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Diet plasticity of the South American sea lion in Chile: stable isotope evidence

Plasticidad de la dieta del lobo marino común en Chile: evidencia mediante isótopos estables

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Resumen.- Estudios de dieta del lobo marino común (LMC) en Chile sugieren que esta especie es un depredador oportunista y generalista, cuya dieta varía dependiendo de la distribución de las especies presas y de las variaciones espacio-temporales en la abundancia de dichas presas. Sin embargo, estos estudios han sido esporádicos, limitados espacialmente y basados en análisis de contenidos estomacales, lo que no permite un análisis integral de la composición de la dieta y de sus potenciales diferencias espacio-temporales. En este estudio se analizó la composición de la dieta del LMC en 3 zonas geográficas de la costa chilena utilizando los isótopos estables de $\delta^{13}\text{C}$ y $\delta^{15}\text{N}$ en muestras de pelo y piel. En la zona norte las principales especies consumidas fueron los peces *Isacia conceptionis* (19,5%) de acuerdo al análisis de piel y *Cilus gilberti* (23,3%) en análisis de pelo; en la zona centro lo fueron *Thyrssites atun* (40,1%) en piel y *Strangomera bentincki* (31,1%) en pelo; mientras que en la zona sur especies de peces pelágicos (como *T. atun* y *Trachurus murphyi*, 20,8%) en piel y salmones de cultivo (20,7%) en pelo. Estas diferencias demuestran que el LMC muestra cambios espaciales en la composición de su dieta. Variaciones entre tejidos, así como con lo registrado en estudios previos, sugiere que esta especie es capaz de adaptarse a variaciones, tanto intra como inter-anales, de la presencia/ausencia de sus presas.

Palabras clave: Modelos mixtos, MixSir, especialización trófica, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, *Otaria flavescens*, Chile

Abstract.- Diet studies of the South American sea lion (SASL) in Chile suggest that this species is an opportunistic and generalist predator whose diet varies depending on the distribution of prey species and spatial and temporal variations in the abundance of these dams. However, these studies have been sporadic, geographically limited and based on stomach content analysis, which does not allow an integral analysis of the composition of the diet of this species and its potential spatial and temporal variability. In this study we analyzed the diet of the SASL in 3 geographic zones of the coast of Chile using analysis of stable isotopes $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ on hair and skin tissues. In the northern zone, the main prey species consumed by SASL were *Isacia conceptionis* (19.5%) for skin and *Cilus gilberti* (23.3%) for hair; in the central zone were *Thyrssites atun* (40.1%) for skin and *Strangomera bentincki* (31.1%) for hair, whereas in the southern zone the main species were pelagic fish (such as *T. atun* and *Trachurus murphyi*, 20.8%) for skin and farm-raised salmonids (20.7%) for hair analysis. These differences indicate variation in the composition of its diet. Variations between the analyzed tissues and also with previous studies suggest that this species is capable of adapting to intra- and inter-annual variations in the presence/absence of its prey.

Key words: Mixed models, MixSir, Trophic specialization, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, *Otaria flavescens*, Chile

INTRODUCTION

South American sea lions (SASL) *Otaria flavescens* (Shaw, 1800) are considered as generalist predators (Capozzo & Perrin 2009), with a diet primarily composed by fish and to a lesser degree by mollusks and crustaceans (Vaz-Ferreira 1982, Crespo *et al.* 1997, Koen Alonso *et al.* 2000). In Chile, Sielfeld *et al.* (1997) found that in the extreme northern part of Chile (18°30'S-26°05'S) the diet was

composed mainly by pelagic species such as anchovy (*Engraulis ringens*) and Patagonian squid (*Loligo gahi*). Aguayo & Maturana (1973) reported that in the central zone, the Patagonian redfish (*Sebastes oculatus*), the South Pacific hake (*Merluccius gayi gayi*) and the Araucanian herring (*Strangomera bentinckii*) were the main prey items, while in the south-central zone (36°30'S-

38°S) benthodemersal species such as the South Pacific hake and the pink cusk-eel (*Genypterus blacodes*) (George-Nascimento *et al.* 1985) were the most common prey. This variation suggests that the SASL is an opportunistic and generalist predator, and that the composition of its diet will depend upon the local abundance of prey species (Aguayo & Maturana 1973, Crespo *et al.* 1997, Koen Alonso *et al.* 2000, Cappozzo & Perrin 2009). However, all these studies have been sporadic, geographically limited and based only on stomach content analysis, which does not allow for an integrated analysis of SASL diet composition and its potential spatial and temporal variability.

Stomach content and scat analyses are the most common and traditionally utilized methods for the reconstruction of the diet in marine mammals (Barros & Clarke 2009). The main advantage of these methods is that they quantify the relative number and size of prey species through identification of hard structures (*e.g.*, otoliths, bones, scales, cephalopod beaks) (Hobson *et al.* 1997). Stomach and scat analyses, however, have a number of limitations. The main disadvantage of these traditional methods is that, unless the sampling frequency is high, each analysis represents a view of the food eaten only during the most recent feeding bout, and does not necessarily reflect the time integrated representation of diet composition (Hobson *et al.* 1994). Errors may also be introduced by factors such as selective retention of remains (*e.g.*, cephalopod beaks *versus* fish bones) and differential degradation of hard structures (Naya *et al.* 2000). Also, actually they are more expensive than other methods (*e.g.*, stable isotopes) because they require more human labor (Newsome *et al.* 2010a). Due to these disadvantages, in recent decades other techniques have been developed to quantify diet composition in both terrestrial and marine consumers, including marine mammals.

Stable isotope analysis has quickly become a widely used tool to study trophic ecology and consumer diet composition (Kelly 2000, Fry 2006, Caut *et al.* 2009). This method is ideal for examining variation in the diet composition, since different tissues integrate dietary inputs over different time periods. For example, blood plasma and liver have a very rapid isotopic incorporation rate relative to whole blood or muscle (Martínez del Río *et al.* 2009). Turnover rate varies according to the metabolic activity of the tissue itself being analyzed, so that changes in the composition of the diet may take from a few days to several weeks to be reflected in the tissue of a predator

(Tieszen *et al.* 1983, Hobson & Clark 1992). Thus most metabolically active tissues, such as skin, have a high turnover rate (Hicks *et al.* 1985), because they interact more with newly ingested nutrients and metabolites in the diet (Tieszen *et al.* 1983). Kurle & Worthy (2001), in a study in terrestrial mammals, indicate that the half-life of carbon isotopes in the skin are among the values of the liver (6.4 days) and muscle (27.6 days). Additionally Hobson (1993) indicates that the isotopic analysis of a tissue represents an integration of the diet of 2-3 times the average life of the isotopes. That is, the skin of sea lions reflects the diet of the animals from twenty days to 3 months ago. Hair, by contrast, is an inert tissue that once synthesized does not show isotope replacement. Therefore, hair based studies reflect the composition of the diet of the animal in this period of time in which the tissue was synthesized (Newsome *et al.* 2009, Orr *et al.* 2011). Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values of a consumer reflect those of its diet, with a selective retention of the heavier isotope (^{13}C or ^{15}N) and excretion of the lighter one (^{12}C or ^{14}N) (Das *et al.* 2003). This selective retention/excretion yields a somewhat predictable isotopic difference between consumer and prey, also known as trophic discrimination (Karasov & Martínez del Río 2007, Crawford *et al.* 2008). $\delta^{15}\text{N}$ values increase by ~3-5‰ per trophic step and thus they are used to quantify the position of a consumer in a trophic web, while values of $\delta^{13}\text{C}$ are generally used to evaluate habitat use (*e.g.*, nearshore *versus* offshore) in marine consumers (DeNiro & Epstein 1978, 1981; Hobson *et al.* 1994).

The first ecological applications of stable isotopes considered only a qualitative comparison of isotope values that are commonly presented in $\delta^{13}\text{C}$ *versus* $\delta^{15}\text{N}$ bivariate space (biplots). However, during the last decade more quantitative measures of trophic position and diet composition have been developed, such as the mixing models that can generate quantitative estimates of the proportional contribution of different prey sources to the diet of a consumer (Phillips & Gregg 2003, Moore & Semmens 2008, Parnell *et al.* 2010). Two of the most commonly used models are MixSIR (Moore & Semmens 2008) and SIAR (Parnell *et al.* 2010). Both of these methods use Bayesian statistics and allow users to input isotopic variance (SD) in prey sources and error estimates for trophic discrimination factors.

Here we present the diet composition of the SASL based on isotopic data ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) from skin and hair samples collected in northern, central, and

southern zones of Chile. The objectives of this study were to: (1) analyze the diet composition of the SASL in these zones of Chile, and (2) determine if there are variations in the diet of this consumer between hair and skin tissues. These results provide novel insight into spatial and/or temporal variation in the diet composition of the SASL that inhabit Chilean waters.

MATERIALS AND METHODS

SAMPLE COLLECTION

From February 2009 to January 2012, skin and hair samples were collected from 94 adult and subadult SASL individuals (48 males, 27 females, and 19 indeterminate) in 3 areas of the Chilean coast: Northern Zone including Isla Choros and Isla Chañaral ($n = 12$) collected in Summer and Autumn; Central Zone including Cobquecura ($n = 16$) collected in Winter; and Southern Zone including different localities off Chiloé Island ($n = 66$) collected in Summer, Autumn months, Winter and Spring (Fig. 1). Samples were obtained with a modified PaxArms.22 caliber rifle using darts specially designed to obtain a small sample of hair, skin and fat without harming the animal. In the same areas we also obtained muscle samples of 28 species of fish, mollusks and crustaceans which are potential prey of SASL in Chile (Table 1). All samples were kept frozen during transport to the laboratory.

SAMPLE ANALYSES

In the laboratory, skin, hair and fat were separated and stored separately. Samples were dried in a drying oven (model UNE400, Memmert, Germany) at 60°C for 72 h. Hair and skin samples were then minced with a scalpel and muscle samples (preys) ground in a porcelain mortar and stored in filter paper. Finally, lipids were removed from samples in a Soxhlet extractor with petroleum ether for 2 h. Samples were then stored in microcentrifuge tubes prior to weighing for stable isotope analysis. A 0.5 (± 0.05) mg subsample of sea lion (hair and skin) and prey (muscle) tissues were sealed into tin capsules for stable isotope analysis. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were determined using a Carlo-ErbaNC 2500 (Milan, Italy) or Costech4010 (Valencia, California, USA) Elemental Analyzer interfaced with a Thermo-FinniganDelta Plus XL isotope ratio mass spectrometer (Waltham, Massachusetts, USA) at the University of Wyoming Stable Isotope Facility (Laramie, WY, USA). Isotopic results are expressed as δ values, $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = 1000 \times [(R_{\text{smp}}/R_{\text{std}}) - 1]$, where R_{smp} and R_{std} are the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratios of the sample and

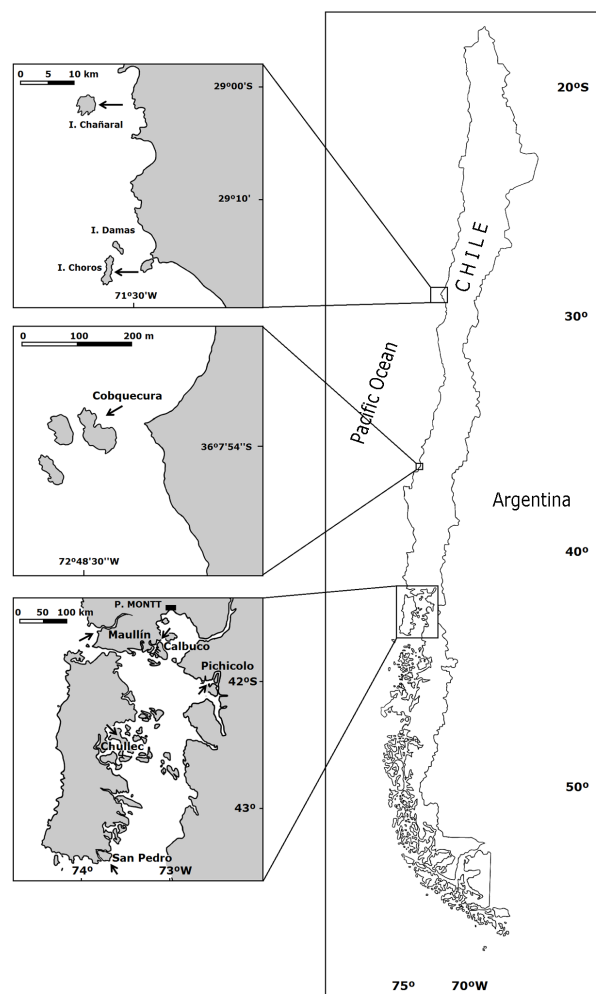


Figure 1. Study area showing the 3 zones of sample collection. Arrows indicate the location of the colonies / Área de estudio en que se indican las 3 zonas de muestreo. Las flechas indican la ubicación de las colonias

standard, respectively. The standards are Vienna-Pee Dee Belemnite limestone (VPDB) for carbon and atmospheric N_2 for nitrogen. The units are expressed as parts per thousand or per mil (‰).

DATA ANALYSIS

The potential prey species were pooled into functional groups, which were defined according to both similarity in the isotopic values and ecological function of prey items. The number of groups for each zone, and the species that were included in each group are indicated in Table 1. To determine the relative contribution of the prey groups to the diet of the SASL, we used the Bayesian stable isotope mixing model MixSIR (Moore & Semmens 2008).

Table 1. Mean individual and group values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and their standard deviations (SD) of the potential prey species of the South American Sea Lion in northern, central and southern zones of Chile and sample number analyzed / Valores promedio individuales y grupales de $\delta^{13}\text{C}$ y $\delta^{15}\text{N}$ y sus desviaciones estándar (SD) de potenciales especies presa del lobo marino común en la zona norte, centro y sur de Chile y número de muestras analizadas de cada grupo (n)

Zone	Prey group	Prey	n	Individual values		Group values	
				$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$
Northern	N1	Ta	6	-17.2 \pm 0.4	19.7 \pm 0.6	-17.0 \pm 0.4	19.6 \pm 0.4
		Tm	4	-16.9 \pm 0.5	19.5 \pm 0.2		
	N2	Cg	3	-16.4 \pm 0.6	20.2 \pm 0.1	-16.4 \pm 0.6	20.1 \pm 0.2
		Sf	3	-16.4 \pm 0.9	20.0 \pm 0.2		
	N3	Mo	2	-15.5 \pm 0.9	20.3 \pm 0.2	-15.5 \pm 0.9	20.3 \pm 0.2
	N4	Gc	5	-17.0 \pm 0.3	19.2 \pm 0.6	-17.2 \pm 0.4	19.4 \pm 0.8
		Sl	3	-17.4 \pm 0.4	19.6 \pm 1.3		
	N5	Pa	4	-16.1 \pm 0.7	19.6 \pm 1.9	-16.1 \pm 0.7	19.6 \pm 1.9
	N6	Ic	3	-16.5 \pm 0.6	18.4 \pm 1.2	-16.5 \pm 0.6	18.4 \pm 1.2
Central	C1	Sb	8	-16.6 \pm 0.4	15.7 \pm 0.7	-16.6 \pm 0.4	15.7 \pm 0.7
	C2	Mg	4	-16.2 \pm 0.2	16.9 \pm 0.3	-16.2 \pm 0.2	16.9 \pm 0.3
	C3	Pa	2	-15.5 \pm 0.1	18.0 \pm 0.6	-15.2 \pm 0.4	17.9 \pm 0.4
		So	3	-14.8 \pm 0.0	17.9 \pm 0.3		
		Gc	3	-15.4 \pm 0.5	17.7 \pm 0.4		
	C4	Ta	2	-17.0 \pm 0.9	18.7 \pm 0.2	-17.0 \pm 0.9	18.7 \pm 0.2
	C5	Ea	3	-15.5 \pm 0.5	16.6 \pm 0.4	-15.5 \pm 0.5	16.6 \pm 0.4
	C6	Cc	2	-14.6 \pm 0.4	16.5 \pm 1.5	-14.6 \pm 0.4	16.5 \pm 1.5
Southern	S1	Om	19	-17.4 \pm 0.8	12.9 \pm 1.1	-17.3 \pm 0.8	13.0 \pm 1.1
		Ok	3	-16.5 \pm 0.1	-13.0 \pm 0.6		
		Ss	1	-17.3 \pm 0.0	13.9 \pm 0.0		
	S2	Dg	2	-16.2 \pm 0.1	16.3 \pm 0.2	-16.2 \pm 0.1	16.3 \pm 0.2
	S3	Su	12	-15.6 \pm 0.4	15.3 \pm 0.3	-15.6 \pm 0.4	15.3 \pm 0.3
	S4	Sc	2	-14.7 \pm 0.4	19.2 \pm 0.3	-14.4 \pm 0.4	18.1 \pm 1.1
		Ma	14	-14.7 \pm 0.5	18.0 \pm 1.1		
		Hl	5	-14.5 \pm 0.3	17.3 \pm 1.0		
		Gs	11	-14.2 \pm 0.3	17.7 \pm 0.9		
		Sa	6	-14.2 \pm 0.2	17.8 \pm 0.5		
		Mm	4	-14.0 \pm 0.7	18.6 \pm 2.0		
	S5	Cc	6	-14.1 \pm 0.1	19.0 \pm 0.8		
		Ta	7	-15.1 \pm 0.3	18.1 \pm 1.0	-15.1 \pm 0.3	17.8 \pm 0.9
		Tm	3	-15.1 \pm 0.4	17.3 \pm 0.4		
	S6	Pa	7	-14.7 \pm 0.6	16.3 \pm 1.4	-14.1 \pm 1.0	15.9 \pm 1.0
		Ph	9	-14.2 \pm 0.9	16.2 \pm 0.5		
		Ea	12	-13.7 \pm 1.2	15.6 \pm 1.0		
	S7	Hp	2	-13.6 \pm 0.4	14.3 \pm 0.1	-13.3 \pm 0.6	14.7 \pm 0.7
		Cs	1	-12.6 \pm 0.0	15.5 \pm 0.0		

Species name: Ta: *Thyrstites atun*; Tm: *Trachurus murphyi*; Cg: *Cilus gilberti*; Sf: *Sciaena fasciata*; Mo: *Menticirrhus ophicephalus*; Gc: *Genypterus chilensis*; Sl: *Seriola lalandi*; Pa: Family *Paralichthyidae*; Ic: *Isacia conceptionis*; Sb: *Strangomera bentincki*; Mg: *Merluccius gayi gayi*; So: *Sebastes oculatus*; Ea: *Eleginops maclovinus*; Cc: *Callorhynchus callorhynchus*; Om: *Oncorhynchus mykiss*; Ok: *Oncorhynchus kisutch*; Ss: *Salmo salar*; Dg: *Dosidicus gigas*; Su: *Sprattus fuegensis*; Sc: *Seriola caerulea*; Ma: *Merluccius australis*; Hl: *Helicolenus lengerichi*; Gs: *Genypterus* sp; Sa: *Salilota australis*; Mm: *Mustelus mento*; Ph: *Paralabrax humeralis*; Hp: *Homalaspis plana*; Cs: *Cancer setosus*.

The strength of this program is that it allows the user to incorporate sources of uncertainty, such as variance in the isotopic composition of prey (sources) or estimated error in trophic discrimination factors (TDFs) between consumer and in this zone prey. Isotopic values of SASL were entered individually (for hair and skin), while isotope values of the prey were entered as means (\pm SD). We used tissue-diet TDF values of $2.5 \pm 0.5\text{‰}$ for $\delta^{13}\text{C}$ and $3.5 \pm 0.5\text{‰}$ for $\delta^{15}\text{N}$ in the mixing model for hair (Hobson *et al.* 1996). For skin we used TDFs values of $2.5 \pm 0.5\text{‰}$ and $3.0 \pm 0.5\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively (Newsome *et al.* 2010a,b). These values are similar to the range reported by Newsome *et al.* (2010b) in vibrissae of the sea otter *Enhydra lutris nereis*, as well as within the range of mean enrichment factors estimated for pinniped tissues (Hobson *et al.* 1996, Lesage *et al.* 2002). We used a standard deviation of 0.5‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. The results obtained in each analysis were grouped into 5 columns that correspond to the probable contributions of each prey group to the diet of each sea lion (5, 25, 50, 75 and 95%). The 50% percentile was used to represent the mean contribution of each prey species, and the 5 and 95% percentiles for the inferior and superior range, respectively.

We analyzed potential differences in prey consumption for each study area. The Shapiro-Wilks and Levene tests were used to test normality and homoscedasticity of variances, respectively (Sokal & Rohlf 2011). When $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values fulfilled these assumptions we used a one way analysis of variance (ANOVA), otherwise we used a Kruskal-Wallis non parametric test. All analyses were performed in STATISTICA 8.0 (StatSoft Inc.), using $\alpha = 0.05$ as significance level.

RESULTS

DIFFERENCES IN THE ISOTOPE SIGNATURE AMONG THE STUDIED ZONES

Table 1 presents mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the prey groups for each of the 3 study zones. For each zone significant differences among isotopic signatures of the prey groups were found: In the northern zone for both, $\delta^{13}\text{C}$ ($F_{6,27} = 4.79$, $P = 0.002$) and $\delta^{15}\text{N}$ ($H_{6,34} = 14.27$, $P = 0.026$), and in the central and southern zones, where the $\delta^{13}\text{C}$ ($F_{5,21} = 13.79$, $P < 0.00001$; $H_{6,126} = 85.90$, $P < 0.0001$, respectively) as well as $\delta^{15}\text{N}$ ($H_{5,27} = 21.11$, $P < 0.001$; $H_{6,126} = 55.40$, $P < 0.0001$, respectively) differ significantly.

Potential differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between

sexes for northern and central zones were not tested due to small sample size. In the southern zone, no differences were found between sexes for skin and hair for $\delta^{13}\text{C}$ ($H_{2,35} = 5.40$, $P = 0.067$; $F_{2,22} = 1.136$, $P = 0.0339$, respectively) and $\delta^{15}\text{N}$ ($H_{2,35} = 1.951$, $P = 0.377$; $F_{2,22} = 3.52$, $P = 0.05$, respectively).

DIET COMPOSITION OF THE SOUTH AMERICAN SEA LION

In the northern zone, analysis of skin showed that the dominant prey groups in the diet of the SASL were N6 (19.5%) and N4 (14.2%), while analysis of hair showed that N2 (23.3%) and N6 (16.8%) were the most important groups (Table 2). No significant differences in the relevance of the different groups to the diet of the SASL in this zone were found, neither for skin ($H_{6,70} = 1.206$, $P = 0.976$) nor for hair ($H_{6,28} = 11.542$, $P = 0.073$) (Fig 2a, 2b). In the Central zone, analysis of skin showed that the dominant group was C4 (40.1%) followed by C3 (13%) and C6 (13%), while analysis of hair indicated that C1 (31.1%) and C4 (13.5%) were the

Table 2. Mean contribution (%), sample number and contribution range of the prey groups in the diet of the South American sea lion according to analysis of skin and hair. The groups with the greatest contribution in each zone are indicated in bold. The mean contribution of each species was estimated using the mean of the 50% percentile for all individuals / Contribución porcentual (%), número de muestras y rango de contribución de los grupos presa en la dieta del lobo marino común de acuerdo a los análisis de piel y pelo. Los grupos con mayor contribución en cada zona se destacan. La contribución promedio de cada especie fue estimada usando el promedio del percentil 50% para todos los individuos

Zone	Prey group	n	Skin		Hair	
			Mean \pm SD	Range	Mean \pm SD	Range
Northern	N1	10	12.8 \pm 4.0	0.4 – 55.6	9.8 \pm 5.9	0.3 – 69.6
	N2	6	11.7 \pm 4.4	0.3 – 50.2	23.3 \pm 31.7	0.2 – 48.0
	N3	2	10.3 \pm 4.9	0.2 – 48.7	4.5 \pm 1.3	0.2 – 25.0
	N4	8	14.2 \pm 3.6	0.5 – 82.8	15.5 \pm 8.1	0.5 – 79.1
	N5	4	12.8 \pm 3.6	0.3 – 76.0	6.7 \pm 2.9	0.2 – 62.6
	N6	3	19.5 \pm 15.7	0.6 – 84.0	16.8 \pm 12.0	0.3 – 73.3
Central	C1	8	5.7 \pm 2.2	0.1 – 31.1	31.0 \pm 16.3	0.7 – 82.3
	C2	4	8.3 \pm 3.3	0.2 – 44.0	11.9 \pm 3.6	0.4 – 53.8
	C3	8	13.0 \pm 5.0	0.3 – 59.7	7.7 \pm 3.9	0.3 – 50.3
	C4	2	40.1 \pm 15.8	1.6 – 89.3	13.5 \pm 10.8	0.3 – 54.1
	C5	3	6.9 \pm 3.0	0.2 – 42.6	10.9 \pm 3.5	0.3 – 51.4
	C6	2	13.0 \pm 8.8	0.4 – 64.6	12.2 \pm 6.7	0.2 – 54.9
Southern	S1	23	11.9 \pm 14.1	0.2 – 81.1	20.7 \pm 16.7	0.4 – 83.7
	S2	2	11.9 \pm 4.3	0.4 – 59.2	10.6 \pm 5.2	0.3 – 63.5
	S3	12	8.1 \pm 2.8	0.3 – 46.7	10.7 \pm 2.8	0.3 – 46.8
	S4	48	19.9 \pm 10.3	0.3 – 68.3	8.5 \pm 4.0	0.2 – 50.0
	S5	10	20.8 \pm 9.2	0.3 – 72.1	8.9 \pm 4.2	0.2 – 53.1
	S6	28	7.8 \pm 2.5	0.3 – 41.9	10.8 \pm 4.1	0.2 – 48.2
	S7	3	5.9 \pm 3.8	0.2 – 46.1	14.7 \pm 9.3	0.2 – 55.6

most important prey groups. Significant differences were found in the contribution to the diet among some of the groups (Fig. 2c, 2d). Finally, in the Southern zone the analysis of skin indicated that the most important prey groups were S5 (20.8%) and S4 (19.9%), while for hair data the relevant groups were S1 (20.7%) and S7 (14.7%). Also, significant differences were found in the contribution to the diet among some of the group, both for skin and hair (Fig. 2e, 2f).

In 2 of the 3 study areas there were variations in diet composition among individuals; in 10 SASL, the consumption of just one prey group was $\geq 50\%$. For example, in the Central Zone one individual was estimated to have consumed 67% C4 (snoek) and another one 65% C1 (Araucanian herring), whereas in the Southern Zone

one individual consumed more than 70% S1 (farm-raised salmonids), while in others salmonids were consumed in trace amounts ($<4\%$).

DISCUSSION

SPATIAL DIFFERENCES IN DIET COMPOSITION

As expected, in the 3 study zones the main prey items in the SASLs diet were fish, which coincides with the reports of other authors, both for Chile and other countries (Aguayo & Maturana 1973, Vaz-Ferreira *et al.* 1982, George-Nascimento *et al.* 1985, Crespo *et al.* 1997, Koen Alonso *et al.* 2000). The only exception was skin in the southern zone, where S6 (crabs) was also an important prey item.

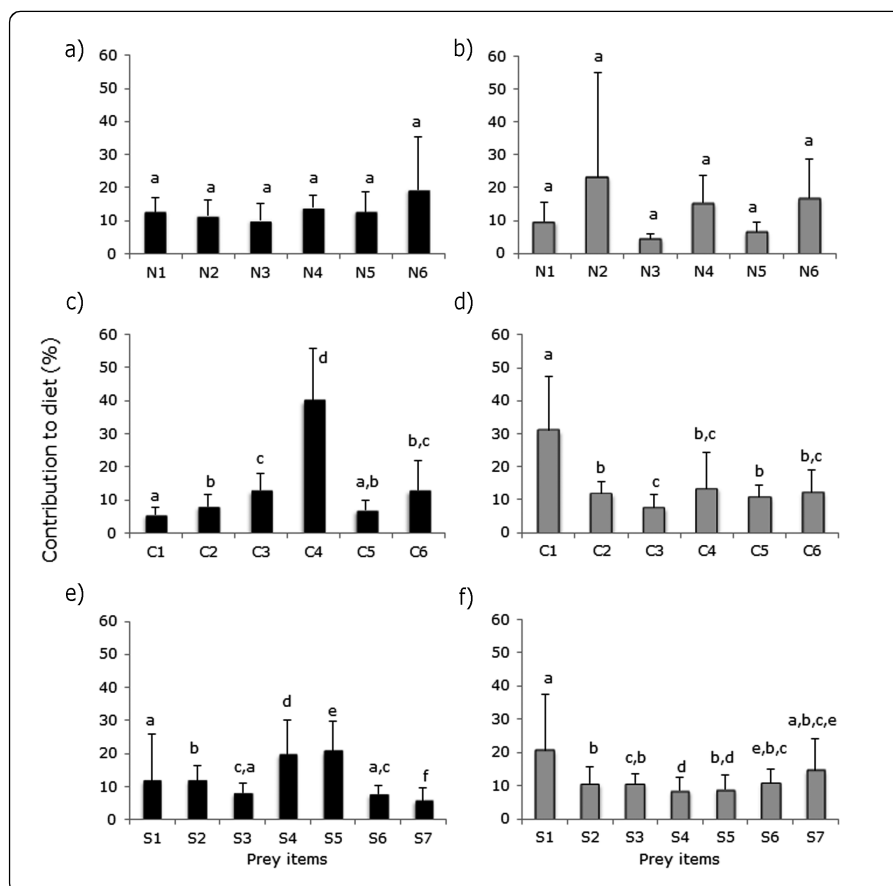


Figure 2. Mean (\pm SD) percentual contribution of the different prey groups into the diet of the South American sea lion (*Otaria flavescens*) in the 3 study areas, and for skin and hair analyses. Black bars (a, c, e) showed the skin results for the northern, central, and southern zones, respectively, while grey bars (b, d, f) showed the hair results for the same zones. Same letters indicated no significant differences among groups / Contribución porcentual promedio de los diferentes grupos de presas en la dieta del lobo marino común (*Otaria flavescens*) en las 3 zonas de estudio, y para análisis de piel y pelo. Las barras negras (a, c, e) muestran los resultados de los análisis de piel en las zonas norte, centro y sur, respectivamente, mientras que las barras grises (b, d, f) muestran los resultados de pelo en las mismas zonas. Las letras iguales indican que no existen diferencias significativas entre los grupos

In the northern zone *Isacia conceptionis* and *Cilus gilberti* were the most important prey item for the SASLs diet, both for skin and hair analyses. Unfortunately, for this zone there are no previous studies with which to compare our results. Aguayo & Maturana (1973) and Sielfeld *et al.* (1997) studied the diet composition of SASL using stomach contents in the zone of Valparaíso and in the extreme north (Iquique), respectively. Aguayo & Maturana (1973) found that the main prey items of sea lions were *Sebastes oculatus* and *Merluccius gayi gayi*, while Sielfeld *et al.* (1997) found that *Engraulis ringens* and *Loligo gahi* were the most important prey. However, the results of these studies are not strictly comparable to our study, since they sampled from different fishing zones. Additionally, in our study no samples of *M. gayi gayi*, *E. ringens* or *L. gahi* were collected, since there is almost no catches of these species in areas close to the study zone (SERNAPESCA 2010). In future studies it would be recommended to collect an even larger number of potential prey species in order to be able to compare with previous studies.

The main prey consumed by the SASL in the central zone, according to both skin and hair analyses, was the *Thyrstites atun*. This may be explained because the *T. atun* is one of the main species captured in this zone; landings of this species in the VIII Region represented 38.4% of the national landing reports (SERNAPESCA 2011). *T. atun* are also captured as by-catch in *Strangomera bentincki* and *E. ringens* fisheries, and sea lions have been observed entering to fish nets to feed on this species (Andrea Nadeau pers. com.). The analysis of hair indicated that *Strangomera bentincki* is another important dietary item in this zone, reaching a mean value of around 30%. *S. bentincki* and *E. ringens* fisheries are the main commercial activity of small pelagic fisheries in central Chile (34°-40°S). *Strangomera bentincki* are captured mainly during the first 6 months of the year, associated with the high seasonality in the abundance and availability of this species (Gatica *et al.* 2007). Given that the analysis of hair represents the diet consumed in austral autumn months (see below), we infer that sea lions take advantage of the higher abundance and availability of this species in this period of the year.

In the southern zone, farm-raised salmonids were the most important prey group for sea lions in the analysis of hair (20.7%). In the case of skin, the principal prey groups were S4 (*Seriotelella caerulea*, *Merluccius australis*, *Helicolenus lengerichi*, *Genypterus* sp., *Salilota australis*, *Mustelus mento*, *Callorhynchus callorhynchus*)

and S5 (*Thyrstites atun*, *Trachurus murphyi*) which corresponded to demersal and pelagic fish, respectively (Table 1). Unfortunately, there are no previous studies of the diet composition of the SASL in this zone to compare with our results. However, Sepúlveda & Oliva (2005) and Vilata *et al.* (2010) indicated a strong interaction between the SASL and salmon farming in the study area, which would explain the high consumption of this diet item, representing > 60% of the diet for same individuals. Also, in the case of demersal and pelagic fish, support of consumption of these preys was obtained from Pavés *et al.* (pers. comm.), who evidenced a strong operational interaction between the SASL and the commercial fisheries of demersal and pelagic species in southern Chile, which captured the same species that we included in our study (e.g., *Thyrstites atun*, *Callorhynchus callorhynchus*, *Genypterus* spp.).

TEMPORAL DIFFERENCES IN DIET COMPOSITION

The central zone is the only sector in which there is a previous study with which to compare, and the results of this study differ from those reported by other authors. Using stomach content analysis, George-Nascimento *et al.* (1985) found that the most important preys consumed by the SASL were the South Pacific hake (*Merluccius gayi gayi*) and the pink cusk-eel (*Genypterus blacodes*). Although samples of hakes were collected and incorporated in our study, it was not an important item in the diet of SASL. The reason may be that the biomass of *M. gayi gayi* decreased drastically as a consequence of overexploitation after the years 2002-2005 (SUBPESCA 2010). Hückstädt *et al.* (2007) found that in this same zone the SASL fed mainly on *T. murphyi*. However, our study is not comparable with that of Hückstädt *et al.* (2007), since we were not able to obtain samples of *T. murphyi*, due to there was no landings of this species during the sampling period. As in the case of the *M. gayi gayi*, the scarcity of this species is due to overfishing; there has been a large decrease in national landings, from 1.3 million tons in 2007 to 0.25 million tons in 2011 (SERNAPESCA 2011). These temporal comparisons may suggest that the drastic decrease of these 2 resource species modified the diet composition of the SASL in recent decades.

It is important to note that the differences in the findings of this study with the results of George-Nascimento *et al.* (1985) may also be due to the particular characteristics of the different methodologies. Stomach content analysis only reveals the main prey items

consumed in the past few days, while the analysis of stable isotopes is very sensitive to the fractioning factors used in the analysis of the diet (Newsome *et al.* 2010a). These factors should be taken into account in comparing studies which use different methodologies.

In addition to long-term (years) temporal variation in the diet composition of the SASL, we also found temporal differences in the short term (months) in the central zone. The importance of the *S. bentincki* in hair may be related to the variability in specific metabolic renewal rates for each tissue, from which information at different time scales may be obtained (Hobson *et al.* 1996, Kelly 2000). Consumption of a given prey species is reflected into the diet in the period in which the tissue is generated. In the case of hair, its shedding in the SASL occurs in austral autumn (Luis Hückstädt *pers. com.*), thus the values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in this tissue reflect the diet consumed during this period of time. Autumn months are those in which herring extraction was highest in the central zone of the country (SERNAPESCA 2010), which could explain why this species was predominant in the diet in the analysis of hair. In the absence of *S. bentincki*, the skin analysis indicated that almost 50% of the diet was composed by *T. atun*, which suggests that this species replaced the *S. bentincki* when the former was not available.

The above suggests that the sea lion is capable of vary its diet not only as a response to the availability of its preys but also given to temporal variation in the abundance of the same preys. Intra-specific temporal variation in diet has also been reported in other species of sea lions, such as in the northern fur seal *Callorhinus ursinus* (Kurle & Worthy 2001), California sea lion *Zalophus californianus* (Costa *et al.* 2007), Antarctic fur seals *Arctocephalus gazella* (Cherel *et al.* 2009) and the Australian sea lion *Neophoca cinerea* (Costa & Gales 2003). According to Estes *et al.* (2003), the overabundance or near extinction of a given prey species may modify the dietary selection of an individual to include or exclude this item, in spite of the high cost this change may entail. Thus the generalist and opportunistic habit of the SASL would allow it to adapt rapidly to this type of change (Cappozzo & Perrin 2009).

TROPHIC SPECIALIZATION?

Although the SASL is considered to be a generalist and an opportunistic predator, in this study we found high inter-individual variation in the diet composition of some of the animals sampled in a same zone. For example, we

found a high consumption of farm-raised salmonids (> 50%) by some animals but almost no consumption (< 4%) by others. This same generalist/specialist disconnection has also been reported for other species of marine mammals, such as the California sea otter (*Enhydra lutris*) (Estes *et al.* 2003). These authors registered a total of 32 prey species for a group of 10 otters; however, each individual otter specialized on feeding on one to 4 species, with very different diets between animals. This foraging behavior has been also reported in different species of otariids, such as in California sea lions (García-Rodríguez & Aurióles-Gamboa 2004), Antarctic fur seals *Arctocephalus gazella* (Cherel *et al.* 2009), and Australian sea lions (Lowther & Goldsworthy 2010, Lowther *et al.* 2011), defining their trophic habits as 'plastic specialists'.

These inter-individual differences may be interpreted as a way of reducing intraspecific competition, in order to maximize foraging success (Hückstädt *et al.* 2012). The results of Estes *et al.* (2003) and Hückstädt *et al.* (2012), along with those reported here suggest that there may be individual specialization in the diet, at least for some individuals of the SASL, although as a group the species appears to be generalist. Further studies will be necessary to confirm specialization in the diet of the SASL, to determine whether this species reduces intraspecific competition by 'sorting out' resources in order to decrease competition with other individuals and thus optimize feeding (Estes *et al.* 2003, Hückstädt *et al.* 2012).

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