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Elephant seals as sentinels of the ongoing changes affecting the Southern Ocean: Disentangling environmental and maternal effects on pup size and body condition

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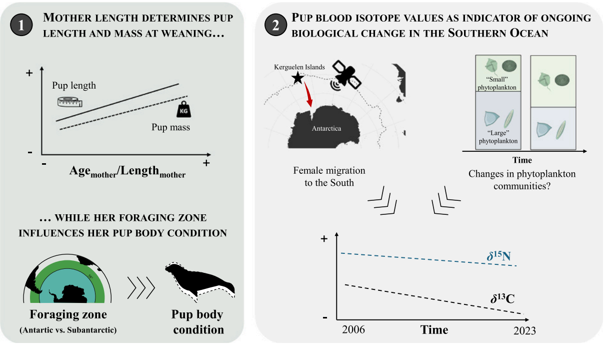
HIGHLIGHTS

- Pup mass and length at weaning depend mainly on maternal length/age in elephant seal
- Pup body condition is shaped by mother foraging environment during pregnancy
- Pup weaning mass and length decreased while body condition improved in Kerguelen SES
- Satellite tracking data indicate a southward shift in SES female at sea distribution.
- Decline in pup δ^{13}C and δ^{15}N values suggests shift in the SO phytoplankton communities

GRAPHICAL ABSTRACT



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ABSTRACT

The weaning mass of southern elephant seal pups (*Mirounga leonina*) is a key predictor of their first-year survival probability. However, variations in pup morphometric characteristics (length, mass and body condition i.e. the residual of the allometric relationship between log(mass) and log(length)) are strongly associated with mother's length and body condition. Leveraging a comprehensive long-term dataset (2006–2024) that integrates morphometric, isotopic, and environmental data, we applied a structural equation model to disentangle the direct and indirect drivers of pup phenotype at weaning. This approach reveals that pup length and mass are primarily determined by maternal length, while pup body condition is mainly shaped by the environmental conditions experienced by the mother during her pre-breeding trip. Our long-term dataset highlights a decline in

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pup weaning mass and length but an increase in their body condition despite an increase in the size of the breeding population. The concurrent decrease in pup blood δ^{13}C and δ^{15}N values, reflecting those of their mother, suggests shifts in southern hemisphere food webs and in the trophic ecology of Kerguelen southern elephant seals. We hypothesize that these changes are mainly linked to shifts in the composition of the phytoplankton community at the base of the trophic chains, which could have downstream effects on intermediate trophic levels and top predators, as well as a southward shift in female at-sea distribution confirmed by the tracking data.

1. Introduction

The observed increase in oceanic temperatures and those predicted by climatic models will have significant and long-lasting effects on marine ecosystems (Forcada and Hoffman, 2014; Weimerskirch et al., 2003). Polar environments are of particular concern, as climate change models forecast that ocean warming will be especially pronounced at high latitudes, potentially leading to significant large-scale effects on the associated marine ecosystems (Constable et al., 2014), and a decrease in marine animal biomass within the 21st century (Lotze et al., 2019). The Southern Ocean (SO), i.e. water masses south of the Subtropical Front, represents 10 % of the Global Ocean and plays a major role in the Earth's climate regulation. It accounts for 70 % of the excess heat storage and 40 % of the global oceanic carbon sink, with the biological pump contributing to approximately one-third of this sink effect (Frölicher et al., 2015). The Southern Annular Mode (SAM) is the dominant driver of SO climate variability (Thompson et al., 2000). It controls the north-south shift in the circumpolar westerly winds and substantially affects SO circulation and CO_2 uptake (Lenton and Matear, 2007). Over the last 50 years, the SAM has become increasingly positive, causing an intensification and southerly shift of westerly winds during the austral summer (Marshall et al., 2013). Positive SAM phases are associated with higher primary productivity south of the Polar Front and in the polar frontal zone due to enhanced upwelling of cold, nutrient-rich waters (Lovenduski and Gruber, 2005), with a one-year lag effect on trophic networks (Oosthuizen et al., 2015) and a two-year lag on the cyclonic field in the polar frontal zone (Meredith and Hogg, 2006). As intense cyclonic activity leads to an increase in primary productivity, the Marshall SAM index is a good proxy for the investigation of prey resources availability for marine predators. However, changes in prey resources availability caused by the SAM are heterogeneous (Del Castillo et al., 2019), and the ecosystems and organisms of the SO may not all experience the same effects. Marine top predators are increasingly employed as sentinel species to detect environmental changes (Hindell et al., 2003), owing to their conspicuous nature and their capacity to integrate environmental signals over time and across space. They reflect or respond to shifts in ecosystem structure and function that may be challenging to identify through direct observations in remote poorly observed regions like the SO (Hazen et al., 2019). Monitoring their populations provides an opportunity to study such changes over extended periods, particularly in the context of ongoing global warming.

In that context, the southern elephant seal (SES) *Mirounga leonina*, is a well-suited sentinel species for detecting changes occurring in the SO and assessing their consequences on marine top-predators, owing to its extensive oceanic habitat which includes the Sub-Antarctic and the Antarctic zones (Hindell et al., 2016). The annual cycle of adult female SES involves two trips to sea, interspersed with two onshore periods of about one month each for breeding (September – October) and moulting (December – February, Condy, 1979). These two terrestrial phases allow to equip with biologging instruments and weigh SES for fine-grained study of their at-sea behaviour including distribution, foraging behaviour, and success. Female SES reproduce for the first time at three to four years of age (Pistorius et al., 2004) and then give birth annually to a single pup weighing ~40 kg. The pups are weaned three weeks after birth and weigh between 60 and 180 kg (Guinet, 1991). Females fast while nursing their pups using the energy reserves accumulated during the eight-month pre-breeding trip at sea (February – October, Jönsson, 1997), meaning that maternal investment is conditioned by prey availability and maternal foraging success during her pre-breeding trip (Fedak et al., 1996). Poor foraging by a female leads to reduced pup weaning mass and lower first-year survival rates (McMahon et al., 2000a, 2017; Oosthuizen et al., 2018), which ultimately results in diminished recruitment of young females into the reproductive population three to four year later. Consequently, monitoring basic parameters such as the number of individuals in the colony and pup weaning mass offers valuable insights into the foraging performance of the mother and can be used as a broad-scale index representing prey availability to adult females during the pre-breeding trip. Complementary to demographic and morphometric analysis, stable isotope analysis of SES tissues provides insights into at-sea diet by broadly determining the trophic levels on which the seals are feeding (^{15}N/^{14}N, δ^{15}N, McCutchan et al., 2003) and foraging habitats (^{13}C/^{12}C, δ^{13}C, Cherel and Hobson, 2007). Interestingly, δ^{13}C and δ^{15}N values in pup blood reflect the foraging ecology of the mother during their pre-breeding trip (Ducatez et al., 2008). Thus, long-term monitoring of weaning mass and isotopic signatures of pup provides a relatively simple means to track temporal changes in prey availability and foraging ecology for adult female SES.

However, a confounding factor is that pup weaning mass is also linked to its length, by an allometric relation, which itself derives directly from their mother's length (Fedak et al., 1996). As SES females grow through most of their life (Bell et al., 1997), older female tend to be larger females and to produce larger and heavier pups (McMahon et al., 2017; Oosthuizen et al., 2015). Until now, no study has focused on the relative contributions of maternal and environmental effects to total phenotypic variance in pup weaning mass over long periods. Understanding the underlying mechanisms that determine pup weaning mass are invaluable as indicators of environmental state because changes in pup mass distribution at weaning over the years can be linked to the environmental conditions experienced by the mother during her pre-breeding trip and/or to the age structure of breeding females. Indeed, a significant increase in the number of young breeding females (i.e. primiparous) in years *n*, who survived of their first-critical year due to favourable environmental conditions in year *n*-3 or -4, may lead to a decrease and/or a change in the distribution of pup mass at weaning, without this being linked to the unfavourable environmental conditions encountered by the breeding females in year *n*. Generalizing to a non-constant growth rate of the breeding population, changes in the distribution of the pup weaning mass may occur, unrelated to the environmental conditions of the current year, solely as a result of a large recruitment of primiparous females (Beltran et al., 2025).

In this study, our objective was to disentangle the contribution of maternal and environmental factors as well as the effect of the age structure of the reproductive females on weaned pup mass variability from the Kerguelen Islands. To achieve this, we (1) quantified the relationships between the morphometric characteristics of pups (length, mass, body condition) and the mothers' length through mother-pup pairs; (2) identified and determined the contributions of variance in pup morphological characteristics into components specifically related to maternal traits, female age-structure and environmental conditions using a structural equation model (SEM) that incorporated a comprehensive set of biological (morphometric, isotopic) and environmental

(Marshall index, wind speed, chlorophyll *a* concentration [Chl*a*]) data collected over an 20-year period.

2. Material and methods

2.1. Study population

Fieldwork was carried out in the southeastern part of the Courbet peninsula at the Kerguelen Islands (49°21′S, 70°18′E), in the immediate vicinity of the Polar Front, as part of long-term scientific programs led by the Centre d'Etudes Biologiques de Chizé. Female SES from Kerguelen Islands show two major foraging areas: the Sub-Antarctic and the Antarctic zone (Mestre et al., 2020) and feed mainly on myctophids (Cherel et al., 2008). Pup and female SES were studied and handled under the ethic (APAFIS) permit 32,407–2,021,071,212,163,407. This project was approved by ComEth Anses/ENVA/UPEC (permit N°19–04021375) and by the TAAF Polar Environment Committee who authorize the conduction of research programs within the "Terres Australes et Antarctic Françaises" Natural Reserve.

2.2. Pup and female morphometric data acquisition

In 2023, mother-pup pairs were selected ($n = 203$). Female length (nose to tail) was measured using a Leica laser telemeter Geosystems BLK3D. Precision was assessed using a subsample of females which that were also anesthetized, using an intravenous injection of Zoletil 100, a 1:1 mixture of tiletamine and zolazepam (McMahon et al., 2000b), and measured to the nearest centimetre. We found no differences in female length between the two methods (telemeter: 232 ± 28 cm; measuring tape: 232 ± 29 cm; $n = 40$; paired *t*-test, $p = 0.99$) with telemeter length and measuring tape length were positively correlated ($R^2 = 0.92$, $p < 0.001$). Pups were measured (± 1 cm) at the end of the weaning period (October–November). Pups were rolled into a net stretcher and weighed (± 1 kg) using a balance attached to an aluminium tripod. Morphometric linear regressions were established to quantify the relationship between mother length ($\text{Length}_{\text{mother}}$) and the length, mass and body condition of the pups at weaning ($\text{Length}_{\text{pup}}$, Mass_{pup}, $\text{Condition}_{\text{pup}}$), with the latter representing the residual of the allometric relationship between log ($\text{Length}_{\text{pup}}$) and log($\text{Mass}_{\text{pup}}$).

2.3. Tracking data acquisition and analysis

Between 2008 and 2024, 163 adult female elephant seals were captured and anesthetized using an intravenous injection of Zoletil 100. Each female was equipped with a head-mounted satellite-relayed data logger (CTD-SRDL, 10.5 × 7 × 4 cm, Sea Mammal Research Unit, St Andrews, UK) that was glued in place. The tagging process did not impact the seals' short-term growth rates nor long-term survival (CTD tag weight representing less than 0.2 % of the total body mass of the seal, McMahon et al., 2008). Female SES movements at sea were monitored using the ARGOS satellite tracking system. To process the tracking data, we first excluded class Z locations, which are the lowest quality measurements provided by ARGOS and we then used the *aniMotum* v1.2–07 R package (Jonsen et al., 2022, 2023) to reconstruct female SES tracks accounting for raw Argos location uncertainty. As SES tracks were highly directional, we used the correlated random walk method to estimate positions at a 12-h interval. We also applied a routing function to adjust the tracks off land with the *pathroutr* v0.2.1 package in R (London, 2021), the speed filter from McConnell et al. (1992) to remove consecutive locations suggesting unrealistic speeds (>20 km/h) and a filter about track length to only consider tracks exhibiting more than 180 positions (3 months). The filtered tracks were analysed to identify potential changes in the latitudinal distribution over years.

2.4. Blood carbon and nitrogen isotope composition measurements

From 2006 to 2023, blood samples from 2258 pups of known sex, length and mass at weaning were collected (from 48 to 238 pups.y^{-1}), with a gap for the year 2017 as pup sampled from this year were originated from another part of the Courbet Peninsula (Mestre et al., 2020). To investigate foraging site fidelity in adult female SES between 2004 and 2024, 250 females were both blood-sampled before their post-moult trip (year *n-1*) and upon their return to land for breeding (year *n*) resulting in sampling in two consecutive years for the same adult female. Blood was collected from the dorsal venous sinus of both pup and female seals using 90 × 1.2 mm (18G) needles. Seventy percent ethanol was added to whole blood, as this preservation method does not alter the isotopic composition (Hobson et al., 1997). Lipids are depleted in ^{13}C relative to proteins and carbohydrates (DeNiro and Epstein, 1977), but the low lipid content of whole blood does not require lipid extraction (Cherel et al., 2005). Blood was either dried in an oven at +40 °C or freeze-dried, then powdered. Subsamples were packed in tin capsules (8 × 5 mm, Elemental Microanalysis Ltd) and weighed (from 0.3 to 0.4 mg). Stable isotopes measurements were performed using a Flash 2000 elemental analyser connected to a Delta V Plus isotope ratio mass spectrometer (Thermo Fisher Scientific). Results are presented in the delta notation (δ) relative to Vienna PeeDee Belemnite (VPDB) and atmospheric N_2 (Air) for δ^{13}C and δ^{15}N, respectively. Normalization was performed using USGS 61 and USGS 63 certified material (US Geological Survey) based on their reference isotope composition values and standard uncertainties (respectively −35.05 ± 0.04 ‰ and –1.17 ± 0.04 ‰ for δ^{13}C, and − 2.87 ± 0.04 ‰ and +37.83 ± 0.06 ‰ for δ^{15}N). We checked C/N ratios of the samples and fixed a threshold of 3.7.

2.5. Structural equation modelling

Structural equation modelling allows the quantification of direct and indirect effects on variables within a presumed causal network (Fan et al., 2016). A positive relationship exists between SAM and wind with higher SAM leading to stronger winds (Lovenduski and Gruber, 2005). Since the process is identical in spring and winter, equality of coefficients for the relations *Wind* ~ *SAM* across both periods has been imposed. The foraging zone (Antarctic or Sub-Antarctic zone) influences the environmental conditions experienced by mother SES. This variable is coded according to a binary factor and assigned based on the probability of assignment to one or the other of the two pre-constructed Gaussian distributions of the mixture model. Winter and spring winds could have opposing effects on [Chl*a*]; thus, they are considered as two distinct but correlated variables due to temporal autocorrelation. We hypothesized that a strong winter wind creates a deep mixing layer that promotes nutrient enrichment of surface waters, while a weak spring wind allows for stratification (Margalef, 1978). The foraging zone might also have an effect on [Chl*a*] (Sokolov and Rintoul, 2007) regardless wind (different nutrient availability, solar energy, temperature) and is modelled by a direct effect. The SAM from two years prior might affect [Chl*a*] through increased vorticity activity (Meredith and Hogg, 2006), which alters nutrient availability (Lutjeharms and Ansorge, 2008). All effects presented here affect maternal quality, that can in turn affect pup morphometry. The positive link between maternal quality (length and body condition) and pup quality has already been established (McMahon et al., 2017; Oosthuizen et al., 2015). In addition to the indirect effect of wind on biometric variables through [Chl*a*], it could directly modify food accessibility by increasing or decreasing the mixed layer depth. Hence, we suggested a direct effect of the wind (spring and winter) on $\text{Length}_{\text{pup}}$ and $\text{Condition}_{\text{pup}}$. The SAM from two years prior might also modify prey accessibility via vorticity activity (Meredith and Hogg, 2006). [Chl*a*] may also influence $\text{Condition}_{\text{pup}}$ through prey abundance and accessibility (Jaud et al., 2012). Furthermore, the foraging zone might have an independent impact on $\text{Condition}_{\text{pup}}$, separate from wind and [Chl*a*], such as different prey accessibility or species. Thus, we modelled a direct effect. The sex of the pup might affect its length and its mass (Oosthuizen et al., 2015), so we include it in the model. The trophic level of the mother could also be an indicator of quality (Ducatez et al., 2008). However, assignment to trophic groups is not independent of assignment to geographical groups, and we do not have elements to specify the direction of a causal relationship. Therefore, we have not included this variable in the model. To model the age structure of the reproductive females, we introduced the recruitment of young reproductive females in year *n* by considering the mean SAM over years *n*-4 and *n*-3. The SAM from 3- or 4-years prior should have an inverse (negative) effect compared to the SAM of the year preceding reproduction n (positive, McMahon et al., 2017). Finally, a temporal trend is noted in environmental data, including an increase in [Chl*a*] (Del Castillo et al., 2019), wind, and SAM (Gillett and Fyfe, 2013). Concurrently, there is a decrease in Mass_{pup} over the years (Mestre et al., 2020). We thus include this trend in possible causal relationships by creating an exogenous variable for year. We impose equality of coefficients for the relations $SAM_{lag2} \sim year$ and $SAM_{lag3,4} \sim year$.

We built four distinct model structures corresponding to combinations of spatially explicit or not, incorporating a temporal dimension or not. We use the *lavaan* R package (Rosseel, 2012) to specify the SEMs. The Marshall index of SAM was extracted for each month from 2002 to 2023 and averaged annually from November to October to align with the life cycle of SES. Wind data were obtained from the Copernicus Marine Services platform at a resolution of 4 km. Spatially, we averaged the values over the entire area and then for the Sub-Antarctic and Antarctic zones, which were defined with a boundary at 58°S (Mestre et al., 2020). Temporally, for each pixel, the data were averaged by month. The winter period was defined as the period with the highest average monthly wind across all years, corresponding to August, September, and October. The subsequent three months (November, December, January) were defined as the spring months. [Chl*a*] data from the ESA Ocean Colour Climate Change Initiative were extracted at a resolution of 4 km. The same spatial processing was applied to the [Chl*a*] data as to the wind data. We calculated monthly average values and visually defined the productive period as October to March. The concentrations for these months were summed to estimate annual primary productivity. All these data used in the SEM are available in **Supplementary Table 1**.

2.6. *Statistical analyses*

Data handling and statistical analyses were conducted using R 4.2.1 and the graphics were created with the *ggplot2* package (Wickham and Chang, 2016). We were not able to identify individuals. However, given the population size of the Kerguelen Islands' elephant seals (~100,000 females, Laborie et al., 2023), their longevity, and their survival rates, we assumed that each measured female corresponds to an independent statistical individual. For population-level comparisons (pup morphometric characteristics and isotope values), each data point was treated as independent. In contrast, to assess interannual consistency in adult female foraging areas (i.e., repeated δ^{13}C measurements), we used Pearson correlation tests as we possess a pair of data per individual, representing repeated values from the same individual across two consecutive years.

2.6.1. *Pup morphometric linear regressions and sex ratio*

The relationships between $\text{Length}_{\text{mother}}$ and $\text{Length}_{\text{pup}}$, Mass_{pup} and $\text{Condition}_{\text{pup}}$ were investigated using Linear Models (LM) and the 203 mother-pup pairs. Given that mother length serves as an approximation of female age (Bell et al., 2005), we included a quadratic term to test for potential effects of senescence. To account for possible sex effects, we conducted an ANCOVA analysis with $\text{Length}_{\text{mother}}$ as a covariate and sex as a grouping variable. The models were compared using the Bayesian Information Criterion (BIC) and the model possessing the lowest value selected. We set a ΔBIC threshold equal to 2, and used the BIC as the selection criterion because it penalizes complexity more strongly than does AIC (i.e. AIC tends to over fit, Garrido et al., 2022). We assessed whether $\text{Length}_{\text{pup}}$, Mass_{pup} and $\text{Condition}_{\text{pup}}$ distributions were compatible with a normal distribution using the Shapiro-Wilk test. To formally evaluate the hypothesis of a mixture of several components, we used the *mclust* R package (Fraley et al., 2012) to approximate the annual pup morphometric characteristics distributions with Gaussian Mixture Models (GMM). For each year, we tested models with one to four components. The number of components was chosen based on the BIC. Exploratory data visualizations of the distributions of $\text{Length}_{\text{pup}}$, Mass_{pup} and $\text{Condition}_{\text{pup}}$ suggested a possible bias towards smaller females with female pup. To deeply investigate this possible bias, we examined whether the sex ratio deviated significantly from 0.5 for each year. We then constructed a binomial family Generalized Linear Model (GLM) with a logit link function, where sex was modelled as a function of $\text{Length}_{\text{mother}}$ to assess whether older mothers tend to have more males.

2.6.2. *Assignment to feeding groups*

To account for the temporal decreasing trend in pup blood δ^{13}C values identified by Mestre et al. (2020), δ^{13}C values were statistically corrected, and GMMs were subsequently applied to the corrected δ^{13}C values. The trend correction for carbon allows for the consideration of all individuals in a single model. Each female was assigned, based on the isotopic composition of her pup, to one of the clusters (Antarctic or Sub-Antarctic for carbon, high or low trophic group for nitrogen) with the *mclust* R package. Females were then grouped by year, and the annual proportion of individuals assigned to each cluster was calculated. To assess foraging site fidelity in female SES, both direct (telemetry) and indirect indicators (δ^{13}C) were used. Fifty-five complete post-moult female foraging trips from 2018 to 2024 were added to those collected by Mestre et al. (Mestre et al., 2020). A LM between blood δ^{13}C values at the time of tag placement (δ^{13}C year *n-1*) and at the time of satellite tag retrieval (δ^{13}C year *n*) was built to investigate foraging site fidelity.

2.6.3. *Selection, sensitivity analysis and validation of the SEM*

For each model structure, we started with the full model and iteratively removed the least significant effects. We used the ΔBIC threshold equal to 2, as the selection criterion. Assignment of pups to clusters in a binary way might be a source of uncertainty as Antarctic and Sub-Antarctic clusters are not well separated. To evaluate whole SEM sensitivity to cluster assignment, we extracted probabilities for each pup to be part of each cluster and then simulated 1000 assignments datasets using a Bernoulli law. We fitted the selected SEM to each dataset and obtained a distribution of parameters. We compared standard deviation from these distributions to standard deviation from one estimation, thus comparing uncertainty due to assignment to uncertainty due to fitting. Finally, we checked model goodness of fit using Comparative Fit Index (CFI, Bentler, 1990) and Standardized Root Mean Squared Residual (SRMR, Pavlov et al., 2021).

3. Results

3.1. *Pup morphometrics and sex-ratio*

Pup length, mass and body condition values for the 2006–2023 period are available in **Supplementary Table 2**. The morphometric data acquired from pup-mother pairs in 2023 are available in the **Supplementary Table 3**. Five of the 17 years sampled exhibited a two-components mixture distribution in Mass_{pup} or $\text{Condition}_{\text{pup}}$ (**Supplementary Fig. 1**). The years showing a two-component mixture distribution for Mass_{pup} and $\text{Condition}_{\text{pup}}$ were not the same, and the occurrence of a two-component mixture distribution within the same sex undermines the hypothesis that this distribution is solely a result of sex. Furthermore, the idea of matching a two-components mixture distribution in $\text{Length}_{\text{mother}}$ with that in Mass_{pup} is untenable because, in 2023, $\text{Length}_{\text{mother}}$ distribution is unimodal, and did not differ from a normal distribution ($p > 0.05$) while Mass_{pup} distribution appeared as a two-components mixture distribution, and the other parameters ($\text{Length}_{\text{pup}}$ and $\text{Condition}_{\text{pup}}$) are unimodal. However, there is a possibility that years with a two-components mixture distribution in $\text{Length}_{\text{pup}}$ due to a two-components mixture distribution in $\text{Length}_{\text{mother}}$ distribution may exist, but as we only have a sufficiently large morphometric female dataset for a single year (2023), it is impossible to test how common or not this was through the study period. A positive and linear relation was observed between pup morphological metrics ($\text{Length}_{\text{pup}}$, Mass_{pup} than for $\text{Condition}_{\text{pup}}$) and mother length (Fig. 1). The relationship was much more marked for $\text{Length}_{\text{pup}}$ and Mass_{pup} than for $\text{Condition}_{\text{pup}}$.

The results of the LM analyses indicated that $\text{Length}_{\text{mother}}$ and $\text{Length}_{\text{pup}}$, Mass_{pup} and $\text{Condition}_{\text{pup}}$ were positively correlated ($p < 0.001$, Supplementary Table 4). A significant effect of sex was observed but only for $\text{Length}_{\text{pup}}$, with males being 3.1 ± 1.1 cm taller than females ($p < 0.01$). For all the pup metrics, senescence did not have a significant effect.

$$\text{Length}_{\text{pup}} = 0.32(\pm 0.04) \times \text{Length}_{\text{mother}} + 3.1(\pm 1.1) \times 1_{\{\text{Male}\}} + \text{constant}$$
$$\text{Mass}_{\text{pup}} = 0.985(\pm 0.087) \times \text{Length}_{\text{mother}}$$
$$\text{Condition}_{\text{pup}} = 0.0024(\pm 0.0006) \times \text{Length}_{\text{mother}}$$

$\text{F} - \text{statistic} = 32.48, \text{R}^2 = 0.38$
$\text{F} - \text{statistic} = 43.87, \text{R}^2 = 0.45$
$\text{F} - \text{statistic} = 6.43, \text{R}^2 = 0.09$

Graphical inspection suggests that small mothers (i.e. primiparous and young mothers), have fewer males than larger mothers (i.e. older mothers; **Supplementary Fig. 2a**) but the result of the GMM on the probability of producing a male as a function of the length of the mother was not significant (CI = 0.38–0.54; $p = 0.08$). Despite this lack of predictive capacity, we found that larger females give birth to more male pups than female pups (**Supplementary Fig. 2b**). We found no evidence for any variation in sex ration from 2006 to 2023, except in a single year 2007 ($p < 0.01$; Supplementary Table 5).

3.2. *δ^{13}C and δ^{15}N values of pup SES*

Pup blood δ^{13}C and δ^{15}N values are presented in Supplementary Table 6. One hundred seventeen samples with a C/N ratio > 3.7, indicative of a high lipid content and consequently depleted in δ^{13}C (DeNiro and Epstein, 1977), were excluded from the statistical analyses. Uncertainty in the measured δ^{13}C and δ^{15}N values does not exceed 0.1 ‰. Pup blood δ^{13}C values range from −23.7 ‰ to −18.0 ‰, with annual means between −21.3 ± 0.8 ‰ and − 20.6 ± 0.8 ‰; while the range of pup blood δ^{15}N values was lower, ranging from 9.8 ‰ to 12.9 ‰ with average annual means between +11.1 ± 0.4 ‰ and + 11.5 ± 0.5 ‰. From 2006 to 2023, an annual decrease in δ^{13}C was found ($\delta^{13}\text{C} = -0.067\ (\pm 0.003) \times \text{year} + 113.6\ (\pm 6.7)$; $n = 2056$, F-statistic = 399.6, df = 2054; $p < 0.001$, $\text{R}^2 = 0.16$) resulting in an overall 1.02 ‰ decrease in the mean δ^{13}C value of pups during the study period (Fig. 2). A second linear model applied on δ^{15}N values of pups suggested a decrease over

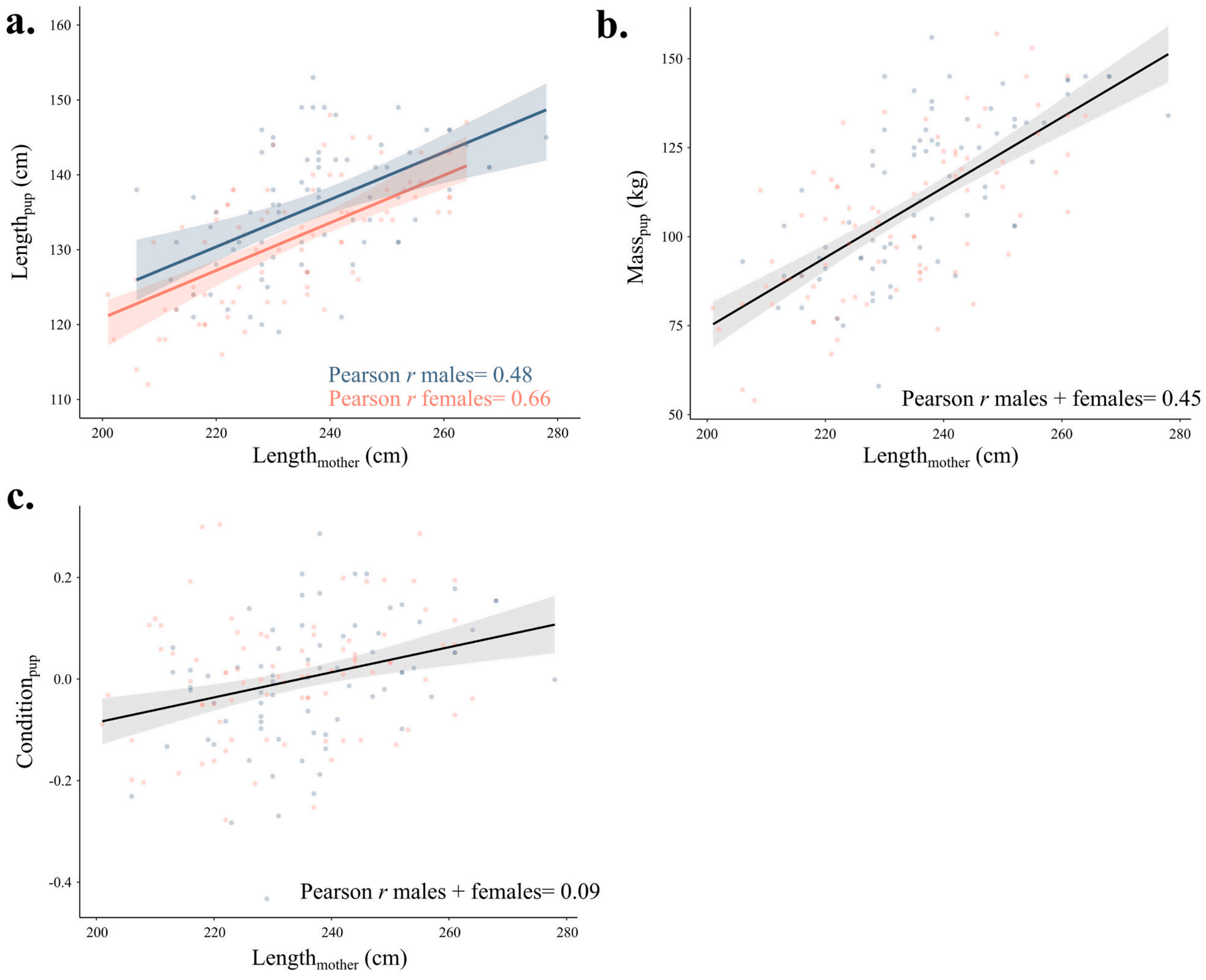

Fig. 1. Relationship between pup morphological metrics and maternal length at weaning. Pup length (**a.**), mass (**b.**) and body condition (**c.**) in relation to the mother's length ($\text{Length}_{\text{mother}}$). The colours represent sex of the pups: blue for males and salmon for females. Lines show the linear model fitted to the data, with the shaded area indicating the 95 % confidence interval.

time (δ^{15}N = −0.014 (± 0.002) × year +38.6 (± 3.1); n = 2056, F-statistic = 76.89, df = 2054, $p < 0.001$, $R^2 = 0.04$) resulting in an overall 0.2 ‰ decrease (Fig. 2). For the year 2023, no relationship was observed between the pup blood δ^{13}C values and Length$_{mother}$ (F-statistic = 2.04, df = 156, $p = 0.15$, $R^2 = 0.01$) nor for δ^{15}N values (F-statistic = 1.94, df = 156, $p = 0.16$, $R^2 = 0.01$; **Supplementary Fig. 3**).

3.3. Foraging area location and fidelity

The duration of female satellite tag transmissions ranged from 29 to 334 days (211 ± 64 d). Most of the females travelled southeast of Kerguelen Islands and a migration of females towards the south was supported by a significant decrease in the mean and mode of the latitudes

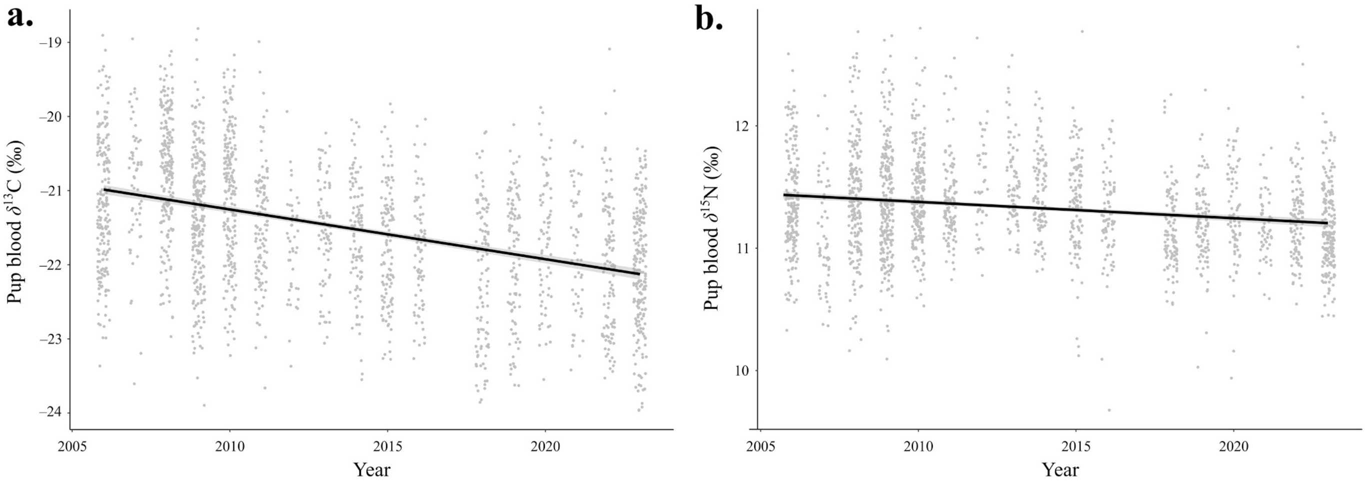

Fig. 2. Linear temporal evolution and its 95% confidence interval of pup blood δ^{13}C and δ^{15}N values. Temporal evolution of δ^{13}C (a.) and δ^{15}N (**b.**) values over the period 2006–2023. Isotopic data for pup measured in 2017 have been excluded as they were acquired on pups from the north part of the Courbet peninsula at the Kerguelen Islands. Lines show the linear model fitted to the data, with the shaded area indicating the 95 % confidence interval.

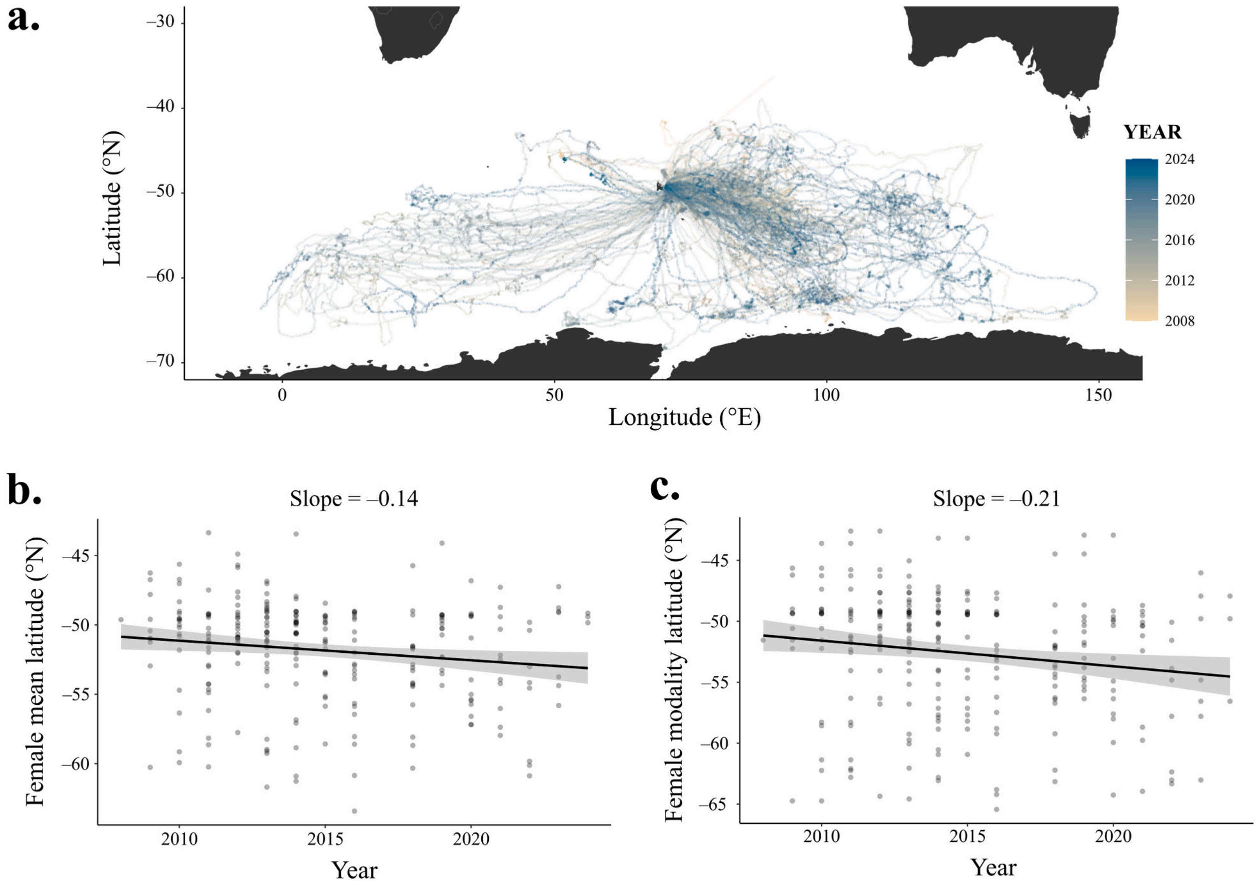

Fig. 3. Telemetry tracking data from SES females satellite tags from the Kerguelen Archipelago. a. Graphical representation of the movements of female SES fitted with ARGOS tracking devices over the period 2008–2024. Evolution of the foraging latitude mean (**b.**) and modality (**c.**) of the female SES over the period 2008–2024. Telemetric data for females in 2017 have been excluded as they were acquired on females from the north part of the Courbet peninsula at the Kerguelen Islands. Lines show the linear model fitted to the data, with the shaded area indicating the 95 % confidence interval.

frequented by the reproductive females (F-statistics = 8.52 and 8.11 respectively, $p < 0.01$, Fig. 3).

The δ^{13}C values of the females were significantly correlated with the mean and the modality of the latitude of their pre-breeding trips at sea ($R^2 = 0.66$, $p < 0.001$, $\rho = 0.8$; Spearman's rank correlation, Supplementary Table 7), with lower δ^{13}C values corresponding to females foraging at high latitude and the inverse (Fig. 4). A positive correlation was observed between the δ^{13}C values measured at the time of tracking device setting (year *n*-1) and those obtained from recaptured individuals in year *n* ($p < 0.001$, $R^2 = 0.37$, Pearson's correlation test). The slope equalled to 0.72 ± 0.11 and indicated that females exhibited high site fidelity.

3.4. Assignment to feeding groups

The sample size and proportion of female individuals assigned to each diet group is provided in Supplementary Table 8. The clusters were not independent as there were consistently more females in low trophic group than in high trophic group, and more females fed in the Sub-Antarctic zone than in the Antarctic zone. For instance, our results showed there are at least twice as many Sub-Antarctic females feeding at high trophic group compared to Antarctic females. The annual proportion of females belonging to each of the geographical groups determined from δ^{13}C values remained stable over time (F-statistic = 0.03, df = 2054; $p > 0.05$), indicating that the equilibrium between the two foraging habitats was maintained (Fig. 5a). On average, 58.6 % of individuals were observed to feed in the Sub-Antarctic zone. On the other hand, the proportion of individuals belonging to the low trophic group exhibited a significant increase ($+0.43 \pm 0.08$ %.yr^{-1}, $p < 0.001$; Fig. 5b).

3.5. Temporal trends in pup morphometric characteristics and isotope values

The ANCOVAs conducted on Length$_{pup}$, Mass$_{pup}$ and Condition$_{pup}$ with year as a covariate and geographical feeding area, trophic groups and sex as factors, revealed identical temporal trends regardless of the geographical, trophic or sex categories (Table 1 and Supplementary Table 9). Model results indicated that Mass$_{pup}$ was significantly affected by year (-0.23 ± 0.08 kg·yr^{-1}), geographical feeding zone of the female (pups from Sub-Antarctic females were + 5.95 ± 0.95 kg heavier than pups from Antarctic females), and sex (males were + 4.85 ± 0.94 kg heavier than females). For Length$_{pup}$, significant effects of year (-0.34 ± 0.04 cm.yr^{-1}), geographical feeding zone of the female (pups from Sub-Antarctic females were 2.1 ± 0.5 cm longer), trophic group (pups from high trophic group females were 1.7 ± 0.5 cm shorter than pups from low trophic group females) and sex (males are 2.1 ± 0.5 cm longer than females) were observed. Finally, significant effects of the year ($+0.0017 \pm 0.0006$ yr^{-1}) and the geographical feeding area of the female were identified on Condition$_{pup}$ (pups whose mother fed in the Sub-Antarctic zone showed values of 0.0316 ± 0.0070 higher than pups whose mother fed in the Antarctic zone).

ANCOVAs results showed trends in pup blood δ^{13}C as a function of year (-0.066 ± 0.002 ‰.yr^{-1}) and trophic group in which the female

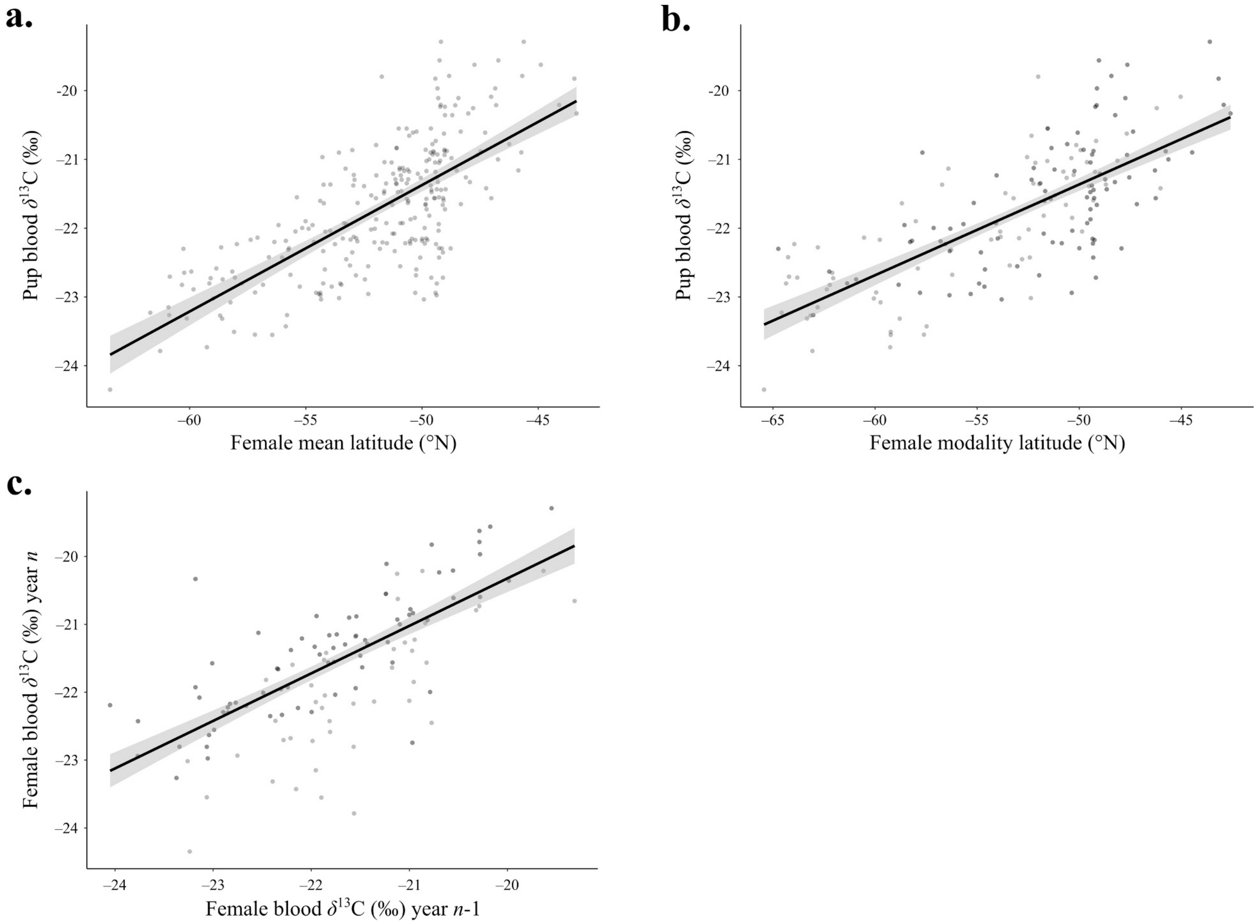

Fig. 4. Blood carbon isotope values of females and pups relative to the latitudes visited by females during their pre-breeding foraging trips. Evolution of the δ^{13}C values in the blood of pups as a function of the mean value (**a.**) and mode (**b.**) of the latitude of the area explored by the female during her pre–breeding trip. (**c.**) Correlation between the δ^{13}C values of the blood of females between year *n* and *n*–1. Lines show the linear model fitted to the data, with the shaded area indicating the 95 % confidence interval.

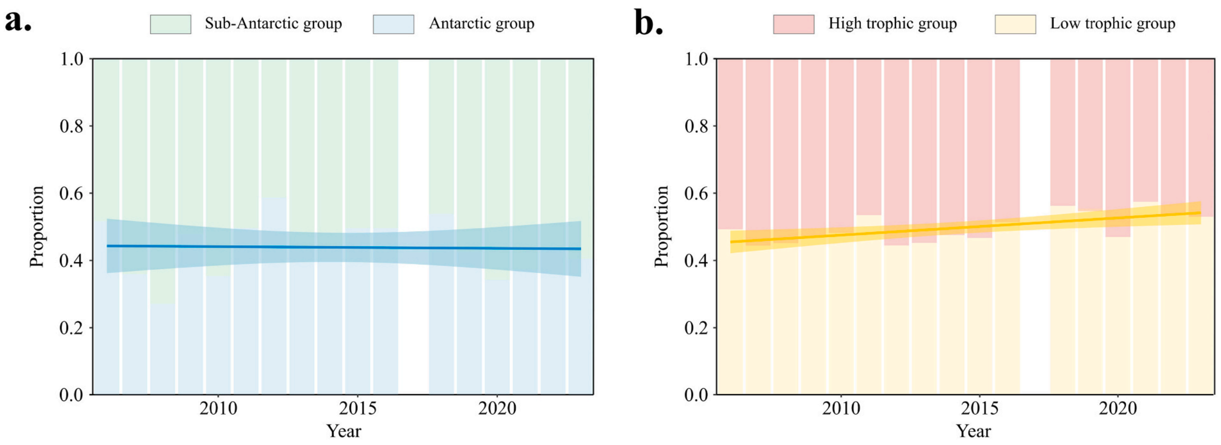

Fig. 5. Evolution of the proportion of assignment to the geographical and trophic groups according to sampling years (from 2006 to 2023). a. Changes in the proportion of individuals assigned to geographic groups. **b.** Changes in the proportion of individuals assigned to trophic groups. Isotopic data from pups in 2017 have been excluded as they were acquired on females from the north part of the Courbet peninsula at the Kerguelen Islands. Lines show the linear model fitted to the data, with the shaded area indicating the 95 % confidence interval.

Table 1

Temporal trends according to group assignments. The reference geographical group is the Antarctic group, the reference trophic group is the lower trophic group, and the reference sex is the female sex.

	Year	Sub–Antarctic group	High trophic group	Male
Length$_{pup}$	−0.34 (± 0.04) cm.yr^{-1}	+2.08 (± 0.47) cm	−1.68 (± 0.50) cm	+2.12 (± 0.46) cm
Mass$_{pup}$	−0.23 (± 0.08) kg.yr^{-1}	+5.95 (± 0.95) kg		+4.85 (± 0.94) kg
Condition$_{pup}$	+0.0017 (± 0.0006) yr^{-1}	+0.0316 (± 0.0070)		
Pup δ^{15}N	−0.006 (± 0.001) ‰.yr^{-1}	+0.118 (± 0.014) ‰	+0.474 (± 0.015) ‰	
Pup δ^{13}C	−0.066 (± 0.002) ‰.yr^{-1}	+1.4 (± 0.022) ‰	+0.222 (± 0.023) ‰	

fed. Pups from high trophic group females possessed δ^{13}C values 0.222 ± 0.023 ‰ higher than pups from low trophic group females. For pup blood δ^{15}N, the results showed a significant effect of year (−0.006 ± 0.001 ‰.yr^{-1}) and geographical feeding zone of the female. Pups from Sub-Antarctic females possessed δ^{15}N values 0.118 ± 0.014 ‰ higher than pups from Antarctic females. For both isotope systems, the sex of the pup had no influence on isotope values.

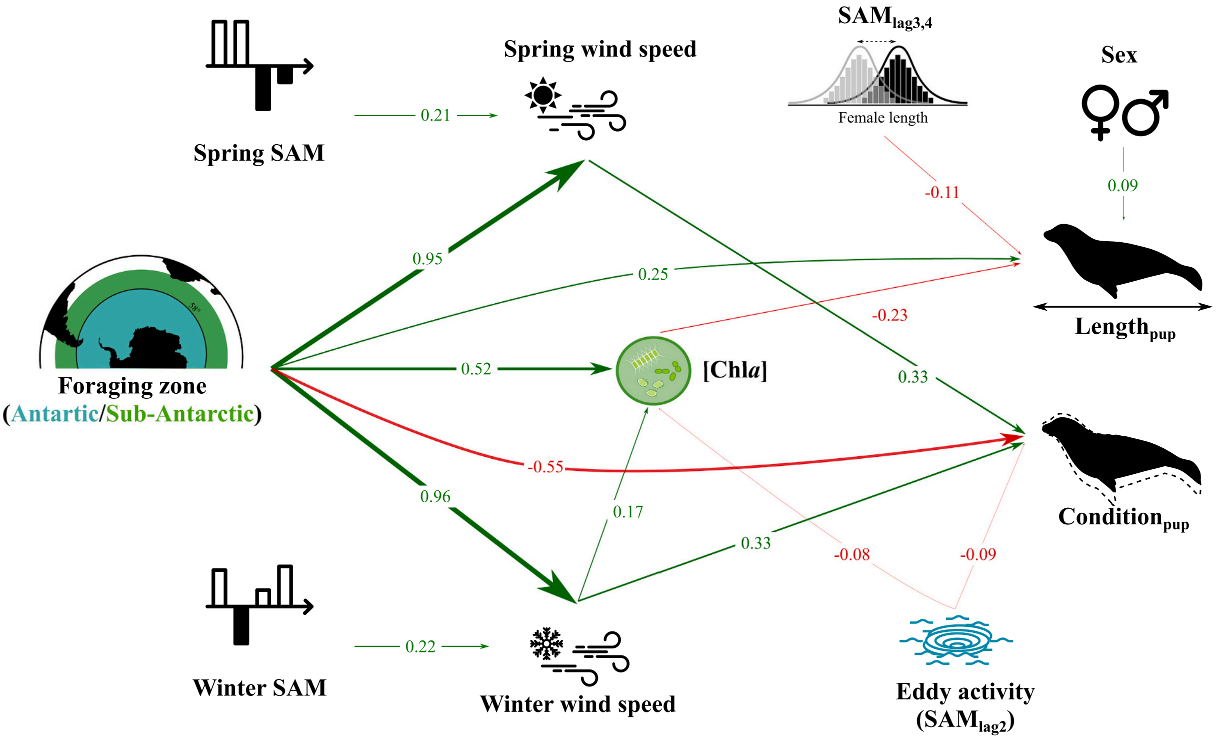

Fig. 6. Plot representing the selected network. The coefficients are standardized coefficients. The thickness of the arrows corresponds to the magnitude of the effect, and their colour to the sign (red: negative; green: positive). For foraging area and sex, the coefficients represent the Sub–Antarctic vs. Antarctic and male vs. female effects respectively.

3.6. *Structural equation modelling*

Since Mass$_{pup}$ and Length$_{pup}$ are interdependent and cannot be processed by SEM, we focused on Length$_{pup}$ and Condition$_{pup}$ for pup morphological characteristics. Four models, corresponding to combinations of spatially explicit model (differentiation between Sub-Antarctic and Antarctic zones) or not, and incorporating a temporal dimension (integration of observed time trends in δ^{13}C and δ^{15}N) or not, were established. Uncertainties due to cluster assignment were of the same order as those due to model fitting and thus have no effect on the selection process of the model (Supplementary Table 10). The model that accounts for the feeding areas of the females without considering the temporal trends appeared to be the most appropriate ($\Delta BIC_{spat/temp.} = 21{,}237$; $\Delta BIC_{spat/no\ temp.} = 0$; $\Delta BIC_{no\ spat/temp.} = 30{,}402$; $\Delta BIC_{no\ spat/no\ temp.} = 9555$). The temporal aspect makes the model too complex, without increasing its explanatory power.

The outputs of the selected model (CFI = 0.908; SRMR = 0.034, Fig. 6), indicate that Length$_{pup}$ is positively influenced by the foraging zone of females and the sex but negatively affected by [Chl*a*] and the recruitment of young breeding females (SAM$_{lag3,4}$). On the other hand, Condition$_{pup}$ is positively related to spring and winter winds whereas the feeding area of females and accessibility of resources by eddy activity have a direct and negative impact.

4. Discussion

4.1. *Pup-mother morphometric relationship and sex ratio*

In this study we detected a positive relationship between the pup length and mass at weaning with mother length, which is increasing with age (Bell et al., 1997, Bell et al., 2005), that is consistent with existing studies (McMahon et al., 2017; Oosthuizen et al., 2015). Here, we did not observe heteroscedasticity of residuals in pup length and mass from longer females, reflecting the variety of ages for the same length (i.e. when female length reached their asymptotic length). The homoscedasticity suggests that it is the mother's length rather than her age that ultimately governs pup length and mass. In addition to these relations, pup body condition increases with mother length meaning an increases in survival rates for pups born to longer and thus older mothers (Postma et al., 2013), leading to greater reproductive success for "older" mothers (Desprez et al., 2014). Indeed, heavier weaned pups could spend more days fasting at-sea during their first foraging trip due to their higher energy stores (McMahon et al., 2000a), which may be what gives them a higher probability of survival than lighter pups.

An additional sex effect on pup length was observed in this study, consistent with past research (McMahon et al., 2017; Oosthuizen et al., 2015). Male pups require greater maternal energy investment than female pups and mother invest more resources in their pups when environmental conditions are favourable (McMahon et al., 2017). Consequently, we might expect a higher incidence of unsuccessful pregnancies when the pup is male leading to sex-ratio alteration in non-favourable years. We only found one year (2007) in which the sex ratio was skewed, and this single example did not allow us to draw any robust conclusions that may inform our expectations of altered sex ratios in years when food is scarce. Similarly, larger females have more energy available than smaller ones (Postma et al., 2013), which could lead to a bias in the sex ratio of pups based on maternal size. While our analyses did not show a clear effect, they do suggest that smaller females, likely primiparous, tend to give birth to females. This skew has been demonstrated in other pinniped species, such as the South African fur seal (Guinet et al., 1998) and the New Zealand fur seal (Bradshaw et al., 2003a) as well as in southern elephant seals (Arnbom et al., 1997). Male mammalian foetuses are generally more costly to produce and have lower viability, so it is probable that smaller females are more likely to miscarry when pregnant with a male foetus (Trivers and Willard, 1973). Our observations for the unique year 2023 warrants replication with a larger sample, as the probability of male or female pup may be influenced by maternal length. If this is the case, changes in the population's age structure could modify the pup sex ratio at birth, potentially affecting trophic networks in the SO, given that males and females forage in different environments (Lewis et al., 2006).

4.2. *Influence of mother trophic strategy on pup morphology*

Depending on the year, the proportion of females belonging to the Antarctic group (from 27 % to 58 %) was slightly lower than reported by Mestre et al. (2020, between 36.5% and 61.5%). These differences likely stem from the use of different algorithms (Hamiltonian Monte Carlo in *rstan* R package vs Expectation-Maximization algorithm in *mclust* here) for the GMM and from close statistical modes of the δ^{13}C values between the Antarctic and the Sub-Antarctic group (respectively −22.3 ‰ and −19.7 ‰). In agreement with Mestre et al. (2020), the pups from Sub-Antarctic females were heavier. We also demonstrated that they were longer and in better condition than pups from Antarctic females. Conjointly, we observed an increase in the proportion of females belonging to the low trophic group. In addition, pups whose mothers belong to the high trophic group (squid-feeders, Cherel et al., 2008), were smaller. To explain these pup morphological differences between mother's trophic strategies, we explored several hypotheses.

First, we hypothesized that females feeding in the Sub-Antarctic could benefit from the proximity of the breeding colony to the feeding ground and by arriving at the Kerguelen Islands in early spring with greater energy reserves that they could allocate to their young due to lowered travel costs (Biuw et al., 2007). In this case, female SES from Sub-Antarctic zone would have a distinct advantage as Antarctic SES exhibited a gradual decline in body condition during this period (Biuw et al., 2007). The foraging behaviour of female SES during their return to the colony remains unclear, but, if it mirrors that of the trip between the colony and the foraging area, the route is typically direct and characterized by a low dive rate *per* kilometre (Biuw et al., 2007). However, the study conducted by Hindell et al. (2022) suggests that SES females had similar body conditions when they arrive on the breeding colony regardless their foraging area. In addition to size, the experience (i.e. primiparous vs. non-primiparous) of the females may also influence pup growth, as non-primiparous females tend to arrive later at the breeding grounds. This delay in arrival can allow them to accumulate a greater absolute amount of body mass, due to their larger size, and thus they will have more energy reserves available to allocate to their pups (Ducatez et al., 2008). Here, this hypothesis could not be tested due to our inability to age breeding females in the absence of a long-term tagging program as the Kerguelen SES population is too large to allow an effective control of tagged individuals. However, estimating age through DNA methylation (Zubakov et al., 2016) could provide a means to test it in the future. Our δ^{13}C data, measured in females during consecutive years, suggest consistent use of the foraging area, a finding in agreement with Bradshaw et al. (2003b) and McIntyre et al. (2017). Site fidelity is established relatively early (∼4 years) in SES life and persists over several years (up to 7 years, Authier et al., 2012; McIntyre et al., 2017) as it may confer ecological benefits to individuals (i.e. familiarity with resources), even when energy gain is not consistently high in all years. Consequently, the hypothesis of geographic segregation and ontogenetic shift with female size can be ruled out (i.e. large females in Sub-Antarctic zone and small ones in Antarctic zone).

The spatial distribution of biological resources in ocean depends upon the physical characteristics of the water column (e.g. temperature, salinity, water chemistry, currents, wind, sea ice concentration; Kogeler and Rey, 1999; Loeb et al., 1997), which are heterogeneous within the SO and could affect the foraging strategy of SES (Hindell et al., 1991; McConnell and Fedak, 1996). As the Sub-Antarctic zone hosts several species of myctophid fish (Sabourenkov, 1991), it is possible that the diet of Sub-Antarctic females differs from that of females feeding along the marginal ice zone, where squid abundance increases with current global change (Caccavo et al., 2021). Given that myctophids are more nutritious than squid and other prey of SES (~30 $kJ.g^{-1}$ compared to ~11 $kJ.g^{-1}$ for salps and ~ 20 $kJ.g^{-1}$ for crustaceans and squids, Schaafsma et al., 2018), we suggested that this nutritional difference could explain the difference in pup body condition from Antarctic and Sub-Antarctic females. To explain the observed difference in pup length between Sub-Antarctic and Antarctic females, the ontogenetic shift hypothesis (i.e. younger females primarily feed on squid, while older females predominantly target myctophids) was ruled out as no significant relationship was observed between mother length and pup blood $\delta^{15}N$ values in 2023. An alternative hypothesis is that, since myctophids are more nutritious than squid, variations in growth patterns could arise depending on the prey availability. Specifically, Sub-Antarctic females that predominantly consume myctophids may exhibit different growth trajectories compared to those that primarily feed on squid which would be in agreement with the observation of smaller pups from Antarctic females. Lastly, individual females' foraging success may be attributed to how they forage rather than where they forage (Field et al., 2001). While there is little evidence of short-term benefits from individual specialization, this does not rule out the possibility that this behaviour may serve to maximize energy gain and reproductive output over an individual's lifetime (Annett and Pierotti, 1999).

4.3. Effects of environmental conditions and age of female reproductive population on weaned pup morphology

Previous work has not partitioned the variance to explain whether the decrease in pup mass is a consequence of a density dependence mechanism alone, or a density dependence mechanism combined with ecosystem changes (Mestre et al., 2020; Oosthuizen et al., 2015). Clarifying the influence of foraging areas, individual traits, and quality in female SES, along with environmental conditions on pup morphometry, would significantly enhance our ability to assess the effect of variations in SO oceanographic conditions and its trophic web. With our structural equation model, we explored the contribution of environmental, maternal and reproductive age-structure factors on pup morphometric variance. SEM outputs indicated that pup body condition was influenced by environmental variables specific to the year (positive effect: winter and spring winds; negative effect: SAM_{lag2} and the Sub-Antarctic fishing zone), while population age structure affected pup length (positive effect: sex, Antarctic fishing zone; negative effect: $SAM_{lag3–4}$, [Chl*a*]). These findings confirm the hypothesis that different processes affect length and body condition in pups. Thus, we can interpret causal relationships regarding pup body condition similarly to causal relationships regarding foraging success. The dependence of the quality of reproduction in SES on annual environmental conditions is a well-documented relationship (McMahon et al., 2017; Oosthuizen et al., 2015) but here we have presented a finer analysis through direct and indirect effects. For instance, the positive relationship between SAM and pup mass, previously established (McMahon et al., 2017), is explained by effects on resource accessibility through wind. However, contrary to existing results (Bailleul et al., 2010; Oosthuizen et al., 2015), we found a negative relationship between eddy activity and fishing success, indicating poorer resource accessibility which could be coupled with lower abundance. Under equal environmental conditions (direct effect only), the Sub-Antarctic zone appears less favourable than the Antarctic zone; however, the overall effect (direct and indirect combined) in the Sub-Antarctic zone on pup body condition is positive, indicating greater maternal gains in this zone due to better foraging conditions.

Contrary to Oosthuizen et al. (2015), we found no relationship between [Chl*a*] and pup body condition. This independence, as well as the lack of dependence of pup length on [Chl*a*], may result from two issues we identified in our model. The first is that we implicitly assumed the effect of [Chl*a*] remains constant over time. The second is related to the integration of temporal trends into the model. One reason the temporally structured model was not selected is the reduction from 6 to 3 exogenous variables while increasing the number of parameters to estimate. The likelihood then decreases significantly, resulting in a higher BIC. We considered not specifying a relationship between SAM at different lags and the year; however, in this case, the *Year* and SAM variables would be correlated, and the signal would be obscured. We did not find a better option to correct these biases. The part of the model dedicated to the length is marked by the effect of the reproduction age structure ($SAM_{lag3,4}$), particularly by the recruitment of young females in their first reproduction. This result is consistent with the negative effect of reproductive population size on pup mass found by Oosthuizen et al. (2015) and interpreted as a possible density-dependent effect. However, our results rather suggest an effect of a change in the age structure of reproductive females.

4.4. Temporal trends

4.4.1. Pup length, mass and condition

Long-term monitoring of the SES population at Kerguelen Islands allowed the identification of trends in weaned pup morphometric characteristics and female trophic ecology. We observed a decrease in pup length and mass, regardless of the foraging area and trophic level of the females. This decline is attributed to an increase in the recruitment of young females (i.e. primiparous) into the reproductive female population. Their integration into the reproductive female population, the consequence of a high survival rates year *n*-3 or − 4, is consistent with an increase in prey availability illustrated by the current observation of global rising in [Chl*a*] (Del Castillo et al., 2019). This is also consistent with the positive growth rate of the Kerguelen population (Laborie et al., 2023). In parallel, pup body condition (i.e. the residuals of the relationship between log(length) and log(mass)) has improved over this period. This enhancement in pup body condition would indicate that female SES forage more effectively or on higher-quality prey (i.e. myctophids; Henschke et al., 2016; Schaafsma et al., 2018). The observed increase in the proportion of low trophic group females, along with the temporal trend of decreasing blood $\delta^{15}N$ values in pups, would lend support to this hypothesis. However, caution is warranted, as the observed decrease in $\delta^{15}N$, could also be influenced by other factors such as changes in composition of the phytoplanktonic communities at the base of the food web.

4.4.2. Towards changes in phytoplanktonic communities in the SO?

Nitrogen isotope fractionation varies within and between groups of marine phytoplankton (Needoba et al., 2003), so, the observed decrease in $\delta^{15}N$ values in pup blood could also result from a shift in the composition of phytoplankton communities at the base of the food web, from diatoms to nano- and picophytoplankton. This hypothesis is consistent with the observed decrease in pup $\delta^{13}C$ values, as phytoplankton type, growth rate, and bloom timing significantly influence their $\delta^{13}C$ values (Bidigare et al., 1997; Deuser, 1970; Hansman and Sessions, 2016; Laws et al., 1995; Popp et al., 1998). Although females seem to migrate southward (an average 3.6° (~400 km) in 18 years), this migration alone would explain only about half of the observed pup blood $\delta^{13}C$ decrease, considering the latitudinal gradient of $\delta^{13}C$ established by Cherel and Hobson (2007). Added to anthropogenic CO_2 emissions (the Suess effect: -0.01 ‰.y^{-1}, Keeling, 1979) this combination would explain for only about 60 %. Changes in phytoplankton communities hypothesis in world oceans due to current global change has been raised by studies using pinnipeds (Hirons et al., 2001), mysticetes (Van Den Berg et al., 2021), odontocetes (Matthews and Ferguson, 2018), and tunas (Lorrain et al., 2020) as ocean sentinels. These changes in phytoplankton community composition, from large to small taxa are thought to be caused and exacerbated by current climate change and are particularly marked in the SO (Cael et al., 2023; Henson et al., 2021). While such a shift across the Southern Ocean remains a working hypothesis, its plausibility is reinforced by documented local changes in phytoplankton community composition in the Northern Antarctic

Peninsula — one of the most rapidly warming regions of the SO, as indicated by climate projections (Clarke et al., 2007) and wide spread changes in SO phytoplankton phenology (Thomalla et al., 2023).

Indeed, in situ measurements in Northern Antarctica Peninsula reported a marked decrease in diatom biomass alongside an increase in the abundance of nanophytoplankton, particularly cryptophytes and small flagellates (Ferreira et al., 2020; Mendes et al., 2013). These changes should lead to major modifications in phytoplankton biomass and community composition, from which two extreme food webs will emerge under contrasting oceanographic conditions in the SO. One supposedly more favourable to upper predators relies on diatoms consumed by krill and then myctophids, while the other based on bacteria and small size phytoplankton cells would enhance the emergence of low energy content gelatinous salps (Pakhomov et al., 2002). Predictions suggest that all regions of the SO will experience changes in phytoplankton productivity and community composition with climate change (Henson et al., 2021), the effect of these changes varying within and among regions with important impact in higher trophic levels. The marked increase in turnover rate of phytoplankton communities in the SO suggests a shift towards more ephemeral species (Henson et al., 2021). This poses a potential challenge for higher trophic level organisms, such as SES, which depend on consistent phytoplankton-driven productivity. As a result, SES may be forced to adapt to a more variable and potentially less nutritious diet.

We have noticed that pups from sub-Antarctic females are in better condition compared to those from Antarctic females likely due to a higher consumption of myctophids. Since global warming, which has a stronger effect at higher latitudes, is expected to have minimal impact on squid given their extreme flexibility and the plasticity of their life-histories (Boyle and Rodhouse, 2008). As such, squid populations are anticipated to persist or even thrive under future climate scenarios (Doubleday et al., 2016). This differential response of prey species to environmental change could have significant consequences for female SES body condition but also for that of their pups which ultimately influence their first-year survival probability (McMahon et al., 2017; Oosthuizen et al., 2018).

Demographic time-series indicate continued decreases in some SES populations (Macquarie Island, Van Den Hoff et al., 2014), while others have remained relatively stable or are increasing (Kerguelen Islands, Laborie et al., 2023; Marion Island, Pistorius et al., 2011). The SES from the Kerguelen Island and Marion Island colonies (McIntyre et al., 2012) feed in regions with high primary production (Stark et al., 2019), implying an increase in prey availability, suggesting greater prey availability. This occurs despite possible shifts in plankton communities, which align with a general increase in [Chl*a*] across the SO, albeit with significant regional variability (Del Castillo et al., 2019). Consequently, the extent to which rising phytoplankton and prey biomasses—versus changes in community composition and prey nutritional quality—affect SES populations remains unclear, particularly in explaining the long-term improvement in pup condition at weaning observed at the Kerguelen colony. In contrast, Macquarie Island SES feed in oligotrophic oceanic regions (Stark et al., 2019), where the poor quality of food caused by changes in phytoplanktonic communities coupled with the limited quantity of resources could contribute, with other environmental factor (i.e. changes in sea-ice extent in the western Ross Sea), to the observed decline (~1 % per year) in their population (Hindell et al., 2017). This likely result in less energy being allocated to pup, reducing their chances of survival during their first year. Changes in phytoplankton community composition, such as a reduction in the proportion of diatoms, could be particularly problematic for SES, as regions with high diatom abundance are associated with greater foraging success (Sari El Dine et al., 2025). In the long term, these biological changes, along with the increasing frequency and intensity of marine heatwaves (Azarian et al., 2024), may negatively impact the population dynamics of SES and the SO trophic webs.

In conclusion, we confirmed a strong relationship between pup morphometric traits and maternal length in southern elephant seals. While maternal length predominantly determines pup length at weaning, pup body condition appears to be more closely linked to environmental resource availability. We therefore recommend using body condition (i.e., measuring mass and length) rather than mass alone as a more robust indicator of maternal provisioning and environmental quality. Relying solely on pup mass may lead to biased interpretations, particularly in years with high recruitment of young, primiparous females tend to produce smaller and lighter pups due to their smaller size than non-primiparous ones. Our long-term monitoring allows us to observe shifts in the pup blood δ^{13}C and δ^{15}N values of Kerguelen SES and changes in the weaning morphology. We further hypothesized that the trends of decreasing length and mass, along with increasing condition, are due to a dual effect. On one hand, an effect of population age/size structure; on the other hand, we suggest an environmental effect, with a change in the composition of phytoplankton communities and associated trophic networks. For the use of SES as indicators of SO ecosystem status, it was crucial to consider these different processes. The recent development of satellite imaging (e.g. ocean colour proxies of phytoplankton community) and amino-acid isotopic analysis of specific compounds (CSIA-AA, Friscourt et al., 2024) will offer excellent prospects for elucidating these changes in phytoplanktonic communities in the SO and assess their ecological consequences. Future research will aim to further characterize the biological component of SO ecosystems using SES as bio-samplers. Emerging onboard technologies, such as miniaturized sonar tag (Molinet et al., 2025), offer promising opportunities to document mesopelagic prey distributions in situ, providing valuable insights into changes in intermediate trophic levels likely linked to shifts in phytoplankton communities. In parallel, amino acid compound-specific stable isotope analyses will enable a shift from individual-based to population-scale assessments of trophic structure. Together, these approaches will enhance the development of ecosystem-based indicators and support conservation efforts and the management of SO food webs.

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CRediT authorship contribution statement

Nicolas Séon: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Vinicius Robert:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Clive R. McMahon:** Writing – review & editing, Resources, Funding acquisition. **Robert G. Harcourt:** Writing – review & editing, Resources, Funding acquisition. **Mark Hindell:** Writing – review & editing, Resources, Funding acquisition. **Alexandra Scheubel:** Writing – review & editing, Methodology. **Gaël Guillou:** Writing – review & editing, Methodology, Data curation. **Paco Bustamante:** Writing – review & editing, Methodology, Funding acquisition. **Baptiste Picard:** Writing – review & editing, Resources, Methodology, Data curation. **Christophe Guinet:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

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Code availability

The R code is available on request. The request should be addressed to Nicolas Séon, Vinicius Robert and/or Christophe Guinet.

Data availability

The data are available either in the main manuscript or in the supplementary materials.

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