

Sexual foraging segregation in South American sea lions increases during the pre-breeding period in the Río de la Plata plume

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ABSTRACT: Stable carbon and nitrogen isotopes in skin and bone of South American sea lions from Brazil and Uruguay were analysed to test the hypothesis that trophic overlap between the sexes is lower during the pre-breeding season than throughout the rest of the year. The isotopic values of skin and bone were used to infer the trophic relationships between the sexes during the pre-breeding period and year round, respectively. Prey species were also analysed to establish a baseline necessary for interpreting the stable isotope ratios of skin and bone. Standard ellipse areas, estimated using Bayesian inference in the SIBER routine of the SIAR package in R, suggested that males and females used a wide diversity of foraging strategies throughout the year and that no differences existed between the sexes. However, the diversity of foraging strategies was largely reduced during the pre-breeding period, with all the individuals of each sex adopting similar strategies, but with the two sexes differing considerably in stable isotope values and the ellipse areas of males and females not overlapping at all. Nevertheless, the results revealed a general increase in the consumption of pelagic prey by both sexes during the pre-breeding period. The progressive crowding of individuals in the areas surrounding the breeding rookeries during the pre-breeding period could lead to an increase in the local population density, which could explain the above reported changes.

KEY WORDS: *Otaria flavescens* · Sexual foraging segregation · Skin · Bone · Stable isotope Bayesian ellipses

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INTRODUCTION

Understanding intersexual differences in behaviour has important implications for breeding biology and population ecology. Although sexual foraging

segregation is a widespread behaviour in the animal kingdom, its underlying causes remain poorly understood (Wearmouth & Sims 2008). Furthermore, although sex-related differences in habitat use or feeding strategies have been previously investigated in

some marine mammal species, they have been less well documented in otariid species (Wearmouth & Sims 2008).

Males and females of the same species often differ in foraging behaviour and diet for at least 4 non-mutually exclusive reasons. The reproductive decision hypothesis attributes sex differences to the differing trade-offs between foraging and other vital activities (e.g. predator avoidance, provisioning of young, mate acquisition) faced by individuals of each sex aiming to maximize their individual fitness (Clutton-Brock & Parker 1992, Jormalainen et al. 2001). The niche divergence hypothesis is based on the fitness benefit of reducing intraspecific competition by individuals of each sex foraging in different locations and/or on different prey species (e.g. Clarke et al. 1998). The sexual size-dimorphism hypothesis predicts that differences in male and female energy requirements, based on differences in body size, can account for sex-specific foraging behaviour (Clutton-Brock et al. 1987, Nagy 1987, Mysterud 2000). Finally, differences in body size may result in differences in access to trophic resources, which may lead to contrasting foraging behaviour and diet composition between the sexes (Le Boeuf et al. 2000, Beck et al. 2003a,b, 2007, Breed et al. 2006).

The keystone importance of body mass in understanding physiological and behavioural variation is well illustrated for sexually dimorphic, air-breathing, marine vertebrates that forage underwater because it largely determines the oxygen stores and the mass-specific rate of metabolism (Miller & Irving 1975, Kooyman 1989, Fowler et al. 2007). Thus, body size differences clearly influence diving skills in pinnipeds since adults of large-bodied species often exploit deep, benthic habitats, whereas those of small-bodied species typically forage in epipelagic habitats (Kooyman et al. 1981, Gentry et al. 1986, Costa 1993, Costa et al. 2004). Likewise, small-bodied females of strongly sexually dimorphic species often have a more pelagic diet than males throughout their life (Le Boeuf et al. 2000, Meynier et al. 2008).

The South American sea lion *Otaria flavescens* is a highly sexually dimorphic species, with adult males weighing about double (300–350 kg) that of adult females (Cappozzo & Perrin 2009). The South American sea lion is often regarded as a benthic forager (Werner & Campagna 1995, Thompson et al. 1998), although available evidence indicates that adults are able to forage both close to the seabed and in mid-water (Werner & Campagna 1995, Soto et al. 2006). As expected from differences in body mass, northern Patagonia sea lion males had been reported to ex-

loit benthic and deeper foraging grounds than females (Campagna et al. 2001, Drago et al. 2009a), although dissimilarities in foraging habits between the sexes have decreased in this area during the last decade (Drago et al. 2009b). Similar patterns have been reported from Uruguay, where adult males and females use similar habitats on an annual basis (Franco-Trecu et al. 2014). Nevertheless, there are reasons to believe that the foraging behavior and diet of the South American sea lion may differ between the sexes during the pre-breeding season.

During the breeding season South American sea lions, scattered along the southwestern Atlantic coast from southern Brazil to southern Argentina (Cappozzo & Perrin 2009), aggregate in few isolated rookeries, resulting in a 2000 km gap between the 2 northernmost rookeries in Uruguay and its closest rookeries in northern Patagonia (Vaz-Ferreira 1982, Grandi et al. 2008). As a result, their local population density appears to be much higher during the pre-breeding (November–December) and breeding (January–February) periods than during the rest of the year (Vaz-Ferreira 1982, Campagna 1985, Rosas et al. 1994). Considering that South American sea lion males may fast during the whole breeding period to defend their territory and mate (Vaz-Ferreira 1975, Campagna & Le Boeuf 1988), local population density can attain high values during the pre-breeding season (Vaz-Ferreira 1982, Rosas et al. 1994). Furthermore, the energetic requirements of males and females may differ during the pre-breeding period from those during the rest of the year for 2 main reasons. On the one hand, females must wean the previous year's pup, put up with the high energetic demands of both late gestation and pup rearing during the first weeks when they do not feed, and provide lipid-rich milk to their pups (Campagna 1985, Oftedal et al. 1987, Campagna & Le Boeuf 1988). On the other hand, males must accumulate resources to invest in reproductive endeavours that would maximise their reproductive success and to cope with prolonged fasting during the breeding season (Vaz-Ferreira 1975, Campagna & Le Boeuf 1988). These concurrent energetic demands may lead to a finer niche partitioning between adults of both sexes during the pre-breeding period.

Stable isotope analysis is a method that is especially well suited to the assessment of temporal variation in trophic habits at different timescales, provided that tissue turnover rates are known, since tissues with different isotopic turnover rates integrate dietary information over different timescales (Dalerum & Angerbjörn 2005). Thus, analysis of a small sample of

predator tissues with differing isotopic turnover rates allows investigation of the animal's diet at different timescales (Dalerum & Angerbjörn 2005). In marine mammals, whereas skin integrates dietary information over a couple of months (Kurle & Worthy 2001, Alves-Stanley & Worthy 2009), bone integrates information over several years (Hobson & Clark 1992a, Riofrio-Lazo & Auriolles-Gamboa 2013). Furthermore, the stable isotope values of the prey species consumed by South American sea lions in Río de la Plata plume and adjoining areas in the southwestern Atlantic indicate that changes in the $\delta^{13}\text{C}$ values of the tissues should primarily reflect changes in the proportion of benthic and pelagic prey items in the diet, whereas changes in the $\delta^{15}\text{N}$ should be primarily linked to changes in trophic level (Bugoni et al. 2010, Vales et al. 2014).

Here we analyse the stable carbon and nitrogen isotopes of bone and skin samples from the South American sea lion to test 2 hypotheses: (1) the consumption of energy rich pelagic prey increases during the pre-breeding season (November and December) compared with the annual average; and (2) the trophic overlap between the sexes is lower during the pre-breeding season than during the rest of the year.

MATERIALS AND METHODS

Sampling

Although the South American sea lion is one of the most frequent pinniped species in southern Brazil that occurs mainly during winter, individuals found along the southern Brazilian coast are part of the breeding stock of Uruguayan rookeries (Rosas et al. 1994, Artico et al. 2010). Indeed, South American sea lions that breed in Uruguay typically disperse throughout the year in the open sea after the breeding season, in an area ranging from northern Argentina to southern Brazil (Vaz-Ferreira 1982, Rosas et al. 1994, Zenteno et al. 2013). Accordingly,

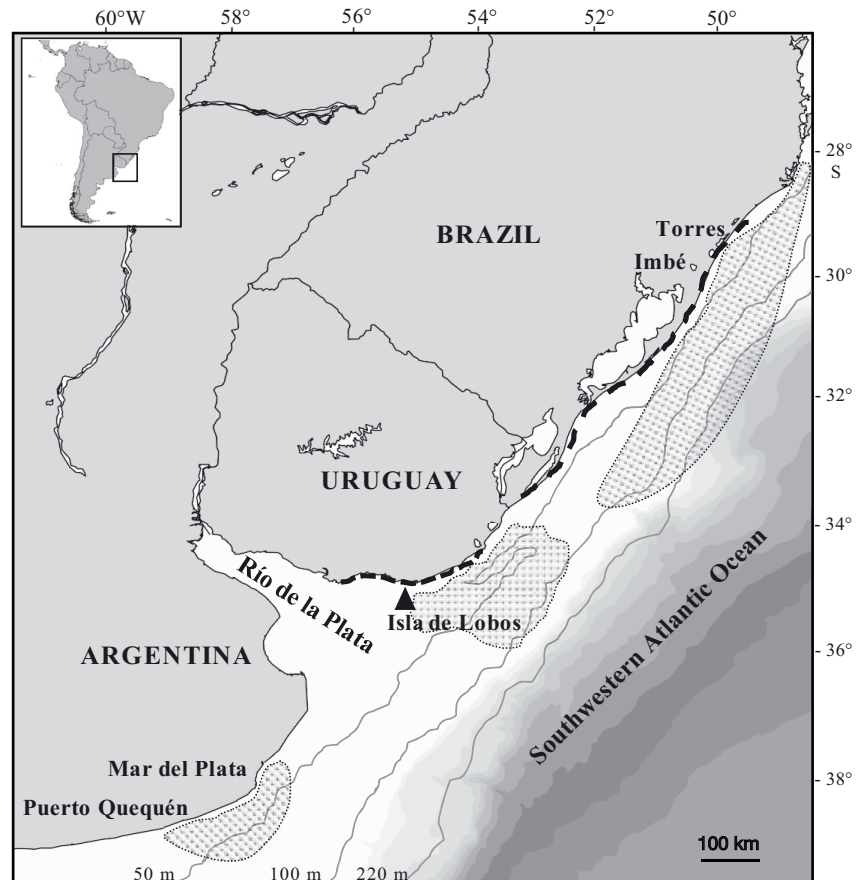


Fig. 1. Study area and sampling location of South American sea lions *Otaria flavescens* and prey species. Dashed lines show sampling location of sea lion skulls from southern Brazil and Uruguay; \blacktriangle : sampling location of sea lion skin samples from Uruguay; stippled areas show location of prey sampling sites off southern Brazil, Uruguay and northern Argentina

bone samples were collected from both sexes of adult South American sea lions that were stranded dead along the coast of the Rio Grande do Sul state (southern Brazil) between 1998 and 2009 and along the Uruguayan coast between 2006 and 2012; skin samples were collected from both sexes of adult reproductive individuals arriving at Isla de Lobos (Uruguay) during the 2009 breeding season (Fig. 1).

Bone samples from Brazilian individuals (10 males and 4 females) were obtained from the skulls of the scientific collection of the Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul (GEMARS) at Imbé (Brazil), while those from Uruguayan individuals (6 males and 10 females) were obtained from the skulls of the scientific collection of the Museo Nacional de Historia Natural (MNHN) at Montevideo (Uruguay). Only adult specimens were considered to avoid any possible age-related bias (Drago et al. 2009a). The age of all the

sampled individuals was estimated by counting growth layers in the dentine of one of their canines (Laws 1952) and ranged from 9 to 15 yr for males and from 7 to 13 yr for females. Sex was determined based on external morphology (e.g. presence of baculum bone in males) during sample collection and eventually assessed using secondary sexual characteristics of the skull following Crespo (1984). The bone sample from the skull of each individual that was used for the isotopic analysis consisted of a small fragment of turbinate bone taken throughout its entire thickness from the nasal cavity. This bone type was selected because it is easy to crush and its sampling does not damage the skull, allowing subsequent studies.

All skin samples were collected in early January from randomly chosen, physically mature sea lions of unknown age (12 males and 10 females). The skin samples were obtained using a biopsy dart (punch tip 5 × 25 mm) shot by means of a CO₂ Dan-Inject Rifle (Børkop, Denmark). Although stable carbon and nitrogen isotope signals in skin do not vary across the body (Todd et al. 2010), all samples were collected from the lumbar region of each specimen.

Samples of prey species consumed by South American sea lions in Río de la Plata plume and adjoining areas (Naya et al. 2000, Riet Sapriza et al. 2013) were collected from northern Argentina and southern Brazil in 2009 to determine their stable carbon and nitrogen isotope values (see Table 1). Samples of prey were provided by local fishermen or collected on board by the staff of the Marine Mammal Laboratory (CENPAT-CONICET) and GEMARS. The stable carbon and nitrogen isotope values from some additional prey (see Table 1) were taken from Bugoni et al. (2010) and Franco-Trecu et al. (2013), after having ascertained that their prey data (i.e. tissue type analyzed, sample preparation procedure and sampling time and location) were appropriate in the context of the present study. All bone samples were cleaned and stored dry, whereas all samples of skin and prey were stored in a freezer at -20°C until analysis.

Stable isotope analysis

Once in the laboratory, samples were thawed, dried in a stove at 60°C for 36 h, and ground into a fine powder using a mortar and a pestle. Lipids were removed from each sample using a chloroform:methanol (2:1) solution (Bligh & Dyer 1959) because lipids are depleted in ¹³C compared with other mole-

cules and variability in lipid content of samples may result in undesirable variability in δ¹³C values (DeNiro & Epstein 1978). Nevertheless, as chemical lipid extraction may lead to unpredictable changes in δ¹⁵N values due inter alia to the inadvertent removal of amino acids (Sotiropoulos et al. 2004, Ryan et al. 2012), we extracted lipids for carbon isotope analysis and used a non-extracted subsample for nitrogen determination. Furthermore, as bone samples contain a high concentration of inorganic carbon that may add undesirable variability to δ¹³C (Lorrain et al. 2003), they were previously treated by soaking in 0.5 N HCl for 24 h to decarbonise them (Newsome et al. 2006). Since HCl treatment adversely affects δ¹⁵N (Bunn et al. 1995), each sample was divided into 2 subsamples—one used for carbon analyses after decarbonation, and the other for nitrogen analyses without decarbonation.

Approximately 1 mg of dried bone, 0.3 mg of skin, and 0.3 mg of white muscle from fish, pleon muscle from crustaceans and mantle from cephalopods were weighed into tin cups (3.3 × 5 mm), combusted at 900°C, and analyzed in a continuous flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA; Thermo Finnigan). Atropine was used as a system check for elemental analyses. Samples were processed at the Centres Científics i Tecnològics of the University of Barcelona.

Stable isotope abundances, expressed in delta (δ) notation, where the relative variations in stable isotope ratios are expressed in per mil (‰) deviations from predefined international standards, were calculated as:

$$\delta^iX = [(iX/iX)_{\text{sample}} / (iX/iX)_{\text{standard}}] - 1$$

where ⁱX is the heavier isotope (¹³C or ¹⁵N), and ⁱX is the lighter isotope (¹²C or ¹⁴N) in the analytical sample and in the international measurement standard (Bond & Hobson 2012); reference standards were the Vienna Pee Dee Belemnite (VPDB) calcium carbonate for δ¹³C and atmospheric nitrogen (air) for δ¹⁵N. Secondary isotopic reference materials of known ¹³C/¹²C ratios, as given by the International Atomic Energy Agency (IAEA, Vienna, Austria), were used for calibration at a precision of 0.2‰. These include polyethylene (IAEA CH₇, δ¹³C = -31.8‰), graphite (IAEA USGS₂₄, δ¹³C = -16.1‰) and sucrose (IAEA CH₆, δ¹³C = -10.4‰). For nitrogen, secondary isotopic reference materials of known ¹⁵N/¹⁴N ratios, namely (NH₄)₂SO₄ (IAEA N₁, δ¹⁵N = +0.4‰ and IAEA N₂, δ¹⁵N = +20.3‰) and KNO₃ (IAEA NO₃, δ¹⁵N = +4.7‰), were used to a precision of 0.3‰.

Data analyses

We compared the stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of prey species among regions (southern Brazil, Uruguay and northern Argentina) using a nested ANOVA, with prey species nested within regions. Two-way ANOVA was used to investigate the differences in bone $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between the sexes and between Brazil and Uruguay. Student's *t*-test was used to detect differences in skin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between males and females from Uruguay.

Tissue-specific prey-to-predator isotopic discrimination factors need to be known to relate stable isotope ratios in the predator to those in its diet (Hobson & Clark 1992b, Bocherens et al. 2014). The prey-to-predator isotopic discrimination factor in skin has been determined for several pinniped species in captivity (Hobson et al. 1996), and the prey-to-predator isotopic discrimination factor in bone has been assessed indirectly for the South American sea lion by Zenteno et al. (2015). While Hobson et al. (1996) reported a prey-to-predator isotopic discrimination factor of +2.3‰ for $\delta^{15}\text{N}$ and +2.8‰ for $\delta^{13}\text{C}$ in skin, Zenteno et al. (2015) found the isotopic discrimination factor of the South American sea lion bone to be $+4.4 \pm 0.8\text{‰}$ for $\delta^{15}\text{N}$ and $+3.5 \pm 0.8\text{‰}$ for $\delta^{13}\text{C}$. Accordingly, stable isotope values in bone and skin were used to calculate the expected stable isotope values in the diet of sea lions throughout the year and during the pre-breeding season, respectively. To do so, the corresponding prey-to-predator isotopic discrimination factors were subtracted from the stable isotope values of bone and skin and means were compared using 2-way ANOVA. We checked the normality of the isotopic values and the homogeneity of variances among groups using Lilliefors test and Levene's test prior to any analyses. Data are always shown as means \pm SDs, unless otherwise stated. All analyses were carried out using SPSS 15.

We estimated the population isotopic niche width using the convex hull area in the isotopic space defined by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Layman et al. 2007). Nonetheless, the use of Euclidean methods (e.g. convex hulls) to define the isotopic niche space of a species in a community (Layman et al. 2007) is subject to sampling biases and is sensitive to sample size (Jackson et al. 2011). The standard ellipse areas estimated by Bayesian inference can incorporate uncertainties such as sampling biases and small sample sizes into niche metrics (Jackson et al. 2011). Thus, we estimated the width of the isotopic niche at the population level using the Bayesian standard ellipse area

(SEA_B) in the function SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011) of the library SIAR (Stable Isotope Analysis in R; Parnell et al. 2010) in the software R (R Core Team 2013). Furthermore, we calculated the magnitude of the isotopic overlap between the sexes at the beginning of the pre-breeding season (skin values) and year round (bone values) based on 100 000 posterior draws of the standard ellipse areas corrected for small sample size (SEA_C) parameters (Jackson et al. 2011). This approach, which is based on Markov-Chain Monte Carlo (MCMC) simulation, assigns measures of uncertainty to construct parameters of ellipses in a way similar to a bootstrap.

RESULTS

Table 1 shows the stable carbon and nitrogen isotope values of the South American sea lion and their prey off southern Brazil, Uruguay and northern Argentina. We found that the prey of the South American sea lion differed statistically in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (nested ANOVA; $\delta^{13}\text{C}_{\text{model}}$: $F_{39,205} = 34.752$, $p < 0.001$, $R^2_{\text{corrected}} = 0.865$; $\delta^{15}\text{N}_{\text{model}}$: $F_{39,205} = 57.408$, $p < 0.001$, $R^2_{\text{corrected}} = 0.915$), both among species (nested ANOVA; $\delta^{13}\text{C}_{\text{species}}$: $F_{37,205} = 31.780$, $p < 0.001$; $\delta^{15}\text{N}_{\text{species}}$: $F_{37,205} = 51.211$, $p < 0.001$) and regions (nested ANOVA; $\delta^{13}\text{C}_{\text{regions}}$: $F_{2,205} = 54.329$, $p < 0.001$; $\delta^{15}\text{N}_{\text{regions}}$: $F_{2,205} = 114.477$, $p < 0.001$). This was because pelagic prey were usually depleted in ^{13}C when compared with demersal prey from the same region, small pelagic fishes were depleted in ^{15}N when compared with medium pelagic fishes and demersal fishes from the same region, and fishes and cephalopods from northern Argentina were usually enriched in ^{15}N when compared with similar species from Uruguay and southern Brazil (Fig. 2).

Adult male and female sea lions did not differ in their bone stable isotope values, with differences between Brazil and Uruguay being statistically non-significant (2-way ANOVA; $\delta^{13}\text{C}_{\text{model}}$: $F_{3,29} = 0.606$, $p = 0.617$; $\delta^{15}\text{N}_{\text{model}}$: $F_{3,29} = 2.613$, $p = 0.073$). Accordingly, adult male and female sea lions had similar diets on an annual basis. Conversely, adult male and female sea lions sampled at the beginning of the breeding season differed significantly in their skin isotope values (Student's *t*-test; $\delta^{13}\text{C}$: $t_{20} = 3.072$, $p = 0.006$; $\delta^{15}\text{N}$: $t_{20} = 11.634$, $p < 0.001$), thus revealing different diets during the pre-breeding period.

Since sea lions from Brazil and Uruguay did not differ in bone stable isotope values, data from individuals of the same sex were pooled for further analyses.

Table 1. Stable isotope values (mean \pm SD) of the South American sea lion *Otaria flavescens* and their prey off southern Brazil, Uruguay and northern Argentina. n (non-bold): sample size; n (bold): number of species; bold isotopic values: gross mean of the prey species by trophic guild. ^aSource: Bugoni et al. (2010); ^bSource: Franco-Trecu et al. (2013)

Scientific name	Common name	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Southern Brazil				
Medium pelagic fish				
<i>Pomatomus saltatrix</i>	Bluefish	5	-16.6 \pm 0.5	18.6 \pm 0.7
<i>Trichiurus lepturus</i>	Cutlassfish	5	-15.7 \pm 0.3	16.6 \pm 0.5
<i>Cynoscion guatucupa</i>	Stripped weakfish	5	-16.5 \pm 0.7	16.0 \pm 0.6
<i>Macrodon atricauda</i>	King weakfish	5	-14.5 \pm 0.6	17.0 \pm 0.3
<i>Trachurus lathami</i> ^a	Rough scad	9	-16.1 \pm 0.1	16.1 \pm 1.1
		5	-15.9 \pm 0.8	16.9 \pm 1.1
Small pelagic fish				
<i>Engraulis anchoita</i> ^a	Argentine anchovy	14	-16.5 \pm 0.5	14.7 \pm 0.5
<i>Sardinella brasiliensis</i> ^a	Brazilian sardine	7	-17.6 \pm 0.6	11.4 \pm 1.0
		2	-17.1 \pm 0.8	13.1 \pm 2.3
Demersal fish				
<i>Menticirrhus americanus</i>	Southern kingfish	5	-15.4 \pm 0.5	16.0 \pm 0.5
<i>Micropogonias furnieri</i>	White croaker	5	-15.7 \pm 0.6	15.3 \pm 0.4
<i>Umbrina canosai</i> ^a	Argentine croaker	10	-15.5 \pm 0.3	16.6 \pm 0.8
<i>Urophycis brasiliensis</i> ^a	Brazilian codling	11	-15.6 \pm 0.5	16.5 \pm 0.7
		4	-15.6 \pm 0.1	16.1 \pm 0.6
Pelagic cephalopods				
<i>Illex argentinus</i>	Argentine short-finned squid	5	-18.1 \pm 0.2	10.0 \pm 0.5
<i>Loligo paelei</i>	Atlantic longfin squid	5	-17.6 \pm 0.2	11.3 \pm 0.5
		2	-17.9 \pm 0.4	10.7 \pm 0.9
<i>Loligo sanpaulensis</i>	Brazilian squid	5	-16.3 \pm 0.1	15.2 \pm 0.3
Sea lion				
<i>Otaria flavescens</i> (♂ Bone)	South American sea lion	10	-12.1 \pm 0.7	20.5 \pm 0.4
<i>Otaria flavescens</i> (♀ Bone)	South American sea lion	4	-12.0 \pm 0.3	20.4 \pm 0.3
Uruguay				
Medium pelagic fish				
<i>Cynoscion guatucupa</i> ^b	Stripped weakfish	6	-15.4 \pm 0.3	17.0 \pm 0.1
<i>Trichiurus lepturus</i> ^b	Cutlassfish	2	-17.3 \pm 0.4	15.4 \pm 1.4
<i>Macrodon atricauda</i> ^b	King weakfish	10	-15.3 \pm 0.3	16.3 \pm 0.2
<i>Merluccius hubbsi</i> (>30 cm) ^b	Argentine hake	1	-16.2	17.9
		4	-16.0 \pm 0.9	16.6 \pm 1.1
Small pelagic fish				
<i>Engraulis anchoita</i> ^b	Argentine anchovy	6	-18.5 \pm 0.3	14.2 \pm 1.0
Demersal fish				
<i>Micropogonias furnieri</i> ^b	White croaker	7	-14.9 \pm 0.1	16.2 \pm 0.1
<i>Umbrina canosai</i> ^b	Argentine croaker	1	-16.0	15.7
<i>Urophycis brasiliensis</i> ^b	Brazilian codling	8	-15.0 \pm 0.7	16.6 \pm 0.7
		3	-15.3 \pm 0.6	16.2 \pm 0.5
Demersal crustaceans				
<i>Pleoticus muelleri</i> ^b	Red shrimp	4	-16.0 \pm 0.3	13.9 \pm 0.2
Pelagic cephalopods				
<i>Loligo sanpaulensis</i> ^b	Brazilian squid	2	-17.9 \pm 0.1	13.7 \pm 0.2
<i>Illex argentinus</i> ^b	Argentine short-finned squid	2	-18.7 \pm 0.2	13.9 \pm 0.7
Sea lion				
<i>Otaria flavescens</i> (♂ Skin)	South American sea lion	12	-13.9 \pm 0.2	21.9 \pm 0.4
<i>Otaria flavescens</i> (♀ Skin)	South American sea lion	10	-14.2 \pm 0.2	19.8 \pm 0.4
<i>Otaria flavescens</i> (♂ Bone)	South American sea lion	6	-12.4 \pm 0.6	21.6 \pm 0.5
<i>Otaria flavescens</i> (♀ Bone)	South American sea lion	10	-12.4 \pm 0.9	20.5 \pm 1.4
Northern Argentina				
Medium pelagic fish				
<i>Merluccius hubbsi</i> (>30 cm)	Argentine hake	3	-18.0 \pm 0.5	15.6 \pm 0.4
<i>Trachurus picturatus</i>	Blue jack mackerel	5	-17.6 \pm 0.3	16.9 \pm 0.5
<i>Stromateus brasiliensis</i>	Butterfish	5	-16.9 \pm 0.6	17.4 \pm 0.4
<i>Cynoscion guatucupa</i>	Stripped weakfish	5	-17.2 \pm 0.2	17.6 \pm 0.3
		4	-17.4 \pm 0.5	16.9 \pm 0.9
Small pelagic fish				
<i>Engraulis anchoita</i>	Argentine anchovy	5	-18.2 \pm 0.3	15.5 \pm 0.5
<i>Sorgentia incisa</i>	Silverside	5	-17.6 \pm 0.3	15.5 \pm 0.2
<i>Merluccius hubbsi</i> (<30 cm)	Argentine hake	2	-18.4 \pm 0.1	14.8 \pm 0.1
		3	-18.1 \pm 0.4	15.3 \pm 0.4
Demersal fish				
<i>Menticirrhus americanus</i>	Southern kingfish	5	-15.0 \pm 0.9	19.1 \pm 1.1
<i>Micropogonias furnieri</i>	White croaker	5	-16.0 \pm 0.3	16.7 \pm 0.5
<i>Paralichthys isosceles</i>	Flounder	5	-16.6 \pm 0.2	17.7 \pm 0.2
<i>Prionotus nudigula</i>	Bluewing searobin	5	-17.0 \pm 0.1	18.0 \pm 0.6
<i>Raneya brasiliensis</i>	Banded cusk-eel	5	-16.2 \pm 0.4	17.4 \pm 0.6
		5	-16.0 \pm 0.7	17.8 \pm 0.9
Demersal crustaceans				
<i>Pleoticus muelleri</i>	Red shrimp	1	-16.4	14.4
Pelagic cephalopods				
<i>Loligo sanpaulensis</i>	Brazilian squid	5	-16.7 \pm 0.2	18.6 \pm 0.2
<i>Illex argentinus</i>	Argentine short-finned squid	5	-17.5 \pm 0.4	14.7 \pm 0.5

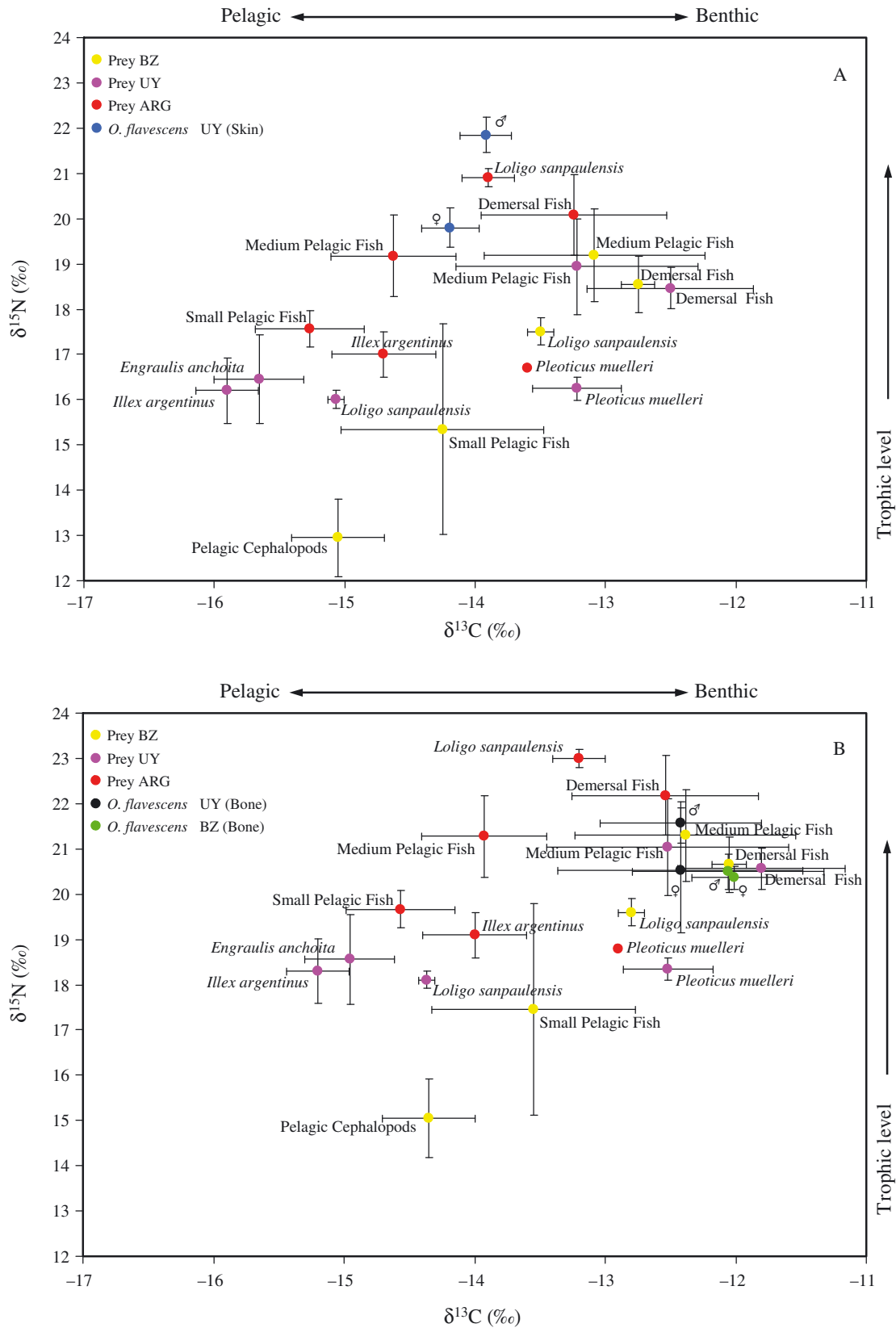


Fig. 2. Bivariate stable isotope values (mean \pm SD) of South American sea lions *Otaria flavescens* from southern Brazil and Uruguay (A) during the pre-breeding period (skin values) and (B) year round (bone values) and values expected if diet was based on a single prey or group of prey. Stable isotope values for expected diets (BZ: southern Brazil; UY: Uruguay; ARG: northern Argentina) differ between panels because of differences in the prey-to-predator discrimination factors of skin and bone (see original data and sample size in Table 1)

Statistically significant differences were found when the expected $\delta^{13}\text{C}$ values of the diet consumed by males and females during the pre-breeding period were compared with that consumed on an annual basis (2-way ANOVA; $\delta^{13}\text{C}_{\text{model}}$: $F_{3,51} = 14.854$, $p <$

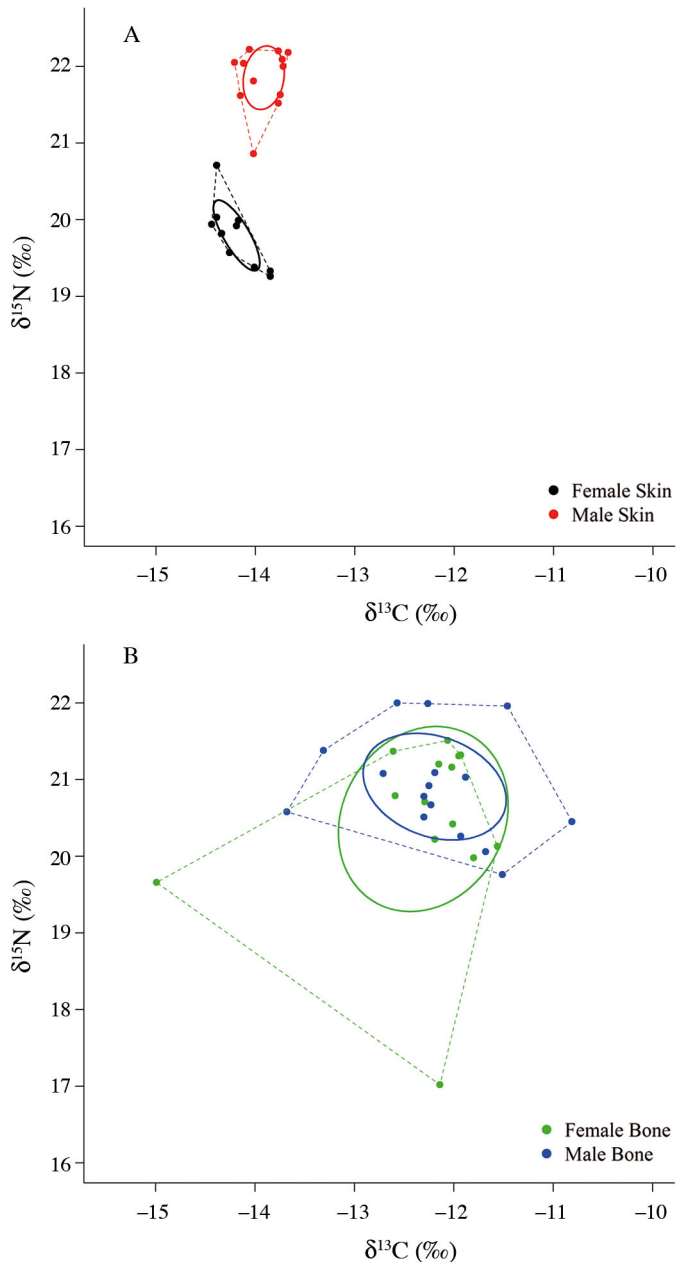


Fig. 3. Bayesian standard ellipse areas (solid lines) and their respective convex hulls (dashed lines) for South American sea lion *Otaria flavescens* (A) during the pre-breeding period (skin values) and (B) year round (bone values), calculated by SIBER using the bivariate isotopic values (solid circles) of each male and female. Stable isotope values for skin and bone of sea lions were not corrected for prey-to-predator isotopic discrimination

0.001, $R^2_{\text{corrected}} = 0.449$). However, these differences were statistically significant only between the pre-breeding and the annual diet (2-way ANOVA; $\delta^{13}\text{C}_{\text{period}}$: $F_{1,51} = 43.581$, $p < 0.001$), without any difference between the sexes (2-way ANOVA; $\delta^{13}\text{C}_{\text{sex}}$: $F_{1,51} = 1.283$, $p = 0.263$) and with a nonsignificant interaction term (2-way ANOVA; $\delta^{13}\text{C}_{\text{interaction}}$: $F_{1,51} = 0.248$, $p = 0.621$).

Statistically significant differences were also found for the expected $\delta^{15}\text{N}$ values of the diet consumed by males and females during the pre-breeding period and that consumed on an annual basis (2-way ANOVA; $\delta^{15}\text{N}_{\text{model}}$: $F_{3,51} = 52.864$, $p < 0.001$, $R^2_{\text{corrected}} = 0.753$). There were significant differences between periods (2-way ANOVA; $\delta^{15}\text{N}_{\text{period}}$: $F_{1,51} = 107.660$, $p < 0.001$), and between the sexes (2-way ANOVA; $\delta^{15}\text{N}_{\text{sex}}$: $F_{1,51} = 33.818$, $p < 0.001$). The interaction term was also significant (2-way ANOVA; $\delta^{15}\text{N}_{\text{interaction}}$: $F_{1,51} = 14.382$, $p < 0.001$) because differences between the sexes were significant only during the pre-breeding period (Fig. 2).

The Bayesian ellipse of females was larger and encompassed that of males when bone data were considered (Fig. 3). The overlap area represented 44.89% of the surface of the female ellipse and 96.0% of the surface of the male ellipse. However, the Bayesian ellipses of males and females had similar areas and did not overlap at all when skin data were considered (Fig. 3). Furthermore, the surface of the Bayesian ellipses based on the skin data was smaller than that based on bone data (female $\text{SEA}_{\text{B(bone)}}$ mean = $3.33\% ^2$, 95% credibility interval of 1.78 to $5.08\% ^2$; female $\text{SEA}_{\text{B(skin)}}$ mean = $0.92\% ^2$, 95% credibility interval of 0.46 to $0.98\% ^2$; male $\text{SEA}_{\text{B(bone)}}$ mean = $1.76\% ^2$, 95% credibility interval of 0.98 to $2.65\% ^2$; male $\text{SEA}_{\text{B(skin)}}$ mean = $0.86\% ^2$, 95% credibility interval of 0.44 to $1.38\% ^2$).

DISCUSSION

Stable isotope analysis has become a standard tool for investigating trophic relationships of wild animals (Newsome et al. 2010, Layman et al. 2012). Their use is based on 3 main assumptions: (1) stable carbon and nitrogen isotopes in the body of an animal come directly from its food; consequently, the stable isotope ratios in their tissues can be used to assess the relative importance of potential prey that differ in stable isotope ratios (DeNiro & Epstein 1978, 1981); (2) the assimilated organic matter is enriched in the heavy isotopes of both carbon and nitrogen when passed from one trophic level to the next, although

that enrichment is greater for nitrogen than for carbon (Michener & Schell 1994); and (3) the rate of change of the stable isotope ratio in each tissue depends on its metabolic rate; hence, the reference time of dietary information is tissue-dependent (Michener & Schell 1994).

Neither prey-to-predator isotopic discrimination factors nor tissue turnover have been determined for the South American sea lion in controlled experiments; thus, extrapolation from studies conducted on phylogenetically close species is required (e.g. Hückstädt et al. 2007, Drago et al. 2010, Vales et al. 2014). We have used this approach to compute the expected stable isotope values of the diet of the South American sea lions as indicated by stable isotope values in skin and bone, considering that the direct comparison of the stable isotope values from tissues differing in discrimination factors may lead to major mistakes (Bocherens et al. 2014). Nevertheless, caution is needed and all the results should be considered as an approximation due to the multiple assumptions involved.

In this context, the reported differences between the sexes in terms of the expected diet stable isotope ratios revealed the preferential consumption of pelagic prey over benthic prey during the pre-breeding period, whereas the opposite was true throughout the year (Fig. 2). This suggests a dietary shift, favouring species with higher energy density, immediately before the onset of the breeding season (Eder & Lewis 2005, Drago et al. 2009b).

The energy density of prey plays a central role in the foraging ecology of at least some otariids (Rosen & Trites 2000, Staniland et al. 2007). The dietary shift observed during the pre-breeding period is consistent with a foraging strategy aiming to maximize energy intake, if energy density was the only criterion for prey selection during key foraging periods with higher energetic demands. Such a dietary shift would allow individuals of both sexes to increase their energy reserves immediately before the onset of breeding, but only if the increased travel cost did not reduce the benefit of preying on offshore pelagic prey with higher energy density (Costa 2008). Our result is congruent with similar findings for the South American sea lions breeding in northern Patagonia, although detailed information about patterns of habitat use during the breeding season have been reported only for females (Drago et al. 2010) and almost nothing is known about males (Campagna et al. 2001). Furthermore, evidence supporting the hypothesis of a general decline in the nutritional quality of the diet after the perinatal period also

comes from studies on milk quality, as the fat content and, therefore, also the energy content of the milk of female South American sea lions was found to decrease after parturition and to increase several months later, just prior to weaning (Werner et al. 1996).

In addition, the isotopic bone data presented here indicate that both males and females sampled in southern Brazil and Uruguay were trophically very similar, since sea lions from the 2 sites did not differ in bone stable isotope values (Fig. 2). Considering that the slow isotopic turnover rate of bone tissue allows integration of the different isotopic values of prey of both ecosystems, this similarity suggests that these animals feed in similar areas and/or share prey species when considering the diet consumed year round. This is probably because sea lions breeding in Uruguay apparently scatter in the open sea from Uruguay to southern Brazil, searching for food after the end of the breeding season (Rosas et al. 1994).

The Bayesian ellipses suggest that male and female sea lions used a wide diversity of foraging strategies throughout the year and that no differences existed between the sexes (Fig. 3). Furthermore, despite the larger body size (hence, larger diving and breath-holding capacity) of male South American sea lions, the diversity of foraging strategies was wider in females. While the latter could result from the influence of a few potential outliers, we think that these extreme points are more likely to reflect the individual trophic specialisation reported for the Uruguayan South American sea lion population (Franco-Trecu et al. 2014). The diversity in the female foraging tactics could reflect the consumption of prey at lower trophic levels and/or the exploitation of more pelagic habitats compared to males, as a means to decrease the intrapopulation niche overlap. Similar to our results with bone tissue, the stable isotope contents of South American sea lion whiskers (that integrate up to 2 or 3 yr of foraging) showed a large overlap of the isotopic niches between the sexes and that females had wider niches than males (Franco-Trecu et al. 2014).

The diversity of foraging strategies was strongly reduced in both sexes during the pre-breeding period, since all individuals increased their consumption of pelagic prey. However, the skin stable isotope values of both sexes differed significantly, with the area covered by the Bayesian ellipses being sharply reduced and the ellipses of males and females not overlapping at all (Figs. 2 & 3).

During the pre-breeding period, the progressive crowding of individuals in the areas surrounding the

breeding rookeries could lead to an increase in the local population density and, therefore, to an overall decrease in the per capita resource share. Sea lion males might also be more efficient foragers than females during key foraging periods, provided that their larger size and physiological abilities enable them to have easier access (capture and handle) to larger and more energetically rewarding prey than females (Page et al. 2005). Thus, considering the isotopic landscape of Río de la Plata plume and adjoining areas (Fig. 2), the per capita consumption of larger pelagic prey at higher trophic levels by male sea lions could be expected to increase during the pre-breeding period, when intraspecific competition between the sexes is stronger due to the concomitant increase in local population density and the necessity to maximize fitness during a period of high energetic demands. This is supported by the significantly higher trophic level of the male diet than that of females during the pre-breeding season, and by the increase in pelagic prey size in accordance with the increase in the trophic level (Figs. 2 & 3). Trophic segregation at this time of year may provide a means of reducing intraspecific competition related to high niche overlap, while permitting males to access higher quality foods needed to face the energetic demands during the breeding period (Beck et al. 2007).

In summary, our results support the niche divergence hypothesis as the most likely explanation for the trophic segregation between the sexes of the South American sea lion. However, this segregation only takes place during the pre-breeding season, when crowding in the areas surrounding the breeding rookeries increases and per-capita resource share declines. Intersexual differences largely vanish during the rest of the year, since individuals of both sexes spread over a huge area and increase both their dietary niche breadth and niche overlap (Fig. 3). This suggests that individual South American sea lions of both sexes could exploit a greater range of habitats and prey when they are more scattered and intraspecific competition is expected to decrease.

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LITERATURE CITED

- Alves-Stanley CD, Worthy GAJ (2009) Carbon and nitrogen stable isotope turnover rates and diet-tissue discrimination in Florida manatees (*Trichechus manatus latirostris*). *J Exp Biol* 212:2349–2355
- Artico LO, Bianchini A, Grubel KS, Monteiro DS and others (2010) Mitochondrial control region haplotypes of the South American sea lion *Otaria flavescens* (Shaw, 1800). *Braz J Med Biol Res* 43:816–820
- Beck CA, Bowen DW, McMillan JI, Iverson SJ (2003a) Sex differences in the diving behaviour of a size-dimorphic capital breeder: the grey seal. *Anim Behav* 64:1–13
- Beck CA, Bowen WD, Iverson SJ (2003b) Sex differences in the seasonal patterns of energy storage and expenditure in a phocid seal. *J Anim Ecol* 72:280–291
- Beck CA, Iverson SJ, Bowen WD, Blanchard W (2007) Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative fatty acid signature analysis. *J Anim Ecol* 76:490–502
- Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. *Can J Biochem Physiol* 37: 911–917
- Bocherens H, Grandal-d'Anglade A, Hobson KA (2014) Pitfalls in comparing modern hair and fossil bone collagen C and N isotopic data to reconstruct ancient diets: a case study with cave bears (*Ursus spelaeus*). *Isotopes Environ Health Stud* 50:291–299
- Bond AL, Hobson KA (2012) Reporting stable-isotope ratios in ecology: recommended terminology, guidelines and best practices. *Waterbirds* 35:324–331
- Breed GA, Bowen WD, McMillan JI, Leonard ML (2006) Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. *Proc R Soc B* 273: 2319–2326
- Bugoni L, McGill RAR, Furness RW (2010) The importance of pelagic longline fishery discards for a seabird community determined through stable isotope analysis. *J Exp Mar Biol Ecol* 391:190–200
- Bunn SE, Loneragan NR, Kempster MA (1995) Effects of acid washing on stable isotope ratios of C and N in penaeid shrimp and seagrass: implications for food-web studies using multiple stable isotopes. *Limnol Oceanogr* 40:622–625
- Campagna C (1985) The breeding cycle of the southern sea lion, *Otaria byronia*. *Mar Mamm Sci* 1:210–218
- Campagna C, Le Boeuf BJ (1988) Reproductive behaviour of southern sea lions. *Behaviour* 104:233–261
- Campagna C, Werner R, Karesh W, Marin MR, Koontz F, Cook R, Koontz C (2001) Movements and locations at sea of South American sea lions (*Otaria flavescens*). *J Zool*

- (Lond) 255:205–220
- Cappozzo HL, Perrin WP (2009) South American sea lion (*Otaria flavescens*). In: Perrin WF, Würsing B, Thewissen JGM (eds) Encyclopedia of marine mammals, 2nd edn. Academic Press, San Diego, CA, p 1076–1079
- Clarke J, Manly B, Kerry K, Gardner H, Franchi E, Corsolini S, Focardi S (1998) Sex differences in Adelie penguin foraging strategies. *Polar Biol* 20:248–258
- Clutton-Brock TH, Parker GA (1992) Potential reproductive rates and the operation of sexual selection. *Q Rev Biol* 67: 437–456
- Clutton-Brock TH, Iason GR, Guinness FE (1987) Sexual segregation and density related changes in the habitat use in male and female red deer. *J Zool (Lond)* 211:275–289
- Costa DP (1993) The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. In: Boyd IL (ed) Marine mammals: advances in behavioural and population biology. Oxford University Press, London, p 293–314
- Costa DP (2008) A conceptual model of the variation in parental attendance in response to environmental fluctuation: foraging energetics of lactating sea lions and fur seals. *Aquat Conserv Mar Freshw Ecosyst* 17:S44–S52
- Costa DP, Kuhn CE, Weise MJ, Shaffer SA, Arnould JPY (2004) When does physiology limit the foraging behaviour of freely diving mammals? *Int Congr Ser* 1275: 359–366
- Crespo EA (1984) Dimorfismo sexual en los dientes caninos y en los cráneos del lobo marino del sur, *Otaria flavescens* (Pinnipedia, Otariidae). *Rev Mus Argent Cienc Nat Bernardino Rivadavia Zool* 13:245–254
- Dalerum F, Angerbjörn A (2005) Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. *Oecologia* 144:647–658
- DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495–506
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341–351
- Drago M, Cardona L, Crespo EA, Aguilar A (2009a) Ontogenetic dietary changes in South American sea lions. *J Zool (Lond)* 279:251–261
- Drago M, Crespo EA, Aguilar A, Cardona L, García N, Dans SL, Goodall N (2009b) Historic diet change of the South American sea lion in Patagonia as revealed by isotopic analysis. *Mar Ecol Prog Ser* 384:273–286
- Drago M, Cardona L, Crespo EA, García N, Ameghino S, Aguilar A (2010) Change in the foraging strategy of female South American sea lions (Carnivora: Pinnipedia) after parturition. *Sci Mar* 74:589–598
- Eder EB, Lewis MN (2005) Proximate composition and energetic value of demersal and pelagic prey species from the SW Atlantic Ocean. *Mar Ecol Prog Ser* 291:43–52
- Fowler SL, Costa DP, Arnould JPY, Gales J (2007) Ontogeny of oxygen stores and physiological diving capability in Australian sea lions. *Funct Ecol* 21:922–935
- Franco-Trecu V, Drago M, Riet-Sapriza FG, Parnell A, Frau R, Inchausti P (2013) Bias in diet determination: incorporating traditional methods in Bayesian mixing models. *PLoS ONE* 8:e80019
- Franco-Trecu V, Auriolles-Gamboa D, Inchausti P (2014) Individual trophic specialisation and niche segregation explain the contrasting population trends of two sympatric otariids. *Mar Biol* 161:609–618
- Gentry RL, Costa DP, Croxall DP, David JP, Davis HM, Kooyman GL (1986) Synthesis and conclusion. In: Gentry RL, Kooyman GL (eds) Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, NJ, p 220–278
- Grandi MF, Dans SL, Crespo EA (2008) Social composition and spatial distribution of colonies in an expanding population of South American sea lions. *J Mammal* 89: 1218–1228
- Hobson KA, Clark RG (1992a) Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. *Condor* 94: 181–188
- Hobson KA, Clark RG (1992b) Assessing avian diets using stable isotopes II: factors influencing diet–tissue fractionation. *Condor* 94:189–197
- Hobson KA, Schell DM, Renouf D, Noseworthy E (1996) Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. *Can J Fish Aquat Sci* 53:528–533
- Hückstädt LA, Rojas CP, Antezana T (2007) Stable isotope analysis reveals pelagic foraging by the Southern sea lion in central Chile. *J Exp Mar Biol Ecol* 347:123–133
- Jackson AL, Parnell AC, Inger R, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. *J Anim Ecol* 80:595–602
- Jormalainen V, Honkanen T, Makinen A, Hemmi A, Vesakoski O (2001) Why does herbivore sex matter? Sexual differences in utilization of *Fucus vesiculosus* by the isopod *Idotea baltica*. *Oikos* 93:77–86
- Kooyman GL (1989) Diverse divers: physiology and behavior. Springer-Verlag, Berlin
- Kooyman GL, Castellini MA, Davis RW (1981) Physiology of diving in marine mammals. *Annu Rev Physiol* 43: 343–356
- Kurle CM, Worthy GAJ (2001) Stable isotope assessment of temporal and geographic differences in feeding ecology of northern fur seals (*Callorhinus ursinus*) and their prey. *Oecologia* 126:254–265
- Laws RM (1952) A new method of age determination for mammals. *Nature* 169:972–973
- Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88:42–48
- Layman CA, Araujo MS, Boucek R, Hammerschlag-Peyer CM and others (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biol Rev Camb Philos Soc* 87:545–562
- Le Boeuf BJ, Crocker DE, Costa DP, Blackwell SB, Webb PM, Houser DS (2000) Foraging ecology of northern elephant seals. *Ecol Monogr* 70:353–382
- Lorrain A, Savoye N, Chauvaud L, Paulet Y, Naulet N (2003) Decarbonation and preservation method for the analysis of organic C and N contents and stable isotope ratios of low-carbonated suspended particulate material. *Anal Chim Acta* 491:125–133
- Meynier L, Morel PCH, Chilvers BL, Mackenzie DDS, MacGibbon A, Duignan PJ (2008) Temporal and sex differences in the blubber fatty acid profiles of the New Zealand sea lion *Phocarctos hookeri*. *Mar Ecol Prog Ser* 366:271–279
- Michener RH, Schell DM (1994) Stable isotope ratios as tracers in marine aquatic food webs. Blackwell, Oxford
- Miller K, Irving L (1975) Metabolism and temperature regu-

- lation in young harbour seals, *Phoca vitulina richardsi* in water. *Am J Physiol* 229:506–511
- Mysterud A (2000) The relationship between ecological segregation and sexual body size dimorphism in large herbivores. *Oecologia* 124:40–54
- Nagy KA (1987) Field metabolic rate and food requirement scaling in mammals and birds. *Ecol Monogr* 57:111–128
- Naya DE, Vargas R, Arim M (2000) Análisis preliminar de la dieta del león marino del sur (*Otaria flavescens*) en Isla de Lobos, Uruguay. *Bol Soc Zool Urug* 12:14–21
- Newsome SD, Koch PL, Etnier MA, Auriolles-Gambao D (2006) Using carbon and nitrogen isotope values to investigate maternal strategies in northeast Pacific otariids. *Mar Mamm Sci* 22:556–572
- Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. *Mar Mamm Sci* 26:509–572
- Oftedal OT, Boness DJ, Tedman RA (1987) The behavior, physiology, and anatomy of lactation in the Pinnipedia. In: Genoways HH (ed) *Current mammalogy*. Plenum Press, New York, NY, p 175–221
- Page B, McKenzie J, Goldsworthy SD (2005) Dietary resource partitioning among sympatric New Zealand and Australian fur seals. *Mar Ecol Prog Ser* 293:283–302
- Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE* 5:e9672
- R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org
- Riet Sapriza FG, Costa DP, Franco-Trecu V, Marín Y and others (2013) Foraging behavior of lactating South American sea lions, *Otaria flavescens* and spatial-resource overlap with the Uruguayan fisheries. *Deep-Sea Res II* 88–89:106–119
- Riofrio-Lazo M, Auriolles-Gamboia D (2013) Timing of isotopic integration in marine mammal skull: comparative study between calcified tissues. *Rapid Commun Mass Spectrom* 27:1076–1082
- Rosas FCW, Pinedo MC, Marmontel M, Haimovici M (1994) Seasonal movements of the South American sea lion (*Otaria flavescens*, Shaw) off the Rio Grande do Sul coast, Brazil. *Mammalia* 58:51–59
- Rosen DAS, Trites AW (2000) Pollock and the decline of Steller sea lions: testing the junk-food hypothesis. *Can J Zool* 78:1243–1250
- Ryan C, McHugh B, Trueman CN, Harrod C, Berrow SD, O'Connor I (2012) Accounting for the effects of lipids in stable isotope (^{13}C and ^{15}N values) analysis of skin and blubber of balaenopterid whales. *Rapid Commun Mass Spectrom* 26:2745–2754
- Sotiropoulos MA, Tonn WM, Wassenaar LI (2004) Effects of lipid extraction on stable carbon and nitrogen isotope analyses of fish tissues: potential consequences for food web studies. *Ecol Freshw Fish* 13:155–160
- Soto KH, Trites AW, Arias-Schreiber M (2006) Changes in diet and maternal attendance of South American sea lions indicate changes in the marine environment and prey abundance. *Mar Ecol Prog Ser* 312:277–290
- Staniland IJ, Boyd IL, Reid K (2007) An energy-distance trade-off in a central-place forager, the Antarctic fur seal (*Arctocephalus gazella*). *Mar Biol* 152:233–241
- Thompson D, Duck CD, McConnell BJ, Garrett J (1998) Foraging behaviour and diet of lactating female southern sea lions (*Otaria flavescens*) in the Falkland Islands. *J Zool (Lond)* 246:135–146
- Todd SK, Holm B, Rosen DAS, Tollit DJ (2010) Stable isotope signal homogeneity and differences between and within pinniped muscle and skin. *Mar Mamm Sci* 26:176–185
- Vales DG, Saporiti F, Cardona L, De Oliveira LR and others (2014) Intensive fishing has not forced dietary change in the South American fur seal *Arctophoca* (= *Arctocephalus*) *australis* off Rio de la Plata and adjoining areas. *Aquatic Conserv Mar Freshw Ecosyst* 24:745–759
- Vaz-Ferreira R (1975) Behavior of the Southern sea lion *Otaria flavescens* (Shaw) in the Uruguayan Islands. *Rapp P-V Reun Cons Int Explor Mer* 169:219–227
- Vaz-Ferreira R (1982) *Otaria flavescens* (Shaw), South American sea lion. In: FAO, UNEP (eds) *Mammals in the seas: small cetaceans, seals, sirenians and otters*, Vol 4. FAO Fisheries Series 5:477–495
- Wearmouth VJ, Sims DW (2008) Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. *Adv Mar Biol* 54:107–170
- Werner R, Campagna C (1995) Diving behaviour of lactating southern sea lions (*Otaria flavescens*) in Patagonia. *Can J Zool* 73:1975–1982
- Werner R, Figueroa-Carranza A, Ortiz CL (1996) Composition and energy content of milk from southern sea lions (*Otaria flavescens*). *Mar Mamm Sci* 12:313–317
- Zenteno L, Crespo E, Goodall N, Aguilar A and others (2013) Stable isotopes of oxygen reveal dispersal patterns of the South American sea lion in the southwestern Atlantic Ocean. *J Zool (Lond)* 291:119–126
- Zenteno L, Crespo E, Vales D, Silva L and others (2015) Dietary consistency of male South American sea lions (*Otaria byronia*) in southern Brazil during three decades inferred from stable isotope analysis. *Mar Biol* 162:275–289

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