

Individual trophic specialisation and niche segregation explain the contrasting population trends of two sympatric otariids

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Abstract Individual specialisation is increasingly recognised to be an ecological and evolutionary process having important consequences for population dynamics of vertebrates. The South American fur seal (SAFS) and the South American sea lion (SASL) are two otariid species with similar ecology that coexist in sympatry in the Uruguayan coast. These two species have contrasting trends and widely different population sizes. The underlying reasons for these population trends, unique in their geographical ranges, remain unknown. We studied the foraging ecology of these otariid species over 2 years at the individual- and population levels using the isotopic ratios ($\delta^{13}\text{C}$ – $\delta^{15}\text{N}$) in whiskers of both sexes. We compared the isotope ratios between species and sexes and used several metrics to characterise the degree of overlap and distinctiveness in the use of isotopic niche space at the individual- and population levels. Interspecific trophic niche overlap was minimal, thus ruling out interspecific competition as the cause for the contrasting population trends of both species. At the intraspecific

level, both species had sexual segregation in their foraging areas, but each species had a large overlap in the isotopic niches between sexes. While SAFS had a wider niche and generalist individuals, SASL had the narrower niche with a higher degree of individual specialisation. Behavioural constraints during the breeding season, intraspecific competition and a major dependence on resources of the Uruguayan coastal shelf may explain why SASL had a higher trophic individual specialisation and a larger vulnerability in a heavily exploited habitat by fisheries and, by consequence, a locally declining population trend.

Introduction

The ecological niche, defined as a n -dimensional hypervolume containing the relevant variables that explain the persistence of a species or a local population, (Hutchinson 1957) is a keystone concept in ecology. It is involved in a wide range of topics ranging from the behaviour and physiology of individual organisms to the structure of communities and ecosystem functioning (Chase and Leibold 2003). However, it has become increasingly clear that the niches of many vertebrate species cannot be assumed to be homogeneous because individuals can substantially differ in their resource use (Bolnick et al. 2003). For instance, many generalist populations that use a wide diversity of resources when examined at the population level are actually an ensemble of specialised individuals that segregate in the niche space (Bolnick et al. 2003, 2007).

Individual specialisation is increasingly recognised to be an ecological and evolutionary process having important influences on population dynamics and community structure of vertebrates (Bolnick et al. 2003; Araujo et al. 2011). Trophic specialisation at the individual level has been

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found in many species such as fish (Brodersen et al. 2012), sharks (Matich et al. 2011), birds (Woo et al. 2008), sea turtles (Vander Zanden et al. 2010) and carnivores (Newsome et al. 2010a). Top predators often play an important role in the structure and dynamics of their communities either through direct effects on their prey or via the indirect impact on species at other trophic levels (Estes et al. 1998; Shurin et al. 2002). In the case of otariids, trophic specialisation could arise because of the individual-level differentiation of resource use and the spatial segregation of foraging areas (Franco-Trecu et al. 2012; Páez-Rosas et al. 2012; Jeglinski et al. 2013). However, to our knowledge, there has been little research on trophic specialisation of otariids including both sexes (Kernaléguen et al. 2012), thus limiting the inferences on the individual behavioural strategies at the population level.

Uncovering the existence of individual strategies in resource use requires showing the consistent differentiation among individuals of a population. In recent years, stable isotopes analysis (SIA) of different tissues has emerged as a key method to investigate the differences in the foraging ecology of pinnipeds (Aurióles-Gamboa et al. 2006; Páez-Rosas et al. 2012; Franco-Trecu et al. 2013). In marine food webs, the prey-to-consumers isotopic ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) enrichment change in a predictable manner in accordance with the specific dietary fractioning (Hobson et al. 1994; Post 2002; Newsome et al. 2007). The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ are used to estimate the trophic position (Post 2002) and the feeding sources used by the predators (DeNiro and Epstein 1978; Bearhop et al. 2004) at different temporal scales depending on the moment of production and the turnover rate of the tissue analysed (Dalerum and Angerbjörn 2005). The SIA of metabolically inert tissues such as tooth dentine and whisker keratin with continuous growth, represent sequential archives that allow inferring foraging strategies at individual level over long periods of time (Zhao and Schell 2004; Kernaléguen et al. 2012; Elorriaga-Verplancken et al. 2013).

Two sympatric otariid species breed in South American coast: the South American fur seal (SAFS), *Arctocephalus australis*, and the South American sea lion (SASL), *Otaria flavescens*. While the Uruguayan SAFS population has steadily increased over the last 17 years, with a current estimated size of 300,000 individuals, the SASL has declined in the same period, and its current population size is about 12,000 individuals (Páez 2006). The underlying reasons for these contrasting trends (Pedraza et al. 2009) that are unique in the geographical ranges of both species (Crespo et al. 2008; Dans et al. 2009) remain unknown. Both species can be considered central place foragers since females regularly return to the rookery to feed the pups (Pyke 1984; Stephens and Krebs 1986). Lactating females from both species must maintain a steady energy supply to their offspring that feed

exclusively on mother's milk for several months. Based on faecal analysis, the SAFS and SASL have been characterised as generalist predators whose diets have similar species composition (Naya et al. 2000, 2002; Szteren et al. 2004). However, using SIA in pup's different tissues, Franco-Trecu et al. (2012) showed that these species were segregated in the isotopic space because SASL breeding females exploited nearshore resources whereas SAFS's used offshore resources during pre- and post-partum periods. Nevertheless, the only study dealing with these two species (Franco-Trecu et al. 2012) evaluated trophic differentiation at the population level without considering potential differences of feeding strategies at the individual level.

In this paper, we test the existence of trophic strategies at the individual- and population levels for two sympatric pinniped species with similar diets (Szteren et al. 2004) having different population trends. We used stable isotope values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in whiskers of the SASL and SAFS from Isla Lobos Uruguay to integrate the spatial and trophic dimensions of the ecological niche of individuals over a long period of time. Considering the estimated growth rates for other otariids species of 0.10–0.17 mm d⁻¹ (Hirons et al. 2001), the time period comprising the whiskers analysed was of approximately 2–3 years. We hypothesised that females of both species would have less variable foraging strategies due to restrictions imposed by maternal care. On the other hand, males could exploit other marine environments including different preys after the breeding season, which would result in males of both species having more distinct and wider isotopic niches than in females over time. Regarding the trophic segregation between SASL and SAFS found by Franco-Trecu et al. (2012) using data for females, we hypothesise that by including isotopic data from the males, the trophic segregation between these two species should decrease. Finally, given that generalist individuals (or populations) often access a wider range of trophic resources and achieve higher fitness (at both individual- and population levels) than specialist individuals in temporally or spatially variable environments (Bolnick et al. 2007), we expect the SAFS population to have a higher trophic niche area and a lower degree of individual specialisation. In contrast, the SASL is expected to have a smaller niche area, stronger resource use specialisation with a larger variety of individual trophic strategies.

Materials and methods

Study site, sample collection and treatment

The SAFS and SASL breed on rocky islands of the Uruguayan continental shelf that are the northernmost breeding sites of both species. Their main rookery is Isla de Lobos

(35°01'S, 54°50'W) located at the easternmost part of the Río de la Plata estuary where a highly dynamic mixing regime results from the mixing of freshwater and seawater because of the convergence of the Brazil and Falklands currents (Ortega and Martínez 2007).

Whiskers of five SASL and five SAFS randomly chosen lactating females were obtained in January 2009 and December 2009, respectively. Lactating females were captured with a hoop net and sedated using ~2 ml of midazolam 0.5 % (Vetcross) in the case of SAFS, while SASL were anaesthetised using isoflurane gas mixed with oxygen (0.5–2.5 %) using a portable-field vaporizer (see Riet-Sapiriza et al. 2013). Whiskers of adult males of both species were collected from dead animals incidentally captured in January 2009 (SASL, $n = 3$) and January 2010 (SAFS, $n = 4$). All procedures of animal manipulation were submitted and approved by the Ethics Committee in Animal Experimentation, Universidad de la República, Uruguay, as valid according to the national laws in animal welfare.

Each whisker was washed with distilled water and phosphate-free soap to remove impurities and divided into approximately 55 fragments, adjusting to the total length of the whisker. To minimise the effect of a strong autocorrelation in the comparison of isotopic profiles, we processed every other fragment of each whisker obtaining a total of 414 fragments of the two sexes and species. Each whisker fragment was immersed in a 1:1 hexane–acetone solution to extract lipids and left until total evaporation (Zeppelin and Orr 2010). We then subsampled each whisker to obtain fragments of *ca.* 0.8 mg (high-precision microbalance Mettler Toledo MX5, precision = 1 μ g) that were stored until isotope determination.

We used a mass spectrometer of continuous flow (CF-IRMS) coupled to an elemental Analyzer PDZ Europe ANCA-GSL (Stable Isotope Laboratory, University of California at Davis) to determine natural carbon and nitrogen abundance and their isotopic ratios with an analytical precision of ± 0.2 ‰ for both isotopes. The resulting isotope ratios for each whisker segment were converted and reported to the conventional values delta (δ) in parts per thousand (‰), according to: $\delta X = [(R/R_{st}) - 1] \times 1,000$, where X stands for ^{13}C or ^{15}N , R is the heavy–light stable isotope ratio of the sample ($^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$), and R_{st} is the heavy–light stable isotope ratio in reference standards, which were the atmospheric N_2 (air) for ^{15}N and for ^{13}C relative to the Pee Dee Belemnite (PDB) standard.

Data analysis

Average isotopic content at species level

We used linear mixed models (Pinheiro and Bates 2000) with Gaussian distributions and identity link functions

to examine the differences between species, sex (both as fixed effects) and their interactions on the average content of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. These models had individual identity as a random effect to account for repeated measures of each response variable on the different fragments of each whisker. This random effect allowed evaluating the extent to which the individuals' isotopic value differentiated from the average profile of the species. We used a continuous autocorrelation function (Pinheiro and Bates 2000) to model the serial correlation of the set of values of the response variables at the individual level. The statistical significance of fixed effects in the mixed models was assessed using Bayesian methods (details in Baayen 2008). Starting from the global model (all fixed effects and their interactions), subsequent models were generated by the stepwise removal of non-significant terms and assessing each simplification with the Akaike information criterion (AIC) using the $\Delta\text{AIC} > 2$ criterion (Bolker 2007). All models considered were subject to the customary residual analyses (Pinheiro and Bates 2000) and were found to have a satisfactory fit (results not shown).

Isotopic niche space use

We characterised the individual use of the isotopic space defined by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using statistical methods developed for home-range analysis (Layman et al. 2007; Sepúlveda et al. 2012). Home ranges are commonly characterised by a set metrics that delimit the zone of its maximum use (minimum convex polygon) or estimate the probability of finding an individual in a given area typically using an adaptive kernel (Worton 1987; Newsome et al. 2012) that minimised the effect of temporal autocorrelation (Fieberg 2007). The percentages of the overall area in the isotopic space used by an individual had a similar interpretation to their common use in home-range analysis. While the 95 % kernel extent denotes the overall area of the isotopic space (resources and foraging areas) used by each individual (or group) over time regardless of frequency of use, the 25 % kernel extent refers to the fraction of the isotopic space that is frequently used and thus likely to be important for a randomly chosen individual. We further characterised the individual- and population-levels patterns of the use of niche space using two metrics. First, we measured the isotopic niche width for each species and sex using the convex hull area calculated as the total area of individual values in the isotopic space encompassed by the minimum convex polygon (Cornwell et al. 2006; Layman et al. 2007). Second, we calculated the individual- and group-levels niches in the isotopic space using the 25 and 95 % kernel density estimates (Sepúlveda et al. 2012) that were employed to estimate their degree of niche overlap at each level. The latter was estimated using the proportion of

each individual (or group) home range (HR) i covered by the home range of another individual (or group) j defined as $HR[i,j] = A[i,j]/A[i]$, where $A[i,j]$ is the area of the intersection between the home ranges of individuals (or group) i and j , and $A[i]$ is the area of the home range of individual (or group) i . We separately compared the magnitude of overlap in the kernel densities at 25 and 95 % between species and sexes using linear mixed models as described above.

We quantified individual specialisation using Bolnick et al.'s (2002) S index (=WIC/TNW) that assesses the proportion of the total niche width (TNW) of a population (or group) that can be attributed to the within individual component (WIC). When the population is made of largely generalist individuals, WIC is a large proportion of TNW (the opposite being true in a population of specialist individuals) (Bolnick et al. 2002). We estimated the WIC as the average of individual kernel densities at 25 and 95 % and the TNW as the total kernel density at the species level. We considered 1–S as the proportion of the TNW explained by variation among the individual niches (WIC) (Bolnick et al. 2003).

All statistical analyses were carried out in R (R Development Core Team 2008) using the `splancs` and `tripack`

libraries (Jombart 2008) to obtain the convex hulls, `adehabitat` (Calenge 2006) for kernel density analysis, `nlme` (Pinheiro et al. 2013) and `lme4` (Bates et al. 2011) for mixed models, and `languageR` (Baayen 2008) to assess the statistical significance of the fixed effects using Bayesian methods.

Results

The average lengths of the whiskers analysed were 132.7 mm (SD = 26.2) and 123.0 mm (SD = 14.3) for SASL and SAFS, respectively. There were significant differences in the mean whisker $\delta^{13}\text{C}$ content between of males and females depending on the species (see interaction sex*species in Table 1). While the average $\delta^{13}\text{C}$ was significantly higher for SAFS females compared with males of the same species, the opposite was true for SASL. Mean $\delta^{15}\text{N}$ values significantly differed between species (but not between sexes), with SASL having higher values than SAFS (Tables 1, 2). For both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, the most parsimonious linear mixed models included a slowly decaying autocorrelation at the individual level of 0.92^γ with γ being the distance in mm between the fragments analysed

Table 1 Linear mixed models for whisker $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value

		Intercept (<i>p</i> value)	Species (SASL) (<i>p</i> value)	Sex (males) (<i>p</i> value)	Species*sex (<i>p</i> value)	AIC	Anova (<i>p</i> value)
$\delta^{13}\text{C}$	Sex*species	−15.30 (0.00)	2.50 (0.00)	0.40 (0.02)	−0.80 (0.002)	361.3	0.002
	Sex + species	−15.16 (0.00)	2.15 (0.00)	−0.01 (0.93)	–	369.0	
	Sex*species (corCAR1)	−15.30 (0.00)	2.53 (0.00)	0.48 (0.01)	−0.94 (0.002)	206.9	<0.0001
$\delta^{15}\text{N}$	Sex*species	17.14 (0.00)	2.84 (0.00)	0.50 (0.18)	−0.58 (0.28)	900.8	
	Sex + species	17.26 (0.00)	2.59 (0.00)	0.25 (0.36)	–	900.0	0.3766
	Species	17.36 (0.00)	2.59 (0.00)	–	–	898.8	<0.0001
	Species (corCAR1)	17.38 (0.00)	2.59 (0.00)	–	–	823.4	<0.0001

Estimates and statistical significance of the fixed factors (sex and species and their interactions) are shown for each variable. The analysis considered the “contrast treatment” option whereby each level of the fixed effects and their interactions was compared with the reference levels: SAFS for species and females for sex. The averages of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (and their standard error) for each combination of Species and sex can be obtained from the fitted coefficients of the fixed effects. The *p* values correspond to the statistical significance of each coefficient of the fixed effects in each model. The AIC are the values of the Akaike information criterion of each model and ANOVA *p* values of the comparison of the deviances between models. The selected models (lowest AIC) for each isotope are in bold and include continuous first order autocorrelation modelled as 0.92^γ , where γ is the distance in mm between consecutive fragments analysed of a whisker

Table 2 Ranges in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, convex hull area and kernel density (25 and 95 %) by groups

Group	$\delta^{13}\text{C}$ (mean, range)	$\delta^{15}\text{N}$ (mean, range)	Convex hull area 95 %	Kernel 25 % area	Kernel 95 % area
SAFS males	−14.9 (−16.6, −13.7)	17.6 (14.3, 20.2)	8.80	0.76	8.44
SAFS females	−15.3 (−16.6, −14.1)	17.2 (14.1, 19.1)	6.80	0.57	7.00
SASL males	−13.2 (−14.8, −12.3)	19.9 (19.1, 21.3)	3.70	0.23	2.54
SASL females	−12.8 (−13.9, −12.2)	20.0 (18.5, 21.6)	3.50	0.56	4.39

SAFS South American fur seal, SASL South American sea lion. Linear model CH-Kernel at 95 %: $y = 0.57 + 0.92^x$ ($p = 0.055$; $R^2 = 0.90$)

of each whisker (Table 1). This decaying function implied that the correlation of isotope readings separated by more than 23 mm (corresponding to four analysed whisker fragments) would not be significantly different from zero (i.e. statistically independent from each other).

SAFS males had the largest niche area in the isotopic space (in units of squared delta isotopic contents) as estimated by the convex hull area (8.8), followed by SAFS females (6.8), SASL males (3.7) and SASL females (3.5) (Fig. 1a). The isotopic niche areas estimated by kernel density had similar ranking, but SASL female areas were

larger than those of SASL males (see Table 2, Fig. 1b). At intraspecific level, 85 % of SAFS females' isotopic niche areas were used by males of the same species, whereas the latter had a more exclusive niche areas that were shared in 75 % by SAFS females (Fig. 1b). In contrast, SASL niche areas had the opposite pattern: 79 % of males' isotopic niche areas were also used by females, and but only 54 % of females' niche areas were used by SASL males (Fig. 1b). At the interspecific level, the individual isotopic niches of females of both species did not overlap whereas those of males only had a small overlap of 16 % for the SASL and 5 % for the SAFL (Fig. 1b). These findings suggest the existence of trophic segregation between species that is similar between sexes (Fig. 1 a, b).

At the individual level, the average isotopic niche areas calculated as 25 and 95 % kernel densities were significantly wider for SAFS than for SASL (25 %: $T = 3.93$, $p = 0.003$; 95%: $T = 4.18$, $p = 0.002$, Fig. 2). In addition, the average overlap between the individual niche areas also calculated as 25 and 95 % kernel densities was significantly higher for SAFS than for SASL (Fig. 2; Table 3). The individual specialisation index (S) was much greater for SAFS than for SASL both at the 25 % (0.963 vs. 0.591) and 95 % kernel densities (0.812 vs. 0.588). These results suggest that the SAFS population was composed by generalist individuals since only between 3.7 and 18.8 % of the TNW could be explained by variation among the individual niches (calculated as $1-S$). In contrast, the SASL population was made of individuals with a medium level of trophic specialisation because 40.9 and 41.2 % of the TNW was due to the differences among individual niches for 25 and 95 % kernel densities, respectively.

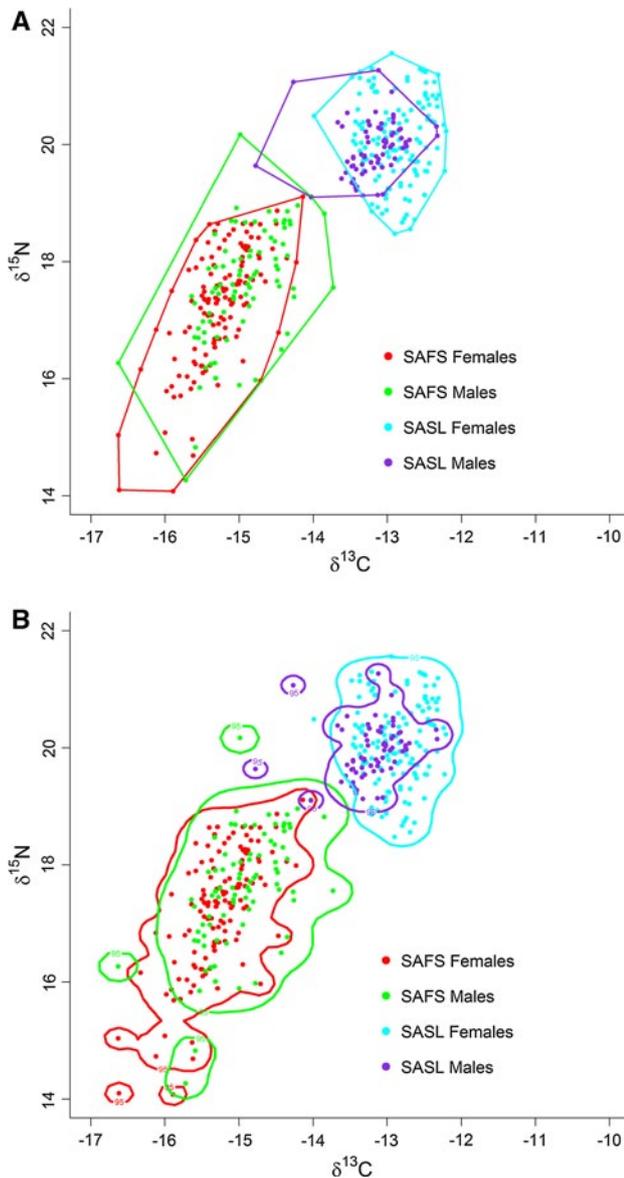


Fig. 1 Isotopic niche area ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) for South American fur seal (SAFS) and South American sea lion (SASL) females and males estimated by **a** convex hull areas and **b** kernel densities at 95 %. Dots represent the isotopic values of successive fragments analysed of a whisker for all individuals of each species and sex

Discussion

We assessed the individual long-term dietary specialisation from two sympatric otariid species using the isotopic ratios in their whiskers (incorporating 2–3 years, see Results). Our results indicate that the isotopic niches of SASL and SAFS have different sizes and that these species have degrees of individual trophic specialisation in the Uruguayan coast. We found that SAFS had a larger trophic niche resulting from generalist individuals, whereas SASL has a smaller niche, and its individuals had a higher degree of trophic specialisation. Characterising individual specialisation and foraging strategies requires having longitudinal data (of isotope profiles, in our case) of the same individual over sufficient length of time. Our sample sizes in terms of individuals may seem limited to some (but they are actually comparable with other studies with otariids: Cherel et al. 2009). However, facing the unavoidable trade-off between having many but more coarsely analysed individual data or

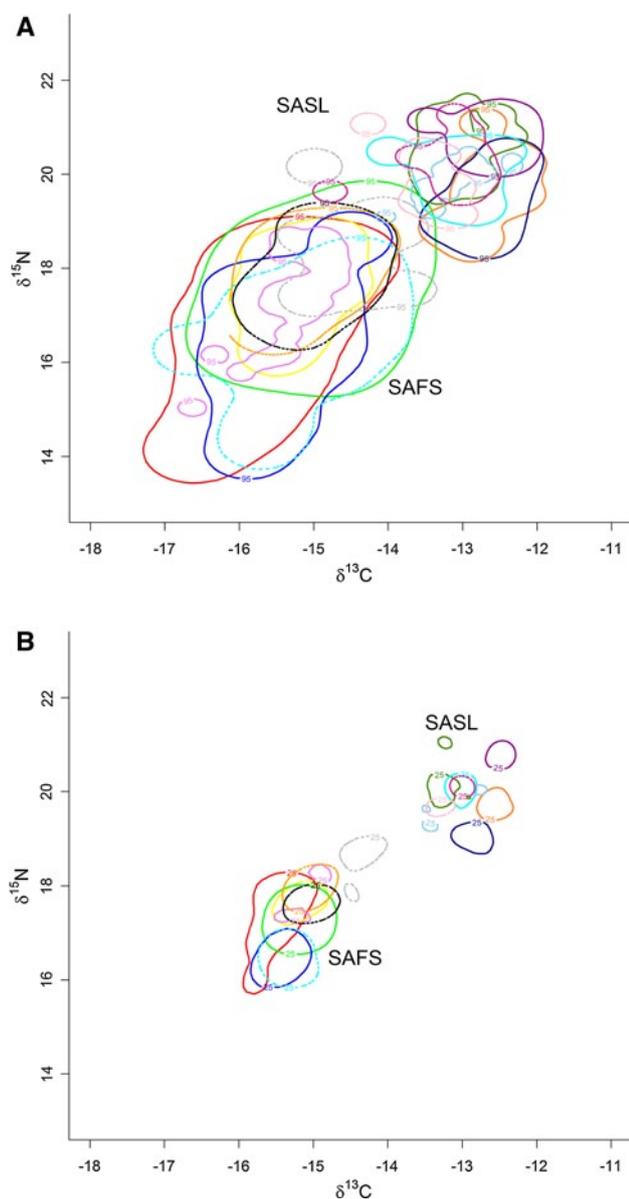


Fig. 2 Individual isotopic niche areas ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) estimated by kernel density for South American fur seal (SAFS) and South American sea lion (SASL) at (a) 95 % and (b) 25 % kernel densities with individuals having different colours

having relatively fewer but more finely analysed isotopic profiles over time, we think that the latter choice may best yield the detailed characterisation of individual profiles over 2–3 years required to test our hypotheses.

Sexual segregation

The existence of overall trophic segregation by sex has already been shown in other species with sexual size dimorphism (Forero et al. 2002; Beck et al. 2007; Cherel et al. 2007; Kernaléguen et al. 2012). Regarding $\delta^{13}\text{C}$, as

Table 3 Linear mixed models for intraspecific overlap between pairs of individual niche areas in the isotopic space estimated by the 25 and 95 % kernel areas

	Intercept (<i>p</i> value MCMC)	Sp (SASL) (<i>p</i> value MCMC)
95 % Kernel overlap model	0.665 (0.00)	−0.165 (0.02)
25 % Kernel overlap model	0.284 (0.00)	−0.141 (0.05)

Estimates are shown with their statistical significance as determined by Markov chain Monte Carlo (MCMC). The analysis considered the “contrast treatment” option showing the average intraspecific overlap of South American fur seals as the Intercept and its average difference with the South American sea lion (SASL) as Sp

it has also been observed in other aquatic environments (France 1995; Newsome et al. 2010b), in Uruguay offshore prey species (deeper waters) have lower $\delta^{13}\text{C}$ value than nearshore (Franco-Trecu et al. 2012). Our results showed that sexual niche segregation more likely occurred in the use of distinct diversity of foraging habitats as reflected by the $\delta^{13}\text{C}$ values and that the differences between sexes in each species varied significantly and in opposite direction along the $\delta^{13}\text{C}$ axis (see significant interaction in Table 1). These results were expected since both SASL and SAFS have sexual dimorphism in body size with males being three times larger than females. Then, differences in $\delta^{13}\text{C}$ contents between sexes may reflect physiological (body mass) or behavioural (parental care) differences. Had males of both species used their higher diving capacity to exploit larger three-dimensional foraging areas, and considering that they are not involved in postnatal care, they could feed farther away from the rookery than females (Campagna et al. 2001) and have exploited wider ranges and more exclusive foraging habitats in $\delta^{13}\text{C}$ (Bearhop et al. 2004).

While SASL males had a lower $\delta^{13}\text{C}$ values than females of the same species, the opposite was true for SAFS. Although the range of $\delta^{13}\text{C}$ was wider for males of both species, we found a large overlapping in the overall areas of isotopic niches between the sexes of both SASL and SAFS (Fig. 1a, b). As reported for other pinniped species (e.g. Weise and Costa 2007), adult females of these species may turn out to have larger mass-specific muscle and total oxygen stores than adult males of similar size. The latter may explain the seemingly surprising result that males, despite not being linked to the colonies, have a similar foraging behaviour than females of California sea lion (*Zalophus californianus*). However, it remains to be explained why the average values of $\delta^{13}\text{C}$ between sexes in these two species differed in opposite directions. We hypothesise that SASL males could be preferentially foraging on more pelagic resources or at more southern areas than SASL females, with the opposite being true for SAFS. In this regard, there have been sightings of SASL males marked

in Mar del Plata, Argentina (38°00'S, 57°33'W) breeding in Isla de Lobos (Giardino et al. 2009) and of SAFS males marked in our study site that were stranded in southern Brazil (VFT unpublished data).

The interpretation of the differences in the isotopic niche areas between sexes may change depending on the method used to quantify them. While niche metrics obtained from convex areas may be influenced by extreme values and thus show biased segregated patterns (Jackson et al. 2011), those based on the kernel density method are more robust and would then be a better representation for the species (or group) use of the isotopic space (Sepúlveda et al. 2012). Contrary to our expectations based on the sexual dimorphism in body size of both species that would allow males to exploit larger preys often at higher trophic levels, the results for $\delta^{15}\text{N}$ showed that both sexes of SASL and SAFS exploited preys at similar trophic levels (Table 1; Fig. 1). In both species, females had wider ranges of $\delta^{15}\text{N}$ (see Table 2) that are associated with a higher consumption of preys at lower trophic levels than males'. The difference in kernel niche area between SASL sexes was related to the wider range of $\delta^{15}\text{N}$ of females (see Table 2). SASL pup physiology imposes restrictions on their mothers (see below) to feed in areas close to the rookery at depth smaller than the diving capacity associated with their large body size (Riet Sapriza et al. 2013) probably consuming preys at lower trophic levels.

Species segregation

We found a strong trophic segregation between species for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Fig. 1). This result confirms that SASL generally consume preys of higher trophic levels in nearshore areas than SAFS (Franco-Trecu et al. 2012). However, the small intraspecific segregation between sexes for $\delta^{13}\text{C}$ led to a small overlap between species on this axis (Fig. 1). The spatial segregation of trophic niches between sympatric species is well known to minimise interspecific competition (Begon et al. 2006). The trophic segregation between SASL and SAFS in the Uruguayan coast implies either the absence or the release from competition of these species. Therefore, the contrasting trends and population abundances between SAFS and SASL would be unrelated to interspecific competition. Another potential cause for the limitation of SASL feeding area is the higher SAFS abundance in the area which would restrict the SAFS to coastal waters, although testing this idea would require an historical approach that the available data in the study area do not allow. In a study conducted at the San Benito Islands, the stable and larger population of the California sea lion (*Zalophus californianus*) share breeding habitat with the less abundant Guadalupe fur seal (*Arctocephalus townsendi*). In this case, the sea lion showed clearly coastal feeding habits

with a large component of fish species in its diet, whereas the fur seal fed mostly on squids (Auriolles-Gamboa and Camacho-Ríos 2007). In another case, the Galapagos sea lion (*Zalophus wolfebaeki*) and Galapagos fur seal (*Arctocephalus galapagoensis*) both have reduced populations and clearly separated feeding grounds and feeding habits (Páez-Rosas et al. 2012). While the case of SAFS and SASL is one in which one species significantly overpasses the other in abundance, it is possible that the density of the SAFS may have some effect on the feeding areas of the SASL. Nevertheless, we think that the patterns we found for SAFS and SASL essentially resemble other cases in which the sea lion feed mostly in coastal waters while the fur seal concentrates its feeding in pelagic waters.

Individual specialisation

There is strong evidence of individual trophic specialisation for many vertebrate species (Bolnick et al. 2003, 2007, 2011) mostly at very short time scales (Woo et al. 2008). In pinnipeds, most evidence is restricted to breeding females that possess fidelity to foraging areas over time (Bona-donna et al. 2001; Chilvers et al. 2005), actively select prey species (Bowen et al. 2002) and have individually distinct diving patterns (Villegas-Amtmann et al. 2008).

The SAFS and SASL had contrasting degrees of individual trophic specialisation. While the SAFS population had a large trophic niche area and was comprised of generalist individuals, SASL has a smaller trophic niche area that was exploited by individuals with a higher degree of individual specialisation. The latter is reflected in the low degree of overlapping between individual niche areas (Fig. 2) and by the index 1–S (proportion of the TNW that could be explained by variation among the individual niches, WIC) for SASL showing that more than 40% of SASL's niche area at the population level corresponded to differentiated niche areas at the individual level. This value of 1–S for SASL lies within the range of values (average = 21 %; range: 0; 62 %) found reported by Bolnick et al.'s (2003) compilation of 79 studies of individual specialisation. The individual-level diversification of the trophic niches here reported for both species concerns a relatively long period of approximately 2–3 years, according to the typical growth rates of pinniped whiskers (Hirons et al. 2001).

Despite of its currently low and declining population size in Uruguay, we believe that SASL's higher degree of individual specialisation may be related to high intraspecific competition. SASL mainly forages in coastal areas that are heavily exploited by both industrial and artisanal fisheries with whom SASL has been shown to have an important degree of spatial overlapping and shared use of fish resources (Riet Sapriza et al. 2013). There have been declining trends in the CPUE for the main fish species in

the Uruguayan coastal areas (Vasconcellos and Haimovici 2006), with the fisheries of many target species being declared overfished (Milessi et al. 2005; Defeo et al. 2009). In a context of resource reduction due to intense competition with coastal fisheries that mainly target whitemouth croaker (*Micropogonias furnieri*, an important prey for SASL (Riet Sapriza et al. 2013), SASL individuals could be forced to diversify their resource use (indicated by $\delta^{15}\text{N}$) and their foraging areas (indicated by $\delta^{13}\text{C}$) so as to minimise the strength of intraspecific interactions (Kobler et al. 2009). However, why did SASL not enlarge its foraging area? While SAFS pups are capable of enduring long periods of fasting (Franco-Trecu 2010), SASL pups can withstand fasting periods of 2 days on average (VFT unpublished data). It is known that infanticide of SASL pups can have an important effect in low-density colonies (Drago et al. 2011), but this behaviour has not been reported for SAFS. The combination of these two features (tolerance to fasting and infanticide) may constrain SASL females to make only short foraging trips and have frequent returns to the rookery; thereby, limiting the extent of their foraging areas (Riet Sapriza et al. 2013). Moreover, the extent and shallowness of the Uruguayan continental shelf (being approximately 200 km with an average depths of 20–30 m) may further constrain the access of SASL females to pelagic resources with higher nutritional value (Drago et al. 2010a) for which they should make longer foraging trips and remain absent for longer periods from the rookery. In contrast, the diets of SASL populations living in areas with narrower and deeper continental shelf are largely comprised of pelagic resources (Hückstädt et al. 2007; Drago et al. 2010b). We believe that the combined influence of behavioural traits and the wide and shallow bathymetry of the Uruguayan continental shelf are key factors shaping the foraging strategies of SASL females. The isotopic specialisation at the individual level in SASL and a major dependence of SASL on resources of the Uruguayan coastal shelf may explain why SASL had a higher trophic individual specialisation, larger vulnerability in a heavily exploited habitat by fisheries and by consequence a declining population trend that is unique in its geographical range. In contrast, the relatively lower individual specialisation found for SAFS would be related with a wider trophic niche at the population level may explain their breeding success and survival rates underlying its observed population trend over the past 17 years (Páez 2000, 2006).

Conclusions

In sum, we have evaluated the trophic segregation of two sympatric otariid species having contrasting population trends. At the interspecific level, the trophic niche overlap

(including both sexes) was rather minimal, which rules out interspecific competition as the cause of the observed population trends of SASL and SAFS in Uruguay. At the intraspecific level, we evaluated the trophic segregation between sexes and individuals. The sexual segregation in the use of foraging areas (indicated by $\delta^{13}\text{C}$) found for both species were opposite for males of SASL and SAFS. This difference probably reflects that capacity or preference of males of each species to exploit different foraging areas. Finally, the species (SAFS) with larger abundance and positive population trend had the largest niche area and showed little individual trophic specialisation, whereas that with smaller abundance and negative population trend (SASL) had the smallest niche area but with a higher individual trophic specialisation. The combined behavioural constraints related to breeding and some key features of the Uruguayan coastal shelf may help explain the contrasting population trends of these sympatric otariid species.

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