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GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Holocene changes in the trophic ecology of an apex marine predator in the South Atlantic Ocean

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Abstract Predators may modify their diets as a result of both anthropogenic and natural environmental changes. Stable isotope ratios of nitrogen and carbon in bone collagen have been used to reconstruct the foraging ecology of South American fur seals (*Arctocephalus australis*) in the southwestern South Atlantic Ocean since the Middle Holocene, a region inhabited by hunter-gatherers by millennia and modified by two centuries of whaling, sealing and fishing. Results suggest that the isotopic niche of fur seals from Patagonia has not changed over the last two millennia (average for the period: $\delta^{13}C_{2200-0BP} = -13.4 \pm 0.5‰$, $\delta^{15}N_{2200-0BP} = 20.6 \pm 1.1‰$). Conversely, Middle Holocene fur seals fed more pelagically than their modern conspecifics in the Río de la Plata region ($\delta^{13}C_{7000BP} = -15.9 \pm 0.6‰$ vs. $\delta^{13}C_{PRESENT} = -13.5 \pm 0.8‰$) and Tierra del Fuego ($\delta^{13}C_{6400-4300BP} = -15.4 \pm 0.5‰$ vs. $\delta^{13}C_{PRESENT} = -13.2 \pm 0.7‰$). In the latter region, Middle Holocene fur seals also fed at a higher trophic level than their modern counterparts ($\delta^{15}N_{6400-4300BP} = 20.5 \pm 0.5‰$ vs. $\delta^{15}N_{PRESENT} = 19.0 \pm 1.6‰$). Nevertheless, a major dietary shift was observed in fur seals from Tierra del Fuego during the nineteenth century ($\delta^{13}C_{100BP} = -17.2 \pm 0.3‰$, $\delta^{15}N_{100BP} = 18.6 \pm 0.7‰$), when marine primary productivity plummeted and the fur seal population was decimated by sealing. Disentangling the relative roles of natural and anthropogenic factors in explaining this dietary shift is difficult, but certainly the trophic position of fur seals has changed through the Holocene in some South Atlantic regions.

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Introduction

Human impacts on marine ecosystems are diverse (e.g. overfishing, pollution, habitat loss, climate change, introduction of exotic species, etc.) and some of them originated a long time ago (Jackson et al. 2001; Erlandson and Rick 2008; Halpern et al. 2008; Lotze and Worm 2009). As a result, the ecosystem structure has been largely modified (Jackson et al. 2001; Erlandson and Rick 2008; Pinnegar and Engelhard 2008) and the modern anthropogenic setting is probably inadequate to understand the original ecological role of those species decimated by human exploitation (Newsome et al. 2007a; Zenteno et al. 2015).

Stable nitrogen and carbon isotope analysis on the remains of ancient organisms offers a unique opportunity to reveal ecological responses to anthropogenic perturbation and/or environmental change over time and to reconstruct their original ecological role (Hirons et al. 2001; Burton et al. 2001, 2002; Newsome et al. 2007a; Zenteno et al. 2015). This retrospective approach is possible because nitrogen and carbon isotope ratios in the tissues of a consumer are expected to reflect that of their overall prey in a predictable way (DeNiro and Epstein 1978, 1981). For aquatic organisms, $\delta^{15}N$ values are well suited to detect changes in trophic level (Minagawa and Wada 1984; Post 2002), while $\delta^{13}C$ values can reveal information on feeding locations, including the relative use of benthic vs. pelagic prey and coastal vs. oceanic prey (Hobson et al. 1994; France 1995). Therefore, information about the diet of vertebrate predators in ancient ecosystems can be derived from the stable isotope ratios of their bones (Schoeninger and DeNiro 1984). Bone is often well preserved in archaeological sites, allowing comparison of isotope ratios from hundreds to thousands of years old (Misarti et al. 2009).

However, when comparing among spatially or temporally separated ecosystems, the $\delta^{15}N$ and $\delta^{13}C$ values of a consumer provide little information about its trophic position or major carbon source. This is because a considerable variation in baseline $\delta^{15}N$ and $\delta^{13}C$ values is expected across ecosystems (Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1999; Post 2002). Therefore, without appropriate estimates of these isotope baseline values, there is no way to elucidate whether variation in the $\delta^{15}N$ and $\delta^{13}C$ values of predators reflects changes in foraging ecology or merely a variation in the isotopic baseline (Post 2002). In this sense, stable isotope ratios in gastropods and bivalves have been proposed as proxies for the isotopic baseline of aquatic ecosystems, as they provide a temporal integration of the seasonal variability in the isotopic values of primary producers (Post 2002; Casey and Post 2011). Molluscs are abundant in archaeological shell middens and the organic matrix of their shells is preserved

in subfossil and fossil specimens, providing a way to reconstruct temporal changes in the stable isotope baseline that offer a benchmark to interpret changes in the isotopic ratios observed in predators (Casey and Post 2011).

Pinnipeds are major top predators in cold temperate coasts worldwide and have been intensely exploited by humans for a long time (Bonner 1982). As a result, declines of pinniped populations have often resulted in density-dependent responses leading to decreased intraspecific competition (Scheffer 1955; Trites and Biggs 1992; Etnier 2004; Hanson et al. 2009; Drago et al. 2010) and dietary changes (Hanson et al. 2009; Drago et al. 2010; Zenteno et al. 2015). As a consequence, the current diet data may provide a biased and incomplete picture of the true behavioural plasticity and ecological roles of extant species in non-anthropogenic settings (Burton et al. 2001; Zenteno et al. 2015).

The southwestern South Atlantic Ocean region offers a unique opportunity to understand the potential changes in the trophic ecology of pinnipeds in response to human exploitation, because of the combination of three factors. Firstly, the history of large-scale removal of predators as a consequence of sealing and fishing has been well documented (Koen Alonso and Yodzis 2005; Drago et al. 2009; Saporiti et al. 2014a). Secondly, modern and ancient pinniped bone material dating back to the Middle Holocene is available from modern scientific collections and from the zooarchaeological record. Thirdly, the occurrence of pinniped remains and mollusc shells in the same zooarchaeological sites (Muñoz 2011; Borella 2014) offers the opportunity to account for changes in the isotope baseline when using stable isotopes to explore potential shifts in the trophic ecology of pinnipeds.

The South American fur seal *Arctocephalus australis* (Zimmermann 1783) was abundant from southern Brazil to Tierra del Fuego for most of the second half of the Holocene and during the colonial period, according to the zooarchaeological record (Schiavini 1993; Inda et al. 2006; Castilho and Simões-Lopes 2008; Muñoz 2011; Bayón and Politis 2014; Borella 2014) and the reports of European explorers like Francis Drake, Louis Antoine de Bougainville and James Cook, among several others (Vales 2015). Pinnipeds, including fur seals, were commonly hunted by Pampean hunter-gatherers on the coast of the Buenos Aires province during the Early-Mid and Middle Holocene (7400–5700 BP), although they were not a major resource during the Late Holocene (3100-430 BP) (Bayón and Politis 1996; Eugenio and Aldazabal 2004; Bonomo 2005; Bonomo and León 2010; Aldazabal et al. 2011; Bayón et al. 2012; Bonomo et al. 2013). Hunter-gatherers inhabiting the coast of northern and central Patagonia exploited pinnipeds with variable intensity from the Middle Holocene to the beginning of the eighteenth century, when coastal areas

were abandoned following the domestication of feral horses of European origin (Gómez Otero 2007a; Moreno 2008; Favier Dubois et al. 2009; Moreno et al. 2011; Borella and Cruz 2012). Finally, exploitation of fur seals and sea lions *Otaria flavescens* in Tierra del Fuego by hunter-gatherers goes back to ca. 6400 BP, i.e. the Middle Holocene, and lasted until the nineteenth century (Schiavini 1993; Orquera and Piana 1999; Zangrando et al. 2014). Nevertheless, pinniped exploitation decreased steadily from 5500 to 5000 BP to the nineteenth century (Zangrando 2009; Zangrando et al. 2010; Tivoli and Zangrando 2011), probably due to resource depression by hunter-gatherers (Zangrando et al. 2014) and/or the decreasing levels of regional marine primary productivity through time (Saporiti et al. 2014b). Whatever the reason, the decline in fur seal population size was not comparable to that experienced as a result of the commercial exploitation by sealers between the eighteenth and twentieth centuries. Although the actual numbers of fur seals harvested in the South Atlantic remains unknown, the species was extirpated from most of their former range by the late nineteenth century (Clark 1887; Townsend 1910; Schiavini 1992; Dickinson 2007). It is worth noting that the decline of sea lions in the Falkland/Malvinas Islands has been attributed primarily to environmental factors (Baylis et al. 2015) and that the collapse of the fur seal population in Tierra del Fuego coincided also with a major decline in marine productivity (Saporiti et al. 2014b).

As a legacy of commercial sealing, the fur seal population is currently reduced to colonies scattered within the boundaries of their original range in the southwestern South Atlantic Ocean (Crespo et al. 2015; Vales 2015), but the ecological significance of such demographic change remains unknown. For instance, fur seals currently forage mainly on small pelagic fishes, squids and crustaceans (Naya et al. 2002; Oliveira et al. 2008a; Baylis et al. 2014; Vales et al. 2015), but nothing is known about their trophic ecology in the past, when populations were certainly much larger (Crespo et al. 2015) and thrived in a different ecological setting.

This study uses stable isotopes of carbon and nitrogen to assess the foraging ecology of South American fur seals inhabiting the coasts of the southwestern South Atlantic Ocean since the Middle Holocene and discuss the relative roles of human exploitation and environmental changes in potential dietary shifts.

Materials and methods

Sampling

Both modern and archaeological samples were collected in three regions of the southwestern South Atlantic Ocean:

Río de la Plata and adjoining areas (from southern Brazil to southern Buenos Aires province, Argentina), northern and central Patagonia (including the coastline of Río Negro, Chubut and northern Santa Cruz provinces, Argentina), and southern Santa Cruz and Tierra del Fuego provinces (Argentina) (Fig. 1). These three regions differ in oceanographic and biogeographic features (Acha et al. 2004; Cousseau and Perrota 2004; Balech and Ehrlich 2008), as well as in the intensity of marine resource exploitation by hunter-gatherers (Orquera and Gómez Otero 2007).

Archaeological bone samples of fur seals were recovered from human occupation sites (e.g. shell middens) dated from the Middle to the Late Holocene (Fig. 1; Table 1). Samples from the archaeological site Túnel VII (ca. 100 BP) are contemporaneous with the depletion of fur seal populations by commercial sealers in Tierra del Fuego, but correspond to animals hunted by native hunter-gatherers (Orquera 2002). Limpet and mussel shells were recovered from shell middens to estimate the baseline of the benthic and pelagic ancient ecosystems, respectively. The ribbed mussel (*Aulacomya atra atra*) and the Magellanic copper limpet (*Nacella magellanica*) were collected from sites in Península Valdés and nearby areas to characterise the base of the food web of northern and central Patagonia. Similarly, the blue mussel (*Mytilus edulis*) and the Magellanic copper limpet were collected from the Beagle Channel to characterise the base of the food web of Tierra del Fuego. As shell middens are scarce in Pampean archaeological sites (Bonomo 2005), no ancient shell samples were available from the Río de la Plata and surrounding areas.

Modern samples of fur seals consisted in small fragments of maxillo-turbinal bones of subadult and adult males collected from skulls housed at three scientific collections: (1) Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul (GEMARS), which contains skulls of individuals belonging to the Uruguayan population (Oliveira 2004; Oliveira et al. 2008b) and collected along the coast of southern Brazil from 1994 to 2011 ($n = 58$) (Vales et al. 2014); (2) Centro Nacional Patagónico (CCT CONICET-CENPAT), which contains skulls of individuals stranded along the coast of Río Negro and Chubut provinces from 1990 to 2013 ($n = 43$); (3) Museo Acatushún de Aves y Mamíferos Marinos Australes, which contains skulls of individuals stranded along the coast of Tierra del Fuego from 1978 to 2008 ($n = 6$). Likewise, modern shell samples of limpet and mussel were collected from December 2009 to February 2010 in Patagonian and Fuegian sites ($n = 5$ individuals per species). All these samples were stored dry until analysis.

Modern potential prey of fur seals previously identified by stomach and scat analysis (Strange 1983, 1992; Schiavini 1993; Naya et al. 2002; Oliveira et al. 2008a;
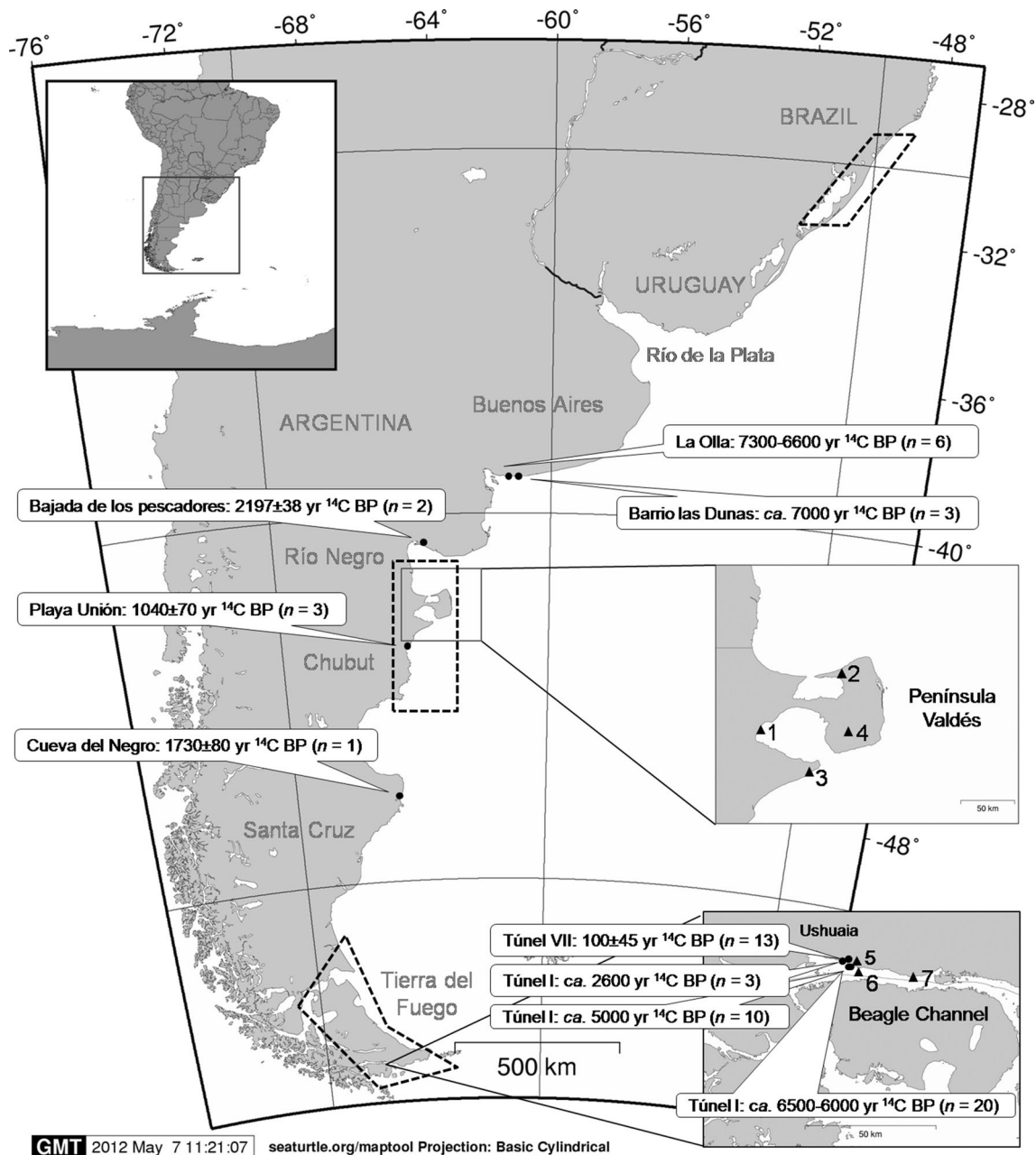
Fig. 1 Map of the southwestern South Atlantic Ocean. *Dotted line polygons* indicate the sampling area of skulls of modern South American fur seals (*Arctocephalus australis*). *Black symbols* show archaeological sites from which the fur seals (*dots*) and shells (*triangles*) were recovered. References for archaeological sites with shells: (1) Ecocentro, hearth 3; (2) Playa Las Lisas 2, midden 2; (3) Cracker 8, level 3; (4) Las Ollas, midden 1; (5) Túnel VII; (6) Shamakush X, layer E; (7) Imiwaia I, layer M and K. Sample size *n* is shown in *parentheses*

Baylis et al. 2014; Vales et al. 2015) were collected in southern Brazil and Buenos Aires province (see for details Vales et al. 2014); off the northern Patagonian coast (see for details Drago et al. 2009; Vales et al. 2015); and off southern Santa Cruz province (from latitude 49° to 52°S) from April 2010 to May 2011, excepting the Fuegian sprat (*Sprattus fuegensis*) collected in April 2000. Sampled

tissues for prey included: white dorsal muscle for fishes, mantle for squids, muscle for Argentine red shrimps (*Pleoticus muelleri*) and the whole body for lobster krill (*Munida gregaria*). All samples were stored in a freezer at −20 °C until analysis. Additionally, stable isotope ratios of some potential prey from southern Brazil were taken from Bugoni et al. (2010).

Table 1 Archaeological sites where the fur seal and shell remains were recovered

Region	Archaeological site	Geographic position	Uncalibrated radiocarbon dating (years ^{14}C BP)	n	Sampled species	References
Río de la Plata and adjoining areas	La Olla 1	38°57′S–61°22′W	From 7300 to 6600	6	*A. australis*	Bayón and Politis (1996), Blasi et al. (2013)
	Barrio Las Dunas	38°59′S–61°20′W	ca. 7000	3	*A. australis*	Bayón et al. (2012)
Northern and central Patagonia	Cracker 8, level 3	42°56′S–64°29′W	5200 ± 70	5	*A. atra atra*	Gómez Otero (2007a)
				2	*N. magellanica*	
	Playa Las Lisas 2, midden 2	42°10′S–64°02′W	2600 ± 60	5	*N. magellanica*	Gómez Otero (2007a)
	Bajada de los Pescadores	40°55′S–64°23′W	2197 ± 38	2	*A. australis*	Borella and Cruz (2012)
	Playa Las Lisas 2, profile 1	42°10′S–64°02′W	2140 ± 50	5	*A. atra atra*	Gómez Otero (2007a)
	Cueva del Negro, grid 1, level 2	47°54′S–65°46′W	1730 ± 80	1	*A. australis*	Beretta et al. (2011), Zubimendi et al. (2011)
	Playa Unión, Barranca Norte 1, hearth 1	43°16′S–65°00′W	1040 ± 70	3	*A. australis*	Gómez Otero (2007a)
	Ecocentro, hearth 3	42°46′S–64°59′W	850 ± 150	5	*N. magellanica*	Gómez Otero (2007a)
	Las Ollas, midden 1	42°38′S–64°05′W	640 ± 40/610 ± 60	5	*A. atra atra*	Gómez Otero (2007a)
Tierra del Fuego	Túnel I, layer E and D (phases I-V)	54°51′S–67°54′W	From 6470 ± 100 to 5840 ± 185	20	*A. australis*	Orquera and Piana (1999), Orquera and Piana (2000), Zangrando et al. (2014)
	Imiwaia I, layer M and K	54°52′S–67°17′W	5940 ± 50/5750 ± 170 5840 ± 45/5710 ± 50	5 5	*M. edulis* *N. magellanica*	Orquera and Piana (1999, 2000)
	Túnel I, layer D (phases VI-VIII)	54°51′S–67°54′W	From 5050 ± 520 to 4590 ± 130	10	*A. australis*	Orquera and Piana (1999), Zangrando et al. (2014)
	Túnel I, layer alfa-X	54°51′S–67°54′W	2690 ± 80/2660 ± 100	3	*A. australis*	Orquera and Piana (1999), Zangrando et al. (2014)
	Shamakush X, layer E	54°51′S–67°51′W	500 ± 100	5 4	*M. edulis* *N. magellanica*	Orquera and Piana (1996), Orquera and Piana (1999)
	Túnel VII	54°51′S–67°54′W	100 ± 45	13 5 5	*A. australis* *M. edulis* *N. magellanica*	Orquera and Piana (1999), Zangrando et al. (2014)

Stable isotope analysis

Bone, shell and prey samples were dried at 60 °C for 36–48 h and ground to a fine powder with a mortar and pestle. Previously, shell surfaces were polished with sandpaper and with a diamond wheel drill to eliminate impurities and then rinsed with distilled water. Lipids were extracted from all samples through sequential soak in a chloroform/methanol (2:1) solution (Bligh and Dyer 1959). Since both bone and shell samples contain high concentrations of inorganic carbon that may bias δ^{13}C values (Lorrain et al. 2003), they were treated by soaking for 24 h in 0.5 and 1 N hydrochloric acid (HCl), respectively, until no more CO_2 was released (Newsome et al. 2006). Since the HCl treatment may alter the δ^{15}N values (Bunn et al. 1995), each sample was split into two subsamples: one was used for δ^{15}N analysis without decarbonising and the other was used for δ^{13}C analysis after decarbonising.

Approximately, 0.60–1 mg of bone, 0.15–16 mg of bivalve and limpet shells, and 0.30–0.50 mg of prey samples were weighed into tin cups, combusted at 900 °C and analysed in a continuous flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA Thermo Finnigan). For shell samples, a CO_2 absorbent for elemental

analysis (CaO/NaOH) was employed to avoid the saturation of the spectrometer during the analysis of the non-decarbonised samples, constituting 90% $CaCO_2$.

Stable isotope abundance was expressed in standard δ notation relative to carbonate Pee Dee Belemnite and atmospheric nitrogen standard scales. Carbon to nitrogen (C:N) atomic ratio was used as proxy for data quality (e.g. an adequate lipid extraction in modern samples (Newsome et al. 2010) and the conservation status of the isotopic ratio in archaeological samples (DeNiro 1985)). Prey, shell and most of the bone samples were analysed at the Centres Científic i Tecnològics of the University of Barcelona (CCiT-UB) at a precision of 0.3‰ for nitrogen and 0.2‰ for carbon. However, some modern fur seal bone samples and samples from the Túnel archaeological locality (Zangrando et al. 2014) were analysed at the Instituto de Geocronología y Geología Isotópica (INGEIS-CONICET/UBA) at a precision of 0.2‰ for both nitrogen and carbon. Therefore, to test whether these data sets are comparable, modern ($n = 5$) and archaeological ($n = 4$) fur seal bone samples were analysed at both laboratories and then paired samples were statistically tested. The isotopic values of fur seal bones analysed at both laboratories were not significantly different (paired t test for archaeological samples: $P > 0.05$, $n = 4$; paired Wilcoxon test for modern samples, $P > 0.05$, $n = 5$); hence, samples were pooled for further analysis.

Data analysis

Changes in the isotopic baseline of each ecosystem through time were evaluated by means of ANOVA or Kruskal–Wallis tests, depending on the fit of the data to parametric requirements. In case of changes of the isotopic baseline and with the aim of making the stable isotope ratios of ancient fur seals comparable with those of modern ones in the current marine ecosystem, baseline correction factors (BCFs) for δ¹⁵N and δ¹³C were computed for each region and epoch. First, isotopic values of mussels and limpets were averaged, thus, integrating the two main trophic pathways (pelagic and benthic) that contribute to the base of marine food webs (Post 2002; Casey and Post 2011). Then, the averaged values of modern shells were subtracted from those of archaeological shells. Second, these estimated BCFs were added to the isotopic values of archaeological fur seal bones; in this way, the stable isotope ratios in ancient fur seal bones can be compared with those in their modern counterparts and with the current topology of the prey community. For those periods where the baseline could not be reconstructed because of the lack of shell samples, a baseline time-weighted average value using the BCFs from the adjacent periods was computed (see Table 2 for details). On the other hand, ancient fur

seal isotopic values from the Río de la Plata and adjoining areas (7000 BP) were corrected using the estimated BCFs from northern and central Patagonia area for 5200 BP (see "Discussion"). For each region, comparisons of baseline-corrected isotopic ratios (δ¹⁵N and δ¹³C) of ancient and modern fur seals were performed.

Age and sex of fur seals were not included in the analyses, as this information was not always available for archaeological individuals. To compare the isotopic composition of fur seal bones directly to those of its prey, the estimated trophic discrimination factors (TDFs) from diet to bone reported for adult males of the species were used (δ¹⁵N = +5.14; δ¹³C = +3.63; Vales et al. 2014).

Results

The δ¹³C values of mussels and limpets from northern and central Patagonia did not change significantly during the last ca. 5200 years (Kruskal–Wallis test *A. atra atra*: $H = 6.962$, $df = 3$, $P = 0.0731$; *N. magellanica*: $H = 4.303$, $df = 3$, $P = 0.2305$). Conversely, the δ¹⁵N values differed significantly over this period of time (Kruskal–Wallis test, *A. atra atra*: $H = 16.655$, $df = 3$, $P = 0.0008$; *N. magellanica*: $H = 13.302$, $df = 3$, $P = 0.0040$). Regarding Tierra del Fuego, the δ¹⁵N and δ¹³C values varied significantly in both species of molluscs throughout the last ca. 6400 years (Kruskal–Wallis test *M. edulis* for δ¹⁵N: $H = 15.44$, $df = 3$, $P = 0.0015$, and for δ¹³C: $H = 12.45$, $df = 3$, $P = 0.006$; ANOVA test *N. magellanica* for δ¹⁵N: $F_{3,15} = 20.61$, $P < 0.0001$, and for δ¹³C: $F_{3,13} = 12.59$, $P = 0.0004$). These results indicate major temporal changes in the isotopic baseline of both regions, highlighting the necessity of correcting the δ¹³C and δ¹⁵N values of fur seal samples from different periods before any comparison (Table 2).

Most C:N atomic ratios lay within the expected range for unaltered bone samples (2.9–3.6; DeNiro 1985), the exception being those samples from the archaeological sites of Barrio Las Dunas and Playa Unión which showed a C:N ratio higher than 3.6 (Table 3). However, as collagen samples with high C:N ratios do not necessary mean isotopic alterations, and the range of δ¹³C and δ¹⁵N values are within the expected isotopic niche of the species (Grupe and Piepenbrink 1987; van Klinken 1999), these latter samples were included in the analyses.

After correcting for changes in the stable isotope baseline (Table 3), ancient fur seals from the Río de la Plata (ca. 7000 BP) were depleted in ¹³C relative to modern ones (Wilcoxon rank-sum test, $W = 12$, $P < 0.0001$; Fig. 2d), whereas no statistically significant changes were found for δ¹⁵N (t test, $T = 1.248$, $df = 8.26$, $P = 0.246$; Fig. 2a). On the other hand, baseline-corrected stable isotope ratios of ancient fur seals from northern and central Patagonia

Table 2 Stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) of modern and ancient shell valves and the estimated baseline correction factors (BCFs) for archaeological fur seal bone samples from northern and central Patagonia, and Tierra del Fuego

Region	Uncalibrated radiocarbon dating (year ^{14}C BP)	Species	$\delta^{15}N$ (‰)	BCF for $\delta^{15}N$	$\delta^{13}C$ (‰)	BCF for $\delta^{13}C$	Sample on which BCF was applied
Northern and central Patagonia	Present	*A. atra atra*	11.4 ± 0.3 (7)	0	−16.6 ± 1.2 (7)	0	
		N. magellanica	11.8 ± 0.5 (5)		−13.5 ± 3.0 (5)		
	610 ± 60/640 ± 40	*A. atra atra*	13.1 ± 0.3 (5)	1.7	−16.2 ± 3.4 (2)	−0.6	
	850 ± 150	*N. magellanica*	13.5 ± 0.9 (5)		−15.1 ± 2.6 (5)		
	1040 ± 70	*A. atra atra*	No data	1.9[ab]	No data	−0.4[ac]	Cueva del Negro Playa Unión
		N. magellanica	No data		No data		
	2140 ± 50	*A. atra atra*	13.7 ± 1.4 (5)	3.0	−14.3 ± 1.2 (5)	0.3	Bajada de los Pescadores
	2600 ± 60	*N. magellanica*	15.7 ± 0.5 (5)		−15.2 ± 2.7 (4)		
	5200 ± 70	*A. atra atra*	14.1 ± 0.2 (5)	2.5	−17.9 ± 0.0 (2)	−2.7	La Olla 1[d]
		N. magellanica	14.1 ± 1.3 (2)		−17.6 ± 0.4 (2)		Barrio Las Dunas[d]
Tierra del Fuego	Present	*M. edulis*	11.9 ± 0.3 (5)	0	−16.7 ± 0.6 (5)	0	
		N. magellanica	10.8 ± 0.3 (5)		−12.6 ± 1.6 (5)		
	100 ± 45	*M. edulis*	13.4 ± 0.8 (5)	1.6	−20.5 ± 0.7 (5)	−5.2	Túnel VII
		N. magellanica	12.5 ± 0.6 (5)		−19.4 ± 2.3 (5)		
	500 ± 100	*M. edulis*	13.4 ± 0.4 (5)	1.5	−14.6 ± 0.3 (3)	0.9	
		N. magellanica	12.1 ± 0.7 (4)		−13.0 ± 2.2 (2)		
	2660 ± 100/2690 ± 80	*M. edulis*	No data	2.1[a]	No data	−0.8[a]	Túnel I, layer alpha-X
		N. magellanica	No data		No data		
	From 5949 ± 50 to 5750 ± 170	*M. edulis*	15.4 ± 1.2 (5)	3.1	−18.2 ± 2.3 (5)	−3.6	Túnel I, layer E and D (phases I-VIII)
		N. magellanica	13.4 ± 0.5 (5)		−18.4 ± 2.1 (5)		

Isotopic values (mean ± SD) are shown with sample size in parentheses

[a] Baseline time-weighted average value from BCFs of adjacent periods were computed for those periods where there is no available isotopic data of shell. For example, for northern and central Patagonia ca. 1000 BP, BCFs for $\delta^{15}N$ and $\delta^{13}C$ values were calculated, respectively as

[b] (0.8 *1.7 + 0.2 *3.0) and

[c] (0.8 *−0.6 + 0.2 *0.3)

[d] BCFs developed from shell samples taken from the northern and central Patagonia region were applied to fur seal samples from these sites located in the Río de la Plata area

(2200–1730 BP and 1000 BP) were similar to those of their modern counterparts ($\delta^{15}N$: Kruskal–Wallis rank-sum test, $H = 0.110$, $df = 2$, $P = 0.946$; $\delta^{13}C$: ANOVA, $F_{2, 46} = 0.709$, $P = 0.497$; Fig. 2b, e). Ancient fur seals from the Río de la Plata (ca. 7000 BP) and Patagonia (1000 BP) exhibited greater variability in $\delta^{15}N$ values than modern individuals (Fig. 2a, b).

The baseline-corrected stable isotope ratios of fur seals from Tierra del Fuego varied through time ($\delta^{15}N$: Kruskal–Wallis rank-sum test, $H = 28.239$, $df = 4$, $P < 0.0001$; $\delta^{13}C$: ANOVA, F4, 47 = 79.96, $P < 0.0001$). Pairwise comparison revealed that ancient fur seals from 6400 to 5900 BP (20.6 ± 0.4‰) and 5000–4300 BP (20.2 ± 0.5‰) were more enriched in ^{15}N than those from the nineteenth century (18.6 ± 0.7‰) and modern periods (19.0 ± 1.6‰), whereas $\delta^{15}N$ values in fur seals from ca. 2600 BP (19.8 ± 1.3‰) did not differ significantly from those of other periods. Also, modern bone samples and those from ca. 2600 BP had greater variability in $\delta^{15}N$ values (Fig. 2c). On the other hand, pairwise comparison

Table 3 Baseline-corrected stable isotope ratios (δ^{15}N and δ^{13}C) of modern and ancient bone samples of South American fur seals from three regions of the southwestern South Atlantic Ocean

Region	Uncalibrated radiocarbon dating (year ^{14}C BP)	Sample size	δ^{15}N (‰)	δ^{13}C (‰)	C:N atomic ratio
Río de la Plata and adjoining areas	7000	9	21.3 ± 1.9	−15.9 ± 0.6	4.0 ± 0.9
	Modern	58	20.5 ± 0.6	−13.5 ± 0.8	3.4 ± 0.2
Northern and central patagonia	2200–1730	3	21.1 ± 1.3	−13.3 ± 0.8	3.4 ± 0.0
	1000	3	21.2 ± 2.6	−13.1 ± 0.2	4.8 ± 0.3
	Modern	43	20.6 ± 1.0	−13.5 ± 0.5	3.3 ± 0.1
Tierra del Fuego	6400–5900	20	20.6 ± 0.4	−15.5 ± 0.6	3.2 ± 0.0
	5000–4300	10	20.2 ± 0.5	−15.3 ± 0.5	3.2 ± 0.0
	2600	3	19.8 ± 1.3	−13.0 ± 0.6	3.3 ± 0.1
	100	13	18.6 ± 0.7	−17.2 ± 0.3	3.2 ± 0.1
	Modern	6	19.0 ± 1.6	−13.2 ± 0.7	3.2 ± 0.1
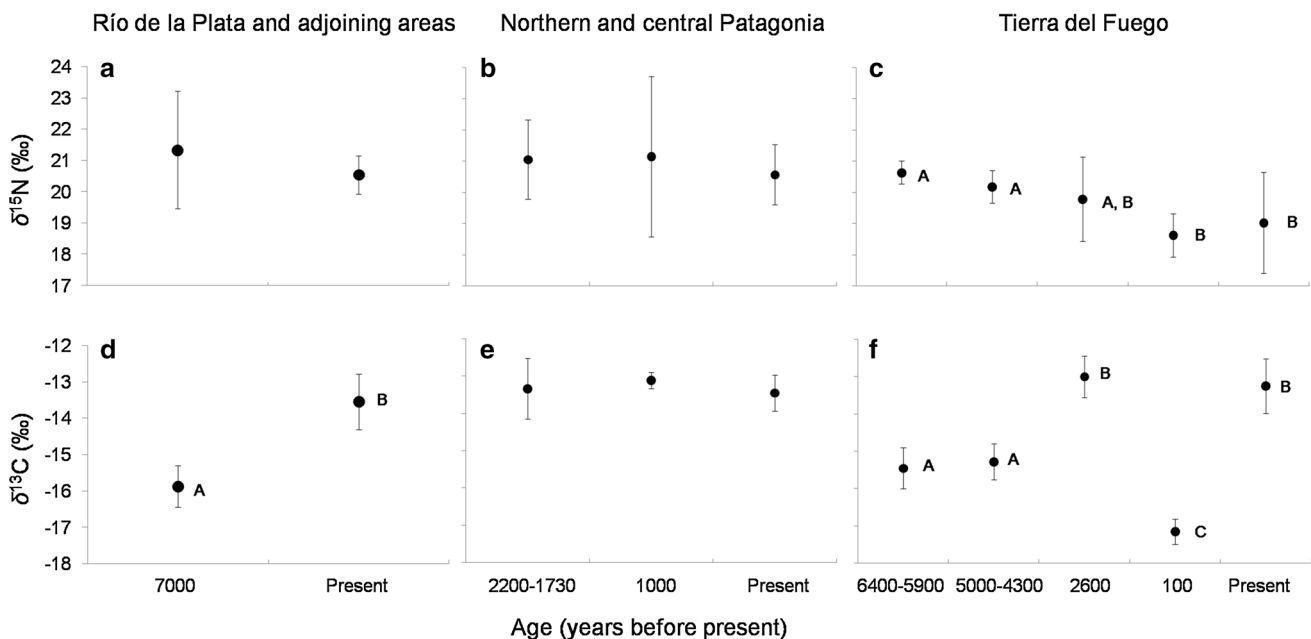
Fig. 2 Mean and standard deviation of baseline-corrected nitrogen (**a**, **b** and **c**) and carbon (**d**, **e** and **f**) stable isotope ratios for ancient and modern bone samples of South American fur seals from the southwestern South Atlantic Ocean. Means with a *different letter* differ significantly ($P < 0.05$)

for baseline-corrected δ^{13}C values indicated that modern fur seals (−13.2 ± 0.7‰) and those from 2600 BP (−13.0 ± 0.6‰) were enriched in ^{13}C as compared with those from 6400 to 5900 BP (−15.5 ± 0.6‰) and 5000 to 4300 BP (−15.3 ± 0.5‰), which in turn were enriched in ^{13}C in comparison to the nineteenth century bone samples (−17.2 ± 0.3‰) (Fig. 2f).

After correcting the δ^{13}C and δ^{15}N values of the predator for diet-to-bone discrimination factor, the bivariate signal of modern fur seals placed well within the isotopic ratios of their potential prey in all three regions (Online Resource

1; Fig. 3). However, fur seals from the Río de la Plata and Tierra del Fuego had a different trophic position in the past, as shown by the δ^{13}C and δ^{15}N values corrected for TDFs and BCFs (Fig. 3a, c).

Discussion

The results reported here reveal major changes in the trophic ecology of South American fur seals during the second half of the Holocene in the Río de la Plata and

Fig. 3 δ^{13}C-δ^{15}N biplots showing the bivariate stable isotope ratios (mean ± SD) of modern (*filled triangles*) and ancient (*empty figures*) South American fur seals and their modern prey (*filled circles*) from the southwestern South Atlantic Ocean, after correcting for baseline (BCFs) and for trophic discrimination factors (TDFs). Regions: **a** Río de la Plata and adjoining areas, **b** northern and central Patagonia, and **c** Tierra del Fuego
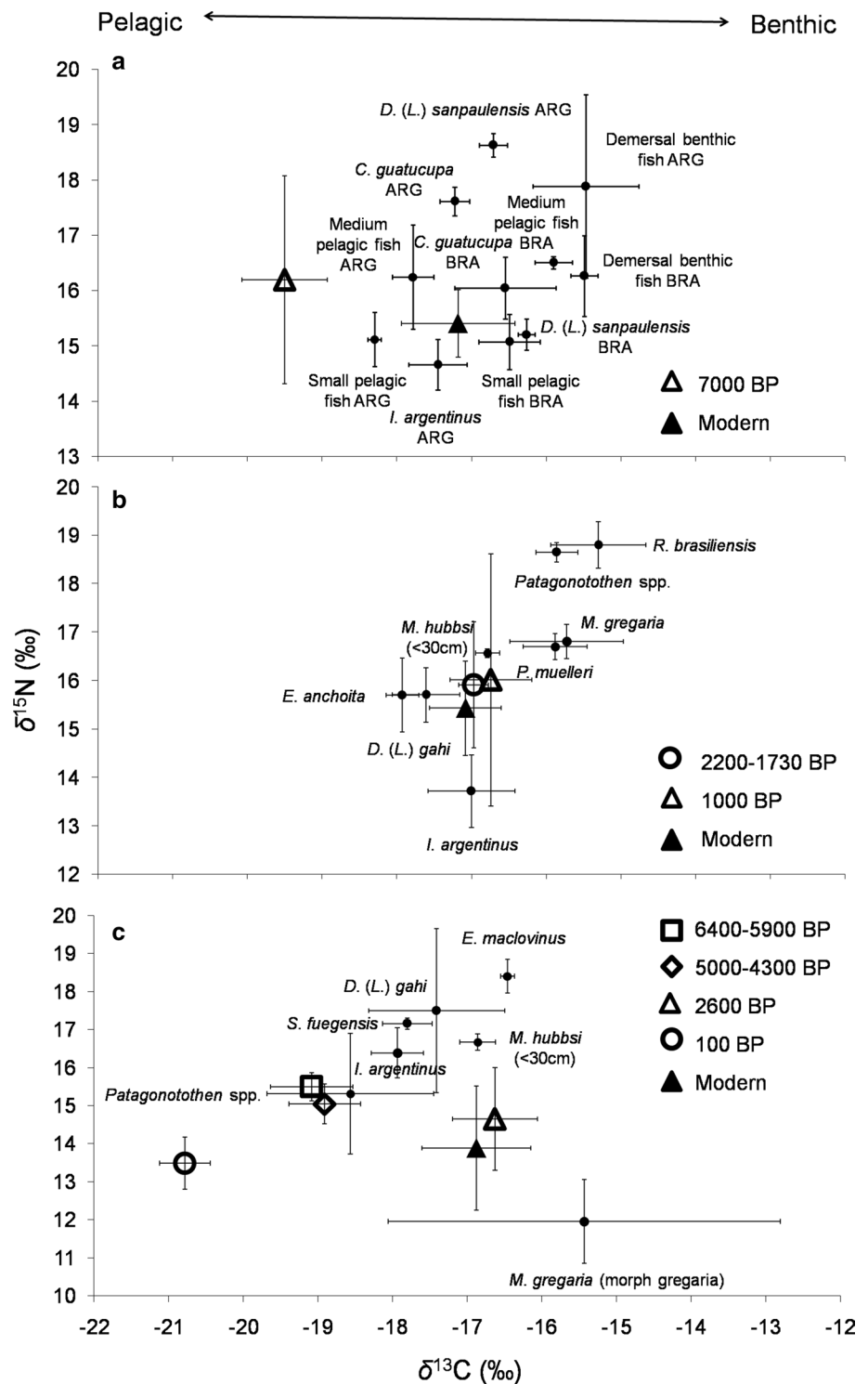
adjoining areas and also in Tierra del Fuego, but little change in northern and central Patagonia. In those regions where dietary shifts have occurred, fur seals varied the relative proportion of pelagic/offshore and benthic/coastal prey in their diets or their trophic position. However, disentangling the relative importance of hunting and environmental

forcing in those dietary changes is difficult, because changes in marine primary productivity and human exploitation often overlapped and might have operated synergistically. Furthermore, changes in the variability of the δ^{15}N values of fur seals among spatially or temporally separated ecosystems cannot be considered indicative of changes in

the diversity of individual foraging strategies, as the variability in the $\delta^{15}N$ values of ancient baselines and prey is unknown (Newsome et al. 2007b; Jackson et al. 2011).

The interpretation of the data reported here relies on four major assumptions:

1. The organic matrix of mollusc shells records the changes in the isotopic baseline of the ecosystem throughout time and the stable isotope ratios in the bones of predators change accordingly (Casey and Post 2011). If so, changes in the isotopic baseline can be accounted for and baseline-corrected samples from different periods can be compared. If not, temporal comparison is meaningless. We believe that there is high likelihood of this assumption being valid because the organic matter of modern mollusc shells is a good proxy of the isotopic baseline of the ecosystem (Saporiti et al. 2014b, 2015) and the atomic C:N ratio of the organic matter recovered from ancient shells was within the range of modern ones, excluding major taphonomic changes.

2. Benthic and pelagic primary producers contributed equally to the nitrogen and carbon pool fuelling the food web and hence one species of limpet (surface-grazing organism) and one species of mussel (filter-feeding organism) can be combined for correcting changes in the stable isotope baseline. The correction factors calculated in that way for $\delta^{15}N$ are unlikely to be affected by changes in the relative contribution of benthic and pelagic primary producers to the pool of organic matter fuelling the food web, as currently herbivores from the benthic and pelagic compartments have similar $\delta^{15}N$ values (Saporiti et al. 2015). Conversely, the correction factors calculated for $\delta^{13}C$ are sensitive to changes in the relative contribution of benthic and pelagic primary producers to the carbon pool, as shells of limpets and mussels usually differ in their $\delta^{13}C$ values (Saporiti et al. 2015). Accordingly, changes in the $\delta^{13}C$ values of fur seals reveal changes in their diets, but may also reveal to an unknown degree changes in the relative contribution of benthic and pelagic primary producers to the carbon pool.

3. The prey-to-predator trophic discrimination factor has not changed through time. If so, shifts in the stable isotope ratios of the predator can be interpreted as dietary shifts within the framework of the current marine ecosystem. Otherwise, temporal comparison still stand, but the use of modern prey to interpret ancient dietary shifts is meaningless. This assumption is likely to be robust, as there is no reason why the prey-to-predator trophic discrimination factor has changed through time in an endothermic carnivore, even if diet changed throughout time.

4. The topology of the prey community within the $\delta^{13}C$–$\delta^{15}N$ space has not changed throughout time, although the actual stable isotope ratios may have changed because of changes in the stable isotope baseline. If so, shifts in the stable isotope ratios of the predator can be interpreted as dietary shifts according to the current topology of the community. In fact, the topology of the prey community within the $\delta^{13}C$–$\delta^{15}N$ space has probably changed over time, but the depletion of pelagic prey on ^{13}C compared with demersal prey and the increase in the $\delta^{15}N$ values with trophic position are expected to last, since these relationships are general across ecosystems (Post 2002).

The results presented here highlight the necessity for reconstructing the isotopic baseline when using stable isotope ratios in palaeoecological studies (Casey and Post 2011; Saporiti et al. 2014a), as the isotopic ratios of mollusc shells showed major significant temporal changes in some regions. Mollusc shells are expected to incorporate any variation in the isotopic ratios of carbon and/or nitrogen produced at the base of the food web (Post 2002; Casey and Post 2011). This includes not only changes in primary productivity (Saporiti et al. 2014b), but also the modification of the $\delta^{13}C$ values after the Industrial Revolution due to the Oceanic Suess effect (Keeling 1979). This is because any effect of anthropogenic CO_2 on the $\delta^{13}C$ composition of marine primary producers is transmitted to their immediate consumers (in this case, limpets and mussels) and the entire food web, finally reaching higher trophic levels. Furthermore, freshwater runoff from rivers and peat bogs may have changed dramatically during the Holocene in response to glacier melting and changes in precipitation (Saporiti et al. 2013) and hence the supply of terrestrial organic matter, which is particularly relevant in some regions of Tierra del Fuego (e.g. Imiwaia I in the Beagle Channel).

Ideally, the isotopic baseline has to be assessed independently for each archaeological site, but this is not always possible for two reasons. First, mollusc shells did not occur at every archaeological site, as it was the case of the region inhabited by Pampean hunter-gatherers (Bonomo 2005). Second, fur seal remains were too scarce in some archaeological sites to allow a meaningful analysis on their own. Stable isotope ratios in the mollusc shells from temporally and geographically nearby sites is the only way to address the first limitation. For this reason, shells from Cracker 8 were used to correct the stable isotope ratios in fur seal samples from La Olla 1 and Barrio Las Dunas, although they were ca. 2000 years apart. Pooling them is reasonable because both groups of samples correspond to the same period (the Holocene Climatic Optimum, 7000–5000 years BP), when the sea level and temperature were higher than today and the influence of the Brazilian current expanded

further south (Aguirre 1993; Codignotto and Aguirre 1993; Ponce et al. 2011). Nevertheless, results should be interpreted with caution until contemporaneous shells are recovered.

In any case, only after correcting the stable isotope ratios in predators to account for changes in the isotope baseline can temporal changes in the $\delta^{15}N$ and $\delta^{13}C$ values be confidently interpreted as shifts in trophic position and in the proportion of pelagic/benthic prey in the diet, respectively. The relevance of using baseline-corrected data is highlighted by a dataset from Tierra del Fuego. Recently, Zangrando et al. (2014) suggested, on the basis of changes in stable isotope ratios and the reduction of jaw size, that the hunting pressure on fur seals by hunter-gatherers could have resulted in changes in the habitat use patterns of fur seals inhabiting the Beagle Channel. However, differences between the diet of fur seals from the Middle and Late Holocene do not hold once the shifts in the isotopic baseline are accounted for (this study), although such correction did not affect the comparisons of stable isotope ratios by time period for male and female fur seals (Zangrando et al. 2014).

Also, it is worth noting that subadult and adult males prevailed in the modern samples of fur seals analysed here, whereas the sex and the age of several individuals recovered from archaeological assemblages were unknown. As stable isotope values of fur seals usually differ between males and females (Franco-Trecu et al. 2014; Zangrando et al. 2014), as well as with the age of the individuals (Vales et al. 2015), the lack of information about the sex and age of the ancient individuals sampled certainly influenced the results. For instance, the maximum differences in average bone stable isotope ratios among different age classes of male fur seals (i.e. yearling, juvenile, subadult and adult) are 1.2‰ for $\delta^{13}C$ and 1.3 ‰ for $\delta^{15}N$ (see Table 1 in Vales et al. 2015), whereas the maximum differences found in average bone stable isotope ratios between sexes are in the order of 0.7‰ for $\delta^{13}C$ and 0.6‰ for $\delta^{15}N$ (see Table 3 in Zangrando et al. 2014). Nevertheless, the differences found between the isotopic values of ancient and modern fur seals from the Río de la Plata and Tierra del Fuego are larger than those above reported, thus indicating that factors other than sex and age are involved.

After accounting for temporal changes in the isotopic baseline, and with the aforementioned caveats in mind, major dietary differences emerge. Ancient fur seals (ca. 7000 BP) from the Pampean coast (Buenos Aires province) were highly depleted in ^{13}C compared with their modern counterparts, which may be indicative of a more pelagic or oceanic foraging behaviour in the past. Middle Holocene Pampean hunter-gatherers exploited coastal resources on a seasonal basis (Bonomo 2005, 2011) and pinnipeds were always second order prey (Bonomo et al. 2013; León

2014), thus suggesting a low rate of exploitation. On the other hand, the Buenos Aires province coastline was placed several kilometres further westward during the Holocene Climatic Optimum (7000–5000 BP), when the sea level and temperature were higher than today (Codignotto and Aguirre 1993; Ponce et al. 2011). This allowed a further southward extension of the Brazilian current and a slightly higher sea surface temperature (ca. 2 °C) than the current one (Aguirre 1993). In turn, higher salinity gradients characterised sites that today are under the influence of the huge Río de la Plata plume and show estuarine/marginal marine conditions (Aguirre et al. 2011). Therefore, the observed shift in the foraging ecology of ancient fur seals (7000 BP) from the Pampean coast may reflect differences in prey availability over the continental shelf in the past and/or the exploitation of alternative foraging areas as a consequence of changes in oceanic productivity and the Brazil Current circulation in the southwestern South Atlantic Ocean during the Holocene (Toledo et al. 2008; Nagai et al. 2010).

In northern and central Patagonia, fur seals had similar diets over the last 2200 years, although ancient fur seals had a higher variability of $\delta^{15}N$ values. Such stability is remarkable, considering that marine primary productivity is currently much lower (Saporiti et al. 2014b). In any case, Late Holocene hunter-gatherers from northern and central Patagonia exploited both terrestrial and marine resources and pinnipeds were a secondary resource (Gómez Otero 2007b; Favier Dubois et al. 2009; Moreno et al. 2011).

Regarding Tierra del Fuego, the foraging ecology of fur seals did not change from ca. 6400 BP to at least 4300 BP, as revealed by baseline-corrected stable isotope ratios. Fur seals prevailed in early zooarchaeological assemblages (ca. 6400–5500 BP) from the Beagle Channel, but their relative importance declined steadily since 5500–5000 BP (Zangrando 2009; Zangrando et al. 2010, 2014; Tivoli and Zangrando 2011). Such decline might be the result of increased or sustained hunting pressure by hunter-gatherers during the Middle–Late Holocene, as the jaw size of the harvested fur seals declined throughout time (Zangrando et al. 2014), or because of a reduction in marine primary productivity (Saporiti et al. 2014b). In any case, the trophic position of ancient fur seals remained the same during most of the Middle Holocene, although fur seals increased the consumption of benthic prey around 2600 years BP.

The fur seal bones recovered from shell middens in the Beagle Channel region and dated to the nineteenth century (dendrochronologically corrected date = 1835 AD; Orquera and Piana 1999) were characterised by low $\delta^{15}N$ and $\delta^{13}C$ values. At that time, exploitation of otariids by the Fuegian hunter-gatherers was greatly reduced (Tivoli and Zangrando 2011; Zangrando et al. 2014) and the fur seal stocks dramatically diminished as a result of commercial sealing in the Beagle Channel region and surroundings

(Clark 1887; Townsend 1910; Schiavini 1992; Orquera 2002; Dickinson 2007). Depletion of pinniped populations as a result of commercial sealing has often resulted in density-dependent responses leading to decreased intraspecific competition (Scheffer 1955; Trites and Biggs 1992; Etnier 2004; Hanson et al. 2009; Drago et al. 2010) and dietary changes (Hanson et al. 2009; Drago et al. 2010; Zenteno et al. 2015). For instance, isotopic results in sea lions from northern Patagonia suggest a dietary shift from pelagic to benthic coastal prey when the population was decimated by commercial sealing in the mid-twentieth century (Drago et al. 2009). Likewise, fur seals from the Beagle Channel underwent a dramatic change in their isotopic niche during the nineteenth century. In the current regional isoscape, low $\delta^{15}N$ and $\delta^{13}C$ values are indicative of foraging grounds in cold and oceanic waters of the Antarctic Convergence (McMahon et al. 2013). We ignore how the regional isoscape was during the nineteenth century, but if it was similar to the current one, myctophid fishes might have had some relevance in the diet of fur seals, as this prey has a highly ^{13}C-depleted signal (Ciancio et al. 2008) and is abundant in the region (Sánchez and de 1995). Certainly, cooler sea surface temperatures observed in the southwestern South Atlantic (Saporiti et al. 2013) during the Little Ice Age (from ca. early fifteenth to nineteenth centuries) may have influenced the distribution of some marine species (e.g. Boretto et al. 2013). In this scenario, an increased availability of prey coming from polar waters to fur seals inhabiting the Beagle Channel region may account for the changes recorded in the stable isotope values in ninetenth century fur seals. Alternatively, the few fur seals hunted by the Fuegian hunter-gatherers at that time might have not been residents of the Beagle Channel region, but migrants coming from other regions if the population had been actually decimated by a combination of reduced oceanic productivity and commercial sealing (Saporiti et al. 2014b). Similarly, the decline of sea lions in the Falkland/Malvinas Islands during the first half of the twentieth century has been attributed to environmental changes triggered by a decrease in sea surface temperature and the associated changes in food availability (Baylis et al. 2015).

The fur seal population from Tierra del Fuego has been recovering since the end of commercial harvesting (Crespo et al. 2015) and little is known about its current diet (Schiavini 1993), but isotopic results are consistent with the diet reported for the species in the nearby Falkland/Malvinas Islands (Strange 1983, 1992; Baylis et al. 2014). In turn, stable isotope ratios in bone of fur seals suggest that the species currently has a trophic position similar to that recorded 2600 years BP, but differs completely from that recorded during most of the Middle Holocene (e.g. 6400–4300 BP).

In conclusion, changes in nitrogen and carbon isotope ratios in fur seal bones could reflect changes in the southwestern South Atlantic ecosystem during most of the Holocene and prior to the commercial sealing era, when fur seal populations were expected to be large and the impact of aboriginal hunter-gatherers on pinniped populations small. On the other hand, the large-scale removal of fur seals and other species since the late eighteenth century may have modified their foraging habits, but the concurrence of environmental changes preclude assessment of the actual impact of commercial sealing on the foraging ecology of this species. In any case, the current trophic ecology of fur seals in some areas of the southwestern South Atlantic Ocean dramatically differs from that during the second half of the Holocene.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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