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Trophic ecology of sooty albatross, segregating mechanisms from the congeneric light-mantled sooty albatross, and conservation implications

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ABSTRACT: The trophic ecology of the Endangered sooty albatross (SA, 4 populations) was investigated using the concept of isotopic niche as a proxy of the trophic niche, and its isotopic metrics were compared with those of the congeneric Near Threatened light-mantled sooty albatross (LMSA, 4 populations). Three features differentiated SA from LMSA. (1) Feather $\delta^{13}C$ and $\delta^{15}N$ values of chicks and breeding adults were overall higher in SA than LMSA. This translates to more northern foraging grounds in the former than the latter species, with SA favouring warmer subtropical waters and LMSA colder waters of the Southern Ocean where they feed in part on low trophic level prey (likely Antarctic krill) at high latitudes. (2) Interestingly, SA from the Atlantic (Gough Island) differentiate from SA of the Indian Ocean (Marion, Crozet and Amsterdam Islands) by adult birds foraging primarily within the Southern Ocean in a similar way as LMSA from South Georgia, Marion, Crozet and Kerguelen Islands. (3) Calculations of the trophic niche width at the population and individual levels showed that SA from the Indian Ocean are specialist populations, while Gough Island SA and the 4 LMSA populations are generalist populations that include both generalist and specialist individuals. Consequently, both the preferential use of warm waters and the narrow trophic niche width of SA from the southern Indian Ocean imply a higher risk for SA than LMSA of being killed by subtropical tuna longline fisheries and being negatively impacted by environmental changes. Conversely, the preferential use of cold waters together with a large trophic niche width of SA from Gough Island suggest fewer negative interactions with direct and indirect human activities.

KEY WORDS: Conservation · Feather · Moult · Procellariiformes · Seabird · Southern Ocean · Subtropics

1. INTRODUCTION

Albatrosses are among the world's most threatened taxa of birds, with all the Southern Ocean species but one being classified from Near Threatened to Critically Endangered on the IUCN Red List (IUCN 2024). The 7 Endangered taxa include 3 *Diomedea* and 3 *Thalassarche* species and the sooty albatross *Phoebetria fusca* (hereafter SA). SA breed on scattered subantarctic and subtropical islands of the Atlantic and Indian Oceans (see Fig. 1), with the total number of adults being estimated at 21 000–29 000 individuals

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(IUCN 2024). Limited information is available to determine population trends, but declines have been reported at all long-term demographic colonies. For example, censuses indicate a 17% decline during 2003–2012 on Amsterdam Island (hereafter Amsterdam), and a 81% decline during the period 1980–2023 on the Crozet Islands (Crozet) (Weimerskirch et al. 2018, Fromant et al. 2024). The decreases result from a low survival caused by mortality associated with fisheries in the subtropics, particularly tuna longliners (Delord et al. 2008, 2013, ACAP 2012).

The trophic ecology of SA is not well detailed, with most studies having been conducted at a few subantarctic breeding sites from the Indian Ocean. Chick food was investigated at the subantarctic Marion Island (Marion) and Crozet (Ridoux 1994, Cooper & Klages 1995, Connan et al. 2014), but little information is available elsewhere (Marchant & Higgins 1990). Tracking using GPS and satellite tags was performed on breeding adults from subantarctic islands (Pinaud & Weimerskirch 2007, ACAP 2012, Schoombie et al. 2017, Carpenter-Kling et al. 2020b, Fromant et al. 2024, BirdLife International 2025), with a few SA having been tracked from the subtropical sites (Delord et al. 2013, Schoombie et al. 2017). Limited isotopic investigations were conducted at Marion and Crozet (Jaeger et al. 2010a, Connan et al. 2014), and an isotopic study on all Southern Ocean albatrosses included 4 SA populations (Cherel et al. 2013).

The aim of the present study was to determine the foraging strategies of SA at the species, population, and individual level using stable isotope analysis. The ecological niche was quantified using the concept of the isotopic niche, with δ^{13}C and δ^{15}N values defining the niche along 2 dimensions reflecting the consumer's foraging habitat and trophic position, respectively (Newsome et al. 2007). Stable isotopes are powerful tools for quantifying foraging strategies at both the individual and population levels, with variance in δ^{13}C and δ^{15}N being a useful proxy for trophic niche width (Bearhop et al. 2004). Feather was the targeted tissue, because keratin is metabolically inert after synthesis (Rubenstein & Hobson 2004), and hence, its isotopic composition reflects diet at the time of feather growth. Following Jaeger et al. (2010a), chick and adult feathers were collected to investigate seasonal changes in the isotopic niche corresponding to the chick-rearing (breeding) period and the poorly known interbreeding period, respectively (SA is a biennial breeder with the consequence that the long interbreeding period spans ~16 mo). This method allows estimating the use of subtropical waters where albatrosses are most at risk.

The trophic ecology of the congeneric light-mantled sooty albatross *P. palpebrata* (hereafter LMSA) was also investigated to help interpretation of SA isotopic values. Breeding sites of LMSA have a circumpolar distribution in subantarctic and Antarctic waters (Marchant & Higgins 1990, Lisovski et al. 2009), and the species is classified as Near Threatened on the IUCN Red List (IUCN 2024). We studied SA and LMSA at 6 breeding sites of the Atlantic and Indian Oceans, which were widely located, from the subtropics to Antarctica (Table 1). Some sites host only 1 population, either SA (Gough Island [Gough] and Amsterdam) or LMSA (South Georgia and the Kerguelen Islands [Kerguelen]), while both species coexist in significant numbers at Marion and Crozet. We posed the following 4 predictions about the food and feeding ecology of SA and LMSA.

1.1. Prediction 1. There is latitudinal segregation between SA and LMSA

Overall, SA would present higher δ^{13}C values than LMSA, which reflects a more northern oceanic distribution of SA because (1) δ^{13}C values increase

Table 1. Estimates of population size (annual breeding pairs) at the 6 investigated breeding sites. SA: sooty albatross; LMSA: light-mantled sooty albatross. Northern Subantarctic Zone: north of the Subantarctic Front; southern Subantarctic Zone: south of the Subantarctic Front

Ocean	Breeding location	Oceanographic zone	SA	LMSA	References
Atlantic	South Georgia	Antarctic Zone	0	5000	ACAP (2012)
	Gough	Northern Subantarctic Zone	2500–5000	0	Cuthbert et al. (2014)
Indian	Marion	Southern Subantarctic Zone	>2200	507	ACAP (2012), Schoombie et al. (2017)
	Crozet	Southern Subantarctic Zone	2040	2300	Weimerskirch et al. (2018)
	Kerguelen	Southern Subantarctic Zone	10	3–5000	Weimerskirch et al. (2018)
	Amsterdam	Subtropical Zone	515	0	Lesage et al. (2024)

with decreasing latitudes in the Southern Ocean (Cherel & Hobson 2007, Quillfeldt et al. 2010), and (2) location of breeding sites, observations at sea together with satellite- and GPS-tracking, and chick diet all concur to indicate a more northern distribution of SA when compared to LMSA (Marchant & Higgins 1990, Carpenter-Kling et al. 2020b, Cherel & Trouvé 2024).

1.2. Prediction 2. Between-population segregation is greater during the breeding period and relaxes during the inter-breeding period

Because albatrosses are central-place foragers during the breeding period, the isotopic values of chicks should reflect the major influence of the local environment surrounding breeding sites, with increasing isotopic values from Antarctic waters (South Georgia) to the subtropics (Amsterdam). By contrast, adult birds are no longer central-place foragers during the long inter-breeding period during which they may disperse over different waters masses, thus increasing their isotopic niche and lowering isotopic segregation between populations (e.g. Jaeger et al. 2010a).

1.3. Prediction 3. SA from Gough Island moult in more southern waters than birds from other sites

A preliminary investigation using δ^{13}C measurements on a single body feather per adult bird suggest that SA from Gough favoured more southern waters during the inter-breeding period than the other SA populations investigated to date (Cherel et al. 2013). This unique at-sea behaviour was tested by measuring several body feathers per bird to better quantify the moulting habitats of individual adult SA from different breeding sites.

1.4. Prediction 4. Populations of SA and LMSA are specialist and generalist populations, respectively

Isotopic measurements of adult LMSA from Crozet and Marion showed that they are isotopic generalist populations including both isotopic generalist and specialist individuals (Jaeger et al. 2010a, Connan et al. 2014). By contrast, isotopic values of SA from Marion suggested a more specialist population (Connan et al. 2014). We tested this on other populations by measuring isotopic values of 4 body feathers per bird and quantifying the within- and between-individual components of the trophic niche width (Bolnick et al. 2003) following Jaeger et al. (2009).

The present work is the last article of a suite of isotopic investigations on the food and feeding ecology of Southern Ocean procellariiforms that were published more than 10 yr ago (Jaeger et al. 2010a, 2013, 2014, Cherel et al. 2013). It includes unpublished isotopic data on chicks and on non-breeding SA and LMSA as well as on the trophic niche width and Bayesian ellipses of the species.

2. MATERIALS AND METHODS

Fieldwork was carried out on 6 archipelagoes and islands located in the 2 oceans where both SA and LMSA breed; the Atlantic (2 localities) and Indian (4 localities) Oceans. The Southern Ocean is defined as the ocean between the Subtropical Front and Antarctica, and the Subantarctic Zone (SAZ) and Antarctic Zone (AZ), as the zones between the Subtropical and Polar Fronts, and between the Polar Front and Antarctica, respectively. The Subtropical Zone (STZ) refers to oceanic waters north of the Subtropical Front (Fig. 1). The Subtropical Front is the boundary between subtropical surface water and cooler, fresher subantarctic surface water, while the Polar Front is most frequently identified by the northernmost extent of the 2°C subsurface temperature minimum (Pollard et al. 2002).

All 6 sampling sites were located either within the Southern Ocean or in warmer fringing waters (Table 1), including 1 Antarctic (South Georgia: 54° S, 38° W), 4 subantarctic (Gough: 40° S, 9° W; Marion: 47° S, 37° E; Crozet: 46° S, 51° E; Kerguelen: 49° S, 70° E), and 1 subtropical (Amsterdam: 37° S, 77° E) localities. Based on estimated feather δ^{13}C isoscapes (Jaeger et al. 2010b), values less than −21.2‰, −21.2 to −18.3‰, and greater than −18.3‰ were considered to correspond to the AZ, SAZ and STZ, respectively.

Body feathers were collected from the lower back and rump of breeding adults, non-breeding birds and from well-feathered chicks over the period 2005–2006. Body feathers were sampled from 6 to 15 randomly chosen birds per group. In albatrosses, body feathers are replaced over several months, probably continuously during the inter-breeding period, and not all are necessarily changed each year (Berruti 1979, Warham 1996). Hence, their isotope values were assumed to represent diet during that period (Cherel et al. 2000, Phillips et al. 2009). Since *Phoebetria* albatrosses are biennal breeders, their internesting period, and hence the temporal window cov-

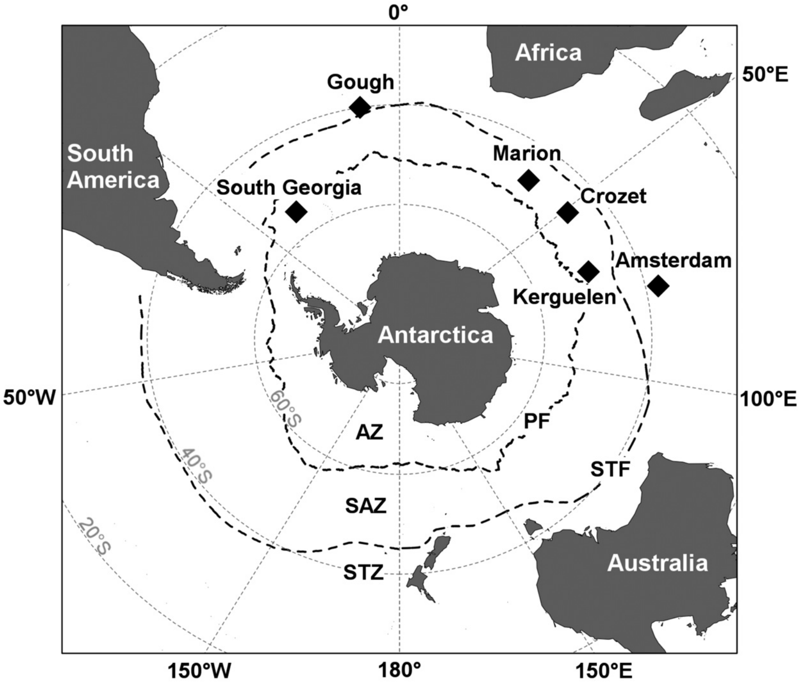

Fig. 1. Location of albatross breeding localities sampled and of the main oceanic fronts and zones of the Southern Ocean. Diamonds show an island or a group of islands. STF: Subtropical Front; PF: Polar Front; STZ: Subtropical Zone; SAZ: Subantarctic Zone; AZ: Antarctic Zone

ered by analyzing body feathers, spans a full year plus a winter.

Isotopic methodology followed Cherel et al. (2013). Prior to analysis, single body feathers were cleaned of surface lipids and contaminants using a 2:1 chloroform:methanol solution for 2 min followed by 2 successive methanol rinses. Feathers were air dried and then homogenized by cutting them into very small pieces that were pooled. One sub-sample was then weighed (~0.4 mg) with a microbalance, packed into a tin cup, and nitrogen and carbon isotope ratios were determined by a continuous flow mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyser (Thermo Scientific Flash EA 1112). Results are presented in the usual δ notation relative to PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate measurement errors <0.10‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. Data were statistically analysed using SYSTAT 12. Values are mean ± SD.

Isotopic measurements were first made on a single whole body feather per bird to characterize the isotopic niche of breeding adults, non-breeding birds and chicks of each population. In a second step, trophic niche width (TNW) and its between-individual (BIC) and within-individual (WIC) components were calculated using 4 body feathers per breeding adult and non-breeding bird (Jaeger et al. 2009, 2010a, 2013). WIC is the average variance of 4 individual feathers and BIC the variation among means of 4 individual feathers. Low and high TNW define isotopic specialist and generalist populations, respectively, with TNW being the variance among all feathers from all individuals of a given population (Bolnick et al. 2003). The relative degree of individual specialization within a given population was subsequently considered to be the proportion of TNW explained by within-individual variation, WIC/TNW (WIC/TNW varies from 0 [maximum variation among individual] to 1 [no variation among individuals]; Bolnick et al. 2003). TNW, WIC and BIC were not calculated from chick data because: (1) the isotopic values of chick feathers represent that of food brought back to the colony by the 2 parents, and (2) all body feathers grow almost synchroneously in chicks, thus lowering greatly the within-individual variance of feather isotopic values (Carravieri et al. 2014).

Isotopic niches of chicks (1 single body feather per bird) and of breeding and non-breeding adults (4 feathers per bird) of the 2 species at the different sites were also compared using Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al. 2011) package version 2.1.9 under R 4.4.1 (R Core Team 2024). As recommended, sample sizes were ≥10 and isotopic values (4 feathers per individual) were scaled and centred (Jackson et al. 2011, Connan et al. 2014). The estimated metrics were total area (TA) of the convex hull encompassed by mean isotopic values of all species in the $\delta^{13}C-\delta^{15}N$ bi-plot space and the standard ellipse area (SEA), which represents the core isotopic niche that contains ~40% of the data regardless of sample size. SEA was corrected for sample size (SEAc), which is a robust approach when comparing small and unbalanced sample sizes. Bayesian SEA (SEAb) was calculated using 10^4 posterior draws to statistically compare niche breadth between species. Potential effects of sexes were not considered because isotopic differences between adult females and males are rarely biologically significant in seabirds (Phillips et al. 2011, but see Jaeger et al. 2014), including LMSA (Phillips et al. 2009).

3. RESULTS

Stable isotopes were measured on 527 body feathers from 209 individuals from 8 populations of SA and LMSA located in the Atlantic and Indian Oceans.

Chicks of SA and LMSA were segregated by their feather isotopic values (MANOVA, Wilks's Lambda, $F_{14,148} = 59.64$, $p < 0.0001$) (Fig. 2, Table 2). Both $\delta^{13}C$ and $\delta^{15}N$ values were overall different ($F_{7,75} = 212.90$ and 47.41, respectively, both $p < 0.0001$). Four features were noticeable: (1) There was no complete overlap of feather $\delta^{13}C$ and $\delta^{15}N$ values between any population of SA and LMSA. The 2 species differed by at least 1 isotopic ratio, with SA chicks generally having higher feather $\delta^{13}C$ and $\delta^{15}N$ values than LMSA (post hoc Tukey's HSD multiple comparison tests, results not shown). (2) Within SA populations, chicks from Amsterdam had higher $\delta^{13}C$ and $\delta^{15}N$ values than the other 3 groups (all $p < 0.0001$). (3) Within LMSA populations, chicks from South Georgia had lower $\delta^{13}C$ and $\delta^{15}N$ values than the other 3 groups (all $p < 0.0001$). (4) SEAc was overall smaller in SA chicks than in LMSA chicks (means: 0.25 and 0.43‰^{2}, ranges: 0.15–0.47 and 0.30–0.72‰^{2}, respectively).

Breeders of SA and LMSA were segregated by their feather isotopic values (Wilks's Lambda, $F_{14,160} = 6.52$, $p < 0.0001$) (Fig. 2, Table 2). Both $\delta^{13}C$ and $\delta^{15}N$ values were overall different ($F_{7,81} = 11.09$ and 6.70, respectively, both $p < 0.0001$). Four features were noticeable from pairwise comparisons: (1) SA from Marion, Crozet and Amsterdam differed from all the LMSA populations by their higher $\delta^{13}C$ and $\delta^{15}N$ values (pairwise comparisons, data not shown). (2) Interestingly, SA from Gough did not segregate from the 4 LMSA populations, neither in their $\delta^{13}C$ nor $\delta^{15}N$ values (all $p \geq 0.524$). (3) SA populations had non-significantly different feather isotopic values, except between birds from Gough and Amsterdam (both $p \leq 0.019$). (4) The 4 LMSA populations had identical feather $\delta^{13}C$ and $\delta^{15}N$ values (all $p \geq 0.979$).

SA chicks from Marion, Crozet and Amsterdam have significantly lower feather $\delta^{13}C$ and $\delta^{15}N$ values than breeding adults (Mann-Whitney U tests, all $p \leq 0.04$, except $\delta^{15}N$ values at Amsterdam, $U = 88.0$, $p = 0.065$). In contrast, values of chicks and breeders from Gough and of all LMSA populations were not different (all $p \geq 0.067$). Breeding adults and non-breeding birds did not generally differ in their isotopic values (Table 2), with only SA $\delta^{15}N$ values from Crozet and LMSA $\delta^{13}C$ values from Kerguelen being significantly, but marginally, different (Mann-Whitney U tests, $U = 25.5$ and 11.5, $p = 0.013$ and 0.044, respectively). At Crozet, breeding SA and LMSA had higher TNW than non-breeding birds (Table 3).

The overall ranges of feather isotopic values were much higher in breeding LMSA ($\delta^{13}C$: 10.6‰, from −27.6 to −17.0‰; $\delta^{15}N$: 7.5‰, from 7.3 to 14.8‰) than in breeding SA from Crozet and Amsterdam ($\delta^{13}C$: 3.7‰, from −19.5 to −15.8‰; $\delta^{15}N$: 5.9‰, from 10.9 to 16.7‰) (Fig. 3 & 4). Accordingly, $\delta^{13}C$ TNW, $\delta^{15}N$ TNW, TA and SEAc were much higher and variable in breeding LMSA at the 4 investigated populations than in SA from Crozet and Amsterdam (Table 3). Interestingly, SA from Gough differed from the other SA populations by having wider ranges of $\delta^{13}C$ and $\delta^{15}N$ values ($\delta^{13}C$: 5.8‰, from −23.1 to −17.3‰; $\delta^{15}N$: 7.6‰, from 7.3 to 14.9‰) (Fig. 3), and their $\delta^{13}C$ TNW, $\delta^{15}N$ TNW, TA and SEAc were medium and close to those of LMSA, respectively (Table 3). Pooling breeders and non-breeders per location highlights the SEA differences between SA from the Indian Ocean and SA from Gough and the 4 LMSA

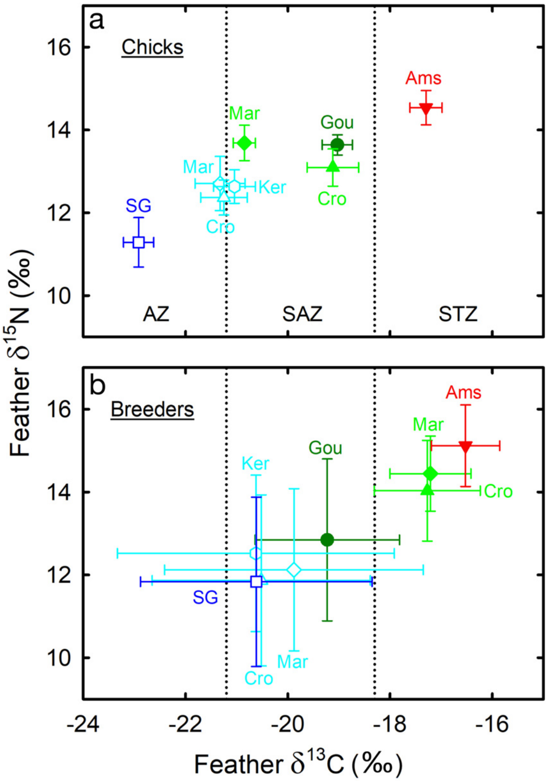

Fig. 2. Mean feather $\delta^{13}C$ and $\delta^{15}N$ values of (a) chicks and (b) breeding adults of sooty albatross (SA, filled symbols) and light-mantled sooty albatross (LMSA, unfilled symbols). Vertical dotted lines: estimated isotopic positions of the Polar and Subtropical Front for feathers. Ams: Amsterdam Island; Cro: Crozet Islands; Gou: Gough Island; Ker: Kerguelen Islands; Mar: Marion Island; SG: South Georgia; AZ: Antarctic Zone; SAZ: Subantarctic Zone; STZ: Subtropical Zone

Table 2. Feather $\delta^{13}C$ and $\delta^{15}N$ values of chicks and of breeding and non-breeding sooty albatross (SA) and light-mantled sooty albatross (LMSA) from various localities of the Atlantic and Indian Oceans. Values are mean ± SD, with isotopic measurements being made on a single body feather per bird

Species	Breeding location	Status	Ind. (n)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
SA	Gough	Breeders	13	−19.2 ± 1.4	12.8 ± 2.0
		Chicks	9	−19.0 ± 0.3	13.6 ± 0.2
	Marion	Breeders	14	−17.2 ± 0.8	14.4 ± 0.9
		Chicks	12	−20.8 ± 0.2	13.7 ± 0.4
	Crozet	Breeders	12	−17.3 ± 1.0	14.0 ± 1.2
		Non-breeders	11	−16.6 ± 0.7	15.1 ± 0.7
		Chicks	10	−19.1 ± 0.5	13.1 ± 0.5
	Amsterdam	Breeders	12	−16.5 ± 0.7	15.1 ± 1.0
		Non-breeders	10	−16.7 ± 0.9	15.4 ± 0.9
		Chicks	10	−17.3 ± 0.3	14.5 ± 0.4
LMSA	South Georgia	Breeders	11	−20.6 ± 2.3	11.8 ± 2.0
		Chicks	10	−22.9 ± 0.3	11.3 ± 0.6
	Marion	Breeders	7	−19.9 ± 2.5	12.1 ± 2.0
		Chicks	7	−21.3 ± 0.5	12.7 ± 0.7
	Crozet	Breeders	10	−20.5 ± 2.1	11.9 ± 2.1
		Non-breeders	10	−19.3 ± 1.5	13.1 ± 1.0
		Chicks	10	−21.3 ± 0.5	12.4 ± 0.4
	Kerguelen	Breeders	10	−20.6 ± 2.7	12.5 ± 1.9
		Non-breeders	6	−18.5 ± 0.9	13.4 ± 0.6
		Chicks	15	−21.0 ± 0.4	12.6 ± 0.4

populations (Fig. 4). In both SA and LMSA, the relative degree of individual specialization within a given population was ≥0.5, with WIC/TNW being high (0.9) for LMSA that breed at Marion.

Feather $\delta^{13}C$ values of adults indicated different moulting strategies between and within species. Three features were particularly relevant: (1) SA from the Indian Ocean primarily moulted body feathers within the STZ and secondarily within the SAZ, with no feathers being synthesized within the AZ (183 [94.3%] and 11 [5.7%] feathers, respectively, for a total of 194 feathers; data from Marion, Crozet and Amsterdam having been pooled) (Fig. 3). (2) By contrast, SA from the Atlantic (Gough) grew feathers primarily within the SAZ, and secondarily within the STZ and AZ (34 [65.4%], 9 [17.3%] and 9 [17.3%], respectively, for a total of 52 feathers) (Fig. 3). (3) Like SA from Gough, LMSA favoured the SAZ over the STZ and AZ for moulting body feathers (107 [54.0%], 47 [23.7%] and 44 [22.2%] feathers, respectively, for a total of 198 feathers; data from South Georgia, Marion, Crozet and Kerguelen having been pooled) (Fig. 5).

For a given albatross population, body feathers of adult birds that were synthesized in different oceanic zones showed different isotopic values (Table 4). Feather $\delta^{15}N$ values overall decreased in the sequence STZ ≥ SAZ > AZ, with all AZ $\delta^{15}N$ values being significantly 3.7–4.7‰ lower than SAZ and STZ values (5 populations, post hoc Tukey's tests, all $p < 0.0001$).

Statistical comparison of isotopic values of feathers synthesized within the same water masses showed a complex pattern between and within albatross species (Table 4). Within the AZ, feather $\delta^{15}N$ values were not significantly different amongst the 5 populations ($F_{4,48} = 0.39$, $p = 0.813$), but $\delta^{13}C$ values of Kerguelen LMSA were lower than those of the 4 other groups ($F_{4,48} = 12.63$, $p < 0.0001$, pairwise comparisons, all $p \leq 0.012$). Within the SAZ, both feather $\delta^{13}C$ and $\delta^{15}N$ values were overall different amongst the 6 populations ($F_{5,143} = 5.00$ and 5.09, respectively, both $p < 0.0001$), but isotopic ranges were small (a maximum of 0.8‰ for both $\delta^{13}C$ and $\delta^{15}N$ values). Within the STZ, feather isotopic values were also different between the 8 populations ($F_{7,231} = 23.09$ and 22.16 for $\delta^{13}C$ and $\delta^{15}N$, respectively, both $p <$

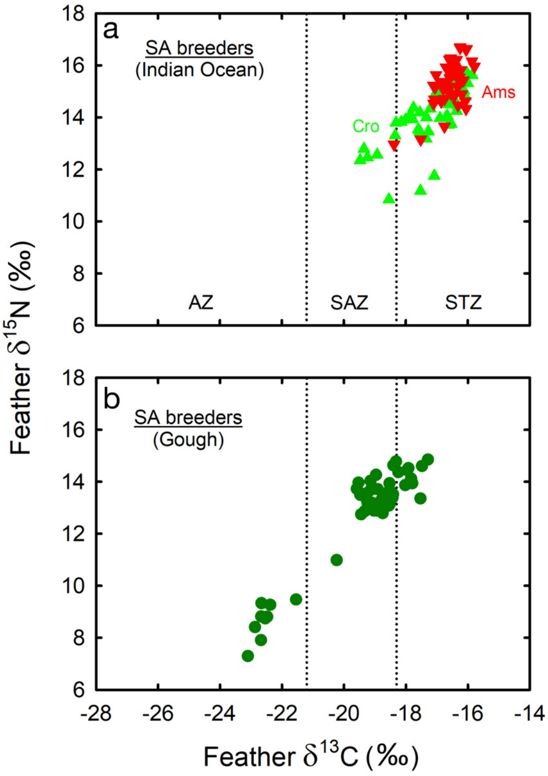

Fig. 3. Individual feather $\delta^{13}C$ and $\delta^{15}N$ values of breeding sooty albatrosses (SA) from (a) the Crozet Islands (Cro) and Amsterdam Island (Ams) and (b) from Gough Island. Vertical dotted lines: estimated isotopic positions of the Polar and Subtropical Front for feathers. AZ: Antarctic Zone; SAZ: Subantarctic Zone; STZ: Subtropical Zone

Table 3. Isotopic niches of breeding and non-breeding sooty albatross (SA) and light-mantled sooty albatross (LMSA) from various localities of the Atlantic and Indian Oceans. Trophic niche width (TNW) and its between-individual (BIC) and within-individual (WIC) components, as well as the total ellipse area (TA), and standard ellipse area corrected for sample size (SEAc) were calculated using 4 body feathers per bird. Values are mean ± SD

Species	Breeding location	Status	Feathers (n)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	TNW (‰) ($\delta^{13}C/\delta^{15}N$)	WIC (‰) ($\delta^{13}C/\delta^{15}N$)	BIC (‰) ($\delta^{13}C/\delta^{15}N$)	WIC/TNW ($\delta^{13}C/\delta^{15}N$)	TA (‰^{2})	SEAc (‰^{2})
SA	Gough	Breeders	52	−19.4 ± 1.6	12.7 ± 2.0	2.4/3.9	1.7/2.7	0.8/1.1	0.7/0.7	2.44	0.62
	Crozet	Breeders	48	−17.2 ± 0.9	14.1 ± 1.1	0.8/1.2	0.4/0.7	0.5/0.5	0.5/0.6	1.67	0.46
		Non-breeders	44	−16.6 ± 0.7	14.9 ± 0.9	0.5/0.8	0.2/0.3	0.3/0.5	0.4/0.4	0.79	0.19
	Amsterdam	Breeders	48	−16.6 ± 0.4	15.4 ± 0.8	0.2/0.7	0.2/0.3	0.1/0.4	0.7/0.6	0.87	0.19
		Non-breeders	40	−16.7 ± 0.6	15.6 ± 0.8	0.4/0.6	0.1/0.3	0.2/0.3	0.4/0.5	0.83	0.20
LMSA	South Georgia	Breeders	44	−20.1 ± 2.0	12.5 ± 1.8	4.0/3.1	2.9/2.2	1.1/0.9	0.7/0.7	2.64	0.72
	Marion	Breeders	28	−19.8 ± 2.7	12.2 ± 2.0	6.9/3.9	6.0/3.6	0.9/0.3	0.9/0.9	2.47	0.91
	Crozet	Breeders	40	−20.2 ± 2.0	11.9 ± 1.9	3.9/3.6	2.6/2.1	1.3/1.5	0.7/0.6	2.45	0.87
		Non-breeders	40	−18.9 ± 1.7	13.1 ± 1.4	2.9/1.8	2.0/1.3	0.9/0.5	0.7/0.7	3.27	0.77
	Kerguelen	Breeders	40	−21.1 ± 3.2	12.1 ± 2.3	9.9/5.2	4.7/2.4	5.2/2.8	0.5/0.5	3.92	1.07

0.0001). Pairwise comparisons indicated 2 remarkable features. (1) Amsterdam SA had higher $\delta^{13}C$ and $\delta^{15}N$ values than all the other 7 groups (but Crozet SA for $\delta^{13}C$). (2) Gough SA had non-significantly different feather $\delta^{13}C$ and $\delta^{15}N$ values when compared to the 4 populations of LMSA (Table 4).

4. DISCUSSION

A limitation of the work is that feather samples were collected ~20 yr ago, while climate change is already operating in the Southern Ocean (Favier et al. 2016, Sallée 2018). However, to what extent climate change is driving changes in the foraging ecology of SA and LMSA is unknown. Hence, the study sets a baseline against which the effects of long-term environmental changes on the isotopic niche of SA and LMSA can be studied across years, breeding sites, and various conditions.

4.1. Prediction 1. There is latitudinal segregation between SA and LMSA

Feather isotopic values of chicks segregated SA from LMSA overall (Fig. 1), which is in agreement with data from Marion Island (Connan et al. 2018). Such an isotopic segregation indicates species-specific differences in the food and feeding ecology of adults during the chick-rearing period. Chick $\delta^{13}C$

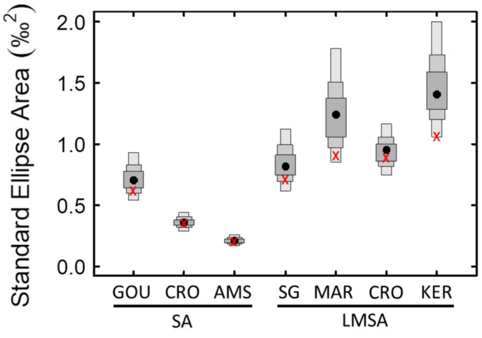

Fig. 4. Bayesian standard ellipse area (SEA) of adult sooty albatross (SA) and light-mantled sooty (LMSA) albatross from various localities of the Atlantic and Indian Oceans. Black dot: SEAb mode; grey rectangles correspond to its credibility intervals at 50, 75, and 95%. Red cross: SEA corrected for sample size (SEAc). AMS: Amsterdam Island; CRO: Crozet Islands; GOU: Gough Island; KER: Kerguelen Islands; MAR: Marion Island; SG: South Georgia

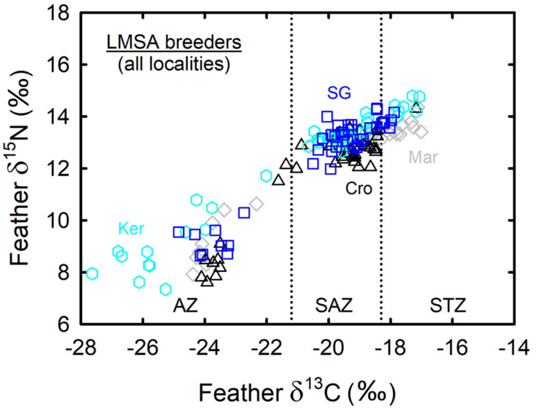

Fig. 5. Individual feather $\delta^{13}C$ and $\delta^{15}N$ values of breeding light-mantled sooty albatrosses (LMSA) from South Georgia (SG), Marion Island (Mar), Crozet Islands (Cro) and Kerguelen Islands (Ker). Vertical dotted lines: estimated isotopic positions of the Polar and Subtropical Front for feathers. AZ: Antarctic Zone; SAZ: Subantarctic Zone; STZ: Subtropical Zone

values of SA were generally higher than those of LMSA, which, owing to $\delta^{13}C$ isoscapes in the Southern Ocean (Jaeger et al. 2010b, Quillfeldt et al. 2010, Carpenter-Kling et al. 2020a), translates into SA foraging at lower latitudes than LMSA. Hence, isotopic investigations agree with the tracking of breeding SA and LMSA at various localities (BirdLife International 2025), including South Georgia (Phillips et al. 2005), Gough (Schoombie et al. 2017), the Tristan da Cunha Group (Schoombie et al. 2017), Marion (Schoombie et al. 2017, Carpenter-Kling et al. 2020a,b), Crozet (Pinaud & Weimerskirch 2007, Delord et al. 2013, Fromant et al. 2024), Kerguelen (Delord et al. 2013), Heard Island (Lawton et al. 2008), Amsterdam (Delord et al. 2013), and Macquarie Island (Weimerskirch & Robertson 1994, Cleeland et al. 2019). Overall, both SA and LMSA fed within the SAZ, with SA foraging also within the warmer STZ and LMSA within the colder AZ during the breeding season.

Feather isotopic values defined 2 groups of breeding birds (Fig. 1). The first one includes the 4 populations of LMSA and the second group clusters the 3 populations of SA from the southern Indian Ocean. Overall, $\delta^{13}C$ values show that LMSA and SA spent the inter-breeding period within the SAZ and STZ, respectively, meaning that LMSA remained within the Southern Ocean all year long, while SA from Marion and Crozet migrated further north after breeding. GLS-tracking of a few adults confirms these results, with LMSA favouring cold waters of the Southern Ocean (Delord et al. 2013, Cleeland et al. 2019), while SA from Marion forage within the SAZ and STZ, and SA from Amsterdam remain within the STZ (Delord et al. 2013, Schoombie et al. 2022).

Isotopic analysis of 4 body feathers per breeding bird allowed detailing in which oceanographic zones albatrosses moulted body feathers. Again, SA and LMSA segregated by their latitudinal habitats, with SA from the southern Indian Ocean moulting their body feathers almost exclusively within the STZ (Fig. 3; Schoombie et al. 2022), while LMSA favoured the SAZ (Fig. 5). A few observations at sea recorded adult SA in wing moult within the STZ, and adult LMSA within the AZ (J. C. Stahl et al. unpubl. data). Interestingly, non-breeding birds showed the same moulting strategy as breeding birds, since feather isotopic values of non-breeders are non-signicantly or marginally different from those of breeders whatever the population of SA and LMSA (Table 2). Hence, feather $\delta^{13}C$ values of chicks, breeders, and non-breeders all verify the first prediction of a latitudinal segregation between SA and LMSA, which is in agreement with at sea observations (e.g. Weimerskirch et al. 1986, Marchant

Table 4. Isotopic values of feathers that grew in different oceanic zones from adult sooty albatross (SA) and light-mantled sooty albatross (LMSA) from various localities of the Atlantic and Indian Oceans. Values are mean ± SD. AZ: Antarctic Zone; SAZ: Subantarctic Zone; STZ: Subtropical Zone

Species	Breeding location	Individuals (n)	Feathers (n)	STZ n	STZ $\delta^{13}C$ (‰)	STZ $\delta^{15}N$ (‰)	SAZ n	SAZ $\delta^{13}C$ (‰)	SAZ $\delta^{15}N$ (‰)	AZ n	AZ $\delta^{13}C$ (‰)	AZ $\delta^{15}N$ (‰)
SA	Gough (UK)	13	52	9	−17.8 ± 0.3	14.2 ± 0.5	34	−19.0 ± 0.4	13.4 ± 0.7	9	−22.5 ± 0.4	8.7 ± 0.7
	Marion (S. Africa)	14	14	13	−17.1 ± 0.7	14.5 ± 0.9	1	−18.8	13.1	0		
	Crozet (France)	23	92	84	−16.7 ± 0.7	14.6 ± 0.9	8	−18.8 ± 0.5	12.6 ± 0.9	0		
	Amsterdam (France)	22	88	86	−16.6 ± 0.4	15.5 ± 0.7	2	−18.4, −18.7	13.0, 13.0	0		
LMSA	South Georgia (UK)	11	44	8	−18.1 ± 0.1	13.8 ± 0.2	27	−19.4 ± 0.6	13.2 ± 0.6	9	−23.8 ± 0.7	9.2 ± 0.6
	Marion (SA)	7	28	11	−17.6 ± 0.4	13.6 ± 0.3	9	−19.0 ± 0.7	13.1 ± 0.3	8	−23.8 ± 0.7	9.2 ± 1.0
	Crozet (France)	20	80	17	−17.4 ± 0.8	14.0 ± 0.8	49	−19.2 ± 0.6	12.9 ± 0.5	14	−23.1 ± 0.9	9.2 ± 1.5
	Kerguelen (France)	16	46	11	−17.7 ± 0.4	14.1 ± 0.5	22	−19.6 ± 0.6	13.3 ± 0.4	13	−25.3 ± 1.5	9.1 ± 1.3

& Higgins 1990), with the limitation that the colonies of origin and breeding status of the individuals observed were unknown.

4.2. Prediction 2. Between-population segregation is greater during the breeding period and relaxes during the inter-breeding period

As expected, feather $\delta^{13}C$ values of chicks increased progressively from the Antarctic South Georgia to the subtropical Amsterdam Island, with chicks from the 4 subantarctic localities having intermediary $\delta^{13}C$ values (Fig. 1). The site-specific $\delta^{13}C$ values highlight the importance of the local environment during the chick-rearing period. This does not preclude adult birds feeding for themselves far from the colonies (Bentley et al. 2024) but indicates that prey for the growing chicks were caught in the vicinity of the breeding sites. Tracking alone provides no precise information about where albatrosses feed during foraging trips, but tracking of a few birds shows that LMSA from Antarctic sites remain within the AZ (Phillips et al. 2005, Lawton et al. 2008) and that SA from Amsterdam forage within the STZ (Delord et al. 2013) during the chick-rearing period.

After breeding, adults increased their foraging range, as indicated by the large SD of their isotopic values. They dispersed widely, generally spending the long inter-breeding period over different water masses. The only exception amongst the 8 populations was SA from Amsterdam that remained all year long within the STZ. However, the different $\delta^{13}C$ values of chicks and breeders indicate different subtropical foraging habitats during the breeding and inter-breeding periods. Indeed, birds spend the inter-breeding period more easterly, to the north of the STZ and in southern Australian waters (Delord et al. 2013). By contrast, feather $\delta^{13}C$ values indicate that SA from subantarctic Marion and Crozet migrated to the STZ during the inter-breeding period, which is in general agreement with the tracking of adult birds (Delord et al. 2013, Schoombie et al. 2022). Finally, feather $\delta^{13}C$ values showed that all 4 populations of LMSA differed from SA by foraging over a larger latitudinal gradient encompassing the AZ, SAZ and STZ during the inter-breeding period.

Feather $\delta^{15}N$ values that were associated with subantarctic $\delta^{13}C$ values were in the range 12–14‰. Such values indicate that SA and LMSA are top predators, with only the wandering albatross having $\delta^{15}N$ values >14‰, and, hence, a higher trophic position, within the diverse subantarctic seabird assemblages (Cherel & Carrouée 2022). Indeed, dietary investigations showed that subantarctic SA and LMSA feed primarily on squid and fish and scavenge on seabirds and marine mammals (Ridoux 1994, Cooper & Klages 1995, Connan et al. 2014). Feather $\delta^{15}N$ values of SA and LMSA that were associated with subtropical $\delta^{13}C$ values were in the range 14–16‰. Those higher values than in the SAZ are more likely explained by the higher $\delta^{15}N$ baseline characterizing the STZ (Altabet & François 1994, Stirnimann et al. 2024) than by a higher trophic position of the birds, which again feed on squid and fish in the subtropics (Cherel & Trouvé 2024, Y. Cherel unpubl. data). By contrast, feather $\delta^{15}N$ values of LMSA that are associated with Antarctic $\delta^{13}C$ values were <12‰ (down to <8‰), and the lower the $\delta^{13}C$ values, the lower the $\delta^{15}N$ values (Fig. 5). Since $\delta^{15}N$ baseline varies little within the Southern Ocean (Altabet & François 1994, Stirnimann et al. 2024), the most likely explanation is that LMSA fed on lower trophic level prey within the AZ compared to the SAZ and STZ. Indeed, LMSA had been observed feeding on Antarctic krill *Euphausia superba* (e.g. Harper 1987), and crustaceans (mainly krill) amount to 40% by mass of food samples at South Georgia, with squid ranking second (46%) and fish third (11%) (Thomas 1982). Hence, low feather $\delta^{15}N$ values likely result from LMSA feeding on krill when they moult within the AZ, with the dietary proportion of krill increasing with increasing latitudes.

In summary, the large feather isotopic variances of adults verify our prediction that isotopic niches widen when SA and LMSA are no longer central place foragers. The study generalizes to albatrosses a previous isotopic investigation on penguins and pinnipeds (Cherel et al. 2007), showing that the isotopic niche (and hence the trophic niche) is larger during the inter-breeding than the breeding period, a concept that can be generalized to the many animals that disperse after reproduction.

4.3. Prediction 3. SA from Gough Island moult in more southern waters than birds from other sites

Feather $\delta^{13}C$ values of SA chicks from Gough highlight the importance of the SAZ for adults to catch prey for their offspring. This foraging pattern is in line with adults from other populations of SA and LMSA feeding near the breeding sites during the chick-rearing period (see above). Isotopic values are also in agreement with tracking conducted earlier during the breeding cycle, which indicate foraging within the

SAZ during the incubation and brood-guard periods (Schoombie et al. 2017).

Isotopic values of breeders from Gough were more puzzling, since they did not follow the pattern of adults from the southern Indian Ocean. Feather values indicate that they foraged from the AZ to the STZ, but favoured the SAZ, and that they had an omnivorous diet during the inter-breeding period (Figs. 2 & 3). Unlike SA from Marion, Crozet and Amsterdam, they foraged within the AZ, where the corresponding low feather δ^{15}N values indicate feeding on various proportions of low trophic level prey, most likely Antarctic krill. To the best of our knowledge, no SA were observed feeding on krill, but Antarctic krill was identified in a few food samples (Ridoux 1994, Cooper & Klages 1995), and satellite-tracked adult SA from Gough disperse widely after reproduction (from 20° to 70° S) mainly within the SAZ and AZ (ACAP 2012).

To sum up, our isotopic investigation confirms that the foraging ecology of adult SA from the subantarctic Gough is unique amongst SA populations, and surprisingly, that it matches closely the trophic ecology of LMSA during the inter-breeding period. Hence, SA from Gough, together with LMSA and to a lesser extent grey-headed albatross *Thalassarche chrysostoma* (Cherel et al. 2013), are the only albatrosses using the high latitudes of the AZ where they feed at least in part on Antarctic krill during their long inter-breeding period.

4.4. Prediction 4. Populations of SA and LMSA are specialist and generalist populations, respectively

Isotopic TNW values clustered breeding adults into 2 groups with either low or high values (Table 3). Considering isotopic gradients in the southern Indian Ocean (Cherel & Hobson 2007, Jaeger et al. 2010b), the 2 groups correspond to isotopic specialist and generalist populations, respectively. Translating isotopic specialists and generalists to trophic specialists and generalists (but see Bearhop et al. 2004), our study highlights 3 major characteristics of SA and LMSA populations: (1) The 4 LMSA populations are all generalist populations, (2) SA populations from the southern Indian Ocean are specialist populations, including birds from Marion (Connan et al. 2014), and (3) unlike other SA populations, SA from Gough is a generalist population. Interestingly, TNW values of non-breeding SA and LMSA from Crozet were lower than those of breeding birds, thus indicating that they used a smaller part of the foraging repertoire of the breeding birds. Feather δ^{13}C values show that non-breeders had a more northern distribution than breeders, with Crozet LMSA foraging more within the STZ and less within the SAZ and AZ, and Crozet SA foraging almost exclusively within the STZ. At Amsterdam, both non-breeders and breeders moulted body feathers within the STZ.

While specialist populations are composed of specialist individuals, generalist populations can be composed of generalist individuals and/or specialist individuals (Bearhop et al. 2004, Jaeger et al. 2009). WIC/TNW values indicate that LMSA populations and SA from Gough included varying proportions of isotopic generalist and specialist individuals. Using a crude limit of 1.0‰ to differentiate TNW of specialists and generalists (Jaeger et al. 2009), the 48 LMSA included 60 and 40% of generalist and specialist individuals, respectively, while the 13 Gough SA included 54 and 46% of generalists and specialists, respectively.

4.5. The competitive exclusion principle and co-existence

In evolutionary biology, 2 species with identical ecological niches cannot stably co-exist (the 'competitive exclusion principle'). Reproductive cycles of SA and LMSA overlap greatly in time (Berruti 1979, Weimerskirch et al. 1986), thus raising the question of year-round co-existence at sea of these phylogenetically closely related species. When breeding in sympatry, SA and LMSA segregated by their feather isotopic values, thus indicating resource partitioning at both Marion and Crozet. Indeed, SA and LMSA chicks are fed either on the same prey species, but in different proportions, or on different prey items. Breeding SA prey more on subtropical squids (e.g. *Histioteuthis bonnellii corpuscula, Taonius expolitus*) in addition to Southern Ocean species (e.g. *Batoteuthis skolops, Histioteuthis eltaninae*) to feed their chicks, while LMSA prey almost exclusively upon Southern Ocean species (e.g. *Galiteuthis glacialis, Moroteuthopsis longimana*), including *Psychroteuthis glacialis*, which is the only endemic squid of the AZ (Cooper & Klages 1995, Cherel et al. 2023, Cherel & Trouvé 2024). Feather δ^{13}C values of breeding adults generalizes this spatial and trophic segregation to the whole cycle including the inter-breeding period at both Marion and Crozet, with SA favoring subtropical waters and LMSA remaining within the Southern Ocean.

The competitive exclusion principle helps understanding the uniqueness of the feeding ecology of Gough SA when compared to other SA populations during the inter-breeding period. No LMSA breed on Gough, and the large LMSA population from South Georgia is located far away both latitudinally (14° difference) and longitudinally (29° difference). The remoteness of Gough likely relaxes potential competition between SA and LMSA for trophic resources in cold waters of the southern Atlantic Ocean during the inter-breeding period. This allows SA to broaden their trophic niche width by foraging from Antarctic to subtropical waters, thus explaining why Gough SA is an isotopic generalist population. Conversely, the specialization of SA from Amsterdam is likely the result of the occurrence of the large population of LMSA from Kerguelen (7° longitudinal difference and 12° latitudinal difference) that compete successfully with the small population of SA for trophic resources during the inter-breeding period. Kerguelen LMSA moulted body feathers within the AZ (28%), SAZ (48%) and also within the STZ (24%), thus likely explaining why Amsterdam SA shifted easterly their foraging grounds to the north of the STZ and in southern Australian waters during the inter-breeding period (see Section 4.2).

4.6. Conservation implications

Generalist strategies are more likely to be favored by organisms in heterogenous and perturbed environments, whereas specialization is thought to be an evolutionary response to an environment that is more stable over space and time (Clavel et al. 2011, Le Viol et al. 2012). In a global change context, reviews on various organisms (Clavel et al. 2011), including birds, have pointed out that generalists and specialist species are 'winning' and 'losing' species, respectively, with larger niche width being a key advantage to cope with human-perturbed ecosystems. Isotopic data showed that LMSA is a generalist species, with its feeding adaptability to forage within different oceanographic zones making it able to face changing conditions. LMSA is thus theoretically less at risk than specialist SA populations from the Indian Ocean and other albatrosses that forage over restricted habitats, as the neritic black-browed albatross *Thalassarche melanophris* (Wakefield et al. 2011) and the resident shy albatross *T. cauta* (Brothers et al. 1998).

A major threat to both SA and LMSA is mortality associated with fisheries, specifically longlining (ACAP 2012). In the Southern Ocean, only fisheries targetting toothfish *Dissostichus* spp. use longlines, which are associated with no or very limited mortality of SA and LMSA (Nel et al. 2002, Delord et al. 2005). By contrast, fishing vessels, especially Asian tuna *Thunnus* sp. longliners, are numerous within the STZ, where they kill many large procellariiforms, including SA and LMSA (Huang & Liu 2010, ACAP 2012). Assuming that the percentage of body feathers moulted within a given oceanic zone translates into a percentage of time spent in that zone, breeding SA from the southern Indian Ocean and LMSA spent overall 94 and 24% of the inter-breeding period within the STZ, respectively. Moreover, all SA from Amsterdam and non-breeders from Crozet spent >97% of the moulting period in the subtropics.

Consequently, both the preferential use of the STZ and narrow TNW of SA from the southern Indian Ocean make them more at risk than LMSA from direct and indirect negative interactions with human activities. Those 2 biological characteristics are, at least in part, the likely explanation of the large population decreases of SA observed at various localities, while LMSA populations have increased or remained stable over the last decades (ACAP 2012, Weimerskirch et al. 2018, but see Schoombie et al. 2016). After an estimated sharp decrease during the period 1972–2000 (Cuthbert & Sommer 2004), the population of SA from Gough now appears stable (Cuthbert et al. 2014), which is consistent with its large TNW and low use of subtropical waters (83% of the inter-breeding period is spent within the Southern Ocean). This unique foraging ecology merits further investigations using a combination of methods to better depict the diet and behaviour at sea of SA from the Atlantic Ocean, not only at subantarctic Gough, but also at the nearby subtropical Tristan da Cunha Group, for which almost no information is available.

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