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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 ($\delta^{15}N$) 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 overexploitation 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, $\delta^{15}N$ values in herbivorous molluscs are expected to reveal $\delta^{15}N$ 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 $\delta^{15}N$ 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 $\delta^{15}N$ 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 Río Negro province (41°1.20′S—41°38.40′S; 64°10.80′W—65°1.20′W), three in Santa Cruz province (47°44.40′S—50°6.60′S; 65°50.40′W—68°27.00′W) and one in Tierra del Fuego province (54°49.20′S; 68°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
$\delta^{15}N$ 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 $\delta^{15}N$ (‰)	Mean Chl-a (mg/m^3)
Nacella magellanica	Río Negro	5	11.8 (±0.5)	1.22 (±2.33)
Nacella magellanica	Santa Cruz	5	12.1 (±0.4)	1.44 (±0.47)
Nacella magellanica	Santa Cruz	5	12.3 (±0.3)	1.55 (±0.30)
Nacella magellanica	Santa Cruz	5	13.0 (±0.5)	1.97 (±0.91)
Nacella magellanica	Tierra del Fuego	5	10.8 (±0.3)	0.86 (±0.12)
Aulacomya atra atra	Río Negro	7	11.5 (±0.3)	1.05 (±1.56)
Aulacomya atra atra	Santa Cruz	5	11.8 (±0.4)	1.44 (±0.47)
Aulacomya atra atra	Santa Cruz	5	12.5 (±0.3)	1.97 (±0.91)
Aulacomya atra atra	Tierra del Fuego	5	11.9 (±0.3)	0.86 (±0.12)

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