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Resource partitioning among air-breathing marine predators: are body size and mouth diameter the major determinants?

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Keywords

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Abstract

Although the body size of consumers may be a determinant factor in structuring food webs, recent evidence indicates that body size may fail to fully explain differences in the resource use patterns of predators in some situations. Here we compared the trophic niche of three sympatric and sexually dimorphic air-breathing marine predators (the South American sea lion, *Otaria flavescens*, the South American fur seal, *Arctocephalus australis*, and the Magellanic penguin, *Spheniscus magellanicus*) in three areas of the Southwestern Atlantic Ocean (Río de la Plata and adjoining areas, Northern Patagonia and Southern Patagonia), in order to assess the importance of body size and mouth diameter in determining resource partitioning. Body weight and palate/bill breadth were used to characterize the morphology of each sex and species, whereas the trophic niche was assessed through the use of stable isotope ratios of carbon and nitrogen. The quantitative method Stable Isotope Bayesian Ellipses in R (SIBER) was used to compute the area of the Bayesian ellipses and the overlap of the isotopic niches. The results showed that morphological similarity was significantly correlated with isotopic distance between groups within the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space in the Río de la Plata area, but not in Northern and Southern Patagonia. Furthermore, resource partitioning between groups changed regionally, and some morphologically distinct groups exhibited a large trophic overlap in certain areas, such as the case of male penguins and male sea lions in Southern Patagonia. Conversely, female sea lions always overlapped with the much larger males of the same species, but never overlapped with the morphologically similar male fur seals. These results indicate that body size and mouth diameter are just two of the factors involved in resource partitioning within the guild of air-breathing predators considered here, and for whom – under certain environmental conditions – other factors are more important than morphology.

Introduction

It has long been acknowledged that the body size of consumers is central to the structure and function of food webs (Elton 1927). This is because it has a strong influence on energy flow, species richness and population densities (Pimm 1982; Hairstone & Hairstone 1993; Elser *et al.* 1996). The size of morphologic structures such as bills or teeth generally scales with body size, and then it has often been used as a morphologic indicator of foraging strategies and the size of the food consumed (Diamond 1973; Grant & Grant 1982; Dayan *et al.* 1990; Karpouzi & Stergiou 2003; Basset & Angelis 2007). Body size also imposes physiologic restrictions on foraging, such as with air-breathing predators for which the interplay of body mass, oxygen stores and metabolic rate determines the duration and depth of their dives (Boyd 1997; Schreer & Kovacs 1997; Kooyman & Ponganis 1998; Watanuki & Burger 1999; Schreer *et al.* 2001; Mori *et al.* 2005; Weise *et al.* 2010).

On these grounds, size-based analysis of food webs assumes that species with a similar body size will have similar diets, and hence the topology of species within the food webs will be largely determined by body size (Jennings 2005). It is in this way that size-based analysis offers a mechanistic, highly reductionist approach that reduces the problem of dealing with thousands of individual trophic links when analysing complex food webs. This explains why size-based analysis of food webs has been used increasingly over the last 25 years to provide generalizations regarding food-web properties (Warren & Lawton 1987; Cohen *et al.* 1993, 2003; Memmott *et al.* 2000; Williams & Martinez 2000; Kerr & Dickie 2001; Leaper & Huxham 2002; Jennings 2005). This approach is certainly a necessary and useful simplification for dealing with a multitude of species whose body masses span several orders of magnitude, from grams (e.g. zooplankton) to kilograms (e.g. fish). However, the relevance of differences in body size may decrease when considering species within the same order of magnitude (e.g. from 1 to 10 kg), a scale in which other factors can be at least as relevant as body size when determining resource use patterns (Layman *et al.* 2005; Akin & Winemiller 2008; Romanuk *et al.* 2011; Madigan *et al.* 2012; Jeglinski *et al.* 2013).

For testing the relative importance of body size and mouth diameter as determinants of feeding habits, a good opportunity can be found in communities of consumers that include sexually dimorphic species with overlapping body sizes. The differences in body size between males and females often result in contrasting diets (Bearhop *et al.* 2006; Drago *et al.* 2009; Weise *et al.* 2010; Silva *et al.* 2014), and related species that differ in body size often have different diets as well (Dellinger & Trillmich

1999; Page *et al.* 2005; Ryan *et al.* 2013; Franco-Trecu *et al.* 2014). In this scenario, it is expected that males and females of sexually dimorphic species will have more similar diets to those of other similar-sized species than to different-sized individuals of their own species. Furthermore, it is also expected that the relationship between morphology and the pattern of resource use partitioning will remain unchanged across time and space, and that differences in body size are the major determinant of resource partitioning.

The Southwestern Atlantic Ocean provides a good location for examining such relationships, for it is here that we can find three co-existing species of sexually dimorphic air-breathing predators: the South American sea lion, *Otaria flavescens*, the South American fur seal, *Arctocephalus australis*, and the Magellanic penguin, *Spheniscus magellanicus* (Vaz-Ferreira 1981, 1982a,b; Scolaro *et al.* 1983; Forero *et al.* 2001). The South American sea lion is one of the largest and most dimorphic otariids (Cappozzo & Perrin 2009), with males being much larger than females (about 350 *versus* 150 kg). The South American fur seal is also dimorphic, with males and females reaching a body mass of 159 and 48.5 kg, respectively (Vaz-Ferreira 1982a). Finally, Magellanic penguins are much less dimorphic, and their body mass is much smaller than the two pinnipeds described above, with females weighing about 3.7 kg and males about 4.5 kg (Scolaro *et al.* 1983; Forero *et al.* 2001). The three species co-exist along 3000 km of coastline, where climatic conditions range from warm temperate in Río de la Plata to cold temperate in Tierra del Fuego. The community of potential prey also varies according to latitudinal changes in productivity, sea temperature and salinity (Cousseau & Perrotta 2000; Miloslavich *et al.* 2011). Body size is known to be an important factor in explaining the intra-specific variability in the diet and foraging tactics of the three species (Drago *et al.* 2009, 2010b; Franco-Trecu *et al.* 2014; Silva *et al.* 2014), but little is known about resource partitioning among species. If the assumptions of a size-based food-web analysis are correct, the trophic relationships within the predator assemblage in the Argentine Sea would be determined solely by body size and mouth diameter. Furthermore, given that the morphology of the three top predators varies only slightly with latitude, their relative position in the food web should remain unmodified along latitudinal gradients.

In this paper we assess the role of body size and mouth diameter in determining resource partitioning among air-breathing predators. To achieve this goal, we measured the distance and the trophic overlap between the isotopic niches of both sexes of the South American sea lion, the South American fur seal and the Magellanic penguin in three areas of the Southwestern Atlantic Ocean. Traditional

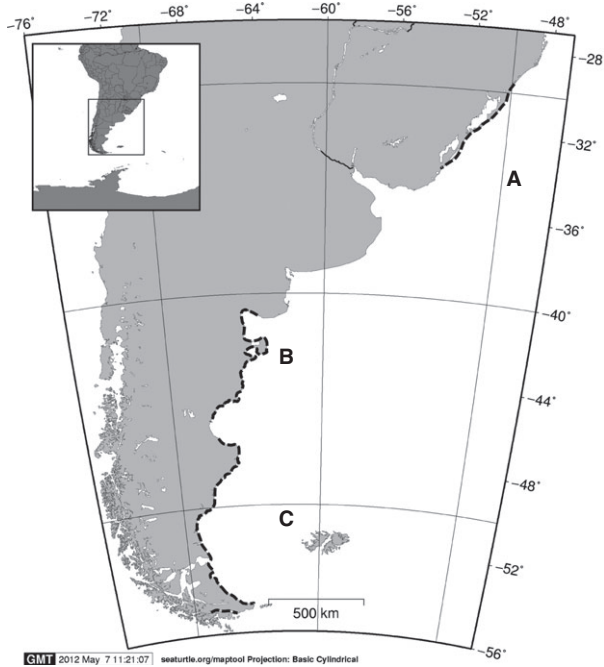


Fig. 1. Study area and zones where sampling was conducted (dashed lines). (A) Río de la Plata area and adjoining areas; (B) northern Patagonia area and (C) southern Patagonia area.

methods for studying resource partitioning among predators are difficult to apply, due to the complexity of the data required and to the impossibility of integrating uneven dietary information (Post 2002; Bearhop *et al.* 2004). Because of this, we analysed the topology of food webs and the trophic niches of single species/groups by using stable isotope data (Bearhop *et al.* 2004; Layman *et al.* 2007; Schmidt *et al.* 2007). Stable isotope data are particularly useful in studying the foraging ecology of marine mammals – and migrating animals in general – because they are a natural tracer of their ingested food and water (Newsome *et al.* 2010). In our case, we applied stable isotope analysis to the study of the trophic organization within a predator community, as this type of analysis provides time-averaged information that incorporates spatio-temporal scales, which are often not considered in traditional studies (Abrantes *et al.* 2014). Moreover, a quantitative method called Stable Isotope Bayesian Ellipses in R (SIBER) has been employed to directly compare isotopic niches across different communities (Jackson *et al.* 2011).

Material and Methods

Sampling

The study area included the southeast coast of South America, from ~29°S to 55°S (Fig. 1). The area has been

divided into the following three sub-areas, according to their oceanographic and biogeographic characteristics (Cousseau & Perrotta 2000; Piola & Falabella 2009): Río de la Plata and adjoining areas (from Southern Brazil to Buenos Aires province, Argentina), Northern Patagonia (Río Negro and Chubut provinces, Argentina) and the Southern Patagonia area (Santa Cruz and Tierra del Fuego provinces, Argentina).

Samples of the maxillo-turbinal bones were collected for both sexes of adult sea lions and fur seals, corresponding to the periods 1988–2010 and 1978–2011, respectively. These came from specimens preserved in the scientific collections of the Museo Acatushún (Ushuaia, Argentina), the Centro Nacional Patagónico (Puerto Madryn, Argentina) and the Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul (Imbé, Brazil). As the dispersal movements of adult sea lions are limited among the three above-mentioned sub-areas (Zenteno *et al.* 2013), stable isotope ratios in bone are expected to integrate the regional diet over a period of ~5 years (Riofrío-Lazo & Auriolles-Gamboa 2013). Magellanic penguins are very distinct from these two species in that they are migratory (Pütz *et al.* 2000, 2007), and their bones will integrate a diet from different regions (Silva *et al.* 2014). For this reason, the tissue selected for the analysis was feather vane from adult males and females found dead at breeding colonies located in Northern and Southern Patagonia. Penguins go through a simultaneous molt, replacing all feathers at the end of the reproductive period (Frere *et al.* 1996); so the isotopic signature of the feather vane informs us about where the feather grew (Hobson 2005). This would be the breeding ground, which is the same every year (Schiavini *et al.* 2005). As there are no penguin breeding colonies in Río de la Plata, we used the claws from both sexes of stranded juvenile penguins found in Southern Brazil because samples from adults were not available. These samples were collected from specimens preserved in the scientific collections of the Centro de Estudos Costeiros, Limnológicos e Marinheiros (Imbé, Brazil). According to claw growth rates (Barquete *et al.* 2013) and the time of collection, the central part of the claw is likely to have formed when the penguins were off the Río de la Plata coast and the basal part when they were off the Southern Brazilian coast. We therefore analysed both sections to assess penguin foraging in the two areas during the winter months. All penguin samples were collected during fieldwork from 2009 to 2011, with the corresponding permissions granted by conservation agencies pertaining to the provinces of Río Negro, Chubut and Santa Cruz in Argentina, and to Rio Grande do Sul in Brazil. No manipulation of living animals was involved in the collection of samples, as all of them came from adults or juveniles found dead at either

the breeding colonies or the migratory grounds. All samples were stored in a freezer at $-20\text{ }^{\circ}\text{C}$ until analysis.

Stable isotope analysis

Bone samples were thawed, dried in an oven at $60\text{ }^{\circ}\text{C}$ for 36–48 h and ground to a fine powder with a mortar and pestle. Lipids were extracted from samples with a chloroform-methanol (2:1) solution (Bligh & Dyer 1959). This is because lipids are depleted in ^{13}C compared with other molecules (DeNiro & Epstein 1977), and lipid concentration in tissues may vary between and within species. As bone samples contain high concentrations of inorganic carbon, which may cause undesirable variability in $\delta^{13}\text{C}$ (Lorrain *et al.* 2003), they were divided into two aliquots. The first was decarbonized by soaking it in 0.5 M hydrochloric acid (HCl) until no more CO_2 was released (Newsome *et al.* 2006). As HCl treatment adversely affects $\delta^{15}\text{N}$ (Bunn *et al.* 1995), the other untreated aliquot was used for $\delta^{15}\text{N}$ analyses. Feathers and claws were washed in a chloroform-methanol (2:1) solution, rinsed thoroughly in distilled water to remove external contamination and dried in an oven at $60\text{ }^{\circ}\text{C}$. The tips (distal part) of the feathers were then cut as finely as possible to allow for precise weighing, while 2-mm-long sections of the claws were sampled from the base and center of the claw. To avoid mixing the older external keratin and the recently deposited inner keratin, samples were collected from along the lateral ridge of the claw.

After this preparation, $\sim 0.7\text{--}1\text{ mg}$ of dried bone, $0.3\text{--}0.35\text{ mg}$ of feathers and $0.23\text{--}0.33\text{ mg}$ of claws were weighed into tin cups ($3.3 \times 5.0\text{ mm}$), combusted at $900\text{ }^{\circ}\text{C}$, and analysed in a continuous-flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA Thermo Finnigan). Stable isotope abundance is expressed in standard δ -notation in [‰] relative to carbonate Pee Dee Belemnite and atmospheric nitrogen. Analyses were performed at the Science and Technology Centres (CCiT) of the University of Barcelona.

Morphologic measurements

Mouth gap was assessed in fur seals and sea lions by measuring palate breadth between postcanines 3 and 4 (see Brunner 2002), and base bill breadth in penguins. Sample size was 20 for each species (10 males and 10 females), except for female fur seals ($n = 7$). Only adults were included (Table 1). Measurements were carried out on skulls from the scientific collections at the Centro Nacional Patagónico (Puerto Madryn, Argentina). Body mass for each species was obtained from the following sources: Bonner (1981), Vaz-Ferreira (1981), Lima & Páez (1995) and Yorio *et al.* (2001).

Data analysis

Due to the differential discrimination that occurs among different tissues in animals, stable isotope values of

Table 1. Sample size and stable isotope ratios of South American fur seals, South American sea lions and Magellanic penguins in the three study areas.

scientific name	tissue	n	$\delta^{15}\text{N}$ (‰) mean (\pm SD)	$\delta^{13}\text{C}$ (‰) mean (\pm SD)
Río de la Plata				
<i>Arctocephalus australis</i> ♀ (Brazil)	Bone	5	18.8 (\pm 1.0)	-13.6 (\pm 0.5)
<i>Arctocephalus australis</i> ♂ (Brazil)	Bone	54	20.6 (\pm 0.6)	-13.6 (\pm 0.8)
<i>Otaria flavescens</i> ♀ (Brazil)	Bone	4	20.4 (\pm 0.3)	-12.0 (\pm 0.3)
<i>Otaria flavescens</i> ♂ (Brazil)	Bone	15	20.7 (\pm 0.5)	-11.9 (\pm 0.7)
<i>Spheniscus magellanicus</i> ♀ (Argentina and Brazil)	Claw	18	15.1 (\pm 1.8)	-16.8 (\pm 0.8)
<i>Spheniscus magellanicus</i> ♂ (Argentina and Brazil)	Claw	20	14.7 (\pm 1.5)	-16.9 (\pm 0.9)
Northern Patagonia				
<i>Arctocephalus australis</i> ♂	Bone	28	20.6 (\pm 1.0)	-13.4 (\pm 0.5)
<i>Otaria flavescens</i> ♀	Bone	11	22.3 (\pm 0.5)	-12.3 (\pm 0.6)
<i>Otaria flavescens</i> ♂	Bone	14	22.2 (\pm 1.0)	-11.9 (\pm 0.6)
<i>Spheniscus magellanicus</i> ♀	Feather	10	19.2 (\pm 1.4)	-16.5 (\pm 0.7)
<i>Spheniscus magellanicus</i> ♂	Feather	7	18.8 (\pm 2.4)	-16.2 (\pm 1.0)
Southern Patagonia				
<i>Arctocephalus australis</i> ♂	Bone	6	19.0 (\pm 1.6)	-13.2 (\pm 0.7)
<i>Otaria flavescens</i> ♀	Bone	10	20.9 (\pm 1.0)	-12.3 (\pm 0.7)
<i>Otaria flavescens</i> ♂	Bone	31	20.7 (\pm 1.2)	-13.1 (\pm 1.1)
<i>Spheniscus magellanicus</i> ♀	Feather	20	18.7 (\pm 1.2)	-16.9 (\pm 0.8)
<i>Spheniscus magellanicus</i> ♂	Feather	18	18.7 (\pm 1.6)	-16.8 (\pm 1.6)

Table 2. Fractionation factors used in this study.

Species	tissue-to-diet		
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	source
<i>Arctocephalus australis</i> (bone)	3.6	5.1	Vales <i>et al.</i> (2014)
<i>Otaria flavescens</i> (bone)	3.5	4.4	Zenteno <i>et al.</i> (2015)
<i>Spheniscus magellanicus</i> (claws)	0.1	3.95	adapted from Cherel <i>et al.</i> (2005)
<i>Spheniscus magellanicus</i> (feathers)	0.1	3.95	adapted from Cherel <i>et al.</i> (2005)

carbon and nitrogen are not directly comparable among bone, claw and feathers (Todd *et al.* 2009). For this reason the rough stable isotope values of both nitrogen and carbon were converted into those expected for muscle using correction factors (Table 2). As discrimination factors from diet to consumer (or *vice versa*) have not been experimentally determined for any of our species and tissues, they were indirectly calculated for pinniped bones (see Vales *et al.* 2014 and Zenteno *et al.* 2015 for details) and, in the case of Magellanic penguins, they were calculated from the values of King and Rockhopper penguin feathers (Cherel *et al.* 2005). As detailed data about discrimination factors in claws are not available, the feather discrimination factor was used instead, as both of them are keratinous tissues.

Six groups (species \times sex) were considered for analysis in Río de la Plata, but only five in Northern and Southern Patagonia, due to the scarcity of suitable skeletal material from female fur seals in those areas. Once the data had been transformed into comparable units, niche similarity was assessed by computing the Euclidean distance between the centroids of groups in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space, whereas morphologic similarity was assessed by computing the Euclidean distance between groups within the morphospace as defined by body size and palate/bill breadth. Niche and morphologic similarities were compared in each area using the Mantel test. We also applied the Bayesian method SIBER (Jackson *et al.* 2011) to compute Layman's metrics (Layman *et al.* 2007). The $\delta^{15}\text{N}$ range (NR), $\delta^{13}\text{C}$ range (CR) and the mean distance to centroid (CD) are measures of the spacing within the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ space. NR is the representation of the vertical amplitude of the isotopic niches, whereas CR gives an idea of the trophic diversity of resources used by predators. CD supplies an indirect measure of the trophic diversity within the top predator community. Mean nearest-neighbor distance (MNND) and the standard deviation of nearest-neighbor distance (SDNND) give a quantitative measure of the relative position between groups within the niche space, and they are used to estimate the extent of trophic redundancy (Layman *et al.* 2007; Jackson *et al.* 2011). Metrics were considered to be different from one area to another if the mean ($\pm 95\%$ credible interval) was different. Finally, SIBER allowed us to calculate both the

area of the frequentist standard ellipses for small sample sizes (SEA_C) and the Bayesian estimate of the standard ellipse and its area (SEA_B). The latter is a metric that, unlike the minimum convex polygon area, makes it possible to compare uneven or small samples, to reduce the error in calculating the isotopic niche by using the ellipses and to preserve the uncertainty of the sampling process. All of these together propagate the error across the measures. The overlap between predators' SEA_C in the three areas was also calculated. All codes for SIBER analyses are contained in the package SIAR (Parnell *et al.* 2010; Parnell & Jackson 2013).

Results

Body mass and the palate/bill breadth of the three top predators were positively correlated, females being lighter

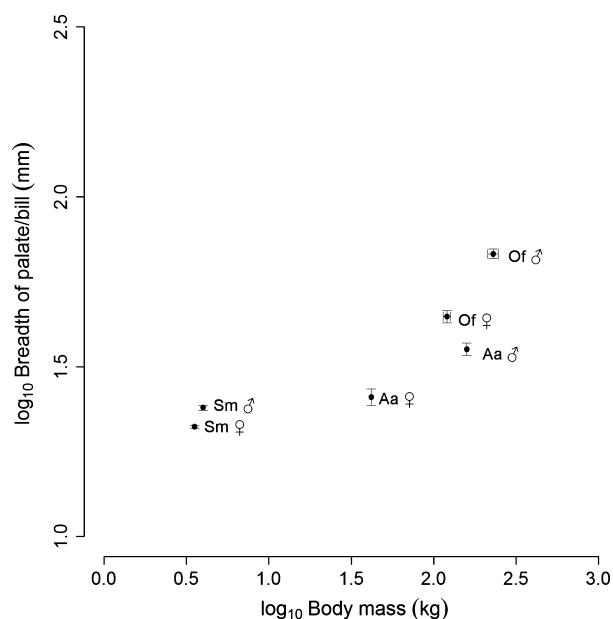


Fig. 2. Plot of the relationship between body mass and breadth of palate/bill in the three top predators split by species and sex: males and females of Magellanic penguin ($\text{Sm}\sigma$ and $\text{Sm}\varphi$), males and females of fur seal ($\text{Aa}\sigma$ and $\text{Aa}\varphi$) and males and females of sea lion ($\text{Of}\sigma$ and $\text{Of}\varphi$). The means and standard deviations (when present) of body mass for each group were obtained from Bonner 1981; Vaz-Ferreira 1981; Lima & Páez 1995; Yorio *et al.* 2001.

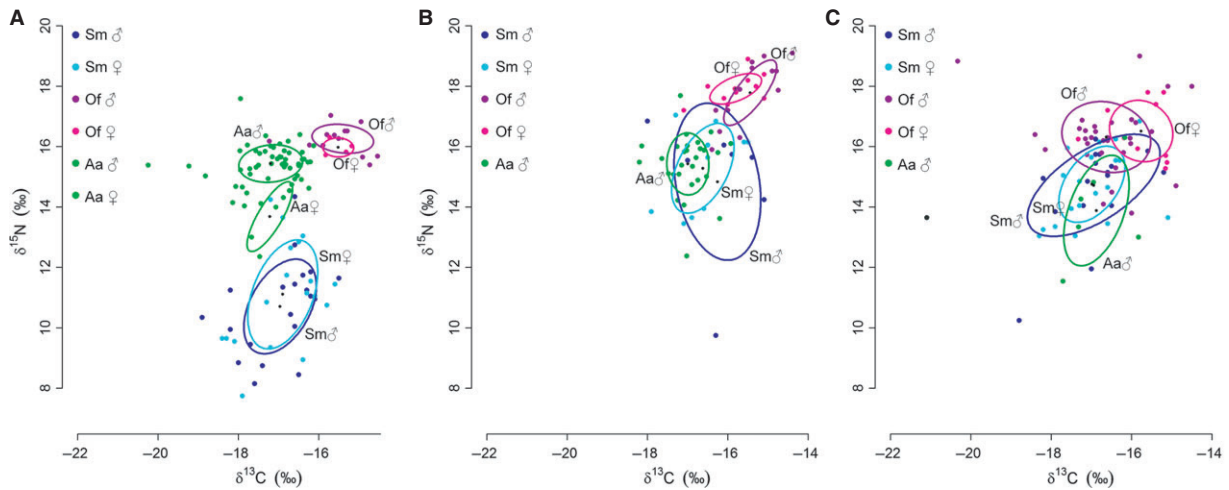


Fig. 3. Isotopic niches of the species described in the text calculated as standard ellipses area corrected for small samples (SEAC). (A) Río de la Plata area; (B) northern Patagonia area; (C) southern Patagonia area. Aa = *Arctocephalus australis*; Of = *Otaria flavescens*; Sm = *Spheniscus magellanicus*.

and with a narrower mouth gape than males for each species (Fig. 2). However, the topology of the same top predators within the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space differed from the morphology-based expectations in two of the three considered regions (Fig. 3). Indeed, morphological similarity and niche similarity were positively correlated only in Río de la Plata (Mantel test $r^2 = 0.679$, $P = 0.025$; Fig. 5). Nevertheless, the niche similarity between female and male sea lions was higher than predicted by morphology. Conversely, the niche similarity between female sea lions and penguins of either sex was lower than that predicted by morphology (Fig. 5). As a consequence of the morphologic prediction, the overlap between the isotopic niches of air-breathing predators inhabiting Río de la Plata (as represented by the standard ellipses in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space) was usually low, with the exception of the two sexes in the penguin and sea lion groups (Table 3, Fig. 3A). A broad overlap was observed between the morphologically dissimilar male and female sea lions, while there was an absence of overlap between the morphologically similar male fur seals and female sea lions.

Morphologic similarity and niche similarity were uncorrelated in Northern Patagonia (Mantel test $P = 0.239$) because the distinct male penguins and male fur seals overlapped in their isotopic niches (Table 3). In fact, the ellipse of male penguins almost completely encompassed that of male fur seals (86.61%), while only 17.05% of the male penguins’ ellipse overlapped with that of male fur seals. As in Río de la Plata, the isotopic niche of female sea lions overlapped with that of male sea lions, but not with that of the morphologically similar male fur seals (Table 3 and Fig. 3). Morphologic similarity and niche similarity were also uncorrelated in Southern Patagonia

Table 3. Overlap as a percentage of standard ellipses corrected for small samples of the three top predators described in the text. The table should be read horizontally, as each number in the cell refers to the percentage of overlap of the area of the group indicated in the row (e.g. 77.97% is the percentage of the ellipses of female sea lions that overlap with the males of the same species, while 26.13% is the percentage of the ellipses of male sea lions that overlap with the females of the same species in Río de la Plata).

	Aa		Of		Sm	
	♀	♂	♀	♂	♀	♂
Río de la Plata						
Aa	♀	1	0	0	0	0
	♂	0	1	0	0	0
Of	♀	0	0	1	77.97	0
	♂	0	0	26.13	1	0
Sm	♀	0	0	0	0	1
	♂	89.69	0	0	0	1
Northern Patagonia						
Aa	♀					
	♂		1	0	0	73.01
Of	♀		0	1	46.36	0
	♂		0	28.22	1	7.12
Sm	♀		38.64	0	0	1
	♂		17.05	0	1.16	35.64
Southern Patagonia						
Aa	♀					
	♂		1	0	8.96	47.71
Of	♀		0	1	53.11	0
	♂		9.15	32.88	1	18.29
Sm	♀		67.46	0	25.34	1
	♂		39.09	11.68	24.09	42.12

Aa, *Arctocephalus australis*; Of, *Otaria flavescens*; Sm, *Spheniscus magellanicus*.

Table 4. SIBER ellipse corrected areas of the three air-breathing top-predators in the three study areas.

Study areas	♀ Aa	♂ Aa	♀ Of	♂ Of	♀ Sm	♂ Sm
Río de la Plata	2.70 (0.84–5.22)	1.62 (1.21–2.07)	1.96 (0.54–4.06)	1.49 (0.81–2.29)	4.52 (2.63–6.74)	4.05 (2.44–5.95)
Northern Patagonia	–	1.87 (1.22–2.59)	1.45 (0.72–2.35)	2.01 (1.07–3.13)	3.50 (1.66–5.73)	7.42 (2.92–13.10)
Southern Patagonia	–	4.37 (1.58–8.06)	2.71 (1.29–4.49)	4.01 (2.70–5.46)	3.06 (1.83–4.47)	6.70 (3.91–9.94)

SIBER, Stable Isotope Bayesian Ellipses in R; Aa, *Arctocephalus australis*; Of, *Otaria flavescens*; Sm, *Spheniscus magellanicus*.

(Mantel test $P = 0.361$), again because the isotopic niches of morphologically dissimilar species overlapped. This was the case for male sea lions and the two sexes of the Magellanic penguin; for male fur seals and the two sexes of the Magellanic penguin; and for female sea lions and male penguins (Table 3). As in the other areas, the sexes of the penguin and those of the sea lion overlapped widely, whereas morphologically similar male fur seals and female sea lions did not overlap.

Finally, Layman’s metrics indicate that the guild of air-breathing predators used a broader diversity of trophic resources in Río de la Plata than in Northern and Southern Patagonia, as the NR and the CD were significantly larger in the former (Figs 3 and 4). However, the metrics of the CR and the trophic redundancy (MNND and SDNND) did not differ between regions (Fig. 4).

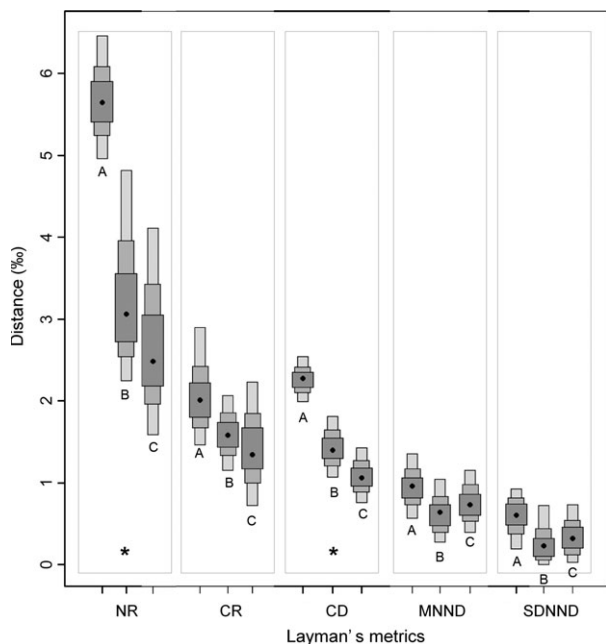


Fig. 4. Probability values of Layman’s metrics in the three study areas: (A) Rio de la Plata area; (B) northern Patagonia area and (C) southern Patagonia area. The asterisks point out significant differences between regions. NR = $\delta^{15}\text{N}$ range; CR = $\delta^{13}\text{C}$ range; CD = mean distance to centroid; MNND = mean nearest neighbour distance; SDNND = standard deviation of nearest neighbour distance.

Discussion

The results reported here indicate that differences in mouth diameter and body size accurately describe resource partitioning among sea lions, fur seals and penguins in some areas of the Southwestern Atlantic (Río de la Plata), but not in others (Northern and Southern Patagonia). This conclusion is based on three different pieces of evidence. Firstly, the distance between predators within the morphospace is correlated with the distance in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space in Río de la Plata (Fig. 5), but not in Northern and Southern Patagonia. Secondly, morphologically dissimilar predators such as male sea lions and male penguins broadly overlap in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space in some regions, whereas morphologically similar predators such as female sea lions and male fur seals never overlap in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space. Thirdly, the topology of the predators within the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space varies regionally, with a positive relationship between overlap and latitude (Table 3 and Fig. 3).

The use of stable isotopes and associated quantitative methods to study the topology of an assemblage of predators within a food web certainly helps us to overcome

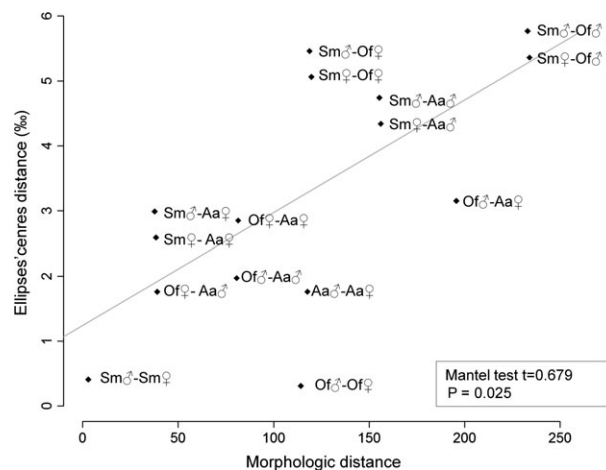


Fig. 5. Correlation in the Rio de la Plata region between morphological distance and trophic distance, calculated as the distance between pairwise centroids in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space. Aa = *Arctocephalus australis*; Of = *Otaria flavescens*; Sm = *Spheniscus magellanicus*. Mantel’s test results are indicated in the box.

some of the complexity of the data required in modeling, as well as the limitations and biases of traditional methods, which are based on stomach content and scat analysis (Post 2002; Bearhop *et al.* 2004). However, methods based on stable isotope ratios are not free from errors and biases. Here, different tissues were analysed to obtain dietary information at comparable regional scales, but data had to be corrected prior to any comparison in order to account for tissue-specific discrimination factors. Although this procedure is conceptually correct, it leads to the introduction of a new source of variability and cannot account for tissue-specific differences in the time span that covers the integration of the stable isotope ratios, which can take several weeks for feathers and years for bone. Another source of potential error is represented by the use of penguins of different age classes, as they may differ in diet. Finally, the use of samples collected over several years might add some variability, although recent analyses have shown that the diets of sea lions and fur seals did not vary during the period considered here (Vales *et al.* 2014; Zenteno *et al.* 2015). All these uncertainties may prevent accurate reconstruction of the diets of the species considered here; however, they do not compromise the conclusion that the topology of the predators within the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space varies regionally and is often independent of the morphology.

According to the optimal foraging theory, predators should maximize their energy intake for the time unit spent foraging (Stephens & Krebs 1986). With pinnipeds this is often achieved by selecting the largest available prey (MacLeod *et al.* 2006). Although detailed studies on pinnipeds and penguins are lacking, the optimal prey diameter for fish is 40–70% of the predator's mouth diameter (Wainwright & Barton 1995). Accordingly, we would expect that the gradient in mouth size would correlate with that of prey size, and therefore male sea lions would consume the largest prey, followed in order by female sea lions, male fur seals, female fur seals and ending with Magellanic penguins of both sexes (Fig. 2). This expectation is true in Río de la Plata, where published dietary information indicates that sea lions consume larger prey than fur seals, which in turn consume larger prey than penguins (Naya *et al.* 2000, 2002; Fonseca *et al.* 2001; Szteren *et al.* 2004; Pinto *et al.* 2007; Franco-Trecu *et al.* 2012, 2014; Vales *et al.* 2014). The results reported here do not provide a direct test of this hypothesis, as they do not incorporate information about prey size. However, the agreement between the distribution of the predator assemblage within the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space and that in the morphospace indicates that body size and mouth diameter are probably the major determinants of the diet of the three species in Río de la Plata. Furthermore, the dietary differences between female sea lions

and male fur seals of similar body size can also be explained by the narrower palate of the latter, which may restrict the consumption of deep-bodied demersal species enriched in ^{15}N (Botto *et al.* 2011; Vales *et al.* 2014). However, morphology cannot explain the dietary overlap between male and female sea lions, thus indicating that factors other than body size are also relevant, as previously reported for other pinniped species (Jeglinski *et al.* 2013).

The matching between morphology and trophic niche vanishes definitively in Northern and Southern Patagonia, where the distance between penguins and sea lions in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space is strongly reduced, despite significant differences in body size and mouth diameter. Furthermore, the isotopic niche of male fur seals in Northern Patagonia is totally encompassed by that of male penguins (Fig. 3B), whereas the niche of male sea lions in Southern Patagonia largely overlaps that of male penguins (Fig. 3C). Penguins forage on small pelagic fishes and squids in Northern and Southern Patagonia (Scolaro *et al.* 1999; Forero *et al.* 2002; Wilson *et al.* 2005). Hence, the reduced distance between the penguins' ellipses to those of male fur seals and male sea lions suggests that pinnipeds consume more pelagic prey at higher latitudes. This interpretation is supported by analyses of sea lion scat and stomach contents in Río de la Plata and Northern Patagonia (Koen *et al.* 2000; Suarez *et al.* 2005). Unfortunately, there is no published information about the diets of fur seals in Northern Patagonia or sea lions in Southern Patagonia. In any case, after comparing Northern and Southern Patagonia with Río de la Plata, SIBER confirmed a reduction in the range of resources used by the predator assemblage. This may explain the increasing overlap between species at higher latitudes and the consequent departure from predictions based on morphology. Similarly, a very high overlap had previously been reported for the isotopic niches of several seabirds foraging off Northern Patagonia, despite large differences in body size (Forero *et al.* 2004).

The poleward decrease in diversity that is characteristic of the Patagonian shelf (Cousseau & Perrotta 2000; Miloslavich *et al.* 2011) may explain this pattern. For instance, deep-bodied sciaenids are a common prey of sea lions in Río de la Plata (Riet-Sapriza *et al.* 2013; Zenteno *et al.* 2015), but they are present only up to the northernmost part of Patagonia (Cousseau & Perrotta 2000; Balech & Ehrlich 2008). Likewise, small, streamlined anchovies (*Engraulis anchoita*) abound in Río de la Plata and Northern Patagonia, where they are distributed all over the continental shelf, and they are an important prey for penguins and fur seals (Scolaro *et al.* 1999; Naya *et al.* 2002). However, anchovies are replaced in Southern Patagonia by the Patagonian sprat (*Sprattus fuegensis*), a

much scarcer species that occurs only along the coast (Cousseau & Perrotta 2000). There is no dietary information about sea lions and fur seals in Southern Patagonia, but in the nearby Falkland Islands (Malvinas), the diets of most air-breathing predators converge on lobster krill, *Munida gregaria* (Thompson *et al.* 1998; Pütz *et al.* 2001; Laptikhovsky 2009). This is also an important prey for fur seals in Southern Chile (Hernández 2012), despite its low energy density (Ciancio *et al.* 2007). Lobster krill is very abundant in the waters of the Southwestern Atlantic (Tappella *et al.* 2002; Clausen *et al.* 2005; Romero *et al.* 2006; Vinuesa & Varisco 2007), where it forms large swarms (Vinuesa & Varisco 2007). Thus, a low diversity of potential prey and the high abundance of lobster krill may explain why morphologically dissimilar predators converge on similar diets in Southern Patagonia. It should be noted, however, that the intensive exploitation of fish, seal and whale populations has dramatically changed the structure of marine ecosystems worldwide (Caddy 1998; Pauly *et al.* 1998; Devine *et al.* 2006) and, hence, the results reported here may not reveal the natural partitioning of resources among the considered species (Saporiti *et al.* 2014).

The reproductive behavior of the three considered species may also explain why the isotopic overlap increases poleward. All three species breed on land and behave as central place foragers during the breeding season, although male sea lions and male fur seals fast at that time (Riedman 1990; Boness 2002; Schiavini *et al.* 2005). Previous research has suggested that breeding imposes serious constraints on the foraging behavior of penguins and sea lions (Drago *et al.* 2010a; Silva *et al.* 2014), but penguins do not breed in Río de la Plata and hence their diet in that area is not influenced by the need to feed their chicks with high-quality food. For penguins from Northern and Southern Patagonia, the stable isotope of feathers reflects only the diet during the final part of the breeding period. This may explain why the ellipses of penguins overlap those of sea lions and fur seals with increasing proportions in those places where the breeding colonies of the three species co-exist.

In conclusion, resource partitioning among the three air-breathing predators considered here varies regionally. Furthermore, body size and mouth diameter successfully predict this partitioning in Río de la Plata but not in other areas. Accordingly, caution is needed when using body size as a proxy for trophic level or ecologic role, as well as when extrapolating patterns of resource partitioning, even if the same species are considered.

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