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Diet composition of an opportunistic predator from an upwelling area in the Southeastern Pacific

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Abstract   The aim of this study was to use scat analysis to analyse the dietary composition of the South American sea lion (SASL, *Otaria byronia*) over a short temporal scale and in different but closely located colonies in the Humboldt Current System of northern Chile. Scat samples were collected at Arica (18°34′S), Iquique (20°48′S) and Mejillones (23°04′S) during the summer (January to March) and winter (July) of 2015. A total of 16 595 individual prey items from nine species were found in 194 of the 215 scat samples. In general, squat lobster (*Pleuroncodes monodon*) was the most important prey item for the sea lion diet, both by number and according to the index of relative importance (%IRI), followed by anchovy (*Engraulis ringens*), which was the most frequent prey item in the scats and the most important by weight. Patagonian squid (*Loligo gahi*) ranked third in importance in the sea lion diet. However, some spatiotemporal variations in the consumption of prey were found. Squat lobster was the most important prey for sea lions in Arica and Iquique, while anchovy was the dominant prey in Mejillones. Regarding seasonal variation, squat lobster was more important in winter than in summer in the three localities, while anchovy was also more important during winter, except in Mejillones where the levels of consumption of this prey were similar in both seasons. These results show that SASL adjust their dietary preferences, modifying the contribution of different prey both spatially and temporally. Spatiotemporal variations in the SASL diet can be explained by temporal changes in the distribution and abundance of their prey.

Key words: Chile, diet composition, *Otaria byronia*, scats, South American sea lion.

INTRODUCTION

The South American sea lion (SASL, *Otaria byronia*) is widely distributed along the Atlantic and Pacific coasts of South America. In the Atlantic, it is found from southern Brazil to the southern tip of South America, including the Falkland/Malvinas Islands (Crespo *et al.* 2012; Pavanato *et al.* 2013). On the Pacific coast, it is found from northern Peru (4°S) to Tierra del Fuego (Crespo *et al.* 2012), with some sightings registered in Ecuador (2°12′S; Félix 2002), and even some occasional observations along the coast of Colombia (2°N; Capella *et al.* 2002). The most recent sea lion counts indicate a population of around 143 000 individuals along the Chilean coast (Venegas *et al.* 2001; Oliva *et al.* 2012; 2016; 2020), with the highest abundances in northern (18°21′S to

25°50′S; 40 000 individuals) and southern Chile (40°20′S to43°38′S; 65 000 individuals).

The SASL diet is composed mainly of fish, and to a lesser extent of mollusks and crustaceans (Vaz-Ferreira 1982). There have been only two studies of the sea lion diet in northern Chile using stomach and scat analyses (Sielfeld *et al.* 1997, 2018). With stomach content analysis, Sielfeld *et al.* (1997) determined that the diet of sea lions around Arica (18°34′S) was dominated by anchovy (*Engraulis ringens*), followed to a lesser extent by Patagonian squid (*Loligo gahi*), cabinza grunt (*Isacia conceptionis*) and paloma pompano (*Trachinotus paitensis*). However, by means of scat analysis, Sielfeld *et al.* (2018) determined that during two periods of El Niño (1997–1998 and 2009–2010), the sea lion diet south of Iquique (20°48′S) was dominated by squat lobster (*Pleuroncodes monodon*), followed by anchovy and Patagonian squid. These changes in diet are associated with temporal and spatial variations in the availability and abundance of

prey caused by climatic phenomena such as El Niño–Southern Oscillation (ENSO; Soto *et al.* 2004, 2006; Sielfeld *et al.* 2018). Due to its ability to respond to environmental changes, this species has been classified as an opportunistic and generalist predator (Koen-Alonso *et al.* 2000; Cappozzo & Perrin 2009). However, it is important to note that the two studies of Sielfeld *et al.* (1997, 2018) were separated by 20 years and under the influence of El Niño events. Thus, the temporal and spatial variations in the SASL dietary composition reported by these authors may be due to long-term environmental changes. Moreover, little is known about potential temporal and/or spatial variations in the dietary composition over a short temporal scale (e.g. seasonal) and in distinct sites located close to each other.

Studies of potential temporal and/or spatial variations in the dietary composition in the short-term are relevant because the SASL diet is composed of species that are also captured by fishers, leading to significant interactions with fisheries (Goetz *et al.* 2008; González *et al.* 2016; Sepúlveda *et al.* 2018). In northern Chile, SASL feeds mostly in shallow (17 ± 2 m diving depth) coastal waters that overlap with fishing areas (Hevia-Álvarez 2013). During foraging trips (which usually last 1–3 days), most animals move in north–south direction, apparently searching for aggregations of specific pelagic resources like anchovy (Hevia-Álvarez 2013). Anchovy is also the main resource for the industrial and small-scale fisheries that operate in the first 20 nautical miles off the coast. Fishing occurs mainly from March to June every year and is constrained by environmental conditions, fishing quotas, and bans due to anchovy reproductive (austral spring) and recruitment (austral summer) periods (Böhm *et al.* 2012). During this period, SASL females congregate in coastal rookeries nursing their pups, which are also learning to hunt and dive in areas close to the colonies (Sepúlveda *et al.* 2001; Acevedo *et al.* 2003). Thus, the nursing periods of SASL coincide with the extraction of pelagic fish by industrial and small-scale fishers in neritic areas. Therefore, the study of the composition and dynamics of the SASL diet is essential to understand and successfully manage the trophic and spatial overlap of SASL with small-scale and industrial fisheries operating in these regions (Crespo *et al.* 2012).

Considering that industrial and small-scale anchovy landings are concentrated in northern Chile, where there is also a large SASL population, we analysed the SASL diet at three geographic locations in northern Chile during two seasons of the year with the aim of analysing potential spatial (Arica *vs.* Iquique *vs.* Mejillones) and temporal (summer *vs.* winter) dietary variations among SASL in the Humboldt Current System in northern Chile.

METHODS

Study area

This study was conducted during the austral summer (January–March) and winter (July) of 2015, at five SASL colonies in northern Chile at three geographic locations: the Punta Blanca and Corazones colonies located south of Arica (Arica, 18°34′S); the Punta Patache colony located south of Iquique (Iquique, 20°48′S); and the Punta Angamos and Punta Campamento colonies on the northern border of the Mejillones Peninsula (Mejillones, 23°04′S; Fig. 1). A recent census of the SASL population reported 4677 animals in these five colonies in summer 2019 (Oliva *et al.* 2020). These locations are separated by distances of 250 km (Iquique-Mejillones) to 500 km (Arica-Mejillones). These distances exceed the average mean distance estimated for foraging trips of SASL individuals along the Atlantic (206 km, Campagna *et al.* 2001) and Pacific coasts (211 km, Hückstädt *et al.* 2014; 100.9 km, Sepúlveda *et al.* 2015), and in the study area (124.1 km, Hevia-Álvarez 2013).

Scat collection and dietary composition

A total of 215 fresh scats were collected at three locations in the summer (Arica = 32, Iquique = 32, Mejillones = 51) and winter (Arica = 29, Iquique = 36, Mejillones = 35) of 2015. Scats at each location were collected and stored individually in plastic bags. In the laboratory, the scats were washed with seawater and fresh running water through different sized sieves (from 0.7 to 2 mm) and preserved in plastic bottles with ethanol (60%). Before analysis, samples were immersed in freshwater for 48 h and washed several times . Using a stereoscopic microscope (20–40×), fish sagittal otoliths, cephalopod beaks and crustacean exoskeletons were identified to the lowest possible taxonomic level using several references, including articles, reports and identification guides (e.g. Pineda *et al.* 1998; García-Godos 2001; Arrieta *et al.* 2010; 2012; Goicochea *et al.* 2012; Puse-Fernández 2012). It was assumed that scats belonged to different individuals based on the following criteria: (i) all scats were collected on a single day per colony, (ii) the number of sea lions in each colony varies from 1088 (in Arica) to 2503 individuals (in Mejillones), and thus the probability of two or more scats belonging to a single animal is very low, and (iii) we covered the entire rookery to avoid the probability of collecting two or more scats from the same individual.

The numerical abundance of fish (NF) per sample was estimated using the maximum number of right or left otoliths in the sample (Koen-Alonso *et al.* 2000; Riet-Sapriza *et al.* 2013) according to the equations:

$$NF = LO + 0.5UO, \text{ if } LO > RO$$

$$NF = RO + 0.5UO, \text{ if } RO > LO$$

where LO, RO and UO are the number of left, right and unassigned otoliths, respectively.
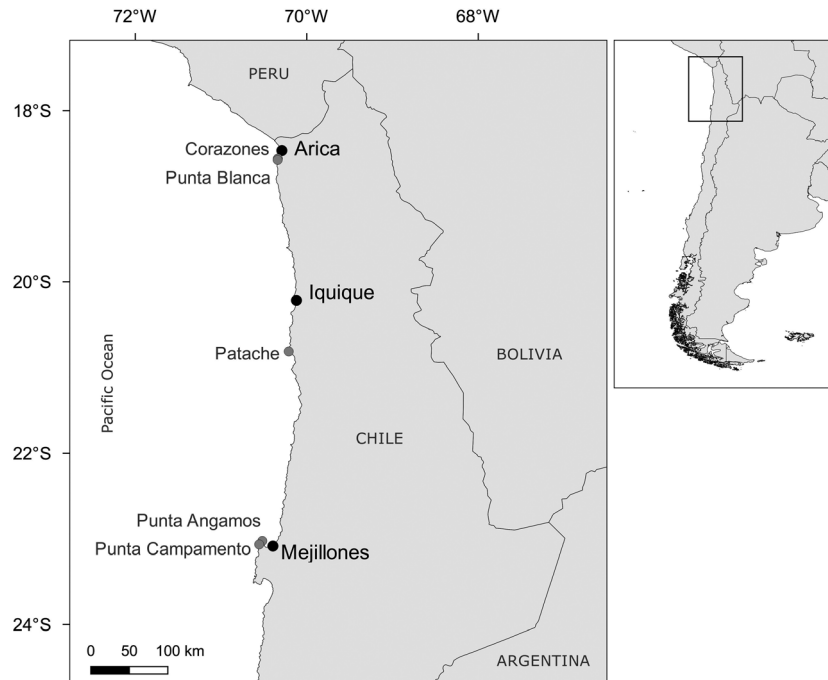
Fig. 1. Study area showing the five sampling colonies (grey dots) for collecting South American sea lion scats at three locations (black dots) in northern Chile during the summer and winter of 2015.

The number of individual crustaceans was estimated using the maximum number of exoskeletons or the number of chelae divided by two. The number of cephalopods was estimated according to the maximum number of beaks recovered per sample (Koen-Alonso *et al.* 2000). The size of prey consumed by SASL was estimated based on the length of the otoliths with no erosion, measured manually, and using allometric regressions of total prey length (TL$_p$) and otolith length (OL) developed for some fish species in northern Chile (Table 1). Otolith size for each species was adjusted according to Jahncke and Rivas (1998), considering that once otoliths cross the digestive tract they are eroded by around 10–15%. The only exception was the Lorna drum (*Sciaena deliciosa*), where no erosion was recorded by the same authors. Thereafter, individual biomass was estimated from regressions between total length (TL) and mass of prey (Table 1). Mass assigned to the squat lobster (4.66 g) was the mean value obtained from direct weight (*n* = 80), obtained from previous studies in the area (Sielfeld *et al.* 2018). Patagonian squid biomass was estimated according to Arancibia and Robothan (1984) assuming a mean weight of 78 g per individual.

Data analysis

We calculated the following indexes to compare the importance of prey species to the SASL diet among seasons and localities: (i) The percentage frequency of occurrence (%FO), which is the percentage of samples in which a prey species is present with respect to the total number of samples; (ii) The percentage by weight (%W), which is the regression-estimated weight of each prey species with respect to the total weight of all samples; (iii) The percentage by number (%N), which is the number of individuals of each prey species with respect to the total number of individuals in all samples; and (iv) The index of relative importance (IRI), estimated as IRI = (%N + %W) × %FO), where %N is the percentage by number, %W is the percentage by weight, and %FO is the percentage of frequency of occurrence (Castley *et al.* 1991; Koen-Alonso *et al.* 2000; Hart *et al.* 2002; Mar-Silva *et al.* 2014). The IRI was expressed as a percentage (%IRI) to facilitate its interpretation, according to Cortés (1997).

Variation in dietary composition among sites and seasons was examined using chi-square tests applied to data on the dietary indexes. To further investigate how the relative importance of prey varies among sites and seasons, the pattern of change in %IRI for selected groups or species was graphed as stacked columns (Fig. 2).

Niche amplitude and trophic level

In order to estimate the level of trophic specialisation, that is the dominance of one or a few prey in the SASL diet in northern Chile, Levin's Standardized Index (Krebs 1999) was calculated as follows:

$$B = \frac{1}{n-1}\left\{\left[\frac{1}{\sum P_j^2}\right] - 1\right\}$$

where *B* is the trophic amplitude standardised on a scale from 0 to 1, P_j is the proportion of prey *j* (%W) in the

Table 1. Mean length (cm) and biomass (g) of prey items identified in South American sea lion scat samples collected at three locations in northern Chile during the summer and winter of 2015, and regression equations of total prey length (TL_p) and otolith length (OL; not corrected) for some fish species in this region

Species	Common name	N	Otolith length (mm)	Fish size (cm)	Individual biomass (g)	Otolith length/fish size ratio	Fish size/individual biomass ratio	Source
Engraulis ringens	Anchovy	3520	2.86 ± 0.56	11.99 ± 2.18	12.43 ± 6.04	TL = (OL*3.33) + 0.798	$W = 0.0078\ TL^{2.9328}$	Jahncke & Rivas (1998) Araya *et al.* (2008)
Normanichthys crockery	Mote sculpin	319	2.50 ± 0.58		2.70 ± 0.19		$W = 0.7867[Ln (OL)] + 2.0018$	García-Godos (2001)
Trachurus murphyi	Jack mackerel	276	2.26 ± 0.87	23.73 ± 0.60	146.82 ± 10.58	TL = (OR-2 1.5)/0.85	$W = 0.014\ TL^{2.923}$	Kaiser (1973) Cubillos & Alarcón (2010)
Odontesthes regia	Chilean silverside	35	2.31 ± 0.51	11.09 ± 2.31	11.39 ± 7.12	TL = −0.614 + 3.85OL	$W = 0.008\ TL^{2.97}$	Jahncke & Rivas (1998) Pavez *et al.* (2008)
Isacia conceptionis	Cabinza grunt	77	3.97 ± 1.36	9.89 ± 3.92	17.06 ± 21.91	TL = 3.6971 $OR^{1.1494}$	$W = 0.0091\ TL^{3.095}$	Goicochea *et al.* (2012), Pérez-Matus *et al.* (2014)
Sciaena deliciosa	Lorna drum	12	4.50 ± 1.92	14.73 ± 6.03	62.48 ± 48.88	TL = −5.88 + 6.2846 OR	$W = 0.0188\ TL^{2.8923}$	Arrieta *et al.* (2010)
Galeichthys peruvianus	Peruvian sea catfish	8	–	27	–	TL = 0.760 $OR^{0.562}$	$W = 0.0306\ TL^{2.5676}$	Castañeda *et al.* (2007)
Pleuroncodes monodon	Squat lobster	12058	–	–	4.66 g/ind	–	–	Sielfeld *et al.* (2018)
Loligo gahi	Patagonian squid	1295	–	–	78 g/ind	–	–	Arancibia & Robotham (1984)

OL, otolith length (mm); OR, otolith radius (=OL/2); TL, fish total length (cm); *W*, fish weight.

SASL diet, and *n* is the total number of prey in the SASL diet. Similarly, the trophic level was estimated as:

$$TL = 1 + \sum_{j=1}^{n} P_j \times TL_j$$

where TL is the trophic level of SASL, P_j is the biomass proportion of each prey *j* (%*W*) in the SASL diet, and TL_j is the trophic level of each prey species *j* according to Fish-Base (Froese & Pauly 2009), or previous studies such as Taylor *et al.* (2008) and Ortiz *et al.* (2013). B_A and TL_i were estimated for each season and locality.

RESULTS

Scat analysis

A total of 16 595 individual prey items of nine species were found in 194 of the 215 scat samples (Table 2), with an estimated weight of 155.2 kg. The fragments found in the scats were mostly crustacean exoskeletons (%*N* = 72.7), teleost fish otoliths (%

N = 25.6) and cephalopod beaks (%*N* = 1.7). Some scats included bird feathers (%FO = 33.4) and pieces of plastic bags (%FO = 3.0).

In general, squat lobster was the most important prey item found in the scats by number and according to %IRI, followed by anchovy, which was the most frequent prey item found in the scats and the most important by weight (Table 2). Patagonian squid ranked third in importance in the sea lion diet. The other prey species represented <2% according to %*N*, %*W* and %IRI.

There were significant differences in dietary composition between summer and winter for all the indexes (%*N*: $\chi^2 = 26.884$, d.f. = 2, $P < 0.001$; %*W*: $\chi^2 = 26.884$, d.f. = 2, $P < 0.001$; %IRI: $\chi^2 = 32.411$, d.f. = 2, $P < 0.001$), with the exception of %FO ($\chi^2 = 4.951$, d.f. = 2, $P = 0.084$). In summer, the SASL diet was dominated by teleost (mainly anchovy), which was the most frequent prey in the scats and the most important by weight and %IRI. The second most important prey species was squat lobster, which was the most numerous. Patagonian squid was third in importance and represented ca.
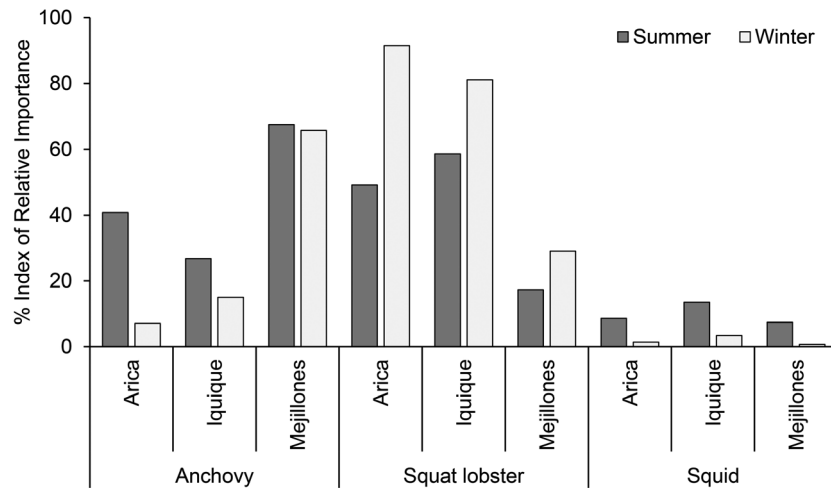
Fig. 2. Index of Relative Importance (%IRI) of dominant prey in the diet of South American sea lions, according to scat samples collected at three localities (Arica, Iquique and Mejillones) in northern Chile during the summer and winter of 2015.

Table 2. Number (N), percentage frequency of occurrence (%FO), percentage by number (%N), percentage by biomass (%W) and percentage index of relative importance (%IRI) of prey items identified from scat samples of the South American sea lion collected during the summer and winter of 2015 in northern Chile

Prey	Summer					Winter					Summer + winter				
	N	%FO	%N	%W	%IRI	N	%FO	%N	%W	%IRI	N	%FO	%N	%W	%IRI
Teleosts															
Anchovy	2419	94.8	36.1	52.5	52.6	1101	78.0	11.1	32.3	23.2	3520	87.0	21.2	43.2	37.3
Mote sculpin	206	45.2	3.1	2.0	1.4	113	30.0	1.1	1.3	0.5	319	38.1	1.9	1.7	0.9
Chilean jack mackerel	258	35.7	3.8	1.6	1.2	18	12.0	0.2	1.1	0.1	276	24.7	1.7	1.4	0.5
Chilean silverside	28	12.2	0.4	0.3	0.1	7	7.0	0.1	0.1	<0.1	35	9.8	0.2	0.2	<0.1
Cabinza grunt	38	10.4	0.6	0.7	0.1	39	18.0	0.4	0.7	0.1	77	14.0	0.5	0.7	0.1
Lorna drum	6	4.3	0.1	1.5	<0.1	6	3.0	0.1	0.5	<0.1	12	3.7	0.1	1.1	<0.1
Peruvian sea catfish	7	5.2	0.1	1.1	<0.1	1	1.0	<0.1	0.2	<0.1	8	3.3	<0.1	0.7	<0.1
Crustaceans															
Squat lobster	3525	79.1	52.6	19.8	35.3	8533	76.0	86.3	56.1	74.1	12058	77.7	72.7	36.5	55.8
Cephalopods															
Patagonian squid	219	63.5	3.3	20.4	9.3	71	34.0	0.7	7.7	2	290	49.8	1.7	14.6	5.3

20% in biomass (Table 2). In contrast, squat lobster was the most important sea lion prey in winter based on number, weight and %IRI, followed by anchovy and then Patagonian squid (Table 2).

Similarly, there was a significant difference in dietary composition among localities for all the indexes (%N: $\chi^2 = 88.81$, d.f. = 4, $P < 0.001$; %W: $\chi^2 = 68.681$, d.f. = 4, $P < 0.001$; %IRI: $\chi^2 = 70.187$, d.f. = 4, $P < 0.001$), with the exception of %FO ($\chi^2 = 7.400$, d.f. = 4, $P = 0.116$). In the Arica and Iquique localities, squat lobster was the most important prey species in the SASL diet by number, weight and according to %IRI (Table 3). In both localities, squat lobster was the dominant prey in the diet of

the SASL during winter, reaching values >80% according to %IRI (Fig. 2). Anchovy, which ranked second in importance in both localities, was more important during summer than during winter according to %IRI (Fig. 2). The opposite pattern was found in Mejillones, where the most important prey item was anchovy, followed by squat lobster and Patagonian squid (Table 3). The contribution of anchovy did not differ significantly between seasons in Mejillones, but squat lobster was more important in winter at this locality (Fig. 2). Finally, the Patagonian squid was third in importance in the sea lion diet and more important in summer than in winter in all three locations.

Table 3. Number (N), percentage frequency of occurrence (%FO), percentage by number (%N), percentage by biomass (%W) and percentage index of relative importance (%IRI) of prey items identified from scat samples of the South American sea lion collected at three locations in northern Chile in 2015

Prey	Arica					Iquique					Mejillones				
	N	%FO	%N	%W	%IRI	N	%FO	%N	%W	%IRI	N	%FO	%N	%W	%IRI
Teleosts															
Anchovy	470	73.8	11.4	21.1	18.8	801	94.1	10	25.8	31.2	2249	90.7	50.4	67.2	68.1
Mote sculpin	12	11.5	0.3	0.4	0.1	102	47.1	1.3	1.3	1.1	205	50.0	4.6	2.6	2.3
Chilean jack mackerel	–	–	–	–	–	3	4.4	<0.1	<0.1	<0.1	273	58.1	6.1	3.2	3.4
Chilean silverside	8	3.3	0.2	0.2	<0.1	2	2.9	<0.1	<0.1	<0.1	25	19.8	0.6	0.3	0.1
Cabinza grunt	8	4.9	0.2	1.4	0.1	5	4.4	0.1	0.1	<0.1	64	27.9	1.4	0.9	0.4
Lorna drum	6	8.2	0.1	4.9	0.3	1	1.5	<0.1	0.1	<0.1	5	2.3	0.1	0.3	<0.1
Peruvian sea catfish	1	1.6	<0.1	0.5	<0.1	2	2.9	<0.1	0.5	<0.1	5	4.7	0.1	1.0	<0.1
Cephalopods															
Patagonian squid	45	39.3	1.1	12.4	4.1	121	32.4	1.5	16.2	5.3	124	41.9	2.8	14.1	4.5
Crustaceans															
Squat lobster	3571	67.2	86.7	59.2	76.6	6971	47.1	87.1	53.1	62.4	1516	74.4	33.9	10.4	21.1

Trophic level and niche amplitude

The trophic level of the SASL in northern Chile was estimated at 4.01 ± 0.17 based on the identification of prey items from scat samples and the biomass contribution and trophic level of each prey species. This index was similar in winter and summer, and among the three localities (Table 4). The trophic amplitude of the SASL in this region was low ($B = 0.33$) and even lower in summer ($B = 0.25$) than in winter ($B = 0.48$). The trophic amplitudes of the SASL at the three localities were lowest in summer. For both seasons, the tropic niche amplitudes of the SASL at Mejillones and Iquique were broader than that of the SASL at Arica in both seasons (Table 4).

Table 4. Niche amplitude (B) and trophic level (TL) of South American sea lions at three localities in northern Chile in summer and winter

Season/locality	B	TL ± SD
Summer	0.25	4.00 ± 0.17
Arica	0.12	3.91 ± 0.14
Iquique	0.23	4.08 ± 0.19
Mejillones	0.36	4.05 ± 0.13
Winter	0.48	4.02 ± 0.17
Arica	0.13	3.85 ± 0.13
Iquique	0.63	4.10 ± 0.19
Mejillones	0.72	4.12 ± 0.12
Total	0.33	4.01 ± 0.17

DISCUSSION

The results of the present study show that in 2015 sea lions in northern Chile preyed on fish, crustaceans and cephalopods, similar to what has been reported elsewhere (e.g. George-Nascimento *et al.* 1985; Koen-Alonso *et al.* 2000). For this study, the SASL diet was composed of a total of nine species, three of them epipelagics (*E. ringens*, *Normanichthys crokeri* and *Trachurus murphyi*), one holopelagic (*P. monodon*), three benthopelagics (*I. conceptionis*, *S. deliciosa* and *Galeichthys peruvianus*) and two neritics (*L. gahi* and *Odontesthes regia*). However, of these nine species, only three were highly dominant: squat lobster, anchovy and Patagonian squid. The results of our study are consistent with most previous studies, which have shown that the SASL diet is composed of a few species, and dominated in frequency and relative importance by two or three species (George-Nascimento *et al.*, 1985; Koen-Alonso *et al.* 2000; Naya *et al.* 2000; Szteren *et al.* 2004; Suarez *et al.* 2005; Riet-Sapriza *et al.* 2013).

Scat analysis is the most widely used non-destructive method to assess mammalian diets (Klare *et al.* 2011). However, because this method is indirect, it can be biased by different factors, including misidentification of prey remains, the effects of scat collection and the under-representation of some prey items (Klare *et al.* 2011; Arim & Naya 2003; Bowen & Iverson 2013). The number of analysed scats is relevant to assess dietary composition in a population because inaccurate conclusions may result if too few

scats are collected (Trites & Joy 2005; Marucco *et al.* 2008). For nine prey species (the number observed for the SASL in our study), the minimum number of scats needed to detect differences between two populations is between 31 and 46, assuming a linear decline in the occurrence of prey (Trites & Joy 2005). The number of scats analysed in our study was in this range, except with Arica in winter (29 samples). In addition to the number of required scats, the use of hard parts in the analysis may also be limited because of hard parts being damaged, totally digested, regurgitated, or even not being ingested during consumption (e.g. soft bodied prey; Cottrell & Trites 2002; Casper *et al.* 2007), and thus, the recovery rates are specific to each species (Cottrell & Trites 2002). Regurgitation of material has been observed with some sea lion species (e.g. New Zealand sea lions (*Phocarctos hookeri*) and Steller sea lions (*Eumetopias jubatus*); Childerhouse *et al.* 2001; Trites *et al.* 2007), and fur seal species (e.g. New Zealand fur seals (*Arctocephalus forsteri*) and Northern fur seals (*Callorhinus ursinus*); Fea & Harcourt 1997; Kiyota *et al.* 1999), which can result in underestimating large cephalopods and large fish (Tollit *et al.* 2006). We caution about the low number of cephalopods found in our study, which could be an underrepresentation due to this behaviour. However, to our knowledge, regurgitation of prey remains has not been documented for the SASL, and thus, we cannot confirm bias in the consumption of this prey group.

Previous studies have reported anchovy as the main sea lion prey in northern Chile (Sielfeld *et al.* 1997) and southern Peru (Vásquez 1995; Zavalaga *et al.* 1998; Arias-Schreiber 2000; Soto *et al.* 2006). However, the results of the present study differ from those reported in the literature, since the squat lobster was the main sea lion prey in northern Chile, followed by the anchovy, and to a lesser extent the Patagonian squid. This difference could be partly explained by the fact that our scat sampling period coincided with the initial phase of the El Niño event of 2015 (NOAA 2019). The abundance of anchovy and squat lobster fluctuated due to interannual climate variability (Blanco *et al.* 2001), which in turn produced variations in their availability for predators. In the case of anchovy, it has been documented that during warm periods such as El Niño, this species disperses and moves to greater depths (Jordán & Chirinos de Vildoso 1965; Arntz *et al.* 1991), which reduces its abundance (Gutiérrez 2001). Conversely, the abundance of squat lobster increases during El Niño events (Sanfuentes 2017). Consistent with our results, Sielfeld *et al.* (2018) registered the squat lobster as the dominant prey in the diet of SASL from Punta Patache, northern Chile, the samples having been collected during two El Niño events (1997–1998 and 2009–2010). Similar results have

been reported in Peru, where anchovy practically disappeared from the diet of the South American fur seal (*Arctocephalus australis*) during the 1982–1983 El Niño (Majluf 1991). Apart from the potential influence of an El Niño event during our study period, the abundance of squat lobster, which is part of the diets of several species (Paredes & Elliot 1997; García-Godos *et al.* 2002; Alegre *et al.* 2014), has increased since the mid-1990s (Gutiérrez *et al.* 2008). Therefore, the change in the availability of prey can also explain the high presence of squat lobster in the sea lion diet.

Although the squat lobster is the main prey of sea lions in northern Chile, some spatiotemporal variations were found in the consumption of prey. Squat lobster was the most important prey for SASL in Arica and Iquique, reaching %IRI values over 80% in both localities in winter. Anchovy ranked second in importance in these two localities, with more consumption in summer. In contrast, anchovy was the dominant prey in the diet of sea lions near Mejillones, and no differences were found in consumptions levels between seasons. Squat lobster was the second most important prey for sea lions in this locality, with higher consumption in winter. These variations in the preferences of sea lions can be explained by spatiotemporal variations in the abundance and distribution of prey, since SASL tend to consume the most abundant prey in the ecosystem (Muñoz *et al.* 2013). It is important to highlight that although the distance between the sampled colonies is greater than the mean distances travelled by the animals when foraging (Mean: 124.1 ± 142.9 km; Hevia-Álvarez 2013), we cannot completely rule out connections among colonies.

It has been reported that the spatial distribution of anchovy varies between winter and summer (Ganoza *et al.* 2000). The distribution of the anchovy broadens to open ocean waters in winter, while in summer its habitat is reduced and individuals are pushed towards the coast, concentrating the stock in coastal waters (Castillo *et al.* 1996; Ganoza *et al.* 2000). These behavioural patterns produce a concentration of anchovy in coastal waters in summer, where presumably it is easier for sea lions to access them, thus increasing the consumption of this prey at this time of the year. In addition, hydroacoustic estimates of abundance show a high density point for anchovies on the coast off Mejillones (Córdova *et al.* 2014), which could explain the greater proportion of this prey in the diet of sea lions near this locality.

There have been few studies into squat lobster abundance and distribution in northern Chile (Acuña *et al.* 2014). As a result, it is difficult to explain the spatiotemporal variations in the contribution of this prey to the sea lion diet. According to Barbieri *et al.* (2001), there is a low squat lobster abundance point

north of 25°S. The bathymetric distribution of squat lobster is conditioned by its reproductive behaviour and the oceanography of the region (Palma & Arana 1997; Rivera & Santander 2005). The reproductive peak of this species occurs yearly between June and July (Gutiérrez & Zúñiga 1977; González *et al.* 2005; Rivera & Santander 2005; Franco-Meléndez 2012), so large gatherings of individuals are expected during this period. Likewise, it is established that female squat lobsters inhabit deeper waters in the early egg-carrying stage (autumn), and as the winter progresses, the percentage of ovigerous females at lower depths increases (Palma & Arana 1997), indicating that ovigerous females migrate to shallower waters in winter to release larvae (Arana & Culquichón 1990; Palma & Arana 1997), so they are concentrated in coastal areas when spawning occurs. This bathymetric change in the distribution and abundance of individuals could make them more available at shallower depths and in more coastal waters at the end of winter. Scat collection was carried out during this season in the last week of July, which coincides with the reproductive peak of the squat lobster. Together with less availability of anchovies along the coast in winter (see above), this explains the greater consumption of squat lobster by sea lions at this time of year.

The trophic level estimates indicate differences in habitat use driven by differences in dietary composition among consumer populations. The trophic level estimations for the different locations and seasons in this study (3.85–4.12) place SASL as a major order predator. These estimations are similar to those of Pauly *et al.* (1998) for SASLs (TL = 4) and Hückstädt *et al.* (2007) for this species in central Chile (TL = 4.57), as well as to estimations for other pinniped species around the world (Pauly *et al.* 1998; Lesage *et al.* 2001). Although trophic levels were similar among all sea lions, there were spatial and temporal variations in the trophic range. The trophic range was lower among sea lions near Arica during (0.12 and 0.13) than among sea lions near Iquique and Mejillones, particularly during the winter months. The narrower trophic spectrum of sea lions near Arica suggests that the diets of these animals consist of fewer prey species than in the diets of sea lions near Iquique and Mejillones. Although the same three main species, squat lobster, anchovy and Patagonian squid, are the main prey for sea lions at all three localities, the sea lions near Iquique and Mejillones also fed on other prey, such as mote sculpin and Chilean jack mackerel, which broadens their trophic spectra.

The results of this study demonstrate that the SASL is capable of varying its diet in response to spatial and temporal variations in the availability of its prey. This spatiotemporal plasticity has also been reported in previous studies (George-Nascimento

et al. 1985; Koen-Alonso *et al.* 2000; Muñoz *et al.* 2013) and among other species of sea lions (e.g. Kurle & Worthy 2001; Costa & Gales 2003; Cherel *et al.* 2009). Future studies should consider estimating prey abundance to corroborate a possible association between prey abundance and the sea lion diet.

AUTHOR CONTRIBUTIONS

Ricardo Sarmiento-Devia: Formal analysis (equal); investigation (equal); methodology (equal); software (equal); writing-original draft (equal). **Maritza Sepúlveda:** Conceptualization (equal); funding acquisition (equal); methodology (equal); project administration (equal); supervision (equal); validation (equal); writing-review & editing (equal). **Guido Pavez:** Formal analysis (equal); investigation (equal); methodology (equal); validation (equal); writing-review & editing (equal). **Jorge Valdés:** Funding acquisition (equal); investigation (equal); supervision (equal). **Anahi Canto:** Data curation (equal); formal analysis (equal); methodology (equal); software (equal); validation (equal). **Muriel Orellana:** Data curation (equal); formal analysis (equal); supervision (equal); validation (equal); writing-review & editing (equal). **Doris Oliva:** Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (equal); supervision (equal); validation (lead); writing-review & editing (lead).

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