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Diet composition and trophic ecology of two Antarctic storm-petrel species

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ABSTRACT

Availability and quality of food shape the distribution and movements of animal populations. In sympatric species, sharing limited resources, coexistence is typically achieved through niche segregation. However, information on dietary niches is lacking particularly for small and elusive seabirds, which often forage in remote oceanic areas. In this study, we aimed to characterize the trophic ecology of two highly pelagic seabird species, Wilson's storm-petrel *Oceanites oceanicus* and Black-bellied storm-petrel *Fregetta tropica*, breeding sympatrically on King George Island, maritime Antarctica, using a combination of methods. Prey species, assayed via metabarcoding of faecal and regurgitate samples, were dominated by teleost fish, primarily lanternfish (Myctophidae), and zooplanktonic crustaceans, mainly krill (Euphausiidae), but also included other prey with lower frequencies of occurrence, such as salps and amphipods. We used carbon and nitrogen bulk stable isotopes and compound-specific isotope analyses of amino acids of blood samples to derive isotopic niches and trophic positions, showing that Black-bellied storm-petrels prey on a slightly higher trophic position than Wilson's storm-petrels (3.7 and 3.5, respectively). Combining results of stable isotope and molecular diet analysis, indicate a diet richer in fish for Black-bellied storm-petrels and thus a potential niche segregation not in regards of general prey spectrum but proportion of specific prey types (prey composition). Additionally, intraspecific segregation in prey spectrum was observed in Wilson's storm-petrels concerning their breeding stage (incubation vs. chick-rearing), suggesting selective chick provisioning. Future studies should investigate a potential interspecific spatial segregation in foraging areas.

1. Introduction

An increasing number of studies demonstrate that animal populations are limited by the abundance and quality of their food and that food availability and accessibility is shaping species distribution and movements (White, 2008; Paredes et al., 2014; Pinsky et al., 2020; Ollus et al., 2023). If resources, such as food resources, are limited in an environment, and sympatric species share the limited resource, the species coexistence is typically achieved through niche segregation. Niche segregation is regarded as a mechanism that reduces competition between co-occurring species and thus facilitates competing species coexistence (Hutchinson, 1959; MacArthur and Levins, 1967; Gravel et al., 2011; Seyer et al., 2020; Petalas et al., 2024; Reyes-Puig et al., 2024). Sympatric species, especially predators like marine seabirds, commonly share resources and congregate at certain sea areas in time and space where their often patchily distributed prey is aggregated, which can lead to interspecific competition due to potential overlap in foraging areas and diet composition (Jessopp et al., 2020; Petalas et al., 2024). This in turn can contribute to dietary and spatial niche segregation/partitioning in sympatric seabirds (Navarro et al., 2013; Robertson et al., 2014; Jessopp et al., 2020; Petalas et al., 2024).

For instance, it is proposed that the co-existence of a large number of Southern Ocean seabirds results from low ecological niche overlaps, reflecting the diversity of their foraging-related life history traits (Cherel et al., 2010; Cherel and Carrouée, 2022). An altered, mainly reduced, food availability, caused by increasing numbers of conspecifics, inter-species competitors or environmental changes, possibly might further increase competition (Łomnicki, 1978; Newton, 1980; Woodward et al., 2010; Piatt et al., 2020). Though having evolved in an isolated and somewhat extreme environment, Southern Ocean biodiversity and food webs belong to the most vulnerable ones (Queirós et al., 2024). The food webs of the Southern Ocean were traditionally described as dominated

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by the crustacean Antarctic krill *Euphausia superba*, playing a pivotal role in supplying various marine predators of the region (Ainley et al., 1984; McBride et al., 2021; Warwick-Evans et al., 2022; Kawaguchi et al., 2024; Queirós et al., 2024). The largest concentrations and highest densities of Antarctic krill occur around the Antarctic Peninsula, in the Scotia and Weddell Seas (McBride et al., 2021). However, since the 1970s, krill stocks, particularly adult population density and the occurrence of very dense swarms, have declined dramatically (Atkinson et al., 2004; Kawaguchi et al., 2024). These changes were associated with latitudinal and longitudinal rearrangement of krill distribution, including a poleward contraction in the Southwest Atlantic, likely exacerbating risk to already declining krill-consuming bird populations (McBride et al., 2021; Kawaguchi et al., 2024). As the Antarctic environment continues to change, some species of marine birds there may decline, particularly along the South Shetland Islands and Antarctic Peninsula, one of the most rapidly warming regions on earth (Warwick-Evans et al., 2021; Dai et al., 2025).

For instance, in the sub-Antarctic, small petrels consume one million tonnes of crustaceans, mainly Antarctic krill, per year. The petrel species dependence on similar prey has led to assumption that interspecific competition could be structuring their communities by foraging niche segregation (Navarro et al., 2013). For example, Blue Petrel *Halobaena caerulea*, Antarctic Prion *Pachyptila desolata*, Common Diving Petrel *Pelecanoides urinatrix* and South Georgian Diving Petrel *P. georgicus* breeding sympatrically on South Georgia operated in very different ecological space (Navarro et al., 2013). However, despite seabirds are important predators in marine ecosystems, in many cases, their functional roles and the limiting effects of the environment on their distributions, remain unclear, amongst other reasons due to a lack of information on what prey they consume (Barrett et al., 2007; Lewison et al., 2012; Philipps et al., 2017; Carreiro et al., 2020; Warwick-Evans et al., 2021; Silva et al., 2024). Generally, of all seabird groups, the diet and feeding ecology of storm-petrels is perhaps the least known (Carreiro et al., 2020), e.g. for sympatrically breeding Antarctic storm-petrels, namely Wilson's storm-petrel *Oceanites oceanicus* and Black-bellied storm-petrel *Fregetta tropica*.

Differences in their foraging areas, i.e. spatial niche partitioning, were assessed by distribution models based on ship surveys around the South Shetland Islands. Black-bellied storm-petrels showed a more heterogeneous distribution, with higher abundance in the Bransfield Strait and further offshore, whereas Wilson's storm-petrels had a highly coastal distribution with the suggestion that this distribution pattern is connected to resource partitioning to reduce competition between the two species (Warwick-Evans et al., 2021). Their dietary niche partitioning was examined using stable isotope analyses (Quillfeldt et al. 2017, 2023; Ausems et al., 2020), as they are assumed to differ in their diet composition during the breeding season (Quillfeldt et al., 2023). Earlier studies used traditional diet analyses and found that that Black-bellied storm-petrels take fish and crustaceans in equal proportions, while Wilson's storm-petrels consume mainly crustaceans (>80 % occurrence), predominantly Antarctic krill (Beck and Brown, 1972; Harper, 1987; Wasilewski, 1986; Croxall et al., 1988; Croxall and North, 1988; Ridoux, 1994; Hahn, 1998a; Quillfeldt, 2002). Interspecific differences in gastrointestinal parasites, linked to the storm-petrel's prey as intermediate host for parasites like cestodes (Fusaro et al., 2023) as well as in elemental concentrations, such as copper (Cu), mercury (Hg), and selenium (Se), in body feather and blood samples (Pacyna et al., 2019; Quillfeldt et al., 2023) both also indicate interspecies differences in foraging behaviour like prey item choice. Following the diet composition differences described previously, Black-bellied storm-petrels are expected to forage at a higher trophic position than Wilson's storm-petrels (Quillfeldt et al., 2017; Ausems et al., 2020). Bulk stable isotope analyses of adult storm-petrels did not unambiguously indicate a higher trophic position for Black-bellied storm-petrels (Quillfeldt et al., 2017; Ausems et al., 2020). Bulk stable isotope value interpretation, particularly in wide-ranging species, can be hampered by stable isotope baseline variations among ecosystems, and for estimations of trophic positions compound-specific isotope analyses of amino acids (CSIA-AA) were shown to be more precise than bulk estimates (Quillfeldt et al., 2017; Thébault et al., 2021; Canseco et al., 2024). A higher trophic position for Black-bellied storm-petrels was shown based on CSIA-AA measured in feather and blood samples, reflecting the moult (non-breeding) and breeding period, respectively (Quillfeldt et al., 2017, 2023), but more information on the diet is needed to fully understand the observed patterns (Quillfeldt et al., 2023). The age of the birds could also be a decisive factor. Black-bellied storm-petrel chicks were probably fed at a higher trophic position (higher δ^{15}N) than adults (Ausems et al., 2020) and in some years Wilson's storm-petrels samples collected at nests, mainly regurgitates from chicks, contained a higher fish content (Quillfeldt, 2002).This leads to the assumption, that to increase their current chick fitness parents may feed their offspring at a different trophic position than they consume themselves by selectively foraging or reserving higher quality prey for chicks, i.e. selective chick provisioning (Browne et al., 2011; Rosciano et al., 2019; Ausems et al., 2020; Quiring et al., 2021; Kennerley et al., 2024). Selective chick provisioning may result in a trophic segregation between adults and chicks, presenting a type of intraspecific niche segregation (Hodum and Hobson, 2000; Alonso et al., 2012; Rosciano et al., 2019).

In the present study, combining DNA metabarcoding of faecal and regurgitate samples, with bulk stable isotope values and compound-specific isotope analyses of amino acids of blood samples, we:

(I) describe and compare the prey spectra of sympatrically breeding Wilson's and Black-bellied storm-petrels on King George Island,
(II) examine differences in their trophic positions, independent of environmental baseline values, and potential interspecific niche segregation, and
(III) in Wilson's storm-petrels, from which we were also able to sample nestlings and generally obtained a higher sample size, evaluate for intraspecific niche segregation by comparing prey composition during incubation and chick-rearing phase to check for selective chick provisioning.

2. Material & methods

2.1. Studied species

Both study species belong to the southern (or austral) storm-petrels (family Oceanitidae) and are highly pelagic seabirds. The Wilson's storm-petrel *Oceanites oceanicus*, Antarctica's smallest endotherm, predominantly breeds in boulder and cliff areas at snow-free zones of the Antarctic continent and surrounding islands, up to the sub-Antarctic zone (Beck and Brown, 1972; Obst and Nagy, 1993; Drucker et al., 2020; Thomas, 2024). The slightly larger Black-bellied storm-petrel *Fregetta tropica* breeds in similar habitats, but has a more northern distribution, with large numbers on Elephant Island, while numbers on sub-Antarctic islands strongly depend on predation (Medrano and David, 2023). Both species breed, often sympatrically, during the austral summer (December to April) in colonies, typically in rock crevices, and perform biparental brood care during the annual breeding attempts with single-egg clutches and a monogamous mating system (Beck and Brown, 1972; Wasilewski, 1986; Quillfeldt et al., 2001; Thomas, 2024). Both are mainly pelagic surface feeders, produce stomach oil for chick provision and usually return to their breeding colonies only at night (Beck and Brown, 1972; Harper, 1987; Obst and Nagy, 1993).

2.2. Field sampling - faecal, regurgitate and blood samples

Field sampling was carried out in the maritime Antarctic at a mixed breeding colony near the Argentine Station 'Carlini' on King George Island/25 de Mayo Island, South Shetland Islands, with nest burrows of the two species situated on basaltic slopes of the old eroded volcano

'Tres Hermanos' (Three Brothers Hill) in the ice-free area of the Potter Peninsula (62°14′S, 58°40′W). Fresh faeces (n = 37) and regurgitates (n = 137) were obtained opportunistically and non-invasively by two ways: either during mist netting captures of adult individuals at night (21:00–01:30 o'clock UTC-3) or during handling adult and nestling birds during controls of marked nest burrows (Table 1). Samples were collected over two breeding seasons 6th February - April 12, 2023 and December 29, 2023 – March 1, 2024 (hereafter referred to as 2023 and 2024) by using disposable plastic or metal spoons and spatulas (to avoid contamination between samples). Individual samples were preserved in an Eppendorf tube with 96 % ethanol and stored dark and frozen (except for transport: approx. 48 h) until DNA extraction. Samples of adults were categorized in three breeding stage categories, depending on the result of the nest check or sampling date: pre-laying and incubation (nest check: adult on egg or December to 14th of January), chick-rearing (nest check: adult with chick or 20th February to April), and unknown stage (15th of January to 19th February).

Blood (~0.2 ml) of adult individuals for stable isotope analyses and molecular sexing (Fridolfsson and Ellegren, 2000) was sampled by puncturing the brachial wing vein with a cannula (⌀ 0.40 × 20 mm, B. Braun SE, Melsungen, Germany), collected with heparinized capillaries (Vitrex Medical A/S, Herlev, Denmark), and stored in ethanol (96 %). For stable isotope analyses, blood samples (n = 24 Wilson's and n = 16 Black-bellied storm-petrels) were oven-dried (60 °C, 24 h, Carreiro et al., 2020) and ground to powder.

2.3. Laboratory and data analysis

2.3.1. Bulk and compound-specific stable isotope analyses

For carbon and nitrogen bulk stable isotope analyses, blood samples (n = 24 Wilson's and n = 16 Black-bellied storm-petrels) were oven-dried (60 °C, 24 h, Carreiro et al., 2020) and ground to powder. Dried, powdered blood (0.39 ± 0.07 mg; n = 24 Wilson's and n = 16 Black-bellied storm-petrels) was weighed into tin cups (5 × 8 mm, IVA Analysetechnik GmbH & Co.KG, Meerbusch, Germany) and sent to the LIENSs laboratory, La Rochelle University. There, carbon and nitrogen isotopic values were measured using a continuous-flow system consisting of an elemental analyzer (Flash 2000; Thermo Scientific, Milan, Italy) equipped with the smart EA option and an autosampler (Zero Blank, Costech, Valencia, CA, United States) and connected via a Conflo IV peripheral to a Delta V Plus isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany). The uncertainty of the reported isotope-delta values was evaluated as the standard deviation of repeated (n = 8) measurements of reference material (USGS61 and USG63, US Geological Survey, Reston, VA, USA). Uncertainty of both δ^{13}C and δ^{15}N values did not exceed 0.10 ‰. Results are given in parts per thousand (‰) in the δ notation and were normalised using reference materials Vienna Pee Dee Belemnite (VPDB) and atmospheric nitrogen (Air-N_2) for carbon and nitrogen, respectively (cf. Quillfeldt et al., 2023).

Compound-specific isotope analyses of amino acids (CSIA-AA) of blood-samples (~6 mg, n = 8 Wilson's and n = 7 Black-bellied storm-petrels) were performed at the UC Davis Stable Isotope facility (USA) as described in Quillfeldt and Masello (2020). Mean standard deviation for sample replicates was ±0.16 ‰ and for reference material replicates ±0.27 ‰. The trophic positions (TP_{CSIA}) of these samples were calculated from nitrogen stable isotope values of glutamic acid (Glx) and phenylalanine (Phe), using a stepwise trophic discrimination factor (see Quillfeldt and Masello, 2020; Thébault et al., 2021 for detailed description) with the following equation:

$$TP_{CSIA} = 2.0 + \frac{\mathrm{Glx} - \mathrm{Phe} - 4.0\,‰ - 3.4\,‰}{6.2\,‰}$$

To calculate trophic positions for all blood samples (n = 40), using their bulk stable isotope values, we used the approach of a linear regression model to study the relationship between TP_{CSIA} and bulk stable isotope values (δ^{13}C and δ^{15}N), as described in Thébault et al. (2021). Trophic positions calculated with the following equation, derived from the linear regression model (Adjusted $R^2 = 0.75$, $F_{2,12} = 21.74$, $p < 0.001$; Fig. S1), are hereafter referred to as TP_{LM}:

$$TP_{LM} = 1.4986 + 0.0046 \times \delta^{13}C + 0.2195 \times \delta^{15}N$$

2.3.2. DNA extraction from faeces and regurgitates

Prior to extraction, the ethanol was evaporated and samples were weighed (faeces: 0.3–240.6 mg, mean: 48.8 mg, regurgitates: 0.5–1186.7 mg, mean 192.8 mg). Faecal samples were used completely, while large regurgitate samples were homogenized and a subsample of the resulting homogenate (~300 mg) was used for DNA extraction. DNA was extracted from the samples using the QIAamp® DNA Stool Mini Kit (Qiagen GmbH, Düsseldorf, Germany), following the protocol of the manufacturer with a few adjustments. To ensure proper DNA extraction by sufficient breaking up and homogenizing diet material, we firstly added 5 to 10 Zirconia beads (⌀ 2.0 mm, Carl Roth GmbH + Co. KG, Karlsruhe, Germany) and used a homogenizer for 1 min and 3000 U/min (BeadBug™ 3, JoJo Life Science U.G., Giengen, Germany). The samples with the beads and with added InhibitEX buffer were placed in the Disruptor Genie™ (Scientific Industries SI™, Bohemia, NY, USA) for 3 min. Furthermore, we increased the incubation time with Buffer AL and proteinase K from 10 to 30 min. During DNA extraction and following laboratory process, we included two negative extraction controls (empty Eppendorf tubes) along with the samples. We determined DNA quantity and quality with the NanoDrop2000c UV–Vis spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA) and the Qubit 4 fluorometer (Invitrogen by Thermo Fisher Scientific Inc., Waltham, MA, USA). If the DNA concentration exceeded 180 ng/μl, the respective samples (n = 5) were diluted to 20 ng/μl.

2.3.3. DNA amplification – amplicon PCRs

We carried out four amplicon PCRs, using a universal marker and three specific markers. Firstly, the 18S small subunit (SSU) rRNA gene in extracted DNA was targeted using the bilaterian-specific primers BilSSU1100F/BilSSU1300R (Jarman et al., 2004). In three taxon-specific PCRs, fragments of the mitochondrial 16S rDNA of krill (Euphausiids) were amplified with primers EuphMLSUF/EuphMLSUR (Deagle et al., 2007) and of crustaceans (Crustacea) with primer pair CRUST16S_F (short)/CRUST16S_R(short) (Berry et al., 2017) as well as a fragment of the mitochondrial 12S rDNA gene of bony fish (Osteichthyes) with the

Table 1
Sampling data of faeces and regurgitates of Wilson's storm-petrels *Oceanites oceanicus* (WSP) and Black-bellied storm-petrels *Fregetta tropica* (BBSP) collected in breeding seasons 2023 (n = 87) and 2024 (n = 87).

	Number of faeces					Number of regurgitates				
	Nest control		Mist netting		Total	Nest control		Mist netting		Total
	2023	2024	2023	2024		2023	2024	2023	2024	
WSP Nestling	14	6	–	–	20	45	9	–	–	54
WSP Adult	1	13	1	1	16	15	36	8	17	76
BBSP Nestling	0	0	–	–	0	0	0	–	–	0
BBSP Adult	0	1	0	0	1	2	1	1	3	7

primers FishF1/FishR1 (Xavier et al., 2018). All PCRs were carried out using 2 × Multiplex PCR Master Mix (Qiagen GmbH, Düsseldorf, Germany), and primers had Illumina overhang adapters (P5 for forward and P7 for reverse primers) attached to allow further PCR-based sample barcoding in preparation for Illumina sequencing. PCR setup and cycling conditions, primer and adapter sequences and fragment sizes are given in Table S1. Negative controls for DNA extraction and negative PCR controls (PCR-grade water) were included in each PCR run. PCR amplicons were visualized using QIAxcel Advanced high-resolution capillary gel electrophoresis (Qiagen GmbH, Düsseldorf, Germany).

2.3.4. Library preparation and Illumina sequencing

A 5 μl aliquot of each amplicon PCR product, which rendered a clear peak (Table S2), was purified using a Cytiva Illustra™ ExoproStar 1-Step Kit for enzymatic PCR clean-up (Cytiva, Marlborough, MA, USA) following the manufacturer's protocol. In 31 cases (Table S2), products of two taxon-specific amplicon PCRs were combined at this step (2.5 μl of each amplicon product, cf. Swift et al., 2018; Marcuk et al., 2024). After this purification, an index PCR was performed in order to individually mark each PCR product with specific Illumina indices (Integrated DNA Technologies, Coralville, IA, USA) added to the P5 and P7 sequencing adapters (Table S3). Resulting index PCR products were purified and normalised with a SequalPrep™ Normalization Plate Kit (Invitrogen by Thermo Fisher Scientific Inc., Waltham, MA, USA), and 2 μl of each normalised and individually tagged sample were pooled to finalise the NGS library. The library was sequenced at SEQ-IT GmbH & Co. KG (Kaiserslautern, Germany) using 250-bp paired-end reads on a MiSeq desktop sequencer (Illumina, San Diego, CA, USA).

2.3.5. Bioinformatics analysis and taxonomic assignment

In order to transform the raw Illumina sequence data received into a list of molecular operational taxonomic units (MOTUs) with assigned taxonomy, a custom workflow in GALAXY was used (Masello et al., 2021; The Galaxy Community, 2024; for detailed steps of the workflow: Supplementary material A1). Subsequently, MOTUs that corresponded to regular field contaminants in faecal and regurgitate samples (bacteria, soil fungi, and bird DNA) were discarded manually (Kleinschmidt et al., 2019). Furthermore, sequences with a length of less than 100 bp, as short fragments are less likely to contain reliable taxonomic information (Deagle et al., 2009), and BLASTn assignment matches of less than 98 % were discarded. MOTUs were assigned to the lowest shared taxonomic level (Kleinschmidt et al., 2019; Table S4). As a further filter step, prey MOTUs were accepted only if they contained a minimum of ten sequences in total. Additionally, we considered read number within the extraction and PCR negative samples for filtering: Two reads for Euphausiidae were present within the negative sample of BilSSU1100F/BilSSU1300R-PCR. Read numbers (maximum of 16 reads) were also low in individual samples for this MOTU, and therefore we removed this MOTU from any sample ($n = 5$ samples for Wilson's storm-petrel and $n = 1$ sample for Black-bellied storm-petrels) that did not amplify with the specific primers (Euphausiidae and Crustacea). All other included negative samples have been free of sequence reads.

2.4. Statistical analysis

Data were analysed and visualized in R (version 4.4.1, R Core Team, 2024; for version information of used packages see Supplementary material A2). Shapiro-Wilk tests were used to check for normality and parametric or non-parametric tests were chosen accordingly.

2.4.1. Statistics of stable isotope data

While carbon stable isotopes values were not normally distributed, nitrogen values were normally distributed (Shapiro-Wilk test: $W = 0.901$, $p = 0.002$ and $W = 0.956$, $p = 0.122$, respectively). As there was no difference for stable isotope values between the sexes, females and males were considered jointly per species (*t*-test $\delta^{15}N$: WSP $t = -0.193$, $df = 18.844$, $p = 0.849$ and BBSP $t = 1.714$, $df = 11.815$, $p = 0.113$; Wilcoxon rank sum test $\delta^{13}C$: WSP $W = 75.5$, $p = 0.770$ and BBSP $W = 39$, $p = 0.494$). To compare isotopic niches between the species we used metrics based in a Bayesian framework within the R package *SIBER* (Stable Isotope Bayesian Ellipses in R; Jackson et al., 2011). Within SIBER standard ellipse area (cf. Jackson et al., 2011) were drawn using nitrogen and carbon stable isotopic values, corrected for small sample sizes (SEAc). Standard ellipses were used to quantify niche width and to compare it between the two species (permutation test with 1000 permutations).

2.4.2. Statistics of DNA metabarcoding data

Valid MOTUs were identified in 87 Wilson's storm-petrel (adults = 68, nestlings = 19) and in seven Black-bellied storm-petrel samples (Table S2). These sample numbers were used to calculate the frequency of occurrence FO (FO% = [n/t] x 100, where 'n' is the number of samples, in which the MOTU was detected, and 't' is the total number of considered samples; Barrett et al., 2007). Since the DNA metabarcoding data are qualitative data, we tested for differences in diet composition at family and genus level with permutation tests in 'VEGAN' (Oksanen et al., 2009). Non-metric Multidimensional Scaling (NMDS, function *metaMDS*) was used to visualise differences between two groups (adult Wilson's storm-petrels vs. adult Black-bellied storm-petrels; adult vs. nestling Wilson's storm-petrels, and pre-laying/incubating vs. chick-rearing adult Wilson's storm-petrels) in diet compositions. NMDS, using rank orders to collapse information from multiple dimensions into usually two dimensions, is generally considered the most robust unconstrained ordination method in community ecology (Faith et al., 1987; Minchin, 1987). The function *metaMDS* allowed us to investigate the agreement between the two-dimension configuration and the original configuration through a stress parameter (stress value < 0.1 = agreement is very good, < 0.2 = good representation). Stress values in present tests were all <0.1 (Fig. 1). We performed Permutational Multivariate Analysis of Variance Using Distance Matrices (PERMANOVA) with the function *adonis* and checked for the multivariate homogeneity of group dispersions (variances) with the function *betadisper*. To assess the dietary overlap of each group according to the presence/absence data at family and genus level, we calculated Pianka's measure of overlap O_{jk} (Pianka, 1986) in 'SPAA' (Zhang, 2016) using the *niche.overlap* function. In order to assess sample sizes covering the prey diversity, particularly for the rather small sample set for Black-bellied storm-petrels ($n = 7$ samples with at least one valid MOTU) we plotted rarefaction curves for MOTUs using the package 'iNEXT' (Hsieh et al., 2016).

3. Results

3.1. Trophic positions & stable isotope analyses

While carbon isotopic values where not significantly different between species (Wilcoxon rank sum test $W = 211.5$, $p = 0.600$), nitrogen isotopic values were higher in Black-bellied storm-petrels (*t*-test $t = 6.208$, $df = 26.732$, $p < 0.001$, Table 2, Fig. 2). Niche width comparison, based on standard ellipse areas, between the species showed no significant difference in area (permutation test $p = 0.763$), however, there is no overlap between the niches, mainly due to the higher nitrogen isotopic values in Black-bellied storm-petrels (Fig. 2). According to stable isotope analyses of blood samples Black-bellied storm-petrels ($TP_{LM} = 3.7 \pm 0.1$, $n = 16$) foraged on a higher trophic position than Wilson's storm-petrels ($TP_{LM} = 3.5 \pm 0.1$, $n = 24$; Welch *t*-test $t = 6.175$, $df = 27.027$, $p < 0.001$; Fig. 2).

3.2. Prey composition based on molecular analyses

In total, 25 prey MOTUs were identified (Table 3; Table S5). Samples included 3.4 ± 2.0 MOTUs, with no significant difference between

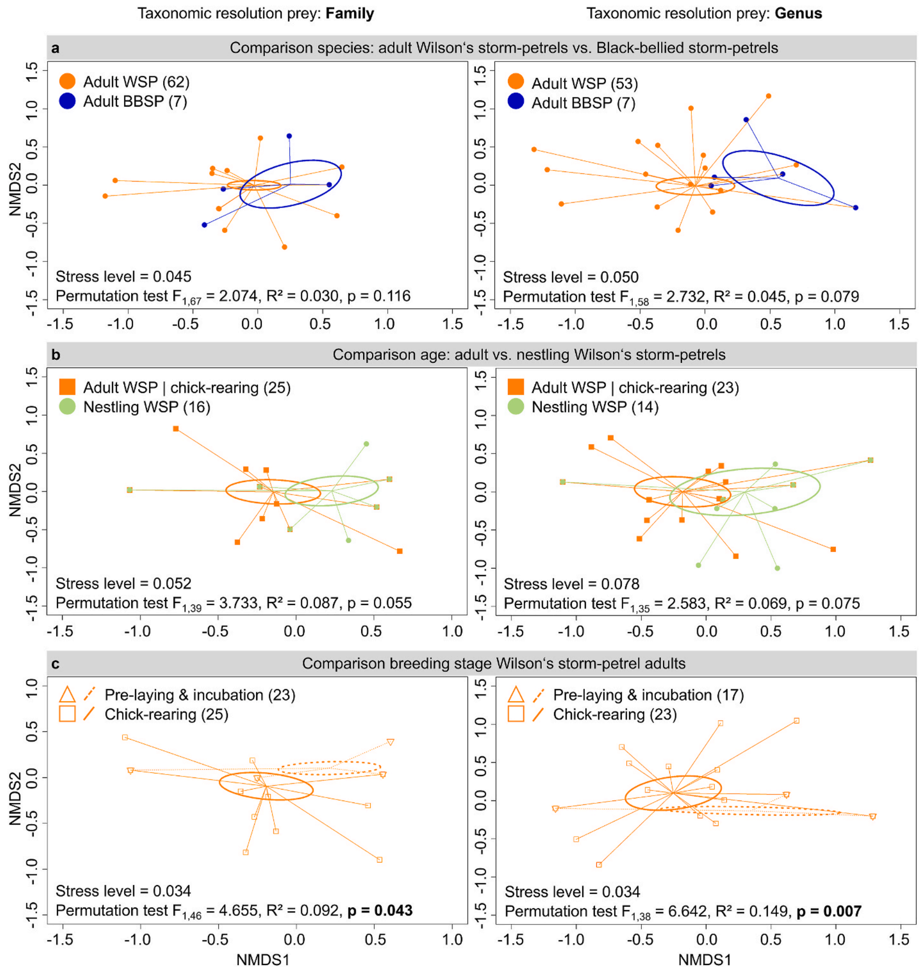

Fig. 1. Non-metric multidimensional scaling (NMDS) plots, depicting the distribution of samples and 95 % confidence ellipses (depicted as circles), display the dissimilarity patterns in prey composition on family (**left**) and genus level (**right**) for Wilson's storm-petrels *Oceanites oceanicus* (WSP) and Black-bellied storm-petrels *Fregetta tropica* (BBSP). NMDS was used to condense multidimensional information into two dimensions and different groups are compared: **(a)** adult Wilson's and Black-bellied storm-petrels (all breeding stages), **(b)** adult and nestling Wilson's storm-petrels during chick-rearing stage, and **(c)** breeding stages in adult Wilson's storm-petrels. Groups are colour- and shape-coded and sample size of each group is given in brackets. Stress level for each NMDS and results of permutation test for differences are shown along each plot. Ellipses represent 95 % confidence intervals around the group centroids, based on Bray-Curtis dissimilarities, for each sample group, calculated using standard errors. Fig. S4 shows the respective distribution of the prey families and genera, removed here to improve readability. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Bulk stable isotope values and SIBER outputs for Wilson's (WSP) and Black-bellied storm-petrel (BBSP) blood samples. Means for $\delta^{13}C$ and $\delta^{15}N$ values, area of the standard ellipse (SEAc, Fig. 1) and calculated trophic position (TP_{LM}) are given. Additionally, means from the breeding season from earlier studies are given with the respective reference.

Species	Sample size	$\delta^{13}C$ [‰] Mean ± SD	$\delta^{15}N$ [‰] Mean ± SD	SEAc	TP_{LM}	Study location	Study
WSP	24	−25.0 ± 0.5	9.6 ± 0.4	0.57	3.5 ± 0.1	South Shetlands (King George Island)	present
	17	−25.9 ± 0.5	9.2 ± 0.4	–	–	South Shetlands (King George Island)	Quillfeldt et al. (2023)
	32	−26.4 ± 0.5	9.9 ± 0.5	–	–	South Shetlands (King George Island)	Ausems et al. (2020)
	19	−20.9 ± 0.8	9.7 ± 0.5	–	–	Kerguelen Islands (Mayes Island)	Quillfeldt et al. (2023)
BBSP	16	−25.0 ± 0.4	10.6 ± 0.6	0.68	3.7 ± 0.1	South Shetlands (King George Island)	present
	19	−25.4 ± 0.4	10.1 ± 0.5	–	–	South Shetlands (King George Island)	Quillfeldt et al. (2023)
	20	−26.7 ± 0.1	11.4 ± 0.5	–	–	South Shetlands (King George Island)	Ausems et al. (2020)
	2	−22.0 ± 0.1	9.9 ± 0.3	–	–	Kerguelen Islands (Mayes Island)	Quillfeldt et al. (2023)

species or age groups of Wilson's storm-petrels (Kruskal-Wallis χ^2 = 3.823, df = 2, p = 0.148, Fig. S2), nor between regurgitates (n = 84) and faeces (n = 10; 3.5 ± 2.0 and 2.7 ± 2.3, respectively; Wilcoxon rank sum test W = 293.0, p = 0.115; Fig. S2). Both storm-petrel species fed on mainly myctophid fish, with Antarctic lanternfish *Electrona antarctica* and Brauer's lanternfish *Gymnoscopelus braueri* showing the highest frequency of occurrence, and Euphausiids, predominantly Antarctic krill *Euphausia superba* (Table 3, Figs. 4 and 5). Other fish and krill species as well as other diet items, such as tunicates like Antarctic salps *Salpa thompsoni*, amphipods like *Eurythenes*, or cephalopod molluscs

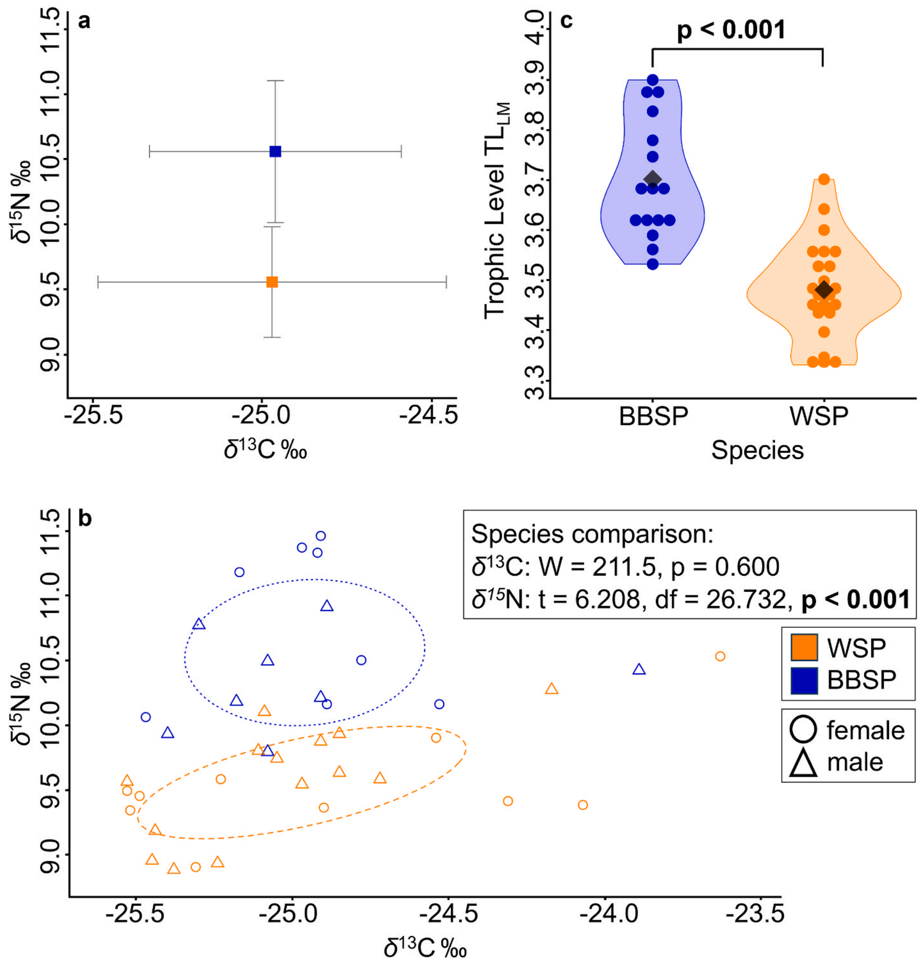

Fig. 2. Comparison on stable isotope values for $\delta^{13}C$ and $\delta^{15}N$ of adult Wilson's storm petrels *Oceanites oceanicus* (WSP, n = 24, orange) and Black-bellied storm-petrels *Fregetta tropica* (BBSP, n = 16, blue) using whole blood samples of adult individuals. (**a**) Biplot with associated species mean values and standard deviation. (**b**) Isotopic niches with ellipses displaying the standard ellipse areas, which contain approx. 40 % of the data, corrected for small sample size (SEAc), constructed using the R package SIBER (Jackson et al., 2011). Individual isotopic values are plotted with circles representing females and triangles males. **(c)** Trophic positions (TP_{LM}) calculated by a linear regression model ($TP_{LM} = 1.4986 + 0.0046 \times \delta^{13}C + 0.2195 \times \delta^{15}N$) derived from TP_{CSIA} (based on from nitrogen stable isotope values of glutamic acid and phenylalanine) and bulk stable isotope values ($\delta^{13}C$ and $\delta^{15}N$). Black-bellied storm-petrels foraged on a higher trophic position than Wilson's storm-petrels (Welch *t*-test t = 6.175, df = 27.027, $p < 0.001$). Displayed are violin plots with the individual data points (blue and orange circles) as dotplots and the mean for each species (black diamonds). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Coleoidea) were identified, but with lower frequencies of occurrence (Table 3). Bilaterian-specific primer revealed prey items mainly on family level or on higher taxonomic levels (Fig. 3), whereas primarily taxon-specific primers for Osteichthyes and Euphausiids identified respective prey items on species level (Fig. 4). Most prey MOTUs (n = 24) were found in samples of adult Wilson's storm-petrels (Table 3), however, this was the group where most samples were collected (Table 1). In adult Black-bellied storm-petrels 11 MOTUs were present. Comparing the two species, Black-bellied storm-petrel samples had a higher frequency of occurrence in the most frequent Teleostei MOTUs, e. g. all samples contained myctophid DNA (Brauer's lanternfish = 85.7 %, and Antarctic lanternfish = 71.4 %), whereas in Wilson's storm-petrel samples the frequency of occurrence of lanternfish was 72.0 % (Brauer's lanternfish = 36.8 %, and Antarctic lanternfish = 38.2 %; Table 3, Fig. 3). Highest frequency of occurrence on species level in adult Wilson's storm-petrel samples was Antarctic krill (44.1 %). In Black-bellied storm-petrels Antarctic krill had a frequency of occurrence of 28.6 %. However, the variation in prey spectrum based on presence/absence consumed by the two species seems rather low (Permutation test on family level $F_{1,67} = 2.074$, $R^2 = 0.030$, p = 0.116, and on genus level $F_{1,58} = 2.732$, $R^2 = 0.045$, p = 0.079; Fig. 1). Higher, but not significant, variation was present, when comparing adult and nestling Wilson's storm-petrels on prey family level (Permutation test $F_{1,39} = 3.733$, $R^2 = 0.087$, p = 0.055), and on genus level (Permutation test $F_{1,35} = 2.583$, $R^2 = 0.069$, p = 0.075; Fig. 1). Significant variation in prey spectra was present when comparing adult Wilson's storm-petrel samples from pre-laying and incubation with ones from chick-rearing stage (Permutation test on family level $F_{1,46} = 4.655$, $R^2 = 0.092$, p = 0.043, and on genus level $F_{1,38} = 6.642$, $R^2 = 0.149$, $p < 0.007$). DNA of Myctophidae and Euphausiidae was present in faecal and regurgitate samples of adult Wilson's storm-petrels in both breeding stages, pre-laying and incubation as well as chick-rearing (Table S5). While Myctophidae and Euphausiidae had the highest frequency of occurrence in both breeding stages, the diversity of consumed prey items was much higher during chick-rearing stage (Fig. 5). Pairwise comparison based on Pianka's measure of overlap (O_{jk}) showed that on family as well as on genus level Wilson's storm-petrel adult samples during chick-rearing and nestling samples are more similar in prey spectra compared to adult samples during chick-rearing and pre-laying/incubation stage (family: $O_{jk} = 0.79$ and $O_{jk} = 0.41$; genus: $O_{jk} = 0.87$ and $O_{jk} = 0.50$, respectively). In both cases, similarity was higher on genus level, opposite to comparing adult Wilson's storm-petrels and Black-bellied storm-petrels with $O_{jk} = 0.67$ on family and $O_{jk} = 0.58$ on genus level. Though rarefaction curves suggest a sufficient coverage (>85 %) was obtained with present sample

Table 3
Frequency of occurrence (FO) for the prey taxa consumed by Wilson's storm-petrels (WSP, *Oceanites oceanicus*), split for adults and nestlings, and adult Black-bellied storm-petrels (BBSP, *Fregetta tropica*) as identified by DNA metabarcoding of faecal and regurgitate samples. Molecular operational taxonomic units (MOTUs), which can be assumed secondary consumption and parasites, are not given here, but see Table S6 and Table S7.

Phylum	Class	Order	Family	Genus/Species	Common Name	FO% WSP adult (68)[a]	FO% WSP nestl. (19)	FO% BBSP adult (7)
Annelida	Polychaeta	Phyllodocida	Syllidae		Necklace worms	5.9	–	–
Arthropoda	Copepoda	Calanoida			Calanoids	1.5	–	14.3
	Malacostraca	Amphipoda	Eurytheneidae	*Eurythenes* sp.	–	4.4	–	–
				Eurythenes gryllus		2.9	–	–
		Euphausiacea	Euphausiidae[b]		Krill	44.1	31.6	28.6
				Euphausia crystallorophias	Ice krill	1.5	5.3	–
				Euphausia frigida	Pygmy krill	–	5.3	–
				Euphausia superba	Antarctic krill	44.1	21.1	28.6
				Thysanoessa macrura	–	8.8	5.3	–
Chordata	Teleostei				Bony fish	77.9	100.0	100.0
		Aulopiformes			Aulopiforms	14.5	21.1	14.3
			Paralepididae	*Notolepis coatsorum*	Antarctic Jonasfish	7.4	21.1	–
		Myctophiformes	Myctophidae		Lanternfish	72.0	78.9	100.0
				Electrona antarctica	Antarctic lanternfish	38.2	36.8	71.4
				Gymnoscopelus sp.	–	39.7	47.4	85.7
				Gymnoscopelus braueri	Brauer's lanternfish	36.8	42.1	85.7
				Gymnoscopelus nicholsi	Nichol's lanternfish	4.4	10.5	–
				Protomyctophum bolini	Bolin's lanternfish	1.5	10.5	–
		Perciformes	Channichthyidae	*Chionodraco* sp.	Chionodraco icefishes	2.9	5.3	14.3
				Neopagetopsis ionah	Jonah's icefish	2.9	10.5	–
			Harpagiferidae	*Harpagifer antarcticus*	Antarctic spiny plunderfish	1.5	–	–
			Nototheniidae	*Pleuragramma antarctica*	Antarctic silverfish	2.9	–	–
Chordata *Tunicata*					Tunicates	2.9	5.3	28.6
	Thaliacea	Salpida	Salpidae		Salps	1.5	5.3	28.6
				Salpa thompsoni	Antarctic salp	1.5	5.3	–
Mollusca	Cephalopoda *Coleoidea*				Octopuses, squids, cuttlefish	4.4	5.3	–

[a] Sample size given here refers to samples, which contained at least one valid mOTU. This sample size was used to calculate the frequency of occurrence (FO).
[b] FO% given as the summary from the respective MOTUs at species level.

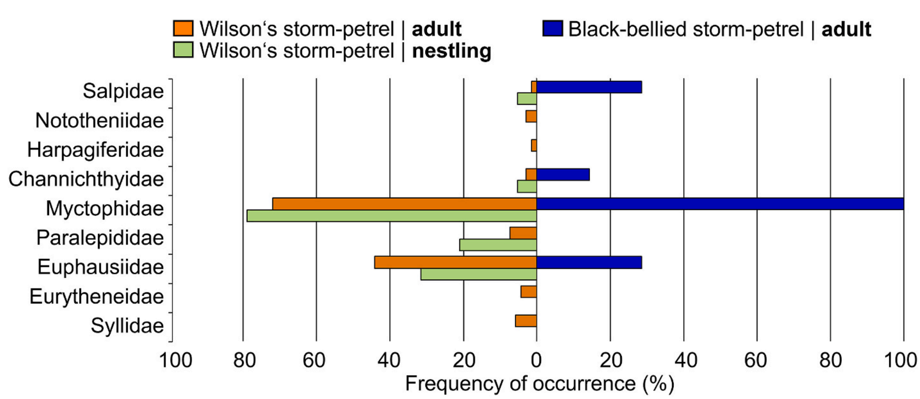

Fig. 3. Frequency of occurrence of diet items that could be determined at least on family level (Table 3), split for the two species and for Wilson's storm-petrels *Oceanites oceanicus* also by age. Shown are the combined results of all four applied primer pairs. Frequency of occurrence was calculated based on the number of samples that contained at least one valid MOTU (BBSP adult n = 7, WSP nestling n = 19, WSP adult n = 68).

sizes (Fig. S3), we refrain from a more detailed analysis of species comparison, as admittedly our sample size of Black-bellied storm-petrels is much smaller compared to the one of Wilson's storm-petrels (Table 1).

3.3. Non-prey DNA in faecal and regurgitate samples

Bilaterian-specific primers amplified DNA of potential parasite species, which may present gastrointestinal parasites and ectoparasites of both storm-petrel species (Table S6). Ectoparasites, feather mites *Ingrassia* sp. and feather lice Philopteridae were present each only in one regurgitate sample of an adult Wilson's storm-petrel (Tables S5 and S6). We detected DNA of Nematoda, namely Rhabditida and Dorylaimina, in adult Wilson's and Black-bellied storm-petrel samples and tapeworms (Eucestoda) in one adult Wilson's storm-petrel (Table S6). Moreover, six MOTUs, most likely presenting taxa from secondary consumption, i.e. prey of the birds' prey, were identified (Table S7).

4. Discussion

Our study allowed us to gain a better understanding of the trophic ecology in two sympatrically breeding storm-petrel species with a focus on the dietary niche partitioning by molecular analysis of prey items and

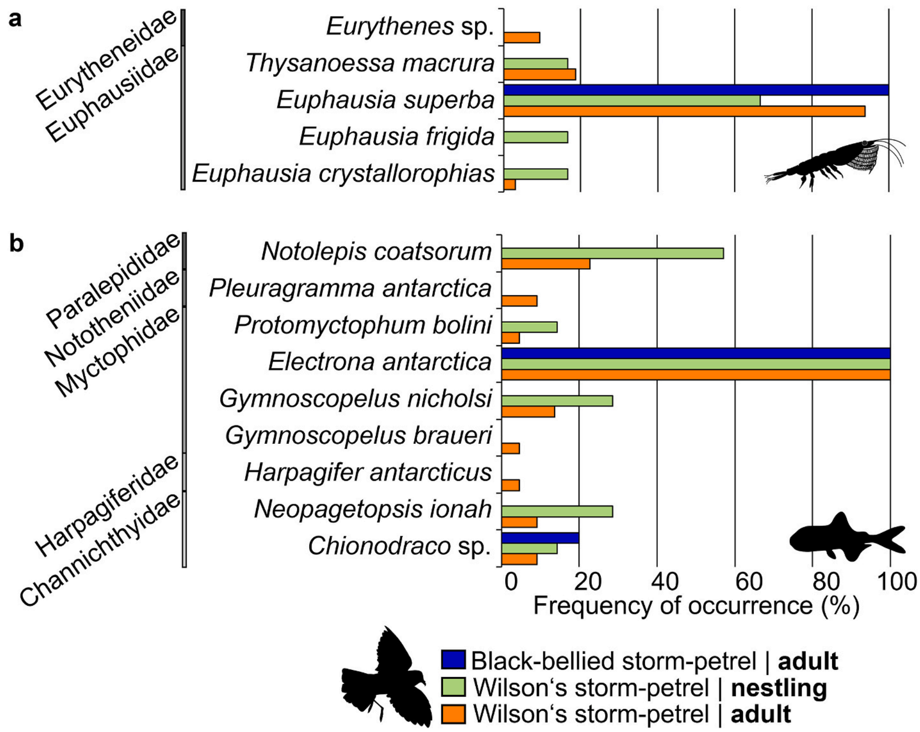

Fig. 4. Frequency of occurrence of diet items, according to the MOTUs, and their respective family of taxon-specific PCR results, split for the two species and for Wilson's storm-petrels (WSP) also by age. **(a)** Combined result of the primers for mitochondrial 16S rDNA of krill (Euphausiids) and of crustaceans (Crustacea) **(b)** result of the primer pair amplifying mitochondrial 12S rDNA gene of bony fish (Osteichthyes). Frequency of occurrence was calculated based on the number of samples that contained at least one valid MOTU for the respective taxon-specific primer **(a)**: Euphausiidae + Crustacea n = 40 samples (BBSP adult n = 2, WSP nestling n = 6, WSP adult n = 32); **(b)**: Osteichthyes n = 34 samples (BBSP adult n = 5, WSP nestling n = 7, WSP adult n = 22)).

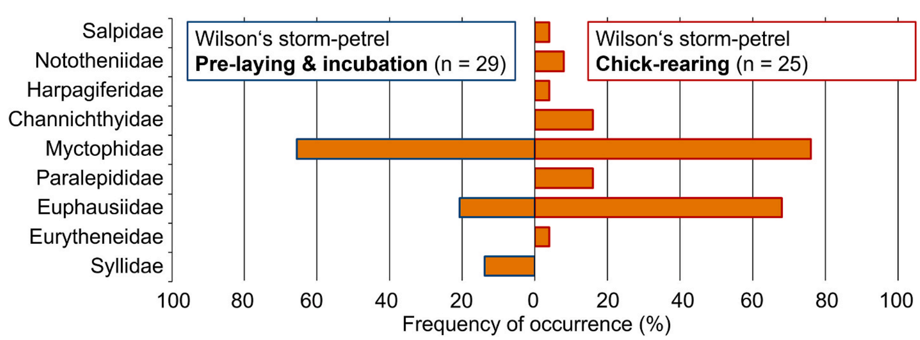

Fig. 5. Frequency of occurrence of diet items, according to the MOTUs, and their respective family in adult Wilson's storm-petrel *Oceanites oceanicus* faecal and regurgitate samples, split by breeding stage: pre-laying and incubation (left, n = 29) vs. chick-rearing (right, n = 25). Shown are the combined results of all four applied primer pairs.

stable isotope values.

4.1. Trophic ecology based on stable isotope values

Our mean stable isotope values in both species were similar with other sampled individuals in the South Shetland Islands, while comparing the values to individuals from other breeding colonies differences become more pronounced (see Table 2). However, a general pattern, in agreement with our study, of higher δ^{15}N values for Black-bellied storm-petrels, while there is no marked difference in δ^{13}C values between the two species, was present in individuals from the South Shetlands (Ausems et al., 2020; Quillfeldt et al., 2023). Sample sizes from subantarctic Kerguelen Islands were too small to verify this pattern there (Table 2). Stable isotope analyses revealed that the species share a similar but not the same isotopic niche, particularly when considering nitrogen isotopic values, with Black-bellied storm-petrels having a slightly larger isotopic niche than Wilson's storm-petrels (Table 2). In the Southern Ocean, δ^{13}C values of seabirds correspond to the latitude of their foraging habitats (Cherel and Hobson, 2007; Lorraine et al., 2009; Quillfeldt et al., 2010; Jaeger et al., 2010), and δ^{15}N values increase with trophic position (Cherel and Hobson, 2007; Cherel et al., 2010; Moreno et al., 2015; Cherel and Carrouée, 2022). Thus, our results from bulk stable isotope analysis indicate that during the breeding season, the individuals of the two species forage around the same latitude i.e. might share foraging areas around the breeding colony, on a large geographical scale according to isoscapes in the Antarctic zone south of 50°S (Jaeger et al., 2010). Differences in the isotopic niche, particularly in nitrogen isotopic values, between the species, suggest that they potentially also differ in their trophic niche. Generally, metabolically active tissues, like blood, provide information about diet in the short-term, i.e. rather short isotopic turnover time, depending on the species metabolism (Silva et al., 2024). Half-lives of carbon and nitrogen in whole blood in Black Oystercatchers *Haematopus bachmani* were 8.6 and 9.3 days, respectively (Carney et al., 2023), and in a summary for different terrestrial and marine bird species range from 4.5 to 29.8 days (Carleton and Rio, 2005). Thus, our blood samples provide information on a time window of around one to four weeks prior sampling, i.e. reflects the breeding season, which was also the time for collecting the faecal and regurgitate samples. While our results, based on blood samples, show that Black-bellied storm-petrels fed at a higher trophic position during the breeding season, the same was shown during moult in the non-breeding season, based on the analysis of feather samples (Quillfeldt et al. 2017, 2023). Calculating the trophic position based on a linear regression derived from CSIA-AA showed that Black-bellied storm-petrels during the breeding season fed at a trophic position of 3.7 ± 0.1, which was higher compared to the one of Wilson's storm-petrels (3.5 ± 0.1). This is in line with the result of Quillfeldt et al. (2023), comparing the trophic position of the two species during incubation period, with trophic positions of 3.8 ± 0.1 for Black-bellied storm-petrels and 3.4 ± 0.1 for Wilson's storm-petrels. Bulk stable isotope results from the two species, sampled at Arctowski station, also indicate, characterised by higher $\delta^{15}N$ values, that Black-bellied storm-petrels forage at a higher trophic position than Wilson's storm-petrels (Ausems et al., 2020). However, linear models based on CSIA-AA cope better with baseline variations of ^{15}N among ecosystems and can determine trophic positions more precisely than bulk $\delta^{15}N$ values independently of baseline effect (McClelland and Montoya, 2002; Ishikawa et al., 2014; Quillfeldt et al., 2017; Quillfeldt and Masello, 2020; Thébault et al., 2021). Thus, we decided for this approach to verify the difference in trophic position for the present samples. Roughly summarised, trophic positions (TP) are defined that organisms between TP 1 to 2 are primary producers, TP 2 to 3 herbivores, TP 3 to 4 omnivores, and TP 4 to 5 piscivores/carnivores (Pauly and Christensen, 1995; Pauly and Watson, 2005). The trophic positions of the storm-petrels (TP_{LM} WSP: 3.3 to 3.7, BBSP: 3.5 to 3.9) are mainly lower, but partly overlap with the trophic positions of myctophid fish, found as prey within our diet analysis, in the Southern Ocean, e.g. *Electrona antarctica* 3.8 ± 0.1, *Gymnoscopelus braueri* 4.0 ± 0.1, *Protomyctophum bolini* 3.9 ± 0.1 (Cherel et al., 2010). Taking into account the lower trophic positions of macrozooplanktonic crustaceans, mainly Euphausiids, ranging between 2.5 and 3.3 (Cherel et al., 2010; Guerreiro et al., 2015), this implies that the storm-petrels, falling between trophic positions of full zooplanktivores (TP ≥ 3) and full piscivores (TP ≥ 4; Miller et al., 2010), prey mainly on macrozooplanktonic crustaceans and a certain part on teleost fish. Whereby the proportion of fish is higher in Black-bellied storm-petrel diet. Linking this result regarding the interspecific difference in trophic position with the outcomes of the molecular diet analysis shows that it matches well with the observed pattern in diet composition.

4.2. Diet composition: prey of Antarctic storm-petrels

The molecular method used in the present study allowed the identification of several prey taxa and particularly for teleost fish and krill with the taxon-specific primers to species level. This overcomes the disadvantage that regurgitated prey material of storm-petrels is highly digested, which often hampers prey species identification (Croxall et al., 1988; Croxall and North, 1988; Ridoux, 1994). To our knowledge, some prey items identified in the present study have not been identified through traditional methods, e.g. Brauer's lanternfish *Gymnoscopelus braueri* and *Chionodraco* sp. for both species (Beck & Brown 197; Obst, 1985; Wasilewski, 1986; Harper, 1987; Croxall et al., 1988; Croxall and North, 1988; Ridoux and Offredo, 1988; Ainley et al., 1984, 1992; Ridoux, 1994; Hahn, 1998a; Quillfeldt, 2002; Jiménez, 2012). However, besides being able to present a list of prey items (Table 3), which particularly for adult Wilson's storm-petrels due to sufficient sample size is likely to cover their prey spectrum largely, in the discussion we focus on more general patterns in their prey composition and especially link them to the results of the stable isotope analysis.

4.2.1. Niche segregation in prey composition between black-bellied and Wilson's storm-petrels

The diet of Wilson's storm-petrels had been analysed in the past by various authors based on morphological prey identification of regurgitates and deceased individuals (Beck and Brown, 1972 and references therein; Obst, 1985; Wasilewski, 1986; Harper, 1987; Croxall et al., 1988; Croxall and North, 1988; Ridoux and Offredo, 1988; Ainley et al., 1984, 1992; Ridoux, 1994; Quillfeldt, 2002; Jiménez, 2012). The studies show that Wilson's storm-petrels mainly prey on crustaceans with krill species often dominating their diet. However, the studies show a range of food items and considerable variations in the diet composition, possibly connected to a difference in the prey availability among the Sub-Antarctic and Antarctic sample sites. Fewer studies thematise the diet of Black-bellied storm-petrels (Harper, 1987; Ainley et al., 1992; Ridoux, 1994; Hahn, 1998a; Jiménez, 2012). A general conclusion, based on traditional morphological prey identification and further more indirect methods, is that the diet of Black-bellied storm-petrels consists of a higher proportion of fish compared to Wilson's storm-petrels, which is dominated by planktonic crustaceans (Hahn, 1998a; Quillfeldt et al., 2023), which indicates despite a present overlap in prey spectrum a potential niche segregation regarding prey composition between the two species. Higher $\delta^{15}N$ values in Black-bellied storm-petrels compared to Wilson's storm-petrels suggest a higher fish component in the diet (Ausems et al., 2020). This is in line with stable isotope results of penguins with fish-eaters having higher $\delta^{15}N$ values than crustacean consumers (Cherel and Hobson, 2007). High Hg concentrations in Black-bellied storm-petrels also indicate a fish-dominated diet (Quillfeldt et al., 2023). Results from our stable isotope analysis, namely higher $\delta^{15}N$ values and a higher trophic position for Black-bellied storm-petrels, line up with the previous findings. Considering the results of the molecular diet analysis, they as well confirm this interspecific difference in prey composition. Even though permutation tests did not point out a significant difference in the prey spectrum and a rather substantial overlap (O_{jk} 0.58 to 0.67) existed for the two species, this result should be verified with more Black-bellied samples included, and a general more equal sample size, as due to the highly unequal sample size in our dataset (limited number of Black-bellied storm-petrel samples) the statistical power to detect compositional differences could have been reduced. Nevertheless, the higher frequency of occurrence in the two most frequent fish species, the myctophid fish *Electrona antarctica* and *Gymnoscopelus braueri*, and a lower frequency of occurrence in Euphausiids, particularly for *Euphausia superba*, in Black-bellied storm--petrels compared to Wilson's storm-petrels, implicate a more fish-rich or crustacean-rich diet, respectively. However, here we additionally have to point out that we focus presence/absence data of prey items and not on proportions of single prey items within a sample, i.e. relative abundance, which would provide additional important information about the relevance of individual prey types and their ratios to each other and thus about interspecific difference in proportional diet composition. Due to differences in the PCR specificity of different primers and targets, it is often not possible to reliably convert sequence count data, most typically relative read abundance (RRA), into dietary profiles with diet component proportions (see e.g. Alberdi et al., 2019; Deagle et al., 2019; Littleford-Colquhoun et al., 2022; Stedt et al., 2025). Therefore, we have not calculated any proportions of prey items from our metabarcoding data. Especially during the breeding season when seabirds are central-place foragers, segregation mechanisms are most important to reduce competition (Jessopp et al., 2020; Cherel & Carrou 2022; Petalas et al., 2024). Within dietary partitioning, species can consume same prey species, but vary on their size (Ross, 1977; Robertson et al., 2014; Seyer et al., 2020). However, with the molecular diet analysis, we were not able to compare prey sizes. In future studies dietary proportions and information on prey size would help considerably to better understand the niche segregation regarding prey composition in the two sympatrically breeding storm-petrel species. Following the assumption that interspecific diet niche partitioning causes interspecific competition to lesser extent and facilitates niche overlap when shared prey is superabundant and easily accessible, such as Antarctic krill *Euhausia superba* in the foraging area of the two species (Croxall et al., 1999; Forero et al., 2004; Weimerskirch et al., 2012; Ausems et al., 2020; Friedlaender et al., 2021), in the future, competition and thus niche partitioning is likely to change between the two species with decreasing krill availability due to global climate change (Atkinson et al., 2004; McBride et al., 2021; Kawaguchi et al., 2024). With ongoing climate change, gelatinous Antarctic salps *Salpa thompsoni* extend their distribution range into historically krill-dominated areas and due to asexual reproduction can increase rapidly (Perissinotto and Pakhomov, 1998; Johnston et al., 2022; Pietzsch et al., 2023). Antarctic salps seem to inhibit Antarctic krill populations, which could trigger cascading effects on krill-predating species (Bitiutskii et al., 2022; Pietzsch et al., 2023). Historically, salps have been considered irrelevant as prey with a high water content and low caloric value per unit volume. However, more recent evidence suggests that salps are more nutritious than previously thought (Henschke et al., 2016; Johnston et al., 2022). In the Southern Ocean, *Salpa thompsoni* and *Ihlea racovitzai* are now recognized as nutritionally important prey items for mammals and birds, having high protein and carbon contents (Dubischar et al., 2012; Henksche et al., 2016). Even if the energetic content of salps is lower than that of crustaceans, the salps move slower and thus predators may need to invest less energy for capturing, thus possibly they constitute an efficient food source (Wang and Jeffs, 2014; Henksche et al., 2016). Whether the diet composition of Antarctic storm-petrels may change to a higher proportion of salps due to likely increased availability of this prey item and simultaneous reduction in krill availability with ongoing climate change, should be monitored in future studies. The only previous record of *Salpa thompsoni* as prey of Wilson's storm-petrels (frequency of occurrence: 3 %) and Black-bellied storm-petrels (17 %) was found in Ainley et al. (1992). We also found salp DNA with a lower frequency of occurrence in Wilson's (1.5 %) than in Black-bellied storm-petrels (28.6 %). In Black-bellied storm-petrel samples Salpidae hence had the same frequency of occurrence as Euphausiidae.

4.2.2. Selective chick provisioning in Wilson's storm-petrels

As the number of active Black-bellied storm-petrel nests has declined sharply in the study colony compared to the past (cf. Hahn, 1998b), we could not obtain any samples of Black-bellied storm-petrel nestlings. The number of Wilson's storm-petrels on King George Island declined by 90 % as well (Ausems et al., 2023). Nevertheless, for Wilson's storm-petrels we were able to compare the diet of adult and nestling individuals. One general common problem is that studies using regurgitates may not fully represent the species diet, as regurgitated food may be intended as food for offspring only (Furness and Baillie, 1981; Croxall et al., 1988; Ausems et al., 2020). Regularly trophic positions between adults and nestlings differ in seabirds, i.e. differences in the prey spectrum and composition exist for self-provisioning and chick provisioning, which can result in selective chick provisioning (Van Franeker et al., 2001; Rosciano et al., 2019; Quillfeldt and Masello, 2020; Quiring et al., 2021; Monier, 2024). In Wilson's storm-petrels, breeding individuals showed a seasonal pattern in diet composition with krill decreasing and alternative prey increasing from the incubation to the chick-rearing period (Quillfeldt, 2002; Quillfeldt et al., 2005). Our molecular diet analysis results also show a higher diversity of prey MOTUs, particularly more fish families, in samples collected in chick-rearing period compared to pre-laying and incubation period. The permutation test validated this significant difference in prey spectrum at prey genus and family level. Confirming this change in the diet from previous research, the data indicates that Wilson's storm-petrels selectively choose alternative prey to krill in order to meet the nutrient demands of their offspring. Strengthening this, Ausems et al. (2020) found that in the two storm-petrel species chick diet niche widths were narrower than adult niche widths, possibly indicating that parents were more selective about prey items they feed their chicks than prey they forage for themselves. For instance, fish has higher calorie and protein content than crustaceans (Ruck et al., 2014; Boenish et al., 2022) and might be thus positive for nestling development. Considering the frequency of occurrence data, this also points in favour of selectively feeding chicks with fish prey, since the nestling samples have a higher FO for teleost fish and a lower FO for Euphausiids than the samples from adult individuals, however, contrary permutation tests could not demonstrate a significant difference in prey spectrum found in adult and nestling samples. Nitrogen stable isotope values considerably overlapping in Wilson's storm-petrel adults and nestlings, also rather argue against a selective chick provisioning (Ausems et al., 2020). As starvation is the main cause for nestling mortality and glucocorticoid excretion data suggest that adults respond to unfavourable conditions by maintaining their own body condition and reducing chick provisioning (Quillfeldt, 2001; Quillfeldt and Möstl, 2003; Büßer et al., 2004), future research could focus on intraspecific dietary segregation, including selective chick provisioning, and year differences due to differences in prey availability in both species.

4.3. Parasite infestation and its connection to prey composition

Differences and changes in diet can influence the richness and load of parasites (e.g. Leung and Koprivnikar, 2019; Lorenti et al., 2025). Habitats with extreme conditions, such as the polar regions, were long considered as 'retreats' for organisms to evade parasites. However, many parasites have successfully adapted to these extreme environments and Antarctic birds are not beyond the effects of parasites (Barbosa and Palacios, 2009; Selbach and Paterson, 2025). Although not the primary focus of this study, the molecular analysis of the faeces and regurgitates revealed data on parasite infestation in the two storm-petrel species, which is likely linked to their prey composition Generally, feather lice and mites as well as cestodes and nematodes are known to infect Antarctic bird species (Barbosa and Palacios, 2009). In accordance with our findings on ectoparasites, feather lice, mainly *Philoceanus robertsi*, and feather mites are described to parasitize Wilson's and Black-bellied storm-petrels (Gressitt, 1967; Horne and Rounsevell, 1982; Fowler and Price, 1987; Quillfeldt et al., 2004; Valim et al., 2006; Han et al., 2021). While handling our sampled birds no obvious signs of damage in the plumage, as can be caused by lice and mites were noticed. Also in line with our results, nematodes of the order Rhabditida, namely *Stegophorus macronectes* and *Seuratia* sp., were proven in carcasses of Wilson's and Black-bellied storm-petrels (Fusaro et al., 2023). Some nematode species, belonging to the suborder Dorylaimina, are found in vertebrates (Anderson, 2000). However, most Dorylaimina species and many Rhabditida species are free-living nematodes in freshwater and soil, including areas on King George Island (Anderson, 2000; Elshishka et al., 2023; Salas et al., 2024). We admittedly cannot exclude to have amplified DNA of free-living nematodes by our analysis method, since MOTU determination to species level in their cases was not possible. While Fusaro et al. (2023) found tapeworms, more precisely *Tetrabothrius* sp., in one individual Black-bellied storm-petrel, we found Eucestoda DNA in one faecal sample of a Wilson's storm-petrel adult. Likewise, Hoberg (1983) reports nematodes and cestodes in adult Wilson's storm-petrels. While ectoparasites intake most likely occurs through preening, infestation by gastrointestinal parasites is largely influenced by the host's feeding habits. Consequently, prey composition and dietary shifts can play an important role in exposure to parasites (Barbosa and Palacios, 2009). Patterns of gastrointestinal parasite infestation in storm-petrels are therefore likely linked to their rather stenophagic diet and prey composition, as many of the parasites have crustaceans and teleost fish as intermediate hosts (Fusaro et al., 2023). Further studies, like our present one, shading light on the prey composition of the species, may help to further unravel host-parasite interactions and transmission routes. Climate change and associated effects may change the dynamics of current host-parasite relationships and further may result in the transmission of novel parasites and diseases to the Antarctic fauna. Thus, further studies of parasites and their interactions with hosts, such as transmission via specific prey species, from the Antarctic fauna are warranted and needed to understand trophic ecology of Antarctic seabirds and their prey (Barbosa and Palacios, 2009; González-Acuña et al., 2021; Fusaro et al., 2023).

5. Conclusion

Understanding trophic relationships and interspecific niche partitioning in dynamic marine ecosystems requires the analysis of diet of the involved species. In the present study, we were able to demonstrate that while sharing general prey spectra Black-bellied storm-petrels fed on a higher trophic position than Wilson's storm-petrels, in line with a higher proportion of fish in their diet composition. However, besides dietary partitioning, investigated here, interspecific segregation can (additionally) take place along multiple dimensions within and across niche spaces, such as on spatial distribution, e.g. spatial segregation in foraging areas (Jessopp et al., 2020; Petalas et al., 2024; Bonnet-Lebrun et al., 2025). While our stable isotope analysis indicates that both storm-petrels share foraging areas around the breeding colony on large geographical scale, there could be a foraging spatial segregation on smaller scale. For instance, there is little overlap in the species abundance hotspots at the Antarctic Peninsula and studies indicate that Wilson's storm-petrels remain in coastal regions, whereas Black-bellied storm-petrels are also abundant further offshore (Quillfeldt et al., 2005; Santora and Veit, 2013; Warwick-Evans et al., 2021). GPS tracking data could be used to investigate potential spatial segregation between the two storm-petrel species during foraging (cf. Dehnhard et al., 2019; Linhares et al., 2024; Petalas et al., 2024; Bonnet-Lebrun et al., 2025).

CRediT authorship contribution statement

Yvonne R. Schumm: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Wiebke C. Schäfer:** Writing – review & editing, Software, Methodology. **Marcela M. Libertelli:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization. **Mara Centurión:** Writing – review & editing, Resources, Investigation. **Laura Reyes Jiménez:** Writing – review & editing, Resources, Investigation. **Paco Bustamante:** Writing – review & editing, Resources, Methodology, Investigation. **Petra Quillfeldt:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Ethical standards

The study involved wild individuals and was carried out under permits from the Argentine Antarctic Institute IAA (permit numbers: #2022-FEAMB-CT-GA-79 and #2023-FEAMB-CT-GA-70).

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107624.

Data availability

Sequences from the diet analysis are deposited at the National Center for Biotechnology Information (NCBI) under the BioProject ID: PRJNA1301642 (https://www.ncbi.nlm.nih.gov/sra/PRJNA1301642) with BioSample accession numbers SAMN50450774 to SAMN50450957. Stable isotope data is deposited at IsoBank (https://isobank.tacc.utexas.edu/) under dataset record ID 913. Used R packages and respective version information are given in Supplementary material A2.

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