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# Ecosystem shifts inferred from long-term stable isotope analysis of male Antarctic fur seal *Arctocephalus gazella* teeth

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ABSTRACT: The Atlantic sector of the Southern Ocean has been rapidly changing over the last century. Many of those changes are driven by climate anomalies such as the El Niño–Southern Oscillation and the Southern Annular Mode, which affect biological processes that scale up the food web. We used $\delta^{13}C$ and $\delta^{15}N$ time series of dentine growth layer groups (as a proxy of individual foraging history from multiple years, n = 41 teeth) to assess temporal shifts in foraging habits of subadult/adult male Antarctic fur seals *Arctocephalus gazella* (AFSs) in 2 areas of high concentration of Antarctic krill *Euphausia superba*: the South Shetland Islands and the South Orkney Islands. Our analyses, which represent the first long-term isotopic assessment of male AFS sampled in Antarctic waters, revealed a significant decrease of $\delta^{13}C$ from 1979 to 2015 and an increase of $\delta^{15}N$ after the late 1990s. The observed changes are likely driven by shifts in latitudinal and longitudinal distribution of krill and increased incorporation of $^{15}N$-enriched sources (higher trophic level prey and/or feeding in different areas) in the most recent period for reasons that are not yet clear. We were able to trace ecosystem changes through isotopic bioarchives of Antarctic fur seals, highlighting the role of this species as an ecosystem indicator of the trophic cascade effects caused by climate change in the Southern Ocean.

KEY WORDS: Climate change · Southern Ocean · Antarctic krill · Antarctic food webs · Ecological time series



## 1. INTRODUCTION

The Southern Ocean environment has been changing rapidly over the last century (Turner et al. 2005, 2016). In the Western Antarctic Peninsula (WAP) and Northern Antarctic Peninsula (NAP), the sea ice season has decreased by 85 d (Stammerjohn et al. 2008), and air temperatures have increased at one of the fastest rates on the planet (0.5°C decade$^{-1}$ from 1951 to 2011) (Turner et al. 2014). Increased ocean warming events have been changing the phytoplankton community structure around the Antarctic Peninsula

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(AP) in recent decades (Montes-Hugo et al. 2009, Mendes et al. 2018). A decrease in large-cell diatoms, increases in cryptophytes that are less suitable for grazing by Antarctic krill *Euphausia superba* (hereafter 'krill') (Haberman et al. 2003) and the concurrent decrease in the sea ice extent negatively affect krill abundance (Massom & Stammerjohn 2010). Current warming seems to be more evident in the southwest AP region, while the north/north-east of the AP and South Shetland Islands switched from a warming trend between the late 1970s and 1990s to cooling between the early 2000s and mid 2010s (Oliva et al. 2017). Positive relationships between krill abundance and the cold La Niña (El Niño–Southern Oscillation [ENSO] negative phase event) (Loeb & Santora 2015) and negative relationships between krill abundance and Southern Annular Mode (SAM) phases (Atkinson et al. 2019) have been recorded. Future climate projections suggest a further reduction in krill abundance (Piñones & Fedorov 2016), where krill-specialist predators will either have to switch to farther offshore and/or more southern foraging habitats, thereby increasing energetic demands, or change their diet (e.g. as simulated for the crabeater seal *Lobodon carcinophaga*, Hückstädt et al. 2020). Moreover, cumulative forcing such as the ongoing development of krill fisheries (Nicol & Foster 2016) will also put further pressure on krill abundance and distributions. Detecting the influence of climate change on the ecology of elusive and long-lived predators such as seabirds and marine mammals is a major analytical challenge. Long time-series monitoring is often required, as responses can take up to several years or even decades to appear (Hindell et al. 2003, Volzke et al. 2021).

Climate change may directly or indirectly affect the phenology, distribution, behaviour and diet of predators (Sydeman et al. 2015). For instance, the more generalist gentoo penguin *Pygoscelis papua* from the WAP is one trophic level higher at present than 40 years ago, which may have guaranteed its foraging success and consequently, its breeding success, and increased abundance today compared to the declining krill-specialist chinstrap penguin *P. antarctica* (McMahon et al. 2019). Long-term analysis of bioarchives of another Southern Ocean sentinel, the Antarctic fur seal *Arctocephalus gazella* (AFS), has revealed a switch to more pelagic/offshore feeding grounds between the 1960s and 2000s in the South Georgia Islands (Hanson et al. 2009) and a possible increase of high trophic level prey contribution to their diet from 1920 to 2000 at the South Shetland Islands (Huang et al. 2011).

The AFS is an important krill consumer (Forcada 2021). The species breeds north and south of the Polar Front (PF), and numbers have been increasing as they recover from over-harvesting that occurred during the $19^{th}$ century (Forcada 2021). The AFS is considered an ecosystem indicator by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), since the proportion of fish to krill in its diet at the South Shetland and South Orkney islands seems to be related to krill availability in the environment (Daneri et al. 2008, Waluda et al. 2010). The species may also complement its diet with penguins (Casaux et al. 2004) and cephalopods (Daneri et al. 1999). However, most of the global AFS population evolved in a context of high krill abundance and could be less fit for consuming other prey (Cleary et al. 2019). Furthermore, positive SAM events have reduced the longevity of adult females and the body mass of pups and have promoted strong selection against homozygous individuals (Forcada & Hoffman 2014). El Niño conditions have been identified as the main cause for lower growth rates in males (Turner 2004), lower pup production (Forcada et al. 2005) and greater foraging efforts by lactating females (Boyd et al. 1994), due to reduced availability of prey (such as krill) in some years.

In the framework of trophic ecology, the analysis of intrinsic chemical tracers such as stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) (see Newsome et al. 2010 for a review) in scientific collections or museum specimens has emerged as a useful approach, since it is possible to compare them with contemporary organisms and expand time-series data sets. Long-term isotopic time series can provide important information about fluctuations in the foraging ecology of organisms (e.g. Hanson et al. 2009, McMahon et al. 2019) and ecosystem structure (e.g. Possamai et al. 2021). Marine mammal teeth are accretionary and metabolically inert bioarchives, which represent an individual and natural chronological record of assimilated diet through deposition of annual growth layer groups (GLGs) (Payne 1978). Therefore, they represent an ideal tissue for longitudinal sampling (i.e. obtaining chronological data) for stable isotope analysis.

Baseline $\delta^{13}C$ and $\delta^{15}N$ information on the Atlantic sector of the Southern Ocean is scarce. However, the information available (Brault et al. 2018, Seyboth et al. 2018, Walters et al. 2020) has helped us understand animal movement and diet through time using isotope proxies. For instance, $\delta^{15}N$ values increase from open ocean to coastal areas (Brault et al. 2018). As sea surface temperature (SST) inversely decreases with latitude, the solubility of $CO_2$ in seawater increases, which results in higher uptake of $CO_2$ during photosynthesis (Goericke & Fry 1994) and strong discrimination against $^{13}$C by phytoplankton, causing zooplankton to incorporate lower $\delta^{13}$C values (Tuerena et al. 2019). This carbon gradient is even more evident in the transition area between the Subantarctic Front (SAF), PF and the NAP, as top predators foraging in the interfrontal zone exhibit higher $\delta^{13}$C values compared to the ones foraging in Antarctic waters (e.g. Martin et al. 2011, Jones et al. 2020, Walters et al. 2020). Furthermore, particulate organic matter has lower $\delta^{13}$C values in offshore waters around the AP and in water masses where cryptophytes predominate over diatoms (Seyboth et al. 2018). The same authors also found higher $\delta^{13}$C and $\delta^{15}$N values in Powell Basin compared to Bransfield and Gerlache Straits.

In this paper, we used $\delta^{13}$C and $\delta^{15}$N time series of bulk dentine GLGs (as a proxy of individual foraging history from multiple years) to assess temporal shifts in foraging ecology of subadult/adult male AFSs from the South Shetland Islands and the South Orkney Islands. We also analysed how biotic and abiotic changes in this ecosystem, along with climate anomalies and krill density, might have affected AFS individuals foraging in this area. We hypothesised that AFS $\delta^{13}$C and $\delta^{15}$N values would increase in response to years of lower krill abundance and SST anomalies driven by SAM positive phases or strong El Niño events, by incorporating higher trophic level prey into their diet. To our knowledge, this is the first long-term isotopic assessment of male AFSs sampled in Antarctic waters.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The study area covers the northernmost part of the Atlantic sector of the Southern Ocean, which includes the NAP and WAP, and the southern Scotia Sea (Fig. 1). The Scotia Sea is bounded to the east by Drake Passage and to the north and south by North and South Scotia Ridges, respectively. The circulation is mainly influenced by the Antarctic Circum-

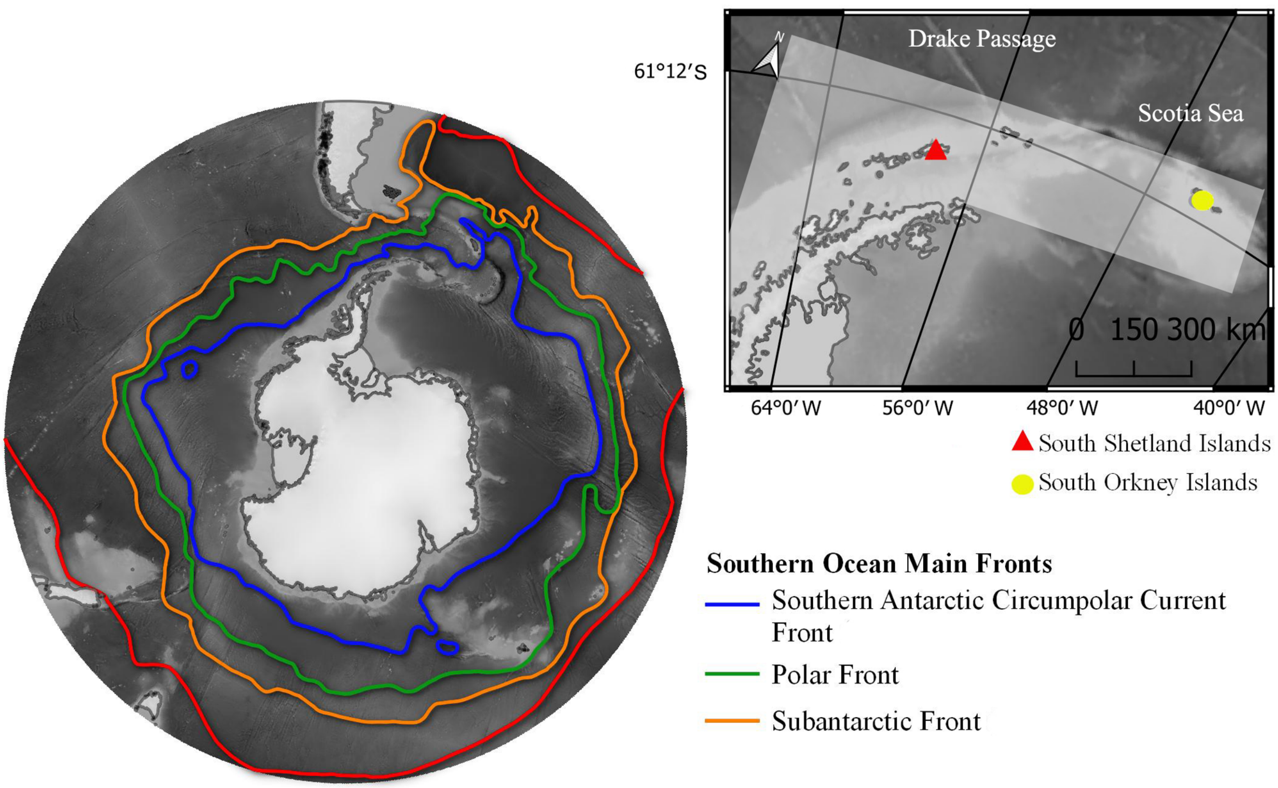


Fig. 1. Study area in the Southern Ocean. The sampling locations for Antarctic fur seal *Arctocephalus gazella* teeth are indicated by a red triangle (King George Island/Isla 25 de Mayo, South Shetland Islands, Carlini Station) and a yellow dot (Laurie Island/South Orkney Islands, Orcadas Station). The main fronts of the Southern Ocean and the area delimited for environmental variable extraction (in transparent white) are also indicated

polar Current (ACC), SAF, PF and Southern ACC Front (Meredith et al. 2001) (Fig. 1), which flows from the edge of the continental shelf to the entire Scotia Sea (Orsi et al. 1995). The NAP circulation is driven by the northeastward flow of the Gerlache Strait Current and the Bransfield Current, which flow in different directions (Zhou et al. 2002). The latter includes anticyclonic eddies and the AP Front, which is a convergence between water masses from the Bellingshausen and Weddell Seas, controlled by seasonal winds and glacial meltwater (Sangrà et al. 2011). The main circulation drivers along the WAP include the AP Front (Moffat et al. 2008) and the continental shelf-break flow of the ACC southern boundary (Ducklow et al. 2012).

### 2.2. Sampling

Teeth were taken from a collection of AFS skulls curated in the Laboratório de Mamíferos Marinos, Instituto Antártico Argentino, La Plata, Argentina. We selected upper canines from male individuals collected between 1991 and 2015 (with a known year of death) in the vicinity of the Argentinian research stations Orcadas (60° 44′ S, 44° 44′ W, Laurie Island, South Orkney Islands) (n = 23) and Carlini (62° 14′ S, 58° 40′ W, King George Island/Isla 25 de Mayo, South Shetland Islands) (n = 10) (Fig. 1, Table 1). Eight teeth collected at one of the Argentinian research stations in the AP/Scotia Sea between 1983 and 1985 were also included, but a precise sampling location for these teeth was not available. Overall, we used the canine teeth of 41 individuals.

### 2.3. Age estimation

We estimated the age of AFSs through the counting of dentine GLGs. Teeth were cut in half longitudinally using a Buehler IsoMet® diamond metallographic low-speed saw, sanded and polished with fine-grit sandpapers (320–12 000), and then decalcified in 25 % formic acid ($CH_2O_2$) for 1 h. We left tooth sections in running water for 12 h to eliminate any influence of acid treatment and then photographed exposed GLGs through a stereomicroscope coupled to a digital camera (Fig. 2). Two independent researchers counted GLGs at least 2 times.

Based on previous studies on the age and growth of the AFS (Payne 1977, 1979), we assigned each GLG to different age classes: yearling (≤1 yr old), juvenile (2–4 yr), subadult (5–8 yr) and adult (≥9 yr). Among the 41 individuals sampled, 28 were adults and 13 were subadults. We also assigned the last GLG to the individual year of death and back-counted calendar years for the previous GLGs.

### 2.4. Sample preparation for stable isotope analysis

To determine the isotopic ratios of dentine samples, we obtained a portion of dentine powder from each GLG using a computer-guided high-resolution Merchantek MicroMill® drilling system. We used a 300 µm drill bit to drill the dentine to a depth of ≤500 µm, to avoid mixing with other GLGs (Fig. 2). Dentine was only sampled when the GLG was wide enough to be individually drilled, which was not always the case for the last GLG of some individuals. About 1 mg of dentine powder from each GLG was weighed into tin capsules (Costech®) ready for stable isotope analysis.

### 2.5. Stable isotope analysis

Stable isotope analysis was performed using a Flash 2000 elemental analyser linked to a Delta V Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific) at the Centro Integrado de Análises, Universidade Federal do Rio Grande. The isotopic ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$, represented by $R$) of the samples are expressed through the delta notation (δ) in parts per thousand (‰) of glutamic acid and caffeine (against Vienna Pee Dee Belemnite) standards for carbon and nitrogen:

$$\delta = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}}\right) - 1 \quad (1)$$

The internal laboratory standards used were caffeine (United States Geological Survey [USGS] 62, $\delta^{13}C = -14.8‰$, $\delta^{15}N = 20.2‰$), glutamic acid (USGS40, $\delta^{13}C = -26.4‰$, $\delta^{15}N = 4.5‰$) international standards, and cane sugar and beet sugar for calibration. Analytical precision was ≤0.07‰ for $\delta^{13}C$ (USGS62) and ≤0.3‰ for $\delta^{15}N$ (USGS40). Accuracy was ≤0.04‰ and ≤0.03‰ for $\delta^{13}C$ and $\delta^{15}N$ (USGS62), respectively, and ≤−0.2‰ and ≤−0.06‰ for $\delta^{13}C$ and $\delta^{15}N$ (USGS40).

### 2.6. Extraction of environmental variables and krill numerical density

We assessed the relationship between $\delta^{13}C$ and $\delta^{15}N$ values in AFS tooth dentine and environmental variables considered to potentially affect their forag-

Table 1. Male Antarctic fur seals *Arctocephalus gazella* used in this study with their respective scientific collection identifier (ID), sampling site, stable isotope values (mean ± SD $\delta^{13}C$ and $\delta^{15}N$ values considering all growth layer groups, i.e. whole tooth), estimated age and year of death

| ID | Site | Mean raw $\delta^{13}C$ (‰) | Mean Suess-corrected $\delta^{13}C$ (‰) | Mean $\delta^{15}N$ (‰) | Age (yr) | Year of death |
|---|---|---|---|---|---|---|
| 83.1[a] | Antarctica[b] | −19.1 ± 1.0 | −19.3 ± 1.0 | 11.0 ± 1.4 | 10 | 1983 |
| 83.2[a] | Antarctica[b] | −19.5 ± 0.6 | −19.7 ± 0.6 | 8.7 ± 1.9 | 14 | 1983 |
| 84.1 | Antarctica[b] | −20.1 ± 1.0 | −20.3 ± 1.0 | 7.7 ± 1.2 | 6 | 1984 |
| 84.2 | Antarctica[b] | −20.7 ± 1.2 | −20.9 ± 1.2 | 7.6 ± 1.1 | 10 | 1984 |
| 85.1 | Antarctica[b] | −20.9 ± 1.1 | −21.1 ± 1.1 | 10.3 ± 0.8 | 11 | 1985 |
| 85.2[a] | Antarctica[b] | −20.8 ± 1.3 | −21.0 ± 1.3 | 9.9 ± 0.9 | 10 | 1985 |
| 85.3 | Antarctica[b] | −19.3 ± 1.4 | −19.5 ± 1.4 | 11.8 ± 1.9 | 11 | 1985 |
| 85.4 | Antarctica[b] | −20.1 ± 0.6 | −20.2 ± 0.6 | 9.6 ± 2.1 | 8 | 1985 |
| 91.2 | South Orkney Islands | −18.1 ± 0.8 | −18.2 ± 0.8 | 11.6 ± 2.2 | 8 | 1991 |
| 91.4 | South Orkney Islands | −20.7 ± 1.2 | −20.9 ± 1.0 | 8.4 ± 1.7 | 8 | 1991 |
| 97.1 | South Orkney Islands | −20.6 ± 0.7 | −20.7 ± 0.7 | 6.7 ± 1.4 | 12 | 1997 |
| 99.3 | South Orkney Islands | −20.8 ± 1.4 | −20.9 ± 1.4 | 11.0 ± 0.7 | 12 | 1999 |
| 99.4 | South Shetland Islands | −20.5 ± 1.6 | −20.6 ± 1.5 | 10.2 ± 0.6 | 10 | 1999 |
| 99.5 | South Shetland Islands | −20.4 ± 1.4 | −20.5 ± 1.4 | 9.4 ± 1.1 | 9 | 1999 |
| 0.3[a] | South Orkney Islands | −20.7 ± 1.1 | −20.8 ± 1.0 | 9.8 ± 1.7 | 11 | 2000 |
| 0.4 | South Orkney Islands | −20.4 ± 1.2 | −20.5 ± 1.2 | 9.8 ± 0.9 | 9 | 2000 |
| 0.5 | South Orkney Islands | −20.9 ± 0.8 | −21.0 ± 0.8 | 8.1 ± 2.2 | 11 | 2000 |
| 0.7 | South Shetland Islands | −20.2 ± 0.9 | −20.3 ± 0.9 | 9.2 ± 0.5 | 7 | 2000 |
| 1.1 | South Orkney Islands | −20.8 ± 0.4 | −20.9 ± 0.4 | 8.3 ± 2.3 | 9 | 2001 |
| 1.2 | South Shetland Islands | −21.3 ± 0.6 | −21.4 ± 0.6 | 9.0 ± 1.2 | 9 | 2001 |
| 2.6 | South Shetland Islands | −21.1 ± 0.9 | −21.2 ± 0.8 | 10.4 ± 0.7 | 11 | 2002 |
| 2.7 | South Shetland Islands | −20.7 ± 0.8 | −20.7 ± 0.8 | 9.3 ± 1.3 | 7 | 2002 |
| 2.8 | South Shetland Islands | −19.0 ± 1.0 | −19.1 ± 1.0 | 9.0 ± 1.8 | 5 | 2002 |
| 2.9 | South Shetland Islands | −20.9 ± 0.8 | −21.0 ± 0.8 | 10.6 ± 1.0 | 11 | 2002 |
| 2.12 | South Orkney Islands | −20.7 ± 0.5 | −20.8 ± 0.5 | 6.9 ± 0.9 | 10 | 2002 |
| 3.2 | South Shetland Islands | −21.1 ± 0.9 | −21.2 ± 0.9 | 8.1 ± 2.2 | 15 | 2003 |
| 5.2[a] | South Orkney Islands | −20.9 ± 0.8 | −21.0 ± 0.8 | 8.7 ± 1.1 | 9 | 2005 |
| 5.4 | South Orkney Islands | −21.8 ± 0.4 | −21.9 ± 0.4 | 8.8 ± 0.4 | 9 | 2005 |
| 5.6 | South Orkney Islands | −20.0 ± 1.1 | −20.1 ± 1.1 | 9.5 ± 1.5 | 8 | 2005 |
| 6.3 | South Orkney Islands | −21.3 ± 0.8 | −21.4 ± 0.8 | 8.5 ± 0.6 | 6 | 2006 |
| 8.2[a] | South Orkney Islands | −20.8 ± 1.3 | −20.9 ± 1.3 | 10.3 ± 1.3 | 11 | 2008 |
| 8.5 | South Orkney Islands | −19.2 ± 1.1 | −19.3 ± 1.1 | 10.8 ± 2.1 | 7 | 2008 |
| 8.7 | South Shetland Islands | −21.2 ± 1.0 | −21.3 ± 0.9 | 8.7 ± 0.6 | 8 | 2008 |
| 9.5 | South Orkney Islands | −20.4 ± 1.7 | −20.4 ± 1.7 | 10.2 ± 1.3 | 7 | 2009 |
| 9.6 | South Orkney Islands | −19.8 ± 1.0 | −19.8 ± 1.0 | 9.3 ± 1.6 | 7 | 2009 |
| 11.7 | South Orkney Islands | −21.4 ± 0.5 | −21.4 ± 0.5 | 8.7 ± 0.7 | 12 | 2011 |
| 12.1 | South Orkney Islands | −20.3 ± 1.1 | −20.3 ± 1.1 | 7.9 ± 1.1 | 9 | 2012 |
| 12.3 | South Orkney Islands | −20.7 ± 1.2 | −20.7 ± 1.2 | 9.9 ± 0.5 | 10 | 2012 |
| 13.1 | South Orkney Islands | −20.6 ± 1.4 | −20.6 ± 1.4 | 9.8 ± 1.3 | 10 | 2013 |
| 13.3 | South Orkney Islands | −20.7 ± 1.0 | −20.8 ± 1.0 | 10.2 ± 0.4 | 11 | 2013 |
| 15.3 | South Orkney Islands | −20.7 ± 1.0 | −20.7 ± 1.0 | 10.5 ± 1.0 | 10 | 2015 |

[a]Last growth layer group not sampled
[b]Samples from the Scotia Sea/Antarctic Peninsula; precise sampling locations were not available

ing habits. All variables were considered as yearly averages (January to December), coinciding with the yearly deposition rate of GLGs. We obtained krill numerical density data (number of post-larval animals under 1 $m^2$ of sea surface) from net sampling surveys compiled by KRILLBASE (Atkinson et al. 2017) (except for the years 1974 and 1979, which were not available). Due to the highly skewed distribution of data, we applied a log transformation. We also obtained SST data from the Extended Reconstructed Sea Surface Temperature v5 (Huang et al. 2017) database derived from the International Comprehensive Ocean–Atmosphere Dataset. Satellite chlorophyll *a* (chl *a*) data between 1998 and 2015 were derived by extracting remote sensing reflectance data from the Ocean Colour–Climate Change Initia-

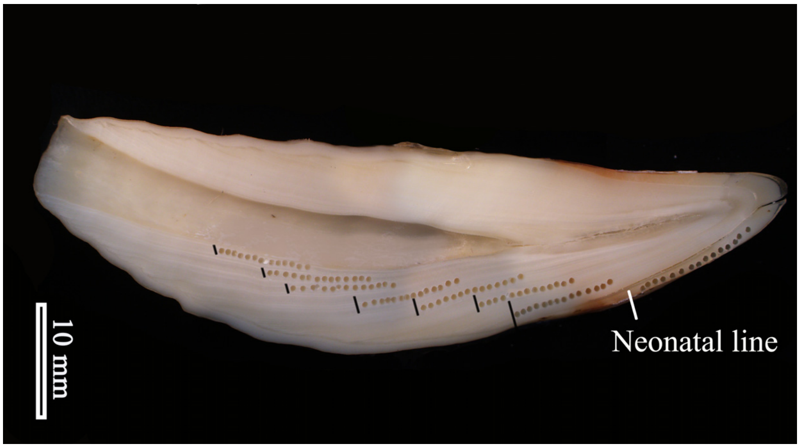


Fig. 2. Sectioned canine tooth of a 7 yr old male Antarctic fur seal *Arctocephalus gazella*. Black lines indicate the positions of growth layer groups. The holes represent the spots where the micro drill extracted dentine powder for $\delta^{13}C$ and $\delta^{15}N$ analysis

tive multi-sensor product v4.2 (Sathyendranath et al. 2019) and applying the OC4-SO regional algorithm (Ferreira et al. 2022). The geographic constraint for data extraction was based on areas of most intensive foraging by 18 male AFS satellite-tagged at the South Orkney Islands (Lowther et al. 2020) (Fig. 1). We also included the observation-based SAM Index (Marshall 2003) and the Oceanic Niño Index (ONI) (NOAA Climate Prediction Center) in our analyses as covariates. Considering the difficulties of detecting climate effects on top predators and nonlinearities between physical and biological processes (Doney et al. 2012), SAM and ONI were tested at 1 yr (referred to as SAM1 and ONI1), 2 yr (SAM2 and ONI2) and 3 yr (SAM3 and ONI3) lags, which is the average time taken for changes to scale up from primary producers to krill (Loeb & Santora 2015, Atkinson et al. 2019) and their predators (e.g. Seyboth et al. 2021). Finally, we also included sampling location (South Orkney Islands, South Shetland Islands and unknown location) as a covariate.

### 2.7. Statistical analysis

To account for the decrease of $^{13}C$ in atmospheric $CO_2$, due to the intensive increase of fossil fuel and methane emissions (known as the Suess effect; Keeling 1979), we corrected $\delta^{13}C$ values considering a decrease rate of 0.005‰ $yr^{-1}$ reported for the period after the 1970s in Antarctica (McNeil et al. 2001). All Suess-corrected values are referenced to the year 2015, which is the most recent year represented in our samples. All $\delta^{13}C$ values have had this correction unless otherwise stated. We assessed differences among GLG age classes using non-parametric Kruskal-Wallis tests and pairwise comparisons through Wilcoxon tests, for both $\delta^{13}C$ and $\delta^{15}N$ values.

For temporal analysis, we employed generalized additive models (GAMs) using penalized regression splines (p-splines) as smoothing functions (R package 'mgcv', Wood 2011) with a Gaussian distribution and an identity link function, for $\delta^{13}C$ and $\delta^{15}N$, separately. Since GLG isotopic values corresponding to yearling and juvenile age-classes were highly variable (Fig. 3), and to avoid any influence of ontogeny, only subadult/adult GLG data were considered. The individual was included as a random effect, and SST, chl *a* (as a proxy for phytoplankton biomass), SAM and ONI lagged indexes, krill density and sampling location as explanatory variables (matched up to

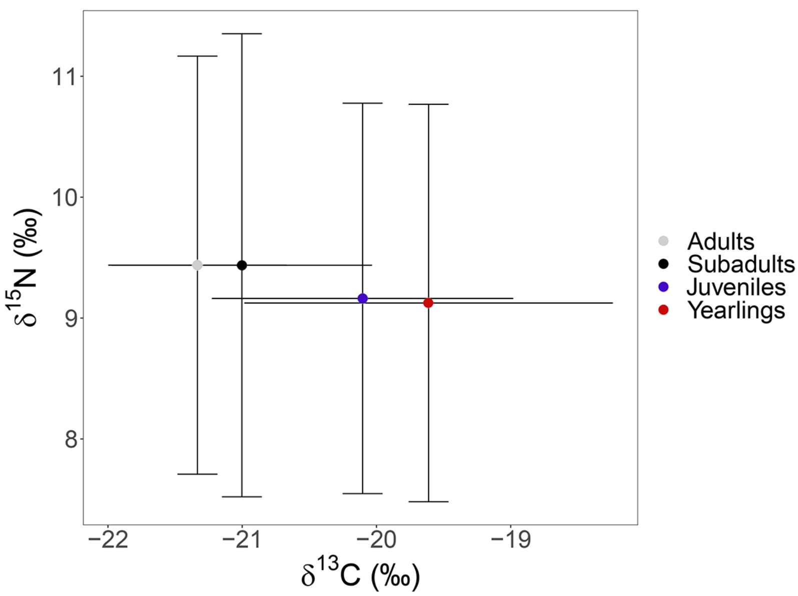


Fig. 3. Biplots of bulk dentine $\delta^{13}C$ and $\delta^{15}N$ (mean ± SD) values of different age classes of teeth growth layer groups from male Antarctic fur seals *Arctocephalus gazella*

the GLG estimated year). Since continuous satellite chl *a* data were only available since late 1997, when the NASA SeaWiFS sensor was launched (Hooker & McClain 2000), we considered 2 different sets of GAMs: one from 1974 to 2015, without chl *a*, and another from 1998 to 2015 including chl *a*.

All models included a continuous autocorrelation function (corAR1) and were subjected to customary residual analysis (e.g. residuals versus fitted values) (Figs. S1–S4 in the Supplement at www.int-res.com/articles/suppl/m695p203_supp.pdf). All statistical analyses were performed in R version 4.0.5 (R Core Team 2021) and a significance level (α) of 0.05 was adopted.

## 3. RESULTS

We obtained stable isotope ratios from 391 GLGs among 41 teeth/individuals (Table 1). Age of the sampled AFSs ranged from 5 to 15 yr (mean ± SD, 9.5 ± 2.1 yr). Mean ± SD of GLG samples per individual was 8.7 ± 2.7 (min = 5, max = 15). The $\delta^{13}C$ and $\delta^{15}N$ values of GLGs ranged from −17.5 to −22.2‰ (mean ± SD, −20.5 ± 1.2‰) and from 4.8 to 14.0‰ (mean ± SD, 9.5 ± 1.8‰), respectively. Two samples with unusually low $\delta^{15}N$ values (3.2 and 3.9‰) were considered outliers and were not included in the statistical analyses.

There was a high intraindividual variability, which was greater for $\delta^{15}N$ values (0.4–2.3‰) compared to $\delta^{13}C$ (0.4–1.7‰) (Table 1) (Figs. S5 & S6). We found statistically significant differences in $\delta^{13}C$ values among age classes ($H_3$ = 98.7, p < 0.01), but not for $\delta^{15}N$ values ($H_3$ = 6.7, p = 0.08). Differences were lower between adult and subadult GLGs (p = 0.02) and between yearling and juvenile GLGs (p = 0.05) compared to yearling/subadult, yearling/adult, juvenile/subadult and juvenile/adult GLGs (p < 0.01) (Fig. 3). This corroborates the eligibility of subadult/adult data for temporal analysis.

Strong collinearity (r > 0.7) was found between SST and the calendar year for data between 1998 and 2015. For this reason, SST was only included in GAMs for the whole time series (1974–2015). All covariates (average annual values) plotted against time are presented in Fig. 4. We considered as linear all covariates that showed effective degrees of freedom (edf) equal to 1 (Zuur et al. 2009), and these were included as parametric coefficients in the GAMs. After checking residual plots, outliers from $\delta^{13}C$ data had to be removed to assure model robustness (24 points from the 1974–2015 model, which included all data from 1974 to 1978, and 10 from the 1998–2015 model).

We found no significant effect of any of the covariates on $\delta^{13}C$ values during the period 1998–2015. However, when including all data in the models (i.e. 1979–2015), a strong effect of the year could be detected (p = 0.003, Table 2), highlighting an evident temporal decrease of $\delta^{13}C$ values (Table 2, Fig. 5). As for $\delta^{15}N$ data, only year showed statistical significance for the most recent period (p < 0.01), when $\delta^{15}N$ values increased (Figs. 5 & 6). Sample origin (South Shetland vs. South Orkney Islands) was also not significant according to GAMs. However, $\delta^{13}C$ values were more variable for South Orkney samples (Fig. 7).

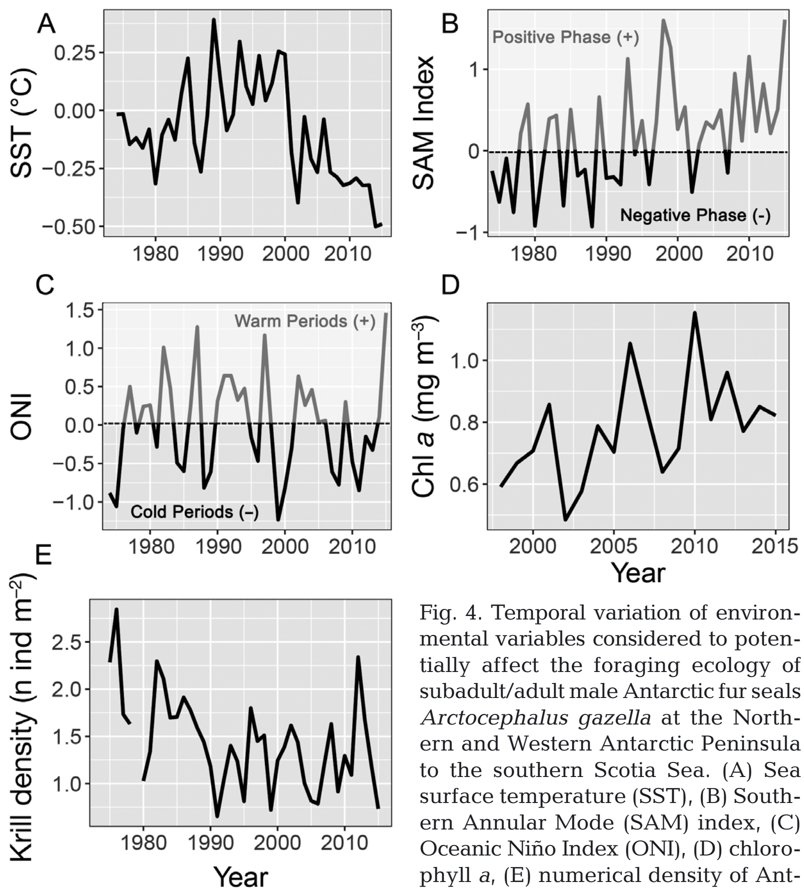


Fig. 4. Temporal variation of environmental variables considered to potentially affect the foraging ecology of subadult/adult male Antarctic fur seals *Arctocephalus gazella* at the Northern and Western Antarctic Peninsula to the southern Scotia Sea. (A) Sea surface temperature (SST), (B) Southern Annular Mode (SAM) index, (C) Oceanic Niño Index (ONI), (D) chlorophyll *a*, (E) numerical density of Antarctic krill *Euphausia superba*

Table 2. Generalized additive models of the relationship between environmental variables/climate anomalies and bulk dentine $\delta^{13}C$ and $\delta^{15}N$ values of teeth growth layer groups (GLGs) of male subadult/adult Antarctic fur seals *Arctocephalus gazella*. Adjusted $R^2$ ($R^2$ adj.), deviance explained, generalized cross-validation (GCV) score and number of samples are shown for each model. Covariates are abbreviated as follows: chl: chlorophyll *a*; sst: sea surface temperature; oni1 (oni2, oni3) = Oceanic Niño Index (ONI) lagged by 1 (2, 3) yr; sam1 (sam2, sam3): Marshall Southern Annular Mode (SAM) Index lagged by 1 (2, 3) yr; krill: Antarctic krill *Euphausia superba* numerical density; local: sampling location; ind: individual; re: random effect. All models included an autocorrelation structure (corAR1). Significant values are marked with asterisks (*p < 0.05; ***p < 0.001)

**1974–2015**

A) $\delta^{13}C$ ~ s(oni3) + s(sam2) + year + sst + krill + oni1 + oni2 + sam1 + sam3 + local + s(ind, re)

$R^2$ adj. = 0.4 Deviance explained = 53.5%
GCV = 0.2 n = 186

| | Parametric coefficients | | | |
|---|---|---|---|---|
| | Estimate | SE | *t* | p |
| Intercept | 76.9 | 32.0 | 2.4 | 0.02* |
| year | −0.05 | 0.02 | −3.1 | <0.01** |
| sst | −0.03 | 0.3 | −0.09 | 0.9 |
| krill | −0.004 | 0.1 | −0.04 | 1.0 |
| oni1 | 0.009 | 0.1 | 0.1 | 0.9 |
| oni2 | −0.1 | 0.09 | −1.1 | 0.3 |
| sam1 | 0.05 | 0.07 | 0.7 | 0.5 |
| sam3 | 0.001 | 0.07 | 0.03 | 1.0 |
| local(SouthShetlandIs) | 0.2 | 0.3 | 0.8 | 0.4 |
| localUnknown | −0.5 | 0.4 | −1.4 | 0.3 |

| | Approximate significance of smooth terms | | | |
|---|---|---|---|---|
| | edf | Ref.df | *F* | p |
| s(oni3) | 1.7 | 2.0 | 0.5 | 0.6 |
| s(sam2) | 1.4 | 1.7 | 0.2 | 0.8 |
| s(ind) | 32.7 | 37.0 | 3.4 | <0.01*** |

Long-term carbon model does not include data from 1974 to 1978

B) $\delta^{15}N$ ~ s(year) + s(sst) + s(oni2) + krill + oni1 + oni3 + sam1 + sam2 + sam3 + local + s(ind, re)

$R^2$ adj. = 0.6 Deviance explained = 66.2%
GCV = 1.8 n = 208

| | Parametric coefficients | | | |
|---|---|---|---|---|
| | Estimate | SE | *t* | p |
| (Intercept) | 10.1 | 0.7 | 14.7 | <0.01*** |
| krill | −0.2 | 0.3 | −0.8 | 0.4 |
| oni1 | −0.2 | 0.2 | −0.9 | 0.3 |
| oni3 | 0.2 | 0.2 | 0.9 | 0.4 |
| sam1 | 0.1 | 0.2 | 0.3 | 0.8 |
| sam2 | 0.04 | 0.2 | 0.2 | 0.8 |
| sam3 | 0.00 | 0.2 | 0.0 | 1.0 |
| local(SouthOrkneyIs) | −0.5 | 0.6 | −0.7 | 0.5 |
| local(Unknown) | −0.7 | 1.2 | −0.6 | 0.6 |

| | Approximate significance of smooth terms | | | |
|---|---|---|---|---|
| | edf | Ref.df | *F* | p |
| s(year) | 2.6 | 3.2 | 1.5 | 0.3 |
| s(sst) | 1.5 | 1.9 | 1.4 | 0.2 |
| s(oni2) | 1.2 | 1.3 | 0.4 | 0.7 |
| s(ind) | 32.4 | 38.0 | 6.6 | <0.01*** |

**1998–2015**

C) $\delta^{13}C$ ~ s(sam2) + s(sam3) + chl + year + krill + oni1 + oni2 + oni3 + sam1 + local + s(ind,re)

$R^2$ adj. = 0.3 Deviance explained = 45.9%
GCV = 0.2 n = 111

| | Parametric coefficients | | | |
|---|---|---|---|---|
| | Estimate | SE | *t* | p |
| (Intercept) | 48.3 | 41.3 | 1.2 | 0.2 |
| chl | 0.03 | 0.4 | 0.07 | 0.9 |
| year | −0.03 | 0.2 | −1.7 | 0.1 |
| krill | −0.06 | 0.2 | −0.4 | 0.7 |
| oni1 | 0.07 | 0.1 | 0.5 | 0.6 |
| oni2 | −0.1 | 0.1 | −0.9 | 0.4 |
| oni3 | −0.03 | 0.1 | −0.3 | 0.8 |
| sam1 | 0.06 | 0.1 | 0.5 | 0.6 |
| local(SouthOrkneyIs) | 0.3 | 0.2 | 1.7 | 0.1 |

| | Approximate significance of smooth terms | | | |
|---|---|---|---|---|
| | edf | Ref.df | *F* | p |
| s(sam2) | 1.9 | 2.2 | 2.7 | 0.1 |
| s(sam3) | 1.4 | 1.6 | 0.4 | 0.7 |
| s(ind) | 16.7 | 26.0 | 1.4 | <0.01** |

D) $\delta^{15}N$ ~ s(sam2) + chl + year + krill + oni1 + oni2 + oni3 + sam1 + sam3 + local + s(ind,re)

$R^2$ adj. = 0.6 Deviance explained = 75.7%
GCV = 1.0 n = 120

| | Parametric coefficients | | | |
|---|---|---|---|---|
| | Estimate | SE | *t* | p |
| (Intercept) | −343.0 | 96.5 | −3.6 | <0.01*** |
| chl | −1.3 | 0.9 | −1.5 | 0.1 |
| year | 0.2 | 0.05 | 3.7 | <0.01*** |
| krill | −0.5 | 0.3 | −1.5 | 0.1 |
| oni1 | 0.4 | 0.3 | 1.3 | 0.2 |
| oni2 | 0.2 | 0.2 | 0.9 | 0.4 |
| oni3 | 0.2 | 0.2 | 0.9 | 0.4 |
| sam1 | −0.001 | 0.2 | −0.003 | 1.0 |
| sam3 | 0.2 | 0.3 | 0.7 | 0.5 |
| local(SouthShetlandIs) | −0.8 | 0.6 | −1.4 | 0.2 |

| | Approximate significance of smooth terms | | | |
|---|---|---|---|---|
| | edf | Ref.df | *F* | p |
| s(sam2) | 1.7 | 2.0 | 1.3 | 0.3 |
| s(ind) | 24.0 | 28.0 | 6.3 | <0.01*** |

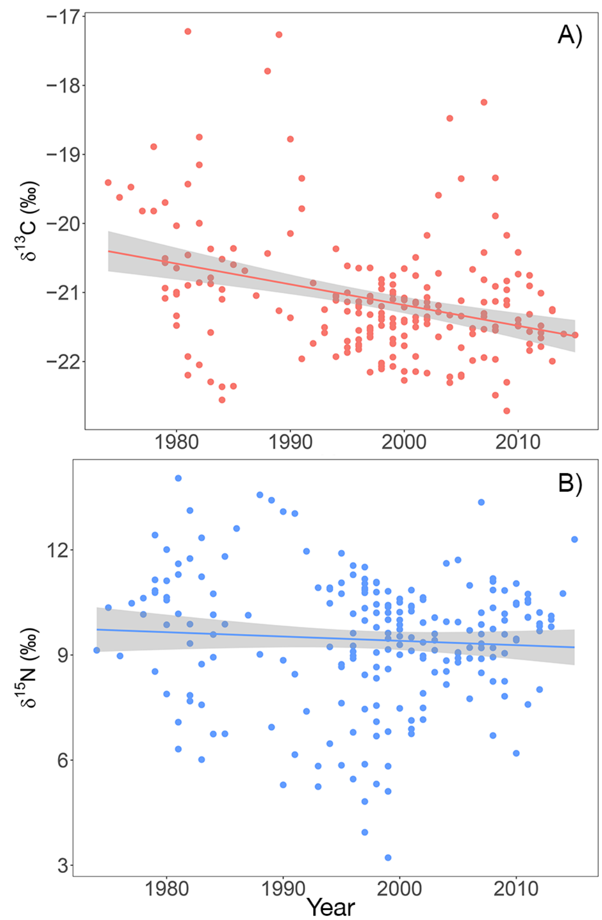


Fig. 5. Temporal variation of bulk dentine (A) $\delta^{13}C$ and (B) $\delta^{15}N$ values of teeth growth layer groups (GLGs) of male subadult/adult Antarctic fur seals *Arctocephalus gazella*. Each point represents the isotopic composition of a different GLG among the 41 individuals analysed. The shaded area corresponds to the 95% confidence interval for predicted values in a linear regression

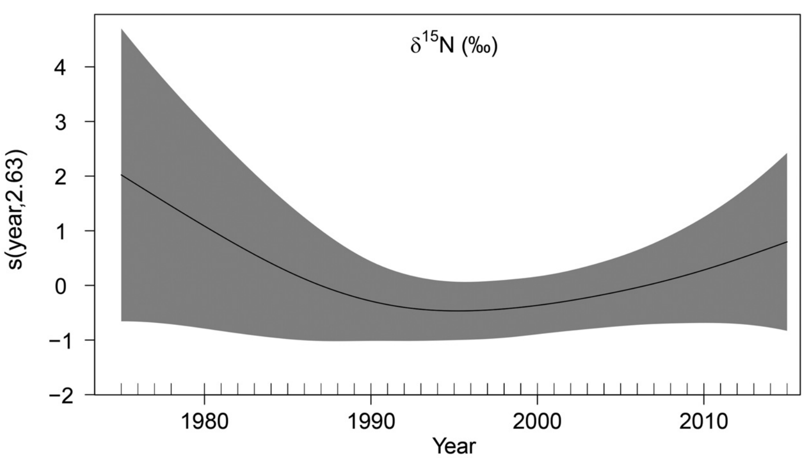


Fig. 6. Generalized additive model estimated p-spline smoothing curves (s; effective degrees of freedom) for bulk dentine $\delta^{15}N$ values of teeth growth layer groups of male subadult/adult Antarctic fur seals *Arctocephalus gazella*. The shaded area indicates the 95% confidence interval

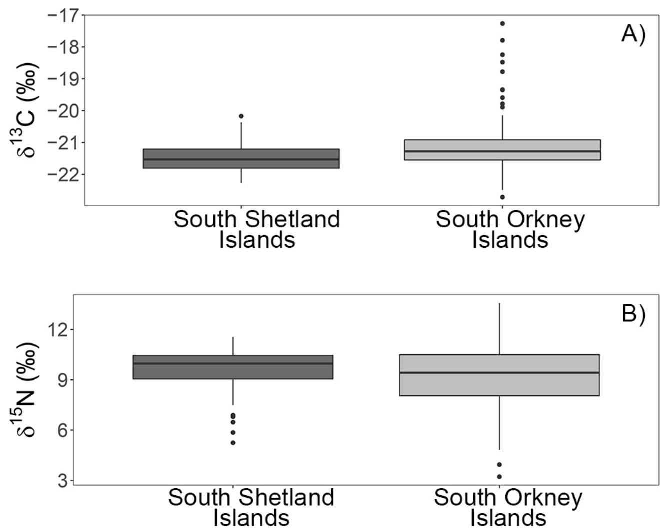


Fig. 7. Bulk dentine (A) $\delta^{13}C$ and (B) $\delta^{15}N$ values of teeth growth layer groups of subadult/adult male Antarctic fur seals *Arctocephalus gazella* according to sample origin

## 4. DISCUSSION

Here we present a 41 year time series of carbon and nitrogen stable isotopes in tooth dentine of subadult and adult male AFSs from the South Shetland Islands and South Orkney Islands. We suggest that individuals followed the distribution shifts of their main prey over time, targeting areas of higher krill concentration, and increased consumption of higher trophic level prey and/or switched to different feeding areas after the late 1990s.

Declining $\delta^{13}C$ trajectories, as found in our study, were previously detected for AFSs in South Georgia (Hanson et al. 2009) and other marine predators in the Southern Ocean, whereby a few hypotheses emerged, from a decline in primary productivity and changes in the phytoplankton community, to a poleward shift in distribution, e.g. rockhopper penguins *Eudyptes chrysocome* (Hilton et al. 2006) and thin-billed prions *Pachyptila belcheri* (Quillfeldt et al. 2010). Different forcing and stressors resulting from climate change may have different implications for phytoplankton (Boyd & Brown 2015, Boyd et al. 2016). For the Southern Ocean, recent evidence has shown a positive trend for chl *a* (Del Castillo et al. 2019), with an indication that blooms are starting earlier than expected (Henson et al.

2018), but the scenario might be different in some regions of the AP. In the NAP, primary productivity and phytoplankton biomass have declined since the early 2000s (Ferreira et al. 2020), which has been accompanied by the replacement of large-cell diatoms by small-flagellated cryptophytes (Mendes et al. 2013, 2018). However, as cryptophytes are a negligible prey for krill (Haberman et al. 2003), and most fishes consumed by AFSs are krill-feeding species (Daneri 1996, Casaux et al. 1998), it is unlikely that this switch in primary producer communities has significantly influenced AFS dentine stable isotope ratios through direct baseline effects. There is also no indication of a significant decline in phytoplankton biomass considering the wide area used by male AFS (from the southern Scotia Sea to the NAP and WAP) as shown by our data.

Furthermore, the highest krill densities in the Atlantic sector of the Southern Ocean were concentrated in its northern part (around the South Georgia region) during the 1920s and 1930s. However, since the 1970s, the distribution has contracted southward and closer to Antarctic continental shelves (Atkinson et al. 2019). This latitudinal distribution shift may have contributed to decreasing $\delta^{13}$C values found in our data through the use of more southerly habitats by AFS over time, if they followed the areas with highest abundances of krill.

Contrary to our expectations, we did not find a relationship between GLG $\delta^{13}$C and $\delta^{15}$N values and climate anomalies or environmental variables that affect the main AFS prey, i.e. Antarctic krill. The yearly deposition of GLGs might have diluted any shorter-term effects, such as climate effects on Antarctic summer, the period when krill becomes most available to predators. Moreover, the relationship between climate anomalies and krill abundance is complex, as there are contrasting reports in the literature.

While Loeb & Santora (2015) found a significant relationship between krill population dynamics and ENSO, Atkinson et al. (2019) found a much stronger influence of SAM. On the other hand, Fielding et al. (2014) and Steinberg et al. (2015) failed to detect significant influences of either one of these climate anomalies on krill in South Georgia and the WAP, respectively. In this study, in addition to not finding an evident relationship between climate anomalies and yearly foraging habits of a krill predator through stable isotope data, we also could not find a relationship between krill numerical density and AFS $\delta^{15}$N values. However, it is important to consider that the wide geographic area in our analyses probably did not capture diverging trends in more specific regions, as precise foraging locations of individuals are unknown.

Although the scientific contribution of KRILLBASE is unquestionable, it is a compilation database, which is not homogeneously distributed in time and space, accounting for only a portion of the krill fishing fleet. Therefore, these data should be interpreted with caution. We also detected an increase in $\delta^{15}$N values in the most recent period (1998–2015), indicating foraging on a $^{15}$N-enriched source. No significant relationships were found between this shift and climate anomalies, SST or primary productivity, and this should be further investigated. As previously stated, the lack of a statistically significant relationship between krill numerical density from KRILLBASE and our stable isotope data does not mean that a decrease in krill abundance in particular areas and years did not occur. Data from AFS scats or another quantitative source of dietary information for recent years are scarce. The only 2 diet assessments for the 2010s in the South Shetland Islands, to our knowledge, showed that krill was still the most important and abundant prey in male scats in the summers of 2012 (Descalzo et al. 2021) and 2019 (Garcia-Garín et al. 2020). As for the South Orkney Islands, the most recent diet information is from 2003, when krill also predominated (Casaux et al. 2016). Our most recent $\delta^{15}$N values are similar to other non-exclusive krill predators from the WAP, such as leopard seals *Hydrurga leptonyx* (Botta et al. 2018).

While there is no evidence to support a long-term decline of krill contribution to AFS diet, some species of penguins such as *Pygoscelis papua* are thriving (Herman et al. 2020) and could have been an attractive alternative prey in the 2000s, as seen during 2001 and 2002 (Casaux et al. 2004). It is also possible that krill dietary shifts in most recent years have contributed to the observed increase in AFS $\delta^{15}$N values. In the context of low diatom abundance, krill might have increased ingestion of other zooplankton taxa, such as copepods (Schmidt & Atkinson 2016), increasing their trophic level. The switch to alternative feeding areas, especially in a context of unstable krill stocks near the AP, is also a possible scenario. While the use of coastal sites seems unlikely, as $\delta^{13}$C values did not increase, individuals might have been feeding in an area of higher $\delta^{15}$N baseline values.

We also have to consider the complexity of food web dynamics in the context of climate change. The responses of AFSs will likely be a function of combined effects from environmental variables and prey abundance, and also the responses of competing predators, such as other krill consumers, e.g.

baleen whales, seals, penguins and fish. For instance, in years of low krill abundance, intraspecific competition increased in the South Orkney Islands (Bertolin & Casaux 2019). Eventually, and in-line with the Van Valen niche variation hypothesis (Van Valen 1965), interspecific competition might lead to specialization in alternative resources. Baleen whales, such as recovering humpback whales *Megaptera novaeangliae* (Zerbini et al. 2019), and *P. papua* (Herman et al. 2020) are only a few examples of krill consumers that have been experiencing population growth over the last years and could pressure AFSs to specialize on alternative and higher trophic level prey, which could also be the case for higher nitrogen ratios found after the late 1990s.

Although not significant according to GAMs, we also found higher values and higher variation (~5 vs. ~2‰) in $\delta^{13}C$ values for individuals sampled around the South Orkney Islands compared to the South Shetland Islands. The South Orkney Islands are an alternative feeding ground for South Georgia males in relation to the AP (Boyd et al. 1998). If individuals sampled in the South Orkney Islands belong to the South Georgia Islands breeding population, this could indicate that some of them forage at lower latitudes, closer to their colonies. While most individuals sampled in the South Shetland Islands (and these probably belong to the Cape Shirreff population) seem to remain at higher latitudes, as corroborated by our lower $\delta^{13}C$ values found for this group, some juvenile and subadult males may disperse towards South Georgia and the South Orkney Islands as well (March et al. 2021). Such movements between different latitudes are likely the reason for this spatial $\delta^{13}C$ variability between AFSs sampled from different sites. For future research efforts, we strongly encourage inter-decadal quantitative assessments of diet composition for AFSs inhabiting the South Shetland and South Orkney Islands, and potential influences of climate anomalies such as ENSO and SAM on resource use. We also recommend that studies similar to this one be performed by sampling females from the same region. Furthermore, coupling satellite telemetry with stable isotope data may increase the chances of detecting small-scale temporal and spatial changes in diet. More telemetry data on both sexes, especially from different years, would also shed light on how their foraging is affected according to different oceanographic and climatic conditions. Finally, compound-specific stable isotope analysis, such as the analysis of $\delta^{15}N$ in amino acids, would also help to disentangle baseline and trophic effects in a temporal context.

Although further studies are necessary, our results add information to the foraging ecology of AFSs at the southern edge of their distribution and highlight the role of this species as an ecosystem indicator. Considering the cumulative pressures of ongoing climate change, it is of paramount importance to continue monitoring AFS populations and other components of the Antarctic ecosystem in order to assure its natural structure, management and conservation, since some of these impacts can be long-lasting and difficult to reverse.

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