



Feeding habits of South American and sub-Antarctic fur seals during their nonbreeding season in the southwestern Atlantic Ocean

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Abstract

Stomach contents of South American (*Arctocephalus australis*) ($n = 219$) (SAFS) and sub-Antarctic (*A. tropicalis*) ($n = 37$) (SFS) fur seals were opportunistically sampled from 1980 to 2021 to examine their feeding habits and resource partitioning in southern Brazil while in their nonreproductive periods. SAFSs mainly consumed abundant coastal pelagic species, such as *Anchoa mitchilli* and *Doryteuthis sanpaulensis*, resulting in high sexual trophic niche overlap. The frequency of occurrence (%FO) of fish prey, especially the overexploited *Micropogonias furnieri*, decreased between 1980–1992 and 2007–2021, while squid increased. For SFSs, offshore squids such as *Ommastrephes bartramii* and *Illex argentinus* were the most important prey considering both sexes in the long-term. The interspecific trophic niche overlap was low, but it is likely underestimated since it increased with the inclusion of scat samples from SFSs. This sample-size effect was also observed in Shannon's diversity index, which was lower for underrepresented SFSs. Marine debris ingestion was detected in both species (SAFS %FO = 2.7; SFS %FO = 8.3), with only flexible plastic material found. This study brings novel information on feeding habits of fur seal species in the extreme south of Brazil, as well as unprecedented information about their ecology during the non-reproductive period.

KEYWORDS

Arctocephalus australis, *Arctocephalus tropicalis*, diet, feeding ecology, long-term analysis, marine debris, stomach contents

Resumo

Conteúdos estomacais de lobos-marinhos-do-sul (*Arctocephalus australis*) ($n = 219$) e lobos-marinhos-subantárticos (*A. tropicalis*) ($n = 37$) foram oportunisticamente amostrados entre 1980 e 2021 para avaliar seus hábitos alimentares e compartilhamento de recursos no sul do Brasil durante o período não-reprodutivo. O lobo-marinho-do-sul consumiu principalmente recursos costeiros pelágicos abundantes, como *Anchoa mitchilli* e *Doryteuthis sanpaulensis*, com alta sobreposição de nicho trófico entre os sexos. A nível populacional, a frequência de ocorrência (%FO) de peixes, especialmente da sobreexplorada *Micropogonias furnieri*, diminuiu entre 1980–1992 e 2007–2021, enquanto a de lulas aumentou. Para o lobo-marinho-subantártico, lulas oceânicas como *Ommastrephes bartramii* e *Illex argentinus* foram as presas mais importantes considerando ambos os sexos a longo-prazo. A sobreposição de nicho trófico entre as espécies foi baixa, mas provavelmente subestimada, uma vez que ela aumentou quando alguns conteúdos fecais dos lobos-marinhos-subantárticos foram considerados. O mesmo efeito do número amostral foi observado no índice de diversidade de Shannon, o qual foi menor para o lobo-marinho-subantártico. Ingestão de resíduos sólidos antropogênicos foi detectada em ambas as espécies (Lobo-marinho-do-sul %FO = 2,7; Lobo-marinho-subantártico %FO = 8,3) e somente material plástico flexível foi encontrado. Esse estudo é o primeiro a avaliar os hábitos alimentares de lobos-marinhos de maneira quantitativa no extremo sul do Brasil, e traz informações sem precedentes sobre sua ecologia fora das colônias reprodutivas.

1 | INTRODUCTION

The subtropical southwestern Atlantic Ocean (SWAO) experiences seasonal influences from sub-Antarctic and tropical waters, which greatly impact biological productivity. The winter and spring months are characterized by higher phytoplankton biomass, thanks to increased nutrient supply from the Patos Lagoon and La Plata River estuaries (Ciotti et al., 1995; Möller et al., 2008). This dynamic supports a high biomass of fish and squid during this period (Castello et al., 1998; Haimovici et al., 1994), creating a biogeographic region where marine mammals from various origins (tropical, sub-Antarctic, and Antarctic) converge (Prado et al., 2016). The coexistence of species in the environment relies on the abundance of resources and favorable levels of competition with conspecifics and others

(Bolnick et al., 2003). However, when sympatric, predators with similar evolutionary backgrounds may engage in intense competition for resources (e.g., Page et al., 2005; Reisinger et al., 2018). This competition potentially result in the exclusion of one species from a feeding area if preferred resources become scarce (Hardin et al., 1960), particularly in cases of overexploitation by fisheries (Jusufofski et al., 2019), or it may lead to diversification of their trophic niches (Svanbäck & Bolnick, 2007).

Pinnipeds (Order Carnivora, Infraorder Pinnipedia) are key components of marine ecosystems and inhabit diverse environments, including polar, tropical, coastal, and pelagic regions (Berta, 2009). The majority of these species are generalist feeders and occupy top positions in food webs (Bowen et al., 2009). Understanding the diet of predators is vital for comprehending the structure of food webs, energy transfer, species interactions, nutritional physiology, and niche specialization (Nielsen et al., 2018). In a community context, dietary data can provide valuable insights into the functioning of ecosystems (Estes et al., 2011). In the Southern Hemisphere, *Arctocephalus* fur seals demonstrate their versatility as consumers by preying on a variety of organisms, including fish, cephalopods, crustaceans, and seabirds (Casaux et al., 2004; Daneri et al., 2008; Makhado et al., 2013; Naya et al., 2002). These records of their diet have proven valuable in assessing predator–prey relationships (Reid & Arnould, 1996; Trites et al., 1997), interactions with fisheries (Machado et al., 2020; Szteren et al., 2004) and ecosystem monitoring (Agnew, 1997).

The South American fur seal (*Arctocephalus australis*) (SAFS) is the most common pinniped species in South America. It coexists with South American sea lions (*Otaria byronia*) along the coasts of Uruguay, Argentina, and the Falklands (Malvinas) Islands in the SWAO (Crespo et al., 2015), as well as Chile and Peru in the Pacific Ocean (Crespo & de Oliveira, 2021; Figure 1). In Brazil, there are no breeding colonies of these species, only haul-out sites: Wildlife Refuge of Ilha dos Lobos, Torres (29°20'S) and Wildlife Refuge of Molhe Leste, São José do Norte (32°11'S) (Procksch et al., 2020). Stranding events of SAFSs peak along the southern Brazilian coast during late winter and mainly consist of recently weaned juveniles and subadult/adult males (Prado et al., 2016). Molecular and morphological data indicate that these individuals originate from Uruguayan colonies, particularly Isla de Lobos (35°01'S, 54°52'W; Figure 1; de Oliveira, Hoffman, et al., 2008). The population of Isla de Lobos is growing at an annual rate of 1.5% (Franco-Trecu, 2017).

Over the past 40 years, another fur seal species has been observed on the southern Brazilian coast—the sub-Antarctic fur seal (*Arctocephalus tropicalis*) (SFS) (Prado et al., 2016). SFSs breed on oceanic islands located north of the Antarctic Convergence (Wynen et al., 2000; Figure 1). The largest breeding site is Gough Island (40°20'S, 09°54'W), which happens to be the closest to Brazil at approximately 4,200 km (Figure 1). This island serves as the primary source of stranded individuals in the area, although dispersion from other sites, such as Crozet Island, has also been identified using molecular markers (Ferreira et al., 2008). The population of Gough Island has successfully recovered following extensive exploitation and is believed to be still growing (Bester et al., 2019). The occurrence of SFSs in Brazilian waters fluctuates over time, and a general decline in numbers was observed between 1992 and 2013 in the southern region (Prado et al., 2016). However, there have been yearly peaks in Brazil, such as in 2002 (in the south) and 2018 (in the southeast) (Prado et al., 2016; Dias et al., unpublished data¹), for reasons that are not yet fully understood.

Fur seals, like other otariids, are sexually dimorphic mammals, with males being two to four times larger than females (Gentry, 2009). This size difference results in higher energy requirements for males. As a result, males possess greater oxygen stores (Boyd & Croxall, 1996), enhanced diving capacity (Weise et al., 2010), and a larger mouth gape (Drago et al., 2018; Segura et al., 2015), enabling them to access different prey and environments. Even as newborns or juveniles, males exhibit faster growth rates and achieve larger body sizes compared to females (Cappozzo et al., 1991). Consequently, otariid sexes often segregate in their resource use (e.g., Drago et al., 2015; Hobson et al., 1997; Kernaléguen et al., 2015), which can be advantageous in reducing intraspecific competition (Albernaz et al., 2017; de Lima et al., 2019, 2022).

Life histories and annual cycles play a crucial role in shaping the foraging movements and habits of fur seals. These species gather in densely populated colonies during late spring and early summer to breed (Kirkwood &

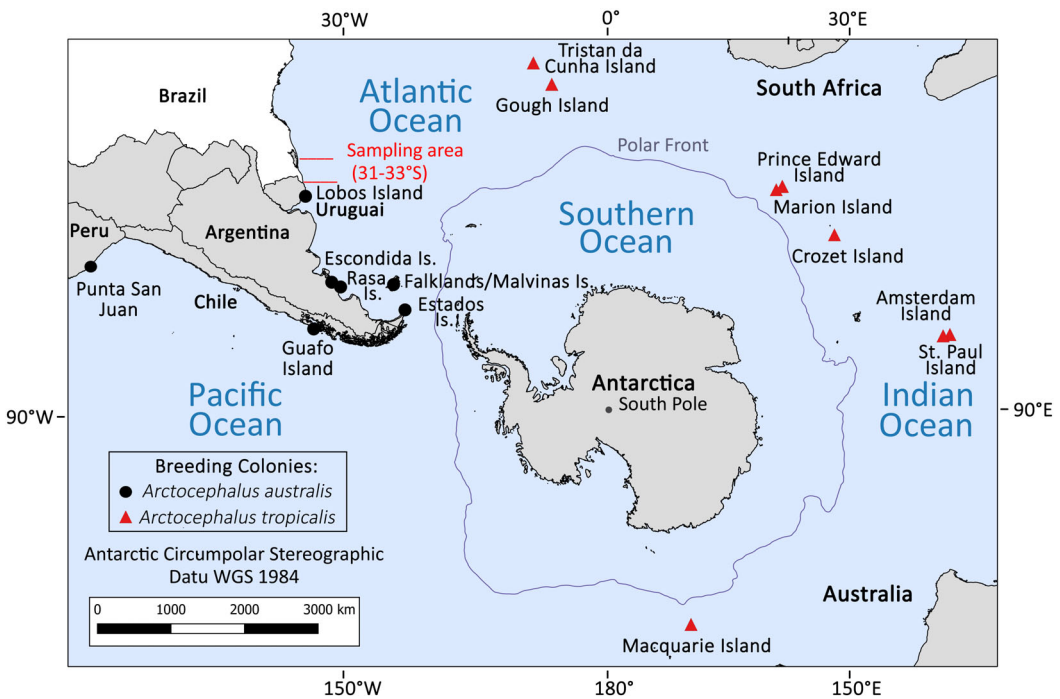


FIGURE 1 Map showing the relative position of the sampling area (southern Brazilian coast, 31°–33°S) in relation to the primary breeding colonies of South American fur seals (*Arctocephalus australis*) (represented by black dots) and sub-Antarctic fur seals (*A. tropicalis*) (represented by red triangles).

Goldsworthy, 2013). The colonies are typically situated on rocky islands near abundant resources because females need to nurse their young on land while also venturing out to sea for feeding throughout the lactation period. This pattern, known as central place foraging, lasts for nearly a year, except for some temperate/polar species (Riet-Sapirza, 2019). As a result, while females remain spatially restricted for the majority of the year, males are able to disperse to distant feeding grounds following the breeding season. The postreproductive dispersion phase is the least understood period of the life cycle for many pinnipeds.

The diet of fur seals during their breeding season, on the other hand, is generally well-documented. In Uruguay, SAFSs primarily consume small pelagic fish and squid (Franco-Trecu et al., 2013; Naya et al., 2002; Szteren et al., 2004). Within their sub-Antarctic range, SFSs mainly feed on myctophid fish (Beauplet et al., 2004; Bester et al., 2021; Makhado et al., 2013), but may also prey on cephalopods (Bester & Laycock, 1985; Makhado et al., 2013), crustaceans (Robinson et al., 2002), and seabirds (Bester et al., 2020). However, there is limited documentation of the feeding habits of these predators after weaning and during postreproductive dispersion. Consequently, their roles as seasonal components of alternative food webs are not well understood (Franco-Trecu et al., 2012; de Lima et al., 2022).

There are various methods to investigate the feeding ecology of pinnipeds, but the most commonly employed approaches involve analyzing the gastrointestinal contents of stranded animals (e.g., Machado et al., 2020) or examining the scat contents collected from breeding (e.g., Franco-Trecu et al., 2013; Makhado et al., 2013; Naya et al. 2002) or haul-out sites (e.g., Daneri et al., 2008). These conventional methods not only offer unique insights about the feeding habits of these animals but also enable the assessment of anthropogenic impacts on marine megafauna, such as ingestion of marine litter (herein, “marine debris”; Ribic et al., 2010). Marine debris can be mistakenly consumed as prey (Santos et al., 2021), accidentally ingested during foraging events, or through secondary ingestion.

In this work, we examine the feeding habits and resource partitioning of two seasonal visitors to the Brazilian coast, the SAFS and SFS, during their nonreproductive periods. We analyze a comprehensive collection of stomach contents spanning a long-term period.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling

The southern Brazilian coast experiences seasonal influences of two major oceanic currents from the SWAO, namely the Brazil and Falkland (Malvinas) currents (Piola et al., 2001). The Falkland (Malvinas) Current transports cold nutrient-rich Sub-Antarctic Shelf Water northward, while the Brazil Current carries warm oligotrophic South Atlantic Central Water southward. The interaction of these water masses at the Brazil-Malvinas Confluence is dynamic, with latitudinal displacement occurring on a seasonal basis (around 33°S in winter and 38°S in summer; Gordon, 1989).

During the cold months, the Falkland (Malvinas) Current strengthens along the eastern South American coast, resulting in a greater influx of nutrients from the Sub-Antarctic Shelf Water to the study area. This nutrient supply is further enhanced by freshwater runoffs of the La Plata River and Patos Lagoon (Garcia et al., 2004), leading to increased primary productivity. The combination of freshwater runoff, the Falkland (Malvinas) and Brazil currents creates the Subtropical Shelf Front (Piola et al., 2008). From spring to winter, the Brazilian Coastal Current flows parallel to the northeast, following the path of the Brazil Current. Although relatively slow, it is highly energetic and productive, as it receives input from sub-Antarctic coastal waters, freshwater discharge, and tropical water (Souza & Robinson et al., 2004). Along the continental shelf break and slope, primary productivity is typically stimulated by occasional export of continental water through the Subtropical Shelf Front, which is influenced by shifts in wind patterns, as well as subsurface upwellings (Braga et al., 2008; Piola et al., 2000).

Between 1980 and 2021, beach surveys conducted from Chuí (33°45'S, 53°22'W) to Mostardas (31°20'S, 51°05'W), Rio Grande do Sul, Brazil, resulted in the sampling of 256 stomachs: 219 from SAFSs and 37 from SFSs. There were no fur seal stomachs sampled between 1992 and 2007, except for one SFS in 2003. Identification of species was based on dental characteristics (e.g., teeth size and shape), external morphology, and fur color pattern (Brunner, 2004; Repenning et al., 1971; Figure 2). Whenever possible, the sex and total body length of the individuals were recorded. Stomachs were removed from the carcasses on-site by cutting at the end of the esophagus and the beginning of the small intestine, and both ends were securely tied with strings to prevent content loss. In most cases, the cause of death could not be determined, unless clear signs of interaction with fishing gear were present (Table S1). The collected stomachs were then packed in plastic bags, labeled, and stored frozen (−20°C) until further processing. Additionally, a total of five scats were collected either when found next to the carcass or manually removed from the intestines, and they were also frozen at −20°C for subsequent analysis.

After thawing, stomachs were subjected to a thorough washing process using running water and a sieve with a mesh size of 0.2 mm. The remaining contents were then transferred to a sorting tray, allowing the retrieval of hard parts of prey items. The sagitta otoliths, found in fish, were carefully separated into right and left, washed, and stored dry. Cephalopod beaks were separated into upper and lower portions and preserved in a mixture of glycerin and 70% ethanol. Feathers or other parts of seabirds were cleaned and stored dry. To determine the minimum number of fish and cephalopods consumed in each stomach, the highest count of either right or left otoliths and upper or lower beaks was considered (Barros & Oddell, 1990). Any marine debris present was meticulously washed using running water, measured, and stored dried.

Prey structures were subjected to digital measurements and photographed using a stereoscopic microscope equipped with a digital camera (OLYMPUS cellSens Imaging Software). Measurements were conducted only for intact or well-preserved structures, considering the longest longitudinal distance for otoliths and the rostral length for beaks of squids or hood length for beaks of octopuses. Otoliths were compared to the reference collection at the



FIGURE 2 Photographs illustrating the distinct characteristics of the two most common fur species found on the southern Brazilian coast: (a) South American fur seal (*Arctocephalus australis*): they can be identified by their relatively long forelimbs, grayish-brown fur slightly lighter below, and post canines with developed accessory cusps; (b) sub-Antarctic fur seal (*A. tropicalis*): these fur seals have relatively short and wide forelimbs, dark gray-brown fur with contrasting pale yellow chest and face, and their upper 4–6 post canines are angled outward from the palate. Photographs courtesy of ECOMEGA-FURG.

Laboratório de Recursos Demersais e Cefalópodes (Universidade Federal do Rio Grande – FURG) and the COSS-Brasil digital collection (<http://www.usp.br/cossbrasil/>; Rossi-Wongtschowski et al., 2016). Beaks were compared to available identification guides (Clarke, 1986; Vaske-Júnior, 2006; Xavier & Cherel, 2009) and the reference collection at CEPsul (ICMBio – Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Sudeste e Sul). Identification of bird parts was accomplished by comparing them to the scientific collection at MUCIN/UFRGS (Museu de Ciências Naturais of the Universidade Federal do Rio Grande do Sul); for further details, refer to Machado et al. (2021).

Due to the absence of hard and digestion-resistant structures, the taxonomic identification of elasmobranchs and crustaceans was challenging. Consequently, only intact or partially digested organisms were identifiable and suitable for quantitative purposes.

Regarding scats, they were thoroughly washed using tiered sieves of mesh diameters of 1.0, 0.5, and 0.025 mm. The material that remained after sieving was carefully sorted, classified, and measured following the same protocol described for the items found in the stomach contents.

2.2 | Statistical analysis

Maturity classes were determined based on approximate total body length of sexual maturity: for SAFS, males ≥ 150 cm and females ≥ 120 cm (Batallés et al., 1990); and for SFS, males ≥ 140 cm and females ≥ 110 cm (Bester & Jaarsveld, 1994). However, the sample size was insufficient to compare diets among different seasons and years, as well as between maturity classes and sexes for SFSs, mainly due to the predominance of adult males in the sample. Regarding SAFSs, we compared diets between sexes and two distinct time periods: 1980–1992 (Period I) and 2007–2021 (Period II), at the population level. However, comparisons between maturity classes were not possible due to the limited representation of adult individuals in our samples. To estimate the total length and mass of fish and cephalopods consumed by fur seals, we utilized otolith and beak measurements along with allometric equations outlined in Table S2.

The significance of each prey in the diet was reported using various metrics, including the frequency of relative occurrence (%FO), numerical contribution (N and %N), reconstructed mass (M and %M), and corresponding prey-specific abundances %PN and %PM. Additionally, we calculated the Prey-Specific Index of Relative Importance (%PSIRI) (Brown et al., 2012):

$$\%PSIRI_i = \frac{\%FO_i \times (\%PN_i + \%PM_i)}{2}$$

To assess differences in prey length or biomass consumed between sexes of SAFSs, and between SAFSs and SFSs, we employed the nonparametric Kruskal-Wallis test. Additionally, we examined the occurrence of different prey types (pelagic, demersal, demersal-pelagic, and benthic) by calculating the percentage of stomachs containing each one, as well as the %FO of marine debris.

To investigate the relationship between fur seal total body length and prey size, we utilized the Pearson correlation coefficient. In cases where data did not follow a normal distribution, we employed the Spearman's rank correlation coefficient instead. To evaluate dietary niche overlap between sexes and periods I and II of SAFSs, we employed the Schoener's Trophic Overlap Index (C) (Schoener, 1970). This index serves as a proxy for resource partitioning and was calculated using the “spaa” package, version 0.2.2 (Zhang & Ma, 2014):

$$C = 1 - 0.5 \left(\sum |Mx_i - My_i| \right)$$

Mx_i represents the proportional reconstructed mass of item i consumed by one group, while My_i represents the proportional reconstructed mass of the same item i consumed by another group. The Schoener's Trophic Overlap Index quantifies the degree of overlap and ranges from zero (indicating no overlap) to one (indicating total overlap) between the two groups.

To assess the diversity of species in the fur seal diets, we calculated the Shannon Diversity Index (H) based on the number of each species found in their stomachs (“vegan” package, version 2.5–7, Oksanen et al., 2012):

$$H = - \sum_{i=1}^S P_i \ln P_i$$

where P_i represents the proportion of the i th species, and S the total number of species found in the samples.

For the statistical analyses mentioned above, only stomach contents were considered. However, in order to facilitate comparison, we also calculated the Shannon Diversity Index and Schoener's Trophic Overlap Index by including information from scats, given our limited sample size for the SFS. All analyses were performed using R (R Core Team, 2021) and a significance level of .05 was used as the threshold for statistical significance.

3 | RESULTS

A majority of the samples ($n = 164$) were collected during the winter months, followed by spring ($n = 51$), autumn ($n = 37$), and summer ($n = 4$). It is worth noting that a substantial number of stomachs were found to be empty: 67.1% of SAFSs and 40.5% of SFSs. Additionally, five SFS scats that were opportunistically sampled were included in the study for qualitative analysis (Table S1) and compared to the stomach contents.

In the southern Brazilian waters, fur seals were found to consume a minimum of 31 prey species belonging to 10 families of teleost fish (Atherinopsidae, Ariidae, Carangidae, Engraulidae, Monacanthidae, Mugilidae, Phycidae, Pomatomidae, Scianidae, Trichiuridae), four families of crustaceans (Cirolanidae, Penaeidae, Portunidae,

Solenoceridae), three families of cephalopods (Argonautidae, Loliginidae, Ommastrephidae), one family of elasmobranch (Arhynchobatidae), and one family of seabird (Spheniscidae) (Table 1). Out of the total 234 prey items ingested, only 34 (14.5%) could not be identified at the species level.

The size of prey items consumed by the fur seals ranged from 42.6 mm to 1,050.2 mm (Figure 3, Table 2). However, no significant relationship was found between the total body length of the fur seals and the size of their prey (SAFS: $r[76] = 0.02$, $p = .9$; SFS: $r[13] = 0.3$, $p = .2$).

3.1 | SAFS

The majority of specimens consisted of males ($n = 123$), followed by females ($n = 70$), and some individuals with undetermined sex. Among the males, 72 were juveniles, 49 were adults, and two lacked information on total body length. Regarding the females, 30 were adults, 39 were juveniles and one lacked information on total body length. The total body length of individuals ranged from 69 to 175 cm ($M = 119.2$ cm, $SD = 30.2$ cm).

Diagnostic remains of prey identified in 72 stomachs (Table S1) represented a minimum of 16 teleost species ($n = 149$, 61.6%), five cephalopods ($n = 74$, 30.6%), five crustaceans ($n = 18$, 7.4%) and one elasmobranch ($n = 1$, 0.4%). The most common prey type consumed was demersal-pelagic (Figure 4).

The total biomass consumed by the SAFSs amounted to 30,152.9 g. The number of prey items per stomach ranged from 1 to 20 ($M = 3.4$, $SD = 4.5$). The diversity of taxa ranged from one to five ($M = 1.3$, $SD = 0.6$). The highest prey richness in the diet was observed in 62 stomachs (Figure S1). The mean biomass per stomach was 76.0 ± 143.4 g, and size of prey ranged from 14.4 to 1,050.2 mm ($M = 132.6$ mm, $SD = 116.5$ mm; Figure 3, Table 2). When considering the entire population, including both sexes, all age groups and all years from 1980 to 2021, the most frequently encountered prey species in the stomachs was *Doryteuthis sanpaulensis* (%PSIRI = 15.0, %FO = 51.4, %N = 23.0, %M = 7.0). However, *Anchoa marinii* had the highest importance in the diet, contributing a larger mass (%PSIRI = 44.1, %FO = 8.3, %N = 19.3, %M = 68.8). *Micropogonias furnieri* also showed a relevant contribution to diet (%PSIRI = 9.1, %FO = 9.7, %N = 9.9, %M = 8.4). The remaining prey items had negligible importance, with %PSIRI values below 5.1 (Table 3, Figure 5).

Anchoa marinii was identified as the most significant prey item in the diets of males (%PSIRI = 36.5, %FO = 10.0, %N = 23.5, %M = 49.5; Table S3). It was followed by *D. sanpaulensis* (%PSIRI = 16.5, %FO = 47.5, %N = 21.8, %M = 11.2), which exhibited the highest %FO, and *M. furnieri* (%PSIRI = 15.0, %FO = 12.5, %N = 11.8, %M = 18.2). Female diets displayed a similar pattern, with the exception of *Stellifer rastrifer*, which demonstrated higher importance (%PSIRI = 12.7, %FO = 4.2, %N = 22.5, %M = 2.9) (Table S3). Despite this, the utilization of the same primary resources resulted in a high dietary niche overlap between the sexes (Schoener's Trophic Overlap Index [C] = 0.6). There were no significant differences observed in mass consumption ($H[1] = 0.1$, $p = .7$) or prey length ($H[1] = 0.3$, $p = .6$). However, male dietary diversity (Shannon Diversity Index [H] = 2.4) was higher compared to that of females ($H = 1.8$).

In terms of temporal analysis, *A. marinii* remained the most important prey based on %PSIRI and M% for both period I and II (Table S4). *Engraulis anchoita* emerged as the third most important prey in period I, following *M. furnieri*, with the highest %N (Table S4). However, it was not found in any stomachs during period II. The Schoener's Trophic Overlap Index (C) indicated high degree of overlap between the two periods (0.7). Conversely, the frequency of occurrence (%FO) of the primary prey items suggested changes between period I and II. While %FO of fish prey such as *M. furnieri* and *A. marinii* decreased (26.7% to 5.3%, 13.3% to 7%, respectively), the squid *D. sanpaulensis* increased significantly from 26.7% to 59.6% (Figure 6). Furthermore, this squid exhibited minor importance in the diet during period I according to %PSIRI (4.6%) but became the second most important resource during period II (21.0%), followed by *S. rastrifer*.

TABLE 1 Prey species consumed by South American fur seals (*Arctocephalus australis* SAFS, $n = 219$ stomachs) and sub-Antarctic fur seals (*Arctocephalus tropicalis* SFS, $n = 37$ stomachs and five scats) on the southern Brazilian coast from 1980 to 2021. The prey types are categorized as: P = pelagic, DP = demersal-pelagic, D = demersal, B = benthic. Prey habitat: C = coastal, O = offshore.

Prey	Common name	Prey type	Habitat	SAFS	SFS
Teleosts					
Atherinopsidae					
<i>Odontesthes bonariensis</i>	Argentinian silverside	P	C		X
Ariidae					
<i>Genidens genidens</i>	Guri sea catfish	D	C	X	X
Carangidae					
<i>Trachurus lathami</i>	Rough scad	DP	C	X	
Engraulidae					
<i>Anchoa marinii</i>	Marini's anchovy	P	C	X	X
<i>Engraulis anchoita</i>	Argentine anchovy	P	O	X	
<i>Lycengraulis grossidens</i>	Atlantic sabretooth anchovy	P	C	X	
Monacanthidae					
<i>Stephanolepis hispidus</i>	Planehead filefish	B	C	X	
Mugilidae					
<i>Mugil</i> sp.			C	X	X
Phycidae					
<i>Urophycis brasiliensis</i>	Brazilian codling	D	C	X	
Pomatomidae					
<i>Pomatomus saltatrix</i>	Blue fish	P	C	X	X
Scianidae					
<i>Cynoscion guatucupa</i>	Striped weakfish	DP	C	X	X
<i>Macrodon atricauda</i>	Southern king weakfish	D	C	X	
<i>Micropogonias furnieri</i>	White croaker	D	C	X	X
<i>Paralichthys brasiliensis</i>	Banded croaker	D	C	X	
<i>Stellifer rastriifer</i>	Rake stardrum	D	C	X	
<i>Menticirrhus</i> sp.			C	X	
Trichiuridae					
<i>Trichiurus lepturus</i>	Largehead hairtail	DP	C	X	X
Elasmobranchs					
Arhynchobatidae					
<i>Sympterygia acuta</i>	Bignose fanskate	D	C	X	
Cephalopods					
Loliginidae					
<i>Doryteuthis sanpaulensis</i>	Sao Paulo squid	DP	C	X	X
<i>Doryteuthis pleii</i>	Slender inshore squid	DP	C		X
<i>Lolliguncula brevis</i>	Atlantic brief squid	B	C	X	
Ommastrephidae					
<i>Hyaloteuthis pelagica</i>	Glassy flying squid	P	O	X	

(Continues)

TABLE 1 (Continued)

Prey	Common name	Prey type	Habitat	SAFS	SFS
<i>Illex argentinus</i>	Argentine shortfin squid	DP	O	X	X
<i>Ommastrephes bartramii</i>	Neon flying squid	P	O		X
Argonautidae					
<i>Argonauta nodosa</i>	Knobby argonauta	P	O	X	X
Crustaceans					
Cirolanidae					
<i>Bathynomus miyarei</i>	Gigant deep-sea isopod	B	C	X	
<i>Excirolana</i> sp.			C	X	
Penaeidae					
<i>Artemesia longinaris</i>	Argentine stiletto shrimp	B	C	X	
Portunidae					
<i>Callinectes sapidus</i>	Blue crab	DP	C	X	
Solenoceridae					
<i>Pleoticus muelleri</i>	Argentine red shrimp	B	C	X	
Seabirds					
Spheniscidae					
<i>Spheniscus magellanicus</i>	Magellanic penguin	P	C/O		X

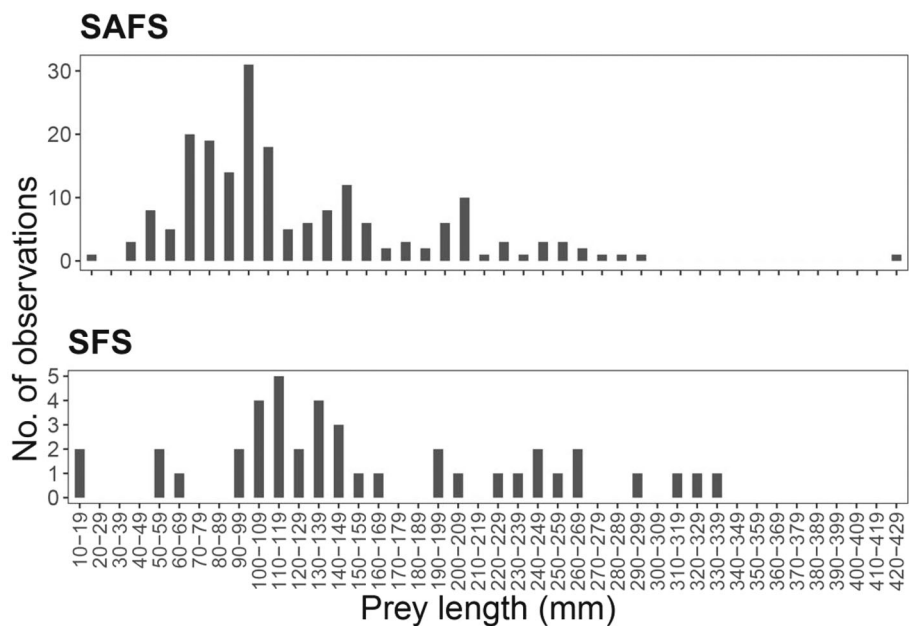


FIGURE 3 Distribution of total lengths of prey consumed by South American fur seals (SAFS, *Arctocephalus australis*) and sub-Antarctic fur seals (SFS, *Arctocephalus tropicalis*) along the southern Brazilian coast from 1980 to 2021, based on the analysis of stomach contents. Two values associated with largehead hairtail (*Trichiurus lepturus*) consumed by a SAFS individual, measuring 1,042.9 and 1,050.2 mm were identified as outliers and therefore excluded from this figure.

TABLE 2 Summary of reconstituted total lengths (mm) and masses (g) of prey consumed by South American fur seals (*Arctocephalus australis*, SAFS) and sub-Antarctic fur seals (*A. tropicalis*, SFS) along the southern Brazilian coast from 1980 to 2021, as determined through the analysis of stomach and scat contents. Total length measurements refer to dorsal mantle length for cephalopods and total body length for fish.

Prey species	SAFS			SFS		
	Total length (mm)		Mass (g)	Total length (mm)		Mass (g)
	Mean ± SD	Range	Mean ± SD	Mean ± SD	Range	Mean ± SD
<i>Odontesthes</i> sp.				132.2 ± 36.9	96.2–285.3	19.5 ± 27.0
<i>G. genidens</i>	14.9	–	31.7	–	–	6.0–150.1
<i>A. marini</i>	78.6 ± 14.1	53.6–102.6	441.6 ± 550.4	80.5 ± 9.9	64.2–96.0	283.4 ± 346.0
<i>E. anchoita</i>	122.9 ± 20.2	89.6–150.0	13.8 ± 7.0	–	4.0–24.8	1.9–1,005.2
<i>L. grossidens</i>	120.4	–	11.4	–	–	–
<i>S. hispidus</i>	91.0					
<i>U. brasiliensis</i>	426.9		681.0			
<i>C. guttucupa</i>	42.6		0.7	144.5	–	30.6
<i>M. atricauda</i>	165.4 ± 11.2	157.5–173.3	34.8 ± 7.7	29.3–40.2	–	–
<i>M. furnieri</i>	199.2 ± 54.4	91.1–294.2	114.4 ± 88.4	6.9–325.7	131.3	23.0
<i>P. brasiliensis</i>	185.4 ± 33.1	93.6–212.3	68.8 ± 27.4	5.2–101.0	–	–
<i>S. rastrifer</i>	115.0 ± 44	77.3–238.5	30.9 ± 51.4	4.8–204.8	–	–
<i>Menticirrhus</i> sp.	286.8		245.4			
<i>T. lepturus</i>	878.6 ± 291.0	542.9–1,050.2	352.7 ± 263.8	48.1–511.2	577.4–613.8	66.0 ± 7.7
<i>Mugil</i> sp.				19.6 ± 7.3	15.4–28.1	178.7 ± 197.9
<i>P. saltatrix</i>				79.5	–	2.9
<i>D. pleii</i>	–		–	260.6	–	175.6
<i>D. sanpaulensis</i>	100.7 ± 51.3	32.1–250.8	49.3 ± 62.4	2.3–292.7	54.3–239.0	67.4 ± 59.5
<i>H. pelagica</i>	99.6 ± 6.3	92.1–107.4	7.1 ± 0.5	6.5–7.6	–	7.4–228.3
<i>L. brevis</i>	79.9		28.0			
<i>I. argentinus</i>	202.7 ± 73.8	93.1–250.8	198.0 ± 124.5	17.6–292.7	153.3–262.0	207.2 ± 80.5
<i>O. bartramii</i>	–		–	316.9 ± 16.8	295.7–332.8	860.0 ± 124.0
<i>A. nodosa</i>	83.1 ± 5.0	79.5–86.6	70.4 ± 11.0	62.7–78.1	–	706.2–980.5

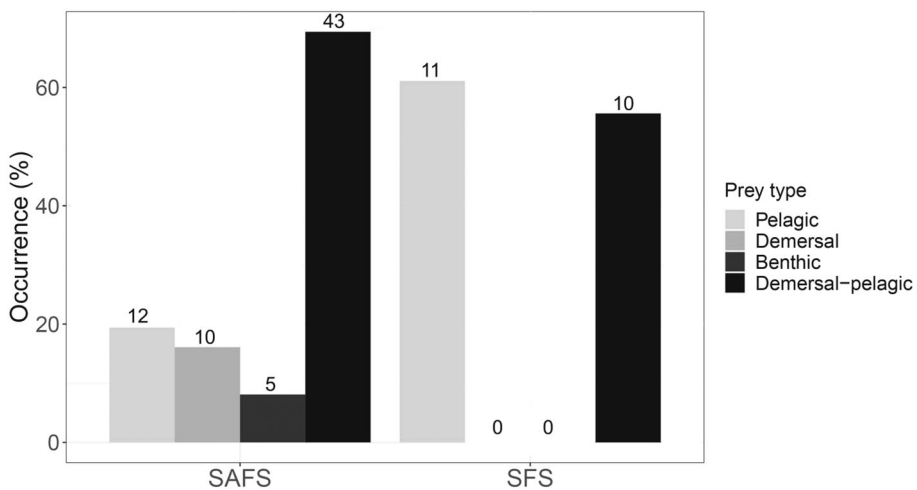


FIGURE 4 Occurrence (%) of prey types in the stomachs of South American fur seals (*Arctocephalus australis*, SAFS) and sub-Antarctic fur seals (*A. tropicalis*, SFS) examined in southern Brazil from 1980 to 2021. Only prey identified at the species level were taken into account. The numbers displayed above the bars indicate the absolute number of stomachs containing each prey type.

The following prey species were recorded in the SAFS diet for the first time: *Genidens genidens*, *Lycengraulis grossidens*, *Stephanolepis hispidus*, *Macrodon atricauda*, *Sympterigia acuta*, *Lolliguncula brevis*, *Hyaloteuthis pelagica*, *Bathynomus miyarei*, *Excirolana* sp., *Artemesia longinaris*, and *Callinectes sapidus*.

3.2 | SFS

Most of the sampled SFSs sampled were males ($n = 29$), followed by females ($n = 4$) and individuals of indeterminate sex ($n = 4$). Among the males, eight were juveniles, and 20 were adults. Regarding the females, two were adults and two were juveniles. The total body length of individuals ranged from 69 to 175 cm ($M = 139.1$ cm, $SD = 25.9$ cm).

Diagnostic prey remains were identified in 21 stomachs (Table S1), representing at least two teleost species ($n = 18$, 27.3%), five cephalopods ($n = 38$, 57.6%), unidentified crustaceans ($n = 8$, 12.1%), and one seabird ($n = 2$, 3.0%). Pelagic species were the most commonly consumed prey type, followed by demersal-pelagic species (Figure 4). In total, a biomass of 6,779.2 g was consumed by the SFS. The number of prey items per stomach ranged from one to 16 ($M = 2.7$, $SD = 3.5$), and the diversity of taxa found ranged from one to three ($M = 1.4$, $SD = 0.7$). The mean biomass per stomach was 199 ± 258.6 g, and prey size ranged from 15.4 to 327.4 mm ($M = 147.6$, $SD = 78.8$ mm; Figure 3, Table 2).

According to the stomach content analysis, *Ommastrephes bartramii* was the most important prey in the SFS diet (%PSIRI = 29.2, %FO = 14.3, %N = 7.6, %M = 50.7) (Table 4). *Illex argentinus* ranked as the second most important prey (%PSIRI = 24.1, %FO = 23.8, %N = 16.7, %M = 31.5), followed by *D. sanpaulensis* (%PSIRI = 15.3, %FO = 42.9, %N = 19.7, %M = 10.9), which was the most frequently consumed item. The remaining prey made minor contributions.

Scats were collected from a total of five fur seals, including three adult males and two juveniles. The analysis of these scats revealed the presence of prey taxa not recorded in stomach contents, such as *A. marinii*, *Mugil liza*, *G. genidens*, *Cynoscion guatucupa*, *M. furnieri*, *Pomatomus saltatrix*, and *Trichiurus lepturus* (Table 1). The size of prey items found in the scats ranged from 28.1 to 613.8 mm (Table 2).

TABLE 3 Summary of prey species composition and the relative importance of prey items, including the frequency of relative occurrence (%FO), numerical contribution (%N and prey-specific %PN), reconstructed mass (M, %M, and prey-specific %PM), and the Prey-specific Index of Relative Importance (%PSIRI), for South American fur seals (*Arctocephalus australis*, SAFS) ($n = 219$) along the southern Brazilian coast from 1980 to 2021.

Prey species	%N	%PN	%FO	M	%M	%PM	%PSIRI
Teleosts							
Ariidae							
<i>Genidens genidens</i>	0.4	0.3	1.4	31.7	0.1	0.1	0.3
Unidentified Ariidae	1.2		2.8				
Carangidae							
<i>Trachurus lathami</i> ^a	0.4		1.4				
Eugraulidae							
<i>Anchoa marinii</i>	19.3	2.3	8.3	20,757.6	68.8	8.3	44.1
<i>Engraulis anchoita</i>	9.5	3.4	2.8	318.8	1.1	0.4	5.3
<i>Lycengraulis grossidens</i>	0.4	0.3	1.4	11.4	0.04	0.04	0.2
Monacanthidae							
<i>Stephanolepis hispidus</i> ^a	0.4		1.4				
Phycidae							
<i>Urophycis brasiliensis</i>	0.4	0.3	1.4	681.0	2.3	1.7	1.4
Pomatomidae							
<i>Pomatomus saltatrix</i> ^a	0.4		1.4				
Scianidae							
<i>Cynoscion guatucupa</i>	0.4	0.3	1.4	0.7	0.002	0.002	0.2
<i>Macrodon atricauda</i>	1.2	0.9	1.4	69.6	0.2	0.2	0.7
<i>Micropogonias furnieri</i>	9.9	1.0	9.7	2,519.9	8.4	0.9	9.1
<i>Paralonchurus brasiliensis</i>	4.5	1.1	4.2	757.0	2.5	0.6	3.5
<i>Stellifer rastrifer</i>	8.2	3.0	2.8	586.8	1.9	0.7	5.1
<i>Menticirrhus</i> sp.	0.4	0.3	1.4	245.4	0.8	0.8	0.8
Unidentified Scianidae	0.4		1.4				
Trichiuridae							
<i>Trichiurus lepturus</i>	1.2	0.4	2.8	1,058.0	3.5	1.3	2.4
Unidentified fish	2.1		6.9				
Elasmobranchs							
Arhynchobatidae							
<i>Sympteria acuta</i> ^a	0.4		1.4				
Cephalopods							
Loliginidae							
<i>Doryteuthis sanpaulensis</i>	23.0	0.4	51.4	2,111.8	7.0	0.1	15.0
<i>Lolliguncula brevis</i>	0.4	0.3	1.4	28.0	0.1	0.1	0.3
Ommastrephidae							
<i>Hyaloteuthis pelagica</i>	3.3	2.4	1.4	42.3	0.1	0.1	1.7
<i>Illex argentinus</i>	2.1	0.4	5.6	792.1	2.6	0.5	2.3

(Continues)

TABLE 3 (Continued)

Prey species	%N	%PN	%FO	M	%M	%PM	%PSIRI
Argonautidae							
<i>Argonauta nodosa</i>	0.8	0.3	2.8	140.8	0.5	0.2	0.6
Unidentified Octopoda	0.4		1.4				
Unidentified Cephalopoda	0.4		1.4				
Crustaceans							
Cirolanidae							
<i>Bathynomus miyarei</i> ^a	0.4		1.4				
<i>Excirolana</i> sp.	0.4		1.4				
Penaeidae							
<i>Artemesia longinaris</i> ^a	0.4		1.4				
Portunidae							
<i>Callinectes sapidus</i> ^a	0.4		1.4				
<i>Callinectes</i> sp.	0.4		1.4				
Unidentified Portunidae	0.4		1.4				
Solenoceridae							
<i>Pleoticus muelleri</i> ^a	0.8		2.8				
Unidentified Amphipoda	0.4		1.4				
Unidentified Bivalvia	1.2		2.8				
Unidentified Brachyura	0.4		1.4				
Unidentified Crustacea	2.1		5.6				

^aAllometric equation not available or otolith/beak could not be measured.

When considering only stomach contents, the trophic niche overlap between SAFSs and SFSs was found to be low (Schoener's Trophic Overlap $[C] = 0.1$). However, when including data from scats, the overlap increased ($C = 0.2$). The diet of SAFSs exhibited higher diversity (Shannon Diversity Index $[H] = 2.4$) compared to SFSs ($H = 1.8$) based on stomach contents alone (Figure S1). However, the difference in diversity became smaller when the scat data were included ($H = 2.1$). There was no significant difference in prey length ($H[1] = 1.4$, $p = .2$) or bio-mass ($H[1] = 3.3$, $p = .07$) consumption between SAFSs and SFSs based on stomach contents alone.

Furthermore, the presence of *Genidens genidens*, *M. liza*, *P. saltatrix*, *C. guatucupa*, *Odontesthes bonariensis*, *A. marinii*, *M. furnieri*, *I. argentinus*, *O. bartramii*, and *D. plei* in the diet of SFSs is being reported for the first time.

3.3 | Marine debris

Marine debris were found in a total of nine stomachs: six SAFSs (%FO = 2.7), including one adult male, two juvenile males, two juveniles of indeterminate sex, and one 147 cm-individual of indeterminate sex (total body length $M = 109.7$ cm, $SD = 31.1$ cm), and three SFSs (%FO = 8.3), including one adult male, one juvenile male, and one 142-cm individual of indeterminate sex ($M = 135.7$ cm, $SD = 16.2$ cm). Out of the four SAFSs that ingested marine debris, none of them had any prey hard parts in their stomachs. The marine debris found in the stomachs was solely composed of flexible plastic, which appeared to originate from plastic bags or packing material. While most individuals had only small and single fragments of debris in their stomachs, one adult male SFS had ingested at least four large plastic fragments measuring between 2.2 and 7.4 cm ($M = 4.6$, $SD = 2.3$ cm; Figure 7).

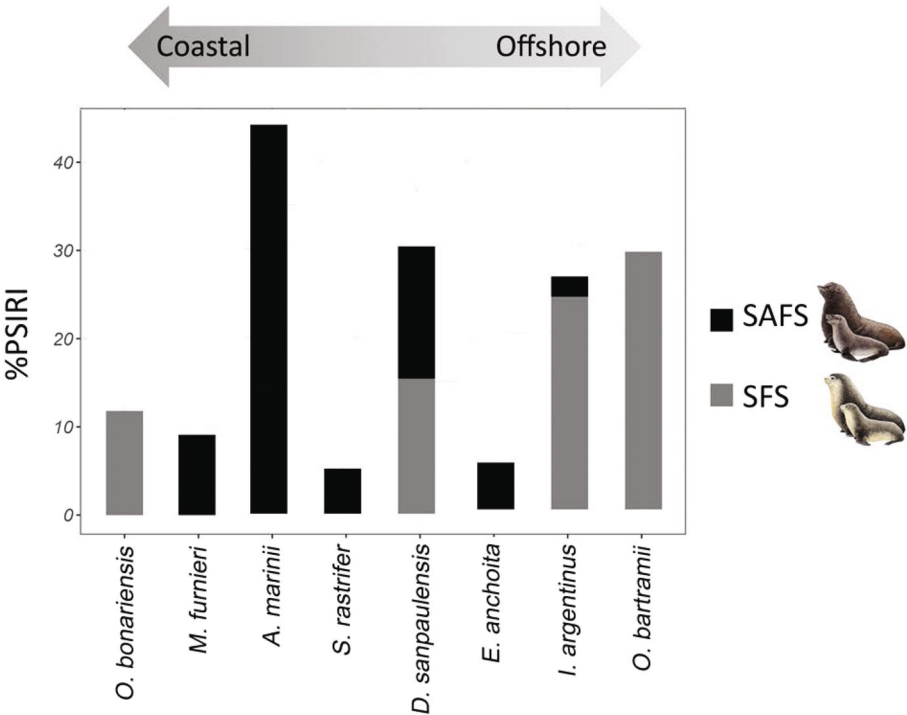


FIGURE 5 Prey-Specific Index of Relative Importance (%PSIRI) for the prey consumed by South American fur seals (SAFS, *Arctocephalus australis*) and sub-Antarctic fur seals (SFS, *Arctocephalus tropicalis*) in the southern Brazilian coast between 1980 and 2021, as determined through stomach content analysis. Fur seal illustrations were obtained from Cárdenas-Alayza (2018) and Hofmeyr and Bester (2018).

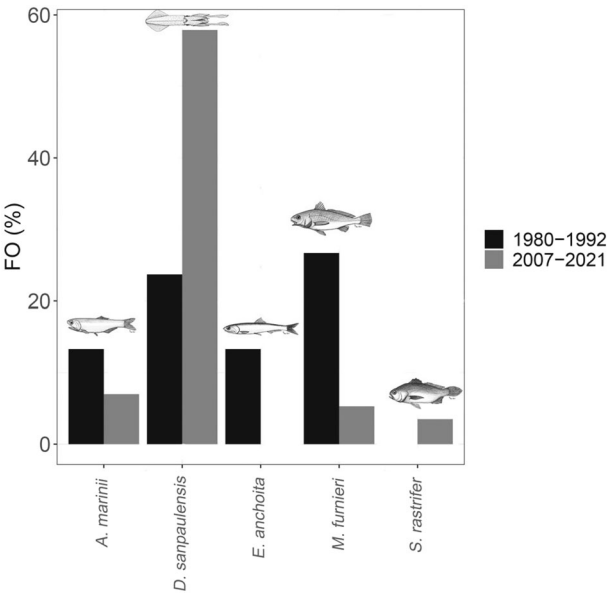


FIGURE 6 Frequency of Occurrence (%FO) of the main prey consumed by South American fur seals (SAFS, *Arctocephalus australis*) the southern Brazilian coast, as determined by stomach content analysis for two distinct periods: Period I (1980–1992) and Period II (2007–2021). Prey illustrations were sourced from Fischer et al. (2011) and Migliavacca & Simone (2020).

TABLE 4 Summary of the prey species composition and the relative importance of prey items for sub-Antarctic fur seals (*Arctocephalus tropicalis*, SFS) ($n = 21$) on the southern Brazilian coast from 1980 to 2021. The relative importance of prey items is presented in terms of the frequency of relative occurrence (%FO), numerical contribution (%N and prey-specific %PN), reconstructed mass (M, %M, and prey-specific %PM), and the Prey-specific Index of Relative Importance (%PSIRI).

Prey species	%N	%FO	%PN	WT	%M	%PM	%PSIRI
Seabirds							
Spheniscidae							
<i>Spheniscus magellanicus</i> ^a	3.0	9.5					
Teleosts							
Atherinopsidae							
<i>Odontesthes bonariensis</i>	21.2	4.8	4.5	165.8	2.4	0.5	11.8
Mugilidae							
<i>Mugil</i> sp.	3.0	4.8	0.6	129.0	1.9	0.4	2.5
Unidentified fish	3.0	9.5					
Cephalopods							
Loliginidae							
<i>Doryteuthis plei</i>	1.5	4.8	0.3	175.6	2.6	0.5	2.0
<i>Doryteuthis sanpaulensis</i>	19.7	42.9	0.5	736.5	10.9	0.3	15.3
Unidentified Loliginidae	3.0	9.5					
Ommastrephidae							
<i>Illex argentinus</i>	16.7	23.8	0.7	2,132.4	31.5	1.3	24.1
<i>Ommastrephes bartramii</i>	7.6	14.3	0.5	3,439.9	50.7	3.6	29.2
Unidentified Ommastrephidae	4.5	9.5					
Unidentified Octopoda	1.5	4.8					
Unidentified Cephalopoda	3.0	9.5					
Crustaceans							
Unidentified Amphipoda	1.5	4.8					
Unidentified Bivalvia	1.5	4.8					
Unidentified Crustacea	9.1	4.8					

4 | DISCUSSION

Through a long-term scientific collection of stomach contents, we have gained valuable insights into various aspects of fur seals in the subtropical SWAO. This includes exploring inter- and intraspecific dietary variations, observing changes in diet over time, and detecting the ingestion of marine debris. In particular, we focused on the feeding habits of the *Arctocephalus* genus in the southern Rio Grande do Sul, which is the region with the highest occurrence of these animals along the Brazilian coast. Surprisingly, this area had not been thoroughly assessed in terms of fur seals' dietary habits until now. Paired data of stomachs and scats also provided insights into transit times of prey hard parts in these species. While there are some limitations to our study, it represents the first comprehensive effort to describe the diet of fur seals in the region using conventional techniques with a high taxonomic resolution. Our findings contribute important new information to the ecological understanding of fur seals during their non-breeding period, which is the least studied phase of their annual life cycle.

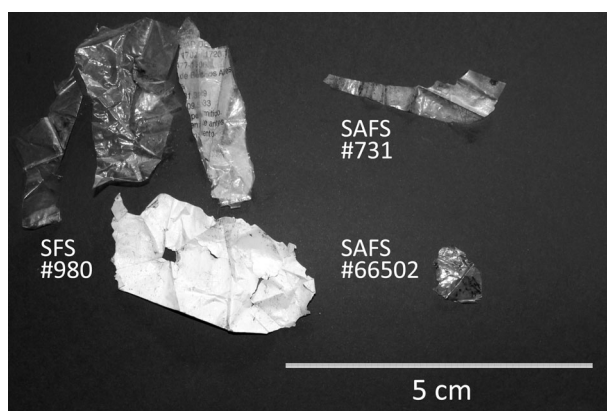


FIGURE 7 Marine debris found in the stomachs of dead South American fur seals (*Arctocephalus australis* – SAFS) and sub-Antarctic fur seals (*Arctocephalus tropicalis* – SFS) along the southern Brazilian coast.

4.1 | South American fur seals

Known for their generalist feeding behavior, SAFSs primarily rely on a limited number of species that are abundant in the subtropical SWAO—mostly demersal-pelagic and pelagic taxa. Among them, the highly significant prey item is *A. marinii*, a pelagic fish that is very abundant along the SWAO's continental shelf (Castello, 1998). The presence of *A. marinii* is closely associated with the cold waters transported by the Brazilian Coastal Current, similar to other engraulid species in the area (Franco et al., 2006). Based on the reconstructed length of fish consumed by SAFSs, it was observed that the majority of *A. marinii* individuals were mature (López et al., 2015).

In our study, another prey of significant importance for SAFSs was the coastal squid *D. sanpaulensis*, which is associated with the Falkland (Malvinas) Current and the Brazilian Coastal Current (Boyle & Roundhouse, 2005). The higher abundance of *D. sanpaulensis* during winter, particularly among coastal squid species, has been attributed to northward intrusions by the Subtropical Shelf Front (Vidal et al., 2013). Based on average reconstructed dorsal mantle length, most squids targeted by fur seals were also mature individuals (Andriguetto & Haimovici, 1996). During late winter and spring, these squids tend to concentrate in the southern-central shelf region (32°S–34°S) at depths of 40–60 m (Andriguetto & Haimovici, 1991; Haimovici & Perez, 1991). Similar to *A. marinii*, *D. sanpaulensis* is currently not targeted by commercial fisheries in southern Brazil (Vidal et al., 2013). Consequently, the interaction between SAFSs and fisheries in the region is expected to be occasional, in contrast to the sympatric South American sea lions (Machado et al., 2020). It is worth noting that *A. marinii* and *D. sanpaulensis* do not appear to be important food sources for SAFSs feeding in the northern Rio Grande do Sul coast (29°S–31°S) (Machado et al., 2020), where *T. lepturus* has been the predominant prey, suggesting spatial variation in feeding habits along the Brazilian coast.

Our study revealed similar feeding habits between males and females. However, there were slight differences in the relative proportions of prey. Females showed an increased importance of *D. sanpaulensis* and a decreased importance of *A. marinii* compared to males. Additionally, we observed a notable contribution of *S. rastrifer* to female diets, which was negligible for males. It is important to note that this contribution was due to a single female that consumed several *S. rastrifer* specimens. This particular occurrence, which took place in August 2007, was likely related to an anomalous advection of tropical water by the Brazil Current to the study area (Segura et al., 2009), which explains the presence of this warm-water fish species (Haimovici, 1997). Our results contrast with information based on stable isotope data that examines resource partitioning between the sexes (de Lima et al., 2019, 2022). The disparity is likely due to the fact that individuals analyzed by de Lima et al. (2019, 2022) were adults, whereas our study primarily focused on juveniles. Furthermore, it is important to consider that stomach contents represent the winter diet and have certain limitations, such as only representing the last meals and having low detection for some taxa. In

contrast, stable isotope data obtained from whiskers reflect the foraging patterns over multiple years (Cherel et al., 2009; McHuron et al., 2016).

Our results, although limited by a small sample size, especially for period I, suggest temporal changes in the feeding habits of SAFSs. The most noticeable difference was the increase in the occurrence of *D. sanpaulensis*, while *M. furnieri* showed a decrease. The stocks of *M. furnieri* were heavily exploited during the 1980s and 1990s, leading to a significant decline in biomass (Vasconcellos & Haimovici, 2006). This decline has also been reflected in the diet of other predators in coastal waters of southern Brazil, such as *Pontoporia blainvillei* and *Tursiops truncatus gephyreus*, which have increased predation on other fish species of low or no commercial value (Botta et al., 2022; Campos-Rangel et al., 2021; Machado et al., 2018; Secchi et al., 2003, 2017). Therefore, it is likely that the overfishing of *M. furnieri* also contributed to its decreased occurrence in the SAFS diet. On the other hand, the mass (M%) of the main resources in the diet, such as *A. marinii* and *D. sanpaulensis*, remained relatively steady over time. However, it is important to note that the Schoener's Trophic Overlap Index only considers M%, which may overestimate the importance of prey of low %FO but high M%, leading to a high overlap between periods. Therefore, this result should be interpreted with caution. The long-term abundance trends of many prey species are currently unknown, and it is possible that there is an ongoing increase in the occurrence of *D. sanpaulensis* on the southern Brazilian coast.

4.2 | Sub-Antarctic fur seals

Considered as opportunistic and pelagic forager throughout its breeding range (Hofmeyr et al., 2016), there is limited information on the diet of SFS diet outside of their colonies. Apart from Brazil, the species has been reported in South Africa (Shaughnessy & Ross, 1980), Gabon (Zanre & Bester, 2011), Ascension Island (Bester, 2021), Uruguay, (González et al., 1994) and Argentina (Bastida et al., 1999). In South Africa, a few stomachs from dead individuals were found to contain beaks from Histioteuthidae squids (Shaughnessy & Ross, 1980). In northern Rio Grande do Sul, Brazil, the consumption of fish and squid, (i.e., *T. lepturus*, *D. sanpaulensis*, and *Argonauta nodosa*) (de Oliveira, Ott, et al., 2008) and penguins (Machado et al., 2021), has also been reported.

In our study, we found evidence that SFSs remain as pelagic foragers outside of their breeding range, with a diet consisting mostly of cephalopods. The offshore squid, *O. bartramii*, is known to occur from the surface to depths of 1,500 m, typically in frontal zones, and is associated with the warm Brazil Current (Araya, 1983; Brunetti & Ivanovic, 2004; Dunning, 1993; Kubodera, 1986). This species contributed the most to the SFS diet according to stomach contents. While it is widely explored in other ocean basins (Nesis, 1987; Roper et al., 1984), it remains an unexplored resource in the SWAO (Brunetti & Ivanovic, 2004). SFSs showed preference for large but immature squids (Jereb et al., 2015). *Ommastrephes bartramii* has also been reported in the diet of other oceanic marine mammals in the region, such as the false killer whale (*Pseudorca crassidens*; Andrade et al., 2002), the killer whale (*Orcinus orca*; dos Santos & Haimovici, 2001), and the pygmy sperm whale (*Kogia breviceps*; Secchi et al., unpublished data²).

Illex argentinus emerged as the second most important resource for SFSs in our study. This squid species is associated with the Brazil-Malvinas Confluence and predominantly inhabits the upper slope, with adults preferring deeper waters compared to juveniles (Haimovici et al., 1998). The average size of *I. argentinus* consumed by SFSs falls within the range of sexual maturity for male individuals (dos Santos & Haimovici, 1997; Haimovici & Alvarez-Pérez, 1990). While this squid species remains underexplored in Brazilian waters, it is heavily target by commercial fisheries in Argentina, Uruguay, and Falkland (Malvinas) Islands (Haimovici et al., 1998). Another noteworthy prey item, *D. sanpaulensis*, suggests that SFSs also venture into coastal waters, possibly when approaching the shore, or while transitioning between coastal and oceanic areas during foraging activities.

The two predation events of *S. magellanicus* documented in our study are part of the first records of penguin predation outside of SFSs colonies (Machado et al., 2021). Unfortunately, due to the advanced stage of digestion, it was not possible to estimate the size and mass of these penguins. These events align with the migratory pattern of *S. magellanicus*, as they move from their southern colonies towards the Brazilian coast (Mäder et al., 2010). In

addition to fish species (represented by *Mugil* sp. and *O. bonariensis*), we also observed a small but not estimated occurrence of crustaceans in the stomachs of SFSs.

The opportunistic analysis of a few scats provided insights into the presence of several fish species that were not detected in the stomachs. These species were all coastal and were also found in the stomachs of SAFSs, including *A. marinii* and *D. sanpaulensis*, which are the primary prey for this subtropical congener species.

4.3 | Trophic niche overlap between South American and sub-Antarctic fur seals, and methodological limitations

Our data suggested a low but potentially underestimated trophic niche overlap between SAFSs and SFSs, as they shared several prey species not detected in both methods (scat and stomach analyses). It is important to acknowledge that the number of stomach samples for the two species is highly unbalanced, and the limited sample size for SFSs likely influenced dietary indexes. Some studies have attempted to determine the necessary sample size of scats or stomachs to detect most common prey species for marine mammals. For example, Trites and Joy (2005) estimated that 59 scats would be required to detect most important prey (>5% of scats) for California sea lions (*Zalophus californianus*). Similarly, Börjesson et al. (2003) found that 35–71 stomachs were necessary to achieve a similar level of confidence for a population of harbor porpoises (*Phocoena phocoena*). Although we probably detected the main prey consumed by SAFSs in southern Brazilian waters, our sample size for sub-Antarctic fur seals is far from ideal. This limitation could have led to an underestimation of the trophic niche overlap between the species, which became more evident when we added scat samples. Additionally, it should be noted that specimens of the two species analyzed in our study also differed in terms of age classes, which can influence their roles as predators considering physical and physiological constraints such as body size, mouth gape, and oxygen stores (Boyd & Coxall, 1996).

However, our data clearly demonstrates that SFSs exhibit a broader range of habitat use compared to SAFSs, which was expected given that SFSs come from distant colonies and would have crossed the entire Atlantic Ocean basin before reaching the study area. This could also explain the lower prey richness and diversity observed for SFSs compared to SAFSs, even when considering a similar number of stomachs analyzed (Figure S1). It is likely that the prey consumed by SFSs in areas far from the Brazilian coast are digested and their remains excreted before reaching coastal waters. This would have more significant implications if foraging events were less frequent during travel, because many individuals are found to have lower-than-average body condition in Brazil (R.C.dL., personal observation).

Increasing sample size of SFSs' stomachs or scats of both species might be difficult, considering that scats are difficult to find in this area and most stomachs are found empty. In light of these constraints, we encourage coupling conventional methods with biomarkers (e.g., stable isotopes, fatty acids) to assess the niche overlap between the two species based on truly assimilated diet over a short time frame.

The use of conventional methods in dietary studies has inherent limitations that should be taken into account (refer to Nielsen et al., 2018 for a comprehensive review). Our analysis of scat and stomach contents has revealed that fish otoliths may be rapidly eliminated in the scats, avoiding the detection of fish consumption by some individual SFSs. This contradicts previous studies that suggested that otoliths are typically fully digested within the stomach due to their delicate composition (mainly CaCO_3 ; Frost & Lowry, 1980; Harvey, 1989). On the other hand, cephalopod beaks, composed of chitin, tend to remain in the stomach for more extended periods (as evidenced by Clarke, 1986; Xavier et al., 2005; this study). Given these findings, we strongly recommend conducting experimental studies on the transit times of different prey remains in one of these species, particularly in SAFSs, which are frequently taken to rehabilitation centers along the Brazilian coast, where a controlled environment can be established.

Prey items that were consumed by SAFSs and SFSs were also observed in the scat and stomach contents of Antarctic fur seals (*A. gazella*) found dead in the same area and period, including *D. sanpaulensis*, and several demersal Scianidae fish (de Lima, 2022). However, due to the limited number of samples, we are unable to investigate their

trophic habits and partitioning with the other two fur seal species. Future sampling efforts are needed to better describe the diet of this species in this region.

We also observed a high occurrence of empty stomachs among SAFSs. Several factors could account for this pattern. Firstly, many individuals in our study were recently weaned and in their first year at sea. Due to their lack of experience, they may struggle to locate food independently, leading to starvation and empty stomachs. The survival rates of weaned individuals are currently unknown. Secondly, in the case of adult SAFSs, their predominantly piscivorous diet, fast digestion rates (Helm, 1984), and/or the last feeding event occurring far from the coast could contribute to the occurrence of empty stomachs. Additionally, we cannot disregard the possibility of sicknesses such as influenza virus and *Mycobacterium pinnipedii* (Tuberculosis) infections (Arbiza et al., 2012; Bastida et al., 1999). However, the health status of pinnipeds stranded in southern Rio Grande do Sul has not been assessed.

Despite the uneven sample size between the two species, our study provides valuable insights into the ecology and occurrence of SAFs and SFSs in the subtropical waters of the SWAO.

4.4 | Ingestion of marine debris

Marine debris are a major and widespread threat to the health of marine biota (Andrady, 2011). While the ingestion of debris has been reported in numerous marine species, its occurrence in fur seals has received limited attention (e.g., de Oliveira, Ott, et al., 2008; Denuncio et al., 2017; Eriksson & Burton, 2003). However, there has been a recent emergence of studies investigating the presence of microplastics in fur seal scats (e.g., Perez-Venegas et al., 2018, 2020). Approximately 80% of marine debris originates from land, with disposable plastic packing materials being the predominant source globally (Auta et al., 2017; Jambeck et al., 2015). Interestingly, our examination of fur seal stomachs revealed the predominance of such materials. Denuncio et al. (2017) reported a prevalence of fishery-related debris in the stomachs of SAFSs from northern Rio Grande do Sul, which differed from our findings. This disparity could be attributed to higher interaction between SAFSs and fisheries in the northern region. A few authors have suggested that the ingestion of marine debris in marine mammals is more common among young individuals (Denuncio et al., 2011, 2017; Di Benedetto & Ramos, 2014), possibly due to playful behavior, curiosity (Laist, 1987) or inexperience during foraging (Baird & Hooker, 2000; Walker & Coe, 1990). Accidental ingestion is also a possibility (Di Benedetto & Awabdi, 2014; Laist, 1987). Although our low sample size was limited, we did observe a slightly higher occurrence of marine debris in stomachs of juvenile fur seals.

The proportion of fur seals affected by debris was relatively higher among SFSs compared to SAFSs. The difference can be attributed to the fact that SFSs originate from distant sub-Antarctic colonies and have a broader foraging range compared to SAFSs, increasing their exposure to marine debris. Additionally, the probability of marine debris ingestion may vary among species depending on their foraging location within the water column (e.g., on the surface versus the bottom; Simmonds, 2012; Tavares et al., 2017) or their prey capture strategies and feeding behavior (Di Benedetto & da Silva Oliveira, 2019). However, these do not seem to differ between these fur seal species.

This study represents the first documentation of marine debris ingestion by SFSs outside of their breeding colonies. Although there are potential negative effects associated with debris ingestion, the small number and size of debris found in the stomachs of fur seals in our study suggest that ingestion did not contribute to the mortality of individuals and is unlikely to pose a serious threat to these species in southern Brazil.

4.5 | Concluding remarks

The postreproductive and postweaning dispersals are the least known phases of most pinniped species, especially those that occur in Brazilian waters. Many individuals may travel to productive feeding areas during this time to avoid intraspecific competition and gather energy reserves. The southern Brazilian coast and adjacent offshore

environments are likely important feeding areas for fur seals during winter and spring. Stomach content analysis indicates a low overlap in resource use between the fur seals in Brazilian waters, suggesting a reduced potential for interspecific competition. However, further investigation is needed as these findings are influenced by sample size, as suggested by previous studies. Contrary to previous isotopic studies (Szteren et al., 2018; Vales et al. 2014), our results suggest long-term shifts in the SAFS diet, and similar feeding habits between sexes. Temporal shifts could be attributed to the overfishing of demersal fish in southern Brazil.

The extra-limital movements of SFSs are poorly understood, particularly the male postreproductive dispersal from the nearest colony to the Brazilian coast, Gough Island. To comprehend their occurrence in subtropical and tropical environments, it is crucial to conduct studies on habitat use and movements. This could be achieved through mark-recapture techniques, biologging and/or stable isotopes. The potential influence of climate and other environmental changes in the Southern Ocean on the occurrence of SFSs in lower latitudes should also be carefully investigated.

Our study highlights the significance of the SWAO as a feeding area for two apex predators. The high productivity of this region during winter and spring attracts SAFSs, especially recently weaned pups, from nearby colonies. Therefore, perturbations on this ecosystem could have negative impacts on the population's fitness and survival. Additionally, the area also serves as a seasonal biogeographic confluence, attracting fauna from different origins (subtropical, sub-Antarctic).

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AUTHOR CONTRIBUTIONS

Renan C. de Lima: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Thaise L. de Albernaz:** Conceptualization; data curation; investigation; writing – original draft; writing – review and editing. **Eduardo R. Secchi:** Conceptualization; data curation; funding acquisition; investigation; supervision; writing – review and editing. **Julieta D. Cebuhar:** Conceptualization; data curation; investigation; visualization; writing – review and editing. **Silvina Botta:** Conceptualization; data curation; funding acquisition; investigation; project administration; supervision; writing – review and editing.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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