



Patterns of fish consumption by hunter-fisher-gatherer people from the Atlantic coast of Tierra del Fuego during the Holocene: Human-environmental interactions

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ABSTRACT

This paper aims to assess changes in the patterns of marine fish consumption by hunter-fisher-gatherer populations in the context of environmental change. To accomplish this objective, we used two methodological approaches: first, stable isotope analysis in ancient and modern shells of limpets and mussels to explore changes in the isotopic baseline and also in fish skeletal remains recovered from different archaeological sites dated to the Middle and Late Holocene of Tierra del Fuego (Argentina); second, a zooarchaeological quantitative analysis of the fish remains from different archaeological sites in the same area and period. Results confirmed that marine primary productivity in the Atlantic coast of Tierra del Fuego decreased throughout the second half of the Holocene, while the contribution of phytoplankton to the carbon pool fueling the coastal food web decreased simultaneously. The quantitative zooarchaeological analysis and the stable isotope analyses in fish remains suggest that in the Atlantic coast there was a variation in the consumption of fish species from offshore to near shore fish species throughout time, mostly because of the declining occurrence of Argentine hake (*Merluccius hubbsi*). This could result from changes in the distribution of the latter and the probability of mass stranding.

1. Introduction

The study of human-environment interactions and the strategies carried out by past societies to deal with ecological changes have been key issues in archaeological inquiry. Since the 1980s, coastal landscapes have been included in this debate with the aim to unravel the role played by the sea and coasts not only in the expansion, evolution and migrations of humans but also in the development of complex societies (Bailey, 2004; Erlandson and Fitzpatrick, 2006; Mearns et al., 2007). As many other ecosystems, marine ecosystems are also sensitive to environmental oscillations, and the archaeological contexts related to coastal resources exploitation are paramount contexts to analyze past human-environment interactions (Pal et al., 2019).

Past societies incorporated marine ecosystems into their way of life

(Mearns et al., 2007). The cold and temperate rocky shores along the Pacific coast of the Americas and the southernmost tip of the Atlantic coast of South America share similar ecosystems, characterized by dense colonies of pinnipeds, extensive intertidal beds of mussels *Mytilus* spp. Linnaeus, 1758, and dense forests of the giant kelp *Macrocystis pyrifera* (Linnaeus) C. Agardh, 1820 (McDonald and Kohen, 1988; Graham et al., 2007; Borsari et al., 2012; Webber, 2014). These coastal landscapes offer highly abundant and predictable marine resources that can be exploited easily and hence facilitated the colonization by humans (Erlandson, 2001; Erlandson and Fitzpatrick, 2006; Boivin et al., 2013). From the first contact between human societies and coastal regions, a progressive process of greater incidence in marine ecosystems was initiated both at local and regional scales (Redman, 1999; Erlandson and Fitzpatrick, 2006; Braje and Rick, 2011). These human impacts on marine

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ecosystems have been accelerating and increasing over time and simultaneously, human population has grown and expanded geographically, in conjunction with the improvement of fishing technology and the beginning of global markets (Grayson, 2001; Anderson, 2008).

However, coastal societies had to cope with natural changes in marine primary productivity and sea surface temperature (SST) and their impacts on marine resources availability (Butler, 2001; Pitcher, 2001). Whereas the intensity of marine primary productivity determines largely the abundance of marine animal resources and their availability for local people (eg. Finney et al., 2002; Saporiti et al., 2014a), changes in SST caused shifts in the latitudinal and/or bathymetric distribution of fish species (Perry et al., 2005; Simpson et al., 2011; Bas et al., 2019, 2020). The way in which human societies dealt with these changes depended on the technological development and innovation, the possibility of exploiting alternative environments and different resources, or the possibility to undertake social changes.

Changes of human consumption and exploitation patterns have been usually reported by traditional zooarchaeological studies as changes in the taxonomic composition of faunal assemblages and changes in the size of the specimens over time (eg. Fitzpatrick et al., 2008; Morales-Muñiz and Roselló-Izquierdo, 2008; Braje and Rick, 2011). More recently, stable isotope analysis has contributed to a better understanding of human impact on the biology of the marine species exploited (eg. Zenteno et al., 2015; Braje et al., 2017) and the response of the associated marine food webs (eg. Saporiti et al., 2014b; Bas et al., 2019). Stable isotope analysis has also been used to assess human paleodiets (eg. Panarello et al., 2006; Kochi et al., 2018) as well as changes in the patterns of human exploitation across environmental gradients (eg. Zangrando et al., 2016; Guiry, 2019).

Isla Grande de Tierra del Fuego (IGTDF hereafter; Fig. 1) is an excellent region to carry out these types of studies and evaluate how human exploitation changed in response to environmental changes, since it has an extensive zooarchaeological record spanning a broad time scale (Muñoz, 2011; Tivoli and Zangrando, 2011; Santiago and Vázquez,

2012; Santiago, 2013; Briz i Godino et al., 2013; Salemmé et al., 2019). Furthermore, the location of the island at high latitude entails major vulnerability to environmental changes as a result of climatic variability (Caniupán et al., 2014) and a low diversity of both terrestrial and marine resources (Miloslavich et al., 2011; Lessa and D'Elía, 2002). IGTDF has been inhabited by different hunter-fisher-gatherer societies at least since the Early Holocene either with navigation technology, as in the Beagle Channel and Strait of Magellan and adjacent seas (Orquera et al., 2011; Torres Elgueta, 2016, respectively), or without it, as in the case of the Atlantic coast of IGTDF (Borrazzo, 2010; Salemmé et al., 2007, 2014, 2019; Santiago, 2013; Briz i Godino et al., 2018).

This paper aims to assess the response of hunter-fisher-gatherer societies inhabiting the Atlantic coast of Tierra del Fuego to changes in the availability of marine resources. We first analyzed the stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in the mollusk shells recovered from archaeological sites located along the Atlantic façade to track changes in primary productivity. Second, we assessed the species identity and analyzed the stable isotope ratios of C of the skeletal remains of fishes to assess the diversity of fish resources exploited.

1.1. Archaeological contexts of Tierra del Fuego study region and regional background

The human occupation of IGTDF began ca. 12,600 cal yr BP (Ozán and Pallo, 2019). During the Middle Holocene, steppe hunter-gatherer populations in Tierra del Fuego based their subsistence on the use of both terrestrial and marine resources, the latter to a lesser extent (Calás, 2009; San Román et al., 2009; Santiago et al., 2011; Torres Elgueta, 2014). The diversity and abundance of terrestrial and marine resources varied temporally and regionally within the island (Santiago and Vázquez, 2012; Tivoli and Salemmé, 2015; Zangrando and Tivoli, 2015; Bas and Lacrouts, 2017).

The Atlantic coast of Tierra del Fuego is characterized by high cliffs and extensive sandy beaches, with great tidal ranges (Isla et al., 2005; Bujalesky, 2007; Montes and Martinioni, 2017); the coasts are exposed

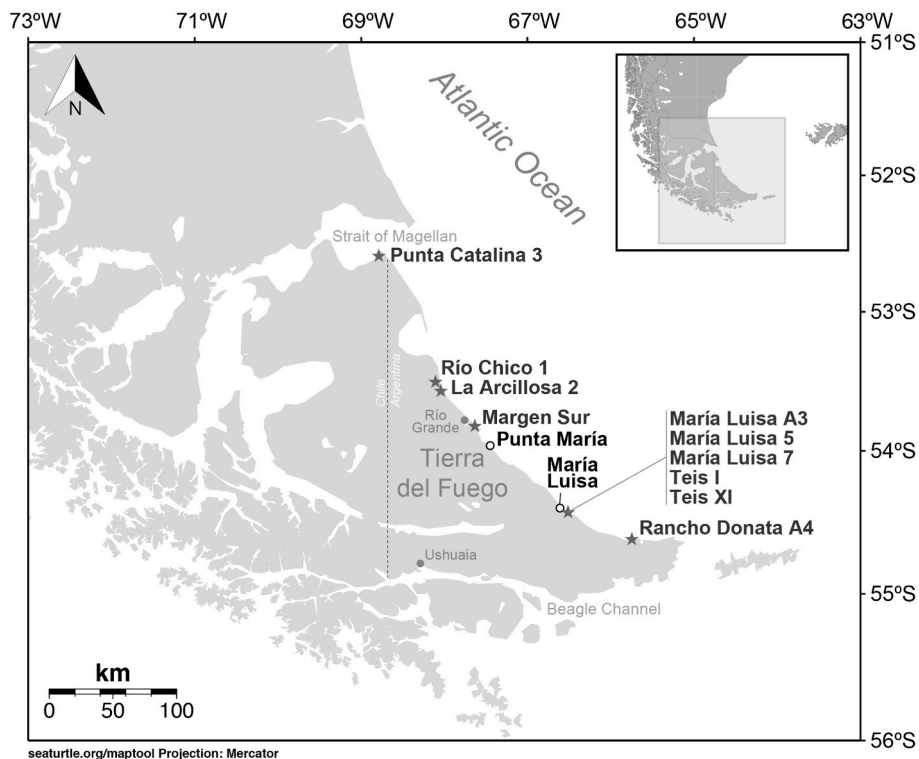


Fig. 1. Isla Grande de Tierra del Fuego (Argentina and Chile). Grey stars indicate archaeological sites used in this study. White circles indicated locations where mollusks were collected (present samples).

to high energy waves and intense westerly winds (Bujalesky, 2007). The earliest evidences of human occupations are dated at 6400 cal yr BP (Favier Dubois and Borrero, 2005; Santiago et al., 2007) and hunter-fisher-gatherer groups lasted until the 19th century. The available archaeological information suggested the exploitation of marine resources, including fish consumption, regardless of the knowledge of navigation technology. Ethnohistorical sources about hunter-fisher-gatherer groups of the Atlantic coast show mainly two fishing techniques developed by its inhabitants: the use of specific bone harpoons or bare hands to obtain the specimens trapped in pools during low tides, and fishing nets made by guanacos' tendons (Segers, 1891; Chapman, 1982; Gusinde, 1986; Coiazzi, 1997). Nevertheless, the evidence of those techniques in the archaeological record is scarce due to preservation conditions. Scheinsohn (1997) points out the existence of a harpoon similar to those that ethnographers indicate to capture fishes in Punta María 2 site, dated on the Late Holocene (Scheinsohn, 1997), as well as lithic sinkers (Scheinsohn, 2013).

From a large-scale perspective, ancient evidences of fishing activities were also detected in the southern portion and northwestern part of the IGTDF, related with hunter-fisher-gatherer societies who developed navigation technology. In the Beagle Channel region, located in the south, human occupations with an intense exploitation of marine resources have been identified from 6400 yr BP (Orquera et al., 2011). The Beagle Channel is a narrow and ancient glacier valley with steep coasts, especially in the central-western areas, with low-intensity tides and waves (Bujalesky, 2007). Fishing played an important role in subsistence practices from the Middle Holocene onwards (Zangrando, 2007). Ethnohistorical and archaeological sources showed that fishing procedures were conducted using harpoons, hooks and lithic weights used to sink fishing lines (Gusinde, 1982; Orquera and Piana, 1999; Bridges, 2000), as well as, the construction of stone structures that would have acted as fishing weirs (Vázquez and Zangrando, 2017). In the northwestern part of the island, in the Strait of Magellan, an interoceanic

channel that has the influence both of the Pacific and Atlantic Oceans, as well as the adjacent areas, the archaeological record confirms that fishing was very relevant for the human subsistence since the Middle Holocene (6000-5500 yr BP). There are presence of fish remains and fishing artifacts, composed particularly by lithic weights probably used to sink fishing lines (Ortiz-Troncoso, 1975; Legoupil 1997; Torres, 2009; Torres and Ruz, 2011), as well as harpoons (Legoupil, 1997).

2. Methods

2.1. Study area and sample collection

To understand the evolution of fish consumption patterns through the Holocene in the Atlantic coast of IGTDF, we considered different kind of data from archaeological sites of the area. All the sites are shell middens of different size dated from the Middle to Late Holocene and their geographical distribution covers approximately 150 km from north to south (Table 1).

Despite the slight differences between the methodological procedures in relation to the excavation of the archaeological sites under study (Fig. 1), there were also similarities such as sediments sieving and the standardized procedures to identify the stratigraphic layers. Regardless that some of them are shell middens the stratigraphic sequence could be accurately traced and the different depositional events have been identified, allowing us a chronological control of the samples used. There were not taphonomy biases since all the sites (unicomponent or multicomponent sites) showed a good resolution and integrity, thus helping us to interpret our results confidently.

In a first analytical stage, we analyzed the stable isotope ratios of C and N in the organic matter matrix of archaeological and modern shells of limpets *Nacella magellanica* (Gmelin, 1791) and mussels *Mytilus chilensis* Hupé, 1854, and the stable isotopes of C in the fish bones recovered from several archaeological sites: RC1, LA2, MS and TXI (Table 1).

Table 1

¹⁴C Archaeological samples used in this paper. * For radiocarbon date calibration, Calib 8.2 program were used (Stuiver et al., 2022) considering South Hemisphere calibration (Hogg et al., 2020; corresponding to "a" superscript) or Marine radiocarbon age calibration curve (Heaton et al., 2020; corresponding to "b" superscript), respectively.

Archaeological site	Lab code	Sample type	Uncal. ¹⁴ C date	Median cal ¹⁴ C date BP *	Two Sigma Ranges	Cultural remains	Reference
Río Chico 1 (RC1)	AA75285	Burned bone	5828 ± 46	6591 ^a	6482–6668	10,776 bone remains (most of them fishes), <i>M. chilensis</i> shells and 1612 lithic artifacts	Santiago (2013); Fig. S1 Santiago et al. (2007) Salemme et al. (2007)
	AA65165	<i>Mytilus chilensis</i>	5856 ± 44	6000 ^b	5764–6209		
	AA 60934	<i>Mytilus chilensis</i>	5508 ± 48	5619 ^b	5414–5862		
La Arcillosa 2 (LA2)	AA102166	<i>Lama guanicoe</i>	5068 ± 66	5778 ^a	5647–5911	<i>M. chilensis</i> shells, less proportion terrestrial and marine vertebrates and lithic assemblage of different raw material and bone artifacts	Salemme et al. (2014) Salemme et al. (2014)
	AA102163	<i>Grampus cf. griseus</i>	5494 ± 65	5603 ^b	5363–5856		
Margen Sur (MS)	AA69655	<i>Homo sapiens</i>	897 ± 38	759 ^a	677–807	Mollusks of six different genera and remains of fish species	Santiago et al. (2011) Salemme et al. (2019)
	AA69657	<i>Mytilus chilensis</i>	1295 ± 50	625 ^b	462–806		
Punta Catalina 3 (PC3)	B-187977	Charcoal	2380 ± 40	2352 ^a	2301–2493	Fishes, cetacean remains and lithic weights	Massone and Torres (2004)
María Luisa A3 (MLA3)	T-13994	Charcoal	1020 ± 80	869 ^a	728–994	<i>Nacella</i> sp. and <i>Mytilus</i> sp. concentrations	Lanata (1995)
María Luisa 5 (ML5)	LP-233	Charcoal	360 ± 50	391 ^a	300–492	Human burial	Lanata (1995)
María Luisa 7 (ML7)	LP-194	Charcoal	690 ± 50	608 ^a	549–670	<i>Nacella</i> sp. and <i>Mytilus</i> sp. concentrations, and lithic and bone tools	Lanata (1995)
Teis I (TI)	DAMS024548	Charcoal	260 ± 21	212 ^a	276–308	<i>Nacella</i> genus, seabirds, fishes and scarce remains of terrestrial and marine mammals	This work
Teis XI (TXI)	AA106348	Charcoal	374 ± 29	393 ^a	317–471	<i>Nacella</i> genus, scarce presence of <i>M. chilensis</i> and other mollusks, marine and terrestrial mammals, fishes and seabirds	Álvarez et al. (2020); Fig. S2 Lanata (1995)
Rancho Donata A4 (RDA4)	LP-252	Charcoal	1380 ± 70	1238 ^a	1175–1357	<i>Nacella</i> sp. and <i>Mytilus</i> sp., birds and fish bones and scarce fragments of pinnipeds and guanaco splinters	Lanata (1995)

It is important to note that limpets are benthic grazers relying largely on microphytobenthos and macroalgae (Rosenfeld et al., 2018), whereas mussels are obligate suspension feeders (Navarro and Winter 1982). Accordingly, limpets reflect the benthic baseline and mussels the pelagic one (Saporiti et al., 2015; Andrade et al., 2016; Riccialdelli et al., 2017). Modern samples of limpets and mussels to obtain the present-day baseline of reference were collected from Punta María and María Luisa beaches, close to some of the archaeological sites included in this paper (Fig. 1 and Table 2).

In the case of fish, bone remains of the following fish species were collected and sampled: Argentine hake *Merluccius hubbsi* Marini, 1933, pink cusk-eel *Genypterus blacodes* (Forster, 1801, eelpout *Austrolycus* sp. Regan, 1913, Patagonian blenny *Eleginops maclovinus* (Cuvier, 1830, Patagonian grenadier *Macruronus magellanicus* Lönnberg, 1907, and snoek *Thyrssites atun* (Euphrasen, 1791 (see Table 3). Since there are not differences in the stable isotope ratios of skeletal elements of fish with acellular bone (Bas and Cardona, 2018), different skeletal elements were analyzed according to availability. Skeletal elements from the neurocranium with the same laterality were preferred, to avoid pseudoreplication. Vertebrae were used otherwise. On that case, they were collected, in each archaeological site, from different quadrants and layers, searching the located as far apart from each other as possible.

In a second analytical stage, we conducted a quantitative zooarchaeological analysis by means of Number of Identified Specimens (NISIP; Grayson, 1984) of fish remains recorded in ten archaeological sites distributed from the Northern to Central-East sections of the Atlantic coast of Tierra del Fuego (Fig. 1; Table 1; see Supporting Information Table S1). The sites were selected considering the available published information about fish remains from the Atlantic coast of Tierra del Fuego (Lanata, 1995; Santiago, 2013; Torres Elgueta, 2014; Bas and Lacrouts, 2017; Saleme et al., 2019) and from unpublished data but available in Museo del Fin del Mundo (Ushuaia, Tierra del Fuego) (see Supporting Information Table S1). For these archaeological sites, fish species were classified as near shore or offshore according to their predominant habitat (Lloris and Rucabado, 1991; Cousseau and Perrotta, 1998).

2.2. Stable isotope analysis

Stable isotope ratios in the tissues of an animal reflect those in its diet and only very small tissue samples are required. The ratio of the stable isotopes of nitrogen ($^{15}\text{N}/^{14}\text{N}$) increases with each trophic position (Minagawa and Wada, 1984; Peterson and Fry, 1987). On the other hand, the ratio of the stable isotopes of carbon ($^{13}\text{C}/^{12}\text{C}$, expressed as

Table 2

Results of GLM with two fixed factors (species and period) performed to assess the temporal variation of the $\delta^{13}\text{C}_{\text{dml}}$ and $\delta^{15}\text{N}_{\text{bulk}}$ values in shells and, when necessary, compensate for any isotopic baseline shift between the periods considered. Shell organic matter has been analyzed for all the samples. RC1: Río Chico 1; LA2: La Arcillosa 2; MS: Margen Sur; TXI: Teis XI; PM: current samples from Punta María; ML: current samples from María Luisa. *N*: sample size; $\delta^{13}\text{C}$ (‰), $\delta^{15}\text{N}$ (‰) and C:N ratio are reported by mean \pm SD. * Denotes statistically significant differences ($P < 0.05$) between ancient and modern samples.

Species	Location	<i>N</i>	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C:N
Limpets	RC1	5	$-12.7 \pm 1.2^*$	$12.2 \pm 0.8^*$	6.28 ± 0.7
	LA2	5	$-15.5 \pm 1.8^*$	$15.1 \pm 1.2^*$	5.74 ± 0.2
	MS	5	$-12.8 \pm 1.4^*$	$14.5 \pm 0.4^*$	5.09 ± 0.5
	TXI	5	$-11.6 \pm 1.4^*$	$12.8 \pm 0.9^*$	5.38 ± 0.7
	PM	5	-8.5 ± 2.0	11.9 ± 0.3	4.72 ± 0.4
	ML	5	-9.3 ± 1.4	10.5 ± 0.4	4.57 ± 0.4
Mussels	RC1	5	$-13.9 \pm 0.6^*$	$13.7 \pm 0.5^*$	3.85 ± 0.2
	LA2	5	$-15.1 \pm 0.6^*$	$14.1 \pm 0.3^*$	3.98 ± 0.1
	MS	5	$-16.9 \pm 1.7^*$	$13.9 \pm 0.5^*$	4.75 ± 0.5
	TXI	5	$-17.6 \pm 0.6^*$	$12.0 \pm 0.6^*$	4.72 ± 0.3
	PM	5	-12.9 ± 0.7	12.1 ± 0.6	3.61 ± 0.1
	ML	5	-13.5 ± 0.5	11.6 ± 0.3	3.66 ± 0.1

Table 3

Stable isotope values in ancient and modern fish bone samples from the Atlantic coast of Tierra del Fuego. Archaeological sites sampled are RC1: Río Chico 1; LA2: La Arcillosa 2; MS: Margen Sur; TXI: Teis XI. *N*: sample size; $\delta^{13}\text{C}$ (‰), $\delta^{13}\text{C}_{\text{corr}}$ (‰) and C:N ratio are reported by mean \pm SD. Correction factor was calculated by difference between mean isotope values of mollusks of modern and ancient samples, respectively.

Species	Location	Sample	<i>N</i>	$\delta^{13}\text{C}$	$\delta^{13}\text{C}_{\text{corr}}$	C:N
Argentine hake (<i>Merluccius hubbsi</i>)	RC1	Vertebrae	5	-14.0 ± 0.7	-11.4 ± 0.7	3.06 ± 0.1
Pink cusk-eel (<i>Genypterus blacodes</i>)	RC1	Basioccipital	5	-16.9 ± 0.5	-14.2 ± 0.5	3.16 ± 0.4
Eelpout (<i>Austrolycus</i> sp.)	RC1	Articular	1	-16.4	-13.8	3.27
Patagonian blenny (<i>Eleginops maclovinus</i>)	LA2	Premaxilla	2	-14.6 ± 0.3	-9.9 ± 0.3	3.24 ± 0.0
Hake (<i>Merluccius</i> sp.)	LA2	Vertebrae	1	-14.1	-9.3	3.57
Patagonian grenadier (<i>Macruronus magellanicus</i>)	MS	Vertebrae	1	-14.6	-10.4	3.24
Patagonian blenny (<i>Eleginops maclovinus</i>)	MS	Premaxilla	3	-16.1 ± 1.2	-11.9 ± 1.2	3.26 ± 0.2
Pink cusk-eel (<i>Genypterus blacodes</i>)	MS	Vertebrae	1	-13.8	-9.6	3.07
Hake (<i>Merluccius</i> sp.)	MS	Vertebrae	1	-16.1	-11.9	3.24
Snoek (<i>Thyrssites atun</i>)	MS	Dentary	1	-12.9	-8.7	2.92
Eelpout (<i>Austrolycus</i> sp.)	MS	Articular	3	-15.3 ± 0.7	-11.0 ± 0.7	3.49 ± 0.2
Patagonian blenny (<i>Eleginops maclovinus</i>)	TXI	Interopercular	1	-9.1	-5.9	3.35
Snoek (<i>Thyrssites atun</i>)	TXI	Cleithrum	2	-12.8 ± 0.4	-9.7 ± 0.4	3.27 ± 0.0
Eelpout (<i>Austrolycus</i> sp.)	TXI	Cleithrum	4	-8.4 ± 1.2	-5.3 ± 1.2	3.39 ± 0.1

$\delta^{13}\text{C}$) depends on the primary carbon sources (France, 1995; Post, 2002) and in the local isospace off Tierra del Fuego allows to differentiate between species relying on phytoplankton and benthic primary producers (Saporiti et al., 2015; Andrade et al., 2016; Riccialdelli et al., 2017).

In order to conduct these analyses, soft tissues were removed from modern limpets and mussels and the shells were rinsed with water, later dried at room temperature and lightly scraped with sand paper to remove epibionts. Shells were later dried in a stove at approximately 50 °C for 24 h. Once dry, each sample was ground to fine powder and divided into two subsamples. Calcium carbonate and lipids have to be removed to obtain unbiased $\delta^{13}\text{C}$ values (Newsome et al., 2006; Bas and Cardona, 2018). One subsample (bulk hereafter) was ground to fine powder with mortar and pestle and approximately 7 mg of modern shell powder was weighed into 5 \times 8 mm tin cups and 14 mg of ancient shell powder was weighed into 5 \times 8 mm tin cups. Another subsample (dml hereafter) were first demineralized by soaking in 1 N HCl until no more CO₂ was released (Saporiti et al., 2014b). After demineralization,

shell_{dml} subsamples were rinsed with distilled water for 24 h, dried again for 24 h at approximately 50 °C and mixed with a 2:1 chloroform:methanol solution to remove lipids. The chloroform:methanol solution was changed overnight until it was transparent. Then, samples were dried again for 24 h at approximately 50 °C and 0.5 mg was weighed into 3.3 × 5 mm tin cups.

The ancient bones samples were ground to fine powder with mortar and pestle, dried again for 24 h at approximately 50 °C and rinsed with a 2:1 chloroform:methanol solution to remove lipids (Folch et al., 1957). The chloroform:methanol solution was changed overnight until it was transparent. Bone samples were dried again for 24 h at approximately 50 °C and demineralized with 0.5 N hydrochloric acid (HCl) until no more CO₂ bubbles were released (Longin, 1971; Newsome et al., 2006). Then, samples were dried again for 24 h at approximately 50 °C and 0.5 mg was weighed into 3.3 × 5 mm tin cups.

All tin cups were combusted at 900 °C and analyzed in a continuous flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA, Thermo Finnigan; www.thermofisher.com) at Centres Científics i Tecnològics de la Universitat de Barcelona (www.ccitub.edu) in Barcelona, Spain. Gases from the combustion of bulk shell samples passed through a CO₂ absorbent column for elemental analysis, containing CaO/NaOH. This was to avoid spectrometer saturation with CO₂, because CaCO₃ constitutes over 90% of the shell's samples and large amount of shell had to be combusted to obtain enough N to measure δ¹⁵N values.

Abundance of stable isotopes is expressed using the δ notation, where the relative variations of stable isotope ratios are expressed as per mil (‰) deviations from predefined reference scales: Vienna Pee Dee Belemnite (VPDB) calcium carbonate for δ¹³C and atmospheric nitrogen (AIR) for δ¹⁵N. However, due to limited supplies, isotopic reference materials, which included known isotopic compositions relative to international measurement standards (VPDB), were analyzed instead. For carbon, isotopic reference materials of known ¹³C/¹²C ratios, as given by the International Atomic Energy Agency (IAEA; www.iaea.org/resources) in Vienna (Austria), were used for calibration at a precision of 0.05‰. These included polyethylene (IAEA CH₇, δ¹³C = -32.1‰), L-glutamic acid (IAEA USGS₄₀, δ¹³C = -26.4‰), and sucrose (IAEA CH₆, δ¹³C = -10.4‰). For nitrogen, isotopic reference materials of known ¹⁵N/¹⁴N ratios were used to a precision of 0.2‰, and these were namely: (NH₄)₂SO₄ (IAEA N₁, δ¹⁵N = +0.4‰ and IAEA N₂, δ¹⁵N = +20.3‰), L-glutamic acid (IAEA USGS₄₀, δ¹⁵N = -4.6‰), and KNO₃ (IAEA NO₃, δ¹⁵N = +4.7‰). Acetanilide and one of the following (polyethylene, UCGMA PF and UCGMA F) were analyzed as internal standards to recalibrate the system once every 12 samples. The raw data were recalculated taking into account a linear regression previously calculated for isotopic reference materials (Skrzypek, 2013). The analytical error was 0.05‰ for δ¹³C and 0.2‰ for δ¹⁵N. For shell samples δ¹³C_{dml} and δ¹⁵N_{bulk} values were used for latter analysis, whereas for fish samples only δ¹³C values were used for latter analysis (see Supporting Information Table S2). Furthermore, the carbon to nitrogen (C:N) atomic ratio of each ancient bone sample was used to assess the efficiency of lipid extraction using the liberal C:N cut-off proposed by Guiry and Szpak (2021).

2.3. Data analysis

Our approach assumes that pelagic and benthic primary producers contribute similarly to the nitrogen and carbon pool fueling the coastal food web off Tierra del Fuego (Saporiti et al., 2015; Andrade et al., 2016; Riccialdelli et al., 2017), and consequently limpets (grazer) and mussels (suspension feeder) can be combined to detect and correct for any changes in the isotopic baseline.

First, the δ¹³C and δ¹⁵N values of limpets and mussels were compared independently using General Linear Models (GLM) as run with two fixed factors (species and period) to assess the temporal variation of δ¹³C and δ¹⁵N value in shells of the Atlantic coast of Tierra del

Fuego and, when necessary, correct for any isotopic baseline shift between different periods considered. This GLM was performed for each archaeological site from the Atlantic coast of IGTF studied here, and the modern conspecifics from Punta María and María Luisa beaches considering geographic proximity, Punta María was compared to RC1, LA2 and MS, and María Luisa was compared to TXI (Fig. 1). Normality and homoscedasticity assumptions were checked by mean of Lilliefors test and Levene test, respectively. The offset in the stable isotope ratios of ancient and modern mollusk species was used as a correction factor to allow the comparison of stable isotope ratios of ancient fish samples (Zenteno et al., 2015; Vales et al., 2017; Bas et al., 2019, 2020).

Second, the average δ¹³C of the fish assemblage from each archaeological site was calculated considering the average δ¹³C value of each species and its proportion in NISP. All these analyses were performed in IBM SPSS Statistics program (Version 23.0.0.2 for Mac).

Third, the proportion of near shore: *Austrolycus* sp., *E. maclovinus*, *Patagonotothen* sp. Balushkin, 1976, *Paranotothenia magellanica* (Forster, 1801); and offshore fish: *Cottoperca gobio* (Günther, 1861), *Salilota australis* (Günther, 1878), *T. atun*, *M. magellanicus*, *G. blacodes*, *Merluccius* sp.; in the fish assemblage was calculated considering the fish remains identified at the species level from the selected archaeological sites, respectively (see section 2.1).

3. Results

The C:N ratio of the organic matrix of limpet shells was higher than that of mussel shells (Table 2) and both were higher than those of fish bone (Table 3). This is because the organic matrix of mollusk shells is a mixture of proteins and chitin, a polysaccharide containing N (Furuhashi et al., 2009), whereas that of fish bone includes only protein (Guiry and Szpak, 2020). Regarding the fish bone samples analyzed here, their C:N ratios were within the limits expected after the successful extraction of lipids (Guiry and Szpak, 2021) and hence their δ¹³C values are expected to be a reliable proxy for habitat.

All the stable isotope ratios were normally distributed and homoscedastic (Table 2). Currently, no statistically significant differences exist between the δ¹³C values of modern mussels and limpets from Punta María and their conspecifics from María Luisa ($F_{(1,16)} = 1.59, p = 0.225$). This is also true for the δ¹⁵N values of mussels ($F_{(1,8)} = 3.28, p = 0.11$; Table 2). However, modern limpets from Punta María have a higher average δ¹⁵N than those from María Luisa ($F_{(1,8)} = 31.53, p < 0.001$; Table 2). As a result, the stable isotope ratios of ancient specimens were compared only to those of the nearby modern sampling site. Differences in the δ¹³C and δ¹⁵N values of ancient limpets and mussels (RC1, LA2, MS and TXI) and their modern conspecifics (PM and ML) were statistically significant (δ¹³C RC1 vs PM: $F_{(1,16)} = 21.65, p < 0.001$; δ¹³C LA2 vs PM: $F_{(1,16)} = 52.61, p < 0.001$; δ¹³C MS vs PM: $F_{(1,16)} = 37.48, p < 0.001$; δ¹³C TXI vs ML: $F_{(1,16)} = 22.42, p < 0.001$, respectively; δ¹⁵N RC1 vs PM: $F_{(1,16)} = 13.41, p = 0.002$; δ¹⁵N LA2 vs PM: $F_{(1,16)} = 70.39, p < 0.001$; δ¹⁵N MS vs PM: $F_{(1,16)} = 109.17, p < 0.001$; δ¹⁵N TXI vs ML: $F_{(1,16)} = 21.76, p < 0.001$, respectively) (Table 2 and Fig. 2). Accordingly, a baseline shift existed between different periods considered for both δ¹³C and δ¹⁵N values. Consequently, the δ¹³C values from ancient fish samples were corrected as follows to allow comparison between different periods: RC1 = 2.64, LA2 = 4.65, MS = 4.22, TXI: 3.18. It is necessary to mention that these analyses were conducted in a small sample size and the spatial variation between ancient and modern datasets could impact the accuracy of the offsets.

Baseline corrected values are shown in Table 3 as δ¹³C_{corr}. According to the archaeological sites sampled, results show a recent increase of the average of δ¹³C values of the fish communities from the archaeological sites located along the Atlantic coast of Tierra del Fuego in the last millennium (Fig. 3).

Near shore species prevailed in the zooarchaeological record of most sites, except one from the Middle Holocene (RC1) and another one from the Late Holocene (RDA4) (Fig. 4).

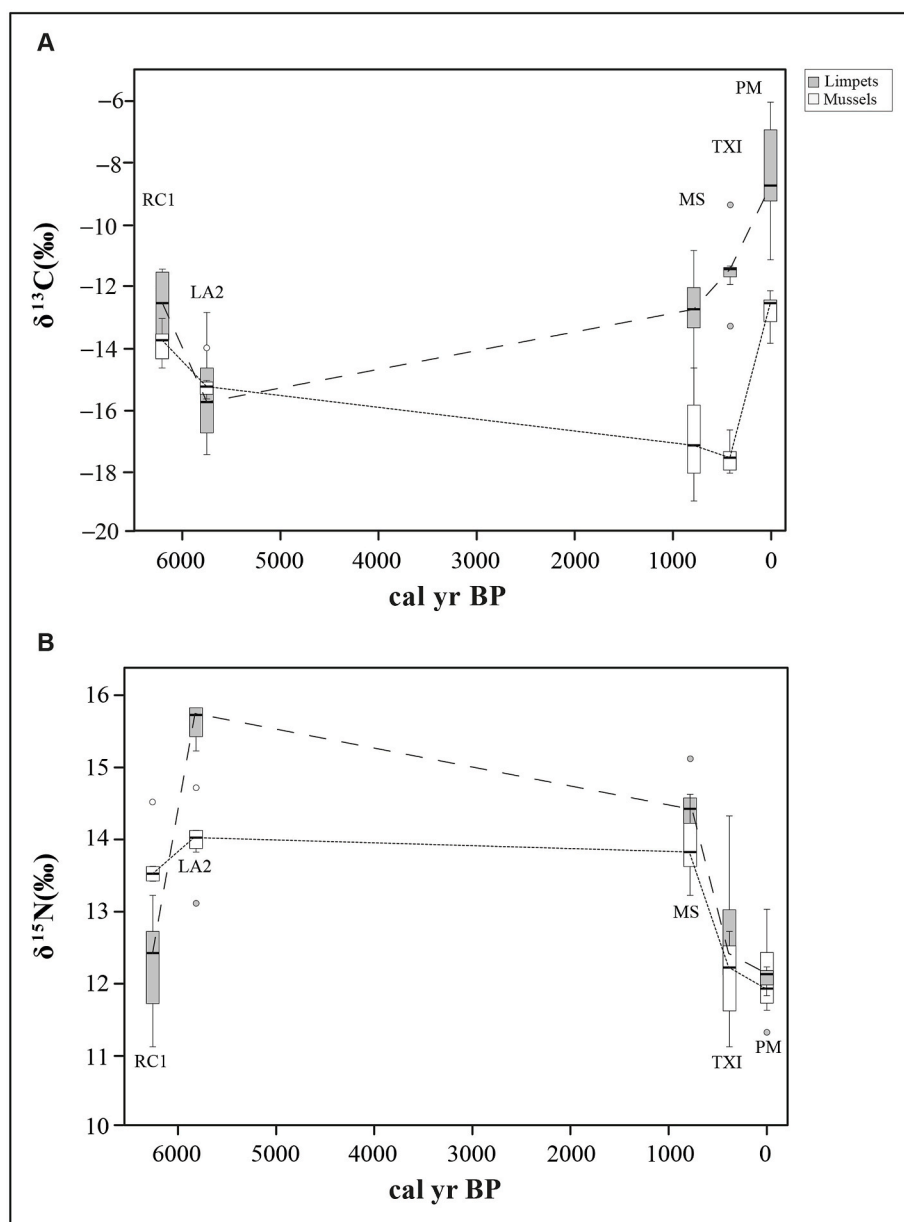


Fig. 2. Box plots showing the evolution of the $\delta^{13}\text{C}$ (A) and $\delta^{15}\text{N}$ (B) values of the two mollusks sampled from the selected archaeological sites of the Atlantic coast of Tierra del Fuego, considering the time scale. Large dashed lines indicate the trend of value changes in limpets, while small dashed lines belong to the trend line for mussels. RC1: Río Chico 1; LA2: La Arcillosa 2; MS: Margen Sur; TXI: Teis XI; from modern samples it was selected PM: Punta María, because modern samples did not present significant differences.

4. Discussion

The results reported here suggested a pattern of coastal fishing since the Middle Holocene, with offshore fish species prevailing only at two of the zooarchaeological sites studied, both dated more than 1000 cal yr BP. Interestingly, marine primary productivity declined during the past 1000 yr, as revealed by the consistent decline in the $\delta^{15}\text{N}$ values of both mussels and limpets, and the presence of offshore fish species declined in parallel in the zooarchaeological record, thus suggesting reduced access to this resource during the past 1000 yr. In the absence of any navigation technology, access to offshore fish species was necessarily opportunistic and relied probably on mass stranding. We hypothesize that mass stranding become extremely rare as primary productivity and the abundance of offshore fish species both declined, which in turn limiting hunter-gather-fisher groups access to offshore fish species. It should be noted, however, that archaeological sites from the Middle Holocene are scarce in our sample and a 5000 yr gap exists between LA2 and MS. We have studied all the archaeological sites known in the study area and hence there is an urgent need to find and study new archaeological sites

from the Middle Holocene in the region.

The reconstruction of the isotopic baseline is a common problem in studies dealing with stable isotope analysis in historical ecology and zooarchaeology (Bailey et al., 2008; Casey and Post, 2011; Saporiti et al., 2014a). This is because stable isotope ratios of primary producers may change throughout time for the same reasons they vary regionally (Somes et al., 2010; Magozzi et al., 2017). Fortunately, there is growing evidence that the organic matrix of mollusk shells offers a good record of temporal changes in the isotopic baseline (Casey and Post, 2011; Saporiti et al., 2014a, 2014b; Misarti et al., 2017) and hence the offset between the stable isotope ratios of modern and ancient samples of the same species allows quantifying such change and calculate a correction factor to allow the comparison of the stable isotope values of other taxa from different periods (Zenteno et al., 2015; Vales et al., 2017; Bas et al., 2019, 2020).

Nonetheless, diagenetic changes in stable isotope ratios may occur, resulting in inconsistent changes in the stable isotope ratios of sympatric taxa across time (Misarti et al., 2017). Here, limpets and mussels exhibit similar temporal trends of variation for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, except for a

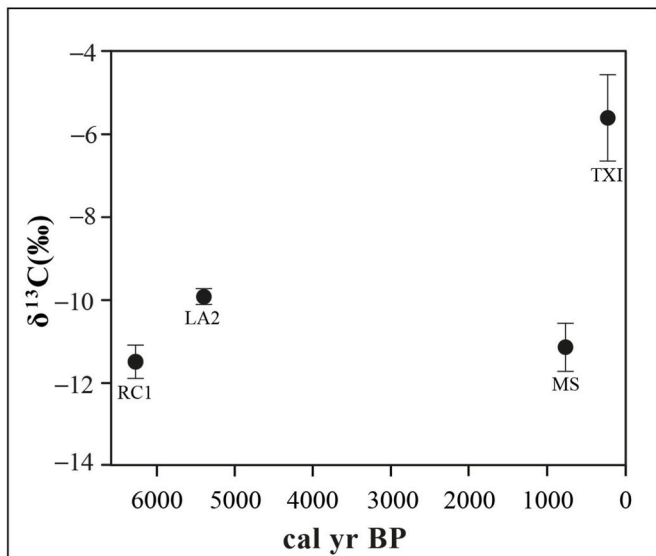


Fig. 3. Set of δ¹³C (‰) values for each fish community sampled from the selected archaeological sites on the Atlantic coast of Tierra del Fuego. The arithmetic mean and standard deviation are shown for each fish community. RC1: Río Chico 1; LA2: La Arcillosa 2; MS: Margen Sur; TXI: Teis XI.

significant drop in the δ¹³C of mussels from MS compared to their ancient conspecifics from LA2, a change not observed in limpets. It should be noted that the baseline of taxa with different feeding strategies may change differently throughout time (Misarti et al., 2017) and that the δ¹⁵N values of both species remained unchanged during the same period. Limpets are generalist grazers (Rosenfeld et al., 2018) whereas mussels are suspension feeders (Navarro and Winter 1982). As a consequence, the stable isotope ratios of limpets depend exclusively on those of microphytobenthos and macroalgae, whereas that of mussels depends on that of suspended organic matter, which in turn is a mixture of phytoplankton, terrestrial detritus and resuspended sediment. Terrestrial plants in Tierra del Fuego are extremely depleted in δ¹³C compared to phytoplankton and macroalgae (Riccialdelli et al., 2017) and hence an increase in the arrival of terrestrial particulate matter to coastal ecosystems at the time the mollusks from MS lived might explain the drop in the δ¹³C values in mussels but not in limpets. This hypothesis is consistent with increased rainfall at the beginning of the last millennia (Tonello et al., 2009; Borromei et al., 2010; Kilian and Lamy, 2012;

Ponce et al., 2017). The parallel evolution of δ¹⁵N in both taxa and the stability from LA2 to MS further support the unparallel evolution of the carbon baselines of mussels and limpets, and not diagenetic changes in mussel shells, as the most likely cause for their dissimilar temporal trends in δ¹³C. This is due to the presence of exogenous sources of protein or extensive protein degradation that should have increased their δ¹⁵N values (Misarti et al., 2017), but they did not change.

On the other hand, the δ¹³C values of limpets and mussels were very similar during the Middle Holocene, but differed largely during the last millennia. Currently, phytoplankton is depleted in ¹³C compared to macroalgae, although the δ¹³C values of red algae are closer to those of phytoplankton than those of brown and green macroalgae (Saporiti et al., 2015; Andrade et al., 2016; Riccialdelli et al., 2017). Kelp thrive in cold water (Graham et al., 2007) and decreasing SST during the last millennia (Bujalesky, 2007; Shevenell et al., 2011; Caniupán et al., 2014) might have triggered the expansion of kelp forests around IGTDF and changes in the community of macroalgae resulting in a broader difference in the δ¹³C values of limpets and mussels that in the Middle Holocene.

The drop in the δ¹⁵N values of both mussels and limpets during the last millennia reported here is consistent with previous studies revealing a similar drop in the Beagle Channel during the second half of the Holocene (Saporiti et al., 2014a; Bas et al., 2019); thus, we can consider this as a regional phenomenon. The long gap between LA2 and MS prevents detailed knowledge of the temporal pattern of that process off the Atlantic coast of IGTDF, but certainly a change in the nitrogen baseline operated in both regions at least during the last millennia. Currently, there is a negative correlation between marine primary production and the δ¹⁵N values of the organic matrix of mollusk shells along the coastline of Argentina (Saporiti et al., 2014a), which suggests that primary productivity might have decreased off Tierra del Fuego at least during the last millennia.

Finally, the δ¹³C values of modern mollusk shells from this region were expected to be depleted in ¹³C compared to ancient ones, because of the Suess effect (Eide et al., 2017). Nonetheless, the δ¹³C values of mollusks showed a downward trend and an increase during the last millennium. This specific shift is much earlier than that caused by the burning of fossil fuels, which would not have caused a significant drop in the δ¹³C values of mollusk shells of IGTDF (Bas et al., 2019; this study). This is consistent with the small intensity of the Suess effect in the South-Western Atlantic Ocean reported by other studies (Eide et al., 2017). Furthermore, changes in the relative contribution of terrestrial detritus, phytoplankton and different groups of benthic primary producers to the C pool fueling the food web, resulting from changes in

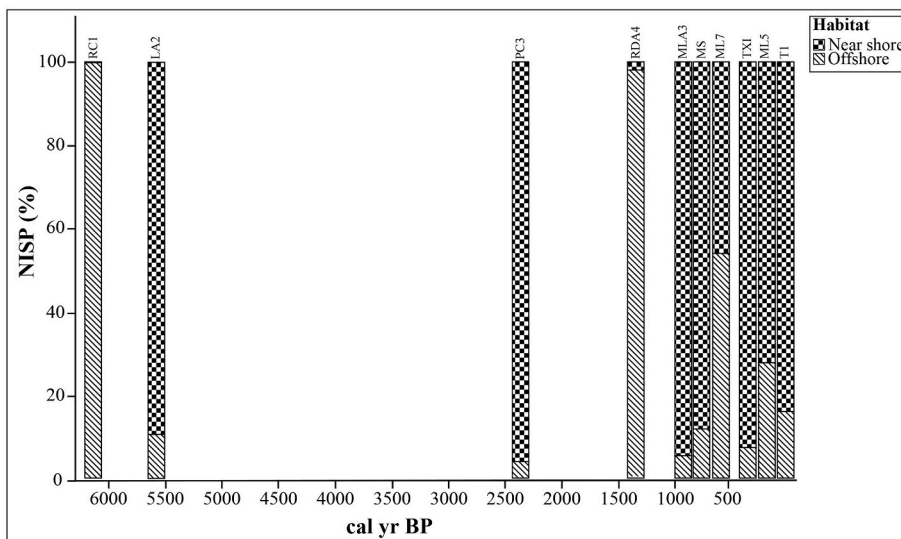


Fig. 4. Temporal variation of the %NISP values of the fish community from the studied archaeological sites in the Atlantic coast of Tierra del Fuego, classified according to habitat. RC1: Río Chico 1; LA2: La Arcillosa 2; PC3: Punta Catalina 3; RDA4: Rancho Donata A4; MLA3: María Luisa A3; MS: Margen Sur; ML7: María Luisa 7; TXI: Teis XI; ML5: María Luisa 5; T1: Teis 1. Offshore species: *C. gobio*, *G. blacodes*, *Merluccius* spp., *M. magellanicus*, *S. australis*, *T. atun*; Near shore species: *Austrolycus* spp., *E. maclovinus*, *Patagonotothen* sp. *P. magellanica*.

freshwater runoff and the communities of benthic macroalgae discussed above have likely masked the Sues effect.

Regardless of the causes of such sources of variability and uncertainty, the average $\delta^{13}\text{C}$ values of the whole fish community consumed by hunter-fisher-gatherer groups from the Atlantic coast of IGTF might have increased in the most recent periods. It should be noted that some fish species inhabiting a broad diversity of habitats and hence taxonomic identity alone is not always a good proxy for habitat. In those cases, $\delta^{13}\text{C}$ may offer a better proxy for habitat, because integrates information on habitat use at an individual level throughout the life of the individual. This is particularly useful in Tierra del Fuego, where phytoplankton and macroalgae differ largely in their $\delta^{13}\text{C}$ values according to Saporiti et al. (2015) and Riccialdelli et al. (2017): $\delta^{13}\text{C}_{\text{phytoplankton}}$ from -24.6‰ to -23.2‰ and $\delta^{13}\text{C}_{\text{macroalgae}}$ from -18.1‰ to -8.4‰ . Therefore, fish individuals inhabiting pelagic and offshore ecosystems off IGTF are expected to have much lower $\delta^{13}\text{C}$ values than those inhabiting nearby benthic and coastal ecosystems, independently on species identity, although the migratory behavior of some species might blur partially those differences. On this ground, the increase of the $\delta^{13}\text{C}$ values of the whole fish community consumed by hunter-fisher-gatherer societies along the Atlantic coast of IGTF in different periods would suggest a habitat shift, from offshore to near shore species, especially in the last five hundred years. Differences in the location of zooarchaeological sites along the coast might be a confounding factor, but currently no differences exist along the studied coastline in the $\delta^{13}\text{C}$ values of the same species, as revealed by mussels and limpets. If this was also true in the past, the increase on the $\delta^{13}\text{C}$ values of the whole fish community consumed by hunter-fisher-gatherers observed in the most recent study site is unlikely to be an artifact caused by the geographical location, but probably reflects a true shift in the habitat of the fish captured. Furthermore, both NISP and $\delta^{13}\text{C}$ values suggest a similar temporal trend, with a prevalence of benthic, coastal species in the most recent period.

Reduced access to offshore fish species during the last millennia, as suggested by the overall evidence reported here, could be related to decreased marine primary productivity and lower SST off the Atlantic coast of IGTF at that time. Marine productivity has been declining in the Atlantic coast of Tierra del Fuego during the last millennium following the results of this study, and it also happened in the Beagle Channel from the Middle Holocene to present (Saporiti et al., 2014; Bas et al., 2019). These fluctuations in marine productivity may affect the food web and marine fauna communities of this region (Hoegh-Guldberg and Bruno, 2010; Simpson et al., 2011).

Changes in SST can also affect the distribution of different fish species according to their ecological plasticity and, as a consequence, their availability to the hunter-fisher-gatherer populations (Perry et al., 2005; Simpson et al., 2011, among others). In IGTF, there were several changes in the SST during the Holocene: the temperature was decreasing gradually until present, with lower temperatures at approximately 5000 yr BP, 1000 yr BP and during the Little Ice Age, between 600 and 300 yr BP (Borromei et al., 2010; Marcott et al., 2013; Caniupán et al., 2014). During the previous stages of Holocene, with a warmer SST than present, some species such as snoek and Argentine hake likely changed their distribution in Tierra del Fuego waters (Bas et al., 2019 and 2020, respectively) and their availability for the human populations decreased. These environmental changes occurred in the entire island.

Consequently, the possible change in fish consumption patterns among hunter-fisher-gatherer societies of Tierra del Fuego through the Holocene could be considered as related to the change of environmental conditions (Bas et al., 2020). At present, in latitude south to 46°S Argentine hake are distributed in deeper and colder waters (average SST off north-eastern Tierra del Fuego is 7°C ; Rivas, 2010) and no coastal spawning aggregation is known (Bezzi et al., 1995; Díaz de Astarloa et al., 2011). Conversely, there is a high population density of Argentine hake with coastal spawning aggregations less than 50 m deep in northern latitudes at 46°S in Comodoro Rivadavia (Bezzi et al., 1995;

Díaz de Astarloa et al., 2011; Botto et al., 2019), where the average SST is 11°C (Rivas, 2010). The average SST in IGTF during the Middle Holocene, RC1 site period, has been reported to be $11\text{--}12^{\circ}\text{C}$ (Nielsen et al., 2004; Bentley et al., 2009; Caniupán et al., 2014). This suggests that Argentine hake would have reached the coast off north-eastern Tierra del Fuego during the summer of the Middle Holocene for spawning, thus becoming vulnerable to hunter-fisher-gatherer people devoid of navigation technology. Consequently, changes in fish species distribution to more coastal and shallow waters, as Argentine hake during the Middle Holocene in this region, could have favored the consumption of a higher diversity of fish species in contrast to the Late Holocene. Nonetheless, it could be also possible that some fish species were available and consumed by mass standings (Zangrando, 2003).

Throughout history, human populations designed different strategies to deal with environmental changes; these strategies may include modifications of social organization, technological innovations, changes in consumption patterns, migrations or the colonization of new spaces, among others. The results presented here could show that in the case of the Atlantic coast the strategy implied a shift in the diversity of species available and consumed. The availability of near shore fishes together with the knowledge and skills related to coastal fishing techniques, the absence of navigation technology, and the opportunity to exploit a broad range of resources along the marine littoral, should have influenced in this subsistence decision. Therefore, the fishing activities of hunter-fisher-gatherer societies of the Atlantic coast of IGTF might have been resilient in order to face to environmental and resources availability changes. Thus, with a scarce labor investment they kept a varied diet avoiding the risk implied in the use of navigation technology in open sea waters.

Considering a regional large-scale perspective, comparing these results with the Beagle Channel region, it was observed that the composition of the fish community exploited over time does not show a clear trend, except in the most modern periods. In the case of the Beagle Channel, fish and seabird consumption increased in the last 1500 yr accompanied with a decrease in the consumption of pinnipeds (Juanmuns, 1996; Orquera et al., 2011; Zangrando and Tivoli, 2015). In the earliest archaeological sites there were already offshore species such as hake and snoek, although in low abundance (Zangrando, 2009), whereas in the archaeological sites from the Late Holocene, there were recorded a great abundance of near shore fish species with presence of hake and snoek until 890 yr BP (Tivoli and Zangrando, 2011). Unfortunately, the stable isotope values of only few fish species from the Beagle Channel have been published until present-day (Zangrando et al., 2016; Kochi et al., 2018; Bas et al., 2019).

Also considering the case of the Strait of Magellan and the adjacent seas, some zooarchaeological studies carried out in archaeological sites (Torres and Ruz, 2011; Torres Elgueta, 2016; Torres et al., 2022) suggested that the importance of fishing was comparable to that of the hunting birds and marine mammals (Morello et al., 2012; San Román et al., 2016). However, the level of fishing, together with hunting of birds, increased between 3500 and 2500 yr BP (Legoupil et al., 2011; Morello et al., 2012; San Román et al., 2016; Torres Elgueta, 2016). During the Holocene near shore fishes such as *E. maclovinus* and also demersal fishes such as *S. australis* (Torres, 2009; Torres et al., 2022) were the most exploited species in this area.

At a regional level, the presence of navigation technology and the broad diversity of fishing techniques in the hunter-fisher-gatherer populations that inhabited the Beagle Channel and the Strait of Magellan and adjacent seas (Torres, 2009; Orquera et al., 2011; Torres Elgueta, 2016, respectively), undoubtedly, allowed them to catch fish species that changed their distribution due to environmental changes in this region and exploit a higher diversity of marine resources through the Holocene compared to hunter-fisher-gatherer groups from the Atlantic coast of IGTF.

5. Conclusions

Despite the small sample size studied in this work, the analysis presented here suggests that the opportunities of hunter-fisher-gatherer people inhabiting the Atlantic coast of IGTF to access offshore fish species declined during the last millennia, when major changes in marine primary productivity and SST affected the region. Such environmental changes might have caused a distribution shift of Argentine hake (Bas et al., 2020) and a general decrease in the abundance of offshore fish species, thus reducing the opportunity for mass stranding. Conversely, hunter-fisher-gatherer people with navigation technology inhabiting other parts of IGTF did not reduced the consumption of offshore fish species (Zangrando and Tivoli, 2015), despite similar changes in marine primary productivity and SST (Saporiti et al., 2014a). This highlights the importance of technology face resource and environmental fluctuations.

Author contributions

MB, MA, IBG and LC conceived and designed the study. MS, FS, MA, IBG and MB conducted the fieldwork. MB and LC conducted laboratory analysis and data analysis. MB and LC wrote the first draft of the manuscript. All authors provided editorial advice and contributed to revisions.

Declarations of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jas.2023.105755>.

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