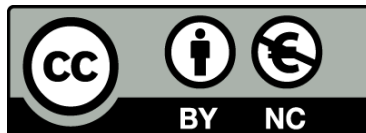


Cambios en la ecología trófica de los depredadores apicales del Mar Argentino durante el Holoceno

Fabiana Saporiti



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Departamento de Biología Animal

Programa de Doctorado en Biodiversidad

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

Changes in the trophic ecology of the apex predators of the Argentine Sea during
the Holocene

Fabiana Saporiti



Changing patterns of marine resource exploitation by hunter-gatherers throughout the late Holocene of Argentina are uncorrelated to sea surface temperature



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ABSTRACT

During the late Holocene, the coastal marine resources of southern South America were exploited by both marine hunter-gatherers with aquatic mobility in the Beagle Channel and the Chilean archipelago and terrestrial hunter-gatherers who inhabited various coastal settings in Argentina. Although the two cultures differed in technology and in historical exploitation patterns, they both used otariids, molluscs, fishes and sea birds as sources of food and raw materials for centuries. Ultimately, their use of these resources, particularly of otariids, declined strongly at different times. Overexploitation has been suggested as the main reason for this pattern, at least in the Beagle Channel, but similar declines in the north Pacific have been attributed to an increase in sea surface temperature (SST). The present paper tests the latter hypothesis in southern South America by using the $\delta^{18}\text{O}$ of bivalve shells (*Aulacomya atra atra* and *Mytilus edulis*) collected at archaeological sites as a proxy for SST and comparing the patterns of $\delta^{18}\text{O}$ with the patterns of resource exploitation by hunter-gatherers. Samples were collected from the Beagle Channel and the central-northern Patagonian coast (north to 43° S) to generate two comparable datasets. The results suggest that SST increased in both areas at the beginning of the late Holocene and was slightly higher than at present during most of that period, except during the Little Ice Age, when values similar to those recorded at the end of the middle Holocene were found. The relative importance of otariids, mainly *Arctocephalus australis*, in the economy of the inhabitants of the Beagle Channel declined as SST increased, but otariid exploitation did not intensify again during the Little Ice Age. On the contrary, the intensity of otariid exploitation in central-northern Patagonia, mainly *Otaria flavescens*, was unrelated to the changes in $\delta^{18}\text{O}$. Thus, changes in SST are unlikely to be the major driver of these resource-exploitation patterns.

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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).

Modern industrial fishing is 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), but overfishing and the ecological extinction of coastal marine megafauna are thought to predate industrialized fishing in many cases. The historical record clearly demonstrates that pre-industrialized 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 pre-

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industrialized 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).

Humans have exploited marine resources for at least 120,000 years (Marean et al., 2007), but fully maritime cultures (*sensu* Lyman, 1991; Orquera and Piana, 1999; Bjerck, 2009) developed only later, during the Holocene. Such cultures were found in the Arctic (Corbett et al., 2008; Hill, 2011), the Pacific coast of the Americas (Gifford Gonzales et al., 2005; Rick et al., 2011) and the Strait of Magellan and the adjoining Fuegian and Chilean archipelagos (Orquera and Piana, 1999; Yesner et al., 2003; Orquera et al., 2011; Tivoli and Zangrando, 2011), among other regions.

Humans colonized the Americas from southern Siberia at the end of the Pleistocene, most likely following two independent dispersal routes (Keefer et al., 1998; Sandweiss et al., 1998; Miotti and Salemme, 2003; Erlandson et al., 2007; Dillehay et al., 2008; Meltzer, 2009; Erlandson et al., 2011). Human groups dispersing along the Pacific coastline possessed the technology required to exploit marine resources, notably fish, birds and molluscs, but the zooarchaeological record suggests that only a few of them had truly maritime economies and that a strong reliance on marine mammals, primarily pinnipeds, developed only much later, during the Holocene (Keefer et al., 1998; Sandweiss et al., 1998; Yesner et al., 2003; Dillehay et al., 2008; Betts et al., 2011; Erlandson et al., 2011; Gifford-Gonzalez, 2011; McKechnie and Wigen, 2011; Moss and Losey, 2011; Orquera et al., 2011; Tivoli and Zangrando, 2011; Whitaker and Hildebrandt, 2011).

The southern end of South America was colonized by humans more than 12,000 years ago (Miotti and Salemme, 2003; Borrero and Miotti, 2008; Dillehay et al., 2008; Orquera et al., 2011), but the archaeological record shows that intense exploitation of marine resources did not develop until approximately 6400 ^{14}C BP in the Beagle Channel (Tierra del Fuego) and along the southern coast of Chile, where fur seals (*Arctocephalus australis*) were the primary prey (Schiavini, 1993; Orquera and Piana, 1999; Orquera et al., 2011; Tivoli and Zangrando, 2011). Marine resources were also exploited approximately 7000–6000 ^{14}C BP by littoral hunter-gatherers (*sensu* Lyman, 1991) inhabiting central and northern Patagonia (Gómez Otero, 2006; Moreno, 2008; Favier Dubois et al., 2009), but more ancient coastal archaeological sites may have disappeared due to rising sea levels during the middle Holocene (Ponce et al., 2011).

The zooarchaeological record and analyses of carbon and nitrogen stable-isotope ratios in human samples from central and northern Patagonia have revealed major regional differences in the use of marine resources (primarily pinnipeds) during the late Holocene, although the consumption of marine resources decreased strongly in all areas after the arrival of Europeans and was completely abandoned in the 17th century (Gómez Otero, 2007; Moreno, 2008; Favier Dubois et al., 2009). Otariids, especially southern sea lions (*Otaria flavescens*), were intensely exploited throughout the late Holocene in the southern province of Santa Cruz (Moreno, 2008). Conversely, the exploitation of sea lions in Chubut province was moderate from 3000 to 1000 years ago, although it intensified from 1000 to 350 years ago (Grammer, 2005; Gómez Otero, 2006, 2007). Finally, the opposite pattern occurred in the northern province of Rio Negro, where intense exploitation of sea lions from 3100 to 2200 years ago was followed by a period of moderate exploitation from 1500 to 420 years ago (Favier Dubois et al., 2009).

Although hunter-gatherers in the Beagle Channel and on the northern Patagonian coast differed dramatically in technology and in historical patterns of resource exploitation (Orquera and Piana, 1999; Moreno, 2008; Orquera and Gómez Otero, 2008; Orquera et al., 2011) (Fig. 1), the use of otariids declined strongly in both

regions after a long period of exploitation (Yesner et al., 2003; Gómez Otero, 2006; Moreno, 2008; Favier Dubois et al., 2009; Tivoli and Zangrando, 2011). Similar declines in pinniped use by maritime hunter-gatherers in the north Pacific have sometimes been linked to increasing sea surface temperatures (Colten and Arnold, 1998; Betts et al., 2011) but are usually attributed to overexploitation in the absence of strong evidence for climatic forcing (Porcasi et al., 2000; Lyman, 2003; Jones et al., 2004; Newsome et al., 2007).

Available pollen and stable-isotope data from Tierra del Fuego have been interpreted as evidence of a rather constant climate through the middle and late Holocene (Heusser, 1984, 1990; Obelic et al., 1998). Accordingly, previous researchers have concluded that changes in the resource-use patterns of hunter-gatherers in the Beagle Channel were not driven by climatic variability (Orquera et al., 2011; Tivoli and Zangrando, 2011). Nevertheless, closer examination of the stable-isotope data reported by Obelic et al. (1998) reveals the prevalence of ^{18}O -enriched samples at the end of the middle Holocene and of ^{18}O -depleted samples during most of the late Holocene, except during the Little Ice Age (Fig. 3). The lowest $\delta^{18}\text{O}$ values were recorded 2500–1500 years ago, and the pattern of resource exploitation by hunter-gatherers changed dramatically after that time (Fig. 3), suggesting that otariids were exploited more intensely during colder periods and hence that some type of environmental forcing was operative. If this hypothesis is correct, a similar pattern should be observed in central and northern Patagonia. Unfortunately, only a few shell-midden samples from this region have been analysed to date (Lanata et al., 2004; Favier Dubois et al., 2009), and the $\delta^{18}\text{O}$ data set is not comparable to that from the Beagle Channel (Obelic et al., 1998). This paper aims to test the hypothesis that the changing patterns of marine resource exploitation by hunter-gatherers along the south-western Atlantic coast of Argentina were driven by climatic variability. To test this hypothesis, two comparable $\delta^{18}\text{O}$ data sets from the Beagle Channel and central and northern Patagonia are generated and 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).

2. Materials and methods

2.1. Bivalve shell samples

Archaeological samples of bivalves were obtained from previous samplings carried out by one of the authors (Julietta Gómez Otero) in central-northern Patagonia and by researchers from CADIC-CONICET, Ushuaia (Luis Orquera, Ernesto Piana and A. Francisco Zangrando), in the Beagle Channel, Tierra del Fuego (Fig. 2). Five shells of rubbed mussel (*Aulacomya atra atra*) were collected from different layers of shell middens in central-northern Patagonia and 5 shells of blue mussel (*Mytilus edulis*) from different layers of shell middens along the Beagle Channel. Because the samples were dated in different laboratories and using different methods, the conventional, non-calibrated radiocarbon dates will be used for all sites (Table 1).

In February 2010, additional samples ($n = 5$ for each species and site) of modern intertidal blue mussels were collected from the Beagle Channel and Buenos Aires province and rubbed mussels from the Beagle Channel and northern Patagonia. Sampling sites were selected to cover the latitudinal range of both species in the south-western Atlantic and to use current $\delta^{18}\text{O}$ values as benchmarks.

2.2. Stable isotope analysis

All bivalve samples were polished with sandpaper and a diamond wheel drill to remove impurities. They were then rinsed with

Table 1
Archaeological sites quoted in the text; the first column represents the sampling areas (see Fig. 1).

Area	Site	Material	Radiocarbon datation (yr ^{14}C BP)	Laboratory	Reference
Central-northern Patagonia	Los Abanicos 1	Charcoal	380 ± 60	LATYR-CONICET-UNLP	Gómez Otero, 2006
Central-northern Patagonia	Las Ollas conchero 1	Shells	610 ± 60/640 ± 60	LATYR-CONICET-UNLP	Gómez Otero, 2006
Central-northern Patagonia	Playa Las Lisas 2 – Perfil 1	Shells	2140 ± 50	LATYR-CONICET-UNLP	Gómez Otero, 2006
Central-northern Patagonia	Cracker 8 – Nivel 3	Charcoal	5500 ± 80	LATYR-CONICET-UNLP	Gómez Otero, 2006
		Shells	5200 ± 70	LATYR-CONICET-UNLP	
Canal Beagle	Túnel VII	Charcoal	100 ± 45	INGEIS (Buenos Aires)	Piana et al., 1992 quoted in Schiavini, 1993
Canal Beagle	Shamakush X site	Charcoal	500 ± 100	INGEIS (Buenos Aires)	Orquera and Piana, 1999 quoted in Tivoli and Zangrando, 2011
Canal Beagle	Mischiuen I Upper C	Charcoal	890 ± 90	INGEIS (Buenos Aires)	Piana et al., 2004 quoted in Tivoli, 2010
Canal Beagle	Imiwaia I (M/K)	Charcoal	5750 ± 170	INGEIS (Buenos Aires)	Piana et al., 1992 quoted in Schiavini, 1993
			5870 ± 150	INGEIS (Buenos Aires)	
			5949 ± 50	Arizona (USA)	

distilled water, dried at 50 °C and ground into a fine powder using a mortar and pestle. The samples were heated at 200 °C for 1 h to remove all organic matter (Dutton and Lohmann, 2002), and aliquots weighing between 40 and 60 µg were acidified in 100% phosphoric acid at 70 °C for 180 s in a Carbonate Kiel Device III (Thermo Finnigan) and analysed using an automated Finnigan MAT-252 isotope-ratio mass spectrometer at the Science and Technology Centres (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 per mil (‰) deviations from predefined international standards, were calculated as

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

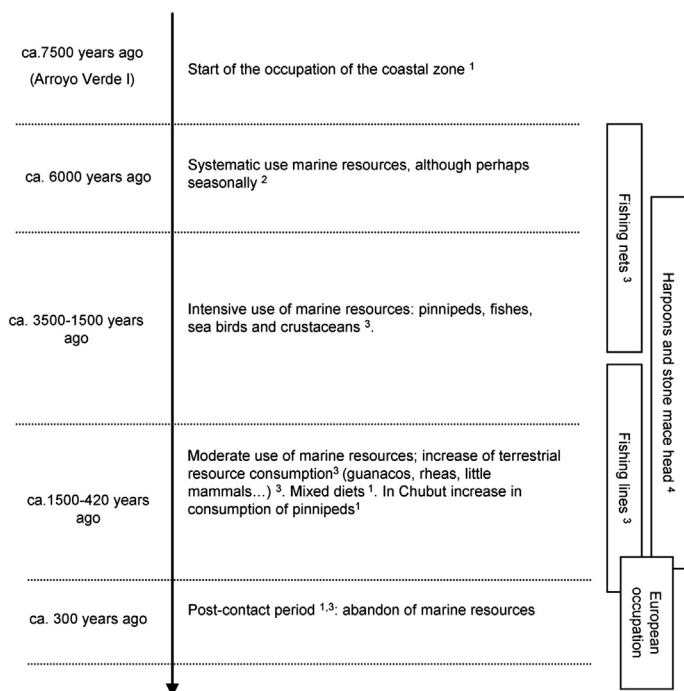
where X is ^{18}O or ^{13}C , R_{sample} is the heavy-to-light isotope ratio of the sample ($^{18}\text{O}/^{16}\text{O}$; $^{13}\text{C}/^{12}\text{C}$), and R_{standard} is the heavy-to-light isotope ratio in the NBS-19 reference standards ($\delta^{13}\text{C}_{\text{PDB}} = +1.95\text{‰}$

and $\delta^{18}\text{O}_{\text{PDB}} = -2.20\text{‰}$) certified by the International Atomic Energy Agency (IAEA, Vienna).

2.3. Archaeological collections for resource use pattern characterization

The collections from five middens excavated at three archaeological sites 40 km apart were used to characterize the pattern of resource use by hunter-gatherers inhabiting the Beagle Channel. One location was situated at Cambaceres Bay and included archaeofaunal samples from stratigraphic layers dated 5940 ^{14}C BP, 1580 ^{14}C BP and from the 19th century. The other middens were located at Estancia Remolino and were dated 4980 ^{14}C BP, 940 ^{14}C BP and 500 ^{14}C BP. There were not significant differences concerning excavation methods, as the same procedures (Orquera and Piana, 1992) were followed. See Tivoli and Zangrando (2011) and references herein for further detail about the sites, dating procedures and collections. The collections from seven middens

a) Northern Patagonia (Chubut/Río Negro)



b) Tierra del Fuego (Beagle Channel)

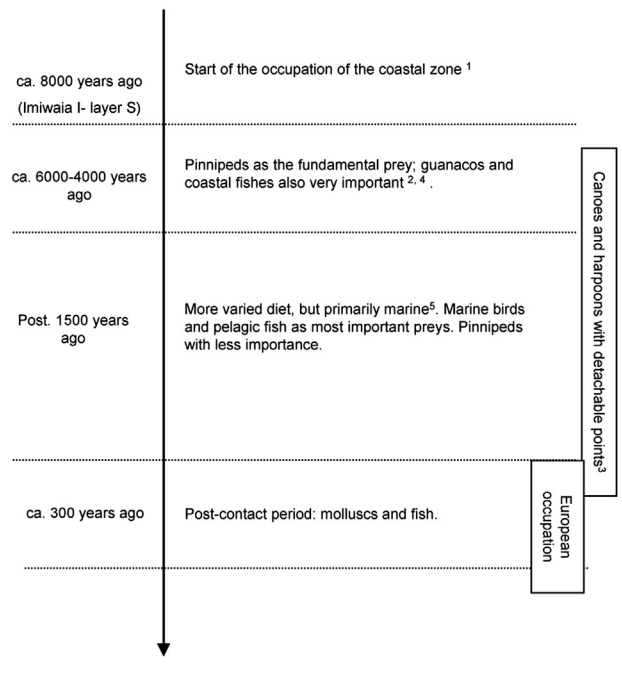


Fig. 1. Subsistence patterns of hunter-gatherers peoples of a) Northern Patagonia; ¹Gómez Otero, 2007; ²Grammer, 2005; ³Favier Dubois et al., 2009; ⁴Moreno, 2008; and b) Tierra del Fuego; ¹Orquera and Piana, 1999; ²Tivoli and Zangrando, 2011; ³Orquera and Piana, 2011; ⁴Schiavini, 1993; ⁵Yesner et al., 2003.

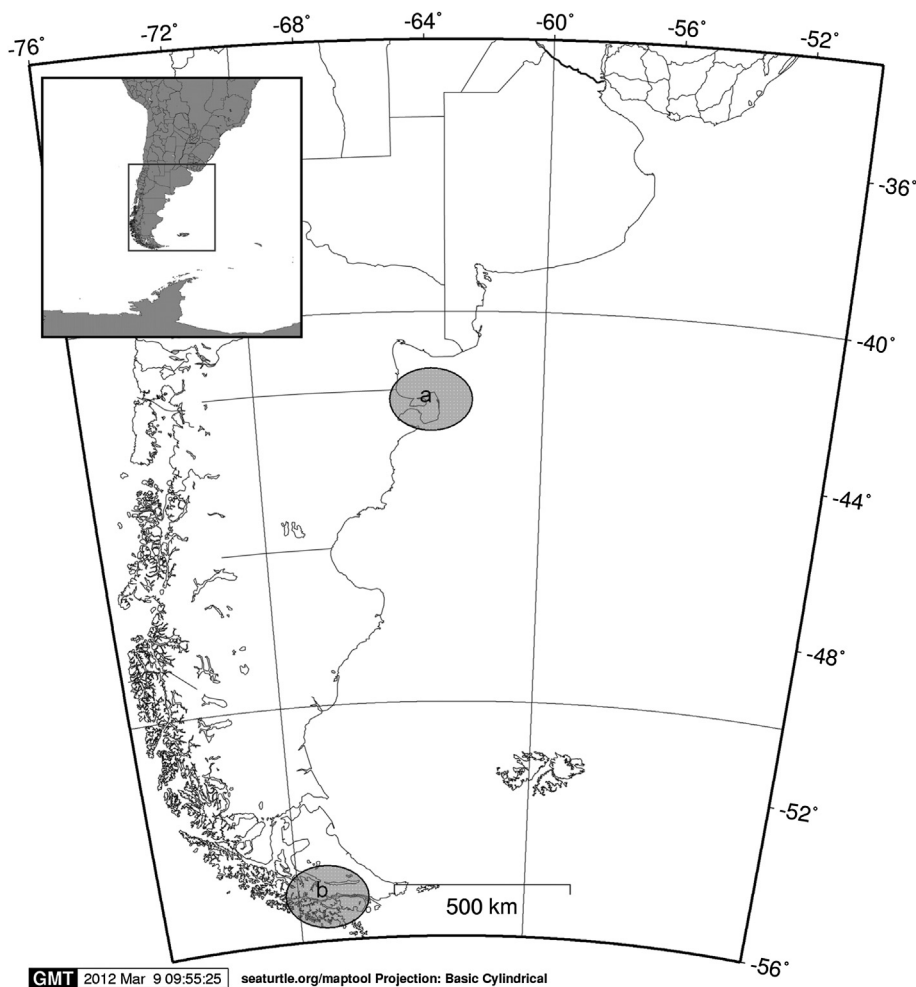


Fig. 2. Map showing approximate sampling localities: a) central-northern Patagonia and b) Beagle Channel.

scattered along 30 km of coastline were used to characterize the pattern of resource use by hunter-gatherers inhabiting northern Patagonia (Favier Dubois et al., 2009).

2.4. Statistical analysis

The normality of the data distribution was tested using the Lilliefors test, and the homoscedasticity was tested using the Levene test. ANOVA was used for multiple comparisons when the data fit the normality and/or homoscedasticity requirements, and the non-parametric Kruskal–Wallis test was used otherwise (Zar, 1998).

The non-parametric Spearman rank correlation coefficient was used to test the association of $\delta^{18}\text{O}$ values and the relative abundance of otariids in the archaeological record, which was assessed using different methods in the collections from the Beagle Channel than in those from northern Patagonia, because of their contrasting characteristics. The relative abundance of otariids was assessed as the percentage of the number of specimens identified at the species level (%NISP) in the collections from the Beagle Channel, because bone material was well preserved and the number of specimens was assessed precisely (Tivoli and Zangrando, 2011). Bone preservation was worse at the archaeological sites from northern Patagonia and therefore numbers of specimens were not 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 using the PASW Statistics 18 software package.

3. Results

The $\delta^{18}\text{O}$ values of blue mussel shells from the Beagle Channel varied dramatically throughout the second half of the Holocene (Kruskal–Wallis test, $\chi^2 = 22.018$, $df = 4$, $N = 25$, $p < 0.001$), but compared to modern blue mussels, zooarchaeological samples were often more enriched in ^{18}O , except those from the Mischiuen I site dated 890 ± 90 ^{14}C BP (Fig. 3e). Notably, the average $\delta^{18}\text{O}$ of the blue mussels from the Mischiuen I site was much lower than that reported for modern blue mussels from the subtropical Buenos Aires province (Fig. 3e); such intense ^{18}O depletion could not be caused by a higher sea surface temperature alone. The most likely explanation is a dramatic decline in salinity, perhaps caused by increased freshwater runoff due to accelerated glacier melting in a slightly warmer climate. Under this scenario, the reconstruction the sea surface temperature based on $\delta^{18}\text{O}$ values may be highly inaccurate.

Differences in the average $\delta^{18}\text{O}$ values of rubbed mussels (ancient and modern) from central-northern Patagonia throughout the past 5500 years were not statistically significant (ANOVA; $F_{4,20} = 2.056$; $p = 0.125$) due to high variability, particularly among

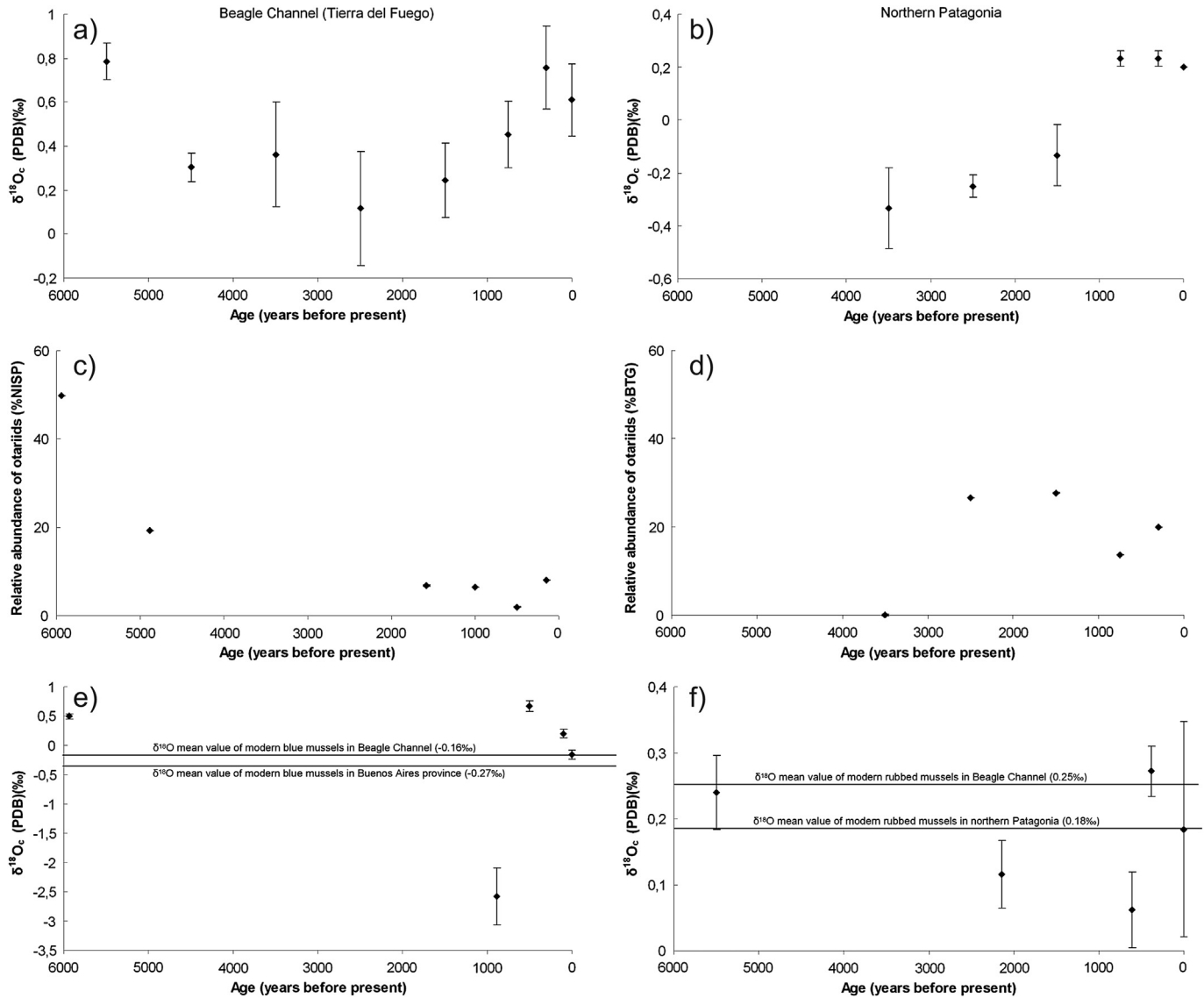


Fig. 3. a) Temporal profiles of oxygen stable isotope ratios in mytilid shells from the Beagle Channel according to Obelicio et al. (1998), b) temporal profile of oxygen stable isotope ratios in mytilid shells from Río Negro, northern Patagonia, according to Favier Dubois et al. (2009), c) temporal profiles of the relative importance of otariids in the zooarchaeological record from the Beagle Channel according to Tivoli and Zangrando (2011), d) temporal profile of the relative importance of otariids the zooarchaeological record from Río Negro, northern Patagonia (Favier Dubois et al., 2009), e) temporal profiles of oxygen stable isotope ratios in mytilid shells from the Beagle Channel according to the present study and f) temporal profiles of oxygen stable isotope ratios in mytilid shells from central-northern Patagonia according to the present study.

modern samples. However, the differences were statistically significant if only zooarchaeological samples were considered (ANOVA; $F_{3,16} = 4.726$; $p = 0.015$). Moreover, the temporal pattern was similar to that reported for the Beagle Channel, with high $\delta^{18}\text{O}$ values at the time when hunter-gatherers began to exploit coastal sites at the end of the middle Holocene, low $\delta^{18}\text{O}$ values during most of the late Holocene (2100–600 ^{14}C BP), high $\delta^{18}\text{O}$ values during the Little Ice Age and declining $\delta^{18}\text{O}$ values during recent centuries (Fig. 3f). Notably, the sea surface temperature during the cold phases corresponding to the end of the middle Holocene and the Little Ice Age was much colder than that currently observed in central-northern Patagonia and close to that currently observed in the Beagle Channel. In contrast, the sea surface temperature during the warmer period between the end of the middle Holocene and the Little Ice Age was slightly warmer than that currently observed in northern Patagonia.

Therefore, the temporal profiles of oxygen stable-isotope ratios in both areas revealed similar patterns, characterized by low

temperatures at the end of the middle Holocene, high temperatures throughout most of the late Holocene, a second cold phase during the Little Ice Age and a recent warming. If the temporal changes in the resource-exploitation patterns revealed by previous zooarchaeological research were caused by climatic variability, they should be parallel in northern Patagonia and the Beagle channel, as both regions showed parallel changes in the oxygen stable-isotope ratios.

However, the resource-exploitation patterns of the Beagle Channel and northern Patagonia were rather different, because otariids occurred throughout the second half of the Holocene in the archaeological record from the Beagle Channel, but were absent from the archaeological sites older than 3000 years ago in northern Patagonia (Fig. 3). Furthermore, the relative importance of otariids in the archaeological record from the Beagle Channel declined steadily during the second half of the Holocene, whereas, the relative importance of otariids in the archaeological record from northern Patagonia increased approximately 2500 years ago, to

decrease slightly 1000 years ago (Fig. 3c–d). Finally, there was no correlation between the $\delta^{18}\text{O}$ values of bivalve shells and the relative abundance of otariids in the archaeological record, either in the Beagle Channel (Rho = 0.500, $p = 0.327$, $n = 5$) or northern Patagonia (Rho = 0.154, $p = 0.801$, $n = 5$). Therefore, their source-exploitation patterns of the two regions were quite different and varied independently, without any relationship with the oxygen stable-isotope ratios in bivalve shells (Fig. 3).

4. Discussion and conclusions

The oxygen-isotope ratios of bivalve shells are currently the most robust proxies for temperature reconstructions and are most likely not affected by ontogenetic changes during bivalve growth (Schöne et al., 2004). However, the reconstruction of palaeotemperatures using the $\delta^{18}\text{O}$ values of bivalve shells can be confounded by variations in salinity (Epstein et al., 1951; Wefer and Berger, 1991; Schöne et al., 2004; LeGrande and Schmidt, 2006) because the $\delta^{18}\text{O}$ values of seawater are influenced by both temperature and salinity (Bowen, 2010). Freshwater runoff into the Beagle Channel is intense (Guerrero and Piola, 1997) and may have varied dramatically during the Holocene in response to glacier melting. Furthermore, palynological analysis has revealed wetter conditions in the Beagle Channel during the second half of the Holocene (Heusser, 1989), possibly resulting in more intense freshwater runoff.

These observations challenge the use of $\delta^{18}\text{O}$ values from bivalve shells for palaeotemperature reconstruction in the Beagle Channel, although Obelic et al. (1998) attempted to overcome this problem using samples from middens located near areas that currently contain “pure seawater”, which in the region has a salinity level of 33 g L^{-1} (Guerrero and Piola, 1997). Samples from middens located near areas that are currently flooded with brackish water were also studied but were not included in subsequent analyses. Palaeotemperature reconstruction using “marine” samples alone revealed no major changes throughout the second half of the Holocene (Obelic et al., 1998), but there is no reason to assume that the distribution of water masses of contrasting salinity within the Beagle Channel has remained unchanged throughout the second half of the Holocene. Thus, the selected middens may not actually have been representative of truly marine conditions. Furthermore, both low salinity levels and high temperatures result in low $\delta^{18}\text{O}$ values. Hence, the alternation of cold and warm periods is not obscured by changes in salinity, although the actual seawater temperature cannot be calculated, and its fluctuations may be magnified by changes in salinity.

When the full data set of Obelic et al. (1998) is considered, a clear pattern emerges, with ^{18}O -enriched samples prevailing at the end of the middle Holocene and ^{18}O -depleted samples prevailing during most of the late Holocene, except during the Little Ice Age (Fig. 3). The data reported here are consistent with this pattern and reveal a parallel pattern for the central-northern Patagonian coast, where $\delta^{18}\text{O}$ values are not confounded by variable salinity because freshwater runoff is currently very low (Guerrero and Piola, 1997) and salinity levels were similar during the middle Holocene, as suggested by a malacological analysis of Quaternary marine terraces (Aguirre et al., 2006). Accordingly, the available evidence confirms the occurrence of a warmer climate in both the Beagle Channel and central-northern Patagonia during the Mediaeval Warm Epoch (Villalba, 1990; Stine, 1994) and of a colder climate during the Little Ice Age (Villalba, 1990; Winkler, 2000; Mauquoy et al., 2004). These findings demonstrate that the climate varied simultaneously in both regions, although contemporaneous seawater temperatures were always lower in the Beagle Channel than off northern Patagonia.

Increasing sea surface temperatures coincided with the decreasing reliance of hunter-gatherers in the Beagle Channel on otariids throughout the first half of the late Holocene (Schiavini, 1993; Tivoli and Zangrando, 2011). However, a causal relationship cannot be determined for at least two reasons. Firstly, otariids consumption did not increase again during the Little Ice Age (Schiavini, 1993; Tivoli and Zangrando, 2011), when sea surface temperature declined. Western exploitation may have decimated fur seals (*Arctocephalus australis*) in Tierra del Fuego at the end of the 18th and beginning of the 19th century (Ratto, 1943; Schiavini, 1992), thus preventing hunter-gatherers from resuming their former exploitation levels during the Little Ice Age. However, fur seal bones were already quite rare in middens $500 \pm 100 \text{ }^{14}\text{C BP}$, when the sea surface temperature had already decreased and European explorers had only recently reached the region. Secondly, male fur seals (*Arctocephalus australis*) represented most of the otariids exploited by hunter-gatherers in the Beagle Channel, and the largest population of the species in the Atlantic currently occurs in subtropical Uruguay (Túnez et al., 2008). Thus, the warm temperatures prevailing during most of the late Holocene most likely did not limit the abundance of this species. In addition, the exploitation of male fur seals would have not severely impacted the population given the high degree of polygyny in this species.

In contrast to the situation in the Beagle Channel, increasing sea surface temperatures during the late Holocene coincided with more intense exploitation of sea lions (*Otaria flavescens*) by hunter-gatherers in central and northern Patagonia, although this intensification began earlier in northern than in central Patagonia (Gómez Otero, 2006; Gómez Otero, 2007; Favier Dubois et al., 2009). Interestingly, reliance on otariids declined 1500 years ago in northern Patagonia (Favier Dubois et al., 2009) and 700 years ago in central Patagonia (Gómez Otero, 2007), although no major change in sea surface temperature was recorded at those times. Thus, the exploitation of otariids in central and northern Patagonia was high when the sea surface temperature was high (at the beginning of the Mediaeval Warm Epoch) and low when sea surface temperature was both low (at the end of the middle Holocene) and high (at the end of the Mediaeval Warm Epoch).

In conclusion, changes in sea surface temperature played only a minor role, if any, in the changing subsistence strategies of hunter-gatherers in northern Patagonia and the Beagle Channel. However, this conclusion does not imply that the abundance of otariids in the south-western Atlantic declined as a result of prolonged exploitation by hunter-gatherers. Otariid populations can be highly sensitive to declines in food abundance and quality (Trites and Donnelly, 2003). Therefore, variations in marine primary productivity in the south-western Atlantic during the second half of the Holocene may better explain the observed variations in the relative abundance of otariids in hunter-gatherer middens, as suggested for the north Pacific (Finney et al., 2002).

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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.2013.03.026>.

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