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Feeding Habits and Individual Specialization in Adult Female South American Sea Lions (*Otaria flavescens*) in Patagonia

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Abstract

Studying trophic feeding habits and their variation over time is crucial for understanding individual and population success. Although many generalist feeders' populations appear to use diverse trophic resources, they are often composed of individuals that specialize in only a subset of these resources, a phenomenon known as individual trophic specialization (ITS). The South American sea lion (SASL) (*Otaria flavescens*), widely distributed along the South American coast, is an opportunistic and generalist predator with a diverse diet, making it a good model for studying ITS. We aimed to estimate the diet composition and the degree of ITS among SASL females on Isla Arce, Argentina, over a period of three years (2012 to 2014). For that, we analysed stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) in vibrissae from 12 females. Over the three years studied, females from this colony primarily fed on pelagic prey. At the population level, the most commonly consumed prey varied between the Argentine anchovy (*Engraulis anchoita*) in 2012 and 2014 and the Patagonian squid (*Doryteuthis gahi*) in 2013. Consuming mostly pelagic resources throughout the year, unlike previous studies in nearby colonies, suggests the existence of different foraging strategies in lactating females. Although the prey contribution varied between years, the analysis indicated that SASL females breeding on Isla Arce show some degree of ITS, which could be a mechanism adopted by individuals to mitigate the potential competition given by sustained population increases.

Key Words: South American sea lion, *Otaria flavescens*, stable isotopes, *Engraulis anchoita*, Patagonian squid, stable isotopes, trophic ecology

Introduction

Understanding the structure and functioning of marine ecosystems requires the knowledge of trophic relationships between species (Raclot et al., 1998). Top predators play a fundamental role in the trophic dynamics of communities. Therefore, studying the feeding habits of different populations is crucial for interpreting their roles in each marine ecosystem (Estes et al., 1998; Pauly et al., 1998).

Individuals within a population are often considered ecologically equivalent, including possessing the same trophic preferences. However, many populations considered generalists are in fact composed of individuals that use small subsets of the total resources utilized by the population, a phenomenon known as individual trophic specialization (ITS) (Bolnick et al., 2002, 2003; Araújo et al., 2011). For a long time, ITS was ignored in ecological studies because it was considered rare or that its impact on ecological processes was not relevant enough to be studied. Currently, a large body of evidence indicates that ITS is widespread in natural populations and may have a profound impact on their ecological and evolutionary dynamics (Bolnick et al., 2003, 2007).

The existence of ITS within a population requires a degree of consistent dietary differentiation among the individuals that comprise it (Bolnick et al., 2002). In recent years, stable isotope ratios in the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of different tissues has become a powerful means to infer consistent individual differences in food-resource use (Paéz-Rosas et al., 2012; Franco-Trecu et al., 2014; Newsome et al., 2015). This technique is based on the fact that the isotopic signatures of the consumers' tissues reflect the isotopic signatures of their prey in a predictable way (DeNiro & Epstein, 1978, 1981). In marine ecosystems, $\delta^{13}C$ values are useful to identify the origin of primary productivity of the foraging habitat, while $\delta^{15}N$ signatures serve as indicators of the trophic level of the consumer (France, 1995; Post, 2002). The biplot representation of $\delta^{13}C$ and $\delta^{15}N$ (i.e., δ-space) enables the estimation of the isotopic niche, which is useful for the study of some characteristics of the ecological niche (Newsome et al., 2007). The axes are divided in two ways: (1) scenopoetic, referring to the bioclimatic zone in which the individual lives and feeds, and (2) bionomic, which defines the resources that animals use (Hutchinson, 1978). In terms of the isotopic niche, the scenopoetic axis is represented by $\delta^{13}C$ and the bionomic axis by $\delta^{15}N$ (Newsome et al., 2007). Due to the properties of the isotopic niche, it may not directly correspond to the trophic niche of a population (Hette-Tronquart, 2019). Instead, it provides insights into trophic interactions and potential habitat utilization patterns of a population, in addition to animal physiology (Shipley & Matich, 2020).

One of the main advantages of stable isotope analysis is that, depending on the animal tissue used and its turnover rate, it can provide information on foraging strategies for periods ranging from days to years (e.g., Inger & Bearhop, 2008). The isotopic signature of metabolically inert tissues reflects the diet at the time of their production, and such tissues with continuous growth (i.e., whiskers, nails) integrate chronological information on the foraging strategies of individuals over long periods of time (i.e., Kernaléguen et al., 2012; Franco-Trecu et al., 2014; Rosas-Hernández et al., 2019). Its application has been particularly important in the study of species that live in habitats that make them difficult to observe and/or that experience large movements such as most marine mammals (Newsome et al., 2010).

The South American sea lion (SASL) (*Otaria flavescens*) is widely distributed on both the Atlantic and Pacific coasts of South America, from Peru to southern Brazil (Vaz Ferreira, 1982). During the fur and oil trade era, between the 18th and 20th centuries, this species was exploited along the Southwest Atlantic coast (Crespo & Pedraza, 1991; Crespo, 2021, 2022; Vales, 2024). However, commercial exploitation was particularly intense during the 20th century, and it is estimated that many populations were reduced to less than 10% of their original numbers once it ceased (Crespo et al., 2021). Although most populations are recovering, in regions like northern and central Patagonia—approximately bounded by 41° and 48° S (Figure 1a & b)—the number of individuals is far from reaching the estimated figures for the period prior to systematic hunting (Romero et al., 2017). The slow recovery has been attributed to diverse reasons such as variations in prey availability due to the expansion of fishing activities in the area (Crespo & Pedraza, 1991; Crespo et al., 1997). This is also the case in the Falkland (Malvinas) Islands, where natural persistent environmental changes that altered the prey availability for SASLs have been suggested as the cause of the decline of this predator in the mid-1900s (Baylis et al., 2015a). On the other hand, SASL populations in southernmost Chile and Uruguay have decreased in recent decades (Venegas, 2001; Franco-Trecu, 2015).

The marine food web of northern and central Patagonia is organized around the Argentine anchovy (*Engraulis anchoita*), hake (*Merluccius hubbsi*), and shortfin squid (*Illex argentinus*) (Angelescu & Prenski, 1987). These three core species support a large number of high trophic-level predators (Koen-Alonso & Yodzis, 2005), including the SASL (Koen-Alonso et al., 2000). In addition, hake and shortfin squid support intensive fishing. For example, during the 2012-2014 period, the Argentine fleet landed 713,407 tonnes of hake (caught south of the 41° S) and 455,454 tonnes of shortfin squid (Navarro et al., 2019). On the other hand, the anchovy is the most abundant small pelagic fish that occurs off Argentina (Hansen et al., 2001), although its fishery is very underdeveloped in Patagonian waters, with reported landings during the 2012-2014 period of 2,546 tonnes (caught south of the 41° S; Navarro et al., 2019).

The SASL is considered a generalist and opportunistic species that uses a great diversity of trophic resources that varies according to sex, ontogeny, location, and environmental availability (Koen-Alonso et al., 2000; Suárez et al., 2005; Soto et al., 2006; Drago et al., 2009a, 2009b, 2015; Riet-Sapriza et al., 2013). Previous studies on the diet of the SASL in northern and central Patagonia through the analysis of stomach contents and feces indicated that females feed mainly on benthic and demersal pelagic prey (Koen-Alonso et al., 2000; Bustos et al., 2012). Additionally, stable isotope analysis in blood tissues of pups—as indicators of the trophic habits of their mothers—provided evidence that females from the Punta León colony (43° 04' S, 64° 29' W) shift their diet from offshore or pelagic prey before parturition to coastal or benthic prey after parturition (Drago et al., 2010).

In many colonies it has been shown that individuals of this species can modify their feeding habits spatially and temporally, both in the short term (Bustos et al., 2012; Muñoz et al., 2013) and in the long term (Baylis et al., 2015b; Cárdenas-Alayza

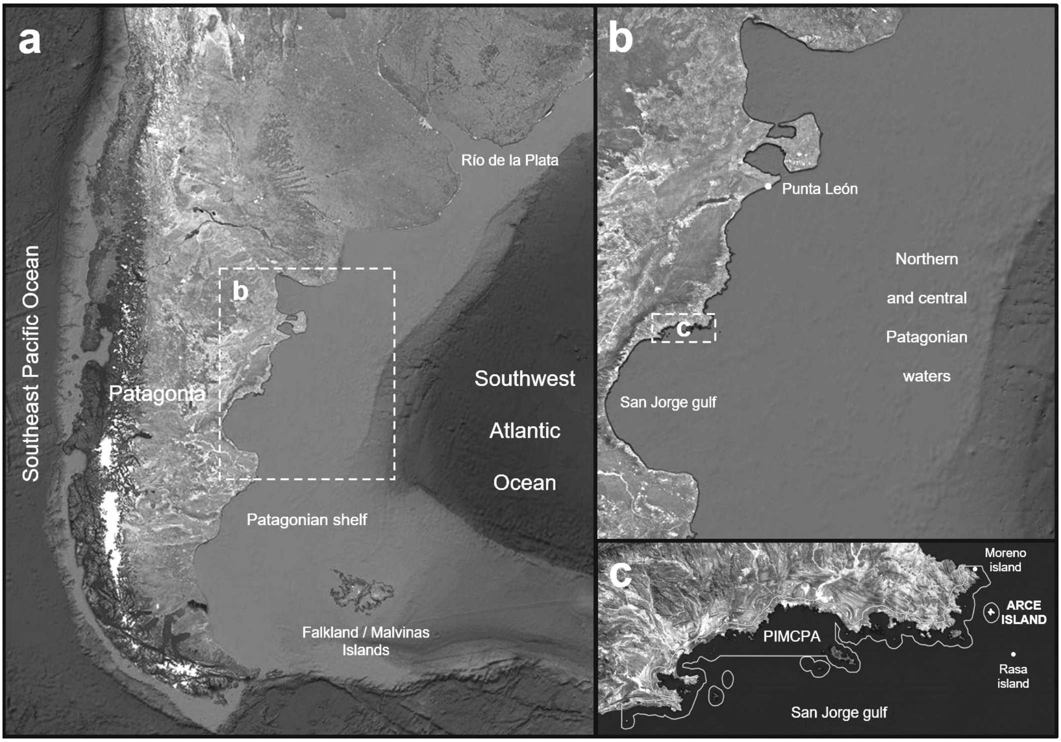

Figure 1. Maps of the study area: (a) southern South America with geographical references mentioned in the text; (b) detail of the northern and central coast of Patagonia (Argentina); and (c) detail of the northern coast of the San Jorge Gulf (Chubut Province, Argentina). The white polygon indicates the limits of the marine protected area Parque Interjurisdiccional Marino Costero Patagonia Austral (PIMCPA). Sampling was carried out in Isla Arce. (Images modified from Google Earth Pro and Bing maps)

et al., 2022), which could allow them to quickly adapt to changes in the environment, such as a drastic decrease in the abundance of certain prey species (Soto et al., 2006; Cárdenas-Alayza et al., 2022). Likewise, recent studies focused on adult female SASLs have revealed various strategies in their feeding habits. In Patagonia and the Falkland (Malvinas) Islands, females from the same and different colonies show differential use of trophic resources and/or foraging areas (Grandi et al., 2020; Riverón et al., 2021). Moreover, patterns of individual trophic specialization have been observed in colonies such as those in Uruguay (Franco-Trecu et al., 2014) and the Falkland (Malvinas) Islands (Baylis et al., 2015b, 2016; Riverón et al., 2021), although information of its variation over time is scarce (Baylis et al., 2015b).

Given the importance of trophic plasticity in individual success and population dynamics by enabling adaptation to environmental changes, the feeding habits and their temporal variations among SASL individuals within a colony on Isla Arce, central Patagonia (Argentina) (Figure 1c), were examined. Focusing on adult females due to their key role in determining population dynamics, we used stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) of whiskers to assess the temporal variations in their diet and the degree of trophic specialization. Adult female SASLs are central place foragers that alternate between foraging trips to sea and nursing on land (Thompson et al., 1998). Due to the restrictions imposed by maternal attendance, during the breeding season, females are expected to minimize their time at sea and maximize the time they spend onshore with their pups. Consequently, mothers were observed to have a more coastal/benthic diet during the breeding season and a more pelagic diet the rest of the year (Drago et al., 2010). Therefore, in this study, it is expected that whisker isotopic values reflect this diet alternation over time. Regarding the degree of individual trophic specialization, considering that the SASL population in northern and central Patagonia is steadily growing (Romero et al., 2017), and given that the increase in population density implies a decrease in the per capita abundance of resources, we hypothesized that the colony on Isla Arce will show a high degree of individual trophic specialization as a mechanism to reduce intraspecific competition (Araújo et al., 2011).

Methods

Study Area

The study area is located within the Parque Interjurisdiccional Marino Costero Patagonia Austral (PIMCPA), a marine protected area on the northern coast of the San Jorge Gulf, Chubut Province, Argentina (Figure 1c). This sector of the coast is characterized by the presence of bays, coves, and numerous islands and islets (Malvicini & Llambías, 1974). The seafloor alternates fine and coarse sediments with rocky bottoms and rocky ridges (Fernández et al., 2003; Sánchez-Carnero & Rodríguez-Pérez, 2021), and depths can reach up to 90 m (Rodríguez-Pérez & Sánchez-Carnero, 2022). Coastal waters are influenced by the Patagonian Coastal Current (i.e., the western branch of the Malvinas/Falkland Current) flowing to the north-northeast over the continental shelf, bringing nutrient-rich, cold, and low salinity sub-Antarctic waters (Palma et al., 2008). In addition, a tidal front near the northern coast of the gulf promotes high biological production, offering feeding and reproductive habitats for fish (e.g., hake and anchovies) and invertebrates (e.g., squids and shrimps). This, in turn, attracts seabirds and pinnipeds that settle on the nearby coasts, as well as several species of cetaceans (Yorio et al., 1998; Acha et al., 2004; Reyes, 2006). Isla Arce (45° 00' S, 65° 29' W) is a rocky island of 0.45 km^2 in area located about 8 km from the mainland. This island harbors a colony of about 900 SASLs (EAC, unpub. data). During the 2015 breeding season (January), 12 lactating female SASLs were randomly captured on the island using hoop nets. They were then sedated using a combination of midazolam 5% and dexmedetomidine (see Katz et al., 2018), and a whisker was extracted from each of them, which was stored in paper for later treatment.

Sample Processing and Stable Isotope Analysis

Each whisker was washed with distilled water to remove impurities and cut into 3-mm-long consecutive sections starting from the proximal end, following the protocol applied to other otariid species (Hirons et al., 2001; Cherel et al., 2009). Each fragment was then immersed in a 1:1 hexane-acetone solution to extract lipids and left until total evaporation. To achieve the required mass (~0.8 mg), each 3-mm fragment of whisker was subsampled, weighed on a high precision microbalance, and stored in tin capsules until isotopic determination.

Nitrogen and carbon isotope ratios were measured by Elemental Analyzer Continuous Flow Isotope Ratio Mass Spectrometry at the Center for Stable Isotopes, University of New Mexico (Albuquerque, NM, USA), using a Costech ECS 4010 Elemental Analyzer (Costech Technologies, Montreal, Quebec, Canada) coupled to a Thermo Fisher Scientific Delta V Advantage mass spectrometer via a CONFLO IV interface (Thermo Fisher Scientific, Waltham, MA, USA). Isotope ratios are reported using the standard delta notation relative to V-AIR and to Vienna Pee Dee Belemnite (V-PDB), respectively. Three internal laboratory standards were run at the beginning, at intervals between samples, and at the end of analytical sessions. Analytical precision calculated from the standards is ± 0.1‰ (1σ standard deviation [SD]) for both $\delta^{15}N$ and $\delta^{13}C$. The resulting isotope ratios for each whisker segment were converted and reported to the conventional values delta (δ) in parts per thousand (‰), according to $\delta X = [(R/Rst) - 1]$, where X stands for ^{15}N or ^{13}C, R is the heavy-light stable isotope ratio of the sample ($^{13}C/^{12}C$ or $^{15}N/^{14}N$), and Rst is the heavy-light stable isotope ratio in reference standards, previously mentioned. As a data quality control criterion, the carbon to nitrogen (C:N) mass ratio of the samples was compared to the theoretical expected weight percent C:N ratios for pure keratin, which is approximately 3.0 (Newsome et al., 2010).

Data Analysis

Vibrissae growth rate estimates for adult female SASLs are 0.15 mm per day (Cardona et al., 2017). As most whiskers were longer than 10 cm (mean = 13.2; SD = 2.98), it was possible to obtain information about the feeding habits within a 3-y period—2012, 2013, and 2014—and to evaluate changes in a medium term. The 2012 analyses were carried out on 10 females instead of 12 because the whiskers of two females were not long enough to integrate three complete years.

Diet Composition—Diet composition was estimated at the population level for each year (2012 to 2014) using mixing models in the 'MixSIAR' package, which allows incorporating a dependency structure among the data of an individual (Stock et al., 2018). The selection of potential prey items to include in the mixing models was based on reports from Jarma et al. (2019) and Koen-Alonso et al. (2000), and were complemented with results of fecal samples collected on Isla Arce and other nearby islands (Isla Rasa and Islote Moreno) between 1999 and 2018 (EAC, unpub. data; Table 1; Figure 1c). Prey isotopic values (mean and SD) were obtained from Drago et al. (2009b) and Vales et al. (2015), while the TEFs used ($\Delta^{13}C = 3.0 \pm 0.5‰$; $\Delta^{15}N = 3.6 \pm 0.5‰$) were determined for SASL whiskers under controlled conditions (Cardona et al., 2017).

Table 1. Relevant prey items in the diet of South American sea lion (*Otaria flavescens*) females according to the literature that were used to run the mixing models. Prey items were selected based on having a percent index of relative importance (%IRI) greater than 1, a percent frequency of occurrence (%FO) greater than 5, or their occurrence in feces. The ecological group for each species is shown in parentheses (P = pelagic, B = benthic, DP = demersal pelagic, and DB = demersal benthic).

Prey species	Selection criterion	Source
Enteroctopus megalocyathus (B)	%FO = 53.8; %IRI = 55.0	Koen-Alonso et al., 2000
Illex argentinus (DP)	%FO = 38.5; %IRI = 17.5	Koen-Alonso et al., 2000
Merluccius hubbsi (DP)	%FO = 34.6; %IRI = 11.9	Koen-Alonso et al., 2000
Raneya brasiliensis (DB)	%FO = 19.2; %IRI = 6.9	Koen-Alonso et al., 2000
Engraulis anchoita (P)	%FO = 15.4; %IRI = 4.4	Koen-Alonso et al., 2000
Doryteuthis gahi (DP)	%FO = 26.9; %IRI = 1.1	Koen-Alonso et al., 2000
Patagonotothen cornucola (DB)	%FO = 7.7; %IRI = 0.6	Koen-Alonso et al., 2000
Paralichthys isosceles (B)	%FO = 7.7; %IRI = 0.4	Koen-Alonso et al., 2000
Doryteuthis sanpaulensis (DP)	%FO = 7.7; %IRI = 0.1	Koen-Alonso et al., 2000
Pleoticus muelleri (DB)	Relevant prey in feces	EAC, unpub. data
Munida subrugosa (B)	Relevant prey in feces	EAC, unpub. data
Seriorella porosa (DP)	%FO = 19.3; %IRI = 9.3	Jarma et al., 2019

The suitability of the selected prey items to run the mixing models was assessed using simulated mixing polygons, which incorporate the standard deviation of the prey and the TEFs used (Smith et al., 2013). The result of this analysis represents the probability that a consumer's diet is adequately represented in the proposed mixing model.

Given that some prey overlap in the δ-space (C and N), as well as having a similar ecological role, they were grouped together to run the mixing models. *Pleoticus muelleri* and *Munida subrugosa* form the group of "decapod crustaceans," while *Raneya brasiliensis*, *Patagonotothen cornucola*, and *Paralichthys isosceles* are combined as "benthic fishes" (see Figure 2). All statistical analyses were performed using *R* software (R Core Team, 2022).

Individual Trophic Specialization—The total niche width (TNW) of the consumer population can be partitioned into two components—(1) the within-individual component (WIC) and (2) the between-individual component (BIC)—such that TNW = WIC + BIC. We quantified individual specialization using Roughgarden's (1972, 1974) ITS index (BIC/TNW) that assesses the proportion of TNW that can be attributed to the BIC. When the population is made of largely generalist individuals, BIC is a small proportion of TNW, with the opposite being true in a population of specialist individuals (Bolnick et al., 2002, 2003).

First, BIC and WIC were estimated, from which the TNW and the ITS index were obtained for each year using both a one-dimensional and a multidimensional approach. For the former, the degree of ITS for ^{13}C and ^{15}N were estimated separately in the 'RInSp' package (Zaccarelli et al., 2013), which performs Monte Carlo resampling to evaluate the statistical significance of the ITS index against the null hypothesis that they are generalist individuals (Zaccarelli et al., 2013). For the latter, a generalized linear mixed model where each of the isotopes (δ^{13}C and δ^{15}N) constituted a niche axis (Ingram et al., 2018) was used. The WIC and BIC variance components were estimated using the 'MCMCglmm' package in *R* (R Core Team, 2022), which employs Bayesian Markov Chain Monte Carlo analysis (Ingram et al., 2018) from which the TNW and the ITS index were then calculated as described above.

Results

The average number of portions per whisker analysed (n = 239 segments) was 19.92 (SD = 4.23), the minimum number of fragments per whisker was 13, and the maximum number was 28. The range of δ^{13}C values was -15.82 to -13.18 (mean = -14.38; SD = 0.39); while for δ^{15}N, the range was 18.71 to 21.14 (mean = 20.25; SD = 0.43) (Figure 2). The average value for each female ranged from -14.56 to -14.09 for δ^{13}C and from

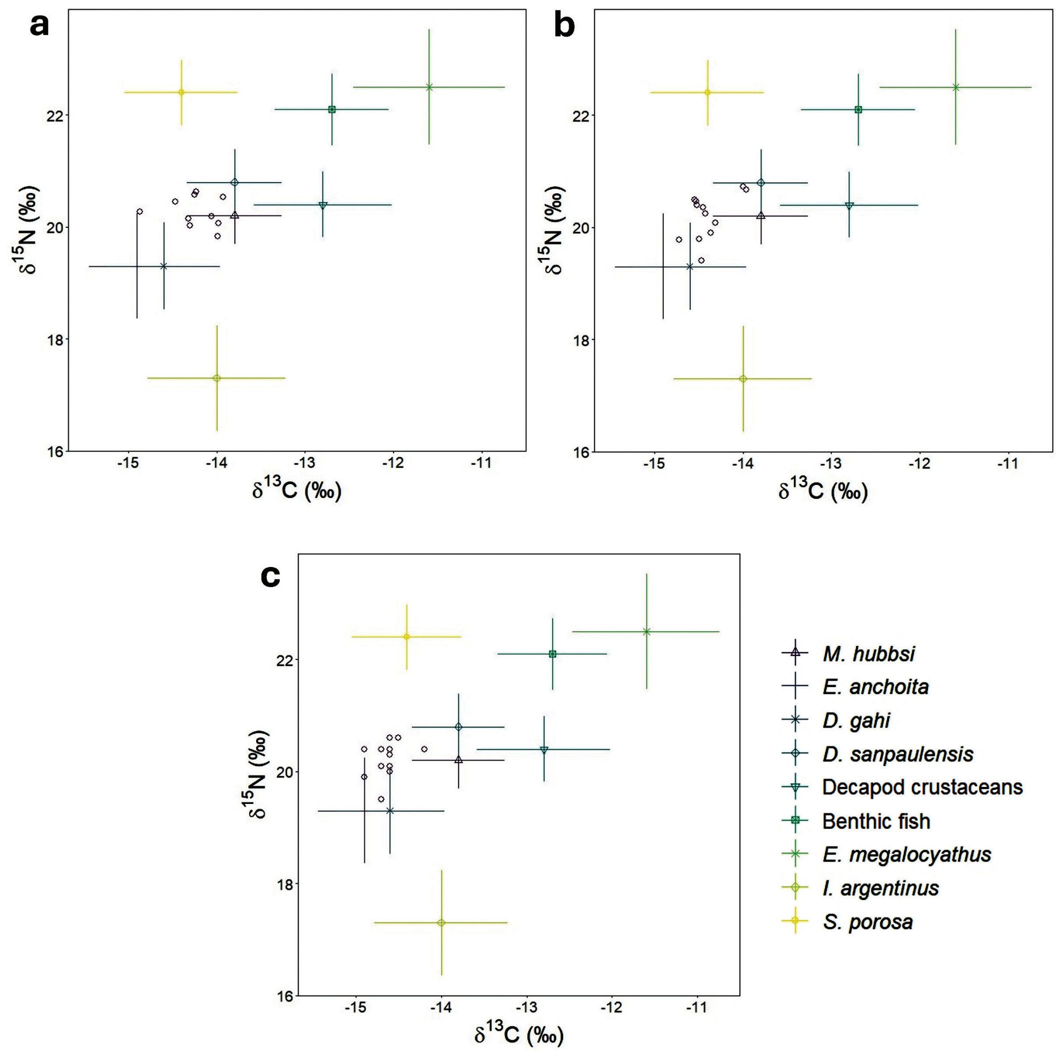

Figure 2. Biplot of δ^{13}C and δ^{15}N for the years 2012 (a), 2013 (b), and 2014 (c) with the isotopic signatures of the whiskers of 12 *O. flavescens* females from a colony on Isla Arce, Argentina (purple circles), and the potential prey species/groups that were selected to analyse the assimilated diet composition using mixing models. The mean of each prey species/group is represented with a different color and symbol, and its standard deviation is represented by error bars.

19.83 to 20.6 for δ^{15}N. Carbon to nitrogen (C:N) mass ratio ranged from 2.70 to 3.60 (mean = 2.82; SD = 0.09).

Diet Composition

In years 2012 and 2014, models predicted that the Argentine anchovy was the most consumed prey by SASL females, contributing 23.4 and 32.2%, respectively, to the diet; while in 2013, it was the Patagonian squid (*Doryteuthis gahi*) with a contribution of 28.5% (Table 2). In all cases, the simulated mixing polygons (Smith et al., 2013) indicated that the proposed mixing models were suitable for estimating the contribution of prey items to the diet of the individuals analysed.

Individual Trophic Specialization

In the one-dimensional analysis, the ITS estimates per year varied between 0.24 and 0.73 for δ^{13}C and between 0.49 and 0.75 for δ^{15}N. In all cases, the null hypothesis that individuals are trophic generalists was rejected ($p \leq 0.05$; Table 3). In the multidimensional analysis, the ITS values for the 3 y analysed varied between 0.45 and 0.72 (Table 3).

Table 2. Average relative importance at the population level of different prey items in the diet of female South American sea lions from a colony on Isla Arce, estimated using mixing models. The 95% confidence interval is shown in parentheses.

Prey	2012	2013	2014
Engraulis anchoita	23.4% (0.3-49.8%)	25.5% (4.4-48.4%)	32.2% (6.0-60.4%)
Doryteuthis gahi	17.9% (0.7-42.9%)	28.5% (6.9-52.0%)	21.9% (0.7-49.5%)
Doryteuthis sanpaulensis	11.4% (0.8-30.3%)	9.6% (0.6-27.6%)	5.0% (0.3-17.9%)
Benthic fish	4.0% (0.1-13.3%)	4.8% (0.1-14.4%)	2.1% (0.1-7.5%)
Illex argentinus	8.5% (1.4-18.2%)	4.2% (0.1-15.7%)	5.3% (0.1-17.8%)
Merluccius hubbsi	11.5% (0.5-32.5%)	5.3% (0.2-16.9%)	4.5% (0.1-15.3%)
Enteroctopus megalocyathus	3.0% (0.2-9.3%)	2.4% (0.0-8.7%)	1.5% (0.0-5.2%)
Decapod crustaceans	5.4% (0.1-16.6%)	2.6% (0.1-10.5%)	2.0% (0.0-7.3%)
Seriolella porosa	14.9% (2.4-29.6)	17.0% (5.2-31.1%)	25.5% (11.0-40.5%)

Table 3. One-dimensional and multidimensional (estimated with a 95% confidence interval) per-year values of the within- and between-individual variance components (WIC and BIC, respectively), total population niche width (TNW), and individual trophic specialization (ITS) for the $\delta^{13}C$ and $\delta^{15}N$ values of SASL females from a colony on Isla Arce. Statistical significance of the ITS index against the null hypothesis that they are generalist individuals: *indicates statistical significance at $p \leq 0.05$ and **indicates statistical significance at $p \leq 0.001$.

	One-dimensional $\delta^{13}C$			One-dimensional $\delta^{15}N$			Multidimensional		
	2012	2013	2014	2012	2013	2014	2012	2013	2014
WIC	0.06	0.02	0.10	0.06	0.05	0.11	0.07 (0.05-0.11)	0.05 (0.04-0.08)	0.13 (0.09-0.18)
BIC	0.07	0.05	0.03	0.07	0.18	0.10	0.09 (0.02-0.22)	0.13 (0.04-0.28)	0.11 (0.02-0.24)
TNW	0.12	0.07	0.13	0.14	0.24	0.21	0.16 (0.06-0.32)	0.19 (0.08-0.35)	0.24 (0.11-0.42)
ITS	0.53**	0.73**	0.24*	0.53**	0.75**	0.49**	0.55 (0.25-0.67)	0.72 (0.55-0.79)	0.45 (0.20-0.56)

Discussion

Diet Composition

Fish were the most frequent prey during the 2012-2014 period, followed by cephalopods. This is consistent with other dietary reports of SASLs in the Southwest Atlantic Ocean, which also identified fishes as the dominant prey taxa (Thompson et al., 1998; Koen-Alonso et al., 2000; Bustos et al., 2012; Machado et al., 2018; Jarma et al., 2019). Building on previous findings that highlighted the dietary patterns of SASL females in northern and central Patagonia, which include a shift from pelagic to benthic prey around the time of parturition, it has been proposed that this dietary flexibility serves to minimize the duration of foraging trips and the time that pups remain unattended during early lactation (Drago et al., 2010). Given this context, and considering that vibrissae record dietary information over several years, it was expected that we would observe changes in isotopic values along the whiskers that would reflect shifts between pelagic and benthic prey consumption. However, our results indicate that female SASLs breeding on Isla Arce primarily rely on pelagic prey year-round (i.e., before and after parturition). Considering all the pelagic species included in the mixture models, their relative importance in the diet at the population level exceeded 85% for all 3 y studied. The consumption of mainly pelagic prey throughout the year (contrary to what was expected) could be an adaptive foraging strategy in response to the variability in prey abundance and availability among different areas. Many otariid species have been observed to vary their diet according to the geographic region and to prey availability (García-Rodríguez & Aurioles-Gamboa, 2004; Cherel et al., 2009; Scherer et al., 2015), including SASLs. Female SASLs that inhabit the Peruvian upwelling ecosystem are exposed to highly stochastic fluctuations in the distribution and abundance of their prey, and they appear to adjust their diets in response to these changes, with the abundance of certain prey in their diets increasing as they became more abundant close to the rookery (Soto et al., 2006; Cárdenas-Alayza et al., 2022). Geographical differences in the diet of the SASLs have also been reported in regions like Chile (Muñoz et al., 2013) and northern Patagonia, where small-scale variations in diet appear to be linked to differential prey availability (Jarma et al., 2019). On the northern and central Patagonian shelf, the distribution and the location of the main anchovy concentrations seem to respond to annual changes in the positions of the marine fronts (Hansen et al., 2001). Therefore, the existence of different foraging strategies in lactating SASL females at a small scale—the SASL colonies of Punta León and Isla Arce are located at a distance of 230 km from each other—may be in response to annual fluctuations in the distribution and abundance of pelagic prey in the region. And when pelagic prey are available near SASL colonies during the reproductive season, lactating females—by undertaking brief foraging excursions—have access to coastal pelagic prey that typically have a higher energy content over benthic alternatives (Eder & Lewis, 2005; Drago et al., 2010).

Individual Specialization

Both the one-dimensional and multidimensional analysis indicated that SASL females breeding on Isla Arce show some degree of ITS. Currently, the SASL population of northern and central Patagonia shows positive growth, with a maximum increase rate of 5.5% (Romero et al., 2017). Previous studies have found a positive relationship between the population density and the degree of ITS in different otariid species (Kernaléguen et al., 2015; Juarez Ruiz et al., 2018), and has been suggested as a foraging strategy that could minimize intraspecific competition (Araújo et al., 2011). Thus, the degree of ITS found in this colony could constitute one of the mechanisms adopted by individuals to mitigate the potential competition given by a sustained population increase. While for years 2012 and 2014 the degree of ITS was moderate, for 2013 it was high. The multidimensional analysis shows that, in 2013, the highest degree of ITS was generated by an increase in inter-individual variance (higher BIC) and a decrease in intra-individual variance (lower WIC) compared to 2012 and 2014. This is consistent with the one-dimensional analysis for $\delta15N$. In 2013, an increase in total niche width (TNW) was also observed, mainly explained by the increase in BIC, increasing the differences between individuals. The higher degree of ITS in 2013 is likely due to greater diversification in the use of secondary resources by females. When the preference for a certain resource is shared, its scarcity can lead to increased competition between individuals to access it within the population (Ferry-Graham et al., 2002). In this context, individuals increase their diet diversification by consuming different secondary resources (Araújo et al., 2011).

In summary, the present study suggests that SASL females breeding on Isla Arce have distinctive foraging patterns compared to nearby colonies as they predominantly consume pelagic prey throughout the year. This is likely due to a higher availability of pelagic resources near the colony, which further corroborates the opportunistic feeding behaviour of the species, characterized by the ability to exploit a wide range of prey types based on availability (Bearhop et al., 2004). It was also found that females of this colony show variability in the degree of ITS, probably as a strategy to mitigate the potential competition given by a sustained population growth. This finding is significant for discussions surrounding the management and conservation strategies for this species, particularly considering the impact intraspecific variation can have in population dynamics (Araújo et al., 2011; Dall et al., 2012). Future studies should integrate foraging habits data with information about local environmental conditions during the period of interest to enhance our understanding of the species' adaptability to environmental changes.

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