



Assessing marine ecosystem complexity: isotopic integration of the trophic structure of seabird communities from the Southern Ocean

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ABSTRACT: Understanding the processes structuring communities is a fundamental goal in ecology and conservation biology. Seabirds are commonly used as sentinels of marine ecosystems, but there is a lack of quantitative information providing a synoptic view of their community structure and of its underlying mechanisms. We used stable isotope analysis of chick feathers to investigate the structure of 2 communities that are representative of the subantarctic (Kerguelen) and Antarctic (Adélie Land) seabird diversity. Total area of the convex hull (a measure of the total $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ niche space) was 8.4-fold higher at the Kerguelen Islands than in Adélie Land, a consequence of the higher seabird diversity at the former locality. Kerguelen seabirds grouped into 2 clusters of oceanic and inshore species, with the latter group not represented in Adélie Land. Communities are primarily structured by the availability of foraging habitats ($\delta^{13}\text{C}$) and then of trophic resources ($\delta^{15}\text{N}$), with body size being a major driving force of trophic position. Ecological characteristics are more important than phylogeny to shape seabird isotopic niche breadth (standard ellipse area corrected for small sample size, SEAc), with no significant differences between Sphenisciformes, Procellariiformes, and Charadriiformes. By contrast, SEAc varies according to foraging guilds, diet, and a specialist–generalist gradient, with ubiquitous seabirds having a 10-fold larger mean SEAc than pelagic divers. This study sets a baseline against which the effects of long-term environmental changes on seabird community structure can be studied across years and conditions, and provides a relevant starting point for the investigation into the effect of climate change on Southern Ocean ecosystems.

KEY WORDS: Habitat · Trophic position · Body size · Penguins · Procellariiformes · Stable isotopes · Antarctica

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1. INTRODUCTION

Understanding the processes that structure communities is a fundamental goal in ecology and conservation biology, with ongoing human-induced environmental changes increasingly affecting the functioning of ecosystems (Hoegh-Guldberg & Bruno 2010). Anthropogenic changes alter energy flow and trophic relationships by increasing or decreasing the amount of primary and secondary production propa-

gating up the food web (Aebischer et al. 1990, Brown et al. 2010, Free et al. 2019). Hence, there is a pressing need to explore the structure of relatively poorly affected communities to investigate how rapid environmental changes will affect even the most remote ecosystems on Earth. Their high position within trophic webs make predators ideal indicators of environmental changes, as they integrate primary and secondary productivities spatially and temporally (Bump et al. 2007, Cury et al. 2011, Sydeman et al.

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2015). The trophic and associated demographic responses of marine predators to variable resource availability are now well documented at the species level (Aebischer et al. 1990, Cury et al. 2011, Barbraud et al. 2012), but few studies have been conducted in communities which integrate multiple trophic levels (TLs) in food webs (Carmel et al. 2013, Moreno et al. 2016).

Seabirds are iconic marine predators that are highly vulnerable to environmental perturbations, making them one of the most endangered avian groups (Dias et al. 2019). They are commonly used as relevant marine sentinels (Sydeman et al. 2015, 2021), because they forage at sea but breed on land where they are easily accessible for building high-quality data sets over the long term (Barbraud & Weimerskirch 2001). Communities of breeding seabirds are very diverse, ranging from a few to tens of sympatric species, with the largest diversity and populations occurring in subantarctic waters (Chown et al. 1998). The Southern Ocean (water masses south of the Subtropical Front) hosts 51 species of Procellariiformes (albatrosses and petrels) that dominate by number (~250 million individuals), and 13 species of Sphenisciformes (penguins) that dominate by mass (~113 million individuals, 90 % of the avian biomass) (Woehler 1993, Van Franeker et al. 1997, Shirihi 2002).

The food and feeding ecology of Southern Ocean seabirds has been intensively investigated at the species level over last decades using a combination of direct (food samples, bio-logging) and indirect (stable isotopes or lipids as trophic markers) methods. Comparatively fewer works have been conducted at the community level ($n \geq 10$ species). Four studies were based on conventional dietary data (Croxall & Prince 1980, Ainley et al. 1984, 1992, Ridoux 1994), two on stable isotopes (Phillips et al. 2009, Connan et al. 2019), and two combining these methods (Rau et al. 1992, Moreno et al. 2016). Results highlighted a combination of various dietary and spatio-temporal mechanisms allowing the co-existence of sympatric seabirds. However, there is still an overall lack of quantitative information to provide a synoptic view of the community structure, especially during the breeding season when seabirds are central-place foragers and thus when segregation mechanisms are the most important, as they allow co-existence by reducing competition.

The stable isotope analysis method emerged in the 1990s as an efficient tool to investigate the trophic ecology of species that are difficult to study in their natural environment, including seabird communities

(Hobson et al. 1994, Forero et al. 2004). Its advantages are numerous, since it allows collecting relevant information at moderate analytical costs along both the scenopoetic (habitat components, $\delta^{13}\text{C}$) and bionomic (trophic components, $\delta^{15}\text{N}$) axes of the ecological niche by using feathers and blood that can be easily and non-intrusively sampled from large numbers of individuals (Newsome et al. 2007, Cherel et al. 2014b). Stable isotope analysis led to the development of the concept of the isotopic niche, which essentially delineates the trophic niche of an animal by representing in δ -space the traditional $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ biplot representation of the isotopic values. This δ -space is comparable to the n -dimensional space that characterizes the trophic niche, because the chemical composition of a consumer reflects its food as well as the habitat in which it forages (Newsome et al. 2007). Further analytical development focused on metrics to quantitatively characterize community-wide aspects of trophic structure (Layman et al. 2007), which were reformulated in a Bayesian framework, allowing robust and direct comparisons of isotopic niches across and within communities and species (Jackson et al. 2011). These new quantitative metrics are now used routinely in isotopic ecology, but studies focused on seabird assemblages have been published only recently (Bodey et al. 2014, Mancini et al. 2014, Connan et al. 2019).

Here, we investigated and compared the isotopic structure of 2 contrasting seabird communities from the remote southern Indian Ocean to establish a baseline for future long-term isotopic monitoring of their trophic structure during the breeding period. Seabirds from the Kerguelen Islands and Adélie Land are representative of those breeding in subantarctic waters and high-Antarctica, respectively. The community from the Kerguelen Islands is one of the most diverse in the world (35 breeding species) (Weimerskirch et al. 1989), while only 8 seabird species breed in Adélie Land (Micol & Jouventin 2001).

Stable isotope analysis was validated in the southern Indian Ocean, with $\delta^{15}\text{N}$ values of seabirds increasing with trophic position (Cherel et al. 2010), and their $\delta^{13}\text{C}$ values decreasing with increasing latitudes and along an inshore–offshore isotopic gradient of habitats (Cherel & Hobson 2007, Jaeger et al. 2010). More specifically, we explored the following issues: (1) the overall diversity of habitats and diets covered by seabird communities by measuring their total isotopic areas, with the prediction of a larger isotopic area in relation to a more diverse community at the Kerguelen Islands than in Adélie Land; (2) the community structuring into distinct sub-assemblages

and their isotopic and biological characteristics, with the prediction of a major importance of the diversity of habitats ($\delta^{13}\text{C}$); (3) the influence of foraging methods and taxonomy on the niche breadth of a species, with the prediction that ecological characteristics are more important than phylogeny; (4) the different TLs encompassed by the community within marine ecosystems and how they are distributed; and (5) the role of body size in shaping the trophic structure of the communities, with the prediction that larger seabird species feed on higher TL prey. Size is the 'master trait' structuring food webs and influencing community ecology (Trebilco et al. 2013, Andersen et al. 2016), including in offshore Kerguelen waters (Hunt et al. 2021).

2. MATERIALS AND METHODS

2.1. Study sites, birds, and sampling

Fieldwork was carried out at Ile des Pétrels, Pointe Géologie Archipelago in Adélie Land, Antarctica (66°S , 140°E), and at the subantarctic Kerguelen Islands in the southern Indian Ocean ($48\text{--}49^\circ\text{S}$, $68\text{--}69^\circ\text{E}$). Pointe Géologie Archipelago lies near the Antarctic Continent, in southern Antarctic waters, while the Kerguelen Islands are located in the northern vicinity of the Polar Front (Park & Gambérone 1997). The Kerguelen Archipelago is surrounded by an extensive shelf and includes a large productive enclosed bay, the Morbihan Gulf (Razouls et al. 1997, Bocher et al. 2001).

Our definition of community is based on taxonomy and corresponds to all breeding seabirds inhabiting a given geographic area, thus sharing a common trophic resource base. The Kerguelen seabird community (35 species) includes 4 penguins and 24 albatrosses and petrels (Weimerskirch et al. 1989), while the species breeding at Ile des Pétrels (2 penguins, 5 Procellariiformes, 1 skua) include all of the high-Antarctic seabirds except one, the Antarctic petrel (Micol & Jouventin 2001). Most species from the 2 communities are summer breeders, although some reproduce either in winter (e.g. emperor penguin and grey petrel) or from mid-winter to mid-summer (e.g. gentoo penguin and Kerguelen petrel); a few large species have a breeding cycle that encompasses both summer and winter seasons (e.g. king penguin and wandering albatross). Guilds were defined according to the seabird feeding methods (functional groups), with species being assigned to 1 of 4 guilds: benthic divers, pelagic divers, surface feeders, and scavengers/

predators; a fifth group ('ubiquitous') included species that forage in various ecosystems (coastal, intertidal, and terrestrial) (Table S1 in the Supplement at www.int-res.com/articles/suppl/m694p193_supp.pdf).

For each seabird species, a few back body feathers were sampled from randomly chosen chicks at the end of the chick-rearing period. The rationale is that feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of chicks are good proxies of the foraging ecology of adult birds during the breeding period, because they integrate the isotopic values of food brought back to the colony by the 2 parents during a well-defined time window. The method allows comparing how species co-exist while foraging for their chicks. All 8 breeding species from Adélie Land were sampled in 2007, while feathers from Kerguelen chicks were collected from 23 species during the period 2000–2014 (Table 1; Table S1). The species included almost all of the representative seabirds of the Kerguelen Islands, except a few species whose colonies are either in too remote places (e.g. grey-headed albatross, soft-plumaged petrel) or whose nests are difficult to locate (e.g. storm petrels). Three species were sampled twice because adults forage in 2 different marine environments, namely in the open and closed sea (Morbihan Gulf). Ten species were sampled over 2 or 3 different years (Table 1). In most cases, inter-annual feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ differences were small ($<0.6\text{‰}$), with no or marginal statistical significance and no or little biological value. We are thus confident that chick $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values represent the average isotopic niches of the species during the study period, and the isotopic data from different years for a given species were therefore pooled.

2.2. Stable isotope analysis

Body feathers of chicks grow almost synchronously and thus present low intra-individual isotopic variation (Carravieri et al. 2014). Hence, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were measured on a single feather per individual. Prior to isotopic analysis, feathers were cleaned of surface lipids and contaminants by immersion in a solution of 2:1 chloroform:methanol for 2 min in a beaker, followed by 2 successive methanol rinses. Each whole body feather was air dried and cut into small pieces with scissors. Sub-samples were then weighed ($\sim 0.3\text{ mg}$) with a microbalance, packed into tin containers, and nitrogen and carbon isotope ratios were determined by a continuous flow mass spectrometer (Thermo Scientific Delta V Advantage) cou-

Table 1. Feather stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), estimated trophic positions (offshore pelagic species), and isotopic niche area estimates of seabirds from Adélie Land (8 species) and the Kerguelen Islands (23 species, 26 populations). Morb: Morbihan Gulf (closed sea) at Kerguelen Islands (see Section 2.1); na: not applicable (see text); SEAC: sample size-corrected standard ellipse area; SEAb: Bayesian standard ellipse area; 95 % CI: upper and lower 95 % credible intervals of SEAb. Values are means \pm SD

Species	Abbreviation	Location	Breeding cycles (sampling years)	n	Feather $\delta^{13}\text{C}$ (‰)	Feather $\delta^{15}\text{N}$ (‰)	Estimated trophic position	SEAC (‰ ²)	SEAb (‰ ²)	95 % CI (‰ ²)
King penguin	KP	Kerguelen	2005–2006	12	-21.6 \pm 0.3	10.5 \pm 0.3	4.6 \pm 0.1	0.27	0.22	0.13–0.43
Emperor penguin	EP	Adélie Land	2007	10	-24.2 \pm 0.3	12.4 \pm 0.4	5.1 \pm 0.1	0.32	0.27	0.14–0.54
Gentoo penguin	GP	Kerguelen	2006	12	-16.5 \pm 1.2	12.4 \pm 0.8	na	1.39	1.51	0.84–2.83
	GP-morb	Kerguelen	2003	10	-14.5 \pm 0.4	13.5 \pm 1.0	na	0.74	0.72	0.35–1.41
Adélie penguin	AP	Adélie Land	2006–2007	10	-23.5 \pm 0.2	10.7 \pm 0.4	4.6 \pm 0.1	0.24	0.22	0.11–0.43
Southern rockhopper penguin	SRP	Kerguelen	2001–2002	11	-19.3 \pm 0.5	8.7 \pm 0.3	4.0 \pm 0.1	0.56	0.46	0.27–0.93
	SRP-morb	Kerguelen	2006–2007	12	-15.3 \pm 0.4	11.5 \pm 0.4	na	0.45	0.40	0.20–0.72
Macaroni penguin	MP	Kerguelen	2006–2007	12	-18.3 \pm 0.5	10.0 \pm 0.5	4.4 \pm 0.2	0.60	0.54	0.30–1.06
Wandering albatross	WA	Kerguelen	2004–2005	15	-19.3 \pm 0.4	14.2 \pm 0.4	5.7 \pm 0.1	0.44	0.40	0.23–0.67
Black-browed albatross	BBA	Kerguelen	2004–2005	18	-18.5 \pm 0.8	12.9 \pm 0.5	5.3 \pm 0.2	0.87	0.87	0.50–1.40
Light-mantled sooty albatross	LMSA	Kerguelen	2004–2005	15	-21.0 \pm 0.4	12.6 \pm 0.4	5.2 \pm 0.1	0.50	0.45	0.27–0.77
Southern giant petrel	SGP	Adélie Land	2006–2007	13	-23.4 \pm 0.3	12.9 \pm 0.4	5.3 \pm 0.1	0.47	0.41	0.23–0.74
Northern giant petrel	NGP	Kerguelen	2004–2005, 2008–2009	22	-19.4 \pm 1.1	13.3 \pm 0.8	5.4 \pm 0.3	1.63	1.74	0.94–3.29
Southern fulmar	SF	Adélie Land	2006–2007	10	-24.1 \pm 0.3	10.4 \pm 0.8	4.5 \pm 0.3	0.79	0.69	0.32–1.38
Cape petrel	CP	Adélie Land	2006–2007	10	-24.7 \pm 0.4	8.8 \pm 0.7	4.0 \pm 0.2	0.59	0.56	0.30–0.17
Snow petrel	SP	Adélie Land	2006–2007	10	-23.3 \pm 0.3	12.3 \pm 0.4	5.1 \pm 0.1	0.38	0.33	0.17–0.68
White-headed petrel	WHP	Kerguelen	2002–2003, 2007–2008	20	-21.5 \pm 0.6	12.3 \pm 0.3	5.1 \pm 0.1	0.44	0.36	0.17–0.76
Great-winged petrel	GWP	Kerguelen	2005	10	-20.0 \pm 0.4	12.9 \pm 0.4	5.3 \pm 0.1	0.44	0.37	0.19–0.80
Kerguelen petrel	KeP	Kerguelen	2008–2009, 2009–2010	18	-22.0 \pm 0.5	11.7 \pm 0.5	4.9 \pm 0.1	0.70	0.66	0.34–1.18
White-chinned petrel	WCP	Kerguelen	2004–2005, 2007–2008	24	-22.1 \pm 0.6	11.6 \pm 0.7	4.9 \pm 0.2	1.11	1.10	0.57–1.88
Grey petrel	GrP	Kerguelen	2002, 2005	25	-19.7 \pm 0.7	13.7 \pm 0.7	5.5 \pm 0.2	0.78	0.71	0.42–1.22
Antarctic prion	AnP	Kerguelen	2007–2008	10	-21.5 \pm 0.5	9.3 \pm 0.4	4.2 \pm 0.1	0.58	0.50	0.26–1.01
Thin-billed prion	TBP	Kerguelen	2002–2003, 2011–2012	21	-22.1 \pm 0.6	8.7 \pm 0.5	4.0 \pm 0.2	0.70	0.67	0.44–1.07
Blue petrel	BP	Kerguelen	2002–2003, 2011–2012	24	-21.9 \pm 0.5	9.6 \pm 0.5	4.3 \pm 0.1	0.72	0.68	0.44–1.03
Wilson's storm petrel	WSP	Adélie Land	2006–2007	6	-24.7 \pm 0.2	10.3 \pm 0.3	4.5 \pm 0.1	0.31	0.22	0.09–0.58
South Georgian diving petrel	SGDP	Kerguelen	2010–2011, 2011–2012	16	-21.3 \pm 0.3	8.8 \pm 0.3	4.0 \pm 0.1	0.25	0.21	0.12–0.38
Common diving petrel	CDP-morb	Kerguelen	2002–2003	17	-17.0 \pm 0.5	12.1 \pm 0.4	na	0.42	0.39	0.24–0.66
Kerguelen shag	KS	Kerguelen	2005–2006	10	-13.8 \pm 1.0	14.0 \pm 0.6	na	2.18	1.80	0.95–3.55
Subantarctic skua	SS-morb	Kerguelen	1999–2000	10	-10.9 \pm 0.7	15.0 \pm 0.6	na	1.07	0.95	0.49–1.93
South polar skua	SPS	Kerguelen	2004–2005, 2009–2010, 2010–2011	32	-21.7 \pm 0.4	10.9 \pm 0.3	na	0.15	0.14	0.07–0.28
Kelp gull	KG	Adélie Land	2006–2007	22	-22.4 \pm 0.3	11.9 \pm 0.7	na	0.58	0.55	0.35–0.84
Kerguelen tern	KT-morb	Kerguelen	2010–2011	7	-12.8 \pm 0.7	13.4 \pm 1.0	na	1.54	1.47	0.64–3.47
		Kerguelen	2013–2014	12	-14.3 \pm 2.6	13.4 \pm 1.1	na	5.60	5.48	3.00–10.39
Black-faced sheathbill	BFS-morb	Kerguelen	2010–2011, 2011–2012	15	-13.4 \pm 1.7	15.0 \pm 1.2	na	4.85	4.80	2.57–8.58

pled to an elemental analyzer (Thermo Scientific Flash EA 1112). Results are presented in the usual δ notation relative to Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated measurement errors $<0.10\%$ for both $\delta^{13}C$ and $\delta^{15}N$. Chick $\delta^{13}C$ and $\delta^{15}N$ values of most Kerguelen species were previously published in a study focusing on mercury contamination in seabirds (Blévin et al. 2013).

2.3. Data analyses

Quantitative metrics based on the position of species in the niche space formed by $\delta^{13}C$ and $\delta^{15}N$ values were applied to estimate isotopic niche breadth (Layman et al. 2007, Jackson et al. 2011). Metrics were calculated using the functions for 'Stable Isotope Bayesian Ellipses in R' (SIBER; Jackson et al. 2011), available within the package 'Stable Isotope Analysis in R' (SIAR; Parnell et al. 2010). Six population metrics were calculated as described below. The first 4 reflect trophic diversity in the $\delta^{13}C$ – $\delta^{15}N$ scatterplot, and the other 2 represent trophic redundancy (how closely positioned species in a given species group are to each other within their respective niches). The metrics are described as: (1) $\delta^{13}C$ range: distance between the 2 species with the most enriched and most depleted ^{13}C values, which indicates the diversity of feeding habitats within a species group (Layman et al. 2007); increased $\delta^{13}C$ range implies more foraging habitats (e.g. pelagic vs. benthic, closed vs. open sea, coastal vs. neritic vs. oceanic, and colder vs. warmer oceanic waters). (2) $\delta^{15}N$ range: distance between maximum and minimum species $\delta^{15}N$ values, which documents trophic length of a species group (Layman et al. 2007). Trophic position (TP) of organisms must be calculated in relation to varying $\delta^{15}N$ baselines, but generally, a larger range in $\delta^{15}N$ values among consumers foraging within the same ecosystem suggests a higher TP and thus a greater degree of trophic diversity. (3) Total area (TA) of the convex hull encompassed by mean isotopic values of all species in $\delta^{13}C$ – $\delta^{15}N$ bi-plot space; TA represents a measure of the total amount of niche space occupied, and thus a proxy for the total extent of foraging diversity within a species group (Layman et al. 2007). (4) Standard ellipse area (SEA): trophic niche breadth of a species (which is to bivariate data what standard deviation [SD] is to univariate data). SEA was corrected for sample size (SEAc), which is a robust approach when comparing small and unbal-

anced sample sizes; SEAc provides an estimation of the core isotopic niche that contains $\sim 40\%$ of the data regardless of sample size; as recommended, all but 2 sample sizes were ≥ 10 (Table 1). The degree of SEAc overlap (%) was estimated to measure isotopic niche overlap between pairs of species (Tables S2 & S3). Bayesian SEA (SEAb) was calculated using 10^4 posterior draws to statistically compare niche breadth between species (Jackson et al. 2011). (5) Mean nearest-neighbor distance: mean of the Euclidean distances to nearest neighbor of each species in bi-plot space, which is a measure of the overall density and clustering of species; a group of species with similar feeding ecologies would show a smaller mean nearest-neighbor distance than a group in which species are more varied in terms of foraging habitats ($\delta^{13}C$) and feeding habits ($\delta^{15}N$) (Layman et al. 2007). (6) SD of nearest-neighbor distance: a measure of evenness of species in the scatterplot, in which low values indicate a more even distribution of species in the isotopic niche space (Layman et al. 2007).

The potential structuring effect of TP was tested on the 2 seabird communities. The concepts of TP and TL are different and complementary. TL is useful to describe both the connectedness web and energy flow web; TL is a natural number that starts from autotrophs (TL = 1) and corresponds with a discrete consumer classification (e.g. primary consumer, TL = 2; secondary consumer, TL = 3) (Ishikawa 2018). By contrast, TP is not a natural number, as it reflects the complexity of most consumers' diet that includes numerous trophic resources (e.g. the global TP of humans is estimated at 2.2; Bonhommeau et al. 2013). The TP of seabirds was estimated using the following equations for blood (Cherel et al. 2010): $TP_x = [(\delta^{15}N_x - 3.4 - 1.7)/3.2] + 3.0$, where $\delta^{15}N_x$ is the nitrogen isotope value of species x , 3.4% is the average value for *Salpa thompsoni*, a dominant herbivorous salp in the Southern Ocean with an assumed TP of 2.0, 1.7% is the enrichment factor between seabird blood and prey muscle, and 3.2% is the average trophic enrichment factor between marine organisms and their food (Sweeting et al. 2007). Since feathers are enriched in ^{15}N compared to blood, feather $\delta^{15}N$ values were first mathematically corrected following an overall regression for all studied seabird species gathered together (Cherel et al. 2014b).

The potential structuring effect of seabird size on TP was tested using adult metrics (structural size, wingspan, body mass) collected by Shirihai (2002) (Table S1). Due to their large ranges, size data were first ln-transformed before testing linearity with TP. Two major limitations precluded performing a gen-

eral analysis including all seabird species: (1) different biological driving forces to dive and fly result in penguins being much larger and heavier than albatrosses and petrels, and (2) different $\delta^{15}\text{N}$ baselines do not allow $\delta^{15}\text{N}$ and thus TP comparison between seabirds foraging in oceanic, coastal, intertidal, and terrestrial ecosystems (Cherel & Hobson 2007). Consequently, the size effect on TP was tested on 2 distinct data sets of offshore pelagic seabirds, namely penguins ($n = 5$, excluding the coastal gentoo penguin and southern rockhopper penguin from the Morbihan Gulf) and Procellariiformes ($n = 18$, excluding the common diving petrel from the Morbihan Gulf), because $\delta^{15}\text{N}$ baseline varies little in oceanic waters of the southern Indian Ocean (Altabet & François 1994).

Data were statistically analyzed using R 3.0.0 and, in few cases, SYSTAT 13. Values are presented as means \pm SD.

3. RESULTS

As expected, large $\delta^{13}\text{C}$ (13.8‰) and $\delta^{15}\text{N}$ (6.3‰) ranges were found amongst chicks of the 31 species (34 populations, 501 sampled individuals) from the 2 pooled communities (Table 1). These ranges suggest

high diversity in the foraging habitats and dietary habits of Antarctic and subantarctic seabirds.

3.1. Communities

3.1.1. Adélie Land

Mean chick feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ranged from -24.7‰ (Cape petrel) to -22.4‰ (south polar skua), and from 8.8‰ (Cape petrel) to 12.9‰ (southern giant petrel), respectively (Table 1). Hence, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges amounted to 2.3 and 4.1‰, respectively (Table 2). TA of the whole community was 4.4‰^2 , while the mean \pm SD nearest-neighbor distance was $0.81 \pm 0.28\text{‰}$. SEAc averaged $0.46 \pm 0.18\text{‰}^2$, and ranged from 0.24 (Adélie penguin) to 0.79‰^2 (southern fulmar). No or little overlap occurred between the core isotopic niches of the species, with limited overlaps (0.09–0.11; Table S2) in SEAc of southern giant petrel and snow petrel (Fig. 1).

3.1.2. Kerguelen Islands

Mean feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ranged from -22.1‰ (white-chinned petrel) to -10.9‰ (Kergue-

Table 2. Trophic niche metrics of seabirds from Adélie Land and the Kerguelen Islands according to communities, feeding guilds, and taxonomy (Orders). TA: total area of the convex hull encompassing the data points (mean isotopic values of species); SEAc: sample size-corrected standard ellipse area; na: not applicable. Values are means \pm SD

Groups	n	Feather $\delta^{13}\text{C}$ range (‰)	Feather $\delta^{15}\text{N}$ range (‰)	TA (‰ ²)	SEAc (‰ ²)	Nearest-neighbor distance (‰)
Adélie Land (all oceanic)	8	2.3	4.1	4.4	0.46 ± 0.18	0.81 ± 0.28
Surface feeders	4	1.4	3.5	1.1	0.52 ± 0.22	1.19 ± 0.67
Procellariiformes	5	1.4	4.1	1.6	0.51 ± 0.19	0.79 ± 0.35
Kerguelen Islands	26	11.2	6.3	36.9	1.11 ± 1.30	0.70 ± 0.54
Coastal, intertidal, terrestrial	11	10.8	4.1	20.4	1.82 ± 1.80	1.34 ± 1.09
Oceanic	15	3.8	5.5	15.9	0.60 ± 0.23	0.77 ± 0.48
Benthic divers	4	5.6	2.6	0.9	1.35 ± 0.62	1.75 ± 1.09
Pelagic divers	6	6.3	2.8	11.5	0.42 ± 0.14	1.73 ± 0.08
Surface feeders	11	3.6	5.5	8.6	0.66 ± 0.21	0.63 ± 0.37
Scavengers/predators	2	2.3	2.4	na	0.89 ± 1.05	3.66
Ubiquitous species	3	1.5	1.6	1.1	4.00 ± 2.16	1.51 ± 0.10
Sphenisciformes	6	7.1	4.8	13.2	0.67 ± 0.39	1.91 ± 0.60
Procellariiformes	14	5.1	5.5	14.5	0.68 ± 0.35	0.64 ± 0.37
Pelecaniformes	2	2.9	1.0	na	1.63 ± 0.78	3.02
Charadriiformes	4	8.9	4.1	7.5	3.04 ± 2.61	3.10 ± 3.17
Two communities pooled						
Pelagic divers	8	na	3.7	na	0.39 ± 0.14	na
Surface feeders	15	na	5.5	na	0.62 ± 0.21	na
Scavengers/predators	4	na	2.4	na	0.71 ± 0.64	na
Sphenisciformes	8	na	4.8	na	0.57 ± 0.37	na
Procellariiformes	19	na	5.5	na	0.64 ± 0.32	na
Charadriiformes	5	na	4.1	na	2.54 ± 2.51	na

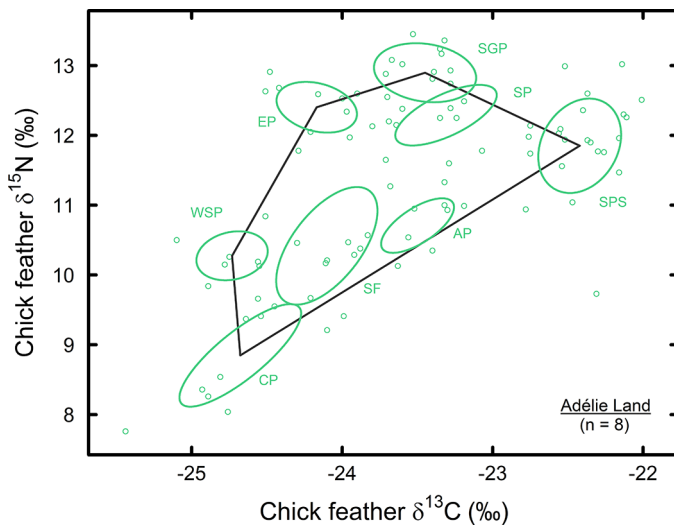


Fig. 1. Sample size-corrected standard ellipse area (SEAc) calculated from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of chick feathers from seabird species breeding in Adélie Land, Antarctica. See Table 1 for abbreviations

len shag from the Morbihan Gulf), and from 8.7‰ (southern rockhopper penguin) to 15.0‰ (Kerguelen shag from the Morbihan Gulf), respectively (Table 1). Hence, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges amounted to 11.2 and 6.3‰, respectively. TA of the whole community was 36.9‰² (Fig. 2), while the mean \pm SD nearest-neighbor distance was 0.70 ± 0.54 ‰ (Table 2). SEAc averaged 1.11 ± 1.30 ‰² amongst the 26 populations, and

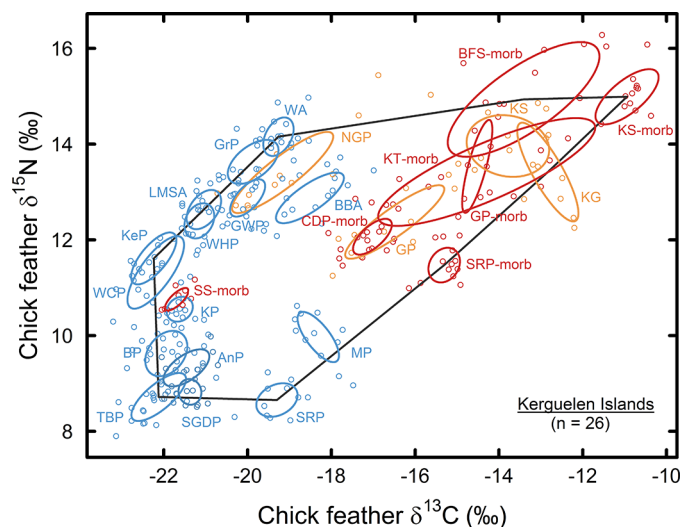


Fig. 2. Sample size-corrected standard ellipse area (SEAc) calculated from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of chick feathers from seabirds breeding in the subantarctic Kerguelen Islands. The community includes species/populations foraging in the closed sea environment of the Morbihan Gulf (red), in the open sea (orange), and in oceanic waters (blue). See Table 1 for abbreviations

it showed a large range of values from 0.15 (sub-antarctic skua) to 5.60‰² (Kerguelen tern) (Table 1).

Feather $\delta^{13}\text{C}$ values drove the segregation of 2 sub-groups within the Kerguelen seabird community, with no $\delta^{13}\text{C}$ values between -18.3 (macaroni penguin) and -17.0‰ (common diving petrel) (Table 1). The subgroup with the most positive $\delta^{13}\text{C}$ values included most of the populations and species that are known to forage in terrestrial, intertidal, or coastal habitats, while the second subgroup included all oceanic species plus 2 outliers, i.e. the northern giant petrel and subantarctic skua, which foraged mainly on land and in coastal waters (Pacoureau et al. 2019, Reisinger et al. 2020). Indeed, cluster analysis using the Bray-Curtis method grouped the 2 latter species with oceanic penguins and Procellariiformes (Fig. 3). The Kerguelen seabird community was thus split into 2 sub-communities composed of (1) oceanic species and (2) all other species and populations

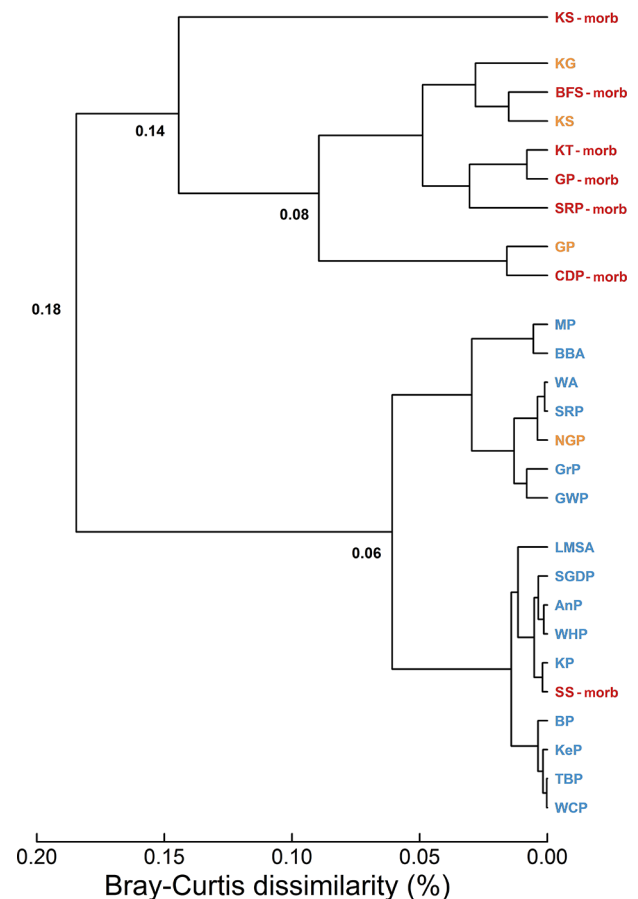


Fig. 3. Dendrogram based on mean $\delta^{13}\text{C}$ values of chick feathers from seabirds breeding at the Kerguelen Islands (red: closed sea; orange: open sea; blue: oceanic). The method uses the Bray-Curtis dissimilarity measure in cluster analysis. See Table 1 for abbreviations

(thus including the northern giant petrel and subantarctic skua). TA, the mean nearest-neighbor distance, and SD of the nearest neighbor distance for the oceanic species and the other group were 15.9 and 20.4‰², 0.77 and 1.34‰, and 0.48 and 1.09‰, respectively. Cluster analysis also allowed splitting the oceanic sub-community into 2 groups that are characterized by higher and lower feather $\delta^{13}\text{C}$ values, with a 1.0‰ gap between values from the great-winged petrel and light-mantled sooty albatross (Fig. 3).

The oceanic sub-community is composed of 15 species whose SEAc averaged $0.60 \pm 0.23\%$ (Table 2). Most (98 out of 105, 93.3%) of the pairwise comparisons showed no overlap between the core isotopic niches of the oceanic species, and 5 (4.8%) of the quantified overlaps were low (0.04–0.26) (Table S3a). However, 2 overlaps (1.9%) were notable (0.43–0.68), i.e. between SEAc of the light-mantled sooty albatross and white-headed petrel, and those of the white-chinned petrel and Kerguelen petrel (Fig. 2). The second sub-community is composed of 11 coastal, intertidal, or terrestrial species and populations whose mean SEAc ($1.82 \pm 1.80\%$) was higher than that of oceanic seabirds (Mann-Whitney $U = 42.0$, $p = 0.035$). Within the second sub-community, a majority of species' SEAc values did not overlap (43 out of 55, 78.2%), and some of the significant overlaps had no ecological value due to geographical mismatches in foraging areas (within and outside the Morbihan Gulf). The only relevant overlap (0.80) occurred between SEAc of the gentoo penguin and Kerguelen tern from the Morbihan Gulf, with most of the core isotopic niche of the former being included within that of the latter (Table S3b). Notably, the 3 species (Kerguelen shag, and gentoo and southern rock-hopper penguins) that were sampled in closed and open sea had smaller SEAc within than outside the Morbihan Gulf (Table 1).

3.2. Isotopic niche breadth and structuration of guilds and orders

When pooling all seabirds from the 2 communities, the mean SEAc was $0.96 \pm 1.17\%$ ($n = 34$). SEAc varied 37-fold, from 0.15 (subantarctic skua) to 5.60‰² (Kerguelen tern) (Fig. 4, Table 1). The 5 foraging guilds from the Kerguelen Islands were segregated by their SEAc values (Kruskal-Wallis $H = 14.32$, $p = 0.006$), which ranged from 0.42 to 4.00‰² in increasing order as follows: pelagic

divers < surface feeders < scavengers/predators < benthic divers < ubiquitous species (Table 2). Notably, the less diverse pelagic divers ($n = 6$) had higher TA (11.5 vs. 8.6‰²), 2.7 times higher mean nearest-neighbor distance (1.73 vs. 0.63‰) but lower SD of nearest-neighbor distance (0.08 vs. 0.37‰) than the more numerous surface feeders ($n = 11$) (Table 2). When pooling species from the 2 communities, the 2 most diverse guilds (pelagic divers and surface feeders) were segregated by their SEAc values ($U = 22.0$, $p = 0.014$). The mean SEAc value of surface feeders did not significantly differ between Adélie Land and the Kerguelen Islands ($U = 30.0$, $p = 0.294$).

Taxonomical analysis indicated that the 4 seabird orders from the Kerguelen Islands did not segregate by their mean SEAc values ($H = 5.01$, $p = 0.171$)

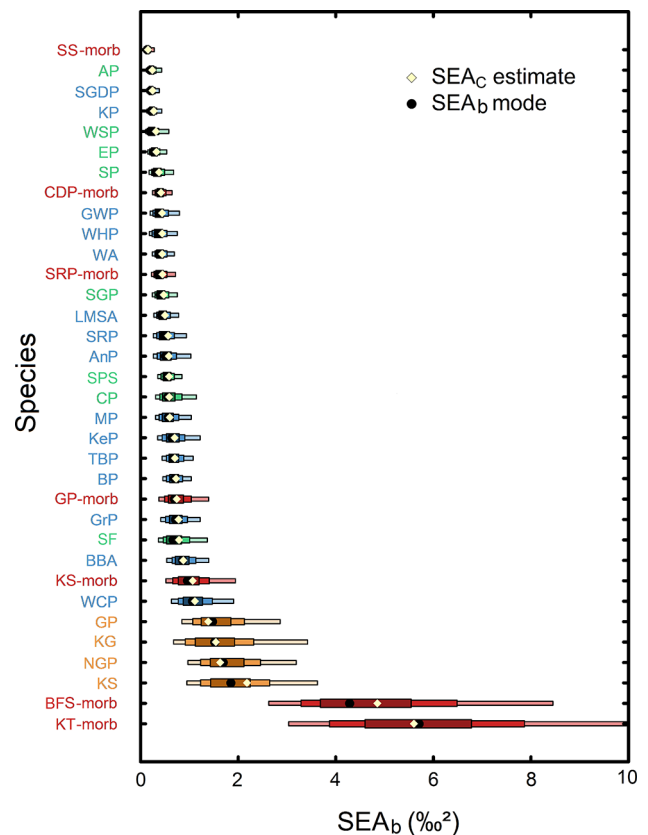


Fig. 4. Bayesian estimates of the standard ellipse area (SEAb) calculated from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of chick feathers from seabirds breeding in Adélie Land (green) and the Kerguelen Islands (red: closed sea; orange: open sea; blue: oceanic). SEAb values were deliberately placed in an increasing sequence to illustrate the diversity of isotopic niche breadth amongst species and populations. Shaded density plots represent 50, 75, and 95% credible intervals, with SEAb mode indicated by a black circle and SEAc by a yellow diamond. See Table 1 for abbreviations

(Table 2). Notably, the less diverse penguins ($n = 6$) had similar TA (13.2 vs. 14.5‰), 3.0 higher mean nearest-neighbor distance (1.91 vs. 0.64‰), and higher SD of nearest-neighbor distance (0.60 vs. 0.37‰) than the more numerous albatrosses and petrels ($n = 14$) (Table 2). When pooling species from the 2 communities, the 3 most diverse seabird orders (Sphenisciformes, Procellariiformes, and Charadriiformes) were not segregated by their SEAc values ($H = 2.42$, $p = 0.298$). The mean SEAc value of Procellariiformes did not significantly differ between Adélie Land and the Kerguelen Islands ($U = 45.0$, $p = 0.353$).

3.3. Offshore pelagic species: structuration by TP and size

Pelagic species of penguins, albatrosses, and petrels from Adélie Land and the Kerguelen Islands were segregated by their estimated TP ($H = 275$, $p < 0.0001$). Species were deliberately placed in a trophic sequence to illustrate the trophic structure of the 2 pooled communities (Fig. 5). Offshore pelagic seabirds from the Southern Ocean fed along a continuum of less than 2 TL (1.7) from 4.0 ± 0.1 (southern rockhopper penguin) to 5.7 ± 0.1 (wandering albatross).

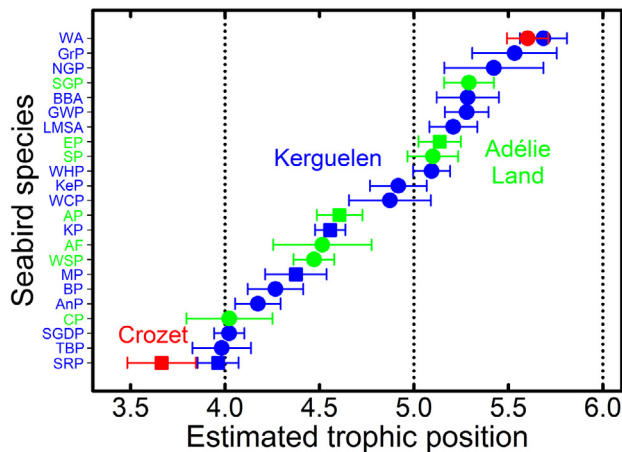


Fig. 5. Trophic positions estimated from chick feather $\delta^{15}\text{N}$ values of offshore pelagic species of penguins ($n = 5$, squares) and Procellariiformes ($n = 18$, circles) from Adélie Land (green) and the Kerguelen Islands (blue). Lowest (southern rockhopper penguin) and highest (wandering albatross) estimated trophic positions of chicks from the Crozet Islands (red) illustrate the overall trophic structure of a third representative seabird community from the Southern Ocean (see Section 4.4). Dotted lines represent the discrete successive trophic levels. Values are means \pm SD. See Table 1 for abbreviations

Overall, size ranged widely within Sphenisciformes and Procellariiformes. Structural size and body mass varied 2.3- and 11-fold in penguins, respectively, and structural size, wingspan, and body mass varied 7.2-, 9.4-, and 226-fold in albatrosses and petrels, respectively (Table S1). Estimated TP correlated positively and linearly with ln-transformed size metrics in both penguins (structural size and body mass: $y = -1.13 + 1.31x$ and $y = 0.66 + 0.43x$, $r = 0.946$ and 0.930 , $F_{1,3} = 25.54$ and 19.23 , $p = 0.015$ and 0.022 , respectively) (Fig. 6) and Procellariiformes (structural size, wingspan, and body mass: $y = 1.87 + 0.78x$, $y = 1.35 + 0.75x$, and $y = 2.87 + 0.30x$, $r = 0.779$, 0.799 , and 0.785 , $F_{1,16} = 24.62$, 28.27 , and 25.77 , respectively, all $p < 0.0001$) (Fig. 7).

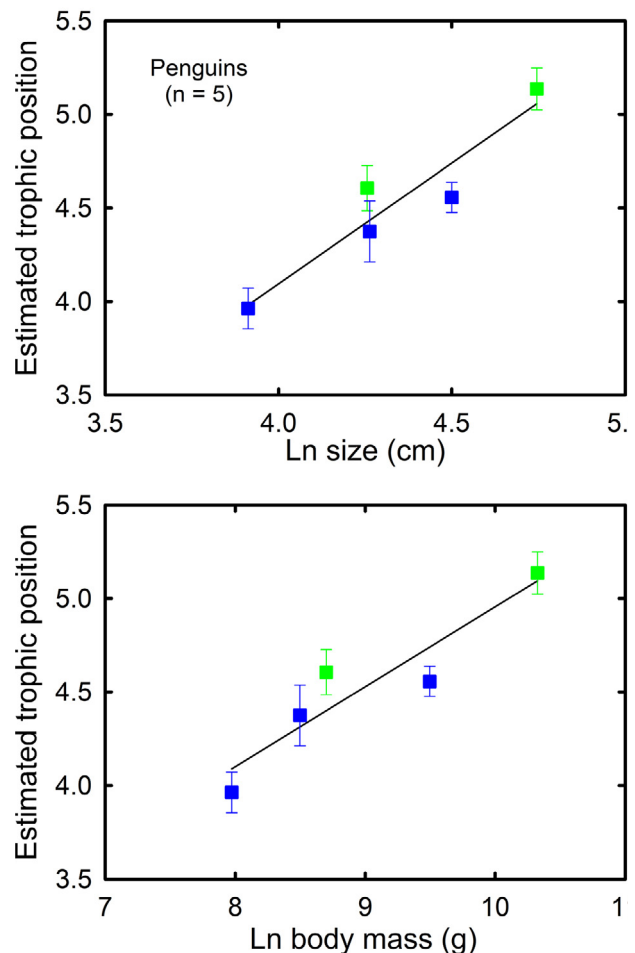


Fig. 6. Estimated trophic positions vs. ln-transformed size metrics (structural size and body mass) of penguins ($n = 5$) from Adélie Land (green) and the Kerguelen Islands (blue). Values are means \pm SD

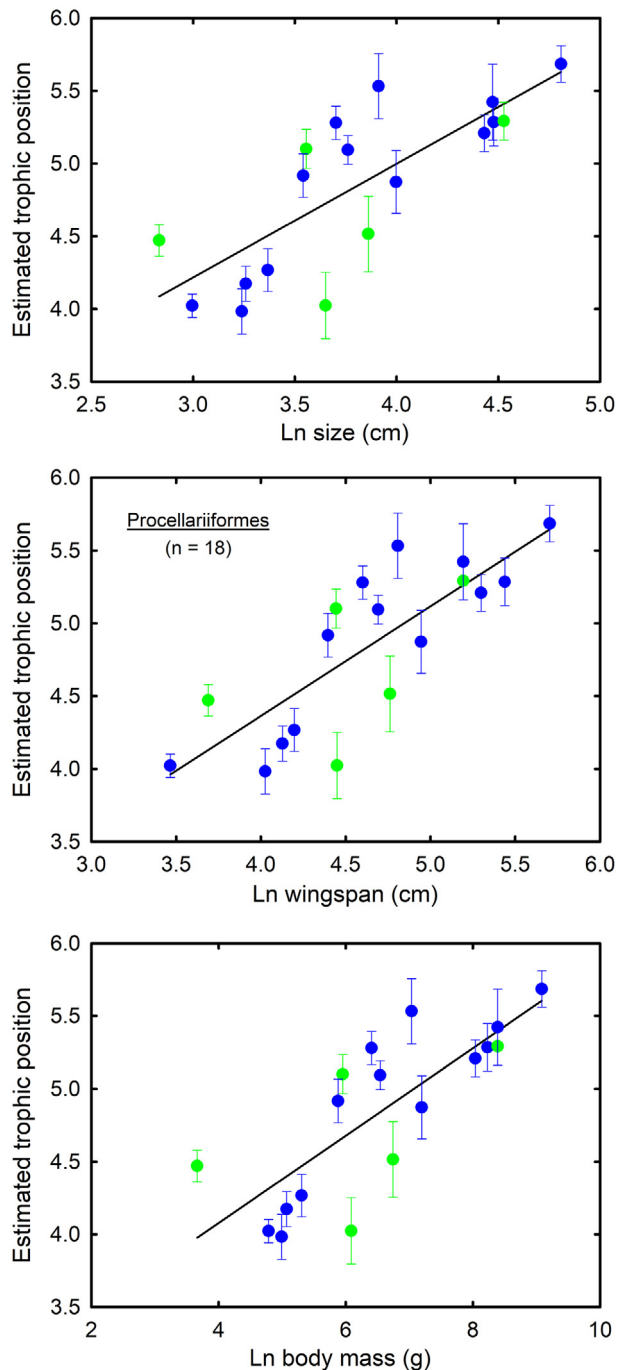


Fig. 7. Estimated trophic positions vs. ln-transformed size metrics (structural size, wingspan, body mass) of Procellariiformes from Adélie Land (green) and the Kerguelen Islands (blue). Values are means \pm SD

4. DISCUSSION

To our knowledge, this study is the first to (1) use quantitative isotopic metrics such as isotopic ellipses to characterize the trophic structure within and

between large seabird communities, (2) describe and compare the isotopic niche of 31 Southern Ocean species according to taxonomy and trophic guilds, representative of the high seabird diversity that characterizes the Southern Ocean, and (3) test the effect of size on the TP of seabirds that were estimated from their measured $\delta^{15}\text{N}$ values. Four main features emerge from the detailed isotopic investigation. (1) TA is much higher at Kerguelen than in Adélie Land, a consequence of the higher seabird diversity at the former locality. (2) The communities are primarily structured by the availability of foraging habitats ($\delta^{13}\text{C}$) and then of trophic resources ($\delta^{15}\text{N}$). (3) Ecological characteristics are more important than phylogeny to shape seabird niche breadth (SEAc). (4) Body size is a major driving force of TP of seabirds.

4.1. Limitations of stable isotope analysis

Conventional dietary analysis and bio-logging provide better trophic and spatio-temporal resolution of seabird foraging ecology than stable isotopes. For example, stomach content analysis allows clarifying taxonomic resolution of food items and estimating their size, but the technique is biased to digestibility rate and to more conspicuous prey items, and is just a snapshot of diet. In contrast, the stable isotope technique is based on food assimilated over time, and isotopic metrics are the most effective and less time-consuming mean to have a synoptic view of the trophic structure of communities and ecosystems (Moreno et al. 2016, this study). However, the method includes some inherent simplifications that must be underlined. (1) The isotopic niche is tightly correlated to the trophic niche, but the 2 concepts are not the same and should not be confused: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values represent 2 dimensions within the multi-dimensional space that defines the trophic niche. Any isotopic difference indicates different trophic niches, but identical isotopic metrics do not indicate identical trophic niches. These limitations are well illustrated by the large SEAc overlaps between the common diving petrel and gentoo penguin (Table S3b), 2 species whose populations are known to segregate by their food and both the horizontal and vertical components of their foraging habitats within and outside the Morbihan Gulf, respectively (Bocher et al. 2000, Lescroël et al. 2004, Lescroël & Bost 2005). (2) In a few cases, there is a mismatch between $\delta^{13}\text{C}$ values and the foraging habitats of the birds, thus illustrating the importance of knowing the basic biology of the targeted species. The low $\delta^{13}\text{C}$

value of Kerguelen subantarctic skuas suggests foraging in oceanic waters, while they feed on land on blue petrels (Pacoureaux et al. 2019). The skua $\delta^{13}\text{C}$ values thus reflect the foraging habitat of blue petrels that travel back and forth to forage in Antarctic waters (Cherel et al. 2002b, 2014a). (3) Isotopic values of chick feathers integrate the feeding ecology of the parents when they forage for their chicks. This does not preclude adult birds foraging differently when they feed for themselves, for example during the long trips and associated distant feeding grounds of Procellariiformes when they use a dual foraging strategy (Weimerskirch et al. 1994, Cherel et al. 2005). However, despite these inherent limitations, the isotopic metrics illuminate the trophic structure of communities, sub-communities, and species (Figs. 1 & 2).

4.2. Isotopic structure between communities

Three main features emerge from the comparison of the isotopic characteristics of the seabird communities from Adélie Land and the Kerguelen Islands. (1) Feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges are higher, thus resulting in an 8.4-fold higher TA at the Kerguelen Islands than in Adélie Land. A higher TA indicates a much larger total extent of foraging diversity within the Kerguelen community. The higher foraging diversity likely results from a higher number of sympatric breeding seabirds at Kerguelen, which can be related to more favorable marine and terrestrial environments in terms of food resources, and of foraging and breeding habitats in subantarctic islands. Alternatively, a higher density of species may induce more prey depletion, possibly forcing species to segregate from each other due to a high competition level driving specialization. (2) Cluster analysis grouped the Kerguelen seabirds into 2 sub-communities marked by their low and high $\delta^{13}\text{C}$ values that characterize oceanic and more inshore species, respectively (Cherel & Hobson 2007, Jaeger et al. 2010). By contrast, all breeding seabirds from Adélie Land were classified as oceanic, with no species showing the high $\delta^{13}\text{C}$ values of the Antarctic coastal and benthic environments (Cherel et al. 2011). The difference between Antarctic and subantarctic communities is likely related to the increasing intense seasonality with increasing latitudes, which is the fundamental driver of life-cycle evolution, thus explaining the lack of resident coastal penguins, shags, and larids in Adélie Land. (3) In agreement with their latitudinal breeding locations, the 2 com-

munities segregate along the scenopoetic axis, since there is no overlap between the feather $\delta^{13}\text{C}$ values of seabirds from Adélie Land and the Kerguelen Islands. The penguins and petrels from Adélie Land showed very low $\delta^{13}\text{C}$ values that characterize high-Antarctica (Cherel 2008). Indeed, breeding birds forage over the Antarctic shelf and its fringing oceanic waters (Zimmer et al. 2008, Jenouvrier et al. 2015, Widmann et al. 2015, Delord et al. 2016, Barbraud et al. 2021), where the species constitute the core of a circumpolar ice-associated seabird assemblage (Ainley et al. 1994, Woehler et al. 2010). By contrast, their $\delta^{13}\text{C}$ values show that Kerguelen seabirds do not forage only in the vicinity of the breeding archipelago. Considering isotopic estimations of the Polar Front and Subtropical Front at -21.2 and -18.3‰ (Jaeger et al. 2010), oceanic seabirds from the Kerguelen Islands forage for their chicks over a wide latitudinal range, encompassing the entire Subantarctic Zone (between the Subtropical and Polar Fronts), the Polar Front, and a part of the Antarctic Zone further south. The 1.0‰ $\delta^{13}\text{C}$ gap between the great-winged petrel and light-mantled sooty albatross highlights 2 subgroups that favor warmer and colder waters, respectively (Fig. 3). Foraging within the Antarctic Zone is in agreement with: (1) the presence of the endemic Antarctic krill *Euphausia superba* in the food of Kerguelen albatross and petrel chicks (Cherel et al. 2002a,b,c, Delord et al. 2010), the tracking of adult birds (Delord et al. 2010, 2013), and the seabird at-sea distribution that defined a circumpolar open-water assemblage whose southern limit is the ice edge (Ainley et al. 1994, Woehler et al. 2010).

To summarize, the higher foraging diversity at Kerguelen than in Adélie Land is primarily driven by the scenopoetic axis, thus underlining the importance of foraging habitat diversity ($\delta^{13}\text{C}$) in shaping seabird communities. The bionomic axis is less relevant, as there are little differences between the overall $\delta^{15}\text{N}$ values (a proxy of TP) and $\delta^{15}\text{N}$ ranges of oceanic seabirds from Kerguelen and Adélie Land. Breeding Antarctic seabirds are trapped by the Antarctic Continent that precludes foraging south of the breeding sites, but they do not feed north of the pack-ice either. By contrast, Kerguelen seabirds forage in coastal and in oceanic waters from north of the archipelago to the ice edge. Subantarctic seabirds underline the trophic connectivity between the Antarctic and subantarctic food webs, and the key role of energy and biomass export from Antarctic waters to sustain subantarctic predators, which is a key element of the functioning of the Southern Ocean (Cherel et al. 2018, Murphy et al. 2021).

4.3. Isotopic segregation within communities

The high degree of isotopic niche separation of seabirds in Adélie Land is a case study with each species having a species-specific non-overlapping niche. Dietary partitioning is remarkable because only 4 prey items form the bulk of the food of air-breathing vertebrates in high-Antarctica: 2 euphausiids and 2 pelagic fish (the neritic ice krill *E. crystallophias* and Antarctic silverfish *Pleuragramma antarcticum*, and the oceanic Antarctic krill and Antarctic myctophid *Electrona antarctica*) (Ainley & DeMaster 1990, Cherel 2008). Seabirds from Adélie Land rely on different proportions of similar prey items, from the krill-eater Cape petrel to the fish-eaters snow petrel and emperor penguin (Fig. 1) (Offredo & Ridoux 1986, Ridoux & Offredo 1989, Cherel 2008).

Isotopic niche overlaps occur more frequently within the Kerguelen community. Most of the isotopic overlaps do not preclude ecological separation, because species segregate through other dimensions of their trophic niches (see above for common diving petrel, gentoo penguin, subantarctic skua, and northern giant petrel). For example, overlaps between the white-chinned petrel and Kerguelen petrel is ecologically minimized by phenology, with the former species breeding later and with a longer breeding cycle than the latter (Jouventin et al. 1985, Weimerskirch et al. 1989). However, the isotopic overlaps between light-mantled sooty albatross and white-headed petrel merit further examination because both species feed on oceanic organisms within the same water masses during the summer breeding periods (Ridoux 1994, Lawton et al. 2008, J. C. Stahl et al. unpublished data).

4.4. Structuring mechanisms

Isotopic niche breadth varies widely amongst seabird species breeding in the Austral Ocean. A key finding is that ecological characteristics appear to be more important than phylogeny to shape niche breadth of penguins, albatrosses, petrels, skuas, and larids. Average SEAc is not significantly different between Sphenisciformes, Procellariiformes, and Charadriiformes, while it is related to seabird ecological characteristics like foraging guilds, diet, and a specialist–generalist gradient. Isotopic niche breadth is strongly related to functional groups of seabirds with ubiquitous species having a 10-fold larger SEAc than pelagic divers. Overall, SEAc of Kerguelen spe-

cies is more structured according to the scenopoetic than the bionomic axis, with a major influence of habitat diversity at different spatial scales. At a large scale, niche breadth is on average 3 times larger in inshore than in oceanic seabirds, with the highest SEAc corresponding to the generalist Kerguelen tern and black-faced sheathbill that forage in coastal, intertidal, and terrestrial environments. The lowest SEAc relates to the specialist subantarctic skua that feeds mainly on a single prey item, the blue petrel (Pacoureaux et al. 2019). At a smaller scale, niche breadth is still related to the diversity of feeding habitats, as illustrated by the larger SEAc in benthic divers that feed on benthic prey (the Kerguelen shag and gentoo penguin) than in divers feeding on pelagic prey (e.g. the rockhopper penguin and common diving petrel). Benthic coastal divers benefit from the mosaic of microhabitats that characterize the shallow-water seafloor (Thrush et al. 2010, Cherel et al. 2011), which contrasts with the more homogeneous pelagic ecosystem. Those microhabitats are fed by various carbon and nitrogen sources that drive small-scale baseline isotopic variability (Gillies et al. 2012), which challenges estimating TP of coastal consumers using their bulk $\delta^{15}\text{N}$ values (Post 2002).

Communities are also structured along the bionomic axis, with TP of oceanic seabirds from Adélie Land and the Kerguelen Islands ranging from 4.0 to 5.7. The distribution of estimated TP provides one of the strongest lines of empirical evidence for the predominance of omnivory (i.e. feeding on more than one TL) in food webs, meaning that seabirds do not distribute in discrete TLs (Cherel et al. 2007), but instead in a continuum of $\delta^{15}\text{N}$ values (Rau et al. 1992, Hobson et al. 1994, Forero et al. 2004) that translates into a continuum of TP (Fig. 5). According to their TP, oceanic seabirds of the Southern Ocean can be defined as meso- to top predators, which revisits the common paradigm of seabirds sharing a place at the top/apex of the food web with large sharks, bony fishes, and marine mammals (Cherel et al. 2008). Oceanic seabirds distribute along almost 3 TLs (from 4 to 6), but their influence on the food web is wider and encompasses 4 TLs. Small petrels include herbivorous zooplankton (TL = 2) in their diet (Ridoux 1994, Cherel et al. 2002a), while large Procellariiformes feed at least in part on high-TP organisms (Cherel et al. 2017, Mills et al. 2021). Interestingly, end-point species were identical for the Kerguelen and the closely related Crozet communities (Fig. 5), from the southern rockhopper penguin (TP = 3.7–4.0) to the wandering albatross (TP =

5.6–5.7), thus suggesting a similar trophic structure within all subantarctic seabird assemblages.

Body size is a key feature of any organism that determines the range of prey sizes it can consume, with larger individuals feeding on larger prey and thus being expected to feed at higher TLs (Cohen et al. 1993). In marine ecosystems, size can be a better predictor of TP than taxonomy (Andersen et al. 2016), because the continuous growth of most organisms is linked to ontogenic dietary shifts (Jennings et al. 2008). In contrast, seabirds have a definite growth, with fledglings almost reaching the adult size. Hence, it can be expected that species itself is a relevant predictor of TP in seabirds, a hypothesis that was rarely tested (Mancini et al. 2014). Oceanic seabirds from Adélie Land and Kerguelen Islands verify the hypothesis since estimated TP of penguins and Procellariiformes is positively related to various size metrics (structural size, wingspan, body mass). The smallest seabirds feed primarily on crustaceans, while the largest species target either micronektonic fish (penguins) or nektonic fish and cephalopods (Procellariiformes) (Offredo & Ridoux 1986, Bocher et al. 2000, Cherel et al. 2007, 2017). The role of body size in shaping the trophic structure of seabird communities was demonstrated both in the Southern Ocean (this study) and in the tropics (Mancini et al. 2014), thus suggesting it is a general feature of large seabird assemblages worldwide.

4.5. Conclusions and perspectives

Co-existence of a large number of Southern Ocean seabirds results from low ecological niche overlaps, which integrate the underlying diversity of their life-history traits related to foraging. Low niche overlaps indicate a low level of species redundancy in polar seabird communities, which contrasts with the isotopic structure of the complex assemblages of tropical fish (Genner et al. 1999), mammals (Dammhahn et al. 2013, Oelbaum et al. 2019), and birds (Symes & Woodborne 2010), including seabirds (Catry et al. 2008). Low isotopic niche overlaps also suggest that trophic resources are limited at both Kerguelen and Adélie Land, thus contrasting with the superabundance of food at a few Southern Ocean localities. In South Georgia, Antarctic krill is the primary prey of most air-breathing predators, with poor-krill years revealing segregating mechanisms that do not operate at their best in normal years (Murphy et al. 2007).

The isotopic structure of Kerguelen and Adélie Land seabird communities can be considered as an

early-21st century baseline. The isotopic niche of seabirds from Adélie Land has likely remained unchanged for decades, because climate warming has not yet greatly affected East Antarctica (Jun et al. 2020), and, accordingly, the isotopic niche of emperor and Adélie penguins has varied little since the 1950s (Jaeger & Cherel 2011). By contrast, museum specimens from Kerguelen Islands have indicated an isotopic shift in the thin-billed prion molting grounds over the last decades (Cherel et al. 2014a). Recent environmental changes have already affected demographic parameters, foraging behavior, and at-sea distribution of subantarctic seabirds, thus defining some species as 'winners' and 'losers' (Connan et al. 2008, Péron et al. 2010, Weimerskirch et al. 2012, Bost et al. 2015). Hence, climate change is already operating in the subantarctic (Favier et al. 2016, Sallée 2018), but to what extent it is driving changes in the trophic structure of seabird communities is unknown. To monitor these ongoing and future changes, chick feathers from representative species have been collected on a yearly basis since 2013 along a latitudinal gradient of breeding localities (including the Kerguelen Islands and Adélie land) to build up an isotopic database in complement to our long-term demographic and tracking studies.

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