Whisker isotopic signature depicts migration patterns and multi-year intra- and inter-individual foraging strategies in fur seals

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The movement and dietary history of individuals can be studied using stable isotope records in archival keratinous tissues. Here, we present a chronology of temporally fine-scale data on the trophic niche of otariid seals by measuring the isotopic signature of serially sampled whiskers.

Whiskers of male Antarctic fur seals breeding at the Crozet Islands, Southern Indian Ocean, Habitat and diet records were interpreted from the δ13C and δ15N values of whiskers that were serially sampled all along their length. The two basic underlying principles were first, that the isotopic composition of whiskers reflects diet at the time of their growth, because keratin is metabolically inert after synthesis (Rubenstein & Hobson 2004) and, second, that otariid whiskers grow continuously at a constant rate and are not shed (Hirons et al. 2001), thus retaining stable isotope records allowing the reconstruction of an individual’s trophic history. Antarctic fur seals are arguably the best studied otariid. However, most work has focused on lactating females, with little information available on individual variations, the inter- breeding period and on adult males (Stanilov 2005).

The present work, therefore, documents the less well-known, cryptic life stage of the species, i.e. the individual at-sea migration patterns of adult males.

2. MATERIAL AND METHODS
Field study was carried out on Possession Island (46°30’S, 51°45’E). One whisker was collected from 10 randomly chosen breeding male fur seals of unknown age during the summer season 2001–2002. Whiskers were cut as close to the face as possible. Prior to the isotopic analysis, they were hand-washed in 100 per cent ethanol and then cleaned in distilled water for 5 min in a ultrasonic bath. Whiskers were measured, dried and cut into 3 mm long consecutive sections starting from the proximal end. Sections (n = 710) were weighed with a micro-balance, packed in tin containers, and carbon and nitrogen isotope ratios were determined by a continuous flow mass spectrometer (Thermo Fisher, Delta V Advantage) coupled to an elemental analyser (Thermo Fisher, Flash EA 1112). Results are presented in the conventional notation relative to Pee Dee belemnite marine fossil limestone and atmospheric N2 for δ13C and δ15N, respectively. Values are mean ± s.d.

Keratinous tissues (including whiskers) are approximately 3% 13C enriched over their diet in pinnipeds (Hobson et al. 1996). Taking into account both the keratinous effect and the latitudinal gradient in blood δ13C values of top predators in the Southern Ocean (Chere1 & Hobson 2007; Chere1 et al. 2007), the isotopic positions of the polar front (PF) and the subtropical front (STF) for fur seal whiskers were estimated at approximately −19 and −16‰, respectively (figures 1 and 2). The subantarctic zone (STZ) is defined as the area north of the STF, the subantarctic zone (SAZ, where the Crozet Islands are located) as the area between the STF and the PF, and the Antarctic zone (AZ) as the area south of PF.

3. RESULTS
The length of whiskers ranged from 84 to 333 mm, and the number of whisker sections analysed for each individual male Antarctic fur seal varied accordingly from 28 to 111 (see the electronic supplementary material). Whisker isotopic signatures were spread over a large range, with δ13C and δ15N values varying from −25.3 to −14.6‰ (a 10.7‰ difference) and from 7.2 to 14.5‰ (7.3‰), respectively. Overall,
4. DISCUSSION

The results of the present study report the migration patterns and long-term intra- and inter-individual variations in the isotopic niche of an otarid species, using whiskers as an archival tissue of the individuals’ foraging history. Consistent isotopic oscillations along whiskers were previously noted in Steller sea lions. Each oscillation was interpreted as reflecting a complete annual migratory cycle, because the estimated whisker growth rate for each oscillation in wild animals was similar to the range of growth rates in captive individuals (Hirons et al. 2001). Estimated whisker growth rates are identical in wild Steller sea lions and Antarctic fur seals (ranges 0.10–0.14 and 0.11–0.16 mm d\(^{-1}\), respectively). Hence, isotopic cyclicity in whiskers of male Antarctic fur seals is likely to record their annual migratory pattern. As whiskers showed on average 4.8 oscillations, and the age of territorial male fur seals varies from 7 to 13 years (Wickens & York 1997), a single whisker recorded a substantial part (37–69%) of the animal’s lifespan.

In the Southern Ocean, \(\delta^{13}C\) values vary with latitudes and along an inshore/offshore gradient (Cherel & Hobson 2007). While we cannot preclude an inshore/offshore influence, the large oscillations in whisker \(\delta^{13}C\) values are likely to represent regular latitudinal movements of the fur seals. At the population level, the range of \(\delta^{13}C\) values and our isotopic estimation of the position of oceanic fronts show that male seals foraged preferentially in SAZ (46% of the 710 whisker sections) and AZ (45%), and marginally in STZ (9%). The synchronous patterns of \(\delta^{15}N\) with \(\delta^{13}C\) values indicate periodic changes in the animals’ diet associated with migration, because variation in the \(\delta^{15}N\) baseline level in the Southern Ocean
cannot alone account for the large range of seal δ¹⁵N signatures (Best & Schell 1996). Indeed, whisker δ¹⁵N values decreased with latitudes from approximately 12.8‰ in STZ to 10.0‰ in AZ, which is in agreement with both a higher δ¹⁵N baseline level in the subtropics (Best & Schell 1996) and fur seals feeding on different species of mesopelagic fishes in subtropical and subantarctic waters (Beaufort et al. 2004; Cherel et al. 2007).

However, the further drop of δ¹⁵N values from approximately 10.0‰ associated with low δ¹³C signatures indicates feeding on lower trophic level prey. The fur seal nitrogen signature is close to that of krill-eating Adélie penguins (Cherel 2008), indicating that, in high-Antarctic waters, adult males from Crozet preyed upon krill, which forms the staple food of the species elsewhere (Staniland 2005).

The isotopic patterns observed show large intra- and inter-individual trophic niche variations in male Antarctic fur seals. Whisker δ¹³C values indicate that the migratory cycle of individuals encompassed either one (n = 3), two (n = 6) or three (n = 1) oceanographic zones, with no seal foraging exclusively in the subtropics. Among the six individuals foraging in the AZ, four seals reached high-Antarctic waters where their δ¹⁵N values showed that they all fed on krill. The isotopic niches of individual males either overlapped or showed some levels of habitat and resource partitioning. Two examples illustrate the inter-individual segregating mechanisms (figure 2). First (figure 2a), the foraging ranges of males #78 and #Y were overall different but overlapped in SAZ, where their δ¹⁵N signatures indicate dietary segregation. Second (figure 2b), their whisker δ¹³C values show that males #M and #Z never foraged in the same habitats for over more than four years. How can we explain the fact that males breeding in the same subantarctic colony did not show any overlap in their foraging habitats? Territorial males fast on land at the beginning of the reproductive cycle (Staniland 2005). They, therefore, retain the isotopic signature of their foraging areas and diets where they build up energy reserves. Thus, the two seals reproduced at Crozet, but one individual did not feed significantly in subantarctic waters when travelling back and forth to its preferred Antarctic foraging grounds.

In summary, whisker isotopic signatures reveal new multi-year migratory patterns of male Antarctic fur seals at both the population and the individual levels. The subsequent step will be to use the method to describe species-, sex- and individual-related foraging strategies allowing the coexistence of two sympatric fur seal species at the Crozet Islands (Cherel et al. 2007). Together with other keratinous tissues (Best & Schell 1996; Cherel et al. 2009), whiskers represent an archive of foraging ecology of wild mammals, thus providing unique opportunities to reconstruct the habitats, diets and environmental conditions experienced by those animals. The method is at its most powerful when used on challenging cryptic species and cryptic life stages.

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