



# NEW INSIGHTS INTO THE TROPHIC ECOLOGY OF SOUTH AMERICAN FUR SEALS BREEDING AT THE FALKLAND ISLANDS

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PREPARED BY NOEMIE FRISCOURT

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## VERSION CONTROL

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3. The holder of proprietary environmental knowledge of the South Atlantic – by continuing to provide the research expertise offered to date.

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## EXECUTIVE SUMMARY

This report presents updated insights into the trophic ecology of South American fur seals (SAFS) breeding in the Falkland Islands, using stable isotope analysis of whiskers to reconstruct individual foraging histories over the past decade. Despite overlapping habitat use, males and females exhibit distinct feeding strategies, with males foraging at higher trophic levels and displaying broader isotopic niches. However, trophic preferences are not strictly sex-specific, as some males showed generalist diets while others were more specialized. Female foraging patterns varied with the breeding cycle and timing of *Doryteuthis gahi* (known locally as loligo) fishing season. Long-term isotopic trends indicate that SAFS have adapted their diet and foraging areas in response to shifting prey availability driven by changes in local fisheries. Declines in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values between 2011 and 2015 reflect a dietary shift to lower-trophic prey like rock cod and Falkland herring, while post-2016 increases in  $\delta^{15}\text{N}$  suggest greater reliance on higher-trophic species such as hake and squid. A sharp drop in isotopic values in 2023 likely signals reduced availability of these key prey items, especially for males, who may be more vulnerable to changes in fishery dynamics and anthropogenic pressures.

## INTRODUCTION

The South American fur seal (*Arctocephalus australis*, hereafter 'SAFS') is a widely distributed marine predator, breeding along the coasts of South America and offshore islands, including the Falkland Islands (Cárdenas-Alayza et al. 2016, Crespo & de Oliveira 2021). Historically, the SAFS was heavily exploited for the fur trade over the past two centuries, leading to a drastic population decline (Crespo et al. 2015, Crespo & de Oliveira 2021). However, recent surveys indicate a recovery, with the Falklands now hosting the largest breeding population (Crespo et al. 2015, Baylis et al. 2019). Despite their ecological importance, the SAFS remains one of the least studied otariid species, particularly in the Falkland Islands, with knowledge of their diet relying on a limited number of studies (Baylis et al. 2014, Baylis et al. 2018a, Jones et al. 2020a, Riveron et al. 2021), and consequently, substantial knowledge gaps remain regarding diet temporal, spatial and sex-based variation (van der Grient et al. 2023).

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Previous dietary studies based on scat analysis indicate that fish dominate SAFS diets, including Falkland herring (*Sprattus fuegensis*) and rock cod (*Patagonotothen* spp.), while squid *Doryteuthis gahi* (known locally as *loligo*), and crustaceans (lobster krill; *Grimothea gregaria*), play a secondary role (Baylis, 2013). Foraging behaviour and diet studies suggest significant differences between colonies and seasons likely driven by variations in prey availability and environmental conditions (Thompson et al. 2003, Baylis et al. 2014, Baylis et al. 2018a). In addition, foraging strategies may also vary at the individual level due to factors such as sex, body size, age, and energetic demands associated with reproductive cycles (de Lima et al. 2021, Riveron et al. 2021) and has implication for capacity to buffer against environmental variability (Bolnick et al. 2003, Araujo et al. 2011).

Obtaining direct information on marine predator diet and habitat use is challenging, particularly for species spending most of their lives at sea, but recent advancements in biochemical tracers (e.g. stable isotopes, DNA metabarcoding) have allowed researchers to address knowledge gaps on the feeding ecology of marine predators (Pethybridge et al. 2018, Trueman & St John Glew 2019, Bestley et al. 2020). Stable isotope analysis is a powerful approach, as it provides information on the food that has been assimilated by the organism, rather than just ingested (Tieszen et al. 1983). The isotopic methodology is based on the predication that stable isotope ratios in the proteins of consumers reflect those of the proteins in their diet in a predictable manner (Hobson & Clark 1992, Hobson et al. 1994). Nitrogen isotope ratios ( $\delta^{15}\text{N}$ ) generally indicate the consumer trophic position, as they increase with trophic level due to the preferential retention of  $^{15}\text{N}$  in body tissues and the excretion of  $^{14}\text{N}$  in waste products (DeNiro & Epstein 1981, Minagawa & Wada 1984, Post 2002). In contrast, carbon isotope ratios ( $\delta^{13}\text{C}$ ) provide information on the geographic origin of prey, as  $\delta^{13}\text{C}$  values varies with latitude and between inshore and offshore regions (Popp et al. 1999, Cherel & Hobson 2007). By analysing  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values from fur seal whiskers, which are metabolically inert and grow continuously over multiple years, we can reconstruct individual foraging histories, track seasonal or interannual shifts in diet, and assess individual specialisation (Cherel et al. 2009, Newsome et al. 2010, Kernaleguen et al. 2015a, de Lima et al. 2021).

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Marine predators are valuable ecological indicators of the status of lower trophic levels and effective tools to monitor changes in remote oceanic environments (Young et al. 2015, Hazen et al. 2019). Monitoring the diet and foraging behaviour of these predators is crucial for understanding their role in food webs, predicting the impacts of environmental changes, and informing effective management and conservation strategies (Boyd et al. 2007). The Falkland Islands marine ecosystem is experiencing increasing pressures from commercial fisheries and hydrocarbon exploration which may impact SAFS populations through direct (e.g. entanglement, pollution) and indirect interaction (e.g. spatial and trophic overlap) (Baylis et al. 2014, Baylis et al. 2018b, Baylis et al. 2021, Riaz et al. 2023, Riaz et al. 2024a). Adult SAFS forage within both the Argentinian and Falkland Islands Exclusive Economic Zone, overlapping with fishing areas and increasing the potential for interactions between seals and fisheries (Baylis et al. 2018b, Riaz et al. 2023, Riaz et al. 2024a). Notably, loligo are important prey for SAFS, are also targeted by local Falkland fisheries. A recent surge in observed SAFS–fishery interactions around the Falklands has raised concerns about potential competition for these shared resources (Baylis et al. 2014, Riaz et al. 2024a, Riaz et al. 2024b). In addition, given the strong environmental variability in the South Atlantic marine ecosystem and its susceptibility to climate change (van der Grient et al. 2023), it is crucial to monitor the diet of SAFS over the years, as well as assess the degree of individual variability within the population to better understand their adaptability to environmental change. This report provides an update in our understanding of the diet of adult South American fur seal breeding in the Falklands Island, using bulk table isotope on male and female whiskers samples. Our aim is to investigate sex-specific and temporal (seasonal and interannual) variations in diet and habitat use, and to quantify individual specialization within and between sexes.

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## METHODS

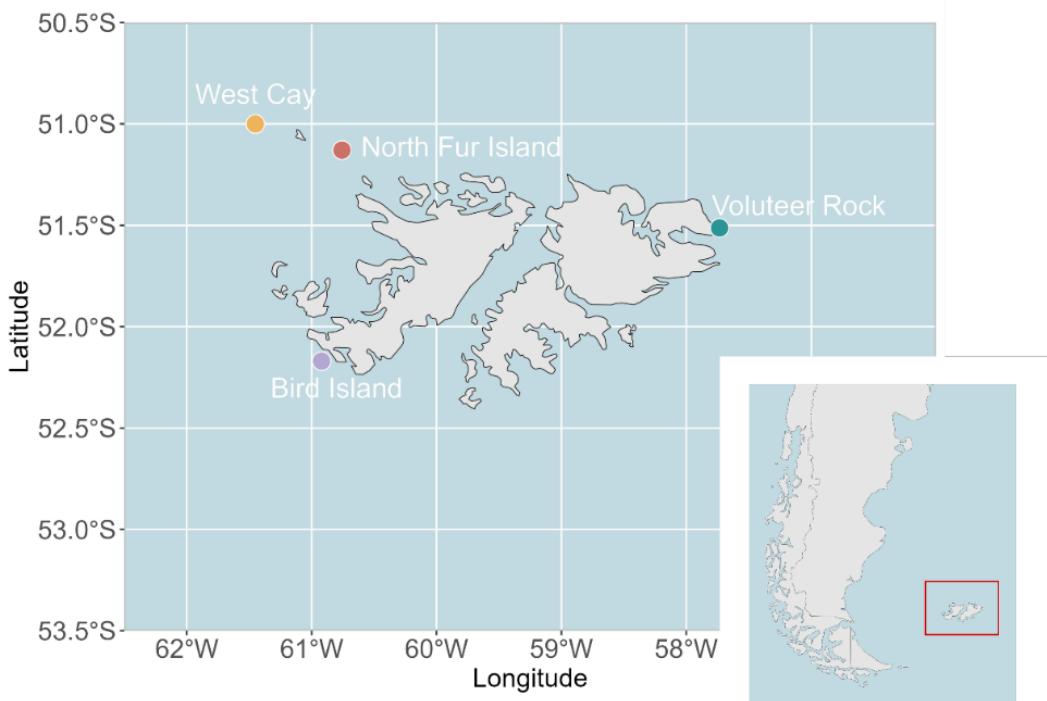
### 1.1. STUDIED SITES AND SAMPLING

The study was conducted in the Falkland Islands, South Atlantic, in 2015, 2017, 2018 and 2023. A total of 34 whiskers were collected from several SAFS breeding colonies (Table 1): North Fur Island (51.13° S, 60.76°W), Volunteer Rocks (51.51° S, 57.73°W), West Cay (51.00° S, 61.45°W), Bird Island (52°17 S, 60°92 W; Fig. 1) and 15 whiskers were sampled from SAFS by-caught at sea. The longest whiskers were removed by snipping it as close to the skin as possible using cutting pliers. The samples were labelled and stored dry in plastic bags until laboratory analysis.

**Table 1.** Locations and number of South American fur seal (*Arctocephalus australis*) whisker samples collected by year and sex at the Falklands Island.

Year	Colony	Sex	Number of whiskers
2015	North Fur island	Female	6
		Male	2
	Volunteer Rock	Male	4
2017	By-caught at sea	Male	6
2018	Bird Island	Female	8
	West Cay	Female	6
	By-caught at sea	Male	9
2023	Bird Island	Male	9

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**Figure 1.** Sample locations of South American fur seals (*Arctocephalus australis*; SAFS) at the Falkland Islands in the South Atlantic: Bird Island ( $n = 17$ ), North Fur Island ( $n = 8$ ), Volunteer Rock ( $n = 4$ ), West Cay ( $n = 6$ ). Nine additional samples were from SAFS by-caught at sea.

## 1.2. STABLE ISOTOPE ANALYSIS

Whiskers were cleaned prior to analysis using a sponge and 95% ethanol followed by an ultrasonic bath of distilled water for 5 min (Kernaleguen et al. 2012, Kernaleguen et al. 2015b). Each whisker was inspected under a microscope for any remaining contaminants and, if necessary, the cleaning process repeated. Vibrissae then were cut into 5 mm long consecutive segments starting from the proximal (facial) end (Baylis et al. 2018a, Riveron et al. 2021). Each 5mm whisker segment were subsample to achieve a target mass of 0.5 mg (based on the requirements of the isotope ratio mass spectrometer), packed into tin containers. Stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopes values of samples from 2015 were analysed by a Carlo-Erba elemental analyser interfaced with a Finnigan Delta Plus XP mass spectrometer (Stable Isotope Laboratory, University of California Santa Cruz, USA), and by a Thermo-Fisher-Scientific Delta XP Plus Isotope Ratio Mass Spectrometer (Scottish Universities Environmental Research Centre, Scotland, United Kingdom) for samples from 2017,

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2018 and 2023. Measurement precision (in standard deviation) was based on within-run replicate measures of the laboratory standards (Light Stable Isotope Lab: pugel, and Scottish Universities Environmental Research Centre: GEL, ALAGEL and GLYGEL). Samples published in Baylis et al. (2018a) had a precision of 0.03‰ for  $\delta^{13}\text{C}$  and 0.06‰ for  $\delta^{15}\text{N}$ , samples analysed in Riveron et al. (2021), had a precision of < 0.17‰ and < 0.22‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively. Stable isotope ratios were measured in parts per mil (‰) deviation from international standards (Vienna-Pee Dee belemnite for carbon and atmospheric air N<sub>2</sub> for nitrogen) according to the following equation:  $\delta X = [(R_{\text{sample}}/ R_{\text{standard}}) - 1] \times 1000$ ; where X is  $^{15}\text{N}$  or  $^{13}\text{C}$  and R is the corresponding ratio of  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ .

## 1.3. DATA ANALYSIS

All analyses were conducted in R version 4.3.0 (R Core team, 2023). As a control for the quality of keratin, we measured the carbon-to-nitrogen ratios (C:N) of each sample (Table 1). The average C:N ratios for whisker segments ranged from 2.7 to 3.5 (mean  $\pm$  SD:  $2.9 \pm 0.1$ ; Table 1), indicating good data quality (Newsome et al. 2010). One sample with a C:N ratio  $> 3.8$  (C:N = 5.1) were excluded from the analysis. One female (No tag, sampled in 2018), has one extreme  $\delta^{13}\text{C}$  value of -18.7‰. While this could represent an outlier, the C:N mass ratio was within acceptable limits, and the value is consistent with those reported for SAFS breeding and foraging over the south part of the Patagonian shelf (Vales et al. 2020), and previous tracking from SAFS from Falkland showed that adult female SAFS forage over the Patagonian shelf (Riaz et al. 2023, Riaz et al. 2024b), suggesting a potential long-distance foraging event for this individual. To avoid biasing broader trends and interpretations, this data point was excluded from subsequent analyses.

**Intra- and inter-annual variability.** We assigned each vibrissae segment to a specific month, based on the tissue growth rate for this species (female: 0.08 mm day<sup>-1</sup>, Lima et al. 2019; male: 0.13 mm day<sup>-1</sup>, Vales et al. 2015), assuming linear and continuous growth for otariid (Hirons et al. 2001, Cherel et al. 2009, McHuron et al. 2016). The date of sample collection was considered the approximate endpoint of tissue synthesis at the vibrissae base. To account for the portion of the whisker that remains under the skin (approximately 5 mm; Baylis A., personal communication), 62 days were added to all time estimates. In addition, each whisker segment was assigned to two

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seasonal categories: one based on the fur seal breeding cycle (breeding season: November–January; post-breeding season: February–October), and another based on the *Doryteuthis gahi* (known locally as *loligo*) fishing (first season: February–May; second season: August–October; or outside the fishing season; Riaz et al. 2024a).

To evaluate the effects of sex, season, year and colony of origin on isotopic values, we applied Linear Mixed Effects Models (LMMs). To account for repeated measures on the same individuals we used individual as random effects. We initially fit a full linear mixed-effects model including interactions between sex, year, and season:  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C} \sim 1 + \text{sex} + \text{season} + \text{year} + \text{sex:season} + \text{sex:year} + (1 | \text{seal})$ . However, the model was rank-deficient due to unbalanced sampling across sex-year combinations, leading to unstable estimates. We therefore retained a simplified model with no interactions,  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C} \sim 1 + \text{sex} + (1 | \text{year}) + (1 | \text{seal})$ , and further explored temporal patterns using separate models for each sex:  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C} \sim 1 + \text{breeding cycle} + \text{loligo fishing season} + \text{year} + \text{colony} + (1 | \text{seal})$ .

**Diet – potential preys.** To explore the potential prey of SAFS we compared the whisker stable isotope values with isotopic values of known or likely prey species reported in previous studies from the Patagonian shelf region (Vales et al. 2015, Handley et al. 2017). These prey species included Falkland herring, rock cod, loligo, lobster krill, common hake (*Merluccius hubbsi*), and southern blue whiting (*Micromesistius australis*; Table 2). Prey values were adjusted for trophic discrimination using  $3.3 \pm 0.3\text{‰}$  for  $\delta^{13}\text{C}$  and  $3.7 \pm 0.3\text{‰}$  for  $\delta^{15}\text{N}$  (Stricker et al. 2015, Beltran et al. 2016), allowing direct comparison with seal values.

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**Table 2.** Mean and standard deviation of the stable isotope values of potential prey of the South American fur seal breeding in the Falkland Islands.

Prey	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Citation
Falkland herring ( <i>Sprattus fuegensis</i> )	$-18.4 \pm 1$	$11.4 \pm 0.5$	Handley et al. (2017)
Rock cod ( <i>Patagonotothen spp.</i> )	$-15.9 \pm 0.3$	$18.6 \pm 0.2$	Vales et al. (2015)
Rock cod ( <i>Patagonotothen ramsayii</i> )	$-18 \pm 0.2$	$12.1 \pm 0.5$	Handley et al. (2017)
Patagonian longfin squid ( <i>Doryteuthis gahi</i> )	$-17.6 \pm 0.4$	$15.7 \pm 0.6$	Vales et al. (2015)
Lobster krill ( <i>Munida gregaria</i> )	$-15.7 \pm 0.8$	$16.8 \pm 0.3$	Vales et al. (2015)
	$-17.4 \pm 0.2$	$12.5 \pm 0.2$	Handley et al. (2017)
Lobster krill ( <i>Munida subrugosa</i> )	$-15.6 \pm 0.3$	$11.9 \pm 0.2$	Handley et al. (2017)
Argentine Short fin squid ( <i>Illex argentinus</i> )	$-17.0 \pm 0.6$	$13.7 \pm 0.8$	Vales et al. (2015)
Argentine Hake ( <i>Merluccius hubbsi</i> )	$-16.8 \pm 0.2$	$16.6 \pm 0.1$	Vales et al. (2015)
	$-18.1 \pm 0.1$	$15.3 \pm 0.1$	Handley et al. (2017)
Southern blue whiting ( <i>Micromesistius australis</i> )	$18.6 \pm 0.4$	$11.2 \pm 0.5$	Handley et al. (2017)

**Individual specialization.** In the past, resources and habitat have been investigated at the population or species level, individuals of a population considered to be ecologically equivalent (Bolnick et al. 2003). However, more recent research has emphasized the importance of exploring ecological variations among individuals within populations (Layman et al. 2007, Araujo et al. 2011). To assess individual specialization in adult female AFS, we calculated a specialization index (S), which quantifies the degree to which individuals use a subset of the population's niche based on within (WIC) and between-individual (BIC) dietary variation (Roughgarden 1972, Roughgarden 1974, Bearhop et al. 2004, Newsome et al. 2012). We estimated BIC as the variance of  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  values across all individuals of the same sex and WIC as the variance within an individual's whisker of the same sex. The specialization index was calculated as  $S = \text{WIC}/(\text{WIC} + \text{BIC})$ , ranging from 0 to 1.

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Individuals were classified as generalists ( $S > 0.5$ ) or specialists ( $0 < S < 0.5$ ) (Hückstädt et al. 2012, Baylis et al. 2015). The specialisation index was estimated for both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  and separately for males and females. To address potential biases in the classification of specialization groups due to variation in whisker length, we tested for correlations between whisker length and specialization index using a Pearson's correlation test. Results showed that the relationship was not significant ( $\delta^{13}\text{C}$   $p=0.9195$ ;  $\delta^{15}\text{N}$   $p= 0.568$ ) and confirmed the reliability of our specialization index.

**Isotopic niche size and overlap.** To compare isotopic niche size and overlap between sexes, we used the R package nicheROVER (Swanson et al. 2015), which estimates a probabilistic niche region in a Bayesian framework. Niche regions were defined as the portion of the  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  isotopic space where the probability of finding an individual from a given group (male or female) is equal to a user-defined threshold. We used 40% and 95% niche regions to represent the core and global niche, respectively. Posterior distributions of group-specific parameters were generated using non-informative priors and 10,000 draws. Niche overlap was estimated as the probability that a randomly drawn individual from one group falls within the niche region of another, yielding asymmetrical overlap metrics.

## 2. RESULTS

We analysed 910 segments from 49 whiskers of adult South American fur seals, including 23 from females and 26 from males. Whiskers represented between 1.4 and 5.4 years per individual (mean  $\pm$  SD:  $2.7 \pm 0.6$  years for males;  $3.6 \pm 0.8$  years for females). Male  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values ranged from 12.5 to 18.3% and from  $-17.6$  to  $-14.0\%$  respectively (Table 3). Female values ranged from 12.2 to 18.3 % for  $\delta^{15}\text{N}$  and from  $-16.8$  to  $-14.1\%$  for  $\delta^{13}\text{C}$  (Table 3). We observed regular oscillations of  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  in numerous individuals of both sex (Fig. 2), with more pronounced fluctuations in  $\delta^{15}\text{N}$  compared to  $\delta^{13}\text{C}$ .

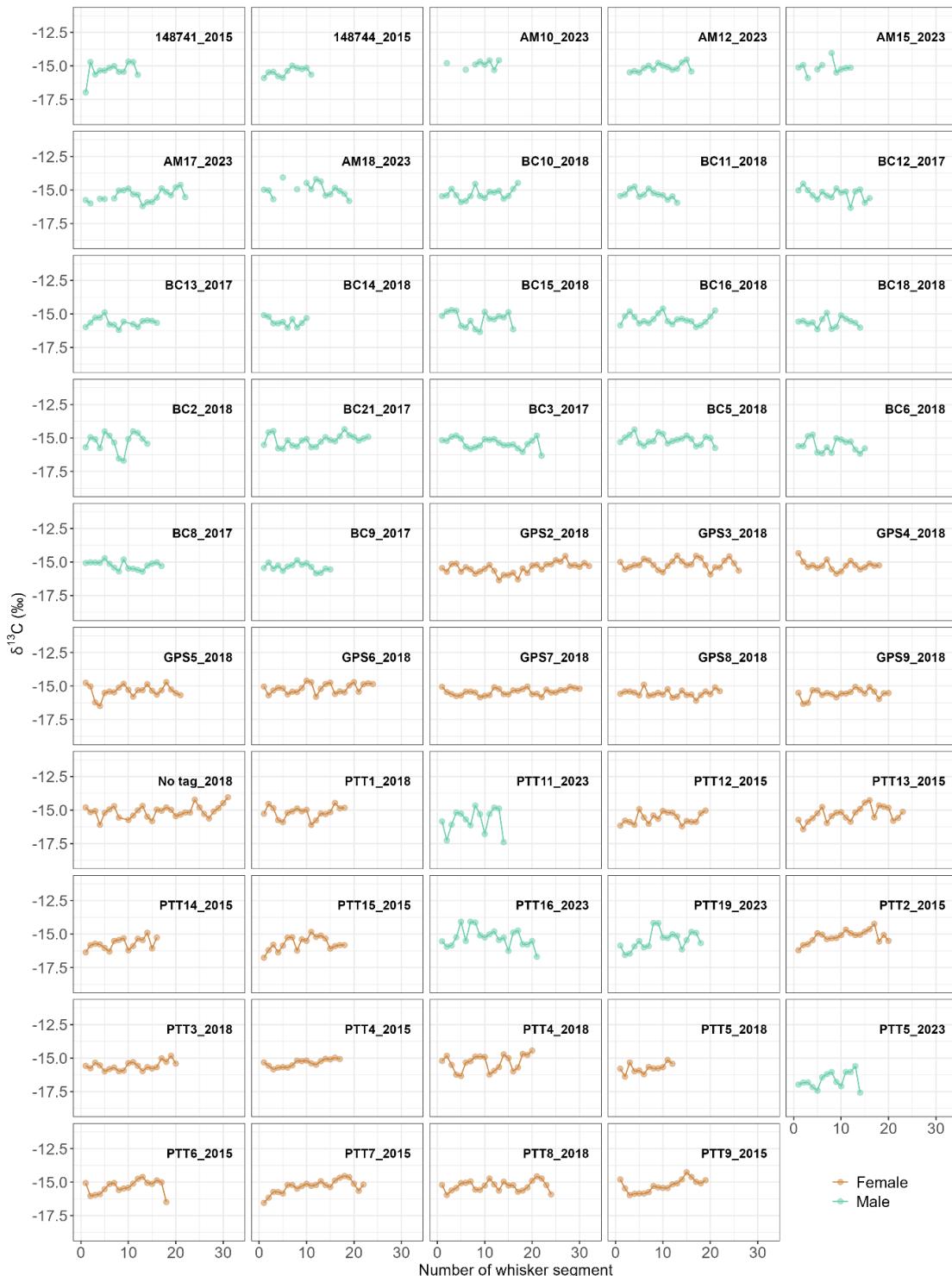
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**Table 3.** Stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope values and C:N mass ratio of segmented whiskers from 49 adult male and female South American fur seals (*Arctocephalus australis*) from the Falkland Islands. Seals were sampled in 2015, 2017, 2018 and 2023 (see Table 1).

	Number of individuals	Number of whiskers segments	C:N mass ratio	Whiskers bulk isotopic values			
				$\delta^{15}\text{N}$ (‰)	Mean $\pm$ SD	Min   Max	$\delta^{13}\text{C}$ (‰)
<i>Population</i>	49	910	2.9 $\pm$ 0.1	14.6 $\pm$ 1.0	12.2   18.3	-15.4 $\pm$ 0.5	-17.6   -14.0
<i>Sex</i>							
Female (♀)	23	420	2.9 $\pm$ 0.0	14.2 $\pm$ 0.9	12.2   18.3	-15.4 $\pm$ 0.8	-16.8   -14.1
Male (♂)	26	490	2.9 $\pm$ 0.1	15.0 $\pm$ 1.1	12.5   18.3	-15.4 $\pm$ 1.1	-17.6   -14.0
<i>Breeding season</i>							
Female (♀)	23	83	2.9 $\pm$ 0.1	14.4 $\pm$ 0.8	12.6   16.9	-15.5 $\pm$ 0.5	-16.5   -14.3
Male (♂)	26	94	2.9 $\pm$ 0.1	15.0 $\pm$ 1.3	12.6   18.0	-15.3 $\pm$ 0.6	-17.4   -14.1
<i>Non-Breeding season</i>							
Female (♀)	23	406	2.9 $\pm$ 0.1	14.2 $\pm$ 0.9	12.2   18.2	-15.3 $\pm$ 0.5	-16.8   -14.1
Male (♂)	26	327	2.9 $\pm$ 0.1	15.0 $\pm$ 1.1	12.5   18.3	-15.4 $\pm$ 0.6	-17.6   -14.1
<i>Year</i>							
2011 (♀)	3	8	2.9 $\pm$ 0.1	15.3 $\pm$ 0.8	14.5   16.3	-15.4 $\pm$ 0.3	-15.8   -15.1
2012 (♀)	9	47	2.8 $\pm$ 0.1	15.1 $\pm$ 1.0	13.5   18.3	-15.1 $\pm$ 0.5	-16.5   -14.2
2013 (♀ + ♂)	16	81	2.9 $\pm$ 0.1	14.8 $\pm$ 0.8	13.0   17.6	-15.3 $\pm$ 0.4	-16.3   -14.1
2014 (♀ + ♂)	26	119	2.9 $\pm$ 0.1	14.4 $\pm$ 1.0	12.5   17.3	-15.4 $\pm$ 0.4	-16.4   -14.2
2015 (♀ + ♂)	35	134	2.9 $\pm$ 0.1	14.1 $\pm$ 0.9	12.2   17.3	-15.4 $\pm$ 0.5	-17.0   -14.4
2016 (♀ + ♂)	29	165	2.9 $\pm$ 0.0	14.4 $\pm$ 1.0	12.6   17.7	-15.4 $\pm$ 0.4	-16.7   -14.5
2017 (♀ + ♂)	29	158	2.9 $\pm$ 0.0	14.5 $\pm$ 0.9	12.6   17.0	-15.3 $\pm$ 0.4	-16.5   -14.4
2018 (♀ + ♂)	23	49	2.9 $\pm$ 0.0	14.6 $\pm$ 1.0	12.8   18.0	-15.3 $\pm$ 0.4	-16.3   -14.3
2019 (♂)	1	1	3.1 $\pm$ NA	15.7 $\pm$ NA	NA	-15.5 $\pm$ NA	NA
2020 (♂)	5	22	2.9 $\pm$ 0.1	15.1 $\pm$ 1.0	13.5   17.2	-15.3 $\pm$ 0.5	-16.7   -14.7
2021 (♂)	9	47	2.9 $\pm$ 0.0	15.2 $\pm$ 1.3	13.1   18.0	-15.4 $\pm$ 0.7	-17.6   -14.2
2022 (♂)	9	54	2.9 $\pm$ 0.0	15.4 $\pm$ 1.2	13.4   18.3	-15.3 $\pm$ 0.8	-17.4   -14.0
2023 (♂)	9	25	2.9 $\pm$ 0.0	14.9 $\pm$ 1.2	12.6   18.0	-15.9 $\pm$ 0.7	-17.3   -14.8

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**Figure 2.** Oscillations in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values along the length of the whisker of adult female (orange) and male (turquoise) South American fur seals (*Arctocephalus australis*) from Falkland Island. Top panel,  $\delta^{13}\text{C}$  values; bottom panel,  $\delta^{15}\text{N}$  values.

# NEW INSIGHTS INTO THE TROPHIC ECOLOGY OF SOUTH AMERICAN FUR SEALS BREEDING AT THE FALKLAND ISLANDS

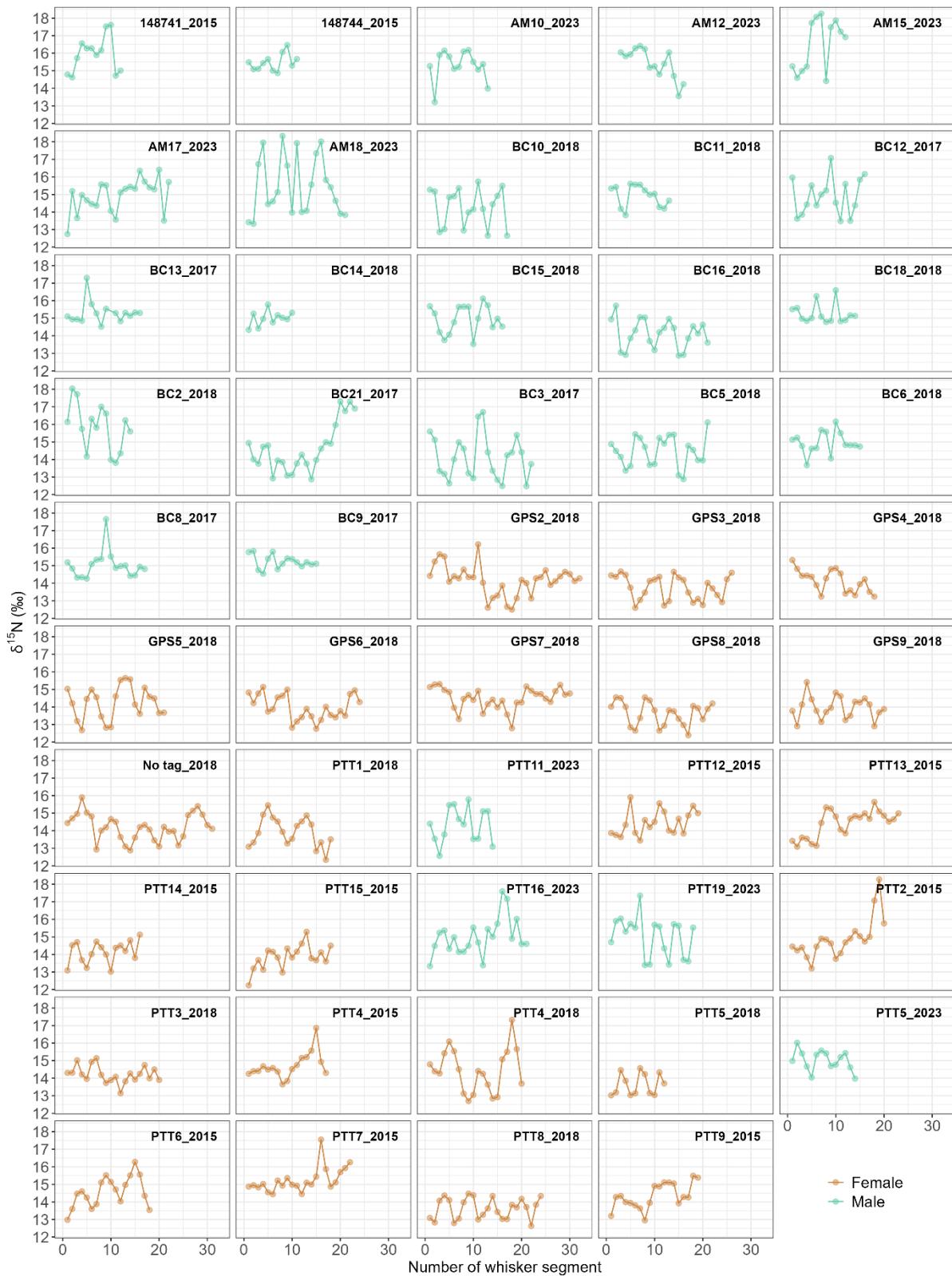
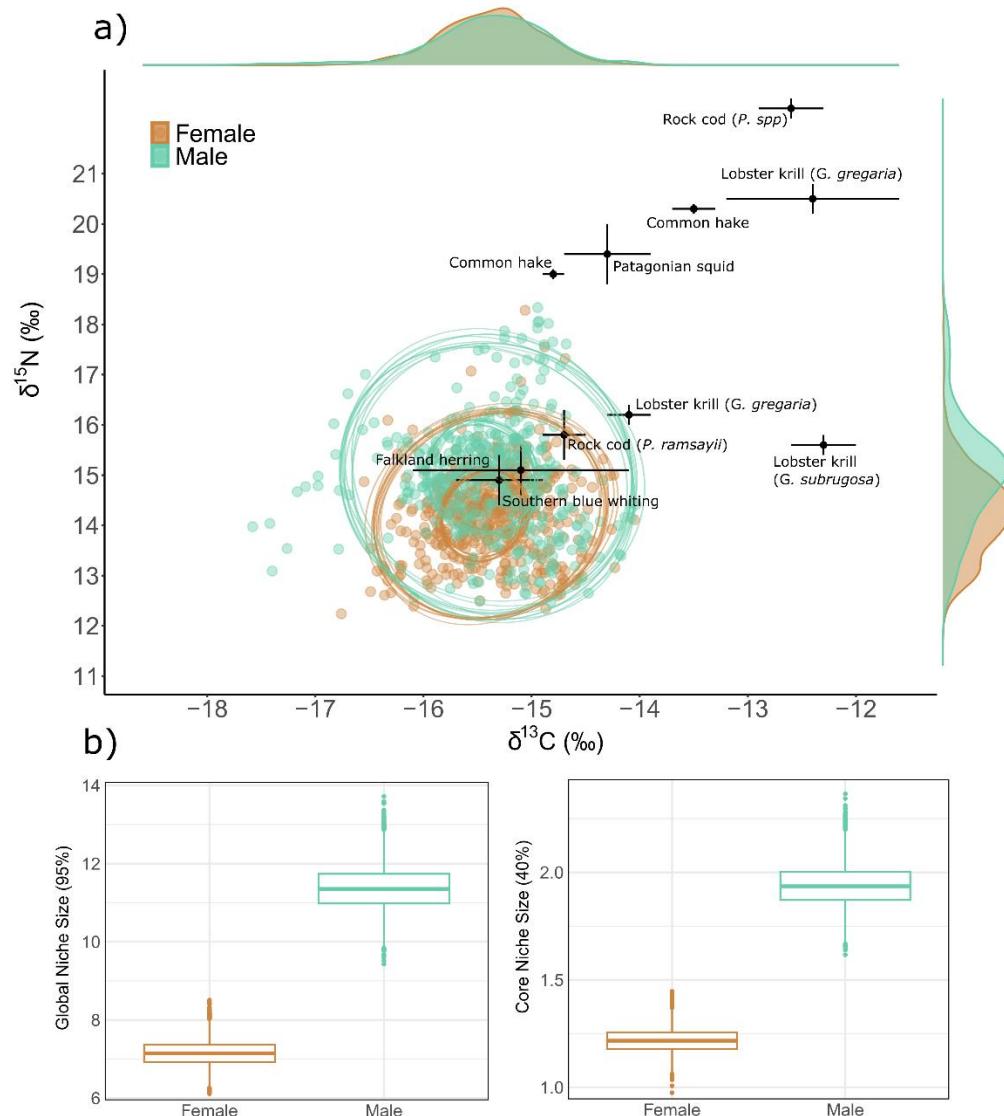


Figure 2. Bottom panel.

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*Potential preys.* Rock cod, Falkland herring, and Southern blue whiting emerged as primary prey, followed by lobster krill, with common hake and Patagonian squid contributing to a lesser extent (Figure 3).



**Figure 3.** a) Variability in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of whiskers of female and male South American fur seal (*Arctocephalus australis*) from Falkland Islands ( $n=49$ ). The estimated 40% (inner, core niche) and 95% (outer, global niche) random ellipses are also shown for both sex. Ten thousand random ellipses were generated for each sex but for clarity only the first 1000 are shown in this figure. Density curves for each isotope and each sex are also drawn marginally along the corresponding axis. b) Boxplot comparing isotopic niche region areas ( $\text{‰}^2$ ) between females and males for the 95% (global niche) and 40% (core niche) thresholds. Sample size is 1000 for each group, based on the random elliptical projections that were generated from this study. Bivariate isotopic signals of the potential prey shown as mean  $\pm$  SD, once corrected in accordance with the corresponding trophic discrimination factor (see the Method section for more information). The two hake values represent Hake from different regions.

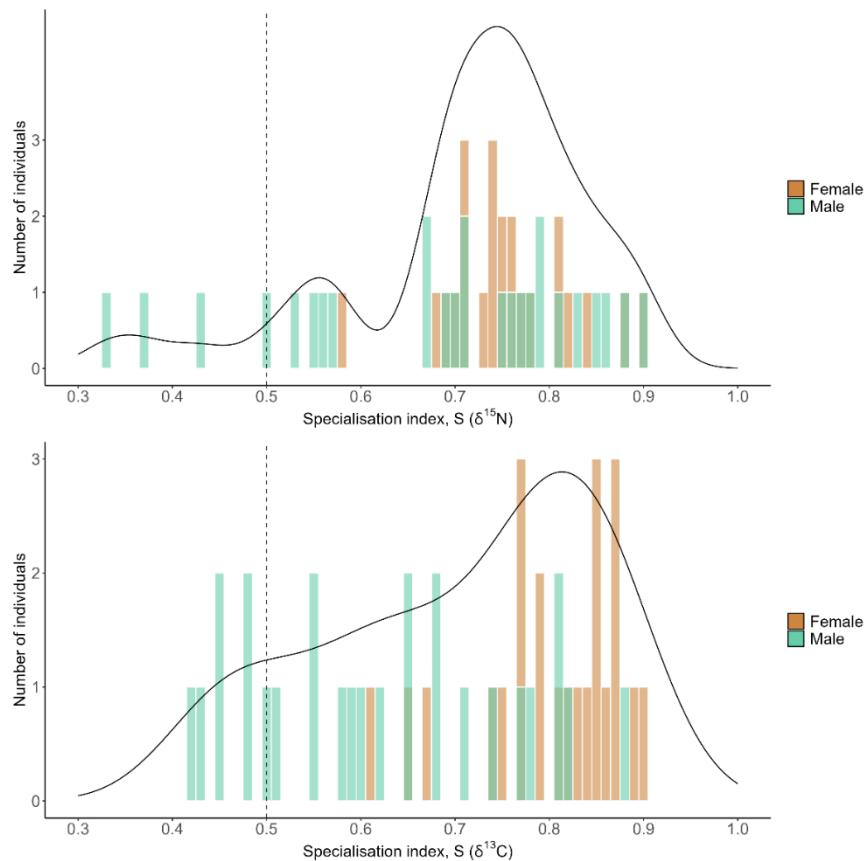
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*Sex-based differences.* There were significant differences in mean  $\delta^{15}\text{N}$  values between female and male South American fur seals, with males having significantly higher  $\delta^{15}\text{N}$  values ( $14.2 \pm 0.9 \text{‰}$  vs.  $15.0 \pm 1.1 \text{‰}$ , respectively, p-value  $<0.0001$ , Table 3 and 4). No significant differences in  $\delta^{13}\text{C}$  values were detected between sex. Niche size estimates differed between sexes (Fig. 3). Males had a larger 95% niche area compared to females, and the same pattern was observed in the 40% core niche size (Fig 3). Niche overlap between sexes was asymmetrical, with 97% of the female niche fell within the male niche, while only 25% of the male niche overlapped with the female niche at the 95% probability level. This pattern was consistent when using the 40% core niche region, with reduced overlap values (43.8% for females into males; 21% for males into females), indicating limited overlap in core dietary space between sexes. These results suggest that males occupy a broader isotopic niche than females, with females using a more restricted subset of the male niche space. Individual specialization indexes showed that SAFS from this population range from extreme specialist to generalist in both diet and habitat use and that there are significant differences between sex. We detected significant differences in  $\delta^{13}\text{C}$  values among females from different colonies. Females from Bird Island had higher  $\delta^{13}\text{C}$  values compared to those from North Fur Island and Volunteer Rock, while females from West Cay also showed higher values than those from Volunteer Rock and North Fur Island. No significant differences were observed among males.

The  $\delta^{13}\text{C}$  specialisation index ranged from 0.61 to 0.90 ( $0.80 \pm 0.08$ ) for females and 0.42 to 0.88 ( $0.62 \pm 0.13$ ) for males, while  $\delta^{15}\text{N}$  specialisation index ranged from 0.58 to 0.90 ( $0.75 \pm 0.07$ ) for females and 0.33 to 0.90 ( $0.68 \pm 0.15$ ) for males (Fig. 4). These results indicate that, although most of the individual are generalist, males exhibited a wider range of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  specialization index values. This suggests greater heterogeneity in individual foraging strategies among males.

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**Figure 4.** Frequency distribution of the individual specialization index ( $S$ ) for  $\delta^{15}\text{N}$  (top panel) and  $\delta^{13}\text{C}$  values (bottom panel) in adult female and male South American fur seals (*Arctocephalus australis*) from Falkland Island ( $n=49$ ). Individuals with  $0 < S < 0.5$  are considered specialists, while those with  $S > 0.5$  are classified as generalists.

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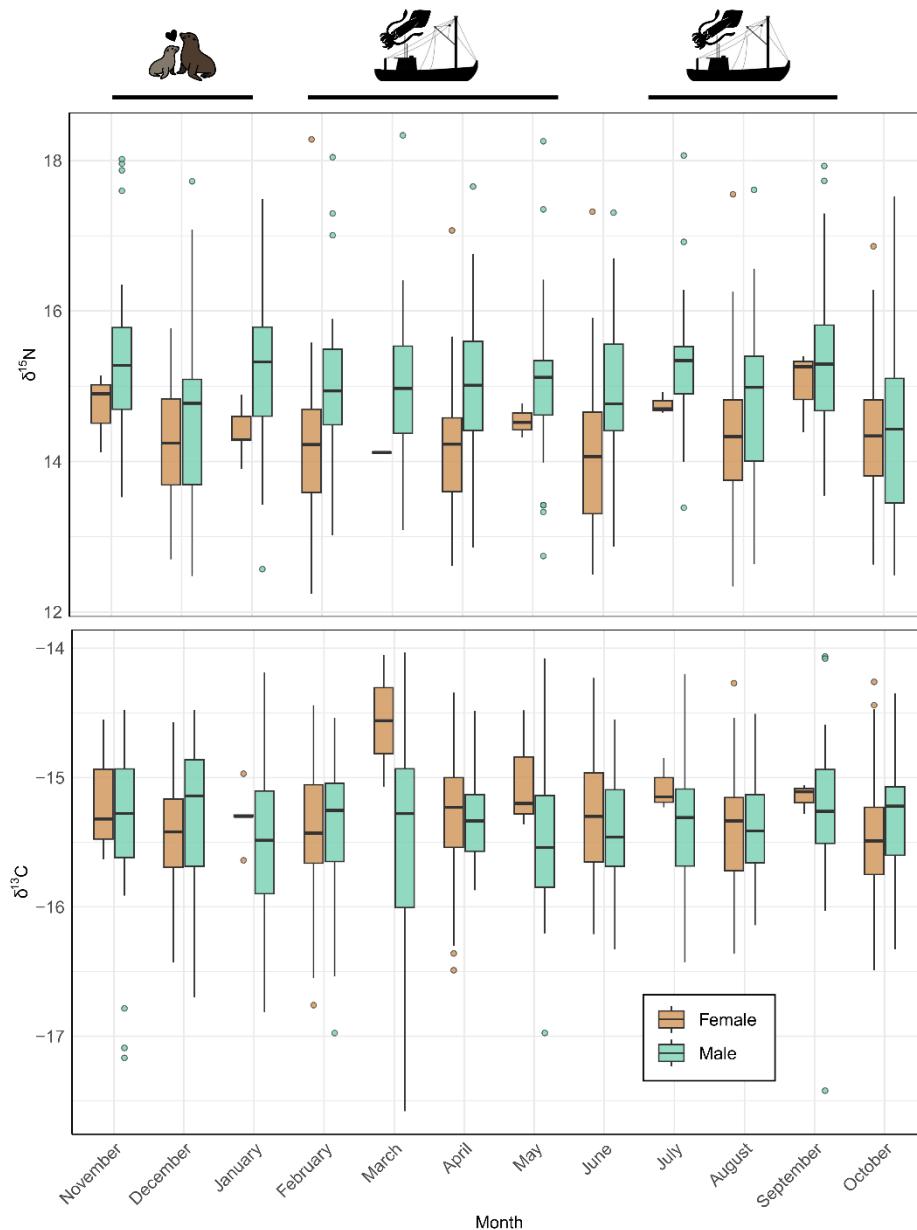


*Intra-annual variations.* No significant variation between months in  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  values were detected (Fig. 5). Females showed higher  $\delta^{13}\text{C}$  values during the post-breeding seasons compared to the breeding season ( $p\text{-value} = 0.0138$ ), and lower  $\delta^{13}\text{C}$  values during the second loligo fishing season compared to both the first season and period out of the fishing season (0.00614 and 0.03955 respectively, Table 4, Fig. 6).

**Table 4.** Results of linear mixed models on  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in adult female and male South American fur seals (*Arctocephalus australis*) whiskers, followed by a Tukey's post hoc test for pairwise comparisons to test significant differences between sex, year, breeding cycle and *Doryteuthis gahi* (known locally as loligo) fishing season. Only significant differences are reported.

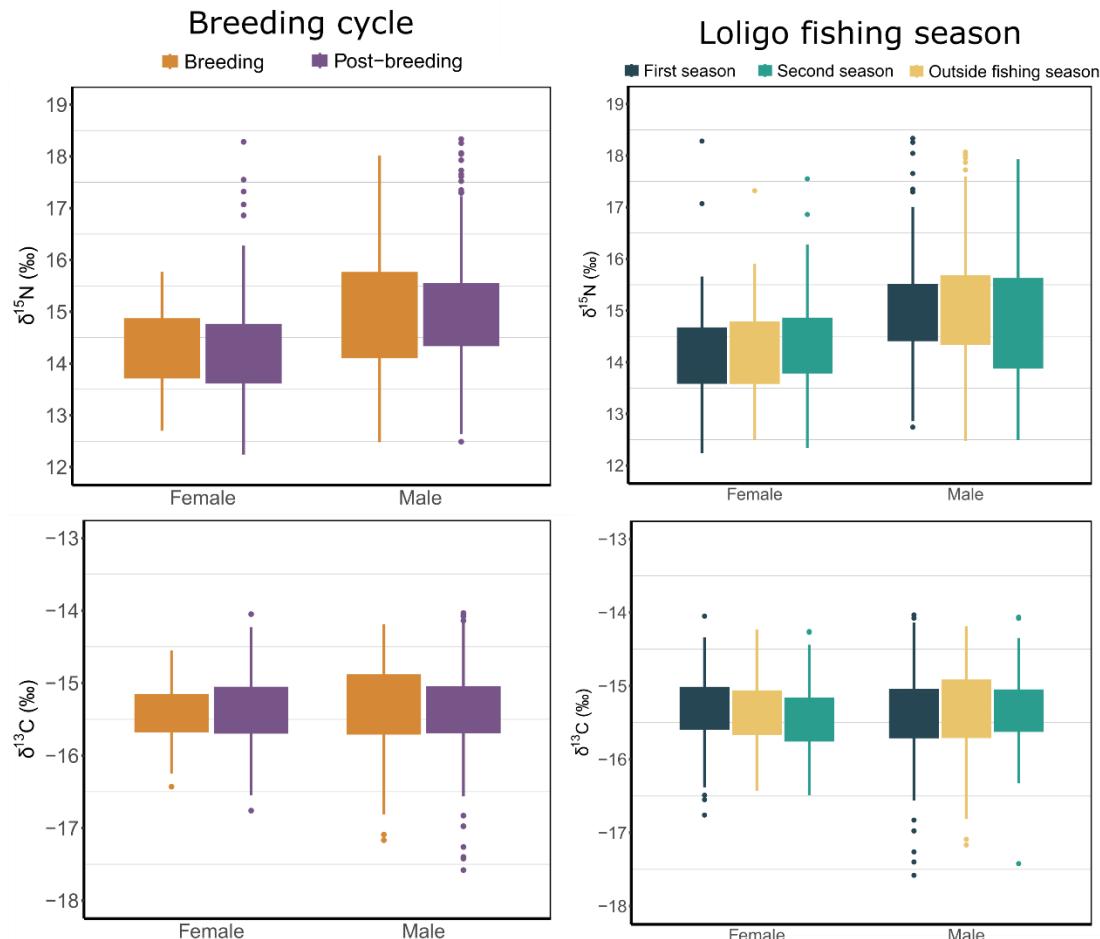
SAFS POPULATION $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ ~ 1 + sex + (1   year) + (1   seal)							
Comparison	$\delta^{15}\text{N}$ Estimate (%)	Std. Error	p-value	Comparison	$\delta^{13}\text{C}$ Estimate (%)	Std. Error	p-value
Male - Female	0.9299	0.1374	<0.0001	NS	NS	NS	NS
FEMALES SAFS $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ ~ 1 + breeding cycle + loligo fishing season + year + colony + (1   seal)							
Comparison	$\delta^{15}\text{N}$ Estimate (%)	Std. Error	p-value	Comparison	$\delta^{13}\text{C}$ Estimate (%)	Std. Error	p-value
2014 - 2011	-1.08	0.27	0.00157	Post-breeding - Breeding	0.15	0.06	0.0138
2015 - 2011	-1.43	0.28	0.00343	Second season - First season	-0.14	0.04	0.00614
2016 - 2011	-1.24	0.35	<0.001	Second season - Outside fishing season	-0.13	0.05	0.03955
2017 - 2011	-0.93	0.28	0.01941	North Fur Island - Bird Island	-0.38	0.10	<0.001
2018 - 2011	-0.94	0.31	0.04664	Volunteer Rock - Bird Island	-0.61	0.11	<0.001
2013 - 2012	-0.45	0.13	0.01657	West Cay - Volunteer Rock	0.43	0.10	<0.001
2014 - 2012	-0.88	0.13	<0.001	West Cay - North Fur Island	0.65	0.11	<0.001
2015 - 2012	-1.24	0.15	<0.001	2014 - 2011	-1.08	0.27	0.00157
2016 - 2012	-1.06	0.15	<0.001	2015 - 2011	-1.43	0.28	<0.001
2017 - 2012	-0.74	0.15	<0.001	2016 - 2011	-1.25	0.28	<0.001
2018 - 2012	-0.74	0.19	0.00259	2017 - 2011	-0.93	0.28	0.01941
2014 - 2013	-0.43	0.11	0.00305	2018 - 2011	-0.94	0.31	0.04664
2015 - 2013	-0.79	0.13	<0.001	2013 - 2012	-0.45	0.13	0.01657
2016 - 2013	-0.61	0.13	<0.001	2014 - 2012	-0.40	0.13	<0.001
2015 - 2014	-0.36	0.11	0.03249	2015 - 2012	-0.49	0.15	<0.001
2017 - 2015	0.50	0.11	<0.001	2016 - 2012	-0.51	0.15	<0.001
2018 - 2015	0.50	0.16	0.03647	2017 - 2012	-0.63	0.15	<0.001
				2018 - 2012	-0.51	0.19	<0.001
				2014 - 2013	-0.30	0.11	<0.001
				2015 - 2013	-0.40	0.13	<0.001
				2016 - 2013	-0.42	0.13	<0.001
				2015 - 2014	-0.36	0.11	0.03249
				2017 - 2015	0.50	0.11	<0.001
				2018 - 2015	0.50	0.16	0.03647
MALE SAFS $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ ~ 1 + breeding cycle + loligo fishing season + year + colony + (1   seal)							
Comparison	$\delta^{15}\text{N}$ Estimate (%)	Std. Error	p-value	Comparison	$\delta^{13}\text{C}$ Estimate (%)	Std. Error	p-value
2015 - 2014	-0.88	0.24	<0.01	2023 - 2021	-0.46	0.12	<0.01
2022 - 2015	0.89	0.26	0.0265	2023 - 2022	-0.60	0.12	<0.01
2023 - 2022	-0.81	0.24	0.0223				

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**Figure 5.** Monthly variation in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values for adult male and female South American fur seals (*Arctocephalus australis*) whiskers from Falkland Islands. The fur seal breeding cycle (breeding: Nov–Jan; post-breeding: Feb–Oct) and *Doryteuthis gahi* (known locally as loligo) fishing seasons (Feb–May, Aug–Oct) are indicated for context.

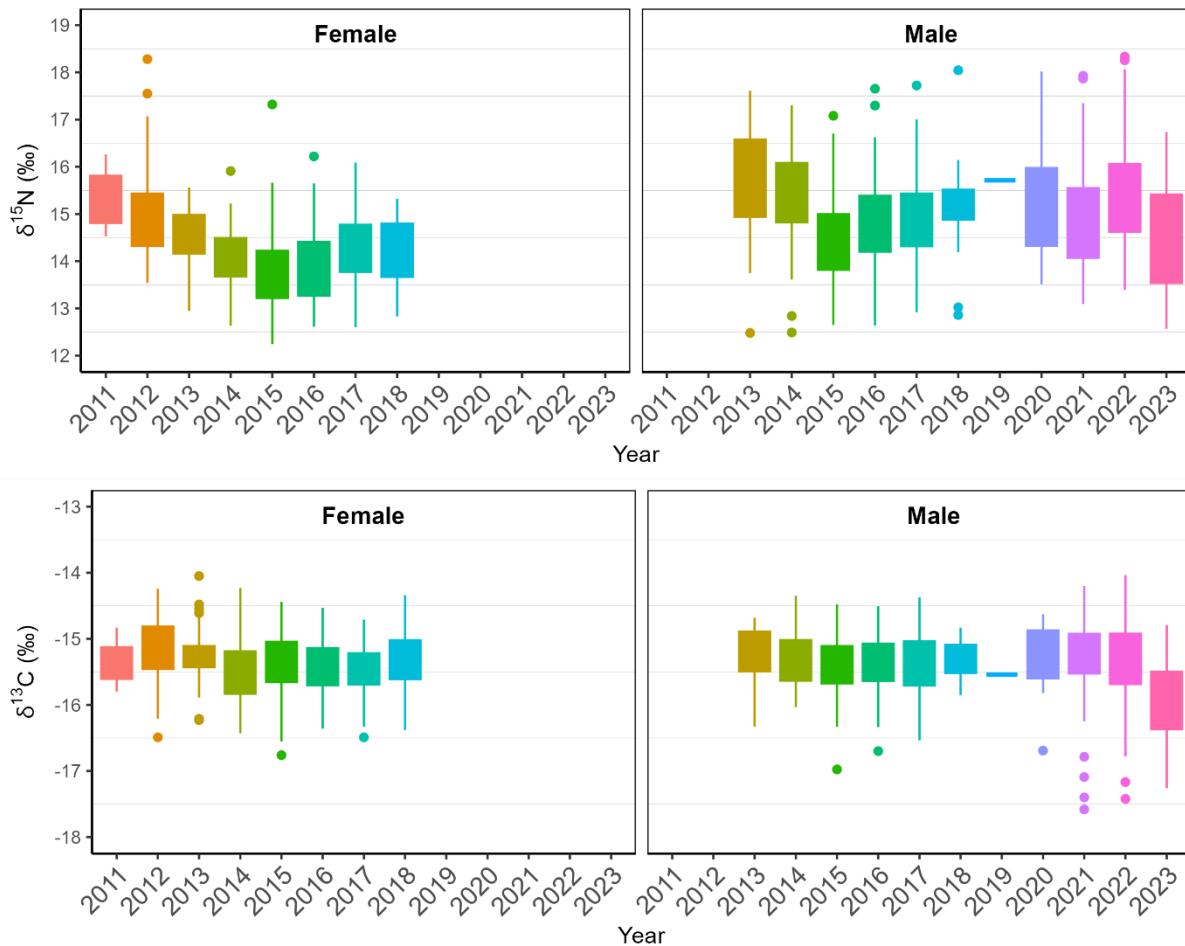
# NEW INSIGHTS INTO THE TROPHIC ECOLOGY OF SOUTH AMERICAN FUR SEALS BREEDING AT THE FALKLAND ISLANDS



**Figure 6.** Variation in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values for adult male and female South American fur seals (*Arctocephalus australis*) whiskers from Falkland Islands, depending on the breeding cycle (breeding: Nov–Jan; post-breeding: Feb–Oct) and *Doryteuthis gahi* (known locally as loligo) fishing seasons (Feb–May, Aug–Oct).

**Inter-annual variations.**  $\delta^{15}\text{N}$  values in female SAFS showed a significant decreasing trend from 2011 to 2015, followed by relatively stable values in 2016 and a slight increase in subsequent years (Table 4; Fig. 7). Males exhibited a similar but less pronounced pattern, with a significant decline in  $\delta^{15}\text{N}$  values in 2015 and a notable increase in 2022 compared to 2015, followed by a significant decrease in 2023 (Table 4; Fig. 7). In males,  $\delta^{13}\text{C}$  values remained relatively stable until a significant decrease in 2023 (Table 4; Fig. 7), while in females,  $\delta^{13}\text{C}$  values were higher in the first half of the study period (2012–2015) compared to the second half (2015–2018; Table 4; Fig. 7).

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**Figure 7.** Variation in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in adult female and male South American fur seals (*Arctocephalus australis*) whiskers from Falkland Island from 2011 to 2023.

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## DISCUSSION

This report provided updated information on the trophic ecology of the South American fur seal breeding at the Falkland Island, using whiskers as a record of the individuals' foraging history.

Despite similar habitat use, our results highlight sex-specific differences feeding habits, with males foraging at higher trophic levels and exhibiting a broader isotopic niche than females. We found trophic preferences that are not strictly sex-based, with males ranging from specialist to generalist. Our analysis revealed that female South American fur seals use different feeding grounds depending on the breeding cycle and the timing of the loligo fishing season. Overall, decadal variation in isotopic values suggests that SAFS adjusted their diet and foraging areas in response to the shifting abundance of key prey species, potentially as an adaption to change in finfish stock in the last decade.

Vibrissae revealed regular oscillations of  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  in numerous individuals, implying that individual regularly change their diet and migrate between isotopically distinct areas. The more pronounced oscillations in  $\delta^{15}\text{N}$  compared to  $\delta^{13}\text{C}$  may indicate stronger temporal changes in diet than in foraging location. Isotopic values of both males and females fell within the range of potential prey previously identified in scat analyses (Baylis et al. 2014), including primarily Falkland herring, southern blue whiting, and rock cod. Lobster krill appeared to contribute to a lesser extent, while a small subset of individuals (mostly males) possibly include common hake and Patagonian squid in their diet.

Our results revealed sex-based difference in trophic preferences. Isotopic values of male SAFS were more enriched in  $^{15}\text{N}$ , diverging from females in the isotopic space, and resulting in male having bigger isotopic niche than females. Males have broader range of prey compared to females, targeting preys of higher trophic levels, probably common hake and Patagonian squid. Dietary differences between adult male and females SAFS are consistent with those seen in other breeding locations including Uruguay and Brazil (de Lima et al. 2019) and other pinniped species with sexual size dimorphism (Kernaleguen et al. 2012, Kernaleguen et al. 2015b, Jones et al.

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2020b). SAFS have strong sexual dimorphism in body size with males being three times larger than females. This larger body size and greater prey-handling capacity may allow males to access larger, higher trophic level prey. Moreover, male and female will also have distinct foraging opportunities during to breeding constraint. Indeed, females narrower niche size could be due to more constraint to central place foraging when taking care of the pup, as foraging trips are limited by the fasting ability of offspring (Thompson et al. 2003). During this period, females may consume lower trophic level prey that is easier to capture or in higher abundance to meet their energetic requirements. Male and female SAFSs exhibited similar  $\delta^{13}\text{C}$  values, suggesting comparable latitudinal foraging ranges, consistent with tracking studies showing that both sexes use similar areas along the Patagonian shelf and shelf break (Baylis et al. 2018b, Riaz et al. 2023). However, we detected a seasonal shift in  $\delta^{13}\text{C}$  values among females, with post-breeding periods associated with higher  $\delta^{13}\text{C}$  values. This pattern may reflect a change in habitat feeding grounds more enriched in  $^{13}\text{C}$ , possibly toward more coastal or higher-latitude areas during the post-breeding period. Foraging trip of adult females vary during the 10 months of lactation, generally becoming longer as the pup grows older (Thompson et al. 2003). Compared to other studies on SAFS, we found a higher isotopic niche overlap between males and females than reported for Brazilian populations (de Lima et al. 2021). Additionally, our females exhibited a broader niche than those in Riveron et al. (2021), despite being from the same population. This highlights the importance of using a sufficient sample size and multi-year data to capture the full extent of individual and population-level variability.

Although characterized as a generalist predator in the past, recent studies have described a more complex picture of the trophic ecology of SAFS (de Lima et al. 2021, Riveron et al. 2021, de Lima et al. 2023). We observed contrasting degrees of individual trophic specialisation both between and within sexes, with specialisation index value of adult male SAFS suggesting higher inter-individual variability, with some males functioning as specialists while others adopt more generalist foraging behaviours. Trophic individual specialisation is common in pinnipeds (Kernaleguen et al. 2015b, Kernaleguen et al. 2016, Cormack et al. 2023), including SAFS (Franco-Trecu et al. 2014, de Lima et al. 2019, de Lima et al. 2021, Riveron et al. 2021). Our findings are consistent with studies from

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SAFS population breeding at higher latitude (Uruguay, Brazil and Argentina), showing that trophic generalist populations are composed of specialist and generalist individuals. Several factors may underlie the observed individual specialization observed. Colony differences among females suggest that local environmental conditions may influence their foraging strategies, consistent with findings from Baylis et al. (2018a). In contrast, no such spatial differences were observed in males, indicating that other mechanisms may drive the variation from specialists to generalists within this group. Previous studies have linked body mass to dietary variation in SAFS (Vales et al. 2015). Larger males may access different, deeper-dwelling prey such as common hake, which occur at greater depths than herring or southern blue whiting (Macchi et al. 2021, van der Grient et al. 2023), possibly contributing to individual specialization. As the SAFS population at the Falkland Island is still growing (Baylis et al. 2019) some individuals may exploit a specific resource and maximize their foraging success and fitness to relax intra-specific competition (Bolnick et al. 2003). Our findings may also not solely reflect intraspecies competition but could extend to interactions with other marine predator species breeding on the Falkland Islands. Trophic overlap between SAFS and other upper-trophic level marine predators at the Falkland Islands is likely (Baylis et al. 2014). For example, Gentoo penguins (*Pygoscelis papua*) at the Falkland Islands exhibit stomach content and stable isotope values similar to those of SAFS, indicating comparable trophic positions, diet and foraging habitats (Handley et al. 2017).

Decadal variation in isotopic values suggests that SAFS have adjusted their diet and foraging habitat over time, likely in response to the shift in abundance of key prey species and the potential impacts of local fisheries. Spatiotemporal shifts in the Falkland Islands trawl fishery from 2011–2023 led to major changes in catch composition, affecting species that are also targeted by SAFS, including rock cod, Patagonian longfin squid, blue whiting and common hake (Baylis et al. 2018b, Riaz et al. 2024a). This have increased the potential for interactions and trophic overlap between the SAFS and local fisheries (Riaz et al. 2024a). Over the past decade, shifts in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in South American fur seals have closely mirrored changes in local fisheries. From 2011 to 2015, declining  $\delta^{15}\text{N}$  values (especially in females) coincided with the rise of rock cod as the dominant catch, suggesting a shift to lower-trophic prey. Over the same period,  $\delta^{13}\text{C}$  values slowly decline,

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indicating a shift in foraging behaviour to more pelagic and northerly areas. After 2016, as rock cod declined, and the fishery transitioned to higher-trophic species like common hake and Patagonian squid.  $\delta^{15}\text{N}$  values began to rise at the same period suggest increased inclusion of those species in their diet and overlap with current fishing activity. An increased consumption of Falkland herring (lower  $\delta^{15}\text{N}$ ) in the late 2010s could explain why  $\delta^{15}\text{N}$  rose only gradually.

In males, the spike in  $\delta^{15}\text{N}$  observed in 2022 may reflect increased consumption of higher-trophic prey such as squid (supporting scat data would be valuable to confirm this trend). By contrast, the sharp decline in both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in 2023 suggests a dietary shift toward lower-trophic prey and more pelagic or northerly foraging areas. This pattern likely reflects a reduced availability of high-trophic prey, as 2023 saw the lowest loligo and hake catches since 2020 and 2019 respectively (Falkland Islands Government 2024). As a result, male SAFS may have relied more heavily on lower-trophic, pelagic species such as Falkland herring during that year. Since males feed more heavily on hake and loligo, both major fishery targets, they may face greater risk of fishery interactions, highlighting potential sex-specific exposure to anthropogenic threats.

Our study provided a better assessment on how the SAFS population breeding at Falkland exploits the resources of the Patagonian marine ecosystem. This report underlines the importance of considering both sex and individual specialization when assessing the foraging ecology and ecological role of this species. We showed the importance of long-term monitoring to detect subtle changes in ecosystem structure and SAFS foraging behaviour, which may be influenced by oceanographic or anthropogenic activities like fisheries. Falkland Islands marine ecosystem susceptible to climate change (Van der Grient 2023), and the potential restructuring of the wasp-waist food web in response to climate change will likely affect differently individual of various foraging strategies. We encourage coupling SIA data with other biomarkers method for future analysis (e.g. DNA on scats) to assess more fine scale evaluation of diet at specie level.

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## ACKNOWLEDGEMENTS

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