Shifting niches of marine predators due to human exploitation: the diet of the South American sea lion (*Otaria flavescens*) since the late Holocene as a case study

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Shifting niches of marine predators due to human exploitation: the diet of the South American sea lion (*Otaria flavescens*) since the late Holocene as a case study

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Abstract.——Stable isotope ratios of carbon and nitrogen in archaeological and modern bone samples have been used to reconstruct the dietary changes of the South American sea lion *Otaria flavescens* from the late Holocene to the present in the southwestern Atlantic. We sampled bones from archaeological sites in northern-central and southern Patagonia, Argentina, and bones housed in modern scientific collections. Additionally, we analyzed the stable isotope ratios in ancient and modern shells of intertidal molluscs to explore changes in the isotope baseline and allow comparison between bone samples from different periods after correction for baseline shifts. Results confirmed the trophic plasticity of the South American sea lion, demonstrated the much larger impact of modern exploitation of marine resources as compared with that of hunter-gatherers, and underscored the dissimilarity between the past and modern niches of exploited species. These conclusions are supported by the rather stable diet of South American sea lions during several millennia of aboriginal exploitation, in both northern-central and southern Patagonia, and the dramatic increase in trophic level observed during the twentieth century. The recent increase in trophic level might be related to the smaller population size resulting from modern sealing and the resulting reduced intraspecific competition. These results demonstrate how much can be learned about the ecology of modern species thanks to retrospective studies beyond the current, anthropogenically modified setting where ecosystem structure is totally different from that in the pristine environments where current species evolved.

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Introduction

Humans have dramatically modified the world by altering biogeochemical cycles and eroding biodiversity (Crutzen 2002; Terborgh and Estes 2010). Large species are particularly vulnerable to human impacts, and many of them declined in population size, or went extinct, before we had the ability to study and understand their ecological significance (Jackson et al. 2001; Martin 2005; Terborgh and

Estes 2010). Nevertheless, biologists still attempt to interpret the biology of extant species as if they had evolved in the current anthropogenic setting (Steadman 2006). In this context, a historical reference point is essential not only for understanding the evolutionary processes that operated in pristine environments, but also for providing goals for restoration and management (Jackson et al. 2001; Terborgh and Estes 2010; Braje and Rick 2011). Although much of the anthropogenic loss of biodiversity has

been caused by the expansion of western societies, aboriginal exploitation also resulted in significant levels of extinction and habitat modification (Jackson et al. 2001; Martin 2005; Terborgh and Estes 2010). Thus, we must study deep time, using the stable isotope ratios in bone collagen to reconstruct paleodiets and trophic levels to understand the natural trophic ecology of modern species in their original environments (Ambrose and DeNiro 1989; Schwarcz 2000).

Human impacts are not limited to terrestrial ecosystems; the world oceans also have been severely affected (Halpern et al. 2008). Eared seals, or Otariids, may exert strong top-down effects on ecosystem structure where abundant enough (Yodzis 1998; Koen-Alonso and Yodzis 2005) and are still major components of coastal ecosystems in the temperate regions of the Southern Hemisphere (Gentry 2009). However, most species of eared seals, commercially exploited for their pelts and fat, were hunted to the brink of extinction throughout the nineteenth and twentieth centuries, and currently some species remain well below their original numbers (Kovacs et al. 2012). Nevertheless, in some regions the human exploitation of eared seals predates the arrival of western sealers by several millennia, thus raising many questions about the actual impact of aboriginal exploitation (Porcasi et al. 2000; Jones et al. 2004; Newsome et al. 2007; Tivoli and Zangrando 2011).

The South American sea lion *Otaria flavescens* is widely distributed along some 10,000 km of the coast of South America (Cappozo and Perrin 2009). According to the zooarchaeological record, pinnipeds and other marine species were widely exploited by the hunter-gatherers inhabiting the Beagle Channel and northern Patagonia during the late Holocene, although the effect of aboriginal hunting on their populations remains uncertain (Schiavini 1993; Orquera and Piana 1999; Gómez Otero 2006; Favier Dubois et al. 2009; Favier Dubois and Kokot 2011; Orquera et al. 2011; Tivoli and Zangrando 2011; Borella and Cruz 2012; Favier Dubois and Scartascini 2012). Modern exploitation through its entire range began in the eighteenth century and lasted until the first half of the twentieth century, by which time the species had been severely depleted

(Cappozo and Perrin 2009). In Uruguay, the population is still decreasing, even though sealing ceased in 1995 (Páez 2006). The population breeding in Argentina experienced a 90% decline from the 1920s to the 1960s and currently is approximately one-third of the original size (Crespo and Pedraza 1991; Dans et al. 2004; Schiavini et al. 2004). Simultaneously, numbers of sea lions declined in the Falkland (Malvinas) Islands, where the small remaining population is less than 1.5% of the original size (Thompson et al. 2005).

South American sea lions are no longer hunted in the region, but the intense exploitation of fishes, squids, and crustaceans experienced during the last 40 years has deeply modified the structure of the ecosystems and caused a dramatic decrease in average fish size (Koen-Alonso and Yodzis 2005; Dato et al. 2006). South American sea lions are generalist predators (Thompson et al. 1998; Koen Alonso et al. 2000; Campagna et al. 2001; Riet-Sapriza et al. 2012) and during the twentieth century they have shifted their diet to adapt to the new environmental conditions created by industrial fishing (Suárez et al. 2005; Drago et al. 2009; Romero et al. 2011), but at the cost of consuming less profitable prey and reducing body size (Drago et al. 2010). Nevertheless, intraspecific competition, and not competition with fisheries, has been proposed to be the major determinant of diet composition in South American sea lions (Drago et al. 2009, 2010), as they consume primarily large prey that feed near the bottom (demersal hereafter) when and where the population is small (Koen Alonso et al. 2000; Drago et al. 2009; Riet-Sapriza et al. 2012) and shift to smaller benthic and pelagic prey when and where the population increases (Suárez et al. 2005; Drago et al. 2009; Romero et al. 2011). If this hypothesis is true, the current trophic niche of South American sea lions would be different from that exploited in the past, when the population was much larger (Rodriguez and Bastida 1998; Dans et al. 2004; Schiavini et al. 2004).

The presence of bones of the South American sea lion in the zooarchaeological record, together with extensive scientific collections of modern skeletal material, offers a unique opportunity to assess the magnitude of change

in the trophic ecology of a marine top predator in response to human exploitation and compare the effect of aboriginal and modern exploitation. To do so, here we analyze the stable isotope ratios of carbon and nitrogen in the bone of ancient and modern South American sea lions from Argentina to assess the dietary changes of the species through the second half of the Holocene and determine the trophic niche of the species in ancient ecosystems. The stable isotope ratios of modern and ancient organisms cannot be compared directly, because temporal variations in the isotopic baseline may exist (Casey and Post 2011). Nonetheless, the proteins that make up the organic matrix of mollusc shells can become encased within mineral crystals and preserved, hence offering a material suitable to reconstructing the changes in the isotopic baseline (Crenshaw 1980; Bailey et al. 2008; Casey and Post 2011). Accordingly, we also analyzed the stable isotope ratios in the shells of modern and ancient limpets and mussels to reconstruct, and compensate for, changes through time in the stable isotope baseline.
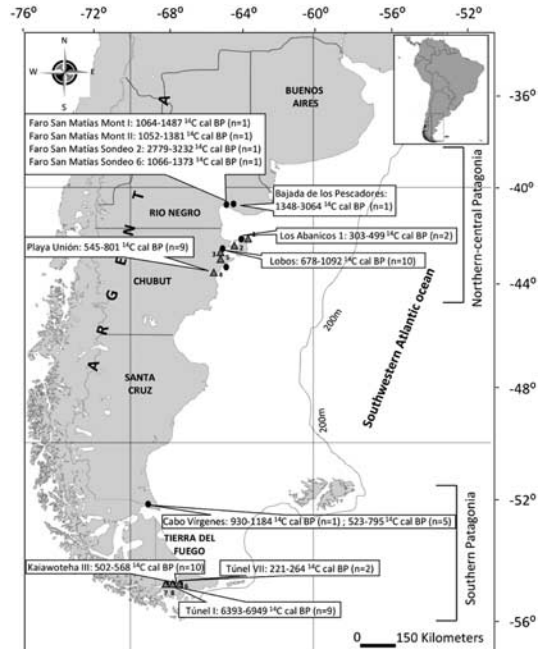

FIGURE 1. Location of archaeological sites from which sea lions and shells were sampled for stable isotope analysis. Sample sizes are listed in parentheses. The filled circles show archaeological sites for sea lions and the triangles denote sites for shells: 1 = Los Abanicos 1; 2 = Las Ollas Conchero 1; 3 = Ecocentro Fogón 3; 4 = Playa Las Lisas 2; 5 = Cracker 6; Túnel VII; 7 = Shamakush X; 8 = Imiwaia I.

Material and Methods

Study Site and Sample Collection.—We measured the stable isotope ratios of carbon and nitrogen of both modern and archaeological bone collagen samples of South American sea lions from two areas in Argentina (Fig. 1), northern-central Patagonia (from 39°S to 46°S) and southern Patagonia (from 46°S to 55°S). Modern samples of turbinate bones from South American sea lions were collected from specimens at the scientific collections at Centro Nacional Patagónico (Puerto Madryn, Argentina) and Museo Acatushún (Ushuaia, Argentina); the corresponding stable isotope ratios of carbon and nitrogen had been published previously elsewhere (Drago et al. 2009). Zooarchaeological bone samples from different skeletal elements were recovered from different layers of shell middens in northern-central Patagonia and southern Patagonia by researchers from Centro Nacional Patagónico, Centro Austral de Investigaciones Científicas, and Instituto Multidisciplinario de Historia y Ciencias Humanas (Table 1).

The samples were dated in different laboratories and using different methods, in particular samples from northern-central Patagonia, where all dated samples were marine shells instead of charcoal. We calibrated radiocarbon ages using the package Clam 2.2 (Blaauw 2010) and the new curve for Southern Hemisphere ShCal13 (Hogg et al. 2013). Reservoir effects data for the northern Patagonia region have emerged only recently, and they suggest variable differences between marine and terrestrial ages (Cordero et al. 2003; Favier Dubois 2009).

From December 2009 to February 2010 we collected the shells of modern molluscs from the two study regions (Supplementary Table). We have also analyzed zooarchaeological shell samples recovered from different layers of shell middens in northern-central Patagonia and the Beagle Channel, Tierra del Fuego (Fig. 1). Clementz and Koch (2001) pointed out that five samples are enough to provide robust estimates of mean and standard deviation for stable

TABLE 1. Ratios of stable isotopes of carbon and nitrogen in the bone tissue of South American sea lions from the archaeological sites of northern-central Patagonia (Río Negro and Chubut) and southern Patagonia (Santa Cruz and Tierra del Fuego).

Sample ID	Archaeological site	Skeletal element	Age (^{14}C ybp)	Calibrated age (^{14}C cal BP (±1σ)[1]	δ^{13}C (‰)	δ^{15}N (‰)	C:N	Reference
northern-central Patagonia								
FSM-SRH	Faro San Matías Mont II	rib	1630 ± 80	1052–1381 (91.1%)[1]	−11.4	22.4	3.3	Borella and Cruz 2012; Favier Dubois et al. 2009
OBS 13	Faro San Matías 6	vertebra	1380 ± 80	1066–1373 (95%)	−11.2	22.4	3.1	
OBS 137	Bajada de los pescadores	sternum	2197 ± 38	1348–3064 (94.9%)	−13.4	21.1	3.6	
OBS 4	Faro San Matías 2	radius	2910 ± 90	2779–3232 (95%)	−13.9	18.1	3.6	
FSM-SRH	Faro San Matías Mont I	rib	1680 ± 90	1064–1487 (94.2%)[1]	−11.9	23.0	3.7	
36	Los Abanicos 1	elbow	380 ± 60	303–499 (95%)	−12.3	21.4	4.0	Gómez Otero 2006
82	Los Abanicos 1	elbow			−11.8	23.8	3.5	
F$_1$ 17	Playa Union	humerus	1040 ± 70	545–801 (94.6%)[1]	−13.7	19.9	3.3	Gómez Otero 2006
FM$_1$13	Playa Union	humerus			−13.1	19.7	4.1	
FM$_1$14	Playa Union	humerus			−13.4	21.0	3.3	
FM$_1$15	Playa Union	humerus			−12.1	20.3	3.0	
FM$_1$16	Playa Union	humerus			−12.3	18.7	3.3	
FM$_1$17	Playa Union	humerus			−12.7	18.9	3.2	
FM$_1$19	Playa Union	humerus			−12.9	22.5	3.3	
FM$_1$20	Playa Union	humerus			−12.3	21.9	3.2	
FM$_1$21	Playa Union	humerus			−12.8	20.3	3.4	
i$_1$ 61	Lobos*	humerus	1290 ± 100	678–1092 (94.2%)[1]	−13.1	21.3	3.8	Serrán et al. 2008
i$_3$ 43	Lobos*	humerus			−13.0	22.0	3.2	
i$_4$ 44	Lobos*	humerus			−13.4	22.3	3.7	
i$_5$ 54	Lobos*	humerus			−11.0	22.2	3.4	
I$_{15}$ C1	Lobos*	humerus			−14.4	22.2	2.7	
I$_{18}$ 89	Lobos*	humerus			−13.6	25.0	3.4	
i 23	Lobos*	humerus			−12.8	21.3	3.3	
i 24	Lobos*	jaw			−14.6	23.2	3.5	
M$_1$1	Lobos*	humerus			−12.0	22.3	3.0	
M$_1$3	Lobos*	humerus			−13.0	22.4	3.8	
southern Patagonia								
CV6 4/-60–65cm	Cabo Vírgenes	rib	1190 + 60	930–1184 (94.7%)[2]	−13.9	20.8	3.4	L' Heureux and Franco 2002
CV20 OF1	Cabo Vírgenes	phalange			−14.8	15.4	3.0	
CV20 OF3	Cabo Vírgenes	skull			−14.5	17.9	3.4	
CV20 OF4	Cabo Vírgenes	skull	1256 ± 50	523–795 (95%)[2]	−12.2	19.1	3.2	Belardi et al. 2011
CV 20 OF6	Cabo Vírgenes	jaw			−12.3	19.6	3.9	
CV20 OF7	Cabo Vírgenes	skull			−14.2	18.8	3.5	
30459	Túnel I, Capa D	jaw	5000–4300	6393–6949 (93.2%)	−11.3	19.6	3.2	Orquera and Piana 1988
33458	Túnel I, Capa D	jaw			−12.4	18.5	3.0	
33459	Túnel I, Capa D	jaw			−11.4	18.7	3.2	
33551	Túnel I, Capa D	jaw			−11.8	18.8	3.2	
33571	Túnel I, Capa D	jaw			−12.5	19.0	3.4	
33717	Túnel I, Capa D	jaw			−12.7	18.4	2.7	

ID	Site/Stratum	Bone	Date (BP)	Range	Ref.	δ13C	δ15N	δ...
34177	Túnel I, Capa D	jaw				−12.3	18.6	3.1
34544	Túnel I, Capa D	jaw				−12.0	18.4	3.9
34751	Túnel I, Capa D	jaw **				−11.6	18.9	3.8
43418	Túnel VII	bone **	100 ± 45	221–264 (17.0%)	Piana et al. 1992	−11.7	18.5	2.7
154286	Túnel VII	bone **	580 ± 45	502–568 (74.2%)	Piana et al. 2007	−11.3	17.7	2.8
OF 2a	Kaiawoteha III, Capa K	humerus				−13.8	17.4	3.5
OF 2b	Kaiawoteha III, Capa K	humerus				−15.6	16.8	3.2
OF 3	Kaiawoteha III, Capa K	coxal				−15.1	16.5	2.9
OF 5	Kaiawoteha III, Capa K	radius				−15.6	16.9	3.4
OF 7	Kaiawoteha III, Capa K	radius				−14.2	17.6	3.7
OF 9	Kaiawoteha III, Capa K	humerus				−14.2	16.3	3.9
OF 10	Kaiawoteha III, Capa K	coxal				−12.6	17.3	4.0
OF 12	Kaiawoteha III, Capa K	maxilla				−12.2	17.8	4.1
OF 14	Kaiawoteha III, Capa K	coxal				−13.2	17.8	3.3
OF 15	Kaiawoteha III, Capa K	maxilla				−14.1	19.2	3.2

*Paleontological site
**Unspecified
[1] The regional marine reservoir effect of 266 ± 51 years was included in the calibration of the samples (Favier Dubois 2009).
[2] The regional marine reservoir effect of 516 ± 85 years was included in the calibration of the samples (Cordero et al. 2003).

isotope ratios in tissues that integrate dietary information over long periods of time, and hence sample size was set at five for each species, locality, and zooarchaeological stratum where available (Supplementary Table). The limpet *Nacella magellanica* was sampled everywhere, but the rubbed mussel (*Aulacomya atra atra*) was sampled in northern-central Patagonia and the blue mussel (*Mytilus edulis*) in southern Patagonia, according to availability in regional shell middens.

Bones of some fish species are abundant in the zooarchaeological record of both northern-central and southern Patagonia (Favier Dubois et al. 2009: Favier Dubois and Kokot 2011; Favier Dubois and Scartascini 2011; Tivoli and Zangrando 2011), but the remains of cephalopods, shrimp and squat lobsters are missing. These taxa are important prey for modern South American sea lions (Thompson et al. 1998; Koen Alonso et al. 2000; Suárez et al. 2005; Romero et al. 2011) and hence necessary for comparisons between the stable isotope ratios of ancient South American sea lions and those of potential prey from the same period and region. For this reason, we analyzed muscle samples from the prey species currently consumed by South American sea lions (Table 2) and inferred the likely stable isotope ratios expected for ancient prey after correcting for the changes in the isotopic baseline revealed by the analysis of mollusc shells. Furthermore, we computed a diet-to-bone discrimination factor by combining published information about diet-to-vibrissa fractionation in marine carnivores (Hobson et al. 1996; Newsome et al. 2010) and the stable isotope ratios of paired samples of vibrissa and bone from eight adult South American sea lions dead-stranded in northern Patagonia between 2006 and 2011 (see below for details about the calculations). This discrimination factor is necessary for comparing the stable isotope rations in the tissue of the predator with those in the tissue of its prey.

Bone and shell samples were stored dry at room temperature. Samples from potential prey were stored at −20°C prior to analysis.

Stable Isotope Analysis.—Bones were cleaned of sediment and dried in a stove at 50°C. Shell samples were polished with sandpaper

TABLE 2.   Ratios of stable isotopes of carbon and nitrogen (mean ± standard deviation) in the muscle of modern potential prey of the South American sea lion off northern-central Patagonia and southern Patagonia.

Species	Common name or synomym	Family	n	$\delta^{13}C$ (‰) (mean ± SD)	$\delta^{15}N$ (‰) (mean ± SD)
northern-central Patagonia					
Demersal					
Enteroctopus megalocyathus	Red octopus	Octopodidae	4	− 14.7 ± 0.6	18.5 ± 1.9
Genypterus blacodes	Pink cusk-eel	Ophidiidae	5	− 14.7 ± 0.4	18.0 ± 0.3
Munida subrugosa	Squat lobster	Galatheidae	5	− 15.7 ± 0.8	16.8 ± 0.4
Octopus tehuelchus	Tehuelchus	Octopodidae	5	− 14.8 ± 0.2	19.9 ± 0.4
Paralichthys isosceles	Flounder	Paralichthyidae	5	− 16.0 ± 0.4	18.0 ± 0.6
Patagonotothen cornucola	*Notothenia cornucola*	Nototheniidae	2	− 15.6 ± 0.1	18.8 ± 0.2
Patagonotothen ramsayi	*Notothenia ramsayi*	Nototheniidae	2	− 16.1 ± 0.2	18.6 ± 0.2
Platyxanthus patagonicus	True crabs	Platyxanthidae	5	− 15.3 ± 0.2	16.3 ± 0.9
Pleoticus muelleri	Red shrimp	Solenoceridae	5	− 15.9 ± 0.4	16.7 ± 0.3
Raneya brasiliensis	Banded cusk-eel	Ophidiidae	5	− 15.3 ± 0.7	18.8 ± 0.5
Pelagic					
Engraulis anchoita	Argentine anchovy	Engraulidae	5	− 18.0 ± 0.2	15.7 ± 0.8
Illex argentinus	Argentine short-finned squid	Ommastrephidae	5	− 17.0 ± 0.6	13.7 ± 0.8
Loligo gahi	Patagonian squid	Loliginidae	5	− 17.2 ± 1.0	16.2 ± 1.2
Loligo sanpaulensis	Brazilian squid	Loliginidae	5	− 16.8 ± 0.2	17.2 ± 0.3
Merluccius hubbsi (≥30cm)	Argentine hake	Merlucciidae	9	− 17.3 ± 0.7	16.2 ± 0.5
Merluccius hubbsi (<30cm)	Argentine hake	Merlucciidae	5	− 17.0 ± 0.5	17.1 ± 0.4
Stromateus brasiliensis	Southwest Atlantic butterfish	Stromatidae	2	− 17.0 ± 0.9	16.2 ± 0.4
southern Patagonia					
Demersal					
Eleginops maclovinus	Patagonian blenny	Eleginopsidae	2	− 16.5 ± 0.1	18.4 ± 0.4
Genypterus blacodes	Pink cusk-eel	Ophidiidae	5	− 17.2 ± 0.8	18.3 ± 0.5
*Macroronus magellanicus**	Hoki	Merlucciidae	5	− 18.2 ± 0.7	13.9 ± 0.7
Munida gregaria	Lobster krill	Galatheidae	5	− 15.4 ± 2.6	11.9 ± 1.1
Paralichthys patagonicus	Patagonian flounder	Paralichthyidae	1	− 15.8	19.0
Patagonotothen ramsayi	Rock cod	Nototheniidae	5	− 18.4 ± 1.4	15.6 ± 2.2
Pleoticus muelleri	Red shrimp	Solenoceridae	5	− 15.6 ± 0.4	15.7 ± 0.5
Psammobatis rudis	Smallthorn sand skate	Rajidae	3	− 14.8 ± 0.8	16.7 ± 0.6
Pelagic					
Illex argentinus	Argentine short-finned squid	Ommastrephidae	5	− 17.9 ± 0.4	16.4 ± 0.7
Loligo gahi	Patagonian squid	Loliginidae	5	− 17.2 ± 1.0	17.3 ± 2.1
Merluccius hubbsi (≥30 cm)	Argentine hake	Merlucciidae	10	− 18.0 ± 0.2	17.2 ± 0.2
Merluccius hubbsi (<30 cm)	Argentine hake	Merlucciidae	3	− 16.8 ± 0.2	16.7 ± 0.3
**Mictophids*	Lanternfish	Myctophidae	17	− 21.9 ± 0.7	11.7 ± 0.9
Sprattus fuegensis	Falkland sprat	Clupeidae	5	− 17.8 ± 0.3	17.2 ± 0.2
Stromateus brasiliensis	Southwest Atlantic butterfish	Stromateidae	5	− 17.8 ± 0.5	15.7 ± 1.2

*Reference: Ciancio et al. 2008

and with a diamond wheel drill to remove impurities and subsequently rinsed with distilled water and dried in a stove at 50°C. White muscle from fish and mantle from squids were thawed and dried in a stove at 50°C. Once dry, all samples were ground to a fine powder with a mortar and pestle. Because shells and bone contain high concentrations of inorganic carbon, which may bias $\delta^{13}C$ values (Lorrain 2003), they were divided in two aliquots. One of them was decarbonized by soaking during in 0.5 N (bone) or 1 N (shell) hydrochloric acid (HCl) until no more CO_2 was released (Newsome et al.

2006). The HCl treatment adversely affects $\delta^{15}N$ values (Bunn et al. 1995), so the other aliquot was not treated with HCl and was used for $\delta^{15}N$ determination. Lipids were extracted from bone samples with a chloroform/ methanol (2:1) solution (Bligh and Dyer 1959).

The vibrissae were washed in methanol in an ultrasonic bath for 20 min in order to remove residual deposits or any lipid contamination from the vibrissae's surface as a result of handling, and then were dried again for 48 hr at 50°C. Vibrissae were cut into 3-mm-long consecutive sections starting from the proximal end. This is

because each section integrates diet during one month (Hirons et al. 2001)

Approximately 0.8 mg of bone, 0.3 mg of vibrissae, 0.4–9.9 mg of shell, and 0.3 mg of white muscle from fish and mantle from cephalopods were weighed into tin cups (3.3 × 5 mm), combusted at 900°C, and analyzed in a continuous-flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA; Thermo Finnigan, Bremen, Germany). Atropine was used as a system check for elemental analyses. Samples were processed at Centres Científics i Tecnològics de la Universitat de Barcelona. The samples from modern South American sea lions had already been analyzed in the same laboratory and the results had been reported by Drago et al. (2009).

Stable isotopes abundances, expressed in delta (δ) notation, in which the relative variations of stable isotope ratios are expressed in parts permil (‰) deviations from predefined international standards, were calculated as

$$\delta X = \left[\left(R_{sample}/R_{standard} \right) - 1 \right] \times 1000 \quad (1)$$

where X is ^{13}C or ^{15}N, and R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios in the sample and standard, respectively. The standards used were Vienna Pee Dee Belemnite (VPDB) calcium carbonate for ^{13}C and atmospheric nitrogen (air) for ^{15}N.

Stable Isotope Discrimination Factors.— Animals are related isotopically to their environment by means of an isotopic diet-tissue discrimination factor (Hobson 1999). These factors vary significantly, within and between species, with diet, physiology, and tissue (Gannes et al. 1997; Olive et al. 2003; Koch 2007). Discrimination factors from diet to enamel and bone have been assessed in ungulates (Passey and Cerling, 2002; Nardoto et al. 2006), but they are unlikely to be useful because enamel and bone may differ in fractionation factors (Riofrío-Lazo and Aurioles-Gamboa 2013) and nutrient routing is different between omnivores and carnivores (Martínez del Rio et al. 2009). For this reason, we have computed a diet-to-bone fractionation factor using published information about diet-to-vibrissa fractionation in marine carnivores (Hobson et al. 1996; Newsome et al. 2010) and

comparing the stable isotope ratios of vibrissa and bone of South American sea lions (eq. 2), as bone is expected to integrate diet over several years (Newsome et al. 2006) and the same is true for long otariid vibrissa, with each few millimeters corresponding to several weeks (Cherel et al. 2009):

$$\Delta_{(bone-vibrissae)} + \Delta_{Means\ Reference}(vibrissae-diet)$$
$$= \Delta_{(bone-diet)} \quad (2)$$

Data Analysis.—The $\delta^{13}C_{shell}$ and $\delta^{15}N_{shell}$ values of limpets and mussels allowed tracking changes in the stable isotope baseline through time. The $\delta^{13}C_{shell}$ and $\delta^{15}N_{shell}$ values of modern and ancient individuals of each species from the same region were compared using the nonparametric Kruskal-Wallis test for multiple comparisons, because the assumptions of normality (using Lilleford test) and homoscedasticity (using Leven test) were seldom met (Zar 1984).

Stable isotope ratios in archaeological and modern bone samples were compared only after correcting for changes in the isotopic baseline (Casey and Post 2011). When statistically significant differences were found between modern and ancient stable isotope ratios, a correction factor was computed as the difference between the average stable isotope ratio of modern and ancient shells from each locality and age. Secondly, the difference was added to the stable isotope ratio of ancient bones from the same locality and age, to allow comparison with modern samples. For instance, if the $\delta^{15}N$ value of modern shells was 2‰ above that of ancient ones, the $\delta^{15}N$ value of ancient bones had to be increased 2‰ to be compared with that of modern bones. When bones came from a stratum without associated mollusc shells, bone stable isotope ratios were corrected using the time-weighted average of the correction factors computed for nearest strata below and above. Ideally, a bottom grazer (limpet) and a suspension feeder (ribbed mussel and blue mussel) were combined from each locality, but this was not always possible. A detailed description of those calculations and the resulting correction factors are shown in Table 3.

Once we had corrected for isotope baseline shifts, we compared stable isotope ratios in

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TABLE 3.   Baseline correction factor for shells and sea lions to each radiocarbon year (ybp) where we obtained samples. Underlined numbers are the correction factors utilized for calculating the weighted values.

Age shell (^{14}C ybp)	Correction Factor (shell) ($\Delta = \delta^{13}$C or δ^{15}N$_{14C\ age\ BP\ shell}$ - δ^{13}C or δ^{15}N$_{0BP}$)				Average correction factors (shell)		Age bone (^{14}C ybp)	Correction factors used for baseline	
	Δ δ^{13}C		Δ δ^{15}N		Δ δ^{13}C	Δ δ^{15}N		Δ δ^{13}C	Δ δ^{15}N
northern-central Patagonia									
	Aulacomya atra atra	*Nacella magellanica*	*Aulacomya atra atra*	*Nacella magellanica*					
380 ± 60	1.5	− 0.9	2.4	3.6	0.3	3.0	380 ± 60	0.3	3.0
610 ± 60	− 0.1	–	1.6	–	− 0.1	1.6	1380 ± 80	− 0.4*[1]	1.8*[2]
640 ± 60							1000 ± 70		
850 ± 50	–	− 1.6	–	1.7	− 1.6	1.7	1630 ± 80		
2140 ± 50	1.8	–	2.2	–	1.8	2.2	1680 ± 90		
2600 ± 60	–	− 1.7	–	3.8	− 1.7	3.8	2197 ± 38	0.1*[3]	3.0 *[4]
5200 ± 70	− 1.8	− 4.1	2.6	2.3	− 2.9	2.5	2910 ± 90	− 1.7	3.8

*[1,2] weighted value calculating by: [1] (0.63 * − 1.6 + 0.33 * 1.8); [2] (0.63 * 1.7 + 0.33 * 2.2)
*[3,4] mean values calculating by: [3] 1.8 and − 1.7; [4] 2.2 and 3.8

southern Patagonia									
	Mytilus edulis	*Nacella magellanica*	*Mytilus edulis*	*Nacellla magellanica*					
100 ± 45	− 3.7	− 6.7	1.5	1.7	− 5.2	1.6	100 ± 45	− 5.2	1.6
500 ± 100	2.1	− 0.3	1.6	1.3	0.9	1.8	580 ± 45	0.9	1.5
890	3.4	–	–	–	− 3.4	1.5	1256 ± 50–1190 ± 60	− 3.4[#1]	1.7[#2]
5940–5710	− 1.5	− 5.8	3.5	2.6	− 3.6	3.1	5000–4300	− 3.6	3.1

[1,2] weighted value, calculated by: [1](0.90 *−3.4 + 0.10 * −3.6); [2] (0.9 *1.5 + 0.10 *3.1)

bone samples with those of modern potential prey, after applying the diet-to-bone discrimination factors for South American sea lions ($\Delta\delta^{13}C = 3.5 \pm 0.8\permil$; $\Delta\delta^{15}N = 4.4 \pm 0.8\permil$) obtained in this study. Mann-Whitney U-tests were used for testing differences in the $\delta^{13}C$ and $\delta^{15}N$ signatures between demersal and pelagic modern prey.

Data are presented as mean $\pm$ standard deviation (SD) and significance was assumed at the 0.05 level. All statistical analyses were carried out with PASW Statistics (Version 17.0 for Windows, SPSS).

Results

Although the $\delta^{13}C_{shell}$ values of the mussels and limpets from northern-central Patagonia did not vary throughout the late Holocene (Fig. 2; Kruskal-Wallis test; *A. atra atra*: $\chi^2 = 9.418$, df $= 4$, $p = 0.052$; *N. magellanica*: $\chi^2 = 5.352$, df $= 4$, $p = 0.253$), those of the mollusc species collected in southern Patagonia exhibited a remarkable variability and changes run in parallel in both species (Fig. 2; Kruskal-Wallis test; *M. edulis*:

$\chi^2 = 15.714$, df $= 4$, $p = 0.003$; *N. magellanica*: $\chi^2 = 11.765$, df $= 4$, $p = 0.008$). Likewise, differences through time in the $\delta^{15}N_{shell}$ values of mussels and limpets were statistically significant both in northern-central Patagonia (Kruskal-Wallis test; *A. atra atra*: $\chi^2 = 19.549$, df $= 4$, $p < 0.001$; *N. magellanica*: $\chi^2 = 17.000$, df $= 4$, $p = 0.002$) and in southern Patagonia (Kruskal-Wallis test; *M. edulis*: $\chi^2 = 15.684$, df $= 4$, $p = 0.001$; *N. magellanica*: $\chi^2 = 14.392$, df $= 4$, $p = 0.002$), and the two species from the same area exhibited the same pattern of temporal variation (Fig. 2) although each region evolved independently. These results revealed major changes in the stable isotope baseline, and hence correction factors were computed for each region and period to allow comparison of the stable isotope ratios in the bone of ancient and modern South American sea lions (Table 3).

Vibrissae were depleted both in ^{13}C and ^{15}N relative to bone (mean $\delta^{13}C$: vibrissae $= -13.1 \pm 0.8$; bone $= -12.3 \pm 0.8$; mean $\delta^{15}N$: vibrissae $= 21.2 \pm 0.9$; bone $= 22.5 \pm 1.5$; $p = 0.01$), which resulted in an average vibrissa-to-bone discrimination factor of $0.8 \pm 0.8\permil$ for $\delta^{13}C$ and
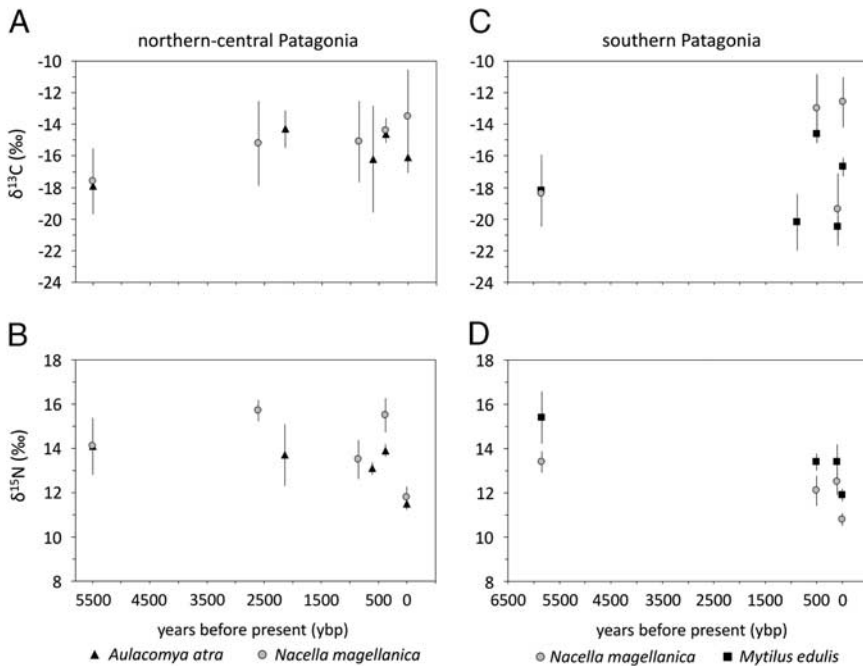

FIGURE 2. Temporal trends throughout the late Holocene of the $\delta^{13}C_{shell}$ and $\delta^{15}N_{shell}$ values is molluscs from northern-central Patagonia and southern Patagonia. Differences through time were statistically significant; except for the $\delta^{13}C_{shell}$ values of *Aulacomya atra atra* and *Nacella magellanica* from northern Patagonia (see the text for details about the statistical analyses).

$1.2 \pm 1.0\%o$ for $\delta^{15}N$. Combining this with the diet-to-vibrissa discrimination factor ($\delta^{13}C = 2.7 \pm 0.7\%o$; $\delta^{15}N = 3.2 \pm 0.5\%o$) reported by Hobson et al. (1996) and Newsome et al. (2010) resulted in a diet-to-bone discrimination factor of $3.5 \pm 0.8\%o$ for $\delta^{13}C$ and $4.4 \pm 0.8\%o$ for $\delta^{15}N$. Bone ($\delta^{13}C = -11.9 \pm 0.4$; $\delta^{15}N = 22.2 \pm 0.8$) was enriched relative to dentine ($\delta^{13}C = -12.0 \pm 0.5$; $\delta^{15}N = 21.4 \pm 0.6$), so the diet-to-dentine discrimination was of $3.5 \pm 0.8\%o$ for $\delta^{13}C$ and $3.6 \pm 0.8\%o$ for $\delta^{15}N$.

The uncorrected $\delta^{13}C_{bone}$ and $\delta^{15}N_{bone}$ values of ancient and modern sea lions are shown in the Table 1. After correction for changes in the isotope baseline (Fig. 3), the $\delta^{13}C_{bone}$ values of modern South American sea lions from northern-central Patagonia were higher than those of the South American sea lions that inhabited the region during the second half of the Holocene ($\delta^{13}C$ Kruskal-Wallis test: $\chi^2 = 7.094$; df = 1; $p < 0.05$) and the same was true for the $\delta^{15}N$ values (Kruskal-Wallis test: $\chi^2 = 43.628$; df = 1; $p < 0.05$). The $\delta^{13}C_{bone}$ values of South American sea lions from southern Patagonia also varied through time ($\delta^{13}C$ Kruskal-Wallis test: $\chi^2 = 5.262$; df = 1; $p < 0.05$), but there were no consistent

differences between modern and ancient South American sea lions. However, the $\delta^{15}N_{bone}$ values of modern South American sea lions from southern Patagonia were higher than those of ancient South American sea lions from that area ($\delta^{15}N$ Kruskal-Wallis test: $\chi^2 = 44.480$; df = 1; $p < 0.05$).

The stable isotope ratios of modern potential prey from northern-central Patagonia and southern Patagonia are shown in Table 2. Demersal fishes from northern-central Patagonia were more enriched than pelagic fishes from the same region in both $\delta^{13}C$ and $\delta^{15}N$ ($\delta^{13}C$; Mann-Whitney $U = 0.000$, $Z = -3.428$, df = 17, $p < 0.000$; $\delta^{15}N$; Mann-Whitney $U = 6.000$, $Z = -2.841$, df = 17, $p < 0.003$), and, accordingly, the simultaneous increase in the $\delta^{13}C_{bone}$ and $\delta^{15}N_{bone}$ values of the South American sea lions from that region throughout the Holocene indicates an increase in the consumption of demersal prey (Fig. 4). Conversely, most pelagic and demersal prey from southern Patagonia exhibit similar $\delta^{13}C$ and $\delta^{15}N$ values ($\delta^{13}C$; Mann-Whitney $U = 7.500$, $Z = -1.934$, df = 13, $p > 0.051$; $\delta^{15}N$; Mann-Whitney $U = 21.000$, $Z = 0.000$, df = 13, $p = 1.000$), although myctophid fishes and the
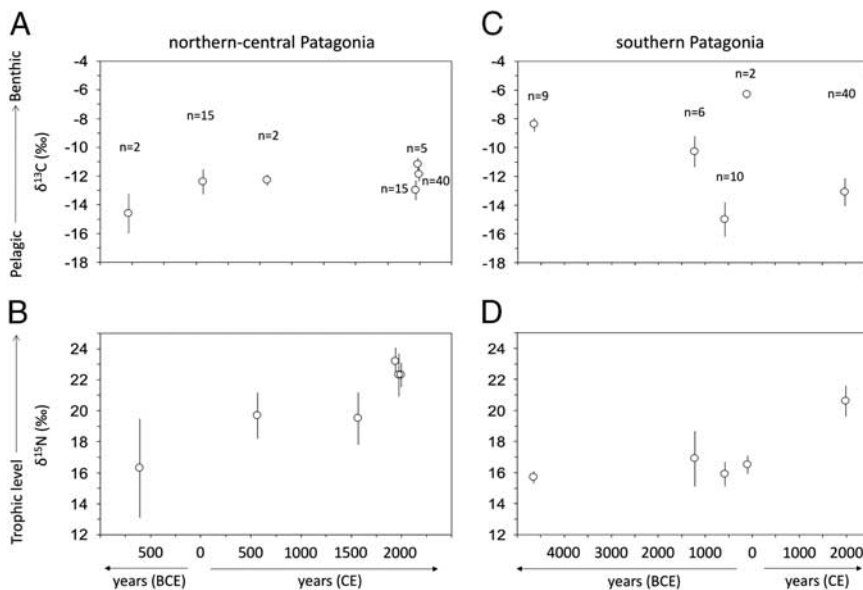

FIGURE 3.   Mean ($\pm$SD) values of $\delta^{13}C_{bone}$ (A, C) and $\delta^{15}N_{bone}$ (B, D) for South American sea lions collected in northern-central Patagonia and southern Patagonia through the middle and late Holocene of Argentina, after being corrected for changes in stable isotope baseline.
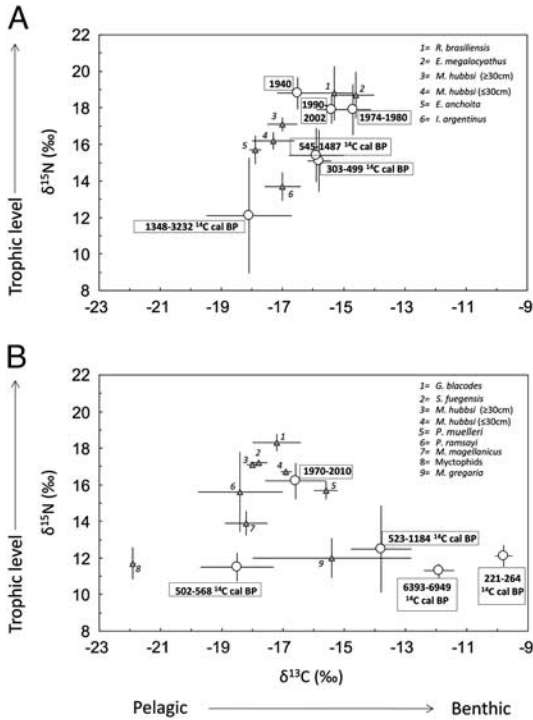
FIGURE 4. Bi-plot of the isotopic signal of the South American sea lion from northern-central (A) and southern (B) Patagonia, after correcting for differences in isotope baseline and for the diet-to-bone fractionation. Circles denote sea lions from different periods and triangles denote main prey.

squat lobster *Munida gregaria* were more depleted in ^{15}N than any other species. Accordingly, the low $\delta^{15}N_{bone}$ values typical of ancient South American sea lions suggest a diet dominated by prey at a low trophic level like *M. gregaria* (Fig. 4), whereas modern South American sea lions consume a larger proportion of prey at a higher trophic level like the rock cod *Patagonotothen ramsayi,* the Argentine hake *Merluccius hubbsi*, and the Argentine shrimp *Pleoticus muelleri*. Interestingly, the two samples from the nineteenth century fell outside the mixing polygon, suggesting they had a totally different diet or came from an area with a different isotopic baseline.

Discussion

The overall evidence reported here indicates that South American sea lions currently forage at a higher trophic level than they did during the late Holocene. Furthermore, those inhabiting northern-central Patagonia forage more benthically than they used to do in the past. Ignorance about the actual age and sex of the ancient South American sea lions recovered from the shell middens, the analysis of different skeletal elements, and the inference made about the stable isotope ratios of ancient prey species might bias the results (Balasse et al. 1999), but the difference between ancient and modern stable isotope ratios is so large that current South American sea lions certainly occupy a totally different trophic level, both in northern-central and southern Patagonia.

The data also reveal the twentieth century as the period when most of the change in the trophic level of South American sea lions happened, following the massive removal of individuals by hunting along the coast of Argentina (Dans et al. 2004; Schiavini et al. 2004; Grandi et al. 2012). Major changes also occurred in southern Patagonia during the early nineteenth century, as all the samples fell outside the mixing polygon formed by the stable isotope ratios of modern prey, even after correction for a shift in the isotope baseline. Western sealing had actually decimated otariid populations in the southern Patagonia during the late eighteenth and the early nineteenth centuries and only isolated otariids were sporadically recorded in the region during the second half of the nineteenth century (Bridges 1949). Rookeries persisted on Staten Island (Argentina), on the Falkland Islands (Malvinas), and in northern Argentina (Bridges 1949; Rodriguez and Bastida 1998; Dans et al. 2004; Dickinson 2007), and the high δ^{13}C values of the sea lion samples recovered at the Beagle Channel from the early nineteenth century are best explained by dispersal from distant areas with a distinct isotope baseline rather than by a dietary shift of the local population.

The dramatic impact of western sealing on the diet and ecology of South American sea lions is in sharp contrast with the rather stable diet of South American sea lions during the period of aboriginal exploitation. Evidence is particularly compelling in southern Patagonia, where the zooarchaeological record spans several millennia and the stable isotope ratios in the bones of South American sea lions were

rather stable. Variability in stable isotope ratios was larger in northern-central Patagonia, but considering the scarcity of samples older than 2000 ^{14}C ybp and the variability associated with the sampling of different skeletal elements, dietary shifts during the aboriginal period are uncertain.

Nevertheless, it should be noted that the diet of South American sea lions inhabiting truly pristine environments remains unknown. Most of the samples analyzed here came from archaeological sites and the oldest skeletal remains of South American sea lions from southern Patagonia are 1000 years younger than the oldest evidence of human exploitation of the marine resources in the area (Orquera and Piana 1988, 1999; Orquera et al. 2011; Tivoli and Zangrando 2011). Likewise, the oldest skeletal remains of South American sea lions from northern-central Patagonia are 3000 years younger than the oldest archaeological evidence of the exploitation of fishes, marine birds, and crustaceans in the area (Favier Dubois et al. 2009; Favier Dubois and Kokot 2011; Favier Dubois and Scartascini 2012; Gómez Otero et al. 2013). Whether such previous exploitation had modified the trophic niche of South American sea lions remains unknown and can be answered only if paleontological sites predating the arrival of humans were discovered.

In any case, the overall evidence indicates that South American sea lions currently forage at a higher trophic level than they did originally and that most of the change was related to human exploitation during the twentieth century. On the contrary, there is no evidence that aboriginal exploitation had a major effect on the trophic ecology of South American sea lions. Accordingly, the current ecology of South American sea lions is a poor guide to understanding the evolutionary forces that operated on the species throughout most of its history. For instance, there is no justification for claims that sexual differences in body mass evolved to reduce trophic overlap, as differences in the diets of male and females vanish as population size approaches carrying capacity (Drago et al. 2009, 2010). Likewise, the pelagic diet of South American sea lions prior to exploitation by western sealers (this study) suggests that the current resource partitioning between demersal South American sea lions and epipelagic South American fur seals (Franco-Trecu et al. 2012) is an artifact resulting from human exploitation, and the same might be true for other sympatric pairs where sea lion and fur seal species differentiate along a demersal-pelagic gradient (e.g., Antonelis et al. 1990; Páez-Rosas et al. 2012).

The results reported here have also implications for conservation. Preventing extinction due to human activity is the first step in wildlife conservation, but restoring the role of species in ecosystem dynamics has to be the long-term goal (Jackson and Hobbs 2009; Terborgh and Estes 2010; Bullock et al. 2011). Legal protection has certainly allowed the partial recovery of the population of South American sea lions in Argentina (Dans et al. 2004; Schiavini et al. 2004; Grandi et al. 2012), but has not restored the ecological role of the species (this study). Fishing is currently the major ecological driver of coastal ecosystems in the southwestern Atlantic (Koen-Alonso and Yodzis, 2005) and has established a new carrying capacity for South American sea lions (Drago et al. 2010). Information about the deep-time ecology of South American sea lions may assist managers in assessing whether the original niche has been restored, independently of population size. Restoring the original trophic ecology of the species is important, because only in this way will the evolutionary forces than once operated on the species also be restored.

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