Journal of Archaeological Science: Reports 18 (2018) 696–707

Contents lists available at ScienceDirect

Journal of Archaeological Science: Reports

journal homepage: www.elsevier.com/locate/jasrep

$\delta^{13}C$ and $\delta^{15}N$ variations in terrestrial and marine foodwebs of Beagle Channel in the Holocene. Implications for human paleodietary reconstructions

Sayuri Kochi[a,*], Suray A. Pérez[b], Augusto Tessone[a], Andrew Ugan[c], Mary Anne Tafuri[d], Jonathan Nye[e], Angélica M. Tivoli[f], Atilio Francisco Zangrando[f]

[a] Instituto de Geocronología y Geología Isotópica, UBA/CONICET, Argentina
[b] Facultad de Filosofía y Letras, Universidad de Buenos Aires, Argentina
[c] Far Western Anthropological Research Group, University of Utah, USA
[d] Dipartimento di Biologia Ambientale, Sapienza Università di Roma, Italy
[e] Department of Earth Sciences, University of California, Riverside, USA
[f] Centro Austral de Investigaciones Científicas – CONICET, Argentina

ARTICLE INFO

Keywords:
Isotopic ecology
Paleodiet
Hunter-gatherers
Tierra del Fuego
Patagonia

ABSTRACT

In this article we evaluate the isotopic variability in $\delta^{13}C$ and $\delta^{15}N$ values of diets among maritime hunter-gatherers of the Beagle Channel (Southern Argentina). A system with two end members –marine and terrestrial resources– is not enough to describe populations with diversified subsistence strategies. Moreover, these marine hunter-gatherers are characterized as highly mobile groups whose foraging ranges comprised not only nearshore areas, but also offshore spaces.

As a first step to distinguish the diversity of prey choices during the Late Holocene, and to improve the accuracy of paleodietary interpretations, we conducted stable isotope analyses on zooarchaeological collections and modern samples of shellfish and plants. We observed that $\delta^{13}C$ and $\delta^{15}N$ values of aquatic animals are more clustered than expected in comparison to modern ecological parameters. Terrestrial prey, such as the guanaco, showed considerable isotopic dispersion in both carbon and nitrogen. While zooarchaeological studies have identified foraging activities in offshore spaces, stable isotope analyses should use different criteria to characterize long-term dietary patterns.

With this local isotopic frame of reference, we re-examined $\delta^{13}C_{collagen}$ and $\delta^{15}N_{collagen}$ measurements of seven adult individuals from the Beagle Channel. Most individuals had marine diets complemented with resources more depleted in ^{13}C and ^{15}N than aquatic prey. While previous interpretations stated that the complementary staple was terrestrial protein, we suggest consumption of shellfish as another possibility. Finally, plants should be reconsidered as a source depleted both in ^{13}C and ^{15}N for mixing models, when typically underestimated in paleodiets from subpolar environments.

1. Introduction

One of the earliest applications of stable isotopes in archaeology focused on distinguishing between the consumption of marine vs. terrestrial resources (Tauber, 1981; Chisholm et al., 1982). These two groups are characterized by a clear contrast in $\delta^{13}C$ and $\delta^{15}N$ distributions (Schoeninger and DeNiro, 1984). However, aquatic environments offer a diversity of isotopically different prey items (Richards and Hedges, 1999; Szpak et al., 2009; Coltrain et al., 2016). $\delta^{13}C$ and $\delta^{15}N$ values of littoral and pelagic primary producers typically differ strongly among habitats, and they are influenced by numerous physical and chemical factors (Casey and Post, 2011). Moreover, some prehistoric populations consumed resources at multiple levels of the local food web (Maschner et al., 2009), which makes understanding the paleodiets of coastal hunter-gatherers even more complex. As such, only with a detailed ecological frame of reference is it possible to distinguish among diverse prey choices and to address broader questions: for example, patterns of foraging ranges and mobility (Weber et al., 2011) or sexual division of labor (Kusaka et al., 2010).

At the southern tip of South America, hunter-gatherer populations of the Beagle Channel (Fig. 1) developed marine foraging strategies from 6400 yr BP until the arrival of European settlers to the region in

* Corresponding author.
E-mail address: sayuri@ingeis.uba.ar (S. Kochi).

https://doi.org/10.1016/j.jasrep.2017.11.036
Received 20 April 2017; Received in revised form 18 September 2017; Accepted 20 November 2017
Available online 26 November 2017
2352-409X/

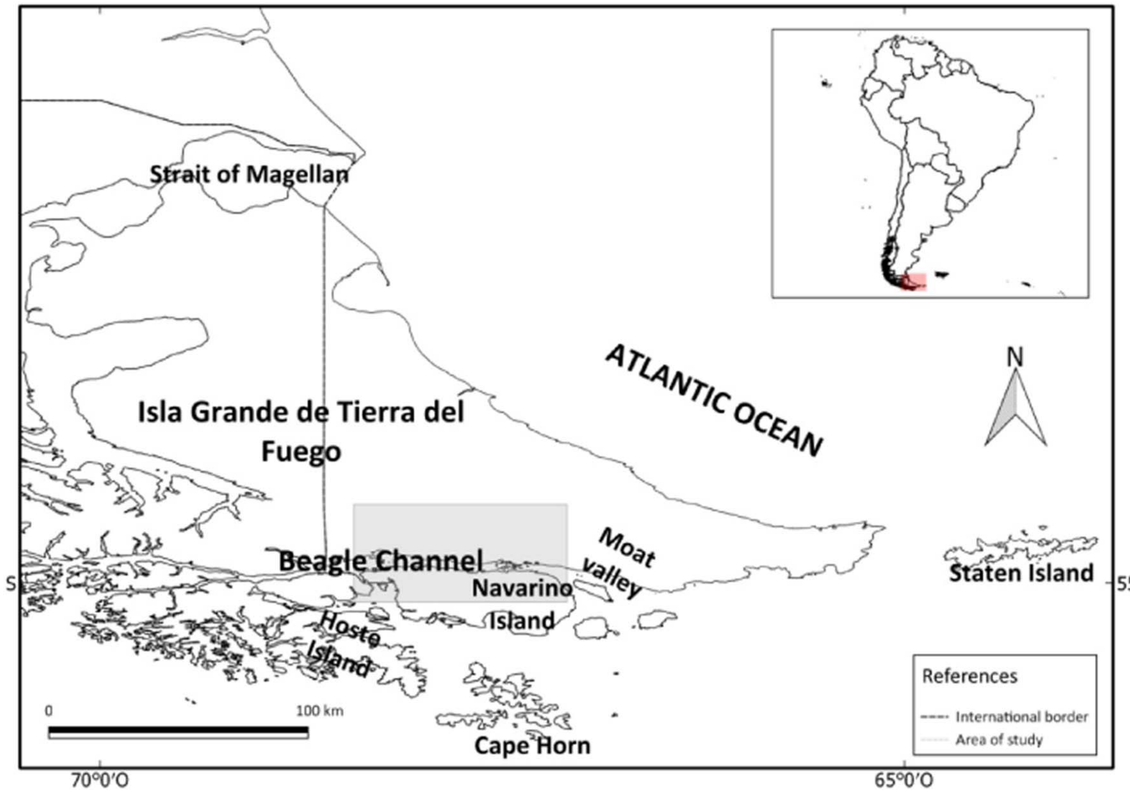

Fig. 1. A map of Southern South America showing the Beagle Channel, where specimens with stable isotopic values originated.

the 19th century. Stable isotope analyses on archaeological human remains from the Beagle Channel indicated that most individuals had marine diets, complemented with terrestrial resources during the Late Holocene (Yesner et al., 1991; Orquera and Piana, 1996; Guichón et al., 2001; Tessone et al., 2003; Yesner et al., 2003; Panarello et al., 2006). Nevertheless, this high latitude coastal environment offered varied potential resources, which required different amounts of labor in their procurement and processing (Orquera and Piana, 1999a; Zangrando, 2009a). As Yesner (1980) stated it is "misleading to lump coastal peoples into a single economic category", and therefore a comprehensive local isotopic ecology (Schwarcz, 1991; Newsome et al., 2007) is required to improve the accuracy of diet reconstructions and ultimately, to identify variations among subsistence strategies of marine hunter-gatherers.

Recent zooarchaeological studies in this area have demonstrated temporal variation in human subsistence activities, showing an expansion of foraging habitats, and an increase of labor investment into fishing activities and capture of birds during the late Holocene (Zangrando, 2009a; Tivoli, 2010; Tivoli and Zangrando, 2011). For example, adult snoeks (*Thyrsites atun*) in the Beagle Channel appear as the most important fish taxa from deep waters only during the last 1000 years (Zangrando, 2009b). Recognized as pelagic predators (Griffiths, 2002), adult specimens of snoeks in the Beagle Channel have only been recorded in deep waters (Fenucci et al., 1974).

While zooarchaeological assemblages and stable isotope studies of human bone inform about different units of analyses and temporal resolution (Barberena and Borrero, 2005), δ^{13}C and δ^{15}N measurements on late Holocene individuals should also detect the consumption of offshore animals. However, it is first necessary to evaluate the amount of isotopic disparity of nearshore and offshore resources as end members (Casey and Post, 2011). Often the end members of interest are not separated enough to provide good resolution in mixing models (Hobson, 1999).

If the isotopic information is not suitable to infer where diets were obtained and, by extension, to analyze the foraging spatial range of the hunter-gatherer groups, then it can be used to discuss possible prey combinations in marine diets of the Beagle Channel. While zooarchaeological studies identify taxon-specific consumption (Barberena and Borrero, 2005; Newsome et al., 2007), isotopic analyses need to aggregate isotopically similar resources for paleodietary interpretations. At this point, the challenge is to combine sources in a logical fashion (Newsome et al., 2004; Phillips et al., 2005) allowing meaningful interpretations about past human behavior. The endmembers defined in ecological studies are not always appropriate to archaeological questions.

The aim of this paper is to generate isotopic reference values for combination of resources in human paleodiets. We determine if the composition of marine diets can be related to the exploitation of different environments by hunter-gatherers, or if is better to analyze the composition of diets according to different criteria. To accomplish this, we characterize isotopic variability in δ^{13}C and δ^{15}N throughout marine and terrestrial food webs of the Beagle Channel by analyzing modern and zooarchaeological samples. First, we describe the ecological setting of this region and expectations about the natural distribution of δ^{13}C and δ^{15}N. Then we introduce the samples and methods used in this study. Finally, we present the isotopic results and we discuss the implications for human paleodiet reconstructions.

1.1. Ecological setting

The Beagle Channel is located at 55° S, along the southern coast of the Isla Grande de Tierra del Fuego. One hundred sixty-five kilometers long, it connects the Pacific and Atlantic Oceans. The Andean Cordillera is situated parallel to the coast in an E-W direction. The climate is classified as oceanic, dominated by a polar maritime air mass throughout the late Holocene (Heusser, 1988). Mean annual temperature is 6 °C and precipitation ranges between 500 and 600 mm (Coronato, 2014).

The subpolar marine ecosystem contains a wide range of species that were consumed by prehistoric populations. Previous zooarchaeological studies (e.g. Zangrando, 2009a, 2009b; Tivoli and Zangrando, 2011), sorted taxonomic groups according to modern ecological parameters, to test hypothesis on landscape use for hunting, fishing or gathering activities in human populations. Nevertheless, isotopic studies need to generate their own frame of reference due to several reasons. Species may have experienced changes in their foraging ecology (Burton et al., 2001) by natural and/or anthropogenic factors, differing present distributions from the past (Szpak et al., 2012; Zangrando et al., 2014a). On the other hand, baseline $\delta^{13}C$ and $\delta^{15}N$ values fluctuate over time (Post, 2002), affecting isotopic values through the food web. Then, to interpret human paleodiets in relation to subsistence strategies in different ecozones, we need to understand the degree of isotopic variation within and among the resources (Phillips, 2012) in the prehistoric environment.

As some marine species change their habitat through their life cycle (Barnes and Hughes, 1999), it may not be suitable to classify faunal species according to where they could be obtained by the hunter-gatherers; but instead, to also take into account general descriptions about the ecological niche of the species (Newsome et al., 2007). We consider the differences between inshore and offshore primary producers in marine systems (France, 1995; Hobson, 1999), the trophic level of the species (Minagawa and Wada, 1984; Forero et al., 2004; Hedges and Reynard, 2007; Ciancio et al., 2008). For terrestrial resources, we include traits of Patagonian forests and herbivores (Tessone, 2010; Fernández and Tessone, 2014; Barberena et al., 2011). This information is useful to model the expectations about differences in $\delta^{13}C$ and $\delta^{15}N$ distributions in the Beagle Channel environment.

1.1.1. Marine environment

In cold temperate coasts, pinnipeds are described as major top predators worldwide (Vales et al., 2017). The South American fur seal (*Arctocephalus australis*) dominates zooarchaeological assemblages from this area (Schiavini, 1993; Orquera and Piana, 1999a). They travel long distances and mostly feed on anchovy, sardines, crustaceans and cephalopod mollusks (Sielfeld, 1999; Falabella et al., 2009). While adult and young male seals spend more time in the water than on land, female fur seals continuously return to the breeding colonies to nurse their pups. However, there are not significant differences between sexes in $\delta^{13}C$ values since 5000 BP (Zangrando et al., 2014b).

The seabirds of Patagonia have a relatively high trophic position (Forero et al., 2004). Migratory birds like the Magellanic penguin (*Spheniscus magellanicus*) forage over 500 km from their colonies. Their diet is mixed, based on fish and squid (Raya Rey and Schiavini, 2000; Silva et al., 2014). Albatrosses (*Diomedea* sp.) are offshore species, which spend most of their time flying over the shelf slope. They feed on crustaceans, squid, fish and carrion (Couve and Vidal, 2003). They only occasionally come to the coast (Falabella et al., 2009).

Fish species with pelagic habits were also consumed by hunter-gatherers, mainly snoeks (*Thyrsites atun*), hake (*Merluccius* sp.) and Patagonian grenadier (*Macruronus magellanicus*). The latter may come closer to the coast in their juvenile stage, and it is a generalist predator with a lower trophic position than the snoeks and hakes. These two epipelagic species are described as consumers of intermediate size fish and squid (Ciancio et al., 2008; Zangrando et al., 2016). In the nearshore marine ecosystem, kelp forests of *Macrocystis pyrifera* constitute an important habitat for several consumers (Riccialdelli et al., 2016). Small fishes of the Nototheniidae family, like the Southern cod (Patagonotothen *sp.*) and Magellanic rockcod (*Paranotothenia magellanica*) inhabit these shallow waters. They are detritivore and small crustacean feeders (Moreno and Jara, 1984; Zangrando, 2009b). Cormorants (*Phalacrocorax* sp.) also feed nearshore, with interspecific differences in foraging behavior (Raya Rey and Schiavini, 2000). The rocky ridges of the intertidal zone are colonized by shellfish communities. The blue mussel (*Mytilus edulis*) is a suspension feeder. They comprise more than 96% of the shell middens of Beagle Channel, being the most common species in these deposits (Orquera, 1999; Orquera and Piana, 2000, 2001; Zangrando et al., 2017).

Typical of estuarine zones is the Patagonian blenny (*Eleginops maclovinus*). It consumes fishes, amphipods and kelps (Lloris and Rucabado, 1991). The Southern river otter (*Lontra provocax*) relies heavily on benthic marine resources like crustaceans and fish (Gomez et al., 2010).

1.1.2. Terrestrial environment

The dominant vegetation types in the terrestrial environment are evergreen and deciduous forests. The most characteristic species are from the *Nothofagus* genera. These trees grow on acidic soils with a poor drainage, rich in organic matter but depleted in nitrogen and other nutrients. However, species of *Nothofagus* in Tierra del Fuego have mycorrhizal associations providing plants with nitrogen (Frangi et al., 2004).

Guanaco (*Lama guanicoe*) was the main terrestrial staple (Orquera and Piana, 1999a). This camelid is defined as an adaptable mixed feeder (Barberena et al., 2009), and analysis of feces found a constant and abundant presence of *Nothofagus* spp. throughout the year (Soler et al., 2013; Arias et al., 2015). A native carnivore is the Fuegian fox (*Lycalopex culpaeus*). They mainly feed on rodents, but aquatic prey is frequent in their diet (Gomez et al., 2010). Neither foxes nor rodents were consumpted by humans, and their presence in archaeological deposits is attributed to taphonomic processes (Santiago and Vázquez, 2012).

1.2. Expectations about the natural distribution of $\delta^{13}C$ and $\delta^{15}N$ values

From the data summarized above, considerable isotopic variability should characterize resources consumed by prehistoric populations of Beagle Channel. Marine ecosystems typically show strong spatial gradients in the distribution of carbon stable isotope values, with nearshore primary producers more enriched in ^{13}C than offshore ones (Clementz and Koch, 2001; France, 1995; Hemminga and Mateo, 1996). In low turbulence areas like kelp forests there is high diffusional resistance to CO_2, which leads to an increased assimilation of heavier ^{13}C isotopes by aquatic plants and more positive $\delta^{13}C$ values among those plants and their secondary consumers.

Conversely, primary producers found in the open water or pelagic habitats have primary producers with lower diffusion resistance and more negative values of $\delta^{13}C$ (Newsome et al., 2010). We expect the carbon isotopic values of animals feeding in the open ocean carbon to be depleted by up to 6‰ relative to the nearshore animals, due to a smaller boundary layer for diffusion. Higher concentrations of dissolved CO_2 and less HCO_3^- in subpolar waters relative to lower latitudes should increase the likelihood of observing depleted carbon isotope values for open ocean animals (Casey and Post, 2011).

Therefore, we expect consumers that are associated with benthic habitats such as littoral fishes like notothenids to have higher $\delta^{13}C$ values than seabirds, pelagic fishes and pinnipeds, which forage across wider areas. Estuarine species should have lower $\delta^{13}C$ values than nearshore animals, due to C_3 terrestrial plant material at the base of the food web. However, the isotopic difference should be minimal, as they also feed frequently in the nearshore area.

In contrast to notothenids closely associated to kelp forests, we expect for intertidal suspension-feeders to be depleted in ^{13}C. The mussel beds may rely mainly on the pelagic production (Jack and Wing, 2011), although they are exposed to a variety of food sources on rocky shores (Richoux et al., 2014). Therefore, mussels also could have $\delta^{13}C$ differences with offshore animals closer to open ocean water. While in ecological studies gastropods are usually analyzed to evaluate benthic sources in a foodweb, we do not include them. Benthic invertebrates were less eaten by hunter-gatherers of the Beagle Channel (Orquera and Piana, 2000, 2001).

Among the many factors which influence the $\delta^{15}N$ values of marine organisms, we focus on the trophic discrimination factor (Minagawa and Wada, 1984; Schoeninger and DeNiro, 1984; Post, 2002; Wolf et al., 2009). Taking into account the stepwise increase in δ^{15}N values up food chains, primary consumers like mussels should exhibit the lowest values of δ^{15}N. From modern ecological studies, we expect the highest δ^{15}N values for seabirds and fur seals. Finally, food sources of estuarine environments are similar to nearshore systems in their nitrogen isotopic composition (Michener and Kaufman, 2007). Knowing that Southern river otter and Patagonian blenny feed on marine prey, they should have δ^{15}N values similar to those of nearshore predators.

We are aware of the complexity of marine food webs, and that coexisting species could feed along a continuum of trophic levels (Hobson et al., 1994; Link, 2002). However, after evaluating the isotopic variability between sources, our aim is to narrow down the diversity of prey in groups useful to refine paleodietary interpretations. The consideration of some differences between nearshore and offshore resources makes sense ecologically, and it is pertinent to archaeological questions (Phillips et al., 2005).

In terms of the terrestrial fauna, we expect to find guanacos depleted in ^{15}N to the same degree as other herbivores of the Patagonian Andean Forest (Tessone, 2010; Tessone et al., 2014; Fernández and Tessone, 2014; Méndez et al., 2014). This pattern was related to the closed nature of the nitrogen cycle in these environments. If this is the case, previous isotopic references for terrestrial foods in the Beagle Channel needs to be reconsidered. Those guanaco bones in previous studies were obtained from archaeological sites situated in the steppe zone (Guichón et al., 2001), which is a drier environment than the forest.

2. Materials and methods

Analyses of δ^{13}C and δ^{15}N were conducted on the collagen of 180 zooarchaeological samples, comprising 13 different taxa. Additionally, we collected 15modern samples of blue mussels (*Mytilus edulis*) and 8 plants from the Magellanic forest (n = 13) in order to estimate the isotopic base line of marine and terrestrial food webs. In total we analyzed 208 samples is.

The faunal bones come from archaeological sites on the north coast of the Beagle Channel, spanning the Middle to Late Holocene. The oldest samples were selected from Second Component of Túnel I site, between 6400 and 4600 yr BP, and Lower Component of Imiwaia I, dated between 6390 ± 50 yr BP and 4900 ± 120 yr BP (Orquera and Piana, 1999a). Late Holocene samples are from the upper layers of these two sites plus five sites postdating 3500 yr BP. Detailed data for each sample is presented in Table A, supplementary material. Specimens were identified at the species or genus level, and were differentiated by anatomical units and side.

The subset of aquatic animals includes 10 samples of albatross (*Thalassarche* sp.), 10 magellanic penguin (*Spheniscus magellanicus*), 11 cormorants (*Phalacrocorax* sp.), 5 Magellanic rockcod (*Paranotothenia magellanica*), 5 Southern cods (*Patagonotothen* sp.), 2 samples of Southern river otter (*Lontra provocax*) and 2 Patagonian blenny (*Eleginops maclovinus*). We also included isotopic data from 46 southern fur seals (*Arctocephalus australis*) analyzed by Zangrando et al. (2014b), and 45 pelagic fishes published in Zangrando et al. (2016). Its sample comprised Patagonian grenadiers (*Macruronus magellanicus*), snoeks (*Thyrsites atun*) and hakes (*Merluccius* sp.). The terrestrial group consists of 38 zooarchaeological and 3 modern samples of guanaco (*Lama guanicoe*), and 3 red foxes (*Lycalopex culpaeus*).

Both δ^{13}C and δ^{15}N measurements on bone collagen of seven adult human individuals from the Beagle Channel have been published (Yesner et al., 1991; Guichón et al., 2001; Panarello et al., 2006). Most of them (Table 1, n = 5) belong to museum collections with scarce contextual information (Yesner et al., 1991; Guichón et al., 2001). According to their associated documents, the remains postdate 1500 yr BP. Only two individuals were recovered in situ. One was AMS dated to 1536 ± 46 yr BPS (Suby et al., 2011); the other was dated to the post-contact period (Panarello et al., 2006).

Bone fragments were cleaned with abrasive elements and ultrasonic baths. Mammal and bird samples of approximately 1 g were first treated with NaOH (0.1 M) for 24 h and demineralized in HCl (2%) for 72 h, changing the acid every 24 h. Subsequently, bone fragments were treated again with NaOH for approximately 24 h. The resulting material was then dried in an oven at 40 °C for 20 h (Tykot, 2004). Approximately 0.3 g of each fish sample was repeatedly soaked in very dilute HCl (0.5%) every 24–48 h (Sealy, 1986). Then, it was rinsed with deionized water and treated with NaOH (0.125%) for 20 h. The collagen extracted was finally dried at 40 °C during 24 h. Plants and soft tissues of mussels were cleaned, dried at 40–50 °C and ground using a mortar and a pestle.

Dried samples were weighed into tin cups and analyzed at the Instituto de Geocronología y Geología Isotópica laboratory (INGEIS, CONICET-UBA), Buenos Aires, Argentina. The isotopic analysis of collagen fraction and soft tissue was performed with a Carlo Erba EA1108 Elemental Analyzer (CHN), connected to a continuous flow Thermo Scientific Delta V Advantage mass spectrometer through a Thermo Scientific ConFlo IV interface.

The conservation status of isotopic signal was evaluated by elemental analysis C/N (DeNiro, 1985). Results are expressed as the ratio of the heavier isotope to the lighter isotope and reported as delta (δ) values in parts per thousand (‰) relative to internationally accepted standards for carbon (VPDB) and nitrogen (AIR). The analytical precision was ± 0.3‰.

Modern mussel samples were adjusted for oceanic Suess Effect using Eq. (1) below, from Misarti et al. (2009):

$$\text{Suess Effect correction factor} = a * exp\ (b * 0.027) \tag{1}$$

a is the maximum annual rate of δ^{13}C decrease (− 0.015‰) due to Suess Effect in the Sub-Antarctic zone (McNeil et al., 2001; Hilton et al., 2006). b derives from the year of death of the animal (2013) minus 1850. Therefore, isotopic δ^{13}C values were corrected for 1.2‰. Modern plants were adjusted by adding 1.5‰ to δ^{13}C measurements (Peterson and Fry, 1987).

To compare the isotopic composition of diets we estimated δ^{13}C and δ^{15}N values of animal protein from bone collagen values. Offsets are $\Delta^{13}C_{protein–collagen}$ = − 2‰ and $\Delta^{15}N_{protein–collagen}$ = + 2‰ for all animals except fish, in which we applied $\Delta^{13}C_{protein–collagen}$ = − 1‰ and $\Delta^{15}N_{protein–collagen}$ = + 2‰ (Fernandes, 2016). Instead of averaging individual samples, we averaged across taxon means to avoid bias towards better represented species.

For protein diet to human bone collagen, we applied discrimination factors of + 5‰ for δ^{13}C and + 5.5 for δ^{15}N (Fernandes, 2016).

3. Results

The δ^{13}C and δ^{15}N results, %C and %N, C:N ratios and collagen yields are presented in the Supplementary material, Table A. Descriptive statistics for δ^{13}C and δ^{15}N values are in Table 2. One sample of *P. magellanica* (code 36630) was eliminated from the analysis, because the C/N presents a value higher than the normal range of 2.9–3.6 (DeNiro, 1985). The rest of the bone samples produced C/N ratios characteristic of well-preserved collagen, assuring primary isotopic signals.

Fig. 2 displays stable isotopes results for different groups of aquatic animals. Data obtained for avian fauna shows a dispersion of 2.8‰ in δ^{13}C values (Fig. 2a). There are no statistical differences between seabirds (One-way ANOVA test, Table 3). However, as the most offshore species among the seabirds analyzed, albatrosses have the most negative average δ^{13}C values (− 13.1‰ ± 0.5‰). In the other extreme, cormorants display the most enriched mean (− 12.7‰ ± 0.3‰). This is in agreement with their feeding in shallow waters and colonies near the coast. Penguins occupy an intermediate position between these two species (− 12.9‰ ± 0.7‰).

Table 1
Available $\delta^{13}C_{coll}$ and $\delta^{15}N$ measurements on human remains from Beagle Channel.

Provenience	Lab code	Sex	$\delta^{13}C_{collagen}$	$\delta^{15}N$	C/N	References
Ushuaia	Without date (Geochron)	Indet.	− 12.6	18.8	Without data (Geochron)	Yesner et al. (1991)
Isla Hoste		Male	− 13.3	17.2		
Isla Hoste		Male	− 16.8	13.2		
Isla Navarino		Male	− 18.5	10.6		
Lauta 2	USF 360	Female	− 12.3	17.3	Without data	Guichón et al. (2001)
Shamakush Entierro	AIE 27573	Male	− 12.4	18.3	3.3	Panarello et al. (2006)
Ea. Harberton	EILAB 87920	Male	− 11.6	18.6	3.2	

The dispersion is wider among $\delta^{15}N$ values, with a range of 6‰, more than one trophic level. The pattern is similar to that observed in carbon isotopes: the heavier mean corresponds to the albatross (18.6‰ ± 0.9‰), whereas penguins have an intermediate average (17.1‰ ± 0.9‰), and cormorants are the most depleted in ^{15}N (15.4‰ ± 0.6‰). Differences are statistically significant (Table 3).

Considering fishes, the input of distinct primary producers in the food web is more likely (Fig. 2b). $\delta^{13}C$ values are dispersed in a considerable range of 4.2‰. The most enriched means are observed in benthic nearshore species as rockcod (− 11.2‰ ± 1.3‰) and Southern cod (− 11.2‰ ± 1.1‰). They have significant differences compared to more offshore species as hakes and snoeks (Table 4). Both have the most negative averages (− 12.8‰ ± 0.7‰ and − 12.6‰ ± 0.7‰, respectively). The Patagonian grenadier has a higher mean than epipelagic fishes (− 11.6‰ ± 0.4‰). The blenny was not included in the ANOVA test, as we have only two samples. It has an average of − 12.1‰ ± 0.6‰, intermediate between the offshore and nearshore fishes. It could be explained by the mixing of depleted terrestrial carbon from the freshwater ecosystem, and the input of more enriched sources from the marine environment.

Although some significant statistical differences are also observed in $\delta^{15}N$ values between different fish species, this does not show a clear pattern. There is a range of 4.3‰ in the $\delta^{15}N$ values, which is expected by the diversity of fish species analyzed. The rockcods have the lightest mean of 14.9‰ ± 0.6‰, followed by the snoeks (15.3‰ ± 0.9‰) and Patagonian grenadiers (15.8‰ ± 0.9‰). Patagonian blenny, Southern cod and hake are the most enriched in the heavier isotope, with a mean of 16.4‰ ± 0.1‰, 16.5‰ ± 0.5‰ and 17‰ ± 0.9‰, respectively.

In aquatic mammals (Fig. 2c), fur seals occupy a tightly clustered isotopic space. They have mean $\delta^{13}C$ values of − 11.8‰ ± 0.5‰ and $\delta^{15}N$ values of 17.3‰ ± 0.6‰. One sample of otter is similar to fur seals in both markers ($\delta^{13}C$ = − 12‰, $\delta^{15}N$ = 18.1‰). The second sample appears as an outlier, and has the highest $\delta^{15}N$ values among all the specimens analyzed ($\delta^{13}C$ = − 9.4‰, $\delta^{15}N$ = 24‰). Despite the fact that it does not have evidence of contamination or degradation, as modern river otters are more depleted in $\delta^{15}N$ (Riccialdelli et al., 2016), we exclude this extremely enriched sample from the subsequent analysis.

Finally, the mussels show the most depleted isotopic values (Fig. 3). The $\delta^{13}C$ mean is − 16.5 ‰ ± 0.6 ‰. The results are on muscle tissues, having different discrimination factors from diet compared to faunal bone collagen. However, they are considerably lighter than the rest of the samples analyzed, probably due to an intake from a different source of primary producers. In previous studies, similar isotopic values of filter feeders were interpreted as showing a large consumption of pelagic producers by this group, with a great influence of phytoplankton and suspended particulate organic matter or SPOM (Riccialdelli et al., 2016). Also the $\delta^{15}N$ average is lower than the rest of the marine samples (11.1‰ ± 0.5‰), which is related to their low trophic level as filter feeders.

Stable isotopes results for terrestrial plants are plotted in Fig. 4. While the primary producers fall in the range expected for C_3 plants, there is a considerable variability between the samples, which can be clearly divided in two groups. Lichens are the samples enriched in ^{13}C, with an average of − 22.6‰ ± 1.2‰. At the same time, they are markedly depleted in ^{15}N. The $\delta^{15}N$ mean is − 16.2‰ ± 1.3‰. The rest of the specimens are C_3 grasses and they display the opposite pattern. $\delta^{13}C$ mean is more negative than the lichens (− 27.9‰ ± 1.1‰) and they have a higher $\delta^{15}N$ mean of 0.7‰ ± 2.4‰.

With respect to terrestrial animals (Fig. 5), the linear dispersion of

Table 2
Descriptive statistics for $\delta^{13}C$ and $\delta^{15}N$ values of all taxa from Beagle Channel. With the exception of mussels and plants, values were measured on bone collagen.

Taxa	n	$\delta^{13}C$ ‰			$\delta^{15}N$ ‰		
		Mean (± SD)	Minimum	Maximum	Mean (± SD)	Minimum	Maximum
Marine							
Southern fur seal	46	− 11.8 ± 0.5	− 12.8	− 10.8	17.3 ± 0.6	15.5	18.7
Albatross	10	− 13.1 ± 0.5	− 14.5	− 12.7	18.6 ± 0.9	17.3	20.6
Penguin	10	− 12.9 ± 0.7	− 13.7	− 11.7	17.1 ± 0.9	14.8	18
Cormorant	11	− 12.7 ± 0.3	− 13.3	− 12.2	15.5 ± 0.6	14.6	16.6
Patagonian grenadier	14	− 11.6 ± 0.4	− 12.2	− 10.8	15.8 ± 1	14.7	18.3
Snoek	14	− 12.6 ± 0.7	− 13.5	− 11.6	15.3 ± 0.9	14	17.7
Hake	17	− 12.8 ± 0.7	− 13.7	− 11	17 ± 0.9	14.8	18.3
Rockcod	4	− 11.2 ± 1.3	− 12.7	− 9.6	14.9 ± 0.6	14.2	15.6
Southern cod	5	− 11.2 ± 1.1	− 12.3	− 9.5	16.5 ± 0.5	15.7	17.1
Mussel	15	− 16.5 ± 0.6	− 17.3	− 15.2	11.1 ± 0.5	10.1	11.7
Southern river otter	2	− 10.7 ± 1.8	− 12	− 9.4	21.1 ± 4.2	18.1	24
Patagonian blenny	2	− 12.1 ± 0.6	− 12.5	− 11.7	16.5 ± 0.1	16.4	16.5
Terrestrial							
Guanaco	41	− 20.9 ± 1.9	− 23.6	− 15.3	1.1 ± 2.3	− 5.3	4.3
Red fox	3	− 18.3 ± 2.3	− 19.9	− 15.7	9 ± 3.4	6.3	12.8
C_3plants	10	− 27.9 ± 1.1	− 30.3	− 26.7	0.7 ± 2.4	− 3.6	3.3
Lichens	3	− 22.6 ± 1.2	− 23.4	− 21.2	− 16.2 ± 1.3	− 17.4	− 14.9

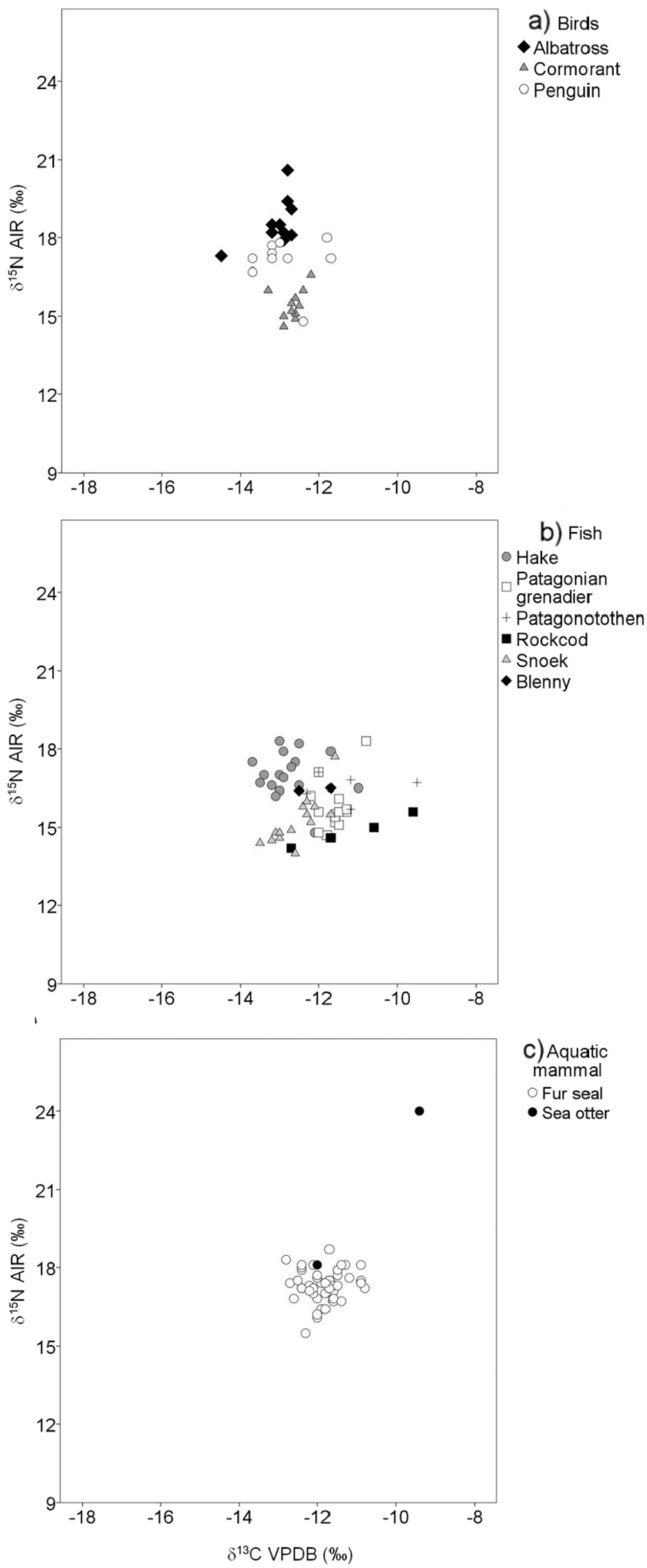

Fig. 2. Stable isotope results for archaeological fauna from Beagle Channel.

guanacos in the isotopic space is strikingly wider for an herbivore. There is a range of 8.3‰ in δ^{13}C values and 9.6‰ in δ^{15}N, but both markers are strongly correlated ($R^2 = 0.75$): this point will be discussed later. The δ^{13}C mean is −20.9‰ ± 1.9‰ and 1.1‰ ± 2.3‰ for δ^{15}N. Compared to guanacos, red foxes have more enriched averages of δ^{13}C and δ^{15}N (−18.3‰ ± 2.3‰ and 9‰ ± 3.4‰, respectively). These results are consistent with their carnivore diet and intake of marine prey, as observed in modern studies.

4. Discussion

4.1. Marine prey

As a first step to characterize the diversity of hunter-gather marine diets in the Beagle Channel, we intended to aggregate prey with similar isotopic values and following ecological criteria. When comparing groups of animals (birds, fishes, aquatic mammals) δ^{13}C values follow the expected patterns for the inshore-offshore gradient. Moreover, the statistically significant differences between means are in agreement with data from ecological studies.

When analyzing the marine food web as a whole, some organisms defined as nearshore -in relation to their habitat- were similarly or more depleted in ^{13}C than offshore species (Fig. 6). Also the distribution of mean δ^{13}C values is very narrow, being 2.4‰ the difference between the highest and lowest mean. The cormorants, which in zooarchaeological studies are defined as nearshore species, have similar δ^{13}C distributions to epipelagic fishes like hakes and snoeks. Mussels can be obtained at the coast but exhibit the most negative δ^{13}C values, most likely feeding on ^{13}C depleted pelagic-derived materials.

We are aware that mussel muscles provide a brief snapshot of the modern aquatic baseline, and that they are influenced by seasonal changes (Richoux et al., 2014). Modern studies in Lapataia Bay, Beagle Channel, (Riccialdelli et al., 2016) found a complicated mixture of marine, estuarine and freshwater inputs in this food web structure. For the species *Mytilus edulis*, the cited study reported a δ^{13}C average of −18.7‰ ± 0.8‰. Even adding 1.2‰ for the Suess effect, they are more depleted than the shellfish samples included in the present study. Despite of the fact that modern shellfish does not account for past isotopic baseline (Casey and Post, 2011), its isotopic analysis suggests that they could be a source depleted in ^{13}C in human diets of Beagle Channel. On the other hand, macroalgae are benthic primary sources with heavier δ^{13}C values, and detritivore fishes feeding in kelp beds presented the most enriched means in ^{13}C.

The distribution of the δ^{13}C values increases gradually across all the species analyzed. Comparing all the taxa at the same time, it is more difficult to separate offshore animals from the nearshore ones; the distribution of δ^{13}C values overlap in species found at different distances from the coast. Miller et al. (2008) mentions aquatic systems where it is not observed δ^{13}C differentiation between nearshore and more offshore species, related to their well-mixed waters. To compare if the Beagle Channel is similar to these cases, it would be necessary to include samples of primary consumers from the benthic community.

While zooarchaeological studies in the Beagle Channel are able to infer the use of inshore-offshore spaces by the hunter-gatherers, stable isotopes analyses on human remains cannot classify the resources in the same manner. Especially, animals as mussels and rockcod, obtained in nearshore zones, occupy both depleted and enriched extremes of δ^{13}C values among aquatic animals. It will be difficult to quantify their proportion in the diet, as the outcome of Bayesian mixing models may be diffuse if the intragroup isotopic variation is larger than intergroup variation; or if there is little variation between source groups (Phillips et al., 2014).

The distribution of δ^{15}N values is represented in Fig. 7. It is similar to the previous figure, in which the distribution of the heavier isotopes increases by degree across the taxa analyzed. This pattern can be related to the access to multiple food sources, high dietary overlap and generalist feeding strategies of marine organisms as stated by Link (2002). Nevertheless, some pelagic animals –albatrosses, fur seals, penguins and hakes– are the most enriched in ^{15}N. It is interesting to find the albatross more enriched in ^{15}N than fur seals, and penguins with similar δ^{15}N values to these pinnipeds. They may occupy similar trophic position in the food web and thus have similar isotopic values,

Table 3
One-way ANOVA test results for isotopic values in archaeological seabirds.

$\delta^{13}C$	Penguin	Cormorant	Albatross
Penguin	–	$p = 0.678$	$p = 0.671$
Cormorant	–	–	$p = 0.222$

$\delta^{15}N$	Penguin	Cormorant	Albatross
Penguin	–	$\mathbf{p = 0.000}$	$\mathbf{p = 0.001}$
Cormorant	–	–	$\mathbf{p = 0.000}$

In bold, significant P values ($P < 0.05$).

Table 4
One-way ANOVA test results for isotopic values in archaeological fishes.

$\delta^{13}C$	Southern cod	Rockcod	Patagonian grenadier	Snoek	Hake
Southern cod		$p = 0.999$	$p = 0.813$	$\mathbf{p = 0.004}$	$\mathbf{p = 0.000}$
Rockcod			$p = 0.666$	$\mathbf{p = 0.002}$	$\mathbf{p = 0.000}$
Patagonian grenadier				$p = 0.078$	$\mathbf{p = 0.001}$
Snoek					$p = 0.977$
$\delta^{15}N$					
Southern cod		$\mathbf{p = 0.004}$	$p = 0.458$	$\mathbf{p = 0.046}$	$p = 0.793$
Rockcod			$p = 0.237$	$p = 0.894$	$\mathbf{p = 0.000}$
Patagonian grenadier				$p = 0.755$	$p = 0.054$
Snoek					$\mathbf{p = 0.002}$

but according to optimal foraging models in archaeology (Winterhalder and Smith, 2000), these aquatic animals imply quite different strategies for exploitation and foraging ranges. As pointed by Britton et al. (2013), high $\delta^{15}N$ values on human samples could not only indicate the consumption of marine mammals such as seals, but also the incorporation of piscivorous seabirds and eggs.

On the other hand, the mussels depleted in ^{15}N would decrease the human $\delta^{15}N$ values towards the lower extreme. We reassert that isotopic analyses on modern mussel are not representative of past baselines of aquatic ecosystems. However, it could be useful to evaluate gathering activities in the intertidal zone (Zangrando et al., 2017). For example, some authors propose that women would pursue predictable, but smaller prey to provision children (Zeanah, 2004). From the

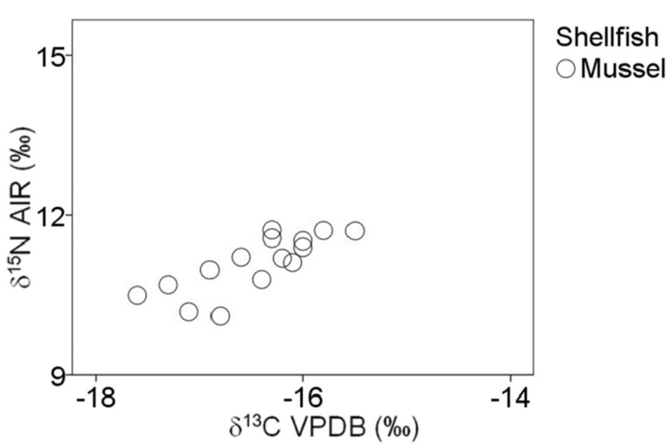

Fig. 3. Stable isotope results for modern mussel muscles from Beagle Channel.

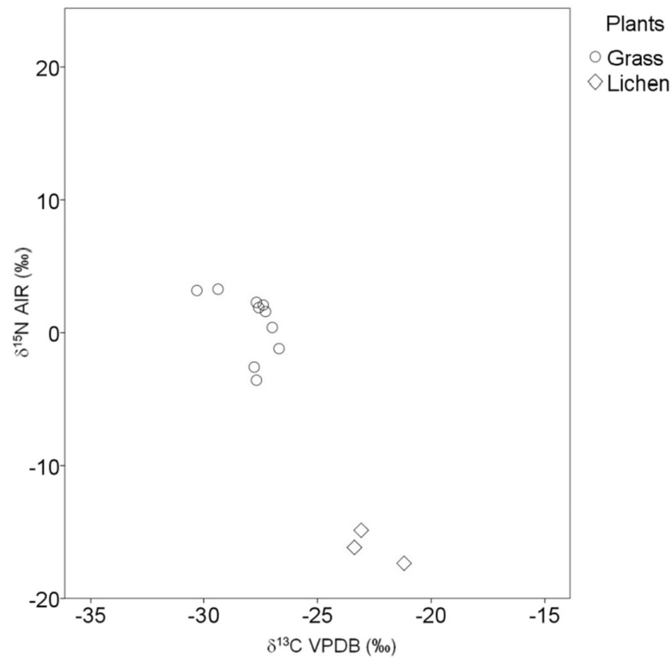

Fig. 4. Stable isotope results for modern terrestrial plants from Beagle Channel.

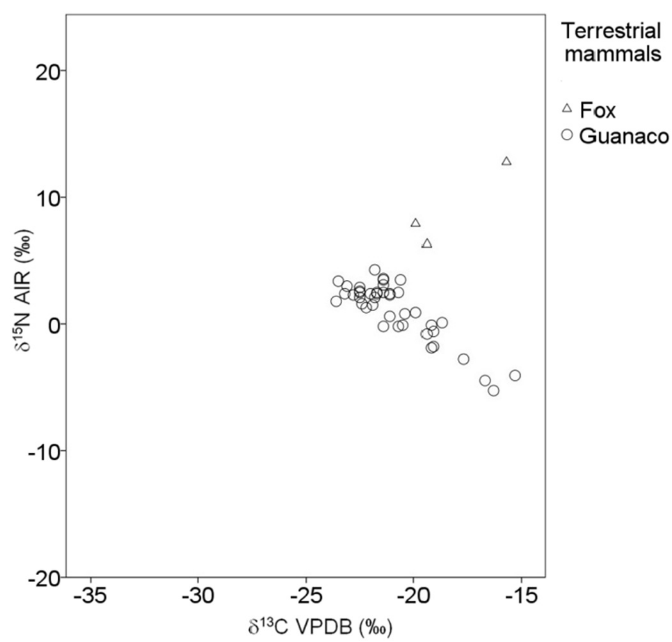

Fig. 5. Stable isotope results for archaeological terrestrial fauna from Beagle Channel.

composition of shell middens in the Beagle Channel, it was estimated that mussels could have contributed between 15 and 20% of the caloric daily requirements (Orquera, 1999). Nevertheless, there is a limitation to infer individual differences in diet related to age, sex, or skill for zooarchaeological studies (Jochim, 1998), while future stable isotopes analyses can evaluate these aspects.

4.2. Terrestrial prey

The $\delta^{15}N$ value for guanaco samples was 1.1‰ ± 2.3‰, notably lower than that previously reported (4.9‰, Guichón et al., 2001). This difference is similar to that associated with the enrichment in ^{15}N across one trophic level. Considering that Tierra del Fuego presents two contrasting vegetal communities, paleodietary interpretations should use

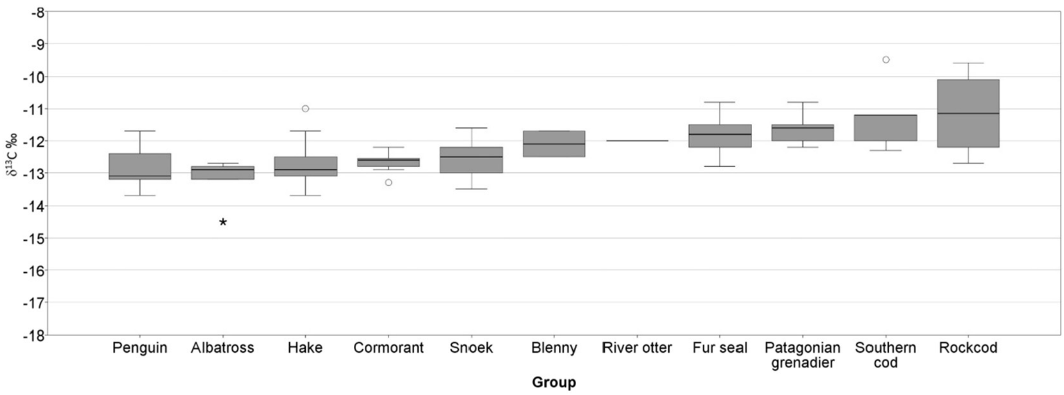

Fig. 6. Comparison of $\delta^{13}C$ values between aquatic vertebrate animals. All values are from bone collagen.

local references for the main terrestrial staple.

The variability of $\delta^{13}C$ and $\delta^{15}N$ values within guanacos from Beagle Channel is also noteworthy, which in turn reflects the widespread dispersion of isotopic values among primary producers of the Magellanic forest. A family group of guanacos occupies a narrow home range that varies between 2 and 9 km^2 (Bilá, 2012), and it is reasonable to find considerable isotopic variations between zooarchaeological samples from different sites. Probably diets of guanacos differ in the proportion of lichens consumed, as observed in other species of herbivores inhabiting temperate and cold forests (Coltrain et al., 2004; Bocherens et al., 2015). Among the plants analyzed in this work, lichens have the highest $\delta^{13}C$ values and the lowest $\delta^{15}N$ values. A similar relation was observed in the isotopic values of guanacos, in which the samples enriched in ^{13}C were ^{15}N depleted. According to microhistological studies of feces, lichens have minor importance in the diet of modern guanacos. However, the amount consumed could be underestimated due to their high digestibility (Bonino and Pelliza Sbriller, 1991; Soler et al., 2012; Soler et al., 2013).

The archaeological implication is that even a simple diet based on one main terrestrial staple may be associated with considerable isotopic variability in the source, and this was pointed as one of the practical difficulties in assessing the trophic level in human paleodiets (Hedges and Reynard, 2007). For hunter-gatherers, who forage over extensive areas, sampling of resources should cover spatial variations in the primary producers which can be transferred to consumers.

4.3. Implications for paleodietary interpretations

To discuss the potential implications of combinations of resources in a diet, we plotted three hypothetical isotopes values on human bone collagen (Fig. 8, grey squares). They are calculated as perfect mixing of different group of resources, and for this reason only serve as general references for qualitative analyses. Then we compare the isotopic measurements on human remains from the Beagle Channel (black dots) against these squares.

Square A represents an individual consuming solely guanacos as the main staple. It has the lowest $\delta^{13}C$ and $\delta^{15}N$ values, as expected for a terrestrial diet in a coastal environment. However, given the isotopic variability within this species it is suggested to use mixing models which can include uncertainties in multiple resources. Plants analyzed in this work are not mentioned as edible in ethnographic records (Orquera and Piana, 1999b) and for this reason we do not include them in the hypothetical terrestrial diet. Nonetheless, it is reasonable to expect that the consumption of plants would reduce human isotopic values in both markers.

One of the two individuals whose diet is mostly terrestrial complemented with marine resources (Yesner et al., 1991, 2003) has a $\delta^{13}C$ value more negative than a diet based only on guanacos. As this difference is minimal, and both guanacos and C_3 plants have considerable variability in $\delta^{13}C$ values, it is difficult to identify a regular ingestion of plants. Although the dependence on gathered plants is low in areas with short growing seasons (Binford, 1990), these resources can contribute from 6 to 15% of the total diet of northern tundra inhabitants (Cordain et al., 2000). Other possibility is that the individual lived in the post-contact period and was consuming non-native foods as bread (Gusinde, 1951). In both cases their contribution to the diet would be underestimated, because $\delta^{13}C_{collagen}$ is skewed towards the isotopic signature of protein (Kellner and Schoeninger, 2007; Froehle et al., 2010, 2012).

Squares B and C are individuals with diets based 100% on marine animals, but with different degrees of reliance on gathered resources. The square B comprises a perfect mixing of all marine resources: mammals, fishes, birds and shellfishes. The square C was calculated as a diet complemented with 20% of shellfish, as estimated by previous zooarchaeological studies (Orquera, 1999). Consumption of these diets

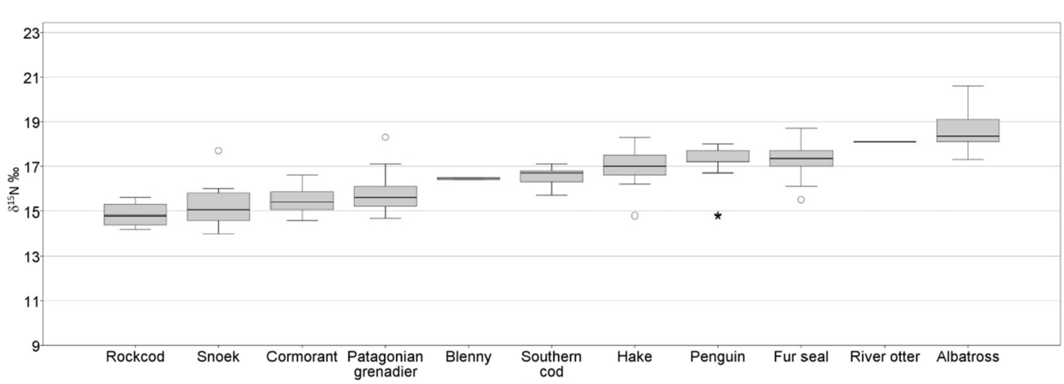

Fig. 7. Comparison of $\delta^{15}N$ values between aquatic vertebrate animals. All values are from bone collagen.

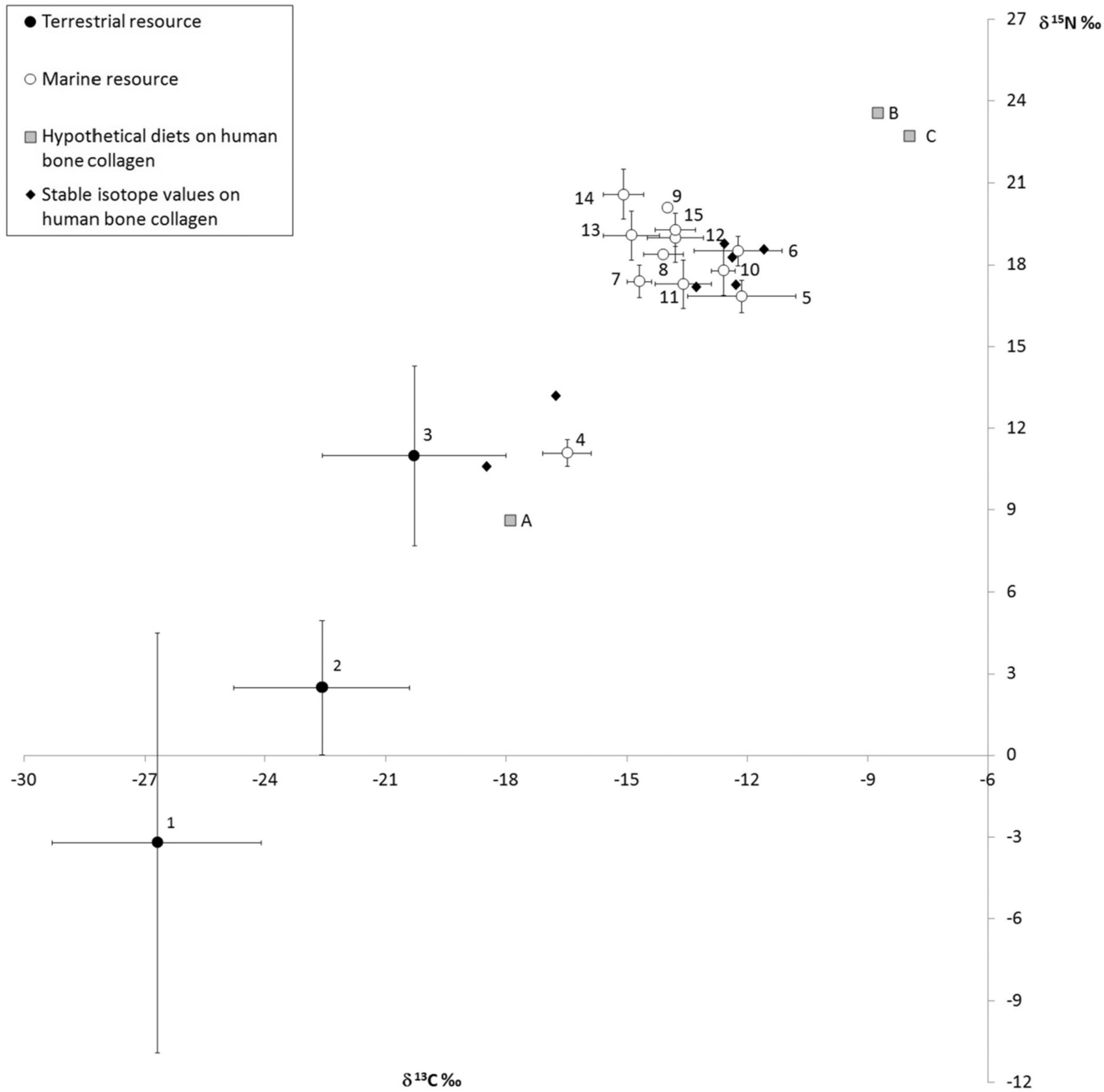

Fig. 8. Mean $\delta^{13}C_{protein}$ and $\delta^{15}N_{protein}$ values (± SD) of all taxa analyzed from Beagle Channel. *Habitat references*: *Terrestrial* (black circle) 1-Plants, 2-Guanaco, 3-Red fox. *Marine* (white circle) 4-Mussel, 5-Magellanic rockcod, 6-Southern cod 7-Cormorant 8-Patagonian blenny, 9-Sea otter, 10-Patagonian grenadier 11-Snoek, 12-Hake, 13-Penguin, 14-Albatross, 15-Fur seal. *Expected isotopic values on human bone* (grey square) *for 100% terrestrial diet*: A-only guanacos as prey. *For 100% marine diet* B-Equal reliance on all marine resources C-Complemented by gathered shellfish. *Available $\delta^{13}C_{coll}$ and $\delta^{15}N$ measurements on human remains from Beagle Channel* (black diamonds).

results in very similar $\delta^{13}C$ and $\delta^{15}N$ values. No matter what criteria is selected to aggregate the marine resources, isotopic record on human bone may be less clear than the zooarchaeological record to distinguish among the different aquatic resources ingested.

The remaining five individuals are quite clustered and close to the enriched extreme of marine diets. However, they have lower $\delta^{13}C$ and $\delta^{15}N$ values than a hypothetical diet based 100% on marine resources, which indicates a minor but regular consumption of terrestrial protein. In most shellmiddens of the central sector of Beagle Channel, since the specialization on maritime resources that began at least 6400 years ago (Orquera et al., 2011), the guanaco has a lower contribution to the zooarchaeological record compared to other species (Zangrando, 2009a). In the eastern sector it is the main staple exploited (Alunni and Zangrando, 2012). Considering that isotope data from human bones informs about the average diet over a longer period than 10 years (Hedges et al., 2007), it is suggested that the eastern sector was occupied for shorter spans or logistical movements; or both isotopic markers on collagen would be more depleted towards a terrestrial diet.

In regard to the capture of pelagic resources such as albatrosses, snoeks and hakes, zooarchaeological studies proposed an increase of their contribution in the diet in the last 1500 years (Tivoli and Zangrando, 2011). The $\delta^{15}N$ values on human bone collagen are not high enough to indicate a substantial intake of these high trophic level resources. Nevertheless, a consumption of shellfish depleted in both isotopes could be masking the ingestion of pelagic preys. Despite the labor required to their processing, bivalves are protein sources readily available and predictable, especially for children and elderly people (Erlandson, 2001). It would not be surprising that mussels were an important staple in the diet, representing more than 20% of the total dietary intake. Finally, there is an obvious sample bias (Milner et al., 2004) as we include only seven individuals in this analysis, so the trend about the regular foraging in offshore patches needs to be tested against a more representative sample of prehistoric individuals and possibly with more isotopic markers (Rossman et al., 2016).

5. Conclusions

Until now, stable isotope studies in Beagle Channel have described paleodiets based on two end members: terrestrial and marine resources. This works analyzed the local isotopic ecology, trying to break down the category of marine diets in its diverse components. Some marine animals from offshore habitats tend to be enriched in ^{15}N. The distribution of δ^{13}C values also varies according to the distance from the shoreline to prey habitats. However, the aggregation of resources in groups blurs the difference in both isotopic markers. δ^{13}C in marine animals are distributed in a narrow range - 2.4‰ between means- to distinguish their consumption separately in mixing models.

Guanacos, the main terrestrial staple, have a high dispersion in both δ^{13}C and δ^{15}N values. As hunter-gatherers foraged over extensive areas, it is important to consider spatial variation in the isotopic values of their subsistence resources and use of mixing models which can deal with several uncertainties in the parameters.

The results of this study suggest that this subpolar marine food web is characterized by a tight clustering of nearshore and offshore groups of resources in isotopic space. Marine mammals are not the only top predators in this food web, in contrast to other high latitude coastal and lacustrine contexts (Richards et al., 2005; Weber et al., 2011; Britton et al., 2013; Coltrain et al., 2016). Seabirds and epipelagic fish such as hake have similar or higher δ^{15}N values. When interpreting high δ^{15}N values in human bone collagen, it is difficult to differentiate diets relying on a high-ranked prey such as the fur seal or a combination of multiple smaller animals. This distinction is central for diet breadth models to detect changes in foraging economies (Winterhalder and Smith, 2000; Richards et al., 2001). Where species differ in their tradeoff but they present similar δ^{13}C and δ^{15}N values, isotopic data need to be complemented with zooarchaeological analyses.

For most adult individuals of Beagle Channel, we observed lower δ^{13}C and δ^{15}N values than expected for a fully marine diet. Previous analyses suggested that these diets were complemented with terrestrial preys as guanacos. However, the consumption of shellfish in great quantities is another possibility, which could explain the slightly depleted values. Also the ingestion of terrestrial plants could be a little higher than suggested from archaeobotanical analyses. With two isotopic markers it was not possible to identify the consumption of nearshore or offshore prey as initially proposed. This aspect of the foraging strategy is better evaluated through zooarchaeological studies. Also the inclusion of other isotopic systems could help answer some of these questions.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2017.11.036.

Acknowledgements

This research was supported by PICT-2013-1011 (FONCYT). Excavations and research in Túnel I, Shamakush I and Imiwaia I sites were conducted by Luis Orquera and Ernesto Piana (CONICET). Daniela Alunni, Germán Pinto Vargas and Martín Vázquez helped with the selection of zooarchaeological samples. Taxonomical identification of terrestrial plants was done by Rosina Soler (CADIC-CONICET). Thanks to Estela Ducos (INGEIS-UBA/CONICET) and Nazareno Piperissa (INGEIS-UBA/CONICET) for the stable isotopes analyses. The authors are responsible for the contents of this paper.

References

Alunni, D.V., Zangrando, A.F.J., 2012. Primeros datos sobre el transporte, procesamiento y consumo de guanacos en la localidad arqueológica Heshkaia (sudeste de Tierra del Fuego, Argentina). Magallania 40 (1), 319–331.

Arias, N., Feijóo, S., Quinteros, P., Bava, J., 2015. Composición botánica de la dieta del guanaco (*Lama guanicoe*) en la Reserva Corazón de la Isla, Tierra del Fuego (Argentina): utilización estacional de *Nothofagus spp*. BOSQUE 36 (1), 69–77.

Barberena, R., Borrero, L.A., 2005. Stable isotopes and faunal bones. Comments on *Milner et al.* (*2004*). Antiquity 79 (303), 191–195.

Barberena, R., Zangrando, A.F., Gil, A.F., Martínez, G.A., Politis, G.G., Borrero, L.A., Neme, G.A., 2009. Guanaco (*Lama guanicoe*) isotopic ecology in southern South America: spatial and temporal tendencies, and archaeological implications. J. Archaeol. Sci. 36 (12), 2666–2675.

Barberena, R., Méndez, C., Mena, F., Reyes, O., 2011. Endangered species, archaeology, and stable isotopes: huemul (*Hippocamelus bisulcus*) isotopic ecology in central-western Patagonia (South America). J. Archaeol. Sci. 38 (9), 2313–2323.

Barnes, R.S.K., Hughes, R.N., 1999. An Introduction to Marine Ecology. John Wiley & Sons.

Bilá, B., 2012. Camélidos sudamericanos. Eudeba.

Binford, L.R., 1990. Mobility, housing, and environment: a comparative study. J. Anthropol. Res. 46, 119–152.

Bocherens, H., Hofman-Kamińska, E., Drucker, D.G., Schmölcke, U., Kowalczyk, R., 2015. European bison as a refugee species? Evidence from isotopic data on early Holocene bison and other large herbivores in northern Europe. PLoS One 10 (2).

Bonino, N., Pelliza Sbriller, A., 1991. Composición botánica de la dieta del guanaco (*Lama guanicoe*) en dos ambientes contrastantes de Tierra del Fuego, Argentina. Ecol. Austral 1, 97–102.

Britton, K., Knecht, R., Nehlich, O., Hillerdal, C., Davis, R.S., Richards, M.P., 2013. Maritime adaptations and dietary variation in prehistoric western Alaska: stable isotope analysis of permafrost-preserved human hair. Am. J. Phys. Anthropol. 151 (3), 448–461.

Burton, R.K., Snodgrass, J.J., Gifford-Gonzalez, D., Guilderson, T., Brown, T., Koch, P.L., 2001. Holocene changes in the ecology of northern fur seals: insights from stable isotopes and archaeofauna. Oecologia 128 (1), 107–115.

Casey, M.M., Post, D.M., 2011. The problem of isotopic baseline: reconstructing the diet and trophic position of fossil animals. Earth-Sci. Rev. 106, 131–148.

Chisholm, B.S., Nelson, D.E., Schwarcz, H.P., 1982. Stable-carbon isotope ratios as a measure of marine versus terrestrial protein in ancient diets. Science 216 (4550), 1131–1132.

Ciancio, J.E., Pascual, M.A., Botto, F., Frere, E., Iribarne, O., 2008. Trophic relationships of exotic anadromous salmonids in the southern Patagonian shelf as inferred from stable isotopes. Limnol. Oceanogr. 53, 788–798.

Clementz, M.T., Koch, P.L., 2001. Differentiating aquatic mammal habitat and foraging ecology with stable isotopes in tooth enamel. Oecologia 129, 461–472.

Coltrain, J.B., Hayes, M.G., O'Rourke, D.H., 2004. Sealing, whaling and caribou: the skeletal isotope chemistry of eastern Arctic foragers. J. Archaeol. Sci. 31 (1), 39–57.

Coltrain, J.B., Tackney, J., O'Rourke, D.H., 2016. Thule whaling at point barrow, Alaska: the Nuvuk cemetery stable isotope and radiocarbon record. J. Archaeol. Sci. Rep. 9, 681–694.

Cordain, L., Miller, J.B., Eaton, S.B., Mann, N., Holt, S.H.A., Speth, J.D., 2000. Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets. Am. J. Clin. Nutr. 71 (3), 1–11.

Coronato, A., 2014. Territorios fueguinos: fisonomía, origen, evolución. In: Tívoli, A.M., Oría, J. (Eds.), Cazadores de mar y tierra. Estudios recientes en arqueología fueguina. Editora Cultural Tierra del Fuego, Ushuaia, pp. 43–63.

Couve, E., Vidal, C., 2003. Birds of Patagonia, Tierra del Fuego & Antarctic Peninsula: The Falkland Islands & South Georgia. Punta Arenas, Fantastico Sur Birding.

DeNiro, M.J., 1985. Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to paleodietary reconstruction. Nature 317, 806–809.

Erlandson, J.M., 2001. The archaeology of aquatic adaptations: paradigms for a new millennium. J. Archaeol. Res. 9 (4), 287–350.

Falabella, V., Campagna, C., Croxall, J., 2009. Atlas del Mar Patagónico. In: Especies y Espacios. Wildlife Conservation Society y Bird-Life International, Buenos Aires.

Fenucci, J., Virasoro, C., Cousseau, M.B., Boschi, E., 1974. Campaña Tierra del Fuego 74. Informe preliminar (Investigación pesquera). In: Contribuciones del Instituto de Biología Marina. 261. pp. 1–37.

Fernandes, R., 2016. A simple(R) model to predict the source of dietary carbon in individual consumers. Archaeometry 58, 500–512.

Fernández, P.M., Tessone, A., 2014. Modos de ocupación del bosque patagónico de la vertiente oriental de los Andes: aportes desde la Ecología Isotópica. Revista Chilena de Antropología 30, 83–89.

Forero, M.G., Bortolotti, G.R., Hobson, K.A., Donazar, J.A., Bertelloti, M., Blanco, G., 2004. High trophic overlap within the seabird community of Argentinean Patagonia: a multiscale approach. J. Anim. Ecol. 73 (4), 789–801.

France, R.L., 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Mar. Ecol. Prog. Ser. 124 (1–3), 307–312.

Frangi, J.L., Barrera, M.D., Puigdefábregas, J., Yapura, P.F., Arambarri, A.M., Richter, L., 2004. Ecología de los bosques de Tierra del Fuego. In: Arturi, M.F., Frangi, J.L., Goya, J.F. (Eds.), Ecología y Manejo de los Bosques de Argentina. La Plata, Editorial de la Universidad Nacional de La Plata, pp. 1–88.

Froehle, A.W., Kellner, C.M., Schoeninger, M.J., 2010. FOCUS: effect of diet and protein source on carbon stable isotope ratios in collagen: follow up to Warinner and Tuross (2009). J. Archaeol. Sci. 37 (10), 2662–2670.

Froehle, A.W., Kellner, C.M., Schoeninger, M.J., 2012. Multivariate carbon and nitrogen stable isotope model for the reconstruction of prehistoric human diet. Am. J. Phys. Anthropol. 147, 352–369.

Gomez, J.J., Gozzi, A.C., Macdonald, D.W., Gallo, E., Centrón, D., Cassini, M.H., 2010. Interactions of exotic and native carnivores in an ecotone, the coast of the Beagle Channel, Argentina. Polar Biol. 33 (10), 1371–1378.

Griffiths, M.C., 2002. Life history of South African snoek, *Thyrsites atun* (Pisces: Gempylidae): a pelagic predator of the Benguela ecosystem. Fish. Bull. 100, 690–710.

Guichón, R.A., Borrero, L.A., Prieto, A.I., Cárdenas, P., Tykot, R., 2001. Nuevas determinaciones de isótopos estables para Tierra del Fuego. Revista Argentina de Antropología Biológica 3 (1), 113–126.

Gusinde, M., 1951. Hombres primitivos en la Tierra del Fuego: de investigador a compañero de tribu. (Escuela de Estudios Hispano-Americanos).
Hedges, R.E., Reynard, L.M., 2007. Nitrogen isotopes and the trophic level of humans in archaeology. J. Archaeol. Sci. 34 (8), 1240–1251.
Hedges, R.E.M., Clement, J.G., Thomas, C.D.L., O'connell, T.C., 2007. Collagen turnover in the adult femoral mid-shaft: modeled from anthropogenic radiocarbon tracer measurements. Am. J. Phys. Anthropol. 133 (2), 808–816.
Hemminga, M.A., Mateo, M.A., 1996. Stable carbon isotopes in seagrasses: variability in ratios and use in ecological studies. Mar. Ecol. Prog. Ser. 140 (1–3), 285–298.
Heusser, C.J., 1988. Deglacial paleoclimate of the American sector of the Southern Ocean: late glacial–Holocene records from the latitude of canal beagle (55° S), argentine Tierra del Fuego. Palaeogeogr. Palaeoclimatol. Palaeoecol. 141 (3), 277–301.
Hilton, G.M., Thompson, D.R., Sagar, P.M., Cuthbert, R.J., Cherel, Y., Bury, S.J., 2006. A stable isotopic investigation into the causes of decline in a sub-Antarctic predator, the rockhopper penguin *Eudyptes chrysocome*. Glob. Chang. Biol. 12 (4), 611–625.
Hobson, K.A., 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120 (3), 314–326.
Hobson, K.A., Piatt, J.F., Pitoccheli, J., 1994. Using stable isotopes to determine seabird trophic relationships. J. Anim. Ecol. 63, 786–798.
Jack, L., Wing, S.R., 2011. Individual variability in trophic position and diet of a marine omnivore is linked to kelp bed habitat. Mar. Ecol. Prog. Ser. 443, 129–139.
Jochim, M.A., 1998. A Hunter-gatherer Landscape: southwest Germany in the Late Paleolithic and Mesolithic. (Springer Science & Business Media).
Kellner, C.M., Schoeninger, M., 2007. A simple carbon isotope model for reconstructing prehistoric human diet. Am. J. Phys. Anthropol. 133, 1112–1127.
Kusaka, S., Hyodo, F., Yumoto, T., Nakatsukasa, M., 2010. Carbon and nitrogen stable isotope analysis on the diet of Jomon populations from two coastal regions of Japan. J. Archaeol. Sci. 37 (8), 1968–1977.
Link, J., 2002. Does food web theory work for marine ecosystems? Mar. Ecol. Prog. Ser. 230, 1–9.
Lloris, D., Rucabado, J., 1991. Ictiofauna del Canal Beagle (Tierra de Fuego): aspectos ecológicos y análisis biogeográfico. Instituto Español de Oceanografía, Madrid (Publicación Especial 8).
Maschner, H.D., Betts, M.W., Cornell, J., Dunne, J.A., Finney, B., Huntly, N., Jordan, J.W., King, A.A., Misarti, N., Reedy-Maschner, K.L., Russell, R., Tews, A., Wood, S.A., Russell, R., 2009. An introduction to the biocomplexity of Sanak Island, western gulf of Alaska 1. Pac. Sci. 63 (4), 673–709.
McNeil, B.I., Matear, R.J., Tilbrook, B., 2001. Does carbon 13 track anthropogenic CO2 in the Southern Ocean? Glob. Biogeochem. Cycles 15 (3), 597–613.
Méndez, C., Barberena, R., Reyes, O., Nuevo Delaunay, A., 2014. Isotopic ecology and human diets in the Forest–steppe ecotone, Aisén region, central-western Patagonia, Chile. Int. J. Osteoarchaeol. 24, 187–201.
Michener, R.H., Kaufman, L., 2007. Stable Isotope Ratios as Tracers in Marine Food Webs: An Update. In: Michener, R., Lajtha, K. (Eds.), Stable isotopes in ecology and environmental science. John Wiley & Sons, pp. 238–282.
Miller, T.W., Brodeur, R.D., Rau, G.H., 2008. Carbon stable isotopes reveal relative contribution of shelf-slope production to the Northern California Current pelagic community. Limnol. Oceanogr. 53 (4), 1493–1503.
Milner, N., Craig, O.E., Bailey, G.N., Pedersen, K., Andersen, S.H., 2004. Something fishy in the Neolithic? A re-evaluation of stable isotope analysis of Mesolithic and Neolithic coastal populations. Antiquity 78, 9–22.
Minagawa, M., Wada, E., 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochim. Cosmochim. Acta 48 (5), 1135–1140.
Misarti, N., Finney, B., Maschner, H., Wooller, M.J., 2009. Changes in northeast Pacific marine ecosystems over the last 4500 years: evidence from stable isotope analysis of bone collagen from archeological middens. The Holocene 19 (8), 1139–1151.
Moreno, C., Jara, H., 1984. Ecological studies on fish fauna associated with *Macrocystis pyrifera* belts in the south of Fueguian island, Chile. Mar. Ecol. Prog. Ser. 15 (1), 99–107.
Newsome, S.D., Phillips, D.L., Culleton, B.J., Guilderson, T.P., Koch, P.L., 2004. Dietary reconstruction of an early to middle Holocene human population from the central California coast: insights from advanced stable isotope mixing models. J. Archaeol. Sci 31 (8), 1101–1115.
Newsome, S.D., Martínez del Río, C., Bearhop, S., Phillips, D.L., 2007. A niche for isotopic ecology. Front. Ecol. Environ. 5, 429–436.
Newsome, S.D., Clementz, M.T., Koch, P.L., 2010. Using stable isotope biogeochemistry to study marine mammal ecology. Mar. Mamm. Sci. 26 (3), 509–572.
Orquera, L.A., 1999. El consumo de moluscos por los canoeros del extremo sur. XXIV. Relaciones de la Sociedad Argentina de Antropología, pp. 307–327.
Orquera, L.A., Piana, E.L., 1996. El sitio Shamakush I (Tierra del Fuego, República Argentina). XXI. *Relaciones de la Sociedad Argentina de Antropología*, pp. 215–265.
Orquera, L.A., Piana, E.L., 1999a. Arqueología de la región del canal Beagle (Tierra del Fuego, República Argentina). (Sociedad Argentina de Antropología).
Orquera, L.A., Piana, E.L., 1999b. La vida material y social de los Yámana. EUDEBA.
Orquera, L.A., Piana, E.L., 2000. Composición de conchales de la costa del canal Beagle (Tierra del Fuego, República Argentina) -primera parte. XXV. Relaciones de la Sociedad Argentina de Antropología, pp. 249–274.
Orquera, L.A., Piana, E.L., 2001. Composición de conchales de la costa del canal beagle (Tierra del Fuego, República Argentina) -segunda parte. XXV. Relaciones de la Sociedad Argentina de Antropología, pp. 345–368.
Orquera, L.A., Legoupil, D., Piana, E.L., 2011. Littoral adaptation at the southern end of South America. Quat. Int. 239 (1), 61–69.
Panarello, H., Zangrando, A.F.J., Tessone, A., Kozameh, L.F., Testa, N., 2006. Análisis comparativo de paleodietas humanas entre la región del canal Beagle y Península Mitre: perspectivas desde los isótopos estables. Magallania 34 (2), 37–46.
Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. 18 (1), 293–320.
Phillips, D.L., 2012. Converting isotope values to diet composition: the use of mixing models. J. Mammal. 93 (2), 342–352.
Phillips, D.L., Newsome, S.D., Gregg, J.W., 2005. Combining sources in stable isotope mixing models: alternative methods. Oecologia 144, 520–527.
Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., Semmens, B.X., Ward, E.J., 2014. Best practices for use of stable isotope mixing models in food-web studies. Can. J. Zool. 92 (10), 823–835.
Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods and assumptions. Ecology 83 (3), 703–718.
Raya Rey, A., Schiavini, A.C.M., 2000. Distribution, abundance and associations of seabirds in the Beagle Channel, Tierra del Fuego, Argentina. Polar Biol. 23 (5), 338–345.
Riccialdelli, L., Newsome, S.D., Fogel, M.L., Fernández, D.A., 2016. Trophic interactions and food web structure of a subantarctic marine food web in the Beagle Channel: Bahía Lapataia, Argentina. Polar Biol. 40 (4), 807–821.
Richards, M.P., Hedges, R.E.M., 1999. Stable isotope evidence for similarities in the types of marine foods used by late Mesolithic humans at sites along the Atlantic coast of Europe. J. Archaeol. Sci. 26, 717–722.
Richards, M.P., Pettitt, P.B., Stiner, M.C., Trinkaus, E., 2001. Stable isotope evidence for increasing dietary breadth in the European mid-upper Paleolithic. Proc. Natl. Acad. Sci. 98 (11), 6528–6532.
Richards, M.P., Jacobi, R.M., Cook, J., Pettitt, P.B., Stringer, C.B., 2005. Isotope evidence for the intensive use of marine foods by late upper Palaeolithic humans. J. Hum. Evol. 49 (3), 390–394.
Richoux, N.B., Vermeulen, I., Froneman, P.W., 2014. Stable isotope ratios indicate differential omnivory among syntopic rocky shore suspension-feeders. Mar. Biol. 161 (5), 971–984.
Rossman, S., Ostrom, P.H., Gordon, F., Zipkin, E.F., 2016. Beyond carbon and nitrogen: guidelines for estimating three-dimensional isotopic niche space. Ecol. Evol. 6 (8), 2405–2413.
Santiago, F., Vázquez, M., 2012. Dietas promediadas: explorando el registro zooarqueológico supra-regional en Tierra del Fuego. Revista del Museo de Antropología 5, 225–238.
Schiavini, A., 1993. Los lobos marinos como recurso para cazadores-recolectores marinos: El caso de Tierra del Fuego. Lat. Am. Antiq. 4 (4), 346–366.
Schoeninger, M.J., DeNiro, M.J., 1984. Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. Geochim. Cosmochim. Acta 48 (4), 625–639.
Schwarcz, H.P., 1991. Some theoretical aspects of isotope paleodiet studies. J. Archaeol. Sci. 18, 261–275.
Sealy, J., 1986. Stable carbon isotopes and prehistoric diets in the south-western Cape Province, South Africa. In: British Archaeological Reports. Vol. 293.
Sielfeld, W., 1999. Estado del conocimiento sobre conservación y preservación de *Otaria flavescens* (Shaw, 1800) y *Arctocephalus australis* (Zimmermann, 1783) en las costas de Chile. Estudios Oceanológicos 18, 81–96.
Silva, L., Saporiti, F., Vales, D., Tavares, M., Gandini, P., Crespo, E.A., Cardona, L., 2014. Differences in diet composition and foraging patterns between sexes of the Magellanic penguin (*Spheniscus magellanicus*) during the non-breeding period as revealed by $\delta^{13}C$ and $\delta^{15}N$ values in feathers and bone. Mar. Biol. 161 (5), 1195–1206.
Soler, R.E., Martínez Pastur, G., Lencinas, M.V., Borrelli, L., 2012. Differential forage use between large native and domestic herbivores in southern Patagonian Nothofagus forests. Agrofor. Syst. 85, 397–409.
Soler, R.E., Martínez Pastur, G., Lencinas, M.V., Borrelli, L., 2013. Dieta estacional de *Lama guanicoe* (Camelidae: Artiodactyla) en un paisaje heterogéneo de Patagonia Sur. BOSQUE 34 (2), 129–141.
Suby, J.A., Zangrando, A.F., Piana, E., 2011. Exploraciones osteológicas de la salud de las poblaciones humanas del canal Beagle. XXXVI. *Relaciones de la Sociedad Argentina de Antropología*, pp. 249–270.
Szpak, P., Orchard, T.J., Gröcke, D.R., 2009. A late Holocene vertebrate food web from southern Haida Gwaii (Queen Charlotte Islands, British Columbia). J. Archaeol. Sci. 36 (12), 2734–2741.
Szpak, P., Orchard, T.J., McKechnie, I., Gröcke, D.R., 2012. Historical ecology of late Holocene sea otters (Enhydra lutris) from northern British Columbia: isotopic and zooarchaeological perspectives. J. Archaeol. Sci. 39 (5), 1553–1571.
Tauber, H., 1981. ^{13}C evidence for dietary habits of prehistoric man in Denmark. Nature 292, 332–333.
Tessone, A., 2010. Arqueología y Ecología Isotópica. In: Estudio de isótopos estables de restos humanos del Holoceno tardío en Patagonia meridional. Facultad de Filosofía y Letras, Universidad de Buenos Aires (Unpublished PhD Thesis).
Tessone, A., Zangrando, A.F.J., Valencio, S., Panarello, H., 2003. Isótopos estables del carbono en restos óseos humanos de la región del canal Beagle, Isla Grande de Tierra del Fuego. Revista Argentina de Antropología Biológica 5 (2), 33–43.
Tessone, A., Fernández, P.M., Bellelli, C., Panarello, H., 2014. $\delta^{13}C$ and $\delta^{15}N$ characterization of modern Huemul (*Hippocamelus bisulcus*) from the Patagonian Andean Forest. Scope and limitations of their use as a geographical marker. Int. J. Osteoarchaeol. 24, 219–230.
Tivoli, A.M., 2010. Exploitation of bird resources among prehistoric sea-nomad societies of the Beagle Channel region, southern South America. Before Farming 2, 1–12.
Tivoli, A.M., Zangrando, A.F.J., 2011. Subsistence variations and landscape use among maritime hunter-gatherers. A zooarchaeological analysis from the Beagle Channel (Tierra del Fuego, Argentina). J. Archaeol. Sci. 38 (5), 1148–1156.
Tykot, R.H., 2004. Stable isotopes and diet: you are what you eat. In: Martini, M., Milazzo, M., Piacentini, M. (Eds.), Physics Methods in Archaeometry. Società Italiana di Fisica, Bologna, pp. 433–444 (Proceedings of the International School of Physics "Enrico Fermi" Course 154).

Vales, D.G., Cardona, L., Zangrando, A.F.J., Borella, F., Saporiti, F., Goodall, R.N.P., de Oliveira, L.R., Crespo, E.A., 2017. Holocene changes in the trophic ecology of an apex marine predator in the South Atlantic Ocean. Oecologia 183 (2), 555–570.
Weber, A.W., White, D., Bazaliiskii, V.I., Goriunova, O.I., Savel'ev, N.A., Katzenberg, M.A., 2011. Hunter–gatherer foraging ranges, migrations, and travel in the middle Holocene Baikal region of Siberia: insights from carbon and nitrogen stable isotope signatures. J. Anthropol. Archaeol. 30 (4), 523–548.
Winterhalder, B., Smith, E.A., 2000. Analyzing adaptative strategies: human behavioral ecology at twenty-five. Evol. Anthropol. 9, 51–72.
Wolf, N., Carleton, S.A., Martinez del Rio, C., 2009. Ten years of experimental animal isotopic ecology. Funct. Ecol. 23, 17–26.
Yesner, D.R., 1980. Maritime hunter-gatherers: ecology and prehistory. Curr. Anthropol. 21, 727–750.
Yesner, D.R., Figuerero Torres, M.J., Guichón, R., Borrero, L.A., 1991. Análisis de isótopos estables en esqueletos humanos: confirmación de patrones de subsistencia etnográficos para Tierra del Fuego. Shincal 3, 182–191.
Yesner, D.R., Figuerero Torres, M.J., Guichón, R., Borrero, L.A., 2003. Stable isotopes analysis of human bone and ethnohistoric subsistence patterns in Tierra del Fuego. J. Anthropol. Archaeol. 22, 279–291.
Zangrando, A.F.J., 2009a. Historia evolutiva y subsistencia de cazadores-recolectores marítimos de Tierra del Fuego. (Sociedad Argentina de Antropología).
Zangrando, A.F.J., 2009b. Is fishing intensification a direct route to hunter-gatherer complexity? A case study from the Beagle Channel region (Tierra del Fuego, southern South America). World Archaeol. 41 (4), 589–608.
Zangrando, A.F.J., Borrazzo, K.B., Tivoli, A.M., Alunni, D.V., Martinoli, M.P., 2014a. El sitio Heshkaia 35: nuevos datos sobre la arqueología de Moat (Tierra del Fuego, Argentina). Revista del Museo de Antropología 7 (1), 11–24.
Zangrando, A.F., Panarello, H., Piana, E.L., 2014b. Zooarchaeological and stable isotopic assessments on pinniped–human relations in the Beagle Channel (Tierra del Fuego, southern South America). Int. J. Osteoarchaeol. 24 (2), 231–244.
Zangrando, A.F.J., Riccialdelli, L., Kochi, S., Nye, J.W., Tessone, A., 2016. Stable isotope evidence supports pelagic fishing by hunter-gatherers in southern South America during the late Holocene. J. Archaeol. Sci. Rep. 8, 486–491.
Zangrando, A.F.J., Vargas, G.P., Tivoli, A.M., 2017. Decreased foraging return in shell-fishing? Species composition and shell size of blue mussel (*Mytilus edulis*) from a late Holocene site of the south coast of Tierra del Fuego. Quat. Int. 427, 160–169.
Zeanah, D.W., 2004. Sexual division of labor and central place foraging: a model for the Carson Desert of western Nevada. J. Anthropol. Archaeol. 23 (1), 1–32.