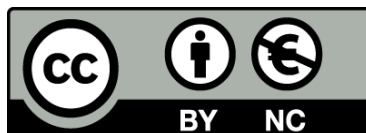


Cambios en la ecología trófica de los depredadores apicales del Mar Argentino durante el Holoceno

Fabiana Saporiti



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Paleoindian pinniped exploitation in South America was driven by oceanic productivity

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ABSTRACT

After centuries of pinniped exploitation, hunter-gatherers from the Atlantic coast of southern South America shifted in several occasions to other animal resources during the second half of the Holocene. The shift has been justified by the overexploitation of pinniped populations although changes in marine primary productivity may be an alternative explanation. This is a critical point, as currently large populations of sea lions and fur seals occur only in areas where marine productivity is high. This paper examines the zooarchaeological record to assess the intensity of pinniped exploitation and the stable isotope ratio of Nitrogen ($\delta^{15}\text{N}$) in mollusc shells collected from archaeological sites as a proxy of marine primary productivity in northern Patagonia and Tierra del Fuego during the second half of the Holocene. The results reveal major fluctuations of marine primary productivity and demonstrate that hunter-gatherers only relied intensely on pinnipeds when marine productivity was high. This finding suggests that the decline in pinniped abundance observed in the zooarchaeological record was caused by a bottom-up control of pinniped population and not by the overexploitation by hunter-gatherers.

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1. Introduction

Concern about the conservation of marine resources has increased during recent decades as evidence that human exploitation has caused major changes in most marine ecosystems has grown (Pauly et al., 1998; Jackson et al., 2001; Pauly et al., 2005). Although recent examples of fisheries recovering after collapse certainly exist (Worm et al., 2009), marine resource exploitation has increased dramatically worldwide during recent centuries (Pauly et al., 2005), and few marine regions remain unaffected by anthropogenic impacts (Halpern et al., 2008). Although modern industrial fishing is the solely responsible for the alteration of offshore and deep-sea ecosystems (Christensen et al., 2003; Myers and Worm, 2003; Lewison et al., 2004; Devine et al., 2006),

overfishing and the ecological extinction of coastal marine megafauna are thought to predate industrialized fishing in many cases.

The historical record clearly demonstrates that preindustrialized European societies overexploited coastal marine mammals (Dulvy et al., 2009) and that European settlement triggered the overexploitation of coastal marine megafauna on other continents (Jackson et al., 2001). However, the impact of other preindustrialized cultures on coastal marine resources remains contentious. An increasing number of multidisciplinary studies examining the interactions between prehistoric peoples and their environments suggest that, at least in some cases, ancient peoples caused cumulative and often irreversible impacts on natural landscapes and biotic resources worldwide (Kirch, 2005).

The study of the Holocene human settlements along the Argentine coast began after 1936, as archaeologists viewed marine resources as minor dietary sources for local hunter-gatherers, who were considered primarily terrestrial (Orquera and Gómez Otero, 2007). Only since the 1980s, with the improvement of archaeological methods and based on the productivity of the seas and the

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high nutritional value of some marine species, was the importance of such resources recognized (Gómez Otero, 2006, 2007; Orquera and Gómez Otero, 2007; Moreno, 2008).

Available evidence indicates that the southern end of South America was colonized more than 12,000 years ago by humans dispersing along the Pacific coastline of the Americas (Miotti et al., 2003; Dillehay et al., 2008; McKechnie and Wigen, 2011; Moss and Losey, 2011; Orquera et al., 2011). These humans possessed the technology to use marine resources, notably fish, birds, and molluscs (Keefer et al., 1998; Dillehay et al., 2008; Betts et al., 2011; Erlandson et al., 2011; Gifford-Gonzalez, 2011), but intense exploitation did not develop until much later, in the Middle Holocene, probably as a consequence of a technological improvement (Yesner et al., 2003; Orquera et al., 2011; Tivoli and Zangrando, 2011). However, the hypothesis that human occupation was earlier than currently thought, especially in certain sectors of the coast where the bathymetry is particularly smooth (Ponce et al., 2011), is still open (Gómez Otero, 2006).

Pinnipeds were especially important prey for both the hunter-gatherers inhabiting the Beagle Channel and the southern coast of Chile, who based their living on marine resources (Schiavini, 1993; Orquera and Piana, 1999; Yesner et al., 2003; Orquera et al., 2011; Tivoli and Zangrando, 2011), and those who inhabited central and northern Patagonia, only partially dependent on maritime resources (Gómez Otero, 2006; Moreno, 2008; Favier Dubois et al., 2009). According to the zooarchaeological record, the human populations inhabiting the Beagle Channel approximately 6000 BP were highly reliant on marine resources, mainly fur seals (*Arctocephalus australis*) which were the main source of food and raw material for many millennia (Orquera and Piana, 1999; Orquera et al., 2011; Tivoli and Zangrando, 2011). Conversely, people inhabiting northern and central Patagonia exploited both terrestrial and marine resources, but the exploitation of pinnipeds, especially sea lions (*Otaria flavescens*), developed approximately 3000 BP, when seasonal settlements were established close to sea lion rookeries (Gómez Otero, 2006; Favier Dubois et al., 2009). Sea lion exploitation was intense in the northern province of Rio Negro from 3100 to 2200 BP and was followed by a period of moderate exploitation from 1500 to 420 BP (Favier Dubois et al., 2009). In contrast, sea lion exploitation in Chubut province was moderate from 3000 to 1000 BP, and intensified from 1000 to 350 BP (Gómez Otero, 2006, 2007).

Although both groups of hunter-gatherers differed dramatically in technology and in historical patterns of resource exploitation (Orquera and Piana, 1999; Orquera and Gómez Otero, 2007; Moreno, 2008; Orquera et al., 2011), everywhere the zooarchaeological record reveals a general decline in the consumption of pinnipeds after several centuries of exploitation (Yesner et al., 2003; Gómez Otero, 2007; Favier Dubois et al., 2009; Tivoli and Zangrando, 2011). Similar declines in the use of pinnipeds by maritime hunter-gatherers in the north Pacific have been on occasions linked to increasing sea surface temperature (Colten and Arnold, 1998; Betts et al., 2011), but most often to over-exploitation by humans in the absence of strong evidence supporting climate forcing (Porcasi et al., 2000; Lyman, 2003; Jones et al., 2004; Newsome et al., 2007). Overexploitation has also been suggested as the reason for the progressive decline in the presence of fur seals in the zooarchaeological record from the Beagle Channel (Orquera et al., 2011; Tivoli and Zangrando, 2011), as the pollen record (Heusser, 1990) and the stable oxygen isotopes (Obelic et al., 1998; Saporiti et al., 2013) suggested no relationship between climate and patterns of resources used by hunter-gatherers during the second half of the Holocene. However, nothing is known about how marine productivity varied throughout that period, a critical point because dense populations

of sea lions and fur seals only thrive in highly productive environments (Bowen et al., 2009).

Primary productivity in coastal areas usually depends on nitrogen availability, which increases due to high freshwater runoff, intense vertical mixing and deep water upwelling (Gruber, 2008). All these processes also promote nitrogen recycling over nitrogen fixation and hence modify the relative abundance of heavy isotopes of nitrogen (^{15}N) in the tissues of aquatic primary producers (Calvert et al., 1992; Wu et al., 1997; Waser et al., 2000). As stable isotope ratios in prey are transferred to their predators, $\delta^{15}\text{N}$ values in herbivorous molluscs are expected to reveal $\delta^{15}\text{N}$ values in primary producers (Post, 2002) and hence inform about primary productivity.

In the intertidal, mussels and limpets are prominent suspension feeders and grazers, respectively (Bigatti and Penchaszadeh, 2008) and their shells often occur mixed with pinniped bones in hunter-gatherers shell middens (Gómez Otero, 2006, 2007; Orquera et al., 2011). Here, the $\delta^{15}\text{N}$ in the protein of the shell of rubbed mussels (*Aulacomya atra atra*) and limpets (*Nacella magellanica*) collected along the coast of Argentina has been measured in order to evaluate the correlation with the marine primary productivity of the water where they live. Once the correlation was confirmed the $\delta^{15}\text{N}$ values of the organic matter from shells collected at hunter-gatherer shell middens have been used as reliable proxies of past marine primary productivity and have been compared to the patterns of marine resource exploitation reported by previous zooarchaeological researchers (Yesner et al., 2003; Gómez Otero, 2006; Moreno, 2008; Favier Dubois et al., 2009; Tivoli and Zangrando, 2011). In this way, the hypothesis that the changing patterns of marine resource exploitation by hunter-gatherers along the south-western Atlantic coast of Argentina were driven by a bottom-up process and not by overexploitation was tested.

2. Methods

2.1. Study area and sampling

Modern mollusc samples ($n \geq 5$ for each species) were collected from December 2009 to February 2010 at six sites along the coastline of Argentina: two in Rio Negro province ($41^{\circ}1.20'S$ – $41^{\circ}38.40'S$; $64^{\circ}10.80'W$ – $65^{\circ}1.20'W$), three in Santa Cruz province ($47^{\circ}44.40'S$ – $50^{\circ}6.60'S$; $65^{\circ}50.40'W$ – $68^{\circ}27.00'W$) and one in Tierra del Fuego province ($54^{\circ}49.20'S$; $68^{\circ}12.00'W$) (Fig. 1). The limpet *N. magellanica* was collected in five sites, and the rubbed mussel *A. atra atra* was collected in four sites (see Table 1). As remotely sensed chlorophyll concentration can be used as an index of the mean water column chlorophyll (Smith, 1981), satellite data (SeaWiFS 9 km; <http://reason.gsfc.nasa.gov/Giovanni/>) were used to determine current (January 2005 to January 2010) average

Table 1
 $\delta^{15}\text{N}$ mean values (with standard deviation) of modern shells of the limpets and rubbed mussels collected along the coast of Argentina. The last column represents the chlorophyll-a levels mean values (with standard deviation) in each sample site.

Species	Province	N	Mean $\delta^{15}\text{N}$ (‰)	Mean Chl-a (mg/m ³)
<i>Nacella magellanica</i>	Rio Negro	5	11.8 (±0.5)	1.22 (±2.33)
<i>Nacella magellanica</i>	Santa Cruz	5	12.1 (±0.4)	1.44 (±0.47)
<i>Nacella magellanica</i>	Santa Cruz	5	12.3 (±0.3)	1.55 (±0.30)
<i>Nacella magellanica</i>	Santa Cruz	5	13.0 (±0.5)	1.97 (±0.91)
<i>Nacella magellanica</i>	Tierra del Fuego	5	10.8 (±0.3)	0.86 (±0.12)
<i>Aulacomya atra atra</i>	Rio Negro	7	11.5 (±0.3)	1.05 (±1.56)
<i>Aulacomya atra atra</i>	Santa Cruz	5	11.8 (±0.4)	1.44 (±0.47)
<i>Aulacomya atra atra</i>	Santa Cruz	5	12.5 (±0.3)	1.97 (±0.91)
<i>Aulacomya atra atra</i>	Tierra del Fuego	5	11.9 (±0.3)	0.86 (±0.12)

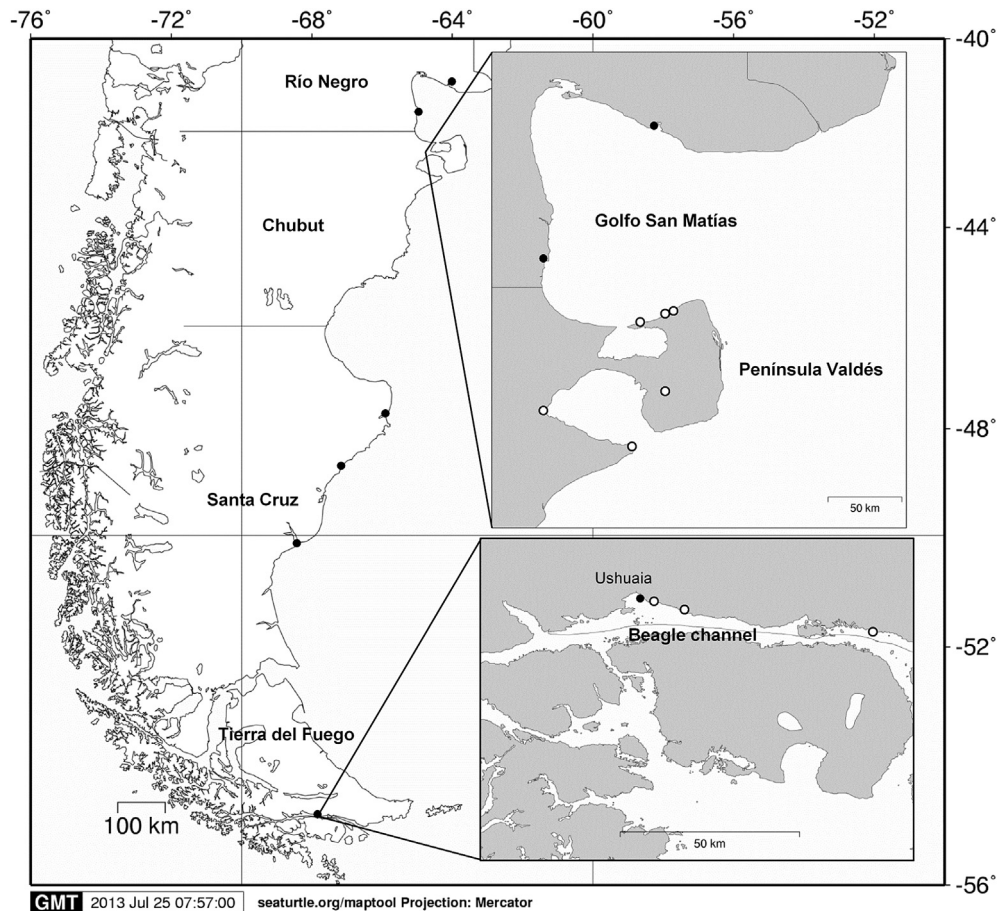


Fig. 1. Map showing approximate sampling localities. Empty circles indicate archaeological samples; filled circles indicate modern samples.

chlorophyll-a levels in each sampling area. Chlorophyll-a is an index of the primary productivity in the oceans (Lorenzen, 1970).

Archaeological shell samples selected for isotopic analysis come from previous fieldwork carried out by authors Julieta Gómez Otero in Golfo San Matías and Península Valdés (northern Patagonia) and Ernesto Piana and colleagues (Luis Orquera and A. Francisco Zangrando) in the Beagle Channel (Table 2). Samples size was five for each species, site, and midden layer where available (Table 3). The samples were dated in different

laboratories and using different methods, in particular samples from northern Patagonia, where all dated samples were marine shells instead of charcoal. Radiocarbon ages were calibrated by the authors using the package Clam 2.2 (Blaauw, 2010) and the new curve for Southern Hemisphere ShCal13 (Hogg et al., 2013). Reservoir effects data for northern Patagonia region are emerging only recently, and they suggest variable differences between marine and terrestrial ages (Cordero et al., 2003; Favier Dubois, 2009). The regional marine reservoir effect of 266 ± 51 years

Table 2
Archaeological sites where shells were recovered. Radiocarbon and calibrated ages were reported.

Area	Site	Material	Radiocarbon age (^{14}C BP)	Calibrated age ^d (^{14}C cal BP ($\pm 1\sigma$))	Laboratory
Northern Patagonia	Las Ollas conchero 1 ^a	Shells	610 \pm 60	268–508 (85.8%) ^e	LATYR-CONICET-UNLP
Northern Patagonia	Ecocentro Fogón 3 ^a	Shells	640 \pm 60	278–519 (92.1%) ^e	INGEIS (Buenos Aires)
Northern Patagonia	Playa Las Lisas 2 – Perfil 1 ^a	Shells	850 \pm 150	281–798 (94.7%) ^e	LATYR-CONICET-UNLP
Northern Patagonia	Playas Las Lisas 2 – Conchero 2 ^a	Shells	2140 \pm 50	1589–1921 (95.0%) ^e	LATYR-CONICET-UNLP
Northern Patagonia	Cracker 8 – Nivel 3 ^a	Shells	2600 \pm 60	2089–2502 (90.1%) ^e	LATYR-CONICET-UNLP
Beagle Channel	Túnel VII ^b	Charcoal	5200 \pm 70	5465–5773 (83.9%) ^e	LATYR-CONICET-UNLP
Beagle Channel	Shamakush X site ^c	Charcoal	100 \pm 45	221–264 (17.0%)	INGEIS (Buenos Aires)
Beagle Channel	Imiwaia I (M/K) ^b	Charcoal	500 \pm 100	498–518 (95.0%)	INGEIS (Buenos Aires)
			5750 \pm 170	6187–6936 (95.0%)	INGEIS (Buenos Aires)
			5870 \pm 150	6310–6989 (95.0%)	INGEIS (Buenos Aires)
			5949 \pm 50	6631–6885 (93.8%)	Arizona (USA)

^a Gómez Otero (2006).

^b Piana et al. (1992).

^c Orquera and Piana (1999).

^d Calibration of radiocarbon ages was carried out by the authors with the program Clam 2.2 (Blaauw, 2010), using the ShCal13 curve (Hogg et al., 2013). The probability is indicated in brackets.

^e the regional marine reservoir effect of 266 ± 51 years was included in the calibration of the shell samples (Favier Dubois, 2009).

Table 3
 $\delta^{15}\text{N}$ mean values (with standard deviation) of archaeological shells of limpets and rubbed mussels used in the paper and collected in previous field work by two of the authors (Julietta Gómez Otero and Ernesto Piana).

Species	Province	Site	Calibrated age (^{14}C cal BP ($\pm 1\sigma$))	N	Mean $\delta^{15}\text{N}$ (‰)
<i>Nacella magellanica</i>	Chubut	Ecocentro Fogón 3	281–798 (94.7%)	5	13.5 \pm 0.8
<i>Nacella magellanica</i>	Chubut	Playas Las Lisas 2 – Conchero 2	2089–2502 (90.1%)	5	15.7 \pm 0.8
<i>Nacella magellanica</i>	Chubut	Cracker 8 – Nivel 3	5465–5773 (83.9%)	2	14.1 \pm 0.8
<i>Nacella magellanica</i>	Tierra del Fuego	Túnel VII	221–264 (17.0%)	5	12.5 \pm 0.8
<i>Nacella magellanica</i>	Tierra del Fuego	Shamakush X site	498–518 (95.0%)	4	12.2 \pm 0.8
<i>Nacella magellanica</i>	Tierra del Fuego	Imiwaia I (M/K)	6187–6936 (95.0%)	5	13.4 \pm 0.8
			6310–6989 (95.0%)		
			6631–6885 (93.8%)		
<i>Aulacomya atra atra</i>	Chubut	Las Ollas conchero 1	268–508 (85.8%)	5	13.1 \pm 0.8
			278–519 (92.1%)		
<i>Aulacomya atra atra</i>	Chubut	Playa Las Lisas 2 – Perfil 1	1589–1921 (95.0%)	5	13.7 \pm 0.8
<i>Aulacomya atra atra</i>	Chubut	Cracker 8 – Nivel 3	5465–5773 (83.9%)	5	14.1 \pm 0.8

was included in the calibration of the shell samples (Favier Dubois, 2009).

For the characterization of resource use pattern by hunter-gatherers inhabiting the Beagle Channel (Fig. 2), we relied on the collections from six middens excavated at two archaeological sites 40 km apart. One location was situated at Cambaceres Bay and included archaeofaunal samples from stratigraphic layers dated 6000 BP, 1500 BP and from the 19th century. The other middens were located at Estancia Remolino and include assemblages dated 4000 BP, 1000 BP and 500 BP. There were no significant differences concerning excavation methods, as the same procedures were followed (see Tivoli and Zangrando, 2011 and references therein for further detail about the sites, dating procedures and collections). The collections from seven middens scattered in Bajo de la Quinta,

Barranco de los Concheros and between Bahía Final 1 and Saco Viejo (northern coast of San Matías gulf), dated between 3430 ± 43 and 450 ± 80 ^{14}C BP, and information about archaeological sites located in Península Valdés, were used to characterize the pattern of resource use by hunter-gatherers inhabiting northern Patagonia (Fig. 3) (Gómez Otero and Suárez, 1999; Gómez Otero, 2007; Orquera and Gómez Otero, 2007; Favier Dubois et al., 2009).

2.2. Analytical methods

Both the archaeological and the modern shell samples were polished with sandpaper and with a diamond wheel drill to remove impurities. Then, they were rinsed with distilled water, dried at 50°C and ground into a fine powder by mortar and pestle. Dried

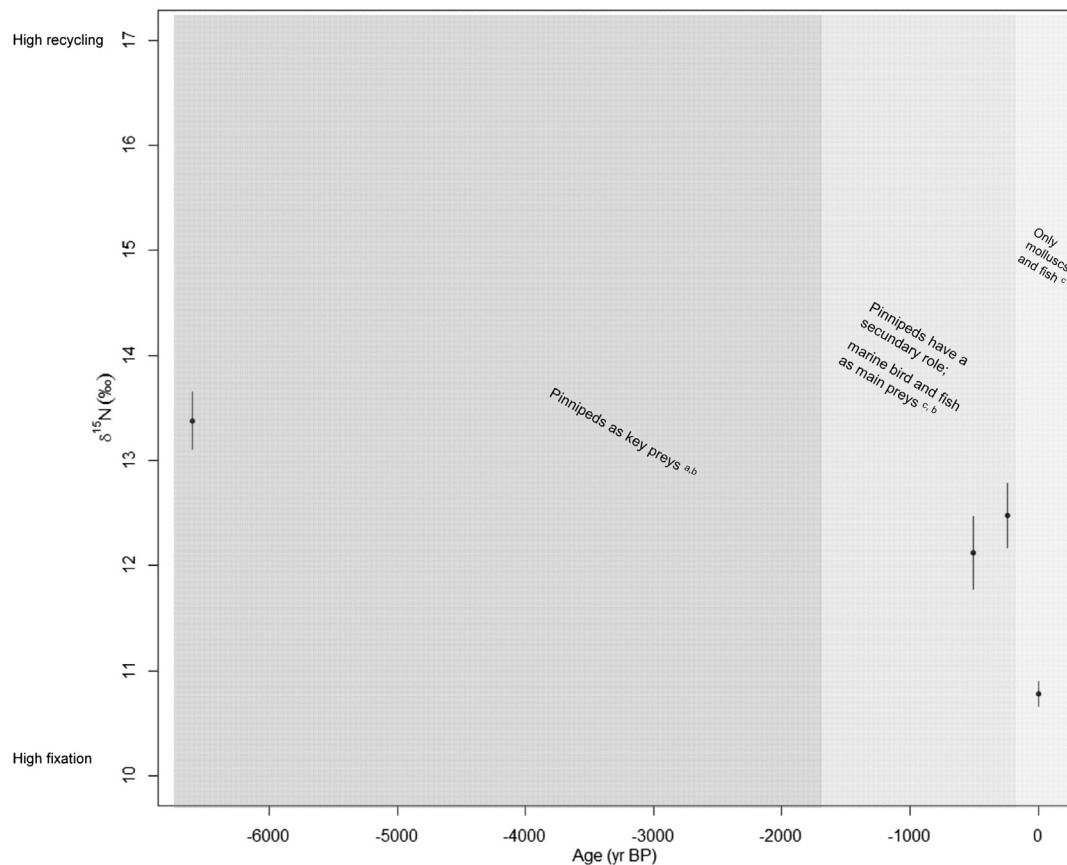


Fig. 2. $\delta^{15}\text{N}$ values in the shell of limpets from the Beagle Channel during the last 6600 years, including modern samples. The background colour represents the relative abundance of pinnipeds for hunter-gatherers in the area. Vertical bars denote standard deviation ($n = 5$). a = Tivoli and Zangrando, 2011; b = Orquera and Piana, 1999; c = Yesner et al., 2003.

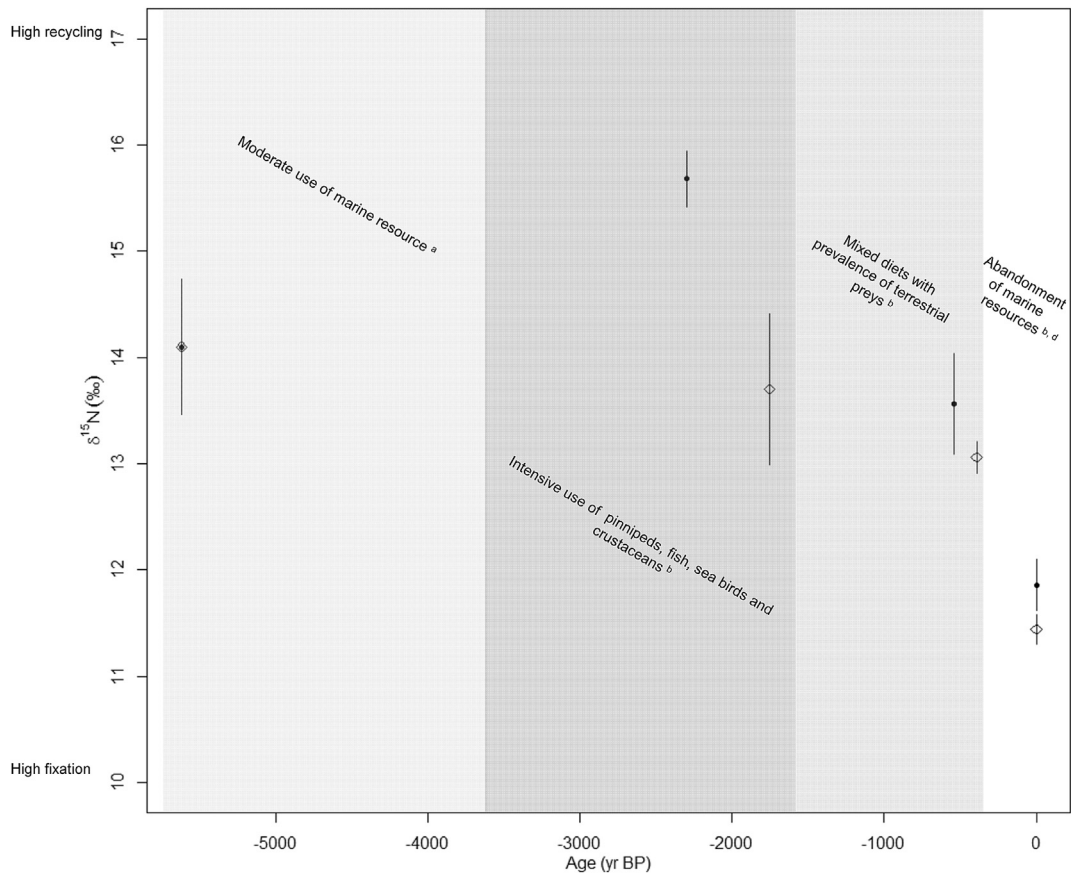


Fig. 3. $\delta^{15}\text{N}$ values in the shell of limpets (solid circles) and rubbed mussels (empty diamonds) from northern Patagonia during the last 6000 years, including modern samples. The background represents the relative abundance of pinnipeds for hunter-gatherers in the area. Vertical bars denote standard deviation ($n = 5$). a = Orquera and Gómez Otero, 2007; b = Favier Dubois et al., 2009; c = Gómez Otero and Suárez (1999); d = Gómez Otero (2007).

powdered samples and secondary reference standards (acetanilide, urea, USGS 40 ($\delta^{15}\text{N} = -4.6\text{‰}$), USGS 34 ($\delta^{15}\text{N} = -1.7\text{‰}$), IAEA N2 ($\delta^{15}\text{N} = +20.3\text{‰}$), IAEA N1 ($\delta^{15}\text{N} = +0.4\text{‰}$), IAEA 600 ($\delta^{15}\text{N} = 1.0\text{‰}$), UCGEMA F ($\delta^{15}\text{N} = +4.6\text{‰}$)) were weighed and analyzed in a continuous flow stable isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA Thermo Finnigan) coupled with an elemental analyzer. We also employed a CO_2 absorbent for elemental analysis (CaO/NaOH) to avoid spectrometer saturation by the CaCO_2 , which constitutes over 90% of the shell. Secondary standards were calibrated with the nitrogen international standard, atmospheric N_2 . Samples were processed at Scientific and Technological Centers (CCiT) of the University of Barcelona.

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

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 10^3$$

where X is ^{15}N , R_{sample} is the heavy-to-light isotope ratio of the sample ($^{15}\text{N}/^{14}\text{N}$), and R_{standard} is the heavy-to-light isotope ratio in reference standards certified by International Atomic Energy Agency (IAEA, Vienna).

2.3. Statistical methods

Normality in data distribution was tested using the Lilliefors test and homoscedasticity using the Levene test. A linear regression was

performed to investigate the correlation between modern shell $\delta^{15}\text{N}$ with chlorophyll-*a*. ANOVA was used for multiple comparisons when data fit the normality and homoscedasticity requirements and the non-parametrical Kruskal–Wallis test was used otherwise.

The percentage of the number of specimens identified at the species level (%NISP) in the collections from the Beagle Channel (Tivoli and Zangrando, 2011) was used to calculate the relative abundance of otariids. Bone preservation was worse at the archaeological sites from northern Patagonia and therefore numbers of specimens had not been assessed (Favier Dubois et al., 2009). As a consequence, the relative importance of otariids in the collections from that area was assessed by calculating the percentage of broad taxonomic groups represented by otariids (%BTG) in each collection. A single collection was analyzed from each zone (Beagle Channel and northern Patagonia) and age. All statistical analyses were conducted with the PASW Statistic 18 software package.

3. Results

As the correlation between modern shell $\delta^{15}\text{N}$ with chlorophyll-*a* was significant for both species (rubbed mussels, adjusted r -squared = 0.340, $n = 22$, $p = 0.003$; limpets, adjusted r -squared = 0.764, $n = 25$, $p < 0.001$), the $\delta^{15}\text{N}$ values of the organic matter from shells collected at hunter-gatherer shell middens have been used as reliable proxies of past marine primary productivity.

The $\delta^{15}\text{N}$ values of rubbed mussel shells from hunter-gatherers shell middens from northern Patagonia were higher than those of modern samples from the same areas (Kruskal–Wallis test,

$\chi^2 = 16.42$, $df = 3$, $N = 22$; $p < 0.01$). The same was true for the $\delta^{15}\text{N}$ values of limpet shells either in northern and central Patagonia (ANOVA $F_{3,13} = 22.00$, $p < 0.001$) and the Beagle Channel (ANOVA $F_{3,15} = 19.97$, $p < 0.001$). Furthermore, the $\delta^{15}\text{N}$ values of limpet shells from northern Patagonia dated 2089–2502 ^{14}C cal BP were significantly higher than those dated ca. 500 cal BP and modern ones. The $\delta^{15}\text{N}$ values of limpet shells from the Beagle channel dated ca. 6600 cal BP were higher than those dated 498–518 ^{14}C cal BP. Thus, stable isotopes analysis indicates that coastal primary productivity during the second half of the Holocene was higher than that currently observed in both areas, although the temporal dynamics differed between the two regions through the second half of the Holocene, as marine primary productivity was much higher at the beginning of human occupation in the Beagle Channel than in more recent periods (Fig. 2) but fluctuated off northern and central Patagonia (Fig. 3). Despite those differences, the periods of intense exploitation of pinnipeds in both regions, indicated as darker shades of colour in Figs. 2 and 3, were characterized by high values of $\delta^{15}\text{N}$ values in mollusc shells.

4. Discussion

Pinnipeds were exploited by hunter-gatherers since the very beginning of coastal settlement at the Beagle Channel, approximately 6400 years ago (Orquera and Piana, 1999; Tivoli and Zangrando, 2011). However, the dietary importance of pinnipeds, mainly fur seals (*A. australis*), declined steadily through the Late Holocene and has been negligible since approximately 1500 years ago (Yesner et al., 2003; Tivoli and Zangrando, 2011), in parallel to the decline of the $\delta^{15}\text{N}$ values of limpet shells. However, this conclusion should be improved by further data for the period between approximately 6000 and 500 years ago, where there are no $\delta^{15}\text{N}$ data. It can be argued that western sealers decimated fur seals (*A. australis*) in Tierra de Fuego at the end of the 18th and beginning of the 19th century (Schiavini, 1993), and hence, impeded the ability of hunter-gatherers to resume former exploitation levels during the Little Ice Age, when $\delta^{15}\text{N}$ slightly rose. However, the occurrence of fur seal bones in middens was already extremely low 500 years ago, when the marine productivity had already decreased and European explorers had just reached the region.

The pattern of pinniped exploitation in northern and central Patagonia is more complex, as hunter-gatherers began the use of marine resources 7000 years ago (Orquera and Gómez Otero, 2007) but only intensified the exploitation of pinnipeds approximately 3000 years ago in Golfo San Matías (Favier Dubois et al., 2009), when the $\delta^{15}\text{N}$ values in mollusc shells increased. The intensity of pinniped exploitation in Golfo San Matías declined approximately 1500 years ago (Gómez Otero and Suárez, 1999). The $\delta^{15}\text{N}$ values of the rubbed mussels are also consistent with this pattern, although differences among Holocene samples were not statistically significant. Finally, coastal areas were abandoned following the domestication of feral horses of European origin at the beginning of the 18th century (Gómez Otero, 2006; Favier Dubois et al., 2009).

In conclusion, the overall evidence suggests that intense exploitation of pinnipeds by hunter-gatherers inhabiting the coastline of the Southwest Atlantic Ocean began when marine primary productivity was high and declined when marine primary productivity decreased. Accordingly, changes in the relative abundance of pinnipeds in the zooarchaeological record more likely reflect a bottom-up control of pinniped populations by marine primary productivity rather than overexploitation by hunter-gatherers. These findings indicate that hunter-gatherers along the south-western Atlantic coast of Argentina did not have a critical role in pinniped population declines, as in other coastal areas of New Zealand and northern Pacific (Anderson, 2008). This is a major

advancement in the archaeology of the Patagonia and revealed that, despite the different mechanisms of livelihood observed in local populations, they had only a minor impact on pinnipeds. In contrast, the prolonged hunt by European sealers was the sole cause of their near extinction in the twentieth century.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quaint.2014.05.015>.

References

- Anderson, A., 2008. Short and sometimes sharp: human impacts on marine resources in the archaeology and history of South Polynesia. In: Erlandson, J., Rick, T.C. (Eds.), *Human Impacts on Ancient Marine Ecosystems: a Global Perspective*. University of California Press, Berkeley, pp. 21–42.
- Betts, M.M., Maschner, H.D.G., Lech, V., 2011. A 4500-year time-series of otariid abundance on Sanak Island, western Gulf of Alaska. In: Braje, T.J., Rick, T.C. (Eds.), *Human Impacts on Seals, Sea Lions, and Sea Otters: Integrating Archaeology and Ecology in the Northeast Pacific*. University of California Press, Berkeley, pp. 93–110.
- Bigatti, G., Penchaszadeh, P.E., 2008. Invertebrados del Mar Patagónico, diagnóstico de la problemática actual y potencial de su conservación y manejo. In: Campagna, C. (Ed.), *El Mar Patagónico, Foro para la Conservación del Mar Patagónico y Áreas de Influencia Referenciales*, pp. 105–133. Puerto Madryn.
- Blaauw, M., 2010. Methods and code for ‘classical’ age-modelling of radiocarbon sequences. *Quaternary Geochronology* 5, 512–518.
- Bowen, G.J., Beck, C.A., Austin, D.A., 2009. Pinniped ecology. In: Perrin, W.F., Wursig, B., Thewissen, J.G.M. (Eds.), *Encyclopedia of Marine Mammals*. Academic Press, pp. 852–860.
- Calvert, S.E., Nielsen, B., Fontugne, M.R., 1992. Evidence from nitrogen isotope ratios for enhanced productivity during the formation of Eastern Mediterranean sapropels. *Nature* 359, 223–225.
- Colten, R.H., Arnold, J.E., 1998. Prehistoric marine mammal hunting on California's northern Channel Islands. *American Antiquity* 63 (4), 679–701.
- Christensen, V., Gue, S., Heymans, J.J., Walters, C.J., Watson, R., Zeller, D., Pauly, D., 2003. Hundred-year decline of North Atlantic predatory fishes. *Fish and Fisheries* 4 (1), 1–24.
- Cordero, R.R., Panarello, H., Lanzelotti, S., Favier Dubois, C.M., 2003. Radiocarbon age offsets between living organisms from the marine and continental reservoir in coastal localities of Patagonia (Argentina). *Radiocarbon* 45, 9–15.
- Devine, J.A., Baker, K.D., Haedrich, R.L., 2006. Fisheries: deep-sea fishes qualify as endangered. *Nature* 439, 29.
- Dillehay, T.D., Ramírez, C., Pino, M., Collins, M.B., Rossen, J., Pino-Navarro, J.D., 2008. Monte Verde: seaweed, food, medicine, and the peopling of South America. *Science* 320, 784–786.
- Dulvy, N.K., Pinnegar, J.K., Reynolds, J.D., 2009. Holocene extinctions in the sea. In: Turvey, S.T. (Ed.), *Holocene Extinctions*. Oxford University Press, Oxford, pp. 129–150.
- Erlandson, J.M., Rick, T.C., Braje, T.J., Casperson, M., Culleton, B., Fulford, B., Garcia, T., Guthrie, D.A., Jew, N., Kennett, D.J., Moss, M.L., Reeder, L., Skinner, C., Watts, J.,

- Willis, L., 2011. Paleoindian seafaring, maritime technologies, and coastal foraging on California's Channel Islands. *Science* 331, 1181–1185.
- Favier Dubois, C.M., 2009. Valores de efecto reservorio marino para los últimos 5.000 años obtenidos en concheros de la costa atlántica norpatagónica (Golfo San Matías, Argentina). *Magallania* 37, 139–147.
- Favier Dubois, C.M., Borella, F., Tykot, R.H., 2009. Explorando tendencias en el uso humano del espacio y los recursos en el litoral rionegrino durante el Holoceno tardío y medio. In: Salemme, M.C., Santiago, M., Alvarez, M., Piana, E.L., Vázquez, M., Mansur, E. (Eds.), *Holoceno*. Editorial Utopía, Ushuaia, pp. 985–998.
- Gifford-Gonzalez, D., 2011. Holocene Monterey bay fur seals. Distribution, dates, and ecological implications. In: Braje, T.J., Rick, T.C. (Eds.), *Human Impacts on Seals, Sea Lions, and Sea Otters: Integrating Archaeology and Ecology in the Northeast Pacific*. University of California Press, Berkeley, pp. 221–242.
- Gómez Otero, J., 2006. Dieta, uso del espacio y evolución en sociedades cazadores-recolectoras de la costa centro-septentrional de Patagonia durante el Holoceno medio y tardío (PhD Thesis). Universidad de Buenos Aires, Buenos Aires.
- Gómez Otero, J., 2007. Isótopos estables, dieta y uso del espacio en la costa atlántica centro-septentrional y el valle inferior del río Chubut (Patagonia, Argentina). In: Morello, F., Martinic, M., Prieto, A., Bahamond, G. (Eds.), *Arqueología de Fuego-Patagonia*. Levantando piedras, desenterrando huesos...y develando arcanos. CEQUA, Punta Arenas, Chile, pp. 151–161.
- Gómez Otero, J., Suárez, F., 1999. Lobos marinos y guanacos: análisis arqueofaunístico de un fogón hallado en la costa del Golfo de San Matías, Península Valdés (Chubut). In: *Resúmenes del XIII Congreso Nacional de Arqueología Argentina*. Universidad de Córdoba, p. 396.
- Gruber, N., 2008. Global modeling of the coastal carbon cycle—a roadmap. *Geophysical Research Abstracts* 10.
- Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. *Science* 319, 948–952.
- Heusser, C.J., 1990. Late-glacial and Holocene vegetation and climate of Subantarctic South America. *Review of Palaeobotany and Palynology* 65, 9–15.
- Hogg, A.G., Hua, Q., Blackwell, P.G., Niu, M., Buck, C.E., Guilderson, T.P., Heaton, T.J., Palmer, J.G., Reimer, P.J., Reimer, R.W., Turney, C.S.M., Zimmerman, S.R.H., 2013. SHcal13 southern hemisphere calibration, 0–50,000 years cal BP. *Radiocarbon* 55, 1889–1903.
- Jackson, J.B., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Eerlandson, J., Estes, J.A., Hughes, S.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–637.
- Jones, T.L., Hildebrandt, W.R., Kennett, D.J., Porcasi, J.F., 2004. Prehistoric marine mammal overkill in the northeastern Pacific: a review of new evidence. *Journal of California and Great Basin Anthropology* 24 (1), 69–80.
- Keefer, D.K., deFrance, S.D., Moseley, M.E., Richardson, J.B., Satterlee, D.R., Day-Lewis, A., 1998. Early maritime economy and El Niño events at Quebrada Tacahuay, Peru. *Science* 281, 1833–1835.
- Kirch, P.V., 2005. Archaeology and global change: the Holocene record. *Annual Review of Environment and Resources* 30, 409–440.
- Lewis, R.L., Freeman, S.A., Crowder, L.B., 2004. Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. *Ecology Letters* 7, 221–231.
- Lorenzen, C.J., 1970. Surface chlorophyll as an index of the depth, chlorophyll content, and primary productivity of the euphotic layer. *Limnology and Oceanography* 15, 479–480.
- Lyman, L.R., 2003. Pinniped behavior, foraging theory, and the depression of metapopulations and nondepression of a local population on the southern Northwest Coast of North America. *Journal of Anthropological Archaeology* 22, 376–388.
- McKechnie, I., Wigen, R.J., 2011. Toward a historical ecology of pinniped and sea otter hunting traditions on the coast of southern British Columbia. In: Braje, T.J., Rick, T.C. (Eds.), *Human Impacts on Seals, Sea Lions, and Sea Otters: Integrating Archaeology and Ecology in the Northeast Pacific*. University of California Press, Berkeley, pp. 129–166.
- Miotti, L., Salemme, M.C., Martita, L., 2003. When Patagonia was colonized: people mobility at high latitudes during Pleistocene/Holocene transition. *Quaternary International* 109–110, 95–111.
- Moreno, E., 2008. *Arqueología y etnohistoria de la costa patagónica central en el Holoceno tardío*. Fondo Editorial Provincial, Secretaría de Cultura del Chubut.
- Moss, M.L., Losey, R.J., 2011. Native American use of seals, sea lions, and sea otters in estuaries of northern Oregon and southern Washington. In: Braje, T.J., Rick, T.C. (Eds.), *Human Impacts on Seals, Sea Lions, and Sea Otters: Integrating Archaeology and Ecology in the northeast Pacific*. University of California Press, Berkeley, pp. 167–195.
- Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283.
- Newsome, S.D., Etnier, M.A., Kurle, C.M., Waldbauer, J.R., Chamberlain, C.P., Koch, P.L., 2007. Historic decline in primary productivity in western Gulf of Alaska and eastern Bering Sea: isotopic analysis of northern fur seal teeth. *Marine Ecology Progress Series* 332, 211–224.
- Obelic, B., Álvarez, A., Argullós, J., Piana, E.L., 1998. Determination of water palaeotemperature in the Beagle Channel (Argentina) during the last 6000 yr through stable isotope composition of *Mytilus edulis* shells. *Quaternary of South America and Antarctic Peninsula* 11, 47–71.
- Orquera, L.A., Piana, E.L., 1999. *Arqueología de la región del canal Beagle (Tierra del Fuego, República Argentina)*. Sociedad Argentina de Antropología, Buenos Aires.
- Orquera, L.A., Gómez Otero, J., 2007. Los cazadores-recolectores de las costas de Pampa, Patagonia y Tierra del Fuego, vol. XXXII. *Relaciones de la Sociedad Argentina de Antropología*, pp. 75–99.
- Orquera, L.A., Legoupil, D., Piana, E.L., 2011. Littoral adaptation at the southern end of South America. *Quaternary International* 239, 61–69.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F.J., 1998. Fishing down marine food webs. *Science* 279, 860–863.
- Pauly, D., Watson, R., Alder, J., 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. *Philosophical Transactions of the Royal Society of London* 29 (360), 5–12.
- Piana, E., Vila, A., Orquera, L., Estévez, J., 1992. Chronicles of the “Ona-Ashaga”: archaeology in the Beagle Channel (Tierra del Fuego-Argentina). *Antiquity* 66, 771–783.
- Ponce, J.F., Rabassa, J., Coronato, A., Borronei, A.M., 2011. Palaeogeographical evolution of the Atlantic coast of Pampa and Patagonia from the last glacial maximum to the Middle Holocene. *Biological Journal of the Linnean Society* 103 (2), 363–379.
- Porcasi, J.F., Jones, T.L., Raab, L.M., 2000. Trans-Holocene marine mammal exploitation on San Clemente Island, California: a tragedy of the commons revisited. *Journal of Anthropological Archaeology* 19, 200–220.
- Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83 (3), 703–718.
- Saporiti, F., Bala, L.O., Crespo, E.A., Gómez Otero, J., Zangrando, A.F.J., Aguilar, A., Cardona, L., 2013. Changing patterns of marine resource exploitation by hunter-gatherers throughout the late Holocene of Argentina are uncorrelated to sea surface temperature. *Quaternary International* 299, 108–115.
- Schiavini, A., 1993. Los lobos marinos como recurso para cazadores-recolectores marinos: el caso de Tierra del Fuego. *Latin American Antiquity* 4 (4), 346–366.
- Smith, R.C., 1981. Remote sensing and depth distribution of ocean chlorophyll. *Marine Ecology Progress Series* 5, 359–361.
- Tivoli, A.M., Zangrando, A.F., 2011. Subsistence variations and landscape use among maritime hunter-gatherers. A zooarchaeological analysis from the Beagle Channel (Tierra del Fuego, Argentina). *Journal of Archaeological Science* 38, 1148–1156.
- Waser, N.A.D., Harrison, W.G., Head, E.J.H., Nielsen, B., Lutz, V.A., Calvert, S.E., 2000. Geographic variations in the nitrogen isotope composition of surface particulate nitrogen and new production across the North Atlantic Ocean. *Deep Sea Research Part I: Oceanographic Research Papers* 47, 1207–1226.
- Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K., Mace, P.M., McClanahan, T.R., Minto, C., Palumbi, S.R., Parma, A.M., Ricard, D., Rosenberg, A.A., Watson, R., Zeller, D., 2009. Rebuilding global fisheries. *Science* 325, 578–585.
- Wu, J., Calvert, S.E., Wong, C.S., 1997. Nitrogen isotope variations in the subarctic northeast Pacific: relationships to nitrate utilization and trophic structure. *Deep Sea Research Part I: Oceanographic Research Papers* 44, 287–314.
- Yesner, D.R., Figuerero Torres, M.J., Guichon, R.A., Borrero, L.A., 2003. Stable isotope analysis of human bone and ethnohistoric subsistence patterns in Tierra del Fuego. *Journal of Anthropological Archaeology* 22, 279–291.