Sharing menus and kids' specials: Inter- and intraspecific differences in stable isotope niches between sympatrically breeding storm-petrels

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HIGHLIGHTS
• 2 species of sympatrically breeding storm-petrels show considerable niche overlap.
• Black-bellied storm-petrel chick diet represents higher trophic level than adults.
• Wilson’s storm-petrel chick and adult diet overlap considerably.
• Chick growth is mainly correlated with hatching date and δ15N of the chick diet.
• Highly productive ecosystems may facilitate considerable foraging niche overlap.

GRAPHICAL ABSTRACT

ABSTRACT
Species sharing resources are predicted to compete, but co-occurring species can avoid competition through niche partitioning. Here, we investigated the inter- and intra-specific differences using stable isotope analyses in the black-bellied storm-petrel (Fregetta tropica) and the Wilson’s storm-petrel (Oceanites oceanicus), breeding sympatrically in maritime Antarctica. We analysed stable carbon, nitrogen and oxygen isotopes in samples representing different life stages; chick down (pre-laying females), chick feather (chick), and adult blood (chick-rearing adults). Pre-laying females had wider stable isotope niches than chicks or chick-rearing adults, due to pre-laying females being free roaming while chick-rearing adults were central-place-foragers. Chicks were fed at a higher trophic level than the adults (higher δ15N), likely to compensate for the high nutritional demands of the growing chicks. Wilson’s storm-petrels showed substantial overlap in stable isotope niches between all life stages, while the black-bellied storm-petrel chicks showed very little overlap. Wilson’s storm-petrel niches significantly overlapped with those of pre-laying and chick-rearing black-bellied storm-petrels, suggesting negligible niche partitioning. Chick growth rate was negatively correlated with chick δ15N values, suggesting nutritional stress resulting in the use endogenous instead of dietary amino acids in protein synthesis. The higher trophic level of the relatively larger black-bellied storm-petrel chicks may be due to their longer stay in the nest, and relatively larger body mass gain, despite chick growth rates being similar to the smaller Wilson’s storm-petrel chicks. Despite breeding sympatrically, the studied storm-petrel species showed considerable overlap in isotopic niches, which may be explained by sharing the same main prey species, reducing the detectability of foraging niche partitioning through stable isotope analyses. We found dietary shifts in black-bellied storm-petrels that are absent in Wilson’s, showing different chick provisioning strategies, and shows that the high productivity of the Antarctic marine ecosystem may facilitate foraging niche overlap of sympatrically living species.

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1. Introduction

According to the niche theory, two or more species cannot permanently and simultaneously occupy exactly the same foraging niche if resources are limited, as interspecific competition would lead to one of them outcompeting the other (Hutchinson, 1957). Therefore, to avoid competition, sympatric species are expected to show foraging niche partitioning through spatial or temporal separation, or through foraging specialisation (Robertson et al., 2014). In sympatric seabird species, spatial foraging niche segregation can manifest, for example, in species foraging at different distances from a shared breeding ground (Barger et al., 2016; Robertson et al., 2014), at different depths in the water column (Masello et al., 2010; Wilson, 2010), or in different front areas (Force et al., 2015). Temporal segregation can occur through alternating foraging areas between species over the season (Clewlow et al., 2019) or day (Wilson, 2010), or staggered breeding (Croallax and Prince, 1980; Hatch and Hatch, 1990). Species with overlapping diets may avoid competition through prey selection, e.g., prey size preferences (Marinello et al., 2019) or generalist vs. specialist foraging (Polito et al., 2015). These preferences can manifest, for example, in differences in morphology, such as in bill shape (Pol et al., 2009) or hunting behaviours (Warham, 1996).

Consequently, niche partitioning results in differences in the size and shape of species’ foraging niches, also described as their niche width (Roughgarden, 1972). Within species, niche widths can vary between colonies (Corman et al., 2016), age cohorts (Pelletier et al., 2014) and the sexes (Miller et al., 2018), and many species show differences in foraging niches between seasons (Cherel et al., 2007; Jaeger et al., 2010). When the availability of a preferred food decreases species may increase the width of their foraging niches (Carvalho and Davoren, 2019), switching to other food sources. Additionally, niche widths may change due to competition; niche widths can increase as the preferred prey becomes unavailable and individuals switch to a wider range of prey (Namgail et al., 2009; Svanbäck and Bolnick, 2007) or decrease as prey availability decreases for the focal species if the preferred prey becomes monopolised by more specialised species with better competitive abilities (Namgail et al., 2009).

The diet of a species determines its place in the food web, or trophic level (Lindeman, 1942). Trophic levels in relatively uncomplicated food webs, such as polar food networks, generally increases from invertebrates to fish, and from short-lived to long-lived prey species, although there is an overlap on species level (Hobson and Welch, 1992; Pauly et al., 1998). Within and between years seabird trophic levels can differ depending on seasonal prey availability, weather conditions or energetic demands (Davies et al., 2009; Moody et al., 2012). Additionally, parents and offspring can differ in trophic level (Davies et al., 2009), as can the sexes (Phillips et al., 2004) due to differing nutritional requirements.

Stable isotope analyses are currently widely used to study animal foraging niches (Newsome et al., 2007; Quillfeldt et al., 2005). They are particularly useful for pelagic seabirds that are important ecosystem components (Furness and Camphuysen, 1997) but challenging to study due to their often inaccessible foraging and breeding locations. Stable carbon and nitrogen isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) are most commonly used (Quillfeldt et al., 2005), because of their link with the food web. $\delta^{15}N$ increases stepwise with trophic level (Minagawa and Wada, 1984). $\delta^{13}C$ is linked to foraging areas: in the Southern Ocean $\delta^{13}C$ of particulate organic matter predictably decreases with latitude (Quillfeldt et al., 2005), related to different water masses (Cherel and Hobson, 2007), and can thus be used to identify foraging areas of seabirds in the Southern hemisphere. In this study, we also analysed $\delta^{18}O$ which like $\delta^{13}C$ differs between water masses but is mainly correlated with temperature (LeGrande and Schmidt, 2006) and freshwater input (Bigg and Rohling, 2000). Thus, including $\delta^{18}O$ allows identifying foraging areas more precisely.

Using stable isotope analyses of the three elements ($\delta^{15}N$, $\delta^{13}C$, $\delta^{18}O$), we aimed to study the extent of isotopic niche partitioning during the breeding season between two species of small, pelagic seabirds breeding sympatrically in maritime Antarctica (Jabłoński, 1986; Sierakowski, 1991; Sierakowski et al., 2017), the black-bellied storm-petrel (Fregetta tropica; hereafter BBSP) and the Wilson’s storm-petrel (Oceanites oceanicus; hereafter WSP). Considering niche theory predictions, the fact that the species share the same guild and overlap in breeding areas, but are of different body size, we expected them to show differences in foraging niches. Previous research (Beck and Brown, 1971; Hahn, 1998a; Quillfeldt, 2002; Ridoux, 1994), although limited, indicated a higher proportion of fish in BBSP than in WSP diets. Following the results of these studies, we expected BBSP to forage at a higher trophic level than WSP, but to show considerable overlap. Further, given documented differences in diet composition, with the diet of the BBSP being more diverse (Beck and Brown, 1971; Hahn, 1998a; Ridoux, 1994), we expected its niche widths to be larger than those of WSP.

Additionally, we investigated the within-species differences in isotopic niches between samples representing different life stages (i.e. chick down representing pre-laying females, adult blood representing chick-rearing adults and chick feathers representing growing chicks), and the correlations between isotopic signatures and chick growth rates (i.e. body mass, tarsus length and wing length). During the pre-laying period, the storm-petrels are free to roam further away from the colony to forage than they are during the chick rearing period, when they have to return to the nest for chick provisioning. Therefore, we expected isotopic niches to be wider during the pre-laying period than during the chick-rearing period, as has also been observed in Arctic Terns (Sterna paradisaea) (Pratte et al., 2018). As $\delta^{15}N$ is often linked to trophic level (Minagawa and Wada, 1984) and thus diet and possibly caloric values, we expected to find the strongest correlation between $\delta^{15}N$ in chick feathers and chick growth rates, compared to $\delta^{13}C$ or $\delta^{18}O$. Furthermore, we expected chicks to be fed at a higher trophic level than adults to meet their high nutritional demands during growth, as has been observed in other seabirds foraging on krill and fish [(Forero et al., 2002; Hodum and Hobson, 2000; Rosciano et al., 2019), but see Booth and McQuaid, 2013].

Since we performed the study for two breeding seasons, due to potential inter-annual differences in storm-petrel prey availability driven by environmental conditions (Siegel, 2012), the inter-annual differences in diet composition should be reflected by differences in isotopic signatures of the sampled tissues (Moody et al., 2012). To control for this inter-annual variability in environmental conditions affecting foraging storm-petrels we compared sea surface temperature and chlorophyll-α (Santora et al., 2017) in potential foraging areas between the studied breeding seasons.

The results of our study are important to understand the functioning of the Antarctic food web that is currently experiencing rapidly occurring changes due to global climate change (Henley et al., 2019) and intensive harvesting of marine living resources (Krüger, 1990). WSP is considered one of the most abundant seabirds worldwide (Warham, 1990), and plays a significant role in the food web of the Southern Ocean and nutrients cycling. BBSP is one of the least studied storm petrels in the sub Antarctic and Antarctic region (e.g., 10 and 15 results total in Web of Science for “black-bellied storm-petrel” and “Fregetta tropica”, respectively). It has only been a subject of a few studies of breeding and foraging ecology, with limited sample sizes ($n = 2–6$) for chicks (Beck and Brown, 1971; Hahn, 1998b), hence basic studies considering the birds foraging ecology are still needed (Büßer et al., 2008). These features underline the importance of fundamental knowledge of foraging ecology of these two species and their use as model organisms for questions regarding the adaptation to environmental variability in the maritime Antarctic (Büßer et al., 2008).
2. Materials and methods

2.1. Study area

In the Austral summer of 2017 and 2018 we studied BBSP and WSP breeding around the Henryk Arctowski Polish Antarctic Station on King George Island, South Shetland Islands, Antarctica (62°09′ S, 58°27′ W) (Fig. A1). The study area is one of the main breeding aggregations of both storm-petrel species in the Admiralty Bay area (Jabłonksi, 1986).

The majority of the nests of both studied species were located in separate colonies. Most WSP nests were located in a colony at Rakusa Point [see Sierakowski et al. (2017) for maps]. However, the BBSP colony at Point Thomas was mixed with some WSP nests. Compared to historical research (WSP n = 140) (Jabłonksi, 1986), we found a similar number of accessible nest burrows but less active nests (WSP n = 44), suggesting relatively low competition over burrows.

### Table 1

Means and standard deviations of the isotopic values for both studied storm-petrel species:

**BBSP** – black-bellied storm-petrel; **WSP** – Wilson’s storm-petrel; n – sample size; chick-rearing – adult blood; Pre-laying – chick down; chick – chick feather (under-tail covert); blood was only collected in 2018; δ18O was only analysed for chick feathers, and not determined separately per year for WSP due to low sample sizes in 2017.

| Species | Life stage | n | Mean ± SD | Mean ± SD |
|---------|------------|---|-----------|-----------|
| **BBSP** | Chick-rearing | 20 | −26.65 ± 0.12 | 11.42 ± 0.49 |
|         | Pre-laying | 10 | −26.54 ± 0.39 | 10.80 ± 0.47 |
|         | Chick | 8 | −27.00 ± 0.20 | 12.87 ± 0.21 |
|         | Pre-laying | 64 | −26.40 ± 0.47 | 9.92 ± 0.47 |
|         | Chick | 56 | −26.94 ± 0.36 | 10.64 ± 0.65 |

| **WSP** | Chick-rearing | 32 | −26.40 ± 0.28 | 9.73 ± 0.55 |
|         | Pre-laying | 64 | −26.36 ± 0.73 | 9.64 ± 0.65 |
|         | Chick | 56 | −26.94 ± 0.36 | 10.64 ± 0.65 |

### Table 2

Bayesian Standard Ellipse Area Overlap for δ13C and δ15N for both studied storm-petrel species: Inter- and intra-specific Bayesian Standard Ellipse Area Overlap between the sampled tissue types for both years pooled; inter-annual overlap for WSP. Overlap was calculated as the percentage of shared area of each individual ellipse with each relevant other ellipse. CI – credible interval of 95%; Chick-rearing – adult blood; Pre-laying – chick down; Chick – chick feather (under-tail covert); BBSP – black-bellied storm-petrel; WSP – Wilson’s storm-petrel. Combinations with a mean overlap of < 5% are bolded and with a mean overlap between 5 and 10% are in italics.

| Interspecific overlap | Species Life stage | n | Mean (%) | Lower CI (%) | Upper CI (%) |
|-----------------------|-------------------|---|----------|--------------|--------------|
| Chick-rearing BBSP WSP | 20 | 31.0 | 4.93 | 65.7 |
| Pre-laying WSP BBSP | 64 | 7.96 | 1.12 | 19.4 |
| Chick BBSP WSP | 56 | 54.6 | 20.0 | 92.1 |
| Chick Pre-laying WSP | 56 | 25.6 | 8.37 | 51.1 |
| Chick chick BBSP | 8 | 5.88 | 0.00 | 56.9 |
| Chick chick Pre-laying WSP | 26 | 1.24 | 0.00 | 10.3 |

| Intraspecific overlap | Species Life stage | n | Mean (%) | Lower CI (%) | Upper CI (%) |
|----------------------|-------------------|---|----------|--------------|--------------|
| Chick-rearing BBSP Pre-laying Chick | 20 | 59.5 | 2.77 | 100 |
| Pre-laying Chick Chick-rearing | 19.1 | 4.71 | 0.00 | 28.8 |
| Pre-laying Chick | 0.59 | 3.85 | 0.00 | 7.45 |
| Chick chick | 5.34 | 4.91 | 0.00 | 31.6 |
| Chick chick | 5.34 | 5.34 | 0.00 | 31.6 |

| Inter-annual overlap WSP | Life stage Year | n | Mean (%) | Lower CI (%) | Upper CI (%) |
|-------------------------|----------------|---|----------|--------------|--------------|
| Pre-laying 2017 2018 | 42.8 | 26.0 | 62.2 |
| Chick 2017 2018 | 67.7 | 37.6 | 94.4 |
| Chick 2017 2018 | 32.8 | 14.7 | 53.0 |
| Chick 2017 2018 | 37.1 | 20.2 | 55.4 |
2.2. Study species

In both BBSP and WSP, the partners share parental duties during the breeding season (Wasilewski, 1986). WSP adults arrive at the colony from September (Sierakowski, 1991) to October (Wasilewski, 1986), and egg-laying occurs from December to February (Wasilewski, 1986). BBSPs breeding on Signy Island have been reported to return to the colony in November, and egg-laying to occur from December to January (Beck and Brown, 1971). Like the other storm-petrel species, they lay a single egg (Carboneras et al., 2017), which is incubated for 38–59 days in WSP and 38–44 days in BBSP. The egg may be left unattended for several days at a time, increasing the time between egg laying and chick hatching (Beck and Brown, 1972, 1971). Fledging takes place after about 60 days (54–69 days) in WSP (Beck and Brown, 1972) and after 65–71 days in BBSP (Carboneras et al., 2017). Fledging during our study period had finished by mid-April (authors’ unpublished data).

The exact ranges of foraging flights during the breeding period are unknown for the studied species, although for WSP they have been estimated to be up to around 200–250 km from the colony (Croxall and Prince, 1980; Pennycuick et al., 1984). Storm-petrels, like other Procellariiformes, may provision their chicks with stomach oil assimilated from ingested prey during longer foraging trips (Obst and Nagy, 1993; Warham et al., 1976).

2.3. Data collection

For the collection of blood/feather samples of adults, we captured individuals by hand while they were incubating in the nest and using mist-nets spread in the colony at night, throughout the chick-rearing period. We collected samples for stable isotope analyses representing three life-stages from adults and chicks. We collected a small amount of blood from adults’ wing veins (BBSP n = 20, WSP n = 32), representing the adult diet during chick-rearing. During the late chick-rearing phase in both studied years, we collected a down sample from each chick (BBSP n = 10, WSP n = 64), representing the maternal, pre-laying diet, and a chick feather sample (i.e. an under-tail-covert; BBSP n = 9, WSP n = 56), representing the chick diet, from each surviving chick, except one BBSP chick that fledged before feather collection. All samples were stored in −20 °C until further processing.

To record chick growth, we performed regular nest checks every three days starting from hatching, weather permitting. We measured chick body mass to the nearest 0.1 g using a digital scale (Pesola PTS3000, Switzerland) and tarsus length to the nearest 0.1 mm using callipers. We started measuring wing length to the nearest 0.1 mm using callipers once pin feathers became visible.

If nests were blocked by snow, we postponed chick measurements until the next check when the nest was open. This was in order to prevent affecting breeding success by damaging the natural insulation.

Fig. 1. Ellipse area overlap for δ13C and δ15N for both studied storm-petrels: Ellipse Areas encompass approximately 95% of the data. A – ellipses for both species in both studied years; B – ellipses for the Wilson’s storm-petrels for 2017 and 2018 (blood was not collected in 2017); C–E – ellipses per life stage; F&G – ellipses per species. BBSP – black-bellied storm-petrels; WSP – Wilson’s storm-petrels; chick-rearing – adult blood, collected throughout the breeding season; pre-laying – chick down; chick – chick feathers (under-tail coverts). See also Table 1 for overlap percentages.
properties of the snow, accidentally getting the chick wet or disturbing it’s hypothermic state (Kuepper et al., 2018).

2.4. Stable isotope analyses

We freeze dried the blood samples for 48 h to prepare them for stable isotope analyses. The feather samples were washed in a 2:1 chloroform:methanol solution and twice in methanol, then air dried for 24 h and cut up into sub-millimetre sections using stainless steel scalpel blades. Stable nitrogen and carbon isotope compositions ($\delta^{15}N$ and $\delta^{13}C$) were analysed using a continues flow system consisting of a Delta V Plus mass spectrometer connected with a Thermo Flush 1112 Elemental Analyzer via Confl flow IV (Thermo-Finnigan/Germany) (Skrzypek and Paul, 2006). We used multi-point normalisation to reduce raw values to the international scale (Skrzypek, 2013), based on international standards provided by IAEA: $\delta^{13}C$ – NBS22, USGS24, NBS19, LSVEC (Coplen, 1996); and for $\delta^{15}N$ – N1, N2, USGS32 and laboratory standards. Stable oxygen isotope composition ($\delta^{18}O$) of chick feather samples was analysed using a TC/EA coupled with Delta XL Mass Spectrometer in continues flow mode (Thermo-Fisher Scientific). The $\delta^{18}O$ results were normalised to the VSMOW scale based on USGS42 and USGS43 and the equilibration method (Coplen and Qi, 2012). All $\delta^{13}C$ results are reported in ‰ on VPDB, $\delta^{15}N$ and $\delta^{18}O$ in ‰ on VSMOW scale (Skrzypek, 2013), with an external analytical uncertainty (one standard deviation) of 0.10‰ for $\delta^{13}C$ and $\delta^{15}N$, and 0.5‰ for $\delta^{18}O$. As we did not lipid-extract the samples, we mathematically corrected the $\delta^{13}C$ measurements for lipid-associated biases using the following equation (Cherel et al., 2014; Post et al., 2007):

$$\delta^{13}C_{\text{corrected}} = \delta^{13}C - 3.32 + (0.99 \times C : N)$$

Additionally, due to differences in isotopic discrimination between tissues blood isotopic signatures should not be directly compared with feather isotopic signatures without controlling for the differences in discrimination factors (Quillfeldt et al., 2008). To calculate the difference in enrichment factors, we used three recaptured individuals in 2018 (1 BBSP, 2 WSPs) with feathers regrown over the season, for which we could calculate the enrichment factors between blood and feathers.

Table 3
Bayesian Standard Ellipse Area Widths for $\delta^{13}C$ and $\delta^{15}N$ for both studied storm-petrel species: The Bayesian Standard Ellipse Areas based on data pooled between both years for both studied species of storm-petrels, and per year for WSP. CI – credible interval of 95%; chick-rearing – adult blood; pre-laying – chick down; chick – chick feather (under-tail covert); BBSP – black-bellied storm-petrel; WSP – Wilson’s storm-petrel.

| Species   | BBSP     | WSP       |
|-----------|----------|-----------|
| Life stage | Lower (%) | Upper (%) | Lower (%) | Upper (%) |
| Chick-rearing | 0.092 | 0.301 | 0.420 | 1.062 |
| 95        | 0.104 | 0.258 | 0.467 | 0.949 |
| 50        | 0.138 | 0.189 | 0.588 | 0.746 |
| Mode      | 0.159 |         | 0.663 |         |
| Pre-laying | 0.189 | 1.279 | 0.856 | 1.690 |
| 95        | 0.253 | 0.980 | 0.940 | 1.550 |
| 50        | 0.385 | 0.610 | 1.109 | 1.312 |
| Mode      | 0.478 |         | 1.208 |         |
| Chick     | 0.047 | 0.353 | 0.478 | 1.000 |
| 95        | 0.060 | 0.265 | 0.527 | 0.907 |
| 50        | 0.093 | 0.154 | 0.628 | 0.754 |
| Mode      | 0.120 |         | 0.688 |         |

Fig. 2. Bayesian Standard Ellipse Areas (BSEA) for $\delta^{13}C$ and $\delta^{15}N$ for both studied storm-petrels: A – BSEAs for both species per tissue for both years; B – BSEAs for the Wilson’s storm-petrels for each year per tissue (blood was not collected in 2017); box width and colour denote credible intervals (thick, dark grey – 50%; medium – 75%, narrow, light grey – 95%); black dots – median. BBSP – black-bellied storm-petrel; WSP – Wilson’s storm-petrel; CR – chick-rearing adult, blood collected throughout the breeding season; PL – pre-laying female, chick down; Ch – chick, chick feathers (under-tail coverts). See also Table 2 for BSEA values.

![Figure 2](image-url)
isotopic signatures synthesised during the same time period (i.e. feather value minus blood value; BBSP: \(\delta^{13}C + 0.64\%o, \delta^{15}N + 0.84\%o\); WSP: \(\delta^{13}C + 0.55\%o, \delta^{15}N + 0.46\%o\)). We then added these differences to the blood isotopic values to correct for the differences in isotopic discrimination before continuing with the statistical analyses.

2.5. Statistical analyses

We performed all statistical analyses in R version 3.6.1 (R Core Team, 2019). When comparing both species, we pooled the data between the years, as we did not have a large enough sample size for BBSP to analyse both years separately. Likewise, we had a too small sample size of \(\delta^{18}O\) in 2017 for WSP. For \(\delta^{13}C\) and \(\delta^{15}N\) we did perform inter-annual comparisons in WSP. For growth rate analyses, we only considered fledged chicks and thus excluded the dead WSP chicks (8 in 2017 and 5 in 2018; no monitored BBSP chicks died).

2.5.1. Stable isotope niches

Due to the fact that \(\delta^{18}O\) was only analysed in chick feathers (BBSP \(n=8\), WSP \(n=31\)), and only for a subset of the WSPs in 2017 (\(n=5\)), and the difference in sample sizes between \(\delta^{13}C\) and \(\delta^{15}N\), and \(\delta^{18}O\), we decided to analyse isotopic niches both including and excluding \(\delta^{18}O\). We started with a MANOVA with a Wilk’s Lambda test \((\text{manova}, \text{package stats})\) to determine if the isotopic signatures differed between the species (BBSP, WSP) and life stages (chick-rearing adult, pre-laying female, growing chick), (i.e. \(\delta^{13}C + \delta^{15}N - \text{species + life stage + species:life stage}\)). We removed the interaction if not significant. Then if we found significant results, we ran another MANOVA between species for each life stage separately (i.e. \(\delta^{13}C + \delta^{15}N - \text{species}\) and within the species between life stages (i.e. \(\delta^{13}C + \delta^{15}N - \text{life stage}\)). For WSP we also added year as a factor (i.e. \(\delta^{13}C + \delta^{15}N - \text{life stage + year}\)) to test for inter-annual variability. If we found significant differences between the species, we used a Welch’s two-sample \(t\)-test \((\text{t.test}, \text{package stats})\) to determine the extent of the difference for each significant isotope. If we found significant differences within species, we used a univariate ANOVA \((\text{aov}, \text{package stats})\) with a Tukey HSD post hoc test \((\text{TukeyHSD}, \text{package stats})\) for each isotope and the three life stages. WSP inter-annual variability was further explored during the chick growth rate analyses, described below.

We determined niche widths and overlap for \(\delta^{13}C\) and \(\delta^{15}N\) using the Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al., 2011). As a measure of foraging niches, we calculated posterior ellipses \((\text{siberMVN})\) for \(\delta^{13}C\) and \(\delta^{15}N\) in all three life stages for both species with \(2 \times 10^4\) iterations, a \(1 \times 10^3\) burnin, thinned by 10 and over 2 chains. We used uninformed priors, as we had no prior knowledge of our expected results. We determined the size of the niche width of each group using Bayesian Standard Ellipse Areas \((\text{bsea}, \text{siberEllipses})\) and then used \(\text{bayesianOverlap}\) to calculate the niche overlap area.

![Fig. 3. Ellipsoid volume overlap for \(\delta^{13}C, \delta^{15}N\) and \(\delta^{18}O\) for chicks of both studied storm-petrels: A – ellipsoids containing ~50% of the data for both studied species in 3D; B–D – ellipse areas containing ~95% of the data for each isotope pair. BBSP – black-bellied storm-petrels; WSP – Wilson’s storm-petrels.](image-url)
between the corresponding Bayesian Estimates for the 95% Prediction Ellipse (BEPE). In contrast to the suggested approach in SIBER, where niche overlap percentage is specified as the proportion of overlapping BEPE relative to the non-overlapping BEPE of both groups combined [i.e. overlapping BEPE/(BEPE group A + BEPE group B – overlapping BEPE)], we calculated niche overlap as the proportion of overlapping BEPE relative to the BEPE of each group separately (i.e. overlapping BEPE/BEPE group A or B). We did so because we were not interested in how much of the area overlapped, but rather in how much of each individual niche (i.e. life stage) overlapped with others.

Additionally, for both species we calculated chick niche widths and overlap including all three isotopes (i.e. $^{13}$C, $^{15}$N and $^{18}$O), following Rossman et al. (2016). We calculated the posterior ellipsoids for all three stable isotopes for chick feathers with 5 × 10$^3$ iterations, a burn-in and adaptation of 1 × 10$^5$, over three chains. We determined the niche width based on the Bayesian Standard Ellipsoid Volume (BSEV) and calculated niche overlap volume of the Bayesian Estimates for the 95% Prediction Ellipsoids (BEPEV), and calculated the percentage niche overlap as the proportion of overlapping BEPEV relative to the BEPEV of each group separately.

2.5.2. Chick growth

Due to logistic reasons and the extended period of egg-laying, we did not find all nests before hatching. In the first field work season (2017) we found five WSP nests before hatching, out of 25 nests followed that year, and one BBSP nest out of six in total. In 2018 we found 16 WSP nests before hatching out of 19 nests in total. We found all three BBSP nests followed in 2018 before hatching.

In order to determine chick growth rates, we calculated the predicted hatching date based on tarsus length (Quillfeldt and Peter, 2000). Firstly, we fitted a Non-linear Least Squares model (NLS) to the tarsus growth data from the chicks with known hatching dates (Fig. A2; Table A1), as tarsus growth follows an S-curve (Fig. A2) (Quillfeldt and Peter, 2000). We did this for both years separately for WSP but pooled the data for BBSP due to low sample sizes (n = 8). Then, we used the inverted NLS model to predict the age based on the tarsus measurement closest to the mid-point between minimum and maximum tarsus length, as an NLS model is most accurate at the linear growth phase. Since the chicks are not born with a tarsus length of zero, maximum tarsus length, as an NLS model is most accurate at the linear tarsus measurement closest to the mid-point between minimum and maximum tarsus lengths measured for the known-age chicks, respectively. From the predicted age, we determined the predicted hatching date (lm, package stats; predicted hatching date = observed hatching date). This method was highly accurate for both species (BBSP $\tilde{\beta} \pm SE = 1.79 \pm 0.130, \bar{t} = 13.83, p < 0.001, adj. R^2 = 0.745$, Fig. A3A; WSP $\tilde{\beta} \pm SE = 0.955 \pm 0.031, \bar{t} = 31.09, p < 0.001, adj. R^2 = 0.780$, Fig. A3B). For comparability, in further analyses we used the predicted hatching date for all chicks.

To examine chick growth rates, we first plotted each parameter (i.e. tarsus growth, wing growth and log transformed body mass growth) against the predicted hatching date. Then, we visually determined the period of linear growth for each growth parameter per species, and per year for WSP (Table A2; Fig. A4). For each species we selected all measurements within this period, and calculated the growth rate as the slope of a linear model ($lm$, package stats). We used Welch’s t-tests to find inter-specific differences in the slope (t.test, package stats), with pooled data for both species. We calculated the variance inflation factor (VIF) (vif, package car) (Fox and Weisberg, 2011) to determine the level of multicollinearity for the growth parameters for both species and the datasets including and excluding $^{18}$O. For BBSP VIF ranged from 1.05 to 2.76 for the data excluding $^{18}$O, and from 1.24 to 3.31 for the data including $^{18}$O. For WSP VIF ranged from 1.02 to 1.42 when excluding $^{18}$O, and from 1.06 to 2.54 when including $^{18}$O. We deemed these values low enough to treat the growth parameters as independent (Neter et al., 1989; Rogerson, 2001).

Because the variance in growth rates (slope of regression for the period of linear growth) was relatively low within species (BBSP tarsus = 0.003, wing = 0.005, body mass = 0.022; WSP tarsus = 0.013, wing = 0.053, body mass = 0.010), and because of the relatively low sample sizes, we bootstrapped (1000 iterations) all analyses considering the effects on growth rates. We used Welch’s two-sample t-tests to determine the inter-annual effects on the slope of each growth parameter for WSP, and each continuous predictor (i.e. $^{13}$C pre-laying, $^{15}$NChick, $^{15}$N pre-laying, $^{18}$O Chick, predicted hatching date) except $^{18}$O Chick. We used a series of Pearson’s correlations to find the effects of each continuous predictor (i.e. $^{15}$N pre-laying, $^{15}$N Chick, $^{18}$O pre-laying, $^{18}$O Chick, predicted hatching date) on the slope of each growth parameter for both species. For BBSP we pooled the data from both years due to the low sample size, but for WSP we analysed the data both pooled between the years and for each year separately. If we found more than one predictor to have significant effect on a growth parameter we bootstrapped a linear model with all significant predictors as main effects, and determined the relative importance of each significant predictor using the lmg metric, which is based on R$^2$ partitioning by averaging over orders as introduced by Lindeman et al. (1980) (calc.relimp, package relaimpo) (Grömpig, 2006).

Table 4

| CI (%) | BBSP (n = 7) | WSP (n = 31) |
|--------|-------------|-------------|
| 2.5    | 0.971       | 0.919       |
| 50     | 2.127       | 1.375       |
| 97.5   | 5.345       | 2.163       |
| Mode   | 1.679       | 1.272       |

Fig. 4. Bayesian Standard Ellipsoid Volume for $^{13}$C, $^{15}$N and $^{18}$O for chick feathers for both studied storm-petrel species: CI – credible interval; BBSP – black-bellied storm-petrel; WSP – Wilson’s storm-petrel; n – sample size.
2.5.3. Environmental conditions in potential foraging areas

To assess inter-annual differences in environmental conditions, we used sea surface temperature [SST4; a night-time algorithm using two bands in the 4 μm atmospheric window, which shows markedly less scatter than the 11–12 μm SST (Minnett, 2010); we used SST4 because of better usable data coverage in the studied buffer zone compared to SST] and chlorophyll-a concentration (chl-a) at the surface layer. We used remote sensing MODIS Aqua satellite data (NASA Ocean Color Web, https://oceancolor.gsfc.nasa.gov/). To establish the environmental parameters, we randomly selected 500 points in the ocean within a 200 km buffer around the studied storm-petrel colonies (Fig. A1B), using ArcMap 10.3.1 (ESRI, 2014). Then, we extracted the SST4 and chl-a values for these points for both studied seasons with a 4 km resolution of monthly composites from November until April (i.e. November 2016 until April 2017 and November 2017 until April 2018), however, due to missing data caused by high cloudiness the sample sizes differed between years and months (see Results). We determined inter-annual differences using a paired Wilcoxon Signed Rank test with continuity correction (wilcox.test, package stats).

Additionally, in 2018, to visualise local δ18O isoscapes (due to a lack of published data from this region), we collected water samples (n = 20) at the end of the storm-petrel nesting period around Admiralty Bay (Fig. A1D), where the studied colonies are situated. All water samples were analysed using an Isotopic Liquid Water and Continuous Water Vapor Analyzer (Picarro 2130) (Skrzypek and Ford, 2014), and results are shown in ‰ VSMOW according to the delta notation (Coplen, 1996), with an external uncertainty for saline water samples (one standard deviation) of 0.10 ‰. Multi-points normalisation was used in order to reduce the raw values to the international scale (Skrzypek, 2013). Normalisation was done based on three laboratory standards, each repeated twice, calibrated against international standards provided by IAEA: VSMOW2, SLAP2 and GISP (Coplen, 1996). We prepared an isoscape map using inverse distance weighted (IDW) interpolation in ArcMap 10.3.1 (ESRI, 2014).

3. Results

3.1. Stable isotopic niches

To determine how the isotopic values differed between the life stages (i.e. adult blood as a proxy for chick-rearing adults, chick down for pre-laying female diet and chick feathers for chick diet) between the species we first considered the full MANOVA model with interaction (Wilk’s Lambda, δ13C + δ15N ~ species + life stage + species:life stage). Since the interaction was not significant (F2, 185 = 1.493, p = 0.228), we removed the interaction term. The results of the model without interaction showed differences in isotopic signatures between the species (F2, 186 = 75.68, p < 0.001) and between the life stages (F2, 186 =...
34.17, p < 0.001). Further analyses showed significantly higher δ15N values for BBSP compared to WSP for all three life stages (Welch’s t-test, pre-laying females t13.17 = 6.571, p < 0.001; chick-rearing adults t38.98 = 10.93, p < 0.001; chicks t31.54 = 19.47, p < 0.001) (Table 1). We found no significant difference in δ13C between the species (ANOVA, F1, 187 = 1.30, p = 0.255), but did between the life stages (F1, 187 = 26.76, p < 0.001) (Table 1).

Within BBSP we found significant differences between the life stages (MANOVA, F2, 35 = 8.15, p = 0.001) in δ15N values (ANOVA, F1, 36 = 13.57, p = 0.001) and δ13C values (F1, 36 = 6.47, p = 0.015). A Tukey’s HSD test showed that chicks had higher δ15N values than both chick-rearing adults (difference = 1.45‰, p < 0.001) and pre-laying females (difference = −0.62‰, p = 0.002) (Table 1). Chick-rearing adults and pre-laying females did not differ in δ13C values (difference = −0.12‰, p = 0.426), chicks had lower δ13C values than both chick-rearing adults (difference = −0.35, p = 0.003), and pre-laying females (difference = −0.46, p < 0.001) (Table 1). Within WSP we found significant differences between the life stages (MANOVA, F2, 149 = 26.06, p < 0.001) in δ15N (ANOVA, F1, 150 = 38.09, p < 0.001) and δ13C (F1, 150 = 22.98, p < 0.001) (Table 1). We found no significant difference in stable isotope signatures between the years for WSP (MANOVA, F2, 116 = 2.693, p = 0.072). Chick-rearing adults and pre-laying females did not have significantly different δ15N values (Tukey’s HSD, difference = 0.20‰, p = 0.257) or δ13C values (difference = −0.04‰, p = 0.936), but chicks had higher δ15N values than both chick-rearing adults (difference = 0.72‰, p < 0.001) and pre-laying females (difference = 0.91‰, p < 0.001), and lower δ13C values (chicks vs. chick-rearing adults difference = −0.54‰, p < 0.001; chicks vs. pre-laying females difference = −0.58‰, p < 0.001) (Table 1).

When we compared chick diets including the δ18O signatures (MANOVA, δ15N + δ13C + δ18O ~ species), we found significant differences between the species (Wilk’s Lambda, F3, 34 = 29.14, p < 0.001) in isotopic signatures for δ18O values (F1, 36 = 5.370, p = 0.026) and δ15N values (F1, 26 = 72.66, p < 0.001) but not δ13C (F1, 36 = 0.774, p = 0.385). Further post hoc analyses showed the difference in δ18O values to be just not significant (t8.027 = 2.071, p = 0.072), and δ15N values to be higher in BBSP than in WSP (t29.27 = 14.841, p < 0.001) (Table 1).

The Bayesian Estimate 95% Prediction Ellipse Area (BEPEA) overlap analyses revealed that between species the chicks showed least overlap in δ13C and δ15N (BBSP vs. WSP mean overlap 5.9%; WSP vs. BBSP mean overlap 1.2%) (Table 2; Fig. 1A). Both chick-rearing adults (BBSP vs. WSP mean overlap 31.0%; WSP vs. BBSP mean overlap 7.96%) (Fig. 1C) and pre-laying females (BBSP vs. WSP mean overlap 54.6%; WSP vs. BBSP mean overlap 25.6%) (Fig. 1E) showed considerable overlap (Table 2). The overlap values were higher for BBSP than for WSP (Table 2;
Fig. 1A), as their niches were smaller than those of WSP for all three sampled life stages (Table 3; Fig. 2A), which meant that a similar overlapping area comprised a larger portion of BBSP BEPEA than of WSP BEPEA.

At the intra-specific level for BBSP, we found the least overlap in the Bayesian 95% Prediction Ellipses of chicks with either chick-rearing adults (chick-rearing adults vs. chicks mean overlap 4.71%; chicks vs. chick-rearing adults mean overlap 5.34%) or pre-laying females (pre-laying females vs. chicks mean overlap 0.59%; chicks vs. pre-laying females mean overlap 2.76%) (Table 2; Fig. 1F). In contrast, chick-rearing adults and pre-laying females showed substantial overlap (chick-rearing adults vs. pre-laying females mean overlap 59.5%; pre-laying females vs. chick-rearing adults mean overlap 19.1%) (Table 2; Fig. 1F). All three life stages were overlapping in WSP (mean overlap range 36.8–93.8%) (Table 2; Fig. 1G). In both species, the maternal pre-laying diet signatures showed the largest niche widths (Table 3;
In WSP the niche widths of chick-rearing adults and chicks were similar, while in BBSP the niche width of chick diet was narrower than either pre-laying diet or chick-rearing adult diet (Table 3; Fig. 2A).

When including δ18Ochick into the analyses, we found negligible inter-specific overlap in Bayesian Estimate 95% Prediction Ellipsoid Volumes (mean overlap <0.001%) for the studied species (Fig. 3). Conversely to the δ13C and δ15N niche widths, we found that the niche widths including δ18Ochick were wider for BBSP than for WSP (Table 4; Fig. 4).

Although we found δ15Npre-laying to be significantly higher in 2017 than in 2018 for WSP (Fig. 5), BEPEAs showed considerable overlap between the years for both pre-laying females and chicks (mean overlap 32.8–67.7%) (Table 2; Fig. 1B). Additionally, the niche widths were similar between the years for both pre-laying females and chicks (Fig. 2B). We found no significant differences in δ13Cpre-laying, δ15Cchick or δ15Nchick between the years (Fig. 5).

### 3.2. Factors affecting chick growth

We found no significant interspecific differences in growth rates for tarsus length (t2,19 = −0.897, p = 0.376, BBSP mean ± SD = 1.01 ± 0.05, WSP mean ± SD = 1.04 ± 0.11), wing length (t2,21 = −0.916, p = 0.366, BBSP mean ± SD = 3.48 ± 0.14, WSP mean ± SD = 3.36 ± 0.42) or body mass (t2,53 = 1.220, p = 0.251, BBSP mean ± SD = 0.08 ± 0.04, WSP mean ± SD = 0.06 ± 0.02). For the WSP chicks we found significant inter-annual differences in body mass growth rate (higher in 2018), tarsus growth rate (higher in 2017) and predicted hatching date (earlier in 2017) (Fig. 6).

For the BBSP chicks the bootstrapped Pearson’s correlation analyses showed a significant positive relationship between tarsus growth and wing growth (Fig. 7A). Additionally, we found a significant positive effect of predicted hatching date and a significant negative effect of δ15Nchick on body mass growth rate (higher in 2017) and predicted hatching dates (both years combined, Fig. 7B). The relative importance of predicted hatching date was higher (mean ± SD lmg = 0.293 ± 0.124) than that of δ15Nchick (mean ± SD lmg = 0.163 ± 0.108) for both years combined (Fig. 7B). The relative importance of predicted hatching date was higher (mean ± SD lmg = 0.163 ± 0.108) than that of δ15Npre-laying (mean ± SD lmg = 0.078 ± 0.058) (Fig. 7D). However, when separating the data for the WSPs between the years, we found a significant positive effect of predicted hatching date on body mass only in 2017 (Fig. 8A) and a significant negative effect of δ15Nchick on body mass growth in 2018 (Fig. 8B).

### 3.3. Environmental conditions in potential foraging areas

We found significant differences between the years in SST4 from November through February (Wilcoxon test, all p < 0.05), with sea surface temperatures from November through February being higher in 2016/17 than in 2017/18 (Table 5; Fig. 9). In March and April temperatures did not significantly differ between the years. Chl-a was significantly different from November through March; for April there was not enough data available due to high cloud cover (Fig. 10). Chl-a concentrations were higher in 2016/17 than in 2017/18 in November and December, but lower from January through March (Table 5).

### 4. Discussion

Our results indicate that BBSPs forage at a higher trophic level than WSPs. All studied life stages (especially chicks) of BBSP were characterised by higher δ15N values than WSP. This observation is consistent with earlier studies suggesting such interspecific differences in trophic levels based on dietary data collected from regurgitations (Furness and Baillie, 1981; Hahn, 1998a; Quillfeldt, 2002). Regurgitation studies may not be fully representative for species’ diet, as regurgitated food is supposed to be intended as chick food only (Furness and Baillie, 1981). Thus, our study, based on stable isotope analyses of samples collected from both chicks and adults provides a more complete picture of the foraging niches of the two species. Interestingly, we found considerable overlap between adult BBSP and WSP isotopic niches, both during the pre-laying period (chick down values) and the chick-rearing period (adult blood values), though in both instances BBSP had on average higher δ15N values. This large degree of overlap may be explained by the importance of Antarctic krill (Euphausia

![Fig. 8. Bootstrapped (N = 1000) Pearson’s correlations between chick growth parameters and predictors and relative importance of multiple significant predictors for both years for the Wilson’s storm-petrels: A – pairwise Pearson’s correlations for 2017; B – pairwise Pearson’s correlations for 2018. Pr. Hatching Date – predicted hatching date. The results are shown as mean (dot) ± the 95% range (i.e. 2.5% and 97.5% quantiles; solid horizontal line). Solid vertical line shows Pearson’s correlation coefficient = 0.0. We assumed significance the 95% range of the Pearson’s correlation coefficient did not overlap 0.0.](image-url)
superba) in the diet of both studied storm-petrel species (Beck and Brown, 1971; Hahn, 1998a; Ridoux, 1994). Foraging on this superabundant (Siegel et al., 2013; Trathan and Hill, 2016), readily available prey may reduce stable isotope niche partitioning, although it does not necessarily eliminate the possibility of interspecific competition (Barlow et al., 2002; Dimitrijević et al., 2018). A study on three closely related

| Month | Chl-a (mg m⁻³) | SST4 (°C) |
|-------|----------------|-----------|
|       | Mean ± SD      | n         | p        | Mean ± SD      | n         | p        |
|       | 2016/17        | 2017/18   |          | 2016/17        | 2017/18   |          |
| Nov   | 0.348 ± 0.146  | 0.303 ± 0.111 | 423 | -0.001 | -0.200 ± 0.193 | -0.772 ± 0.111 | 15 | <0.001 |
| Dec   | 0.464 ± 0.302  | 0.426 ± 0.265 | 425 | -0.001 | 0.951 ± 0.598  | 0.316 ± 0.368  | 186 | <0.001 |
| Jan   | 0.303 ± 0.181  | 0.325 ± 0.186 | 358 | 0.001  | 1.479 ± 0.777  | 1.241 ± 0.746  | 382 | <0.001 |
| Feb   | 0.313 ± 0.199  | 0.387 ± 0.272 | 398 | -0.001 | 1.882 ± 0.960  | 1.357 ± 0.747  | 372 | <0.001 |
| Mar   | 0.222 ± 0.081  | 0.894 ± 0.933 | 323 | -0.001 | 1.217 ± 0.828  | 1.285 ± 0.654  | 351 | 0.674  |
| Apr   | 0.261 ± NA     | 0.415 ± NA   | 1   | NA     | 0.823 ± 0.797  | 0.870 ± 0.510  | 309 | 0.408  |

Table 5: Environmental conditions (chlorophyll-a concentrations (chl-a) and sea surface temperatures (SST4)) in potential foraging areas of the studied storm-petrels: Environmental conditions (chl-a and SST4) as obtained from randomly selected points in a buffer of 200 km around the colonies. Significant (paired Wilcoxon Signed Rank test with continuity correction) p-values (<0.05) are bolded. See also Fig. 8. SD – standard deviation; n – sample size; NA – not available.

Fig. 9: Sea surface temperatures in potential foraging areas for both studied storm-petrel species. Pairwise sea surface temperature (SST4) comparisons between years per sampled month. Sample sizes are shown in brackets. For more details see Table 4 and Fig. A1.
fulmarine petrels breeding sympatrically in Antarctica revealed no significant stable isotope niche segregation between at least two species for feathers and egg membranes, and among all species during incubation as reflected by blood (Dehnhard et al., 2019). Of four species of sympatric planktivorous petrels breeding on Bird Island, South Georgia, two showed partial stable isotope niche overlap (Navarro et al., 2013). The lack of considerable stable isotope niche partitioning in sympatrically breeding species sharing the same guild may be explained by foraging behaviour differences [e.g. diving behaviour (Navarro et al., 2013)], or because the species’ diets truly overlap due to generalist diets (Dehnhard et al., 2019) or focusing on superabundant prey (this study).

To increase the fitness of their current offspring seabird parents may provision their chicks at a higher trophic level than they consume themselves (Forero et al., 2002; Hodum and Hobson, 2000; Rosciano et al., 2019), by selectively foraging for higher quality prey (Kwasniewski et al., 2012) or reserving high quality prey for chick provisioning (Dänhardt et al., 2011). We found that $\delta^{15}$N values of BBSP chicks were higher than those of adults, which may suggest a fish-richer diet. Fish prey has been shown to have higher caloric values than crustaceans (Ruck et al., 2014), and a higher calcium content (Clarke and Prince, 1980), a mineral that is especially important for rapidly growing chicks (Hurwitz et al., 1995). In contrast, WSP chick diet showed considerable overlap with adult diets. Instead of differences in diet causing differences in $\delta^{15}$N values, BBSP chick $\delta^{15}$N values might have been inflated due to nutritional stress in the chicks. Nutritional stress can lead to the use endogenous instead of dietary amino acids in protein synthesis (Hobson et al., 1993), increasing the $\delta^{15}$N values due to nitrogen fractionation. Nutritional stress may be caused by periods of fasting and facultative hypothermia (Beck and Brown, 1971; Cruz et al., 2012; Hobson et al., 1993; Kuepper et al., 2018; Polito et al., 2011).

We suggest that the overlap in diet between adults and chicks might be an effect of prioritising food security over its nutritional value. WSP preferring to forage on the readily available superabundant Antarctic krill over fish might mean higher food security, such that a higher trophic level diet does not induce a higher chick fitness if it means more

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**Fig. 10.** Chlorophyll-$\alpha$ concentrations in potential foraging areas for both studied storm-petrel species. Pairwise chlorophyll-$\alpha$ (chl-$\alpha$) concentration comparisons between years per sampled month. Sample sizes are shown in brackets. For more details see Table 4 and Fig. A1.
a frequent, and stable food supply (Morrison et al., 2014). The smaller WSPs may also be less adapted to catch and handle fish prey than the larger BBSPs. Storm-petrel fish prey is often larger than krill (Ruck et al., 2014), and WSP have smaller culmen (mean 12.6 mm) (Beck and Brown, 1972) than BBSP (mean 15.3 and 15.1 mm for males and females respectively) (Beck and Brown, 1971). There may thus be a threshold size for chicks before they are able to handle fish prey. Our study and previous research (Hahn, 1998a; Quillfeldt, 2002; Ridoux, 1994) do not allow us to distinguish why exactly WSP prefers provisioning their chicks with krill over fish, but their foraging strategies seem heavily reliant on krill. Indeed, WSP change their provisioning strategy based on actual krill abundance (Gladbach et al., 2009; Quillfeldt and Peter, 2000), and breeding success decreases in years with low krill abundance (Büßer et al., 2004).

The difference in nutritional demands between the chicks of both species, such that BBSP parents forage at different trophic levels for their chicks than themselves but WSP parents do not, might stem from the difference in body size and thus metabolic rates between both species (Dunn et al., 2019; Warham, 1996); a higher metabolic rate at sea is expected for heavier seabirds, here for BBSP compared to WSP (Birt-Friesen et al., 1989). While we did not find differences in chick growth rates between the chicks of both species, BBSP chicks do stay in the nest for a longer period of time than WSP chicks and consequently have a longer growth period especially considering body mass gain (Fig. A4). BBSP chicks might have been fed at a higher trophic level than WSP chicks level due to higher nutritional demands, like in black-legged kittiwakes (Rissa tridactyla) (Merkling et al., 2012). BBSP chicks have to grow relatively more from hatching (e.g. the mean body mass at hatching was 10.7 g for WSP (n = 19) and 14.8 g for BBSP (n = 4), while the maximum observed chicks masses were 48.7 g for WSP and 127.8 g for BBSP, a gain of 5.4 times the initial mass for WSP and 8.6 times the initial mass for BBSP). This difference in mass gain could explain the inclination for a bigger shift in trophic level from adults to chicks in BBSP compared to WSP. Additionally, chick feather isotope composition reflects the diet input during the whole growth period, and the effect of a shift in prey types later in the season may thus be confounded for WSP. BBSP may have been provisioning their chicks at a higher trophic level from hatching, thus showing a clearer distinction in trophic level between adults and chicks.

In the adults of both BBSP and WSP we found that the pre-laying female (i.e. chick down) stable isotope niches were widest compared to the other measured life stages, confirming our hypothesis that free roaming adults have wider isotopic niches (Pratte et al., 2018). BBSP showed no difference in δ13C in adult-derived samples (i.e. blood and chick down), but did have higher δ15N values in chick-rearing diets compared to pre-laying diets. This may indicate a shift in the trophic level of the diet (Minagawa and Wada, 1984) but not in foraging area locations (Cherel and Hobson, 2007; Quillfeldt et al., 2005). Both WSP adult-derived samples however, showed no significant difference in isotopic signatures, indicating both similar diets and foraging locations throughout the breeding season. Additionally, we found that chick diet niche widths were narrower than adult niche widths, which may indicate that parents were more selective about prey items they feed their chicks than prey they forage for themselves. Alternatively, many central-place foraging seabirds, including Procellariiformes and likely European storm-petrels (Hydrobatidae pelagicus) (Bolton, 1996) and its sub-species the Mediterranean storm-petrel (H. p. melitensis) (Albores-Barajas et al., 2011), alternate long foraging trips for self-maintenance and short foraging trips for chick provisioning visiting different foraging areas (e.g. Chaurand and Weimerskirch, 1994; Jakubas et al., 2012). The difference in the duration and distance of the foraging flights, could also explain the difference in foraging niche widths between adults and chicks as the shorter trips would cover a smaller range of stable isotope values that change with foraging area, and a smaller range of potential prey types.

Interestingly, while the BBSP isotopic niches were narrower than the WSP niches when considering the δ13C:δ15N space, they were wider when including δ18O. This is likely due to the low sample size (BBSP n = 8), but alternatively may indicate that BBSP parents forage in a wider range of areas from shore to off-shore locations (Bigg and Rohling, 2000). BBSPs breeding on the South Shetland Islands have been shown to prefer foraging further off-shore than WSPs (Santaora et al., 2017), which is confirmed by the tendency for higher δ18O,δ15N chick values in BBSP than in WSP. Conversely, δ13C did not differ between BBSP and WSP, reinforcing the suggestion that the difference in stable isotope niche widths was due to low sample size. However, BBSP might have been foraging in the same water mass (similar δ13C) but further from shore. Additionally, the scale at which changes in δ13C and δ18O occur was not necessarily the same, and could explain why differences in one were picked up by statistical analyses but not in the other.

We found a positive correlation between hatching date and body mass and tarsus growth for the BBSP chicks, and a positive correlation between hatching date and body mass growth for the WSP chicks. In WSP the effect of hatching date on chick growth was much stronger than any other significant effect when analysed together (Fig. 7B & D). Due to the short Antarctic summer and subsequent crash in food availability (Biggs et al., 2019), chicks have a strict deadline for fledging and late chicks may have to grow faster to be ready to leave the nest in time (VanHeezik et al., 1993). The positive correlation between BBSP wing growth and δ13C, pre-laying may be explained in context of carry-over effects from maternal nutrients in eggs to chick isotopic signatures. Lower δ13C have been correlated with lower body conditions in blue-footed booby (Sula nebouxii) chicks (Cruz et al., 2012). If this relationship is also present in pre-laying females, then pre-laying females with lower body conditions might have had chicks slower growing wings. Alternatively, as lipids are depleted in δ13C, pre-laying females foraging on high lipid prey [e.g. fish over krill (Clarke and Prince, 1980)] might have had chicks with slower growing wings. However, we have no data on pre-laying diets or their lipid contents, and thus can only speculate on the reason for the positive relationship between δ13C, pre-laying and chick wing growth for BBSP, as the issue is apparently understudied and requires further investigation (Bond and Jones, 2009).

Similar to other studies on chick growth (Cruz et al., 2012; Trueman et al., 2005), we found that higher δ15N,δ18O values were correlated with lower body mass growth rates in BBSP. This correlation was stronger than the significant effect of hatching date when analysed together (Fig. 7A & C). For WSP we also found a significant negative correlation between body mass growth and δ15N,δ18O but only in 2018. Those negative correlations may be due to nutritional stress in the chicks (Hobson et al., 1993), increasing the δ15N values due to nitrogen fractionation. However, in most species δ15N goes up with age and size, including Antarctic krill (Polito et al., 2013) and fish (Pinkerton et al., 2013), suggesting a correlation between prey age and chick growth rate. Additionally, in Antarctic krill, the relative lipid content in immature is higher than in adults (Clarke, 1984), implying that juvenile krill should be preferred over adults in terms of nutritional quality. Krill size decreases closer to shore (Siegel et al., 2013), possibly indicating a preference for larger krill and thus older krill, contradicting the positive effect of juvenile krill. However, in WSP we found a positive correlation between δ18O,δ15N,δ18O and tarsus growth rate. Sea water δ18O generally decreases closer to shore, especially in bays and estuaries, due to fresh water input which has lower δ18O values than ocean water, indicating a positive effect of foraging further off-shore. However, locally we found that in Admiralty bay ocean δ18O values were higher than in the surrounding open ocean of the Bransfield Strait (Fig. A1D), likely caused by local currents and upwelling zones pushing δ18O richer water masses up along the shore line (Campos et al., 2013; Rakusa-Suszczewski, 1980). These findings show that while δ18O may be useful when studying potentially large (foraging) areas, local systems might be more complex.
When separating the effects on chick growth rates per year for the WSPs, we found significantly earlier hatching dates in 2017 compared to 2018. Additionally, we found significantly higher body mass growth rates in 2018 than in 2017, but lower tarsus growth rates. We found no significant differences in isotopic values during the breeding period, but pre-laying δ¹⁵N values were higher in 2017 than in 2018. These differences in chick growth rates and hatching dates might be due to the inter-annual environmental differences in sea surface temperature and chlorophyll-a concentrations (Figs. 9 & 10), which likely had an effect on krill abundance (Hill et al., 2013; Loeb et al., 1997; Marrari et al., 2008). Looking at the factors affecting chick growth rate, we found that the significant negative correlation between δ¹⁵N pre-laying and body mass growth observed in the pooled WSP dataset disappeared when separating the years. As there were also significant inter-annual differences in δ¹⁵Npre-laying and body mass growth, we assume those to be the base for the significant effect in the pooled dataset. Additionally, we found a significant positive effect of hatching date on body mass growth, which disappeared in 2018 though not in 2017, indicating that this effect is not solely due to inter-annual differences in body mass growth and hatching dates. In 2018 we found a significant negative effect of δ¹⁵N chick on body mass growth, which was not apparent in 2017. These differences in significant effects between the years could be connected with the inter-annual differences in hatching dates, weather conditions or food availability; possibly due to the later hatching dates in 2018 (longer snow cover retention spring blocking access to the nest burrows) all chicks were restricted by the short summer so that hatching date did not affect body mass growth as strongly as in 2017. The higher SST4 and chl-a concentrations early in the season in 2016/17 compared to 2017/18 (Figs. 9 & 10) and their subsequent effect on krill abundance (Hill et al., 2013; Marrari et al., 2008) may have had lasting effects through the breeding seasons. Moreover, the increased precipitation in 2018 (Michielsen et al., 2019) caused increased snow blocking of the nests throughout the season, which in turn lead to more nutritional stress due to fasting and facultative hypothermia (Beck and Brown, 1971; Cruz et al., 2012; Hobson et al., 1993; Kuepper et al., 2018; Polito et al., 2011) and thus higher δ¹⁵Nchick in chicks with higher stress levels and lower growth rates (Hobson et al., 1993). This effect may not have been apparent in 2017 as nutritional stress levels may have been lower and more similar between the chicks.

5. Conclusions

Our study is one of the first to show the differences in stable isotope niches between species and life stages in seabirds (Gladbach et al., 2007; Pratte et al., 2018). In contrast to WSPs, we found that the trophic level of BBSP chicks differed from adults, likely as a result of the specific requirements of growing and developing nestlings. The results revealed some limitations of regurgitation studies as the diet of chicks may be different from adults. Additionally, combining stable isotope data with chick growth rate data allowed us to better understand inter-specific and inter-annual differences in the relationship between diet and chick growth. Despite the expected niche partitioning driven by sympatric breeding and sharing the same guild, the studied storm-petrel species showed, similarly to some other Antarctic predators, considerable isotopic niche overlap during the breeding season. The large overlap is likely due to their reliance on similar prey types, most notably the superabundant Antarctic krill. Its high availability may have reduced interspecific niche partitioning, though interspecific competition may still play an important role in the Antarctic food web (Barlow et al., 2002; Dimitrijević et al., 2018), especially if krill abundance decreases due to global climate change (Hill et al., 2013; Loeb et al., 1997). Our study revealed dietary shifts in BBSPs that are absent in the WSPs, showing different chick provisioning strategies, and shows that the productivity of the Antarctic marine ecosystem may facilitate foraging niche overlap of sympatrically living species.

CRediT authorship contribution statement

Anne N.M.A. Ausems: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing - original draft, Visualization, Project administration. Grzegorz Skrzypek: Formal analysis, Resources, Writing - review & editing. Katarzyna Wojciszalnis-Jakubas: Methodology, Investigation, Writing - review & editing. Dariusz Jakubas: Conceptualization, Methodology, Validation, Investigation, Writing - review & editing, Supervision, Project administration, Funding acquisition.

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

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