# Analysis of stable isotope ratios in blood of tracked wandering albatrosses fails to distinguish a δ13C gradient within their winter foraging areas in the southwest Atlantic Ocean

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| Abstract: | RATIONALE: The main limitation of isotopic tracking for inferring distribution is the lack of detailed reference maps of the isotopic landscape (i.e. isoscapes) in the marine environment. Here, we attempt to map the marine δ13C isoscape for the southwestern sector of the Atlantic Ocean, and assess any temporal variation using the wandering albatross as a model species.<br>METHODS: Tracking data and blood and diet samples were collected monthly from wandering albatrosses rearing chicks at Bird Island, South Georgia, during the austral winter between May and October 2009. δ13C and δ15N values were measured by mass spectrometry in plasma and blood cells, and related to highly accurate data on individual movements and feeding activity obtained using three types of device: GPS, activity (immersion) loggers and stomach temperature probes.<br>RESULTS: The tracked birds foraged in waters to the north or northwest of South Georgia, including the Patagonian shelf-break, as far as 2000 km from the colony. The foraging region encompassed the two main fronts in the Southern Ocean (Polar and Subantarctic fronts). δ13C values varied by only 2.1 ‰ in plasma and 2.5 ‰ in blood cells, and no relationships were found between δ13C values in plasma, and mean latitude or longitude of landings or feeding events of each individual.<br>CONCLUSIONS: The failure to distinguish a major biogeographic gradient in δ13C values suggest that δ13C values in the south Atlantic Ocean are fairly homogenous. There was no substantial variation among months |

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| | either in δ13C or δ15N values of plasma or blood cells of tracked birds. As birds did not show a significant change in diet composition or foraging areas during the study period, these results provide no evidence for major temporal variation in stable isotope ratios in consumer tissues, or in the regional marine isoscape in the austral winter of 2009. |
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# Analysis of stable isotope ratios in blood of tracked wandering albatrosses fails to distinguish a $\delta^{13}C$ gradient within their winter foraging areas in the southwest Atlantic Ocean

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**Short title: Spatiotemporal isotopic variation in southwestern Atlantic waters**

## ABSTRACT

**RATIONALE:** The main limitation of isotopic tracking for inferring distribution is the lack of detailed reference maps of the isotopic landscape (i.e. isoscapes) in the marine environment. Here, we attempt to map the marine $\delta^{13}$C isoscape for the southwestern sector of the Atlantic Ocean, and assess any temporal variation using the wandering albatross as a model species.

**METHODS:** Tracking data and blood and diet samples were collected monthly from wandering albatrosses rearing chicks at Bird Island, South Georgia, during the austral winter between May and October 2009. $\delta^{13}$C and $\delta^{15}$N values were measured by mass spectrometry in plasma and blood cells, and related to highly accurate data on individual movements and feeding activity obtained using three types of device: GPS, activity (immersion) loggers and stomach temperature probes.

**RESULTS:** The tracked birds foraged in waters to the north or northwest of South Georgia, including the Patagonian shelf-break, as far as 2000 km from the colony. The foraging region encompassed the two main fronts in the Southern Ocean (Polar and Subantarctic fronts). $\delta^{13}$C values varied by only 2.1 ‰ in plasma and 2.5 ‰ in blood cells, and no relationships were found between $\delta^{13}$C values in plasma, and mean latitude or longitude of landings or feeding events of each individual.

**CONCLUSIONS:** The failure to distinguish a major biogeographic gradient in $\delta^{13}$C values suggest that $\delta^{13}$C values in the south Atlantic Ocean are fairly homogenous. There was no substantial variation among months either in $\delta^{13}$C or $\delta^{15}$N values of plasma or blood cells of tracked birds. As birds did not show a significant change in diet composition or foraging areas during the study period, these results provide no evidence for major temporal variation in stable isotope ratios in consumer tissues, or in the regional marine isoscape in the austral winter of 2009.

**Keywords:** *Diomedea exulans*; Isoscapes; Oceanic front; Seabird; South Georgia

## INTRODUCTION

The study of movements of marine wildlife is crucial for the conservation and sustainable use of marine resources. Stable isotope analysis (SIA) provides a novel and powerful tool for tracing animal movements because by analysing the appropriate tissues we can link isotopic information to specific geographic areas, and hence determine foraging areas of individuals.[1,2] A prerequisite of isotopic tracking is the identification and validation of isotopic geographic gradients (i.e. isoscapes) in marine environments that can be used to improve our understanding of the foraging ecology (distribution, trophic level and diet) of predators.[3] There is a great deal of interest in the mapping of marine isoscapes, as their limited availability reduces the inferences that can be drawn from isotopic approaches.[4]

Although there is a general lack of observational data on spatial isotopic variability within the marine realm,[5] previous studies have nevertheless been able to detect broad latitudinal gradients from the tropics to the poles in carbon isotope ratios (i.e. in $\delta^{13}$C) at the base of the food web (i.e. in plankton) mirroring those in particulate organic matter.[6,7] Typically, pelagic ecosystems at higher latitudes have much lower $\delta^{13}$C values than at lower latitudes. This broad $\delta^{13}$C latitudinal gradient in baseline values from polar to equatorial waters, is propagated through the food chain up to marine top predators, such as seabirds.[2] As $\delta^{13}$C values vary little up the food chain, the carbon isotope ratio typically reflects the consumer's foraging habitat (i.e. carbon source), which is largely influenced by latitude in pelagic ecosystems, and between inshore and offshore environments.[8–11] On the other hand, stable isotope ratios of nitrogen (i.e. $\delta^{15}$N) mainly reflect the consumer's trophic position, as there is a stepwise enrichment of $^{15}$N between prey and predators.[9,12,13] Since isotopic patterns in food-webs can differ spatially, information on residency periods and movement patterns can be acquired by measuring isotope ratios in consumer tissues such as blood and keratin-based tissues that can frequently be sampled in the field with minimal disturbance or other impacts.[3,14] In this context, stable isotopes are being used increasingly to study spatial ecology as they have the advantage that the individual need be sampled only once, whereas many electronic tracking devices need to be deployed and the animal later recaptured for data retrieval.[15] Although isoscapes do not provide the fine-spatial scale detail obtained with electronic devices, they improve our understanding of animal movement within the marine realm, and support marine spatial planning and conservation efforts.[5]

The southwestern sector of the Atlantic Ocean includes two main oceanic fronts, namely the Antarctic Polar Front (PF) and the Subantarctic Front (SAF), which in this region are steered into meandering paths by the Patagonian Shelf and by the complex bathymetry of the Scotia Sea.[16,17] The region from 40ºS to 62ºS is characterized by a noticeable decline in $\delta^{13}C$ values with latitude at the base of the food web, particularly south of South Georgia and in the Drake Passage from 53ºS to 62ºS, where values decrease from approximately -23 to -30 ‰, respectively.[6,7,18] In contrast, $\delta^{13}C$ values are more homogeneous in waters from the North Scotia Ridge (which extends from South Georgia to the Patagonian Shelf) north to the subtropics, i.e., 40-53ºS and 38-60ºW. This region encompasses the two main oceanic fronts, but the latitudinal and longitudinal gradients in $\delta^{13}C$ are indistinct, with values ranging from -19 to -23 ‰ at the base of the food web.[6,18] Few studies have validated isoscapes for top predators in the Southern Ocean[3,11] and, to our knowledge, none has done so using a combination of stable isotope analyses, highly accurate GPS tracking, and data on timing of feeding events for the Atlantic sector of the Southern Ocean during the austral winter. In addition, knowledge of temporal variation in isotopic ratios is essential to determine the robustness of isotopic tools [19], but is still limited for taxa in pelagic ecosystems.[1]

The wandering albatross (*Diomedea exulans*) was chosen as a model top predator species because these are large animals that forage over vast areas of the Southern Ocean during the breeding season.[20] Wide-ranging seabirds might be very good samplers for the construction and validation of marine isoscapes from local to continental scales.[3] Wandering albatrosses from South Georgia are known to forage between 28ºS (off Brazil) and 63ºS (Antarctic Peninsula shelf) and from 19ºW (off Tristan da Cunha) to 68ºW (Patagonian Shelf and oceanic waters south of Cape Horn) during the chick-rearing period, which includes the austral winter.[20] Thus, given their wide geographical range, we expect a positive relationship between $\delta^{13}C$ values and mean latitudes of foraging areas of tracked birds, given the positive $\delta^{13}C$ gradient at the base of the food web in the region (from approximately -18 ‰ at 28ºS to -30 ‰ at 63ºS).[18] The main objectives of this study are to: 1) validate the marine $\delta^{13}C$ isoscape for top consumers in the southwest sector of the Atlantic Ocean during the austral winter, and 2) assess monthly differences (from May to October) in stable isotope ratios (i.e. temporal variation).

## EXPERIMENTAL

### Fieldwork

Fieldwork was carried out on wandering albatrosses rearing chicks at Bird Island (54ºS 38ºW), South Georgia, from May to October 2009 (austral late autumn to early spring; hereafter termed the austral winter). Thirty-six breeding adults were fitted with devices, but one bird returned only in January 2010, and so samples were available from a total of 35 birds (see Table 1). Each individual bird was fitted simultaneously with a GPS and activity (saltwater immersion) recorder (AR) and, when possible, a stomach temperature probe (Table 1) (see Ceia et al.[21] for detailed specifications on the devices). The devices were removed and a blood sample (1 ml blood from the tarsal vein) was collected at the end of the subsequent foraging trip. The trip duration of each bird was recorded. Additionally, stomach contents were sampled by water-offloading following Xavier et al.[20] Capture, deployment or retrieval of devices, collection of samples and release took 10–15 min. No birds were sampled more than once, nor a sample taken from the partner of a previously sampled bird. The blood samples were separated into plasma and blood cell fractions within 2-3 hours using a centrifuge (15 min at 3 000 rpm) and subsequently stored frozen until isotopic analysis.

### Diet sampling

Food samples collected from each individual reflected recent prey ingestions. Following Xavier et al.,[20] regurgitates were separated into oil and solid mass and each component (cephalopod, fish, crustacean and carrion) was weighed separately.

### Stable isotope analysis (SIA)

We analysed $\delta^{13}C$ and $\delta^{15}N$ values in plasma and blood cells from each adult (N = 35, Table 1). Although there is overlap in the synthesis of plasma and blood cells, each tissue has a different turnover rate and therefore represents different timescales in terms of diet integration. Plasma turnover rate is high, with a half-life of components of up to one week, whereas the turnover rate of blood cells is typically slower, with a half-life of several weeks, and retaining information on diet in the 4-5 weeks prior to sample collection in wandering albatrosses.[22] Hence, the isotopic signature of plasma was representative largely of diet during the single trip in which each bird was tracked (mean trip duration ± SD for the 35 birds = 6.5 ± 5.0 days).

Samples were freeze-dried and homogenized prior to SIA. The low lipid level of blood cells and of whole blood does not affect their $\delta^{13}$C values, but the high and varying lipid concentrations of plasma can result in depletion of $^{13}$C.[13,23] Hence, lipids were removed from plasma but not blood cells using successive rinses in a 2:1 chloroform–methanol solution. The means ± SD in C:N mass ratio of the blood cells and delipidated plasma was 3.27 ± 0.07 and 3.37 ± 0.03, respectively (N = 35 birds); no monthly differences were found in C:N mass ratio for both tissues (see Table 2). The values are thus below the 3.50 threshold which correspond to a low lipid concentration in tissue.[24]

Nitrogen and carbon isotope ratios were determined by a continuous-flow isotope ratio mass spectrometer (Delta V Advantage, Thermo Scientific, Bremen, Germany) coupled to an elemental analyser (Flash EA1112, Thermo Scientific). Approximately 0.3 mg of each sample was combusted in a tin cup for the simultaneous determination of nitrogen and carbon isotope ratios. The results are presented in δ notation as deviations from the standard references in parts per thousand (‰) according to the following equation: $\delta X = [(Rsample / Rstandard) -1]$, where X represents $^{13}$C or $^{15}$N and Rsample the ratios $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectivelly. Rstandard represents the international reference standard Vienna PeeDee Belemnite (V-PDB) and atmospheric nitrogen (AIR) is the standard for $\delta^{13}$C and $\delta^{15}$N values, respectively. Replicate measurements of internal laboratory standards (acetanilide STD: Thermo scientific—PN 338 36700) indicate precision <0.1 ‰ for both $\delta^{13}$C and $\delta^{15}$N values.

### Tracking, activity (immersion) and stomach temperature probe analysis

All the 36 activity recorders were retrieved and downloaded successfully (one in January 2010). The activity recorders check for saltwater immersion every 3 s, recording every change of state from wet to dry, or *vice versa*, that lasts ≥6 s. GPS data were obtained from 33 of the 36 loggers deployed, of which 27 recorded data during the whole trip. Data from all birds with complete trips, and from two birds in which the GPS recorded for >84% of the foraging trip, were included in analyses; the remaining four bird tracks were excluded because the GPS recorded positions for <55% of the trip. This resulted in a total of 29 birds with reliable GPS data (see Table 1). The GPS loggers (median error of <10 m) were set to record location every 20 min. GPS and activity (immersion) data were used simultaneously to determine latitude and longitude of landing events on the water that accounted >10 mins. between consecutive tracking points (i.e. 20 mins.), which was assumed to correspond to a feeding attempt. From the 26 birds equipped with a stomach temperature probe (STP), a total of 23 were retrieved, 22 of which downloaded successfully; data from 17 of these loggers were used in further analyses (Table 1). The data on temperature recorded every 20 s by the STPs were combined with GPS and activity (immersion) data to estimate the latitude and longitude of prey ingestions (feeding events). Changes in temperature <4 ºC usually reflect ingestion of water or very small prey and were excluded from the analyses.[25] There were highly significant positive Pearson correlations between mean latitude and longitude of attempted (from immersion data) and successful prey captures (from STP data) (latitude: $r = 0.96$, $F_{1,15} = 197.8$, $p << 0.001$; longitude: $r = 0.98$, $F_{1,15} = 430.8$, $p << 0.001$) indicating minor bias between mean geographic positions calculated using these two approaches. Hence, to maximise sample sizes (because STP data were unavailable for some individuals), we relate stable isotope ratios in blood to the mean location of prey capture attempts as well of prey ingestions by each indvidual.

## Data analysis

Due to small sample sizes within each month, we used the non-parametric Kruskal-Wallis test, followed by multiple comparisons, to examine differences between months in $\delta^{13}C$ and $\delta^{15}N$ values, diet composition, trip duration and mean positions (latitude and longitude) of attempted and successful prey captures. According to Boecklen et al.[1] we considered two main sources of variation in isotopic values: diet and trophic position. However, the properties of the consumer such as age, body size, body condition, physiology among others, may also contribute to variation in isotopic signatures, as secondary mechanistic factors.[1,2] We checked for possible $\delta^{13}C$ biogeographic gradients using Pearson's correlation, to identify relationships between the $\delta^{13}C$ values of plasma and mean foraging locations of each bird. In these analyses, latitude and longitude data were $\log_{10}$-transformed to fit a normal distribution. We used ArcGIS v.10.1 (ESRI, Redlands, CA, USA) to plot the distribution of the mean location of prey capture attempts by each tracked bird, and used a natural neighbour interpolation in the Spatial Analyst Tool to model and visualize geographic gradients in $\delta^{13}C$ values of plasma within the foraging area during the austral winter (Fig. 1).

## RESULTS

Overall, $\delta^{13}C$ values for the 35 wandering albatrosses sampled from May to October, i.e., throughout the austral winter, varied between -21.3 and -19.1 ‰ in plasma, and between -21.2 and -18.7 ‰ in blood cells. $\delta^{15}N$ values ranged from 13.6 to 15.1 ‰ in plasma and from 13.5 to 14.7 ‰ in blood cells. We found no differences between months (from May to October) in the mean $\delta^{13}C$ and $\delta^{15}N$ values of either plasma or blood cells in all study birds, or if the analysis is limited to the 29 birds for which GPS and immersion data were available, or just the 17 birds for which there were usable data from all three kinds of device (Table 2).

There was no significant effect of month on the mean duration of foraging trips for the entire sample ($H_{5,35} = 6.1$, $p = 0.30$), nor the subsets of birds for which GPS and immersion data were available ($H_{5,29} = 5.8$, $p = 0.33$) or those for which GPS, immersion and STP data were obtained ($H_{3,17} = 1.4$, $p = 0.71$). Overall, the diet of the 35 birds sampled was composed mainly of fish (59.4 % by mass) and cephalopods (38.4 %), a small amount of carrion (2.2 %) and trace amounts of crustaceans (0.02 %). Despite a decrease in the consumption of fish in September and October and a consequent increase in the consumption of cephalopods during the same months, no significant differences between months were observed in the proportions of each category of prey either in samples from all birds, or just from those for which all three types of tracking data were obtained (Table 2).

All the 29 birds for which GPS data were obtained travelled north or northwest of South Georgia during their foraging trips; mean latitude and longitude of all feeding attempts (immersion events that lasted >10 mins.) on these trips were distributed from 40ºS to 54ºS and 37ºW to 54ºW, respectively. This region encompasses the two main ocean fronts (PF and SAF), and the shelf that extends from South Georgia west to the Burdwood Bank (Fig. 1). Depth varied from 100 to 6000 m at these locations. The overall mean latitudes and longitudes did not differ significantly by month for wandering albatrosses from which both GPS and activity data were obtained, although small differences were detected in latitude between September and May (p = 0.043), and longitude between August and May (p = 0.048) (Table 2). No significant differences were found between months in the mean latitudes and longitudes of feeding (Table 2).

No linear relationships were found between the $\delta^{13}C$ values of plasma and the mean latitude (r = 0.08, $F_{1,27} = 0.2$, p = 0.66) or longitude (r = 0.34, $F_{1,27} = 3.5$, p = 0.07) of feeding attempts of the 29 wandering albatrosses from which GPS and immersion data were obtained. Similarly, no relationships were found between the $\delta^{13}C$ values and the mean latitude (r = 0.11, $F_{1,15} = 0.2$, p = 0.68) or longitude (r = 0.20, $F_{1,15} = 0.6$, p = 0.45) of feeding events based on the STP data.

## DISCUSSION

During this study, wandering albatrosses from Bird Island foraged exclusively to the north or northwest of the colony, in the vicinity of South Georgia or Shag Rocks, or towards the Patagonian Shelf. This region encompasses the Antarctic Polar Front (PF), the Subantarctic Front (SAF) and the northern extension of the Subantarctic Front (SAF_N), and is consistent with the foraging distribution identified in past tracking studies of wandering albatrosses breeding at Bird Island, although of considerably smaller range.[20] Based on a previous analysis of the stable isotope data in this paper, but with a different focus, Ceia et al.[21] demonstrated that the tracked birds showed high short-term (within season) consistency in foraging habitat (i.e. carbon source) and trophic level. It is therefore probable that these individual wandering albatrosses tended to concentrate their foraging in particular areas on consecutive trips during the chick-rearing period.

No relationships were found between $\delta^{13}C$ values and mean latitudes or longitudes of the individual trips, suggesting there was no consistent biogeographic gradient in $\delta^{13}C$ values in waters north and northwest of South Georgia to *ca.* 40º S. Overall $\delta^{13}C$ values in the blood of the sampled wandering albatrosses showed limited variation (by 2.1 ‰ in plasma and 2.5 ‰ in blood cells) despite the differences in individual foraging areas, which were across a region that encompasses two main oceanic fronts (Fig. 1). These results thus contrast with the larger range of $\delta^{13}C$ values (-

24 to -19 ‰) and their positive relationship with foraging latitudes for the same species at approximately the same latitudes, and including the same oceanic fronts, in the south Indian Ocean from January to March 2008 (i.e. during the austral summer).[3] During this study, the lowest $\delta^{13}$C values (around -21 ‰) were observed in birds that had fed near the confluence of the Antarctic Polar Front (PF) and the Subantarctic Front (SAF), in the eastern extent of the overall foraging area, *ca*.500-600 km north of the study site (Fig. 1). The particularly complex oceanography of this region results from variable bathymetry, intense eddy formation and meandering of the ocean fronts and currents,[26] such that these are poorly associated with latitude.[16,17,27] However, isotope data (particularly $\delta^{13}$C) are broadly indicative of water mass and not of latitude by itself .[11] As a result, the lack of consistency in the latitudinal stratification of the different water masses confuses the stable isotope signals and presumably weakens the isotopic gradient,[28] especially during the winter when the ocean is more agitated. According to Graham et al.[6] and Quillfeldt et al.,[18] this region of the southwest Atlantic is characterized by much higher $\delta^{13}$C values at the base of the food web, with an indistinct isotopic gradient, whereas waters south of the Antarctic Polar Front show a clearer decline in $\delta^{13}$C values with latitude. Although the observed latitudinal and longitudinal range of the tracked birds (i.e. from 40ºS to 54ºS and from 37ºW to 54ºW) was smaller than expected, the range of the observed $\delta^{13}$C values in both plasma and blood cells of sampled birds (Table 2) are consistent with reported values for organisms at the base of the food web for this region (from -19 to -23 ‰),[6,7,18] considering an expected enrichment between the base of the food web and top predators in $^{13}$C of about 1 ‰.[29] This region shows little variation in carbon stable isotope values at the base of the food web and our results also suggest fairly homogeneous $\delta^{13}$C values at the level of a top consumer around South Georgia and up to a distance of approximately 2000 km northwest, towards the Patagonian Shelf. However, only part of the southwest Atlantic was 'sampled' in comparison to the whole region foreseen, which may have weakened and masked the biogeographic gradients in $\delta^{13}$C values expected for the region, as some studies of stable isotope analysis in lower trophic-level organisms suggest.[7,30] As the tracked wandering albatrosses did not travel south of the colony, we were unable to map the $\delta^{13}$C isoscape in Antarctic waters towards the Antarctic Peninsula, where a positive relationship between $\delta^{13}$C values and latitude would be expected ,[6,7,18] as, in fact, seems to occur in the Southern Ocean in general.[3,8,11]

There was no consistent effect of month on stable isotope ratios in plasma or blood cells of the sampled birds, nor on diet composition or the mean latitudes and longitudes of feeding areas, which suggests that baseline isotope ratios showed little variation during the study period (i.e. austral winter 2009). Currently, there is a large gap in our knowledge of temporal isotopic variation worldwide.[1] However, the $\delta^{13}$C and $\delta^{15}$N values of top consumers integrate those of multiple prey (fish and squid) and may not necessarily reflect the lack of such variation at the base of the food web. Few previous studies have incorporated data on temporal variation (within and between years) in $\delta^{13}$C and $\delta^{15}$N values (but see Quillfeldt et al.[31]), although this is potentially an important reason for variation between top consumers of different species or populations in pelagic ecosystems of the Southern Ocean,[9,32] and the North Atlantic.[33] Several authors suggested that overall variation in stable isotope values measured in predator tissues is more likely to be related to variation in their diets and foraging distributions,[34–36] but the temporal shifts and biogeographical trends in baseline isotope ratios should be considered in order to avoid misinterpretations in future studies as suggested by Quillfeldt et al.[31] Baseline and lower trophic level organisms may show substantial spatiotemporal isotopic heterogeneity[7,30,31] and local enrichment in $^{13}$C in phytoplankton during periods of elevated primary productivity will influence isotopic values of upper trophic level organisms.[37] Our results suggest that there is limited temporal variation in $\delta^{13}$C and $\delta^{15}$N values of top consumers in our study region during the austral winter of 2009, but of course, variation in isotope ratios could be more substantial in the long-term.

Although wide-ranging seabirds, and particularly wandering albatrosses, could be powerful samplers for the validation of marine isoscapes,[3] it should be noticed that seabirds may present some limitations to infer about spatiotemporal variation in marine isoscapes. This is because wandering albatrosses, and seabirds in general, are apex predators that feed on higher trophic level prey that integrate (and then buffer) spatiotemporal isotopic variations (especially at the base of the food web). The general limitations are (i) that wandering albatrosses feed at multiple locations along the track and on prey of different species and size and potentially of widely-differing isotope signatures, and (ii) these prey themselves move both horizontally and vertically in the water column, so their isotope ratios will not necessarly reflect $\delta^{13}$C values in the ocean at the point of capture. In addition, (iii) ingestion of fisheries discards (from benthic discards or bait that could be from anywhere originally) can complicate matters even further.[38] On the other hand, particular caveats of this study may bias the overall results because (iv) the overall distribution of all the single mean locations from each bird provides a relatively poor overall spatiotemporal coverage, with only a few locations in the northwest and during June and October, and (v) plasma turnover rate is up to one week such that if the bird fitted with a GPS returns within a few days, it could be possible to still reflect some isotopic signal from the previous foraging trip (although birds showed a high individual consistency in the foraging niche, particularly over the short time-period).[21] Giving all these limitations, we can argue that for this region the gradient was likely to be weak or indiscernible at the top consumer level, resulting in fairly homogeneous $\delta^{13}C$ values, in contrast with the results in the southern Indian Ocean.[3] However, this may not be true for organisms at lower-trophic levels, although the complex oceanographic features of this region (compared with the southern Indian Ocean with better stratified frontal systems and less eddies and retroflection of currents) suggests that the issue is more of changes in $\delta^{13}C$ values with water mass, rather than latitude.

## Conclusions

Our study examines the $\delta^{13}C$ isoscape for a top consumer, the wandering albatross, in the southwest Atlantic Ocean north of South Georgia during the austral winter (May to October 2009). Although this region includes the two main oceanic fronts (Polar and Subantarctic fronts), our results suggest a fairly homogeneous $\delta^{13}C$ isoscape at the level of a top consumer, in comparison with the more pronounced isotopic gradient with latitude that occurs further south, as indicated in previous studies. We did not find any evidence of major temporal variation in stable isotope values in blood of the tracked birds during the study period, suggesting a consistent pattern during the winter season in this region at the level of a top predator. However, isoscapes may vary from one year/season to another and assumptions about baseline isotope values from different water masses cannot automatically be extrapolated from one geographic area to another broadly similar area. Future studies should attempt to validate isoscapes in different marine environments and assess temporal isotopic variation across larger spatiotemporal scales at both baseline and higher trophic levels.

Once validated, isoscapes can provide valuable insights into the distribution of many marine species that can be sampled at different levels of the foodweb, with applications that range from conservation management, e.g., identification of biodiversity hotspots, to addressing potential conflicts with commercial interests such as fishing, particularly in regions that are as vulnerable as those around Antarctica.

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## REFERENCES

[1] W. J. Boecklen, C. T. Yarnes, B. A. Cook, A. C. James. On the use of stable isotopes in trophic ecology. *Annu. Rev. Ecol. Evol. Syst.* **2011**, *42*, 411.

[2] R. Ramos, J. González-Solís. Trace me if you can: the use of intrinsic biogeochemical markers in marine top predators. *Front. Ecol. Environ.* **2012**, *10*, 258.

[3] A. Jaeger, V. J. Lecomte, H. Weimerskirch, P. Richard, Y. Cherel. Seabird satellite tracking validates the use of latitudinal isoscapes to depict predators' foraging areas in the Southern Ocean. *Rapid Commun. Mass Spectrom.* **2010**, *24*, 3456.

[4] Y. Cherel, M. Corre, S. Jaquemet, F. Ménard, P. Richard, H. Weimerskirch. Resource partitioning within a tropical seabird community: new information from stable isotopes. *Mar. Ecol. Prog. Ser.* **2008**, *366*, 281.

[5] G. J. Bowen, J. B. West, B. H. Vaughn, T. E. Dawson, J. R. Ehleringer, M. L. Fogel, K. Hobson, J. Hoogewerff, C. Kendall, C.-T. Lai, C. C. Miller, D. Noone, H. Schwarcz, C. J. Still. Isoscapes to address large-scale earth science challenges. *Eos, Trans. Am. Geophys. Union* **2009**, *90*, 109.

[6] B. S. Graham, P. L. Koch, S. D. Newsome, K. W. Mcmahon, D. Aurioles, Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems, in *Isoscapes: Understanding Movement, Pattern, and Process on Earth through Isotope Mapping*, (Eds: J.B. West, G.J. Bowen, T.E. Dawson, K.P. Tu). Springer Netherlands, Dordrecht, **2010**, pp. 299–318.

[7] G. Stowasser, A. Atkinson, R. A. R. McGill, R. A. Phillips, M. A. Collins, D. W. Pond. Food web dynamics in the Scotia Sea in summer: A stable isotope study. *Deep Sea Res. Part II* **2012**, *59-60*, 208.

[8] Y. Cherel, K. Hobson. Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar. Ecol. Prog. Ser.* **2007**, *329*, 281.

[9] P. Quillfeldt, R. McGill, R. Furness. Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel. *Mar. Ecol. Prog. Ser.* **2005**, *295*, 295.

[10] S. D. Newsome, C. M. Rio, S. Bearhop, D. L. Phillips. A niche for isotopic ecology. *Front. Ecol. Environ.* **2007**, *5*, 429.

[11] R. A. Phillips, S. Bearhop, R. A. R. McGill, D. A. Dawson. Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. *Oecologia* **2009**, *160*, 795.

[12] A. L. Bond, I. L. Jones. A practical introduction to stable-isotope analysis for seabird biologists: approaches, cautions and caveats. *Mar. Ornithol.* **2009**, *37*, 183.

[13] Y. Cherel, K. A. Hobson, S. Hassani. Isotopic discrimination between food and blood and feathers of captive penguins: implications for dietary studies in the wild. *Physiol. Biochem. Zool.* **2005**, *78*, 106.

[14] K. A. Hobson. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* **1999**, *120*, 314.

[15] G. J. Bowen. Isoscapes: spatial pattern in isotopic biogeochemistry. *Annu. Rev. Earth Planet. Sci.* **2010**, *38*, 161.

[16] H. Orsi, T. Whitworth, W. D. N. Jr. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep Sea Res. Part I* **1995**, *42*, 641.

[17] J. B. Sallée, K. Speer, R. Morrow. Response of the antarctic circumpolar current to atmospheric variability. *J. Clim.* **2008**, *21*, 3020.

[18] P. Quillfeldt, J. F. Masello, R. A. McGill, M. Adams, R. W. Furness. Moving polewards in winter: a recent change in the migratory strategy of a pelagic seabird? *Front. Zool.* **2010**, *7*, 15.

[19] T. Chouvelon, J. Spitz, F. Caurant, P. Mèndez-Fernandez, A. Chappuis, F. Laugier, E. Le Goff, P. Bustamante. Revisiting the use of δ15N in meso-scale studies of marine food webs by considering spatio-temporal variations in stable isotopic signatures – The case of an open ecosystem: The Bay of Biscay (North-East Atlantic). *Prog. Oceanogr.* **2012**, *101*, 92.

[20] J. C. Xavier, P. N. Trathan, J. P. Croxall, A. G. Wood, G. Podestá, P. G. Rodhouse. Foraging ecology and interactions with fisheries of wandering albatrosses (*Diomedea exulans*) breeding at South Georgia. *Fish. Oceanogr.* **2004**, *13*, 324.

[21] F. R. Ceia, R. A. Phillips, J. A. Ramos, Y. Cherel, R. P. Vieira, P. Richard, J. C. Xavier. Short- and long-term consistency in the foraging niche of wandering albatrosses. *Mar. Biol.* **2012**, *159*, 1581.

[22] S. A. Carleton, C. M. del Rio. The effect of cold-induced increased metabolic rate on the rate of 13C and 15N incorporation in house sparrows (*Passer domesticus*). *Oecologia* **2005**, *144*, 226.

[23] Y. Cherel, K. A. Hobson, H. Weimerskirch. Using stable isotopes to study resource acquisition and allocation in procellariiform seabirds. *Oecologia* **2005**, *145*, 533.

[24] D. M. Post, C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi, C. G. Montaña. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **2007**, *152*, 179.

[25] H. Weimerskirch, D. Pinaud, F. Pawlowski, C. A. Bost. Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. *Am. Nat.* **2007**, *170*, 734.

[26] M. R. Mazloff, P. Heimbach, C. Wunsch. An eddy-permitting Southern Ocean state estimate. *J. Phys. Oceanogr.* **2010**, *40*, 880.

[27] R. G. Peterson, L. Stramma. Upper-level circulation in the South Atlantic Ocean. *Prog. Oceanogr.* **1991**, *26*, 1.

[28] S. Laakmann, H. Auel. Longitudinal and vertical trends in stable isotope signatures (δ13C and δ15N) of omnivorous and carnivorous copepods across the South Atlantic Ocean. *Mar. Biol.* **2010**, *157*, 463.

[29] B. J. Peterson, B. Fry. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* **1987**, *18*, 293.

[30] K. Schmidt, A. Atkinson, D. Stubing, J. W. McClelland, J. P. Montoya, M. Voss. Trophic relationships among Southern Ocean copepods and krill: some uses and limitations of a stable isotope approach. *Limnol. Oceanogr.* **2003**, *48*, 277.

[31] P. Quillfeldt, K. Ekschmitt, P. Brickle, R. A. R. McGill, V. Wolters, N. Dehnhard, J. F. Masello. Variability of higher trophic level stable isotope data in space and time – a case study in a marine ecosystem. *Rapid Commun. Mass Spectrom.* **2015**, *29*, 667.

[32] M. Forero, J. González-Solís, K. Hobson, J. Donázar, M. Bertellotti, G. Blanco, G. Bortolotti. Stable isotopes reveal trophic segregation by sex and age in the southern giant petrel in two different food webs. *Mar. Ecol. Prog. Ser.* **2005**, *296*, 107.

[33] J. L. Roscales, E. Gómez-Díaz, V. Neves, J. González-Solís. Trophic versus geographic structure in stable isotope signatures of pelagic seabirds breeding in the northeast Atlantic. *Mar. Ecol. Prog. Ser.* **2011**, *434*, 1.

[34] M. Polito, H. Lynch, R. Naveen, S. Emslie. Stable isotopes reveal regional heterogeneity in the pre-breeding distribution and diets of sympatrically breeding *Pygoscelis* spp. penguins. *Mar. Ecol. Prog. Ser.* **2011**, *421*, 265.

[35] F. R. Ceia, V. H. Paiva, V. Fidalgo, L. Morais, A. Baeta, P. Crisóstomo, E. Mourato, S. Garthe, J. C. Marques, J. A. Ramos. Annual and seasonal consistency in the feeding ecology of an opportunistic species, the yellow-legged gull *Larus michahellis*. *Mar. Ecol. Prog. Ser.* **2014**, *497*, 273.

[36] J. Navarro, J. González-Solís, G. Viscor. Nutritional and feeding ecology in Cory's shearwater *Calonectris diomedea* during breeding. *Mar. Ecol. Prog. Ser.* **2007**, *351*, 261.

[37] R. D. Pancost, K. H. Freeman, S. G. Wakeham. Controls on carbon isotope fractionation by diatoms in the Peru upwelling region. *Geochim. Cosmochim. Acta* **1997**, *61*, 4983.

[38] L. Bugoni, R. A. R. McGill, R. W. Furness. The importance of pelagic longline fishery discards for a seabird community determined through stable isotope analysis. *J. Exp. Mar. Biol. Ecol.* **2010**, *391*, 190.

# TABLES

**Table 1.** Number of GPS, AR (activity (immersion) recorders) and STP (stomach temperature probes) loggers deployed, retrieved and downloaded successfully, and blood and diet samples obtained, from wandering albatrosses breeding at Bird Island by month from May to October 2009.

| 2009 | May | June | July | August | September | October | Total |
|---|---|---|---|---|---|---|---|
| **Deployments** | | | | | | | |
| GPS | 6 | 6 | 6 | 8 | 6 | 4 | 36 |
| AR | 6 | 6 | 6 | 8 | 6 | 4 | 36 |
| STP | 6 | 6 | 6 | 8 | 0 | 0 | 26 |
| **Retrievals** | | | | | | | |
| GPS | 6 | 4 | 6 | 8 | 6 | 3 | 33 |
| AR | 6 | 6 | 6 | 8 | 6 | 4 | 36 |
| STP | 6 | 6 | 4 | 7 | - | - | 23 |
| **Downloaded successfully** | | | | | | | |
| GPS | 6 | 4 | 6 | 8 | 6 | 3 | 33 |
| AR | 6 | 6 | 6 | 8 | 6 | 4 | 36 |
| STP | 6 | 6 | 3 | 7 | - | - | 22 |
| **Combined devices with successful data** | | | | | | | |
| GPS and AR | 6 | 3 | 6 | 6 | 5 | 3 | 29 |
| GPS, AR and STP | 6 | 3 | 3 | 5 | - | - | 17 |
| **Tissue samples for stable isotope analyses and diet samples** | | | | | | | |
| Plasma | 6 | 6 | 6 | 8 | 6 | 3 | 35 |
| Blood cells | 6 | 6 | 6 | 8 | 6 | 3 | 35 |
| Regurgitates | 6 | 6 | 6 | 8 | 6 | 3 | 35 |

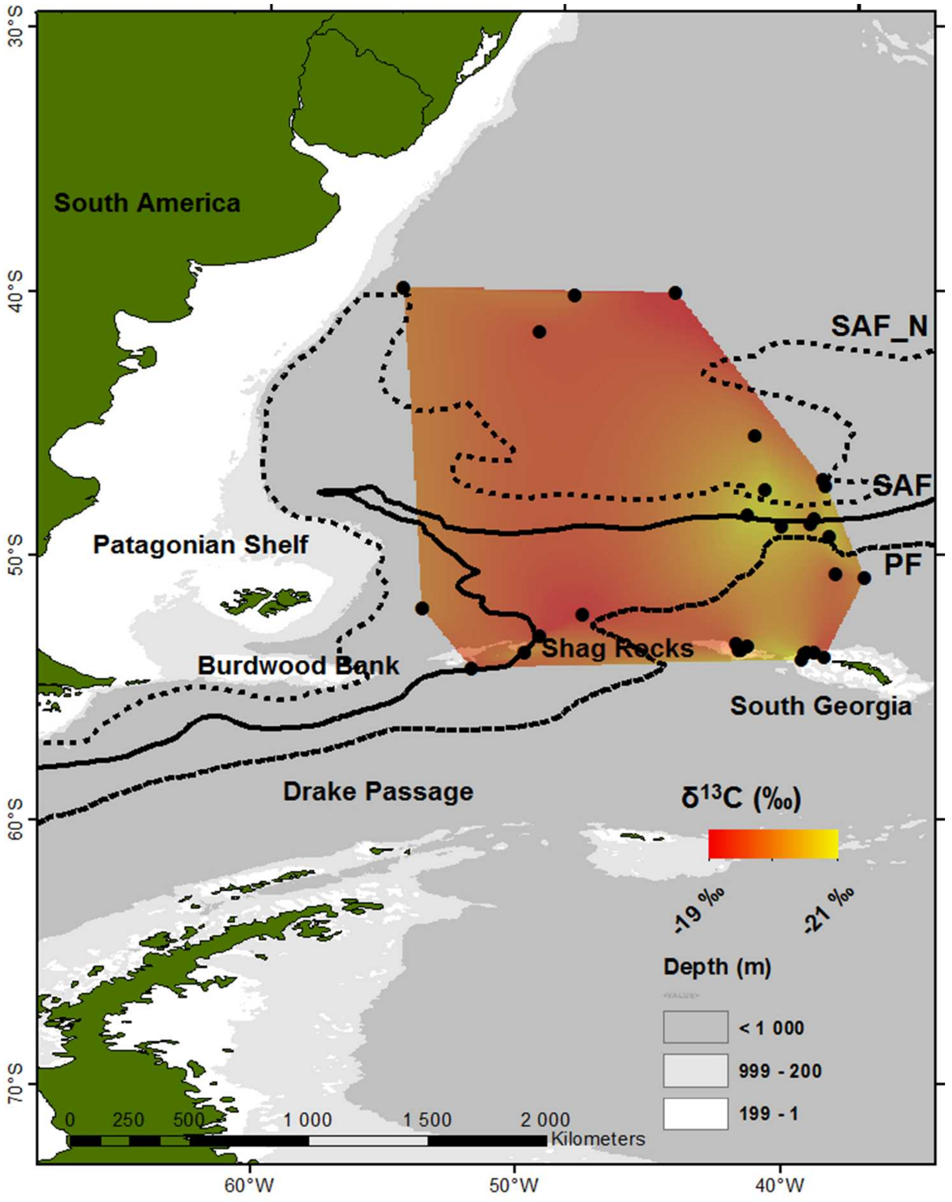
**Table 2.** Comparison of foraging parameters (trip duration, mean latitude and longitude), stable isotope values ($\delta^{13}$C and $\delta^{15}$N), and C:N mass ratio in blood cells and delipidated plasma, and diet composition (proportion by mass of fish, cephalopods, crustaceans and carrion, based on the stomach contents) of breeding wandering albatrosses sampled at Bird Island, South Georgia, from May to October 2009. Values are means ± SD. Identical superscript letters indicate significant differences between months (multiple comparisons). Stable isotope analysis (SIA); activity (immersion) recorders (AR); stomach temperature probes (STP).

| **2009** | | | | | | | Kruskal-Wallis test | |
|---|---|---|---|---|---|---|---|---|
| **A. All birds (n=35)** | May (n=6) | June (n=6) | July (n=6) | August (n=8) | September (n=6) | October (n=3) | $H_{(5,35)}$ | P |
| Trip duration (days) | 3.2 ± 1.4 | 6.3 ± 4.9 | 5.7 ± 3.1 | 6.0 ± 5.3 | 11.3 ± 6.5 | 6.5 ± 5.1 | 6.1 | 0.30 |
| SIA | | | | | | | | |
| Plasma $\delta^{13}$C (‰) | -19.9 ± 0.6 | -20.2 ± 0.6 | -20.5 ± 0.4 | -19.7 ± 0.5 | -19.9 ± 0.6 | -20.1 ± 0.8 | 7.0 | 0.22 |
| Plasma $\delta^{15}$N (‰) | 14.5 ± 0.5 | 14.4 ± 0.4 | 14.2 ± 0.5 | 14.5 ± 0.4 | 14.1 ± 0.4 | 14.2 ± 0.5 | 4.5 | 0.47 |
| Plasma C:N mass ratio | 3.37 ± 0.02 | 3.40 ± 0.04 | 3.35 ± 0.02 | 3.36 ± 0.02 | 3.38 ± 0.05 | 3.35 ± 0.02 | 7.9 | 0.16 |
| Blood cells $\delta^{13}$C (‰) | -20.4 ± 0.6 | -20.2 ± 0.3 | -20.3 ± 0.3 | -20.1 ± 0.3 | -19.8 ± 0.6 | -19.7 ± 0.9 | 3.6 | 0.61 |
| Blood cells $\delta^{15}$N (‰) | 14.0 ± 0.2 | 14.1 ± 0.3 | 14.1 ± 0.3 | 14.1 ± 0.4 | 14.1 ± 0.3 | 14.3 ± 0.4 | 2.2 | 0.82 |
| Blood cells C:N mass ratio | 3.27 ± 0.03 | 3.26 ± 0.04 | 3.27 ± 0.05 | 3.31 ± 0.14 | 3.26 ± 0.04 | 3.25 ± 0.05 | 1.2 | 0.95 |
| Diet | | | | | | | | |
| Fish (% by mass) | 63.0 ± 41.5 | 55.2 ± 48.3 | 63.5 ± 49.6 | 64.2 ± 37.9 | 29.1 ± 38.3 | 1.4 ± 2.3 | 7.7 | 0.17 |
| Cephalopods (% by mass) | 34.0 ± 42.4 | 44.8 ± 48.3 | 36.5 ± 49.6 | 22.8 ± 33.2 | 70.9 ± 38.3 | 90.1 ± 13.8 | 7.0 | 0.22 |
| Crustaceans (% by mass) | 0.3 ± 0.7 | 0 | 0 | 0 | <0.1 | 0 | 4.0 | 0.56 |
| Carrion (% by mass) | 2.7 ± 6.6 | 0 | 0 | 13.0 ± 28.1 | <0.1 | 8.5 ± 14.8 | 5.6 | 0.34 |
| **B. GPS and AR (n=29)** | May (n=6) | June (n=3) | July (n=6) | August (n=6) | September (n=5) | October (n=3) | $H_{(5,29)}$ | P |
| Trip duration (days) | 3.2 ± 1.4 | 5.4 ± 7.3 | 5.7 ± 3.1 | 4.8 ± 4.6 | 10.7 ± 7.1 | 6.5 ± 5.1 | 5.8 | 0.33 |
| Latitude in ° (of feeding attempts) | -53.6 ± 0.4$^{a}$ | -49.1 ± 8.0 | -50.2 ± 2.1 | -49.7 ± 3.6 | -44.8 ± 6.0$^{a}$ | -50.2 ± 2.4 | 9.7 | 0.08 |
| Longitude in ° (of feeding attempts) | -45.4 ± 5.3$^{a}$ | -44.0 ± 8.8 | -42.2 ± 5.7 | -38.8 ± 1.1$^{a}$ | -44.1 ± 4.3 | -41.6 ± 5.4 | 10.0 | 0.07 |
| SIA | | | | | | | | |
| Plasma $\delta^{13}$C (‰) | -19.9 ± 0.6 | -20.4 ± 0.8 | -20.5 ± 0.4 | -19.8 ± 0.5 | -19.8 ± 0.5 | -20.1 ± 0.8 | 5.7 | 0.33 |
| Plasma $\delta^{15}$N (‰) | 14.5 ± 0.5 | 14.4 ± 0.6 | 14.2 ± 0.5 | 14.4 ± 0.5 | 14.2 ± 0.3 | 14.2 ± 0.5 | 2.4 | 0.79 |
| Blood cells $\delta^{13}$C (‰) | -20.4 ± 0.6 | -20.3 ± 0.4 | -20.3 ± 0.3 | -20.3 ± 0.1 | -19.6 ± 0.5 | -19.7 ± 0.9 | 5.5 | 0.36 |
| Blood cells $\delta^{15}$N (‰) | 14.0 ± 0.2 | 14.0 ± 0.5 | 14.1 ± 0.3 | 14.0 ± 0.4 | 14.2 ± 0.2 | 14.3 ± 0.4 | 2.8 | 0.73 |
| Diet | | | | | | | | |
| Fish (% by mass) | 63.0 ± 41.5 | 67.3 ± 56.7 | 63.5 ± 49.6 | 80.7 ± 26.3 | 34.9 ± 39.7 | 1.4 ± 2.3 | 8.0 | 0.16 |
| Cephalopods (% by mass) | 34.0 ± 42.4 | 32.7 ± 56.7 | 36.5 ± 49.6 | 15.4 ± 27.0 | 65.1 ± 39.7 | 90.1 ± 13.8 | 7.3 | 0.20 |
| Crustaceans (% by mass) | 0.3 ± 0.7 | 0 | 0 | 0 | <0.1 | 0 | 3.4 | 0.64 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Carrion (% by mass) | 2.7 ± 6.6 | 0 | 0 | 3.9 ± 7.5 | <0.1 | 8.5 ± 14.8 | 3.7 | 0.59 |
| **C. GPS, AR and STP (n=17)** | May (n=6) | June (n=3) | July (n=3) | August (n=5) | September (n=0) | October (n=0) | $H_{(3,17)}$ | P |
| Trip duration (days) | 3.2 ± 1.4 | 5.4 ± 7.3 | 4.9 ± 2.6 | 3.6 ± 3.7 | | | 1.4 | 0.71 |
| Latitude in ° (of prey ingestions) | -53.6 ± 0.3 | -50.0 ± 6.4 | -50.5 ± 2.7 | -49.6 ± 4.2 | | | 3.2 | 0.36 |
| Longitude in ° (of prey ingestions) | -44.2 ± 4.3 | -43.3 ± 7.4 | -44.6 ± 6.1 | -39.2 ± 1.3 | | | 6.1 | 0.10 |
| SIA | | | | | | | | |
| Plasma$\delta^{13}$C (‰) | -19.9 ± 0.6 | -20.4 ± 0.8 | -20.4 ± 0.3 | -19.7 ± 0.4 | | | 4.5 | 0.21 |
| Plasma $\delta^{15}$N (‰) | 14.5 ± 0.5 | 14.4 ± 0.6 | 14.3 ± 0.5 | 14.5 ± 0.5 | | | 0.8 | 0.84 |
| Blood cells $\delta^{13}$C (‰) | -20.4 ± 0.6 | -20.3 ± 0.4 | -20.3 ± 0.2 | -20.2 ± 0.1 | | | 0.8 | 0.85 |
| Blood cells $\delta^{15}$N (‰) | 14.0 ± 0.2 | 14.0 ± 0.5 | 14.0 ± 0.2 | 14.1 ± 0.4 | | | 0.9 | 0.83 |
| Diet | | | | | | | | |
| Fish (% by mass) | 63.0 ± 41.5 | 67.3 ± 56.7 | 60.8 ± 53.4 | 80.9 ± 29.4 | | | 1.4 | 0.72 |
| Cephalopods (% by mass) | 34.0 ± 42.4 | 32.7 ± 56.7 | 39.2 ± 53.4 | 18.2 ± 29.2 | | | 1.2 | 0.76 |
| Crustaceans (% by mass) | 0.3 ± 0.7 | 0 | 0 | 0 | | | 1.8 | 0.61 |
| Carrion (% by mass) | 2.7 ± 6.6 | 0 | 0 | 0.9 ± 1.9 | | | 1.2 | 0.76 |

## FIGURE LEGENDS

**Figure 1.** Estimated isoscape after natural neighbour interpolation from $\delta^{13}C$ values of delipidated plasma of the 29 wandering albatrosses tracked with both GPS and activity loggers between May and October 2009 from Bird Island, South Georgia. Points represent the mean latitude and longitude of feeding attempts calculated for each bird from immersion data (wet events that lasted >10 mins.). Bathymetry is presented as greyscale (downloaded from http://www.ngdc.noaa.gov/mgg/ global/global.html, blended ETOPO1 product, grid of 0.01°). The main oceanic fronts as described in Sallée et al.[17] are indicated as follows: PF - Antarctic Polar Front, SAF - Subantarctic Front and SAF_N - northern extension of the Subantarctic Front.



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