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Squid in the diet of Antarctic fur seals: potential links to oceanographic conditions and Antarctic krill abundance

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ABSTRACT: Understanding how changes in oceanographic conditions affect predators and their prey is fundamental for interpreting variability in natural marine ecosystems. At South Georgia, Antarctic fur seals *Arctocephalus gazella* are known cephalopod predators and potential indicators of changes in regional environment conditions and prey availability. The cephalopod component of the diet of Antarctic fur seals at South Georgia was assessed using lower beaks found in scats collected over 5 consecutive years (2009–2013) under known variable oceanographic conditions. In years of unusually warm oceanographic conditions around South Georgia and low Antarctic krill *Euphausia superba* density, the number of squids *Slosarczykovia circumantarctica* increased in the seals' diet. Moreover, stable isotope analysis of beaks showed that *S. circumantarctica* exhibited higher $\delta^{15}N$ values in years that were associated with an offshore habitat (lower $\delta^{13}C$ values) where Antarctic fur seals had been foraging. This study provides evidence of the ecological links between the feeding behaviour of Antarctic fur seals, their main cephalopod prey, Antarctic krill densities and oceanographic conditions.

KEY WORDS: Southern Ocean · *Arctocephalus gazella* · *Slosarczykovia circumantarctica* · Stable isotope analysis · Oceanographic conditions

1. INTRODUCTION

Determining how physical processes (e.g. ocean warming, movement in frontal regimes, sea-ice area) influence inter-annual ecological processes in marine ecosystems is essential to interpret and predict the natural variability and their responses (Reid & Croxall 2001, Turner et al. 2014, Gutt et al. 2015). Oceanographic conditions also influence and affect ecosystem trophic dynamics. Unusual years with low productivity and prey availability can influence all trophic levels of the marine food web (Xavier et al. 2013), changing the foraging ecology and the diet of many top predators (Murphy et al. 2007).

Antarctic fur seals *Arctocephalus gazella* are one of the major consumers in the Atlantic sector of the Southern Ocean (Doidge & Croxall 1985). As top predators, they can be an indicator of changes in prey availability and environmental conditions, particularly around South Georgia (Reid 1995, Klages 1996, Staniland & Robinson 2008) where 95% of the world's population breed (54.42° S, 36.58° W; Reid & Croxall 2001, Forcada & Hoffman 2014). During the breeding season in the Austral summer, female Antarctic fur seals forage almost exclusively around South Georgia, feeding on Antarctic krill *Euphausia superba* (hereafter krill), fish (including icefish *Champsocephalus gunnari*)

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and squid (North et al. 1983, Doidge & Croxall 1985, Reid & Arnould 1996, Staniland & Boyd 2003), with shifts in food-web structure between years of high and low krill availability observed (Murphy et al. 2007, Forcada & Hoffman 2014). However, no relationships with other prey are known, including with regionally relevant pelagic squid *Slosarczykovia circumantarctica* (Rodhouse et al. 1992b, 1996). Moreover, with ongoing environmental changes (Croxall et al. 1999, Fielding et al. 2014), more information is needed on the effects of extreme oceanographic conditions. In 2009, exceptionally high sea surface temperatures (SST) were recorded for many consecutive months around South Georgia, with a much higher mean SST compared to the long-term average (Hill et al. 2009, Xavier et al. 2017). Indeed, the lowest density (17.6 g m^{-2}) of krill since annual surveys began in 1997 was observed in 2009 (Hill et al. 2009, Fielding et al. 2014). Thus, a detailed study of consecutive years is needed to assess annual variation of prey availability to Antarctic fur seals under unusual oceanographic conditions.

Antarctic cephalopods have been studied considerably through the diet of their predators (Cherel et al. 2004, Collins & Rodhouse 2006), as cephalopod beaks are resistant to digestion and have proved to be useful for a variety of studies on marine ecology (Xavier et al. 2016a). Beaks can accumulate in stomachs for months, and can be found in faecal material and regurgitates (Clarke 1962, Xavier & Cherel 2009). The squid *S. circumantarctica* is mainly present around the Antarctic Peninsula and South Georgia (Xavier et al. 2016b). It is one of the most common cephalopod prey in the diet of various Antarctic predators, including Antarctic fur seals, but little is known about its biology and ecology (Lipinski 2001, Xavier & Cherel 2009). Furthermore, its variability in the fur seals' diet could be a relevant indicator in understanding possible changes in the seals' feeding behaviour (Staniland & Robinson 2008).

Stable isotope analysis of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) in cephalopod beaks can be used to infer habitat and trophic ecology (Cherel & Hobson 2005) and are related to the foraging ecology of their predators (Seco et al. 2016a). The value of $\delta^{15}N$ reflects the trophic position, as consumers are typically enriched ~3‰ in ^{15}N relative to their prey (Hobson & Welch 1992, Rosas-Luis et al. 2017). $\delta^{13}C$ is mainly used to determine the primary source of carbon — reflecting an observed latitudinal gradient — but can also indicate inshore versus offshore plankton, pelagic versus benthic habitats (Hobson et al. 1994) and is typically used as proxy for the distribution of marine organisms.

Overall, in this study we aimed to (1) analyse the cephalopod component of the diet of Antarctic fur seals at South Georgia in 5 consecutive years, (2) analyse the habitat and trophic ecology, through stable isotopic analysis, of the most abundant squid (*S. circumantarctica*) in the diet of Antarctic fur seals in an ecological perspective and, equally important, (3) compare the relationships of the cephalopods in the diet of Antarctic fur seals with known oceanographic conditions and krill density. Finally, we discuss how the interaction between Antarctic squid and Antarctic fur seals can be used as an environmental indicator for Antarctic pelagic marine ecosystems.

2. MATERIALS AND METHODS

This study was conducted at 2 sampling locations on South Georgia: Bird Island (54° S, 38° W) and King Edward Point (54° S, 36° W). Between 2009 and 2013, a total of 3649 scat samples of Antarctic fur seals were collected. Ten scats were collected weekly, when possible, following methodology of previous studies (Reid 1995). Only fresh, complete scats were collected. Scats were washed and prey items, such as fish otoliths, crustacean carapaces and cephalopod beaks, were identified and measured.

Upper and lower cephalopod beaks were counted and lower beaks were identified to species level using Clarke (1986) and Xavier & Cherel (2009). The lower rostral length (LRL) (Fig. A1 in the Appendix) was measured to the nearest 0.01 mm using a digital calliper or a graticule in a stereomicroscope, depending on beak size. The frequency of occurrence (FO, %) of cephalopods in the diet (number of scat samples containing a specific cephalopod species divided by the total number of scats samples analysed), the proportion (n, %) of lower beaks (number of lower beaks of a certain species divided by the total number of lower beaks) and the contribution to the diet by estimated mass (%) (estimated mass of all individuals of a certain cephalopod species divided by the total estimated mass for all cephalopod individuals) were calculated (see Table 1). Estimated mass was calculated using allometric equations from published guides (Xavier & Cherel 2009). To investigate potential changes in the seals' feeding strategies, krill biomass was obtained from Fielding et al. (2014) using acoustic at-sea surveys and compared with data from the most important cephalopod(s) consumed. The acoustic survey (December–February) occurred entirely during the breeding season of Antarctic fur seals and within their foraging area (Staniland & Robinson 2008, Fielding et al. 2014).

For stable isotopic analysis, a minimum of 10 lower beaks yr^{-1} were randomly selected and analysed (except in 2012, when less than 10 beaks were found) (see Table 2). The entire lower beak was used for these analyses — which provides an integrated, lifetime signal of diet and geographic position, albeit biased towards more recent periods when mass increments are greater — following previous studies (Cherel & Hobson 2005, Seco et al. 2016b). Beaks were cleaned with 70% ethanol, stored in separate microtubes and dried in an oven. After drying, the beaks were milled using a mixer miller (MM400; Retsch®). Stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) were determined using a continuous flow isotope ratio mass spectrometer at the Marine and Environmental Sciences Centre (Figueira da Foz), following Seco et al. (2016b). Results are presented in δ notation as deviations from standard references in parts per thousand (‰) according to the following equation:

$$\delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1000 \qquad (1)$$

where X represents ^{13}C or ^{15}N and R_{sample} represents the ratios $^{13}C/^{12}C$ or $^{15}N/^{14}N$. R_{standard} represents the international reference standard ratios for Vienna Pee-Dee Belemnite (V-PDB) and atmospheric N_2 (air) for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Values of $\delta^{13}C$ of other cephalopod species (the oceanic squid *Gonatus antarcticus* collected from albatrosses breeding at South Georgia and the coastal octopod *Paraledone turqueti* from Patagonian toothfish captured around South Georgia) were also analysed to compare with *Slosarczykovia circumantarctica* signatures to determine their likely habitat (i.e. inshore or offshore).

To characterise the inter-annual variability in the oceanographic conditions around South Georgia, we extracted the historical monthly sea surface temperature anomalies (SSTa) for the austral summer months (January–March) between 2009 and 2013, within the probable foraging range of Antarctic fur seals (area between 49–60° S and 31–43° W) (Staniland & Robinson 2008, Arthur et al. 2017). Data were extracted from http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/.weekly/. This area covers the entire South Georgia coastal/inshore portion, as well as the initial open ocean/offshore part used by the Antarctic fur seals in their longer foraging trips (i.e. 500 km).

Statistical analyses and graphs were made using GraphPad Prism® v.6.01 and R v.3.3.2 (R Development Core Team 2018). All statistical analyses used a significance level of $\alpha = 0.05$ and were preceded by a Shapiro-Wilk normality test. If data followed a normal distribution, a Bartlett's test was performed to test homogeneity. Means were compared using *t*-tests and ANOVA for parametric data, and Mann-Whitney and Kruskal-Wallis tests for non-parametric data. Multiple comparisons were performed using Tukey's and Dunn's multiple comparisons tests for parametric and non-parametric data, respectively. Pearson's correlation was used to test for the different relations. Bayesian stable-isotopic mixing models (Jackson et al. 2011) were performed to establish isotopic niche for each year. Overlap between ellipses were also examined to assess if individuals shared the same isotopic niche. These analyses were performed using the 'SIAR' package in R.

3. RESULTS

3.1. Inter-annual characterisation of cephalopods in the Antarctic fur seal's diet

The 2 sampling locations (Bird Island and King Edward Point) showed no significant difference in any of the parameters evaluated (*t*-tests: LRL: $t = 0.63$, $p = 0.55$; mantle length [ML]: $t = 0.03$, $p = 0.97$; frequency: $t = 1.50$, $p = 0.17$; and number of beaks: $t = 1.56$, $p = 0.16$), so the data from the 2 sites were pooled together.

A total of 263 lower beaks from 8 cephalopods species were identified from 89 scats during 5 yr period (Table 1). The year 2009 had the highest diversity and number of beaks, while 2012 had the lowest. No correlation was found (Pearson's correlation, $r = -0.52$, $p = 0.36$) between the number of scats and the number of species identified in each year. Overall, *Slosarczykovia circumantarctica* was the most dominant species by number of beaks and FO in all years studied as well as when data from all years were combined (Table 1). Moreover, *S. circumantarctica* was also the most important cephalopod species in terms of estimated mass for 4 out of the 5 years (Table 1). The squid *S. circumantarctica* showed a significant difference both in FO (ANOVA: $F_{3,12} = 7.93$, $p < 0.01$) as well as in number of beaks found in scats (ANOVA: $F_{3,12} = 14.79$, $p < 0.01$) compared to the other 3 main squid prey species — *Psychroteuthis glacialis*, *Fillipovia knipovitchi* and *Kondakovia longimana*.

Table 1. Frequency of occurrence (FO), number of beaks (n) and total mass (*M*, in g) for each identified cephalopod species found in the scats of Antarctic fur seals *Arctocephalus gazella* at South Georgia between 2009 and 2013. The frequency shown is relative to the number of scats containing cephalopods, not to the total number of scats per year

Taxon	2009						2010						2011						2012						2013					
	FO	%	n	%	*M*	%	FO	%	n	%	*M*	%	FO	%	n	%	*M*	%	FO	%	n	%	*M*	%	FO	%	n	%	*M*	%
Slosarczykovia circumantarctica	21	67.74	71	81.62	366.73	28.53	22	91.67	69	89.62	410.25	78.45	12	75	40	85.1	216.59	37.71	4	50	9	75	49.94	2.82	5	50	38	86.37	179.7	66.67
Psychroteuthis glacialis	5	16.12	5	5.75	83.54	6.49	4	16.67	4	5.2	59.58	11.39	4	25	4	8.51	148.54	25.81	–	–	–	–	–	–	–	–	–	–	–	–
Fillipovia knipovitchi	3	9.67	3	3.45	631.7	49.13	–	–	–	–	–	–	2	12.5	2	4.25	188.49	32.81	–	–	–	–	–	–	4	40	5	11.36	80.57	29.88
Kondakovia longimana	1	3.22	1	1.14	6.33	0.49	2	8.34	3	3.89	13	2.42	–	–	–	–	–	–	3	38	3	25	1719	97.2	1	10	1	2.27	9.31	3.45
Gonatus antarcticus	1	3.22	2	2.3	17.64	1.37	1	4.16	1	1.29	40.5	7.74	1	6.25	1	2.14	21.29	3.67	–	–	–	–	–	–	–	–	–	–	–	–
Martialia hyadesi	1	3.22	2	2.3	82.19	6.39	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Histioteuthis atlantica	1	3.22	2	2.3	45.94	3.57	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Galiteuthis glacialis	1	3.22	1	1.14	51.9	4.03	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total	–	–	87	–	1286	–	–	–	77	–	523	–	–	–	47	–	574.21	–	–	–	12	–	1769	–	–	–	44	–	269.6	–

From 2009 to 2013, there were no significant differences in the average size of LRL or ML for each species. In relation to the number of beaks found throughout the years for each species, there were significant differences only for *S. circumantarctica* between 2009 and 2010 versus 2012 (ANOVA: $F_{7,28} = 15.36$, $p < 0.01$).

3.2. Stable isotope analysis of *S. circumantarctica* (2009–2013)

Stable isotopic analysis showed no significant differences between the 2 sampling locations in both the $\delta^{13}C$ and $\delta^{15}N$ values (*t*-test: p = 0.34, p = 0.81, respectively), so these data were grouped. Individually, the values of $\delta^{13}C$ for *S. circumantarctica* ranged from −24.82‰ (2009) to −17.34‰ (2010) throughout the 5 years; 2009 and 2011 had the lowest $\delta^{13}C$ values, while 2012 had the highest values (Table 2). Indeed, values of $\delta^{13}C$ showed significant differences among the studied years (ANOVA: $F_{4,41} = 2.76$, p = 0.04) (Fig. 1). $\delta^{15}N$ values varied between +1.12‰ (2011) and +7.27‰ (2013), with more pronounced and significant differences than $\delta^{13}C$ values (ANOVA: $F_{4,\,41} = 10.26$, $p < 0.01$) (Fig. 1). The years 2009 and 2013 presented similar $\delta^{15}N$ values (+5.85 and +5.84‰, respectively), with the highest $\delta^{15}N$ values, while 2012 was the year with the lowest value (+3.42‰) (Table 2). There was no correlation between $\delta^{15}N$ values and LRL (Spearman correlation, r = −0.07, p = 0.61).

From the Bayesian mixing model, our ellipses showed a high overlap with all years except 2009

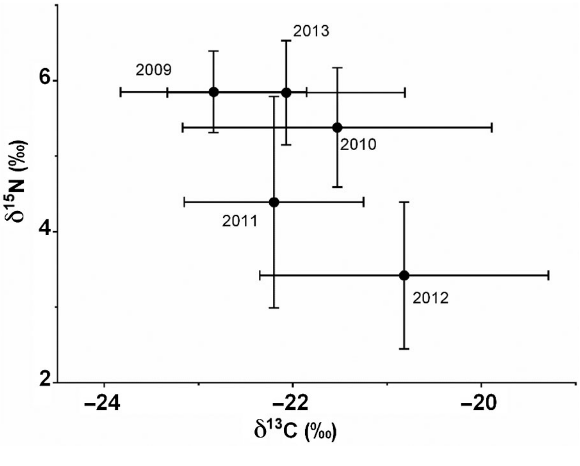

Fig. 1. Mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ values from the beaks of *Slosarczykovia circumantarctica* found in Antarctic fur seal scat, analysed for each year shown

Table 2. General characteristics of *Slosarczykovia circumantarctica* beaks found in Antarctic fur seal scat from South Georgia. Isotopic values of shown are the mean of the set for each year. LRL: lower rostral length

Year	n	LRL (mm)		$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)		C:N (mass ratio)
		Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD
2009	17	2.2 ± 0.4	1.8, 3.2	−22.8 ± 0.9	−24.8, −20.9	+5.85 ± 0.5	+4.8, +6.8	3.5 ± 0.2
2010	10	2.2 ± 0.2	1.9, 2.6	−21.5 ± 1.6	−23.2, −17.3	+5.38 ± 0.8	+4.3, +6.5	3.6 ± 0.3
2011	10	2.7 ± 0.2	2.3, 3.1	−22.2 ± 0.9	−23.6, −20.3	+4.39 ± 1.4	+1.1, +6.2	3.5 ± 0.3
2012	7	2.1 ± 0.3	1.6, 2.4	−20.8 ± 1.5	−24.0, −19.3	+3.42 ± 1.0	+2.4, +4.7	4.0 ± 0.4
2013	10	2.4 ± 0.2	2.1, 2.7	−22.1 ± 1.3	−24.4, −19.8	+5.84 ± 0.7	+4.8, +7.3	3.3 ± 0.1

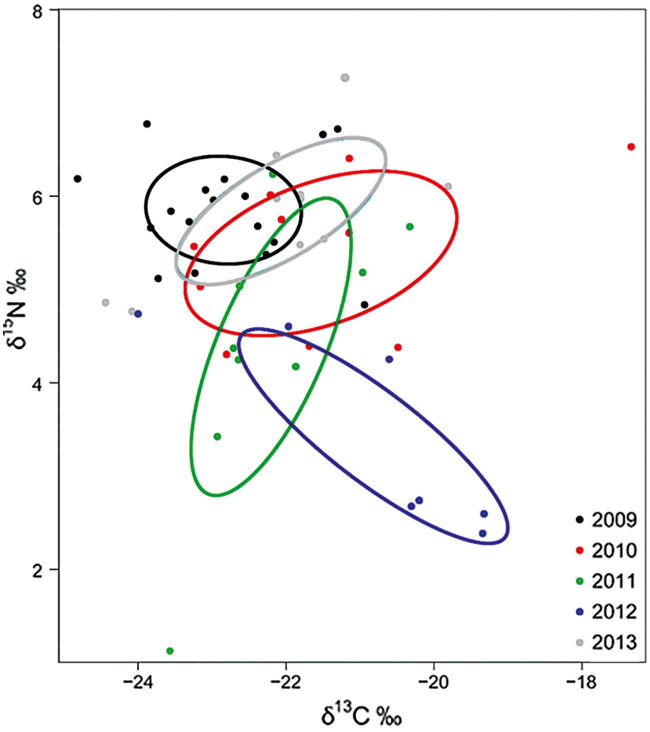

Fig. 2. Bayesian standard ellipse areas displayed for the lower beaks of *Slosarczykovia circumantarctica* found in Antarctic fur seal scat each year

and 2012, which exhibited zero overlap. Also in 2012, values of $\delta^{13}C$ and $\delta^{15}N$ were more separated from the rest (i.e. lower overlap with all the other years) (Fig. 2).

Comparing $\delta^{13}C$ values, *Paraledone turqueti* values were significantly higher than *S. circumantarctica* (all years) (t-test with Welch's correction: $t = 4.97$, $p < 0.001$) but there were also significant differences compared to *G. antarcticus* ($t = 2.40$, $p = 0.04$). However, when analysing $\delta^{13}C$ values, year-by-year significant differences were only found between *S. circumantarctica* and *G. antarcticus* in 2012 ($t = 2.94$, $p < 0.02$), and with *P. turqueti* in every year except 2012 ($t = 1.90$, $p = 0.08$) (Fig. 3).

3.3. Cephalopod prey, oceanographic conditions and Antarctic krill densities

The number of squids (mainly *S. circumantarctica*; see above) consumed by Antarctic fur seals contrasted with the density of krill over the 5 yr (Fig. 4). There was a negative correlation between krill density and the number of cephalopod beaks found in the fur seals' scat (Pearson's correlation, $r = -0.96$; $p < 0.02$).

During the summer months (breeding period of Antarctic fur seals) there were significant differences in SSTa across the 5 yr (ANOVA: $F_{4,8} = 34.65$, $p < 0.01$). The years 2009 (0.78 ± 0.30°C) and 2011 (0.44 ± 0.28°C) showed the highest (positive) values of SSTa, which means that SST was much higher relative to the average of 1981 to 2008. The years 2012 (−0.61 ± 0.46°C) and 2013 (−0.16 ± 0.39°C) had the lowest (negative) values of SSTa, as those were the coldest

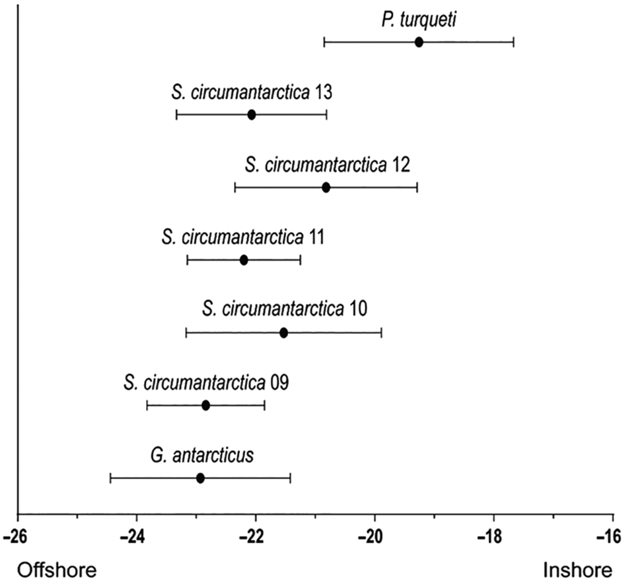

Fig. 3. Mean (±SD) $\delta^{13}C$ values of *Slosarczykovia circumantarctica* beaks found in Antarctic fur seal scat from the different years (09: 2009; 10: 2010; 11: 2011; 12: 2012; 13: 2013); *Pareledone turqueti* and *Gonatus antarcticus* are reference values for shelf and offshore waters, respectively

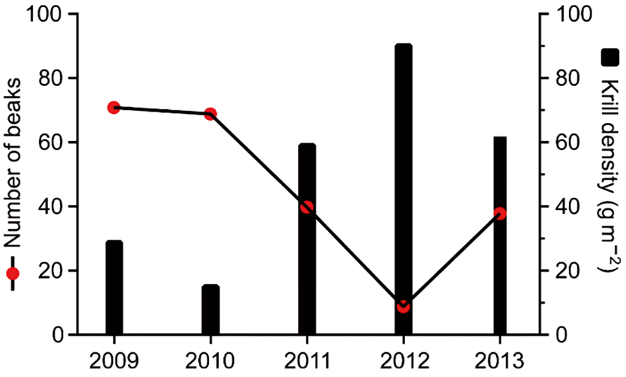

Fig. 4. Simplified relationship between density of Antarctic krill *Euphausia superba* (summer season) (black bars) and number of *Slosarczykovia circumantarctica* beaks collected in Antarctic fur seal scat (red circles) during the 5 yr study (2009–2013)

years. Although there was no significant relationship between SSTa and krill density (Pearson's correlation, r = −0.65, p = 0.23), the highest krill abundance occurred during the lower SST year (i.e. 2012).

Overall, the years with the lowest abundance of krill (e.g. 2009) were the years of the highest fur seal consumption of squid (mainly *S. circumantarctica*), which also corresponded to the unusually high SSTa.

4. DISCUSSION

This study provides detailed information on the cephalopod component of the Antarctic fur seal diet, as well as evidence of inter-annual variations over a 5 yr period (2009–2013). The differences seen among years in the diet were negatively correlated with krill abundance around South Georgia, in which the regional oceanographic conditions may also have had their influence (SSTa are associated with lower krill abundance around South Georgia; see below). Our results indicate that the squid *Slosarczykovia circumantarctica* was the most important cephalopod prey for Antarctic fur seals in all years studied. Also, to better understand this predator–prey interaction, we describe the habitat and trophic ecology of *S. circumantarctica* during this 5 yr period in relation to the foraging ecology of Antarctic fur seals.

4.1. Cephalopod component of Antarctic fur seal diet

All 8 species of cephalopods identified in the fur seal diet over the 5 yr of the study (Table 1) were pelagic squid species found at, and south of, the Antarctic Polar Front (APF) (Collins & Rodhouse 2006, Rodhouse et al. 2014, Xavier et al. 2016b). The 4 most common species (*S. circumantarctica*, *Psychroteuthis glacialis*, *Fillipovia knipovitchi* and *Kondakovia longimana*) showed no differences in either LRL or ML across all years. This suggests that Antarctic fur seals feed on prey of similar sizes, independent of prey availability or environmental conditions (Rodhouse et al. 1992a, Xavier et al. 2003). Indeed, these estimated prey sizes are in line with other studies from other Antarctic fur seals colonies (South Shetland Islands, Kerguelen Islands) (Daneri et al. 1999, 2008, Harrington et al. 2017).

S. circumantarctica was the most important squid species in the fur seals' diet (Table 1). This was expected, as it is one of the most abundant squid species in the Southern Ocean and is found near the surface, where fur seals are known to forage (Rodhouse et al. 1992a, Arthur et al. 2017). It is also the primary squid taken by fur seals at South Georgia and other colonies, as reported in previous studies (Reid 1995, Daneri et al. 1999, Staniland et al. 2007, Lea et al. 2008), and occurs in the diet of many other predators (Table A1 in the Appendix).

The squid species *Gonatus antarcticus*, *Histioteuthis atlantica* and *P. glacialis* were recorded for the first time in the diet of Antarctic fur seals at South Georgia (Table 1). Their previous absence in samples was probably due to changes in availability, the depth that *G. antarcticus* and *H. atlantica* inhabit (which is typically beyond the maximum diving range of the fur seals; <500 m) (Staniland & Boyd 2003, Collins & Rodhouse 2006) and/or due to the higher number of scats analysed here compared to previous studies. These opportunistic catches may have occurred during their daily vertical migration to the surface or in shelf areas where squid are constrained to shallower maximum depths (Collins & Rodhouse 2006, Rodhouse 2013). *P. glacialis* is an Antarctic squid distributed closer to the Antarctic continent, and it is very common in the diet of fur seals from southern colonies around the Antarctic Peninsula and South Shetland Islands (Daneri et al. 1999, Burdman et al. 2015). The occurrence of *P. glacialis* and *Galiteuthis glacialis*, species that are usually found further south, was possible due to the low krill abundance in that year. Low krill abundance in the shelf water zone can force predators to search in more distant waters for prey, therefore providing the opportunity to catch these oceanic squid species (Staniland & Boyd 2003, Collins & Rodhouse 2006, Staniland et al. 2007). Known warmer water species (i.e. *Martialia hyadesi* and *H. atlantica*) were found in the seals' diet only in 2009, a year typified by unusually high temperatures in inshore waters around South

Georgia, bringing these species closer to the island (Xavier et al. 2017). It appears that regional changes in water temperature have little effect on squid ecology, yet increased temperatures could act in favour of more northern species, which could be the case of these both species (Rodhouse 2013, Xavier et al. 2016b).

Of the 8 species of squid found in the fur seals' diet, *P. glacialis* and *G. glacialis* are considered to have a circumpolar distribution, inhabiting oceanic waters near the Antarctic continent (Filippova & Pakhomov 1994, Xavier et al. 2016b). *S. circumantarctica*, *G. antarcticus*, *K. longimana* and *F. knipovitchi* cover a large latitudinal range, inhabiting sub-Antarctic and Antarctic waters (Collins & Rodhouse 2006, Xavier et al. 2016b), in contrast to the 2 remaining species (*M. hyadesi* and *H. atlantica*) which inhabit warmer sub-tropical (oceanic and shallow) waters (Pereira et al. 2017). This distribution suggests that Antarctic fur seals typically feed on oceanic squid species, predominantly in offshore habitats.

4.2. Habitat and trophic ecology of *S. circumantarctica*

In the Southern Ocean, there is a well-defined $\delta^{13}C$ gradient, with values decreasing with latitude and increasing in shallow coastal waters (Jaeger et al. 2010, Guerreiro et al. 2015). Our mean $\delta^{13}C$ values from all years were higher than −22.9‰ (referring to the APF; Cherel & Hobson 2007, Jaeger et al. 2010), suggesting that our specimens were mainly of sub-Antarctic origin. However, our Bayesian mixing model revealed that *S. circumantarctica* occupies a vast range of habitats, with $\delta^{13}C$ values ranging from sub-Antarctic and/or shelf waters (−17.3‰) to very low latitudes corresponding to Antarctic waters (−24.8‰). Also, the high overlap in most of the years suggests that *S. circumantarctica* inhabit a relatively constant latitudinal range.

Values of $\delta^{13}C$ from *S. circumantarctica* reported from around Kerguelen Island were lower (−25.1‰; Cherel & Hobson 2005) than ours. Similarily, comparision of our $\delta^{13}C$ values with other Antarctic cephalopod species ($\delta^{13}C$ range: *Kondakovia longimana* −25.7 to −21.3‰; *G. antarcticus* −25.0 to −18.7‰) shows that *S. circumantarctica* can share the same habitat area (Guerreiro et al. 2015, Queirós et al. 2018). These results suggest that *S. circumantarctica* occupies both sub-Antarctic and Antarctic regions, and that the APF does not act as a biological barrier to the species (Collins & Rodhouse 2006, Rodhouse et al. 2014, Xavier et al. 2016b).

When comparing $\delta^{13}C$ values of *S. circumantarctica* to inshore and offshore species around South Georgia (*P. turqueti* and *G. antarcticus* as a reference for $\delta^{13}C$ values), the habitat of *S. circumantarctica* in 2012 (Fig. 3) was associated with inshore habitat, while in all the other years it was associated with offshore habitat. Indeed, there was a clear difference in values of $\delta^{13}C$ between 2009 and 2012. Such a result may possibly be due to 2012 individuals being sub-adults, inhabiting more inshore/shallow waters than the adults in 2009, since squid normally perform ontogenetic changes (Cherel & Hobson 2005). Early stages of development (e.g. sub-adults) are thought to inhabit inshore and shallow waters (which may have occurred during 2012), while as adults they move offshore and into deeper waters (Cherel et al. 2009, Golikov et al. 2018) (however, we note that carbon also can change with source waters from year to year) (Ceia et al. 2015). Although there was no difference in LRL size, 2012 presented the lowest average as well as the lowest recorded value. The $\delta^{15}N$ values also support this trend, with 2012 individuals having much lower values relative to the other years. In fact, our isotopic niches corroborate this hypothesis, as 2012 exhibited a major separation from the other years. It appears that the main habitat of *S. circumantarctica* is the oceanic / pelagic area, overlapping with the foraging range of Antarctic fur seals (Staniland & Boyd 2003, Staniland et al. 2007, Arthur et al. 2017).

Differences found in $\delta^{15}N$ values between the studied years (e.g. 2009 vs. 2012) may be related to changes in prey type, size, life stage, or changes in nitrogen cycling—patterns also found in other squid species throughout the world (Jennings et al. 2002, Seco et al. 2016b). Squid habitat could also be a reason for this difference, since the type of prey can change according to the type of habitat (e.g. moving more offshore or inshore, which indeed occurred in these years), thus causing changes in $\delta^{15}N$ values (Stowasser et al. 2012, Seco et al. 2016b). Their presence in the diet of various predators and the differences in carbon signatures suggests that *S. circumantarctica* may have a capacity to adapt to variations in oceanographic conditions. Since *S. circumantarctica* always occupied similar spatial habitats in our study, even during 2009 (the year with unusual oceanographic conditions), such results suggest that mesoscale changes in oceanographic conditions are unlikely to have an effect on the distribution of *S. circumantarctica* in our study region. Still, the influence of oceanographic conditions on the distribution and ecology of Antarctic squid remains little explored (Xavier et al. 2018). Given the predator–prey link between Antarctic fur seals and *S. circumantarctica*, it is important to understand if there is any relationship between fur seal consumption and *S. circumantarctica* habitat and trophic ecology.

Although the relationship was not statistically significant, there was an observed trend towards a higher consumption of *S. circumantarctica* by Antarctic fur seals when the squid are at a higher trophic level and associated with offshore environments. Also, the differences in stable isotopes suggest different habitats of *S. circumantarctica*: during 'good' krill abundance years, it is possible that Antarctic fur seals feed on krill closer to the colony, and on smaller amounts of squid inshore. During 'bad' krill abundance years, Antarctic fur seals feed more offshore, and include higher amounts of squid. Thus, isotope values can be indicators of the foraging that the fur seals are performing to feed (see below). This reasoning concurs with previous studies that have shown squid were only consumed by Antarctic fur seals on trips to offshore areas (Staniland & Boyd 2003, Staniland et al. 2007).

4.3. Cephalopod prey, oceanographic conditions and Antarctic krill densities

There were significant inter-annual variations in the consumption of squid (determined by number of beaks identified in seal scat) between 2009 and 2012. In fact, in 2009 the highest diversity (Table 1, Fig. 4; all 8 cephalopod species occurred) and the highest number of cephalopod beaks was recorded (n = 87). The squid species *M. hyadesi*, *H. atlantica* and *G. glacialis* appeared exclusively in this year. 2009 also had the highest SSTa (compared to the long-term average at South Georgia) (Whitehouse et al. 2008, Pereira et al. 2018). Indeed, one phenomenon that marks 2009 as unusual was the occurrence of one of the strongest El Niño Southern Oscillation (ENSO) events ever recorded (Hill et al. 2009). El Niño is a phenomenon characterised by high sea surface and air temperatures, which resulted in the unusual temperatures recorded around South Georgia. These high temperatures occurred for 9 consecutive months and coincided with extremely low catches in local fisheries and poor breeding success of top predators at South Georgia, including Antarctic fur seals (Hill et al. 2009, Fielding et al. 2014, Xavier et al. 2017). Our results showed that in years with low krill density there was higher consumption of squid by Antarctic fur seals, suggesting a degree of prey switching. Penguins and squid are known to offer an alternative and abundant energy source for Antarctic fur seals breeding on other sites, such as the Antarctic Peninsula, in years of low availability of krill (Daneri et al. 2008). This apparent prey switching or foraging niche expansion and change in the feeding behaviour of Antarctic fur seals in years of low krill abundance has been observed in other species breeding on South Georgia, including Gentoo penguins *Pygoscelis papua*, macaroni penguins *Eudyptes chrysolophus* and grey-headed albatrosses *Thalassarche chrysostoma* (Waluda et al. 2010, Horswill et al. 2016, Xavier et al. 2013, 2017). In contrast, during 2012, a year characterized by low temperatures and high levels of marine productivity in inshore waters (Fielding et al. 2014, this study), there was a high abundance of krill in the waters of South Georgia. This was the year with the lowest consumption and diversity of squid, supporting the hypothesis that squid (particularly *S. circumantarctica*) is an alternative prey for Antarctic fur seals in years of low krill abundance.

The Commission for the Conservation of Antarctic Living Resources (CCAMLR) have developed management strategies for Antarctic fisheries, such as krill, by including the relationships between prey ingested by predators and the populations of target species (Constable 2002, 2011). Our results describe changes in the feeding behaviour of Antarctic fur seals regarding squid consumption that appear to be influenced by oceanographic conditions and krill abundance, although other factors (e.g. prey availability, predator's ability to catch prey) can affect these relationships. An understanding of prey switching (squid or other prey items) and alternative energetic pathways within the food web are important in any ecosystem-based management program — especially for an abundant predator such as the Antarctic fur seal. We have also demonstrated how these animals can be used to sample the marine environment and aid in our understanding of more cryptic species.

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Appendix

Fig. A1. Measurement of lower rostral length (LRL) of beaks of *Slosarczykovia circumantarctica* found in Antarctic fur seal scat

Table A1. Presence of *Slosarczykovia circumantarctica* in the diet of Antarctic top predators among different sites on Southern Ocean. (FO: percentage of beaks of *S. circumantarctica* relative to the total number of cephalopod beaks found)

Predator	Location	FO (%)	N	Source
Antarctic fur seal *Arctocephalus gazella*	South Georgia (winter)	50	1	Reid (1995)
	South Georgia (summer)	28.57	2	Reid & Arnould (1996)
	South Shetland Islands	60	9	Daneri et al. (1999)
	South Shetland Islands	25	2	Harrington et al. (2016)
	South Orkney Islands	78.78	26	Daneri et al. (1999)
	Kerguelen Islands	70.58	12	Lea et al. (2008)
Elephant seal *Mirounga leonina*	King George Island	5.68	24	Piatkowski et al. (2002)
	King George Island	13.98	27	Burdman et al. (2015)
	Heard Island	2.70	40	Slip (1995)
	Heard Island	1.31	7	Green & Burton (1993)
	Macquarie Island	2.19	25	Green & Burton (1993)
	South Georgia	17.94	192	Rodhouse et al. (1992a)
Weddell seal *Leptonychotes weddellii*	McMurdo Sound	82.97	39	Burns et al. (1998)
Grey-headed albatross *Thalassarche chrysostoma*	Prince Edward Island	1	3	Richoux et al. (2010)
Wandering albatross *Diomedea exulans*	South Georgia	0.2	25	Xavier et al. (2003)
White-chinned petrel *Procellaria aequinoctialis*	Crozet Islands	42	16	Connan et al. (2007)
Antarctic prion *Pachyptila desolata*	Kerguelen Islands	19.75	16	Cherel et al. (2002)
Patagonian toothfish *Dissostichus eleginoides*	Crozet Islands	13.11	115	Cherel et al. (2004)
	Kerguelen Islands	2	28	Cherel et al. (2004)
	South Georgia	6.74	12	Xavier et al. (2002)
	South Georgia	7.20	12	Pilling et al. (2001)
Lanternshark *Etmopterus* cf. *granulosus*	Kerguelen Islands	18.75	3	Cherel & Duhamel (2004)
Sleeper sharks *Somniosus* cf. *microcephalus*	Kerguelen Islands	2	11	Cherel & Duhamel (2004)
Macaroni penguin *Eudyptes chrysolophus*	South Georgia	13.60	3	Croxall et al. (1999)
Gentoo penguin *Pygoscelis papua*	South Georgia	100	3	Croxall et al. (1999)
	South Georgia	7	4	Xavier et al. (2017)
	South Georgia	40	2	Xavier et al. (2018)

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