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Intensive fishing has not forced dietary change in the South American fur seal Arctophoca (=Arctocephalus) australis off Río de la Plata and adjoining areas

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ABSTRACT

1. South American fur seals (*Arctophoca australis*) inhabiting the Río de la Plata plume and adjoining areas are known to forage upon a wide range of prey (i.e. pelagic, demersal and benthic species).

2. Since the 1960s, trawlers have operated in the area, targeting primarily demersal and benthic species. Carbon and nitrogen stable isotope ratios from 54 adult male fur seals dead stranded along the coast of southern Brazil from 1994 to 2011 were analysed to investigate whether the intensification of fishing in Río de la Plata and adjoining areas since the mid-1990s has reduced the availability of benthic and demersal prey to the growing population of South American fur seals.

3. No significant correlation between δ^{13} C or δ^{15} N values and stranding year was found, thus revealing that fur seals maintained a steady diet over 17 years.

4. Reconstruction of the isotopic landscape of the study area using potential prey of fur seals showed a spatial segregation, with prey from southern Brazil typically enriched in ¹³C and depleted in ¹⁵N compared with those from northern Argentina. Most adult male fur seals relied mainly on small pelagic fishes and squid captured on the continental shelf, whereas medium pelagic and demersal–benthic prey played a minor role in the diet.

5. It is concluded that South American fur seals rely on pelagic resources (i.e. small pelagic fish and squid) more strongly than previously thought and that their diet does not reflect the varying abundance of demersal–benthic resources in the area.

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6. As long as small pelagic fish remain under-exploited in the area, competition between fisheries and fur seals is not expected. However, it is difficult to foresee how changes in the structure and dynamics of the ecosystem caused by fisheries may affect South American fur seal conservation in the long term. Copyright © 2013 John Wiley & Sons, Ltd.

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INTRODUCTION

Fisheries have dramatically modified the structure and dynamics of most marine ecosystems around the globe not only because they have removed a large biomass of target and non-target species, but also as a result of physical impact produced by bottom trawling, the increased rates of nutrient turnover caused by discarded fish and organic detritus, and persistent mortality caused by lost gears (Goñi, 1998; Pauly et al., 1998; Halpern et al., 2008). Marine megafauna is particularly vulnerable to these changes and the decline of stocks of large fishes, sea turtles and marine mammals are a worldwide feature (Jackson et al., 2001; Myers and Worm, 2003; Lewison et al., 2004; Trites et al., 2006). Nevertheless, populations of some eared seals (Otariidae), one of the major components of the biota of the eastern Pacific, the southern Atlantic and the Southern Ocean, are currently increasing after having been pushed to the brink of extinction by decades of severe exploitation (Kovacs et al., 2012).

The South American fur seal, *Arctophoca australis* (synonymy *Arctocephalus australis*) breeds from Peru to Uruguay and was intensely exploited across its whole range until recently (Vaz-Ferreira, 1982; Arnould, 2008). By the late 1940s, the population in Uruguay was at its lowest levels (Vaz-Ferreira, 1950; Lima, 1998). Since then the population has increased steadily, although commercial sealing continued until 1991 (Vaz-Ferreira, 1982). At present, the largest world rookeries are found in Uruguay (Naya *et al.*, 2002) and due to its large and increasing population size the species is classified as Least Concern on the IUCN Red List (IUCN, 2012).

The continental shelf along the south-western Atlantic is influenced by the encounter of the Brazil current (southern-flowing, oligotrophic, warm and high salinity tropical waters) with the Malvinas/Falkland current (northward-flowing, nutrient-rich, cold and low salinity sub-Antarctic waters) and the freshwater runoff from Río de la Plata and Lagoa dos Patos (Longhurst, 1998; Möller *et al.*, 2008). Hence, the whole area is characterized by high primary productivity (Garcia and Garcia, 2008) that supports several populations of high trophic level predators and large fisheries (Haimovici *et al.*, 1998).

The foraging grounds of the South American fur seals that breed in the Uruguayan rookeries span from central Argentina to southern Brazil (Pinedo, 1986, 1998; Dassis et al., 2012). Although they are trophic generalists with the potential to prey upon several species, a few species dominate their diet (Naya et al., 2002). Scat and stomach content analyses have revealed that the major prey consumed in the areas influenced by the Río de la Plata plume are striped weakfish (Cynoscion guatucupa), anchovies (Anchoa marinii and Engraulis anchoita), cutlass fish (Trichiurus lepturus) and squids (e.g. Loligo sanpaulensis), with Argentine hake (Merluccius hubbsi), rough scad (Trachurus lathami), white (Micropogonias furnieri), croaker southern kingcroaker (Menticirrhus americanus), Argentine croaker (Umbrina canosai), Brazilian codling (Urophycis brasiliensis) and Argentine seabass (Acanthistius brasilianus) as secondary species (Nava et al., 2002; Szteren et al., 2004; Oliveira et al., 2008a). More recently, a study based on stable isotope ratios (δ^{13} C and δ^{15} N) in serum and skin of pups from Isla de Lobos (Uruguay) concluded that breeding females exploit mainly pelagic resources, probably anchovies and squid (Franco-Trecu et al., 2012). Nevertheless, diet seems to vary strongly between years probably following changes in prey availability (Naya *et al.*, 2002).

Fishing exploitation of small pelagic fish and squid is poorly developed in southern Brazil (Haimovici et al., 1998; Santos and Haimovici, 2000; Gasalla et al., 2005) and anchovies (Engraulis anchoita) are under-exploited in Argentina (Hansen, 2004), where large fisheries for Argentine hake and shortfin squid (Illex argentinus) exist (Brunetti et al., 1998; Bertolotti et al., 2001). In addition, trawlers have operated on the continental shelf of Brazil, Uruguay and northern Argentina since the 1960s, with a dramatic increase in fishing effort in the late 1980s and mid 1990s (Valentini et al., 1991; Haimovici et al., 1998; Bertolotti et al., 2001; Jaureguizar and Milessi, 2008; Defeo et al., 2011). Landing biomass, catch per unit effort and mean trophic level of landings remained stable during the initial period but declined dramatically by the mid-1990s. For instance, landings of hake in the region peaked at 521000 tons in 1991, just to decline dramatically afterwards (Odebrecht and Castello, 2001). Likewise, demersal landings in Uruguay increased six-fold from 1975 to 1981. yielding in the following 10 years, up to 140000 tons per year; however, landings of Argentine hake, white croaker and striped weakfish decreased in the following years owing to over-exploitation (Defeo et al., 2011). Between 1976 and 1994, total landings of the demersal fisheries in southern Brazil. dominated by sciaenids, fluctuated between 46000 and 75000 tons (mean 59000 tons) (Haimovici, 1998). At present, many demersal stocks are fully exploited or over-exploited (Haimovici, 1998; Jaureguizar and Milessi, 2008; Defeo et al., 2011).

Intensive fishing is known to have adversely affected several marine mammal populations in South America. For instance, the dramatic population declines experienced by the Peruvian population of the South American fur seal, which appear linked to ENSO variability (Arias-Schereiber and Rivas, 1998; Arias-Schereiber, 2000; Oliveira *et al.*, 2009), have been magnified by the high levels of ecosystem alteration caused by intensive fishing (Coll *et al.*, 2008; Kovacs *et al.*, 2012). In northern Patagonia, the development of industrial fishing has probably reduced the carrying capacity for the South American sea lion (Otaria flavescens) (Drago et al., 2010); and at the same time sea lions showed a dietary shift as part of a density-dependence process (Drago et al., 2009a). Furthermore, declining abundance of demersal fishes in southern Brazil (Haimovici, 1998) has been found to cause a major dietary shift in the franciscana dolphins (Pontoporia blainvillei) (Secchi et al., 2003). However, the impact of fishing intensification on the food availability for South American fur seals remains unknown (IUCN, 2012). Particularly, nothing is known about the response of fur seals to the changes caused in Río de la Plata and adjoining areas by fishing development despite expressions of concern, because some of the targets of the fishery are also consumed by fur seals (Naya et al., 2002; Szteren et al., 2004). this reason, De María et al. (2012) For recommended extending the studies on the feeding ecology of South American fur seals to determine potential areas of conflict and overlap with fisheries in the use of resources.

Traditionally, diets have been described from direct observation or the identification of hard remains (e.g. fish bones, cephalopod beaks) from stomach contents and scats. Unfortunately, the diets of most species of marine mammals are poorly understood owing to incomplete sampling across time and space (Trites, 2001). Alternatively, stable isotope analysis is a standard tool for the study of marine mammal ecology (Newsome et al., 2010a) and has allowed the reconstruction of dietary changes in some species through the analyses of specimens in museum and zooarchaeological collections (Hirons et al., 2001a; Newsome et al., 2007; Drago et al., 2009a). This retrospective approach is possible because the stable isotope ratios (δ^{15} N and δ^{13} C) in the diet of a consumer are reflected in its tissues in a predictable way (DeNiro and Epstein, 1978, 1981). While $\delta^{15}N$ values provide data on trophic level (Post, 2002), δ^{13} C values can reveal information on feeding locations, including the relative importance of benthic and pelagic prey in the diet (France, 1995; Hobson et al., 1995; Drago et al., 2009a; Pinela et al., 2010). Bone collagen is a slow turn-over tissue which in large adult mammals is expected to integrate stable isotope ratios over several years (Hirons et al., 2001a). This tissue acts as a

long-term integrator of isotopic fluctuations, which makes it useful for comparing the isotope ratios of many individuals over long periods of time (Schoeninger and DeNiro, 1984; Lee-Thorp *et al.*, 1989; Hirons *et al.*, 2001a; Drago *et al.*, 2009a). Therefore, the use of stable isotope ratios in bone samples is an adequate method to assess potential dietary changes of a predator population over long timescales. Nevertheless, to obtain a high level of resolution in the interpretation of trophic interactions, stable isotopes must be used in conjunction with other information, such as direct diet analyses (Post, 2002).

This paper uses stable isotope ratios in bone to investigate whether the intensification of fishing in Río de la Plata and adjoining areas in the mid-1990s (Haimovici, 1998; Bertolotti *et al.*, 2001; Jaureguizar and Milessi, 2008; Defeo *et al.*, 2011) has reduced the availability of benthic and demersal prey to the growing population of South American fur seals.

MATERIALS AND METHODS

Sampling

The study was conducted on samples from 54 male fur seals found dead stranded along the coast of southern Brazil (from 29°19'S, 49°43'W to 31°15'S, 50°54'W) from 1994 to 2011. Samples consisted of small fragments of maxillo-turbinal bones collected from fur seal skulls belonging to the collection of the Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul (GEMARS), at Tramandaí, Brazil. Morphological and molecular evidence show that South American fur seals dead stranded along the Brazilian coast belong to the Uruguayan population (Oliveira, 2004; Oliveira *et al.*, 2008b). All samples were stored dry until analysis.

Potential prey of South American fur seals previously identified by stomach and scat analysis (Naya *et al.*, 2002; Szteren *et al.*, 2004; Oliveira *et al.*, 2008a) were collected from northern Argentina and southern Brazil. The total length range of analysed prey were within the ranges reported for the diet of fur seals in the area (Naya *et al.*, 2002; Szteren *et al.*, 2004; Oliveira *et al.*, 2008a). Samples from northern Argentina were obtained from fishermen at Mar del Plata ($38^{\circ}08'S$, $57^{\circ}32'W$) and Puerto Quequén ($38^{\circ}35'S$, $58^{\circ}42'W$), whereas samples from southern Brazil were obtained from local fishermen in Imbé ($29^{\circ}58'S$, $50^{\circ}07'W$), Torres ($29^{\circ}19'S$, $49^{\circ}43'W$) (Rio Grande do Sul), and coastal waters off Santa Catarina ($26^{\circ}14'-29^{\circ}06'S$, $46^{\circ}28'-48^{\circ}26'W$; Figure 1). White dorsal muscle was sampled for fishes and mantle for cephalopods. All samples were stored in a freezer at $-20^{\circ}C$ until analysis. Additionally, stable isotope ratios of some potential prey from southern Brazil were taken from Bugoni *et al.* (2010).

Age determination

Some eared seal species show dietary changes with age (Hobson and Sease, 1998; Newsome *et al.*, 2006; Drago *et al.*, 2009b; Orr *et al.*, 2011). In addition, prey-to-predator discrimination factor is expected to change between growing (e.g. yearlings) and non-growing (e.g. adult) animals (Martínez del Rio *et al.*, 2009). Therefore, to avoid undesired variability only adult specimens older than 8 years (Batallés *et al.*, 1990) were used in the study.

Individual ages were estimated from counts of growth layer groups (GLGs; Scheffer, 1950) in the dentine and/or in the cementum of different teeth. Two different techniques were used: thin ground sections of undecalcified teeth, and decalcified and stained thin sections made with a freezing microtome. The technique employed depended on the availability of teeth from each individual (canines, incisors or post-canines) and it was assumed that one GLG is deposited per year (Schiavini et al., 1992; Crespo et al., 1994; Molina-Schiller and Pinedo, 2004). Teeth were read three times by at least two readers. Subsequent readings by the same reader were spaced by at least 1 week. When readings were coincidental, that age was assigned to the individual. Whenever counting differed by less than 10% of the average of the three reads, the mean of the readings was taken as the age of the specimen (Calzada et al., 1994). Where counts exceeded this arbitrary limit, teeth were re-examined or another tooth was prepared.

Stable isotope analysis

In the laboratory, samples were dried in an oven at 60°C for 36 h and ground to a fine powder with



Figure 1. Map of the Río de la Plata and adjoining areas. The thick line indicates the sampling area of fur seals in southern Brazil, points indicate the location of prey sampling sites (Brazil and Argentina) and the triangle marks Isla de Lobos (Uruguay), main rookery of South American fur seals (*Arctophoca australis*) in the world.

mortar and pestle. Lipids were removed from all samples with a chloroform/methanol (2:1) solution (Bligh and Dyer, 1959). Bone samples were divided into two aliquots. One of them was soaked for 24 h in 0.5 N hydrochloric acid (HCl) for decalcification and used to determine δ^{13} C (Newsome *et al.*, 2006; Hanson et al., 2009). Since HCl treatment affects δ^{15} N (Bunn *et al.*, 1995), the other aliquot was not treated with HCl and used for the $\delta^{15}N$ analysis. Approximately 1 mg of dried bone and 0.3 mg of muscle of fish and cephalopods were weighed into tin cups $(3.3 \times 5 \text{ mm})$, combusted at 900°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 relative to carbonate Pee Dee Belemnite and atmospheric nitrogen. Analyses were performed at the Centres Científics I Tecnològics of the University of Barcelona.

Data analysis

Normality of the data was tested with a modified Shapiro-Wilks test and the relation between

isotopic concentration and stranding year was investigated by linear regression analysis for normal data and non-parametric Spearman's p correlation for non-normal data.

Two-way ANOVA was used to analyse the effects of area (southern Brazil vs northern Argentina) and prey species (*E. anchoita*, *T. lathami*, *C. guatucupa*, *M. furnieri*, *M. americanus* and *L. sanpaulensis*) to test the hypothesis that stable isotope ratios differed between the northern and southern part of the Río de la Plata plume. A Tukey test was used as a post-hoc test.

The relative contribution of potential prey to the diet of male fur seals was calculated using the Bayesian mixing model SIAR (Stable Isotope Analysis in R; Parnell *et al.*, 2008), where only a selection of prey previously identified in stomach and scat analysis (Naya *et al.*, 2002; Szteren *et al.*, 2004; Oliveira *et al.*, 2008a) were included, as the use of too many prey species in the model reduces the information provided by the outcome (Parnell *et al.*, 2008). Diet reconstruction through mixing models is possible only if trophic discrimination factors are known, i.e. how δ^{13} C and $\delta^{15}N$ values vary from diet to predator, and are both tissue and species dependent (Newsome et al., 2010a). Controlled experiments in captivity have demonstrated that blood, skin and vibrissae of pinnipeds are enriched in ¹³C and ¹⁵N when compared with the stable isotope ratios in the diet (Hobson et al., 1996), but nothing is known about the diet-to-bone discrimination factor in pinnipeds. Discrimination factors from diet to mammal bone have been determined experimentally only for pig (Nardoto et al., 2006), but this is unlikely to be a good animal model for fur seals because the nutrient routing in omnivores and carnivores is different (Martínez del Rio et al., 2009). Therefore, an indirect approach was used to calculate the diet-to-bone discrimination factor.

Diet-to-vibrissae discrimination factors have been determined experimentally for seals and California sea otters (Hobson et al., 1996; Newsome et al., 2010b). Vibrissae of fur seals grow continuously and at least two annual cycles are recorded in each vibrissa longer than 7 cm (Hirons et al., 2001b; Cherel et al., 2009). Bone is also expected to integrate diet over several years (Hirons et al., 2001a). Accordingly, differences in the stable isotope ratios of bone and vibrissae from individuals from the same sex, age class and populations are expected to reveal differences in diet-to-tissue discrimination factors and can be used transform the published diet-to-vibrissae to discrimination factors into diet-to-bone factors. Following that rationale, the vibrissae of five adult male fur seals $(\delta^{13}C = -14.30 \pm 0.31\%)$; $\delta^{15}N = 18.58 \pm 0.25\%$) and bone samples from 28 adult male fur seals from the same population $(\delta^{13}C = -13.36 \pm 0.51\%; \delta^{15}N = 20.56 \pm 1.01\%)$ were analysed. Then, the average vibrissae-to-bone offset was computed ($\delta^{13}C = +0.93$; $\delta^{15}N = +1.99$) and a diet-to-bone discrimination factor ($\delta^{13}C = +3.63$; $\delta^{15}N = +5.14$) was estimated by adding the average diet-to-vibrissae discrimination factor ($\delta^{13}C = +2.70$; $\delta^{15}N = +3.15$) reported by Hobson *et al.* (1996) and Newsome et al. (2010b) to the average vibrissae-to-bone offset.

All statistical analyses were performed with the InfoStat software package (Di Rienzo *et al.*, 2011), unless otherwise stated.

Stable isotope ratios of potential prey species of fur seals from the two areas studied are shown in Table 1. Potential prey from northern Argentina were usually depleted in ¹³C and enriched in ¹⁵N when compared with the same species from southern Brazil (two-way ANOVA; δ^{13} C: $F_{11, 48} = 37.41, P < 0.001; \delta^{15}N: F_{11, 48} = 134.10,$ P < 0.001); although the species x area interaction term was statistically significant for both isotopes $(\delta^{13}C F_{11, 48} = 8.12, P < 0.001; \delta^{15}N: F_{11, 48} = 12.3,$ P < 0.001). Such interaction can be attributed to the fact that even though all Argentine prey are enriched in $\delta^{15}N$ compared with their Brazilian counterparts, differences were not statistically significant for Argentine anchovy and rough scad (Tukey post hoc test, P > 0.05). The same was true for the δ^{13} C, where most Argentine prev are depleted in relation with Brazilian ones, though differences were not statistically significant for São Paulo squid, white croaker, striped weakfish and southern kingcroaker (Tukey post hoc test, P > 0.05). Nevertheless, benthic fish from the two regions were more enriched in ¹³C than any other group of potential prey and small pelagic fishes from both regions were more depleted in ¹⁵N than any other group, with the exception of Argentine shortfin squid that showed the lowest values of ¹⁵N (Figure 2). Accordingly, a general decrease in the consumption of benthic fish should produce a simultaneous reduction of both δ^{13} C and δ^{15} N in fur seals.

The δ^{13} C values of male fur seal ranged from -16.62to -12.50 % (mean = -13.56; SD = 0.79) and those of δ^{15} N from 19.18 to 22.73 ‰ (mean = 20.58; SD = 0.62). Carbon to nitrogen (C:N) ratio ranged from 2.75 to 3.48 (mean = 2.95), indicative of unaltered collagen in bone samples (DeNiro, 1985; Table 2). There was no correlation between δ^{15} N or δ^{13} C and the stranding year (δ^{15} N: r^2 = 0.01, P = 0.46; δ^{13} C: Spearman's p = 0.12, P = 0.39; Figure 3). After correcting the δ^{13} C and δ^{15} N values for diet-to-bone discrimination, the bivariated signal of most adult male fur seals lay within a polygon formed by small and medium pelagic fish from northern Argentina and southern Brazil, Argentine shortfin squid from northern Argentina, and São

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Table 1. Stable isotope ratios (δ^{13} C and δ^{15} N) of the potential prey of South American fur seal (*Arctophoca australis*) from southern Brazil (BRA) and northern Argentina (ARG)

Species	Common name	Area	n	δ^{13} C (‰) (mean ± SD)	δ ¹⁵ N (‰) (mean±SD) 15.07±0.50	
Small pelagic fish Engraulis anchoita *	Argentine anchovy	BRA	5	-16.49 ± 0.41		
Medium pelagic fish	Cutless fish		5	15 72 + 0.24	16 59 + 0 54	
Trachurus lathami *	Rough scad	BRA	5	-16.08 ± 0.10	16.38 ± 0.34 16.43 ± 0.91	
Demersal-pelagic fish <i>Cynoscion guatucupa</i>	Striped weakfish	BRA	5	-16.55 ± 0.68	16.05 ± 0.56	
Demersal-benthic fish						
Micropogonias furnieri	White croaker	BRA	5	-15.74 ± 0.60	15.33 ± 0.36	
Menticirrhus americanus	Southern kingcroaker	BRA	5	-15.36 ± 0.46	16.04 ± 0.49	
Umbrina canosai *	Argentine croaker	BRA	5	-15.37 ± 0.27	16.92 ± 0.35	
Urophycis brasiliensis *	Brazilian codling	BRA	5	-15.49 ± 0.45	16.78 ± 0.39	
Demersal–pelagic cephalopod						
Loligo sanpaulensis	São Paulo squid	BRA	5	-16.26 ± 0.11	15.21 ± 0.28	
Small pelagic fish						
Engraulis anchoita	Argentine anchovy	ARG	5	-18.24 ± 0.30	15.46 ± 0.54	
Merluccius hubbsi (<30cm)	Argentine hake	ARG	2	-18.36 ± 0.09	14.77 ± 0.04	
Medium pelagic fish						
Merluccius hubbsi (>30cm)	Argentine hake	ARG	3	-17.98 ± 0.49	15.58 ± 0.43	
Trachurus lathami	Rough scad	ARG	5	-17.58 ± 0.34	16.91 ± 0.53	
Demersal-pelagic fish						
Cynoscion guatucupa	Striped weakfish	ARG	5	-17.22 ± 0.20	17.61 ± 0.26	
Demersal-benthic fish						
Micropogonias furnieri	White croaker	ARG	5	-15.97 ± 0.31	16.71 ± 0.46	
Menticirrhus americanus	Southern kingcroaker	ARG	5	-14.97 ± 0.87	19.06 ± 1.08	
Demersal-pelagic cephalopod						
Loligo sanpaulensis	São Paulo squid	ARG	5	-16.71 ± 0.19	18.63 ± 0.21	
Illex argentinus	Argentine shortfin squid	ARG	5	-17.45 ± 0.39	14.66 ± 0.46	

*Stable isotope values taken from Bugoni *et al.* (2010). n: sample size.



Figure 2. Isotopic landscape showing the stable isotope ratios (δ^{15} N and δ^{13} C) of adult male South American fur seals (*Arctophoca australis*) and its potential prey grouped by trophic guilds (mean ± SD) from southern Brazil and northern Argentina. Key: fur seals (black circles), Brazil (empty figures), Argentina (full figures), small pelagic fish (triangles), medium pelagic fish (squares), demersal-benthic fish (circles), Striped weakfish (rhombus), demersal-pelagic cephalopods (crosses).

Table 2. Stable isotope ratios (δ^{13} C and δ^{15} N) of skull bone from adult male South American fur seals (*Arctophoca australis*) dead stranded in southern Brazil during the period 1994–2011

Sample ID	Age (yr)	Stranding year	δ ¹³ C (‰)	δ ¹⁵ N (‰)	C:N ratio
GEMARS 0185	9	1994	-16.62	20.53	3.11
GEMARS 0259	12	1995	-15.60	20.50	3.48
GEMARS 0263	8	1995	-12.87	20.52	2.92
GEMARS 0278	10	1995	-13.31	20.80	3.00
GEMARS 0280	9	1995	-13.09	20.43	2.79
GEMARS 0293	9	1995	-13.11	20.93	2.90
GEMARS 0297	8	1995	-13.87	20.53	3.19
GEMARS 0302	*	1995	-13.34	20.81	3.17
GEMARS 0368	9	1996	-12.97	20.07	2.81
GEMARS 0429	10	1997	-14.51	19.29	2.82
GEMARS 0436	12	1997	-14.22	19.18	2.84
GEMARS 0450	10	1997	-13.34	21.23	2.87
GEMARS 0537	9	1998	-14 32	22.73	3 38
GEMARS 0544	10	1998	-1340	20.74	3 13
GEMARS 0581	13	1990	_12.58	20.74	2.83
GEMARS 0582	10	1999	_12.30	20.04	3.05
GEMARS 0584	10	1000	12.78	20.55	2.05
CEMARS 0586	10	1999	12.04	10.46	2.07
GEMARS 0580	10	1999	-13.23	21 50	2.04
GEMARS 0580	0	1999	-13.09	21.50	2.94
CEMARS 0569	11	2000	-12.74	20.75	2.94
GEMARS 0055	12	2000	-13.04	19.88	3.07
GEMARS 0001	10	2000	-12.02	19.70	2.81
GEMARS 0681	12	2000	-13.50	21.11	2.93
GEMARS 0694	12	2000	-13.19	20.55	2.88
GEMARS 0/21	9	2000	-14.15	21.19	2.82
GEMARS 0/2/	9	2000	-14.33	21.00	3.03
GEMARS 0/39	13	2000	-14.44	19.82	2.93
GEMARS 0830	9	2002	-12.90	20.18	2.92
GEMARS 0901	8	2002	-15.19	20.17	2.96
GEMARS 0958	11	2003	-14.08	20.23	2.87
GEMARS 0960	11	2003	-14.27	19.80	3.12
GEMARS 0969	13	2003	-13.63	20.08	2.76
GEMARS 1014	10	2003	-13.55	20.58	2.83
GEMARS 1065	12	2003	-14.09	20.41	2.85
GEMARS 1087	11	2003	-13.93	20.46	3.14
GEMARS 1113	11	2003	-12.78	20.72	2.92
GEMARS 1114	12	2003	-13.84	20.91	2.97
GEMARS 1128	8	2003	-13.71	20.98	3.15
GEMARS 1133	11	2003	-14.32	20.37	3.22
GEMARS 1185	12	2004	-12.87	20.57	3.20
GEMARS 1230	12	2005	-13.10	19.68	2.96
GEMARS 1277	10	2006	-13.57	21.16	2.98
GEMARS 1310	11	2008	-13.94	21.00	2.93
GEMARS 1330	14	2009	-12.84	21.54	2.84
GEMARS 1343	11	2009	-13.24	20.59	2.88
GEMARS 1413	12+	2010	-12.84	20.53	2.78
GEMARS 1448	14	2011	-13.23	21.00	2.82
GEMARS 1449	13	2011	-13.53	20.81	2.90
GEMARS 1450	11	2011	-12.50	21 17	2.75
GEMARS 1452	14	2011	-13.13	21.32	2.88
GEMARS 1457	9+	2011	-14 16	19 60	2.00
GEMARS 1458	0	2011	-13.28	20.56	2.73
GEMARS 1450	0	2011	_13.20	20.30	2.75
GEMARS 1453	7 10±	2011	_13.25	20.77	2.70
GLIMANS 1403	10+	2011	-13.20	20.72	2.71

*No teeth available for age determination, adulthood inferred from body total length.

Paulo squid and striped weakfish from Brazil (Figure 2). Accordingly, SIAR showed that male fur seals foraged all over the river plume and consumed primarily small pelagic fishes, squid and

hake, with a minor contribution of larger pelagic species like cutlass fish and striped weakfish (Figure 4). It should be noted that two highly ¹³C depleted male fur seals, dead stranded in 1994 and



Figure 3. (a) Linear regression and (b) non-parametric correlation between stranding year and the stable isotope ratios (δ^{15} N and δ^{13} C) of skull bone from adult male South American fur seals (*Arctophoca australis*) from southern Brazil.



Figure 4. SIAR analysis outcome showing the estimated contribution of prey to the diet of adult male South American fur seals (*Arctophoca australis*). The mean contribution of each prey is shown above each box-plot. Median 50%, 75% and 95% credibility intervals (respectively dark grey, light grey and white boxes) of the posterior probability distributions of proportions in diet are shown.

1995, lay outside the isotopic landscape of the Río de la Plata region (Figure 2).

DISCUSSION

Most of the prey species collected in northern Argentina and southern Brazil differed in stable isotope ratios, thus revealing a spatial segregation between the two ecosystems. Usually, potential prey from southern Brazil were enriched in ¹³C as compared with those from northern Argentina, a pattern probably related to the high levels of ¹³C depleted phytoplankton and detritus from freshwater helophytes present in the river plume (Botto et al., 2011) as well as the absence of submerged macrophytes (Mianzan et al., 2001), such as seagrasses and macroalgae, which are usually more enriched in ¹³C than phytoplankton (Drago *et al.*, 2009a). On the other hand, the ^{15}N enrichment of potential prey from northern Argentina could reflect large inputs of sewage from Buenos Aires and Montevideo cities (Acha et al., 2003; Botto et al., 2011). Spatial segregation in the isotopic landscape is evident for small and medium pelagic fish along the $\delta^{13}C$ axis and for striped weakfish, São Paulo squid and demersal benthic fish along the $\delta^{15}N$ axis; however, some prev species did not match that distribution.

Despite the observed spatial segregation of fish stocks revealed by stable isotopes, SIAR supported the hypothesis that the foraging grounds for the South American fur seals that breed in Uruguay span a huge area including the plume of Río de la Plata and southern Brazil, as previously suggested (Pinedo, 1986, 1998; Dassis *et al.*, 2012).

Scat and stomach content analysis conducted in Uruguay and southern Brazil have identified striped weakfish, anchovies, cutlass fish and squids as the most important prey for the species in the region (Naya *et al.*, 2002; Szteren *et al.*, 2004; Oliveira *et al.*, 2008a). The results reported here are in agreement with previous findings, but highlight the greater importance of small pelagic fish (anchovies) and squids in the diet of adult male South American fur seals, as has also been suggested recently for females (Franco-Trecu *et al.*, 2012). Nevertheless, the contribution of juvenile hake (<30 cm) is probably overestimated by the SIAR model, as they have an isotopic signal very similar to that of anchovies and the occurrence of hake remains in scats is negligible (Nava et al., 2002; Szteren et al., 2004). Differences with previous studies can be attributed to the biases inherent to each methodology. First, none of the previous work relying on scat or stomach content analyses discriminated individuals by sex or age classes (Naya et al., 2002; Szteren et al., 2004; Oliveira et al., 2008a), whereas in the present study sampling was focused only on adult males. Therefore, it is expected that differences arise when comparing diet from individuals differing in sex and age classes. For instance, lactating females are more restricted to forage near the rookeries during the breeding season, thus reducing prey selectivity (Naya et al., 2002). Second, scat and stomach content analyses are highly sensitive to seasonal changes, as they just reveal the last meals. In contrast, stable isotope ratios in bone are expected to integrate diet over several years (Hirons et al., 2001a; Newsome et al., 2006; Drago et al., 2009a). Third, prey hard parts are not excreted in the same proportions that they have been ingested, so the estimated contribution of different prev species to diet may be significantly biased in scat based studies (Casper et al., 2006). Fourth, stable isotope analysis can be biased due to the uncertainty about the actual diet-to-predator discrimination factor (Newsome et al., 2010a).

Despite all these shortcomings, the overall evidence from scat (Naya et al., 2002; Szteren et al., 2004), stomach contents (Oliveira et al., 2008a), and stable isotope analyses (Franco-Trecu et al., 2012; this study) indicates that South American fur seals inhabiting the Río de la Plata plume and adjoining areas rely primarily on small pelagic fishes and squid. However, two of the male fur seals analysed showed a different pattern with strongly depleted ¹³C values, thus suggesting alternative foraging areas and/or a different diet. There are records of the presence of South American fur seals at the shelf-break (Bastida and Lichstchein, 1984), and accessibility to the shelf-break has been suggested to rule the distribution of the rookeries of South American fur seals in the south-western Atlantic (Túnez et al., 2008). Besides, myctophid fish are typical inhabitants of the continental shelf-break (Hulley, 1990) and are characterized by a highly ¹³C depleted signal (Ciancio *et al.*, 2008). Therefore, it is possible that myctophids have some relevance in the diet of South American fur seals, at least at certain times or for some individuals in the population, just like they have in South American fur seals from southern Chile (Seguel *et al.*, 2013) and other species of fur seals (Acuña and Francis, 1995; Klages and Bester, 1998; Robinson *et al.*, 2002; Beauplet *et al.*, 2004; Forcada and Staniland, 2008; Boren, 2010).

Cutlass fish, striped weakfish and perhaps myctophids, may be consumed by adult male fur seals at certain periods, but they are certainly minor components in the diet of fur seals on an annual basis. Despite changes in the ecosystem, the diet of fur seals remained essentially pelagic for at least 17 years. Therefore it is concluded that the likely per-capita reduction in the availability of demersal and benthic species caused by simultaneous fishery development (Haimovici, 1998; Bertolotti et al., 2001; Jaureguizar and Milessi, 2008) and increase of the fur seal population (Vaz-Ferreira, 1982; Túnez et al., 2008; Franco-Trecu et al., 2012) has not resulted in a reduction in the consumption of demersal species, contrary to the pattern reported for the South American sea lion in northern Patagonia (Drago et al., 2009a). Several explanations can account for this fact: a preference for feeding on the most abundant and widespread small pelagic fish (i.e. Argentine anchovy) in the south-western Atlantic ecosystem (de Ciechomsky and Sánchez, 1988), as already reported for South American fur seals in Peru (Majluf, 1989); the existence of a mechanism for trophic segregation between sympatric fur seals and sea lions in the area (Franco-Trecu *et al.*, 2012); and limited underwater time and thus, restricted access to benthic resources for smaller body sized fur seals, compared with sea lions (Gentry et al., 1986; Kooyman, 1989; Costa 1991, 1993; Costa et al., 2004). All this results in a higher reliance on pelagic resources in the long term, independently of the abundance of demersal and benthic resources, as already reported for other fur seal species (Páez-Rosas et al., 2012).

As long as small pelagic fish remain under-exploited in the area, competition between fisheries and fur seals is not expected, but the indirect consequences of changes in the ecosystem structure and dynamics caused by intense fishing (Jaureguizar and Milessi, 2008) are hard to predict. For instance, the interactions between fur seals and other anchovy predators are poorly known, but suggest that overfishing of hake and weakfish may have resulted in increased anchovy availability for fur seals. Likewise, the interactions between fur seals and other marine mammals in the area remain unknown. These issues can be explored only through ecosystem modelling and the basic parameters of an Ecopath mass balance trophic model for Río de la Plata have been published recently (Bergamino et al., 2012). However, essential information about the South American fur seal population is still missing and for this reason, a precise and updated estimation of population size becomes essential, once its diet has been assessed, to establish effective conservation and management measures for this species. Besides South American fur seals, several other high trophic level predators are under a dynamic process throughout the south-western Atlantic Ocean, where most of them are increasing their populations in a scenario of resource depletion; hence, also for them it is necessary to know the basic information to approach the reality of the ecosystem as a whole.

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