RAPID COMMUNICATIONS IN MASS SPECTROMETRY
Rapid Commun. Mass Spectrom. 2010; **24**: 3456–3460
Published online in Wiley Online Library (wileyonlinelibrary.com) DOI: 10.1002/rcm.4792

RCM

Seabird satellite tracking validates the use of latitudinal isoscapes to depict predators' foraging areas in the Southern Ocean

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Received 11 July 2010; Revised 15 September 2010; Accepted 15 September 2010

Stable isotopes are increasingly being used to trace wildlife movements. A fundamental prerequisite of animal isotopic tracking is a good knowledge of spatial isotopic variations in the environment. Few accessible reference maps of the isotopic landscape (''isoscapes'') are available for marine predators. Here, we validate for the first time an isotopic gradient for higher trophic levels by using a unique combination of a large number of satellite-tracks and subsequent blood plasma isotopic signatures from a wide-ranging oceanic predator. The plasma $\delta^{13}C$ and $\delta^{15}N$ values of wandering albatrosses ($n = 45$) were highly and positively correlated to the Southern Ocean latitudes at which the satellite-tracked individuals foraged. The well-defined latitudinal baseline carbon isoscapes in the Southern Ocean is thus reflected in the tissue of consumers, but with a positive shift due to the cumulative effect of a slight ^{13}C-enrichment at each trophic level. The data allowed us to estimate the carbon isotopic position of the main oceanic fronts in the area, and thus to delineate robust isoscapes of the main foraging zones for top predators. The plasma $\delta^{13}C$ and $\delta^{15}N$ values were positively and linearly correlated, thus suggesting that latitudinal isoscapes also occur for $\delta^{15}N$ at the base of the food web in oceanic waters of the Southern Ocean. The combination of device deployments with sampling of relevant tissues for isotopic analysis appears to be a powerful tool for investigating consumers' isoscapes at various spatio-temporal scales. Copyright © 2010 John Wiley & Sons, Ltd.

Stable isotopes, particularly those of carbon and nitrogen, are increasingly being used to examine the diets, habitats, feeding zones, and migratory connectivity of animals.[1–4] The stable isotope method relies on the assimilation and fixation of intrinsic isotopic markers from the food into the tissues of consumers. The carbon isotopic signature ($\delta^{13}C$) changes little with each trophic step.[5,6] If the $\delta^{13}C$ value differs among regions, it can be used to estimate the foraging areas of a migratory organism from its food intake in the different regions.[7] The power of $\delta^{13}C$ as a proxy of animal foraging habitats is thus related to the knowledge of the extent and pattern of its spatial variations in the environment. In contrast to $\delta^{13}C$, there is a stepwise enrichment in the ratio of nitrogen isotopes ($\delta^{15}N$) from one trophic level to the next.[5,6] $\delta^{15}N$ values have consequently been used to investigate animal trophic levels and predator-prey relationships. Nonetheless, when comparing among ecosystems, the $\delta^{15}N$ value of an organism alone provides little information about its absolute trophic position. This is because there is variation among ecosystems in the $\delta^{15}N$ at the base of the food web. Without an appropriate estimate of the isotopic baseline in each system, there is no way to determine if variation in the $\delta^{15}N$ of an organism reflects changes in food web structure or just a variation in the $\delta^{15}N$ at the base of the food web.[5] Thus, the usefulness of both carbon and nitrogen isotopes as proxies of the ecological niche relates primarily to the knowledge of their spatial variations in the environment.

In marine systems, gradients in stable isotopes (hereafter ''isoscapes'') at the base of the food web have been described at very large spatial scales.[8,9] Few regional maps of marine isoscapes are available,[10] making this a main limitation of the isotopic method.[11] Many studies investigated the feeding ecology of challenging long-ranging migrating species and the life stages of seabirds and marine mammals using their $\delta^{13}C$ and $\delta^{15}N$ values as proxies of their foraging habitats and trophic levels, respectively.[2,4,12] For top predators, the estimate of foraging habitats from $\delta^{13}C$ values is often obscured not only because of a lack of knowledge of basal isoscapes in the relevant marine areas,[13] but also because there is a substantial difference in $\delta^{13}C$ values between the base and the apex of a given trophic web. This isotopic difference results from the successive small ^{13}C enrichment occurring at each trophic level and from various intrinsic and extrinsic factors that can affect the enrichment factors of different organisms and tissues all along the food web.[5,6]

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Consequently, the best way to interpret the carbon signature of top predators would be to describe $\delta^{13}C$ isoscapes using top predators themselves.

In the Southern Ocean, there is a well-defined latitudinal gradient in carbon isotopic values of particulate organic matter.[14] The assumption that this gradient in marine $\delta^{13}C$ values at the base of the food web should also be reflected in organisms at higher trophic levels was previously tested in top predators (e.g. seabirds), but either there was no control for organisms and tissue types,[15] animals were not tracked,[16] or sampling was carried out on feathers.[13] Body feathers do not allow an accurate comparison of device and isotopic tracking, because the precise timing of their synthesis during the extended seabird moulting period is not known (but see Ramos *et al.*[17] for flight feathers of birds with a known moulting pattern). Hence, a call was recently made for the development of approaches that combine the tracking of seabirds and marine mammals using electronic devices with isotopic analysis of relevant tissues.[13]

Here we report the isotopic carbon and nitrogen signatures of a top predator that was simultaneously satellite-tracked, our main goal being to validate and quantify the relationship between predator $\delta^{13}C$ values and latitudes in the Southern Ocean.[16] We chose a large seabird, the wandering albatross *Diomedea exulans*, as an animal model, because the species forages widely from Antarctic to subtropical waters during the incubation period.[18] The geographical range of wandering albatrosses therefore spans baseline gradients in carbon isotopic composition of oceanic waters,[2,14] thus potentially inducing large inter-individual variations in bird $\delta^{13}C$ values. We used plasma collected at the end of the individual foraging trips as a relevant tissue to investigate the albatross feeding habitat, because the turnover of carbon in plasma is high with a half-life of about 4 days,[19] a shorter period than the duration of incubating trips that average 10–14 days.[18]

EXPERIMENTAL

Fieldwork

Field study was carried out on Possession Island (46°30′S, 51°45′E), Crozet Archipelago. As the south-western Indian Ocean is marked by the strong confluence of the Subantarctic and Subtropical Fronts (STF),[20] the Subantarctic Zone (SAZ, where Crozet Islands are located) is defined as the area between the STF and the Polar Front (PF). The Subtropical Zone (STZ) is the area north of STF and the Antarctic Zone (AZ) as the area south of PF (Fig. 1). STF separates waters of the Southern Ocean from the warmer and saltier waters of STZ.[21]

Using the Argos system, 45 wandering albatrosses were satellite-tracked for a single foraging trip during the incubation period (from 15 January to 13 March 2008). Birds were fitted with solar panel-powered satellite transmitters (PTTs-100, Microwave Telemetry Inc., Columbia, MD, USA) attached to the back feathers. Albatross blood was collected from the tarsus vein of the 45 tracked birds on their return to the colony. Whole blood was centrifuged and plasma samples were subsequently kept at −20°C until isotopic analysis.

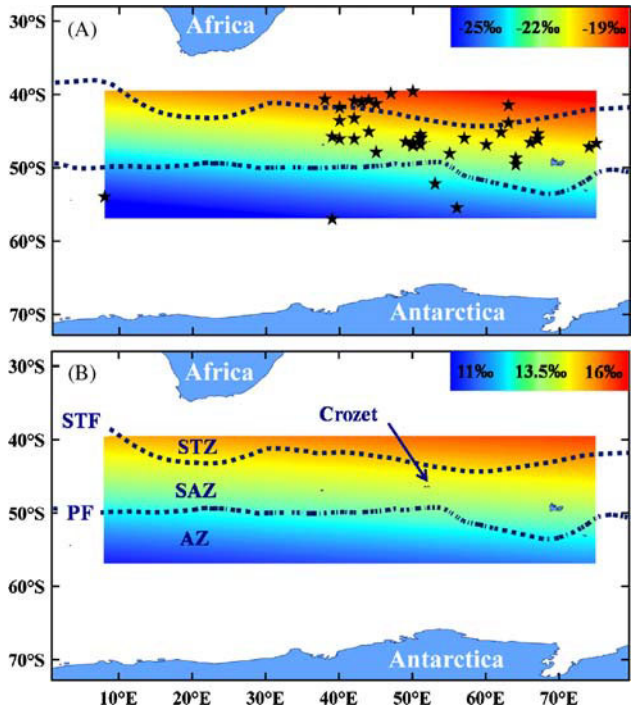

Figure 1. The calculated (A) $\delta^{13}C$ and (B) $\delta^{15}N$ isoscapes after interpolation from the isotopic signatures of plasma of wandering albatrosses that were simultaneously satellite-tracked. Stars represent the distribution of longitude and mean latitude of feeding calculated for each wandering albatross (N = 45). Abbreviations: AZ, Antarctic Zone; PF, Polar Front; SAZ, Subantarctic Zone; STF, Subtropical Front; STZ, Subtropical Zone.

Tracking analysis

From satellite locations, the times spent by sector (resolution: 1° square) were estimated for each individual albatross and used as an estimation of its main foraging areas.[22] Two proxies were then calculated from the times spent by sector to perform linear comparisons between the birds' isotopic signatures and their foraging areas. First, the latitude and longitude of the 1° square where the albatross spent the longest period of time were noted for each bird. Secondly, since no significant correlation was found between longitude and plasma isotopic signature (see Results section), the mean foraging latitude for each bird was also calculated. The time spent in a 1° latitude band, obtained by summing the 1° squares of this latitude (i.e. longitude integrated), was divided by the total trip duration to obtain a ratio of time spent at this latitude. Each ratio was then multiplied by its related latitude, and these values were finally summed to calculate the mean foraging latitude for a given bird. Arcview 10.0 (ESRI) was subsequently used to plot the distribution of each albatross feeding square (N = 45), and a polynomial interpolation in the Geostatistical tool allowed modelling and visualization of the latitudinal trends in $\delta^{13}C$ and $\delta^{15}N$ within the albatross foraging area (Fig. 1).

DOI: 10.1002/rcm

Stable isotope analysis

Since lipids can affect plasma $\delta^{13}C$ values,[23] they were removed from plasma using cyclohexane.[24] In brief, 4 mL of cyclohexane were added to about 0.5 mg of dried plasma. The solution was homogenized in an ultrasound bath (5 min) and then agitated (1 h). The sample was centrifuged, the supernatant containing the lipids was disposed of, and the remaining pellet was dried at 60°C. Sub-samples of the pellets (from 0.3 to 0.4 mg) were weighed with a micro-balance and packed in tin containers. The C/N mass ratio of the delipidated plasma averaged 4.1 ± 0.2 ($N = 45$), with no relationship between C/N and $\delta^{13}C$ values (data not shown), thus indicating that there was no lipid effect on the plasma $\delta^{13}C$ values.[25] The carbon and nitrogen isotope ratios ($\delta^{13}C$ and $\delta^{15}N$, respectively) were determined by a continuous flow mass spectrometer (Thermo Fisher, Delta V Advantage, Waltham, MA, USA) coupled to an elemental analyser (Thermo Fisher, Flash EA 1112). The results are presented in the conventional notation relative to PeeDee belemnite marine fossil limestone and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated measurement errors of <0.15‰ and <0.20‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Data were analyzed using Matlab 7.0 (MathWorks, Natick, MA, USA). The values are mean ± standard deviation (SD).

RESULTS

The duration of foraging trips of incubating wandering albatrosses averaged 10.8 ± 6.0 days. As expected, their satellite tracks encompassed a large latitudinal area, from Antarctic to subtropical waters (Fig. 1), and their corresponding plasma $\delta^{13}C$ and $\delta^{15}N$ values ranged from −25.0 to −19.1‰ (average: -21.2 ± 1.3‰), and from 11.2 to 15.8‰ (average: 14.0 ± 0.8‰), respectively. The plasma $\delta^{15}N$ and $\delta^{13}C$ values were positively and linearly correlated ($y = 0.58x + 26.24$, $R = 0.84$, $p < 0.0001$).

In a first analysis, the latitude and longitude of the sector where each albatross spent the longest period of time during its single trip were compared with its plasma $\delta^{13}C$ and $\delta^{15}N$ values. The plasma carbon and nitrogen signatures were positively correlated to latitude (Pearson's correlation, $R = 0.77$, $p < 0.0001$ and $R = 0.73$, $p < 0.0001$, respectively), but not to longitude ($R = 0.10$, $p = 0.543$ and $R = -0.02$, $p = 0.901$, respectively) of that sector. The marked latitudinal gradient and lack of longitudinal variations are well visualized by isoscape maps drawn using interpolations from the plasma $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 1). In a second analysis, the mean foraging latitudes of the 45 albatrosses were compared with their plasma isotopic values (Fig. 2). The plasma carbon and nitrogen signatures were again highly and positively correlated to latitude (Pearson's correlation, $R = 0.87$, $p < 0.0001$ and $R = 0.81$, $p < 0.0001$, respectively). The corresponding calculated regressions ($y = 0.31x - 7.10$ and $y = 0.20x + 23.03$ for $\delta^{13}C$ and $\delta^{15}N$, respectively) allowed us to estimate the $\delta^{13}C$ values of the main fronts for plasma, i.e. ~ −22.9‰ for PF at ~51°S, and ~ −20.1‰ for STF at ~42°S (corresponding $\delta^{15}N$ values: ~12.8‰ and ~14.6‰, respectively).

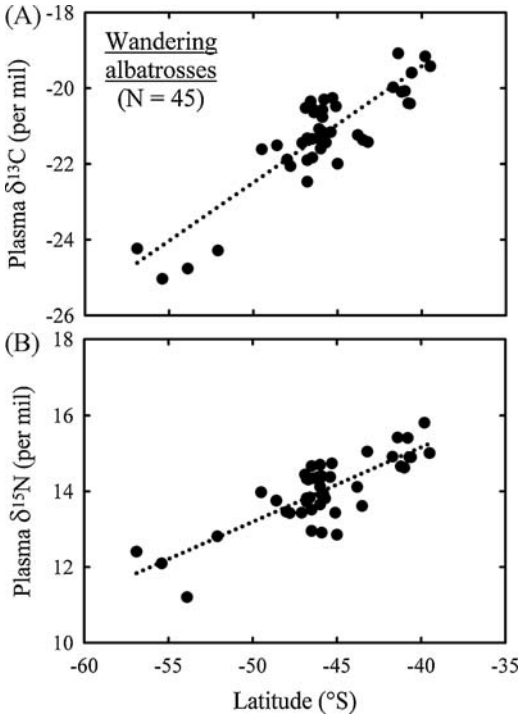

Figure 2. Plasma (A) $\delta^{13}C$ and (B) $\delta^{15}N$ values of wandering albatrosses versus their mean foraging latitudes calculated from their satellite tracking.

DISCUSSION

Here we validate isotopic gradients on top consumers by using a unique combination of satellite-tracks and isotopic signatures of relevant tissues from a wide-ranging oceanic predator. Geographical isotopic gradients have already been depicted in top consumers (e.g. in north-eastern Pacific pinnipeds),[3] but they were not validated by tracking the same individual animals during the time window corresponding to protein turnover in their isotopically analyzed tissue.

As expected, the well-defined latitudinal, but not longitudinal,[16] baseline carbon isoscapes in the Southern Ocean allow us to estimate the latitudes at which consumers forage. However, several intrinsic methodological limitations partially hinder the relationship between albatross tracking and isotopic signatures. Tracking alone does not inform about where and when prey are caught. Since wandering albatrosses feed all along their foraging trips,[26] the single plasma signature per trip integrates not only prey taken at the mean foraging latitude, but also elsewhere during the trip. For example, isotopic values of prey caught in subantarctic waters near the colony lowered (increased) the isotopic signatures of albatrosses that also fed in subtropical (Antarctic) waters. Within that context, the highly positive correlation between the 'diluted' plasma $\delta^{13}C$ values and mean foraging latitudes (Fig. 2) is particularly relevant, underlining the strength of the latitudinal $\delta^{13}C$ isoscapes within the Southern Ocean. Noticeably, the overall latitudinal $\delta^{13}C$ decrease between subtropical and Antarctic waters is lower in predators than at the base of the food web (~5–6 vs. ~8‰) and, at a given latitude, predators are ^{13}C-enriched over baseline levels.[14,16]

DOI: 10.1002/rcm

These differences reflect the cumulative effect of a slight ^{13}C-enrichment at each trophic level,[6] together with different life history traits between short-lived phytoplankton and long-lived predators that integrate and buffer all along the food web short-term variations in baseline isotopic levels.

The lack of longitudinal $\delta^{13}C$ gradient refers to the latitudinal annular structure of the Southern Ocean worldwide, with water masses and fronts with different physical and biological characteristics encircling the Antarctic continent.[21] Consequently, the spatial accuracy of the determination of consumers' foraging areas using their $\delta^{13}C$ values operates more at a large geographical scale, that of water masses and fronts, than latitude *per se*.[13,16] Thus, predators foraging within the same hydrological features would retain the same $\delta^{13}C$ values. Indeed, king penguins from Crozet and Kerguelen Islands that forage at the PF but in different longitudinal areas of the southern Indian Ocean have identical carbon signatures.[16] In the same way, the paradoxical different isotopic signatures of copepods caught at the same latitude in the southern Atlantic Ocean were attributed to a regional longitudinal difference in hydrography, i.e. a northward extension of the PF.[27]

A main result of the present work is the estimated isotopic position of PF and STF at −22.9 and −20.1‰ using albatross plasma. These values compare well with those previously obtained with penguin blood, i.e. −22.5 and −19.7‰, respectively.[16] The 0.4‰ more positive values for whole blood than plasma is probably related to tissue-specific characteristics (e.g. metabolic routing, turn-over rates and discrimination factors). In the same way, feathers are consistently ~1.3‰ ^{13}C-enriched over blood components[28] and, accordingly, the feather isotopic positions of the PF and STF were estimated at −21.2 and −18.3‰, respectively (authors' unpublished data). These isotopic locations of fronts can be used as reference $\delta^{13}C$ isoscape values to estimate the foraging zones of Southern Ocean consumers using blood and keratin-based tissues that are commonly and non-destructively sampled in the field. Whole blood and feathers are metabolically active and inert tissues, respectively, enabling the investigation of different time periods corresponding to the seabird breeding and poorly known inter-nesting period, respectively.[11]

Unlike $\delta^{13}C$, $\delta^{15}N$ is strongly sensitive to trophic level.[5,6] Indeed, $\delta^{15}N$ values of penguins living in the Southern Ocean are more affected by their diet than by the latitudinal locations of their breeding colonies.[16] This does not preclude, however, a baseline effect on the nitrogen isotopic signature of oceanic predators.[29] Within that context, the positive relationship between plasma $\delta^{15}N$ values and latitudes can be explained by two non-exclusive ways: a dietary shift of wandering albatross and/or of its prey, and a change in baseline nitrogen signature with latitude. In agreement with the first hypothesis, wandering albatrosses from Crozet Islands mainly feed on adult squids, including Antarctic, subantarctic and subtropical species,[30,31] which are known to prey more upon lower trophic-level prey in Antarctic waters than further north.[32] In agreement with the second hypothesis, the baseline $\delta^{15}N$ level in the Southern Ocean is depleted compared with lower latitudes. The main feature is a marked decline in the nitrogen signature of particulate organic matter at the STF,[33] with moderate declines occurring further south within the Southern Ocean.[34] Interestingly, albatross $\delta^{15}N$ and $\delta^{13}C$ values are positively and linearly correlated, as are the carbon and nitrogen signatures of beaks from colossal squids.[35] The fact that two different organisms with different isotopic signatures present the same relationship with similar slopes of the regression lines suggests concomitant changes in baseline $\delta^{15}N$ and $\delta^{13}C$ values with latitudes. More information is clearly needed to quantify this latitudinal effect, because it is a crucial point for better interpretation and comparison of the nitrogen signature, and thus the trophic position, of predators foraging in different water masses of the Southern Ocean.[4,12,15]

CONCLUSIONS

Tracking of animals offers us an excellent opportunity to describe marine isoscapes within their foraging areas. We concur with Phillips *et al*.[13] in recommending this approach to increase our knowledge of the marine environment at various spatio-temporal scales. The primary advantage of the stable isotope method is that initial marking of individuals is not necessary and that every capture provides information on origin. In this sense, every capture becomes a recapture,[36] and the method also reduces both animal stress and field work. Once validated and the isoscapes described, it can be successfully applied at low cost on a large number of individuals and species, thus complementing the use of more expensive electronic devices at the population and community levels, respectively.

Acknowledgements

The authors thank M. Berlincourt and H. Mahéo for their help in the field, G. Guillou for stable isotope analysis, and D. Besson, K. Delord, K. Heerah and M. Louzao for processing data. The present work was supported financially and logistically by the programme REMIGE – ANR Biodiversité 2005-011, the Fondation Prince Albert 2 de Monaco, and the Institut Polaire Français Paul Emile Victor (IPEV Program N° 109).

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DOI: 10.1002/rcm