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## Decreased foraging return in shellfishing? Species composition and shell size of blue mussel (*Mytilus edulis*) from a Late Holocene site of the South Coast of Tierra del Fuego

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### ABSTRACT

This paper presents a systematic analysis of the shellfish assemblages recovered from Heshkaia 35, an archaeological site located in the southern tip of South America. Possible arguments concerning to environmental variations and resource depression are considered in an attempt to explain taxa composition and shell size. Results are also discussed in light of expectations based on optimal foraging models and taking into account other factors beyond biological parameters. Shellfishing activities were focused on small mussels, with statistical significant changes in mean shell size along the archaeological sequence of the site. Current knowledge about past variations in sea surface temperature does not seem to explain changes in shell size. Gathering of small mussels appears to be the corollary of resource depression at a local scale. This interpretation reinforces arguments that foraging decisions would have derived from territorial packing on the southeastern coast of Tierra del Fuego during the Late Holocene.

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### 1. Introduction

Archaeological arguments about shellfishing behavior are commonly based on taxonomic composition of shell assemblages and average shell size of mollusks. Both aspects are critical for understanding how shellfish were exploited by human societies in the past. Shell remains are ubiquitous in archaeological middens along the south coast of Tierra del Fuego (Orquera and Piana, 1999a, 2009; Zangrando, 2010; Zangrando et al., 2011). Mollusks were key dietary and technological resources in the subsistence of coastal and marine hunter–gatherers through the Middle and Late Holocene. Archaeomalacological studies developed in this region have used diverse analytical techniques for the reconstruction of the importance of shellfish in prehistory as well as for the understanding of shell midden formation (Orquera, 1999; Orquera and Piana, 1999a, 2000, 2001; Colonese et al., 2011; Verdún Castelló, 2011, 2014b; Colonese et al., 2012).

In the recent literature, studies from many parts of the world have identified a reduction in mean shell size, which is considered

as evidence of reduced foraging returns of shellfish (e.g., Raab, 1992; Mannino and Thomas, 2002; Erlandson et al., 2008; Jerardino et al., 2008). These studies are mainly based on the well-established assumptions from evolutionary foraging models. The prey choice model is the most widely used; assuming that foragers are trying to maximize the rate of energy input, the model predicts that they should preferentially pursue resources with higher post-encounter return rates. If higher ranking resources decline, then foragers should respond by taking lower profitability resources. Central place foraging has also been applied to shellfish procurement (e.g., Bird et al., 2002; Codding et al., 2014). These models predict that once a forager has acquired a resource, she or he should take decisions about what is the best strategy to transport that resource to the central place. Under the assumption that foragers are attempting to maximize the rate at which resources are transported to a central place, the model predicts that the individuals may decide to discard low-utility items (e.g., shell) in the field and returning to their central place with only high-utility parts (i.e., edible tissue) than making a greater number of trips delivering both high and low-utility parts. Bird et al. (2002) demonstrate through the Meriam case in Australia that shellfish assemblage composition may vary independently of prey choice model, and show that relatively high-ranked molluscs are likely to be under-represented in residential places while low-ranked shellfish are likely to be over-represented.

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Shell size is imperative for evaluating these basic assumptions. However, marine shells are usually fragmented in archaeological sites of Tierra del Fuego, and the loss of original size of archaeological valves does seriously reduce their potential for the average shell size reconstruction. This condition is commonly observed in many archaeological sites around the world, and archaeologists have applied various methods to reconstruct complete size shells from dimensions of features which survive on fragments (e.g., Buchanan, 1985; Ford, 1989; Jerardino et al., 1992; Jerardino, 1997; Peacock, 2000; Jerardino and Navarro, 2008; Randklev et al., 2009; Yamazaki and Oda, 2009; Faulkner, 2010; Campbell, 2012). Previous studies developed in the north coast of the Beagle Channel have obtained average shell size from several archaeological sites by measuring *in situ* unbroken valves through the excavation of a column section of the shell midden (Orquera and Piana, 2000). Although systematic studies in the region show that this method is useful, variability across space of the archaeological midden cannot be procure (Orquera and Piana, 2000, pp. 254).

The aim of this paper is to test ideas about foraging behavior in shellfishing activities in southern South America through the assessing of the variability in taxonomic composition, fragmentation and shell size in the Heshkaia 35 archaeological site, a blue mussel-dominated shell midden located in the south coast of Tierra del Fuego (Fig. 1). To achieve this objective and considering the background presented above, two methodological requirements are developed. First, the profitability of some Sub-Antarctic shellfish taxa are evaluated and foraging expectations are elaborated for assessing the archaeological evidence. Second, valve and umbo proportions of blue mussel (*Mytilus edulis*) were used to calculate original shell size of archaeological samples by allometric coefficients.

## 2. Current shellfish community at the Heshkaia locality

The south coast of Tierra del Fuego is included in the Patagonian cold estuarine zone (Acha et al., 2004). This marine ecological zone is part of the biogeographic Magellanic Province. A sea surface temperature of 6.5°C (annual average) was recorded in the Beagle Channel, with a maximum of 10 °C in February and a minimum of 3 °C in August (Iturraspe et al., 1989). The sea water salinity varies

from 27 to 31‰. The south coast of Tierra del Fuego is part of the Fuegian Andes environment, and its physical features are composed mainly by Late Jurassic volcanic beds (Lemaire Formation), which are covered by Cretaceous marine rocks (Yahgan Formation) (Kranck, 1932; Caminos, 1980). Pleistocene glacial deposits and Holocene marine terraces are also prominent features of coastal geomorphology (Rabassa et al., 1990).

Today, long stretches of gravel and sandy beaches dominate the coastal environment of the Heshkaia archaeological locality. These beaches are interrupted by rocky ridges (Yahgan Formation) colonized by shellfish communities. The sandy substrate of the subtidal would not have favored the development of these resources, so that the exploitation of shellfish would have been largely conducted on rocky ridges of the intertidal zone. In fact, most mollusk species of economic interest were accessible in the intertidal, an area of easy access to humans (Fig. 2a). Blue mussel (*Mytilus edulis*), Magellan mussel (*Aulacomya ater*) and other small *Brachidontes* mussels (e.g., *Brachidontes rodriguezii*) are the predominant species, which form dense beds covering the rocky shores of the Heshkaia locality (Fig. 2b). These bivalve mollusks, specially the blue mussels, are the most common in shell middens of the south coast of Tierra del Fuego (Orquera, 1999; Orquera and Piana, 2000, 2001; Verdún Castelló, 2011). Gastropod species of economic interest are less abundant and have different distribution in the intertidal. Small groups of limpets, particularly *Nacella deaurata* and *Nacella magellanica*, sea snails (e.g., *Acanthina monodon*) and chitons (*Polyplocophora*) inhabit semi-vertical rocks of the low-intertidal (Fig. 2c). Limpets of the *Fissurella* genus are also presented (Fig. 2d).

Due to the presence of toxic red tide in the region, shellfish community was not exposed to intensive human exploitation over the past two decades. The current representation of sizes in mussels can be used in this manner as a hypothetical parameter for natural populations under non-exploitation conditions. During low tide, it is possible to obtain blue mussels with a wide size range (18–71 mm), with a mean shell size of  $35.8 \pm 5.5$  in the upper intertidal, an average value of  $44.7 \pm 5.4$  in the mid-intertidal, and  $59.6 \pm 5.9$  in the low part of the intertidal (Fig. 3). Since the maximum size recorded for this species is 85 mm, it is possible to suggest that humans could have had an optimal and simple access to this resource in the past. Mussel beds are composed mainly by

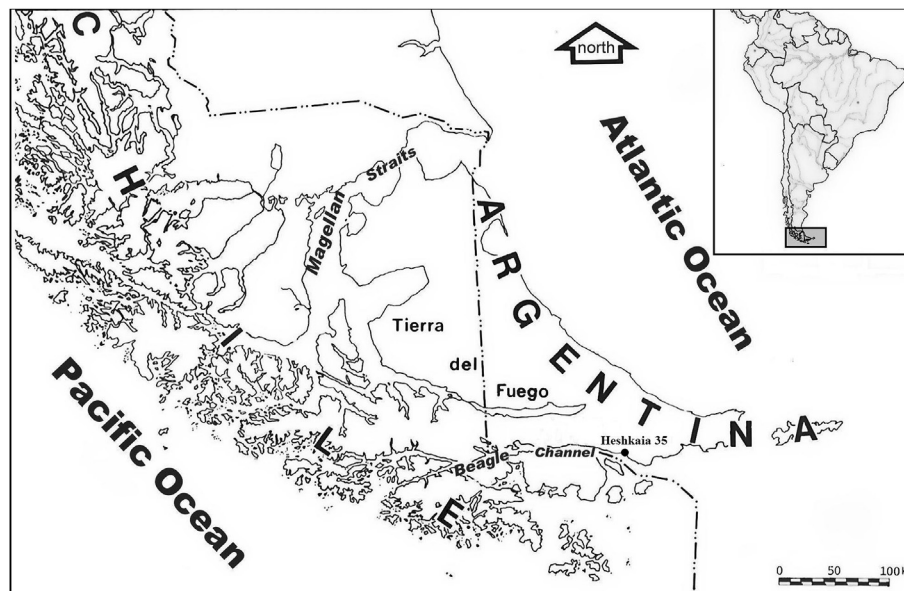


Fig. 1. Geographical location of the Heshkaia 35 archaeological site.



**Fig. 2.** Coastal setting and main shellfish species of the intertidal at the Heshkaia locality: (a) General view of a coast section of the locality with low tide; (b) Beds of mussels covering rocky ridges (yellow scale is equal to 1 m); (c) Group of gastropods in the low intertidal (*Nacella deaurata*, *Nacella magellanica*, and *Acanthina monodon imbricate*); (d) Bed of Chilean blue mussel associated with limpets and one isolated individual of *Fissurella*.

blue mussels, but small *Brachidontes* mussels are also abundant. The size of this species does not exceed 40 mm. Magellan mussels are also present, but normally in small sizes (<50 mm) considering that this species can reach 120 mm.

### 3. Shellfish profitability and archaeological implications

For analyzing the profitability of shellfish, we considered the predictions based on the combined scheme of each taxon post-encounter return rate (Kcal/h), and the likelihood of field processing rate measured through the meat:shell ratio (Coddling et al., 2014). Return rates (Kcal/h) are used to establish a shellfish ranking with the intention of assessing predictions of the prey choice model: if the resource with higher return rate is abundant,

do not affect the returning rates in the transportation to central place. The field processing is unlikely in this situation, both for high- or low-ranking resources. High-ranking taxa with very low meat:shell ratios are not expected to be observed in archaeological assemblages, since their shells should be extracted previous to transportation, even over short transport distances to the central place (Bird and Bliege Bird, 2000). Differences in the frequency of occurrence of present intertidal shellfish species and taxa (Ojeda et al., 2014) may suggest differential encounter rates for shellfish species during foraging activities. Table 1 provides mean values for post-encounter return rates (Kcal/h), meat:shell ratios, and frequencies of occurrence for taxa potentially exploited by the pre-historic inhabitants of Heshkaia. This information is also organized in Fig. 4 following the model proposed by Coddling et al. (2014).

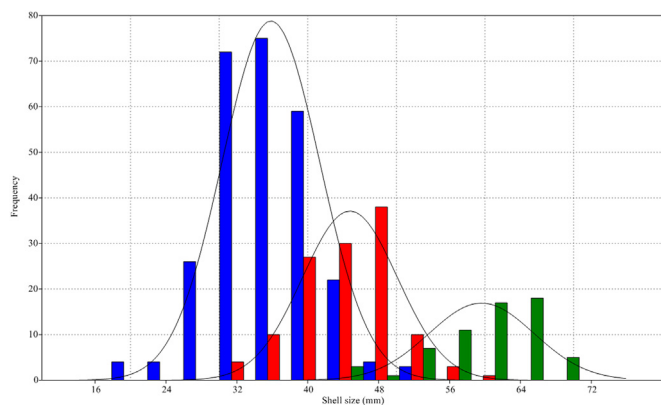
**Table 1**

Data on shellfish returns, meat:shell ratios and frequencies of occurrence ordered by return rate (Kcal/h). Post-encounter return rates (Kcal/h) and transport costs (meat:shell ratio) for limpet, sea snail and blue mussel were calculated considering energy values published by Orquera (1999). We considered proxy data for chitons from Coddling et al., 2014. Encounter rates (frequencies of occurrence) were taken from Ojeda et al. (2014).

Taxa	Common name	Kcal/h	Meat:shell ratio	Frequency of occurrence
Fissurellidae	Limpet	7769	1.97	0.69
Nacellidae	Limpet	2933	1.29	14.50
Muricidae	Sea snail	2197	0.55	2.10
Poliplacophora	Chiton	446–2228	1.16	1.70
Mytilidae: <i>Mytilus edulis</i>	Blue mussel	631	0.12	75.70

then foragers should only take this resource in procurement activities. However, as the availability of the highest ranking resource declines, foragers should start to take lower ranking resources in rank order (Smith, 1983; Bettinger, 1991). Meat:shell ratios can be used in combination with return rates for evaluating predictions of the central place foraging models (Coddling et al., 2014). High meat:shell ratios indicate that low-utility items, shell in this case,

The gastropod *Fissurella* is the taxon with higher post-encounter return rate, thus a high representation in the archaeological middens would be expected. Moreover, given its high meat:shell ratio, completed individuals would also be expected to be transported to the middens proportionally to the frequency with which they are taken. However, this taxon has a low occurrence in the intertidal indicating low encounter rates. Lower ranked taxa, as



**Fig. 3.** Shell size frequencies (lengths) of Chilean blue mussels from three different levels in the intertidal: upper intertidal (blue), middle intertidal (red), and low intertidal (green). Lengths were taken from three samples of two liters. Valve dimensions were measured with digital caliber (0.1 mm). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sea snails (Muricidae) and chitons (Poliplacophora), have also low occurrence; likewise, it is not expected that these taxa dominate shell midden compositions. With similar post-encounter returns to sea snails and chitons but moderate occurrence, limpets (Nacellidae) should come to be more represented in the archaeological record among gastropods. The meat:shell ratios indicate that limpets and chitons are less likely to be field processed than sea snails.

Blue mussels show the lower net utility and the lower meat:shell ratio (Fig. 4). If we only consider post-encounter return rates, this taxon should rarely appear in archaeological middens. However, mussels have by far the higher occurrence in the intertidal zone of the south coast of the Beagle Channel, implying extremely high encounter rates. The information provided above about the current shellfish community at the Heshkaia locality clearly supports this prediction. Given the low return rate of this taxon, field processing is not expected. Since processing times are the same regardless of blue mussel size, smaller individuals indicate reduced foraging return rates (Whitaker, 2008). It seems to be quite apparent in terms of the standard measures. Our experimental work indicates that “large” mussels that are 60 mm long have a post-encounter return rate of 1168 kcal/h, “middle-size” mussels (45 mm) have a return rate of 523 kcal/h, and in “small” mussels

(35 mm) the return rate is 260 kcal/h. Tides on Beagle Channel have a maximum of 1.6 m range (Servicio de Hidrografía Naval, Argentina), so there are no constraints or important differences in terms of costs among various prey sizes during shellfish collecting.

Life-history parameters, such as maturation rates, have also been suggested as a reliable proxy to evaluate human impacts on prehistoric shellfish communities and the relative susceptibility of a taxon to overexploitation (Whitaker, 2008; Coddling et al., 2014; Whitaker and Byrd, 2014). Blue mussels can reach maturity at the first year of age, with 30 mm of shell size approximately (Lasta et al., 1998). First sexual maturity of this taxon has also been recorded for lower shell sizes: 25 mm (Oehrens Kissner and Kroeck, 2005) and 16 mm (Vinueza, 1979). This indicates very rapid maturation rates, implying that blue mussels are resilient to overexploitation.

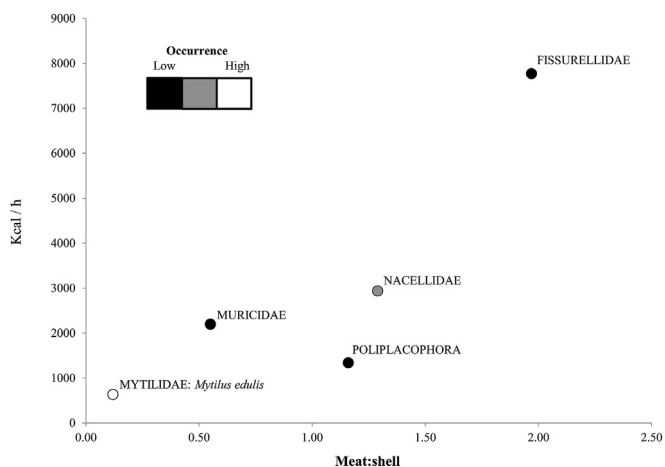
#### 4. Case study

Heshkaia 35 is a shell-bearing midden in the Moat Bay (Tierra del Fuego, Argentina; Fig. 1). It is located at an altitude of 20 m above present sea level and 200 m from the current shore line (54°56'58.9"S–66°49'22.5"W). Heshkaia 35 covers a surface of 120 m<sup>2</sup> and includes a shell mound of 0.6 m of maximum thickness. This site was recently excavated to obtain archaeological and paleoecological information for the area (Zangrando, 2010; Zangrando et al., 2014). One of the purposes was to undertake detailed studies of the abundant shellfish remains present in the site.

##### 4.1. Excavation, stratigraphy and chronology

A total surface of 19 m<sup>2</sup> was excavated to the glacial deposits (till), among which 8 m<sup>2</sup> were excavated over the shell-bearing midden as Trench II (Fig. 5). The excavated material was sieved over 1.5 mm mesh.

Five main stratigraphical layers were observed. Layers A and B were defined according to the natural horizons of the present soil (8 cm thick): Horizon A with a high dense of roots and accumulation of organic material (e.g., tree leaves, bark pieces), and Horizon B characterised by a dark brown silt matrix. Archaeological materials are presented in Layer B. Layer C is a superimposed series of 10 dense shell-bearing middens. Three radiocarbon dates, two from the bottom of the layer (656 ± 35 [AA90434] -charcoal- and 499 ± 37 [AA103903] -guanaco bone-) and another from the top (532 ± 35 [AA98121] -charcoal-), have been obtained indicating



**Fig. 4.** Relationship between post-encounter return rates and meat:shell ratio according to the information presented in Table 1. Frequencies of occurrence are indicated from low (black) to high (white).



**Fig. 5.** Picture showing shellmidden at Trench II of Heshkaia 35.

that the formation of the shell bearing midden took place between 650 and 500 cal years BP (Calib 6.0 [2 $\sigma$  – SHCal04], McCormac et al., 2004). Abundant archaeological materials were recovered along the whole sequence (Alunni and Zangrando, 2012; Zangrando et al., 2014). The glacial deposit (till) was defined as Layer T and it was archaeologically infertile.

#### 4.2. Sampling

Bulk samples of sediments were obtained from contiguous sectors of Trench II for each stratigraphical subunit of Layer C to assess variability of shellfish composition across space. Ten samples with an original volume of around 4 L were sorted in laboratory through the following steps: 1. Drying of sediments; 2. Measuring of weight of the total samples; 3. Sieving over a 1.5 mm mesh and sorting out the different components: shell remains, sediment, charcoal, bone remains and artefacts; and 4. Measuring of weight of each of the separate elements.

Weight frequencies of the main shell midden components are shown in Table 2. In general, shell content predominates over fine sediment and other elements which are included in the deposits. Higher frequencies of fine sediment are observed in C20 and C30, which is something expected considering that those are the sub-superficial stratigraphic units in contact with the Layer B (current soil).

**Table 2**  
Weights (g) and relative frequencies (%) of the main shell midden components.

Samples	Shell		Sediment (fine)		Sediment (gravel)		Charcoal		Bone		Total Weight (g)
	Weight (g)	%	Weight (g)	%	Weight (g)	%	Weight (g)	%	Weight (g)	%	
C20	992.6	37.2	1578.6	59.2	52.1	2.0	36.5	1.4	7.6	0.3	2667.4
C30	955.0	40.4	1306.7	55.3	46.0	1.9	53.2	2.3	1.7	0.1	2362.6
C40	1407.4	55.1	1065.4	41.7	28.7	1.1	49.6	1.9	3.9	0.2	2554.9
C50	1078.3	44.2	1246.6	51.1	40.9	1.7	69.7	2.9	3.9	0.2	2439.4
C70	1658.2	65.1	820.9	32.2	19.4	0.8	45.6	1.8	3.9	0.2	2547.9
C80	1677.2	59.2	1051.5	37.1	39.2	1.4	63.5	2.2	2.5	0.1	2833.8
C100	1132.3	46.2	1248.1	50.9	5.1	0.2	58.4	2.4	9.6	0.4	2453.5
C120	1733.5	59.3	1134.3	38.8	5.9	0.2	47.6	1.6	3.8	0.1	2925.1
C140	1750.9	59.7	1117.7	38.1	6.12	0.2	52.8	1.8	6.2	0.2	2933.7
C150	1597.4	54.7	1232.4	42.2	14.7	0.5	73.5	2.5	2.1	0.1	2920.1
General	13982.6	52.5	11802.2	44.3	258.1	1.0	550.4	2.1	45.2	0.2	26638.5

## 5. Methods

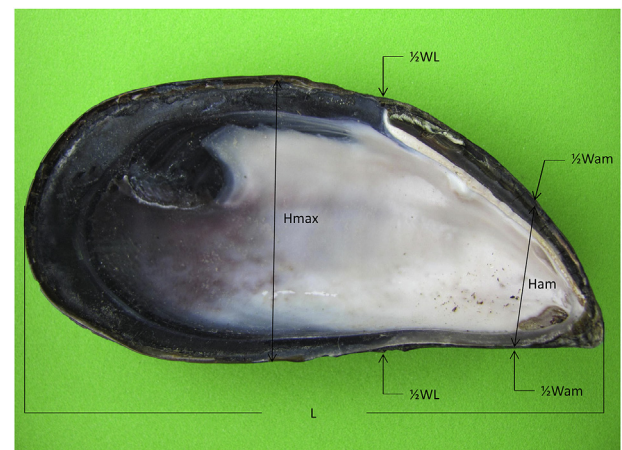
Whole specimens and fragments of shell remains were identified wherever possible to generic or specific level, and minimum number of individuals (MNI) were established for each taxon. For bivalves, the highest number of either left or right hinges was considered to determine the MNI. For gastropods, the number of apices was counted. For chitons, the highest number either anterior or posterior valves was used to establish the MNI.

Completeness and fragmentation indices were assessed to evaluate the preservation status of the blue mussel specimens. The former was determined for each umbo, according to the remaining valve, as follows: “complete or almost complete” (approximately 90% of valve remaining), “partially fragmented” (nearly to 60% of valve remaining), and “highly fragmented” (about 30% of valve remaining). Applying the method of Zohar et al. (2001) for fish-bones, weighted mean indexes [WMI =  $\Sigma (Wi \cdot Xi) / 100$ ] were calculated to standardized the degree of completeness for umbones from each stratigraphical subunits of Layer C, where (Wi) is the relative frequency of umbones and (Xi) represents each fragmentation categories. The fragmentation index was determined by the ratio between the weight of fragments and the total weight of blue mussel shell remains; values near to 0 indicate very low rate of

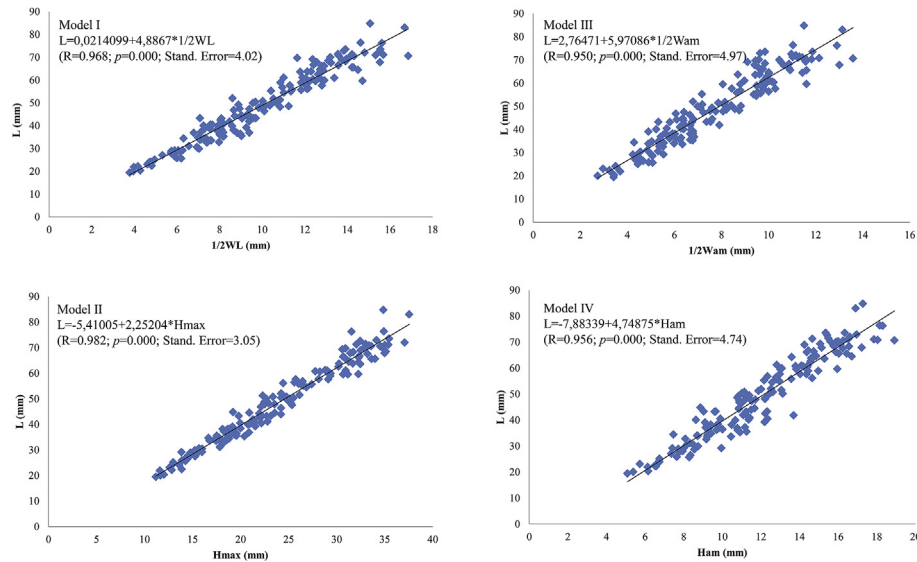
fragmentation, while values near to 1 show that the assemblage is highly fragmented.

Metrical data on blue mussel shells were partially obtained by measuring the total length of unbroken shells. However, in this case study, the high degree of fragmentation did not allow to acquire size observation from all the shells. Size ranges of mussels can be obtained from archaeological samples by measuring the maximum prismatic band width of valves (Buchanan, 1985). But this technique was recently evaluated in *Mytilus edulis*, and it was shown that prismatic band width had no capacity to predict shell length (Campbell, 2012, pp. 97–101). Following the proposal of Campbell (2012; see also Campbell, 2014; Campbell, 2015), valve and umbo dimensions of *Mytilus edulis* were used here to predict original length of archaeological samples by allometric coefficients. Other regression-based approaches have been recently developed on *Mytilus californianus* shell dimensions from archaeological site located on the Pacific Coast of North America (Campbell and Braje, 2015; McKechnie et al., 2015; Singh and McKechnie, 2015).

Three valve dimensions were measured with digital caliber (0.1 mm) (Fig. 6): shell length (L), shell height (Hmax) and maximum valve width ( $\frac{1}{2}$ WL). Two dimensions near the umbo were measured by the same system: the height of the umbo (Ham) at the cross-section at the posterior ends of anterior muscle scars and the valve width at anterior muscle cross-section ( $\frac{1}{2}$ Wam). The allometric relationships between shell length with each one of the other



**Fig. 6.** Picture of blue mussel valve showing dimensions measured (following Campbell, 2012). References: Shell length (L); shell height (Hmax); maximum valve width ( $\frac{1}{2}$ WL); height of the umbo (Ham); anterior muscle cross-section ( $\frac{1}{2}$ Wam).



**Fig. 7.** Allometric relationships between shell length with each one of the other valve and umbo dimensions of the Chilean blue mussel;  $N = 160$ , all measurements in XY axes are expressed in mm.

valve and umbo dimensions were analyzed separately with linear regression. Four models were established with strong relationships and statistically significant (Fig. 7). Models based on umbo dimensions (Models III and IV; Fig. 7) appear to be very convenient for highly fragmented shell middens, however they depend on the good identification of the anterior muscle scars. The recognition of these features was difficult in shell samples of Heshkaia 35: as most of the interior valves were eroded, the muscle scars were difficult to recognize. Measurements by the maximum valve width at posterior edge of ligament (Model I) allowed to obtain a higher amount of measurements than the maximum shell height (Model II) which was more constrained by the shell completeness.

frequency in the top layers (C20–C80), but without dominating the shell middens. Limpets have moderate to low frequencies along the stratigraphical sequence; the highest frequency (nearly 25%) of this resource is recorded in the topmost layer (C20). Sea snail frequencies show a moderate increase in C100. The gastropod *Fissurella*, small gastropods (*Siphonaria* sp. and *Pareuthria plumbea*), and chitons have low frequencies throughout the sequence. Following the interpretation of Whitaker (2008) for small shells, valves of *Siphonaria* sp. and *Pareuthria plumbea* can be considered “riders” in the usual zooarchaeological sense (Binford, 1978), and they should not be pondered as food resources.

**Table 3**  
Taxonomic composition of Layer C by MNI values.

Samples	Bivalvia			Gastropoda					Chiton (Poliplacophora)	Total	
	Mytilidae		Magellan mussel ( <i>Aulacomya ater</i> )	Nacellidae		<i>Siphonaria</i> sp.	Limpet ( <i>Fissurella</i> sp.)	Sea snail ( <i>Muricidae</i> : <i>Acanthina monodon</i> )			Buccinidae: <i>Pareuthria plumbea</i>
Blue mussel ( <i>Mytilus edulis</i> )	Small Brachidontes mussel ( <i>Brachidontes</i> sp.)	Limpet ( <i>Nacella deaurata</i> )		Limpet ( <i>Nacella magellanica</i> )							
C20	97	95	1	42	26	0	1	3	0	6	271
C30	207	73	0	10	12	14	0	5	0	1	322
C40	359	155	0	35	23	5	1	14	0	3	595
C50	269	93	1	19	20	21	3	5	0	4	435
C70	392	178	0	54	60	5	2	5	0	1	697
C80	342	179	0	11	16	11	2	3	1	1	566
C100	76	7	1	7	7	0	1	28	0	2	129
C120	323	39	2	20	18	11	3	1	0	1	418
C140	476	56	0	5	5	15	1	5	0	1	564
C150	332	21	1	5	4	8	0	5	0	2	378
Total	2873	896	6	208	191	90	14	74	1	22	4375

## 6. Results

MNI values are shown in Table 3. Blue mussel is the dominant species throughout the Heshkaia 35 sequence, with higher frequencies (77–84%) in basal subunits (C120, C140 and C150). In upper layers (C20–C100) blue mussel frequencies show a moderate drop (36–64%). Small *Brachidontes* mussels increase in

Completeness values (WMI) of blue mussel shells do not show significant variation in the stratigraphy of Layer C, with frequencies ranging between 31.2 and 44.3. Basing on the weights of all shell remains, fragmentation indexes display more differences among the distinct subunits providing values between 0.44 and 0.89 (Table 4). Subunits C20, C30 and C100 present the lower completeness values combined with the higher fragmentation indexes.

**Table 4**  
Fragmentation indices from different stratigraphic units of Layer C; \* Weighted Mean Index.

Stratigraphical subunits	Frequency of umbones (%) by fragmentation categories			WMI*	Umbone weight (g)	Fragment weight (g)	Total weight (g)	Fragmentation index
	90%	60%	30%					
C20	1.0	2.1	96.9	31.2	45.5	170.8	216.3	0.79
C30	1.0	2.9	96.1	31.4	118.6	360.4	479.0	0.75
C40	10.0	11.7	78.3	39.5	346.2	466.6	812.8	0.57
C50	1.1	4.8	94.1	32.1	199.2	391.2	590.4	0.66
C70	16.3	15.1	68.6	44.3	444.9	355.8	800.7	0.44
C80	9.4	11.7	78.9	39.1	364.2	632.1	996.3	0.63
C100	1.3	1.3	97.4	31.2	49.3	395.6	444.9	0.89
C120	3.4	4.3	92.3	33.3	335.1	789.8	1124.9	0.70
C140	4.0	7.6	88.4	34.7	444.1	730.8	1174.9	0.62
C150	2.4	5.4	92.2	33.1	297.8	749.2	1047	0.72

Mean shell sizes ( $\pm$ SD) of the blue mussel individuals for each stratigraphical layer are presented in Table 5. The general mean shell size recorded for the site is  $31.7 \pm 7.1$  mm. The biggest shell sizes are recorded at the base of the deposit and the smallest one in the topmost layer. The non-parametric Kruskal–Wallis test shows that the mean sizes of blue mussel decrease significantly from the bottommost layers to the upper units of Layer C ( $p = 0.000$ ), denoting statistically significant differences between the cluster comprised by the three lowest units (C120, C140 and C150) and the superior levels. However, the low number of measurements obtained for C20, C30 and C100 subunits can be ascribed to differences in shell preservation and could biased the statistical results about mean mussel size between lower and superior levels.

**Table 5**  
Mean shell size ( $\pm$ SD) on blue mussel for the different stratigraphic units of Layer C; lengths were calculated by Model I (see Fig. 6).

Subunit	N	Mean (mm)	SD $\pm$	Max. (mm)	Min. (mm)
C20	3	27.70	5.05	32.93	22.84
C30	8	31.75	3.51	36.74	25.09
C40	78	30.67	6.65	47.52	15.27
C50	16	34.12	5.83	42.05	23.14
C70	123	29.61	6.67	45.52	14.51
C80	72	30.76	6.45	42.93	15.93
C100	2	30.37	3.19	32.63	28.12
C120	25	34.29	8.62	60.23	20.72
C140	55	34.12	6.16	48.28	21.38
C150	26	37.79	9.37	56.02	13.31
General	408	31.65	7.14	60.23	13.31

## 7. Discussion

Procurement of shellfish was narrowly focused on low-ranking mussels at Heshkaia 35. Extremely low frequencies of Fissurellidae do not match with predictions derived from the post-encounter return rates and meat:shell ratios (see Table 1 and Fig. 4). However, it cannot be founded surprising if we considered the extremely low frequencies of occurrence of that taxon in comparison to those of lower ranked shellfish. Limpets (Nacellidae), with high post-encounter return rates are less represented in the archaeological deposit than bivalves, but again this seems to find an explanation in its lower encounter rate. Sea snails (Muricidae) and chitons (Poliplacophora), with slightly high return rates than mussels, have also very low occurrences in the intertidal, which can also explain the low representations of those shellfish in the shell assemblage of Heshkaia. It is noteworthy that meat:shell ratios of gastropods do not justify field processing for transportation to the site. Thus, the low frequencies recorded along the

whole sequence of Heshkaia 35 (Table 3) appear to represent proportionally the amount of shellfish taken in procurement activities, and the composition of shell assemblages appears to do not be biased by differential transportation of shell material. Results show that shellfish exploitation was shaped by the encounter rates of the different taxa, and not mainly by their post-encounter return rates (Kcal/h) and meat utilities. Thus, since higher ranked taxa (gastropods) continue to appear in shell assemblages in similar proportions to their occurrence in the intertidal, the focused exploitation on blue mussels is not necessary the byproduct of a decreased foraging return in shellfish collecting.

Other factors may have also influenced the shellfish collecting during the occupations of Heshkaia. Some studies have pointed out that not in all conditions the net caloric return for larger individuals exceed the net caloric return for smaller individuals (e.g., Bird and Bliege Bird, 1997; Whitaker, 2008). This perspective ponders shellfishing as part of a broader system of foraging decisions, where a very low-risk practice can be performed by women with young children, children and the elderly (Whitaker and Byrd, 2014). The example of shellfishing among the Meriam foragers is illustrative: children take lower profitability resources because they have slower walking speeds than adults, which results in them having lower encounter rates with highly profitable resources (Bird et al., 2002; Bliege Bird and Bird, 2002). Similarly, young foragers could have experienced different constraints than adults in Tierra del Fuego during shellfish collecting. While mussels can be easily recovered by hand without much effort, limpets require the use of sticks, more effort and skill. This difference in the harvesting strategy of shellfish is well documented in ethnographic documents (Orquera and Piana, 1999b, pp. 162–170). If young foragers contributed actively in collecting practices at the Heshkaia locality, then the deposition of mussels in the shell assemblage of Heshkaia 35 would have seen favored by social factors.

The analysis shows that shellfish exploitation at the Heshkaia 35 site focused on small blue mussel sizes (Table 4). This condition can be viewed as the result of climatic and/or anthropogenic resource depression. The growth rates of open coast mollusc species are influenced by the sea surface temperature (SST), being relatively low temperature conditions physiologically more efficient, while conversely relatively warm SST would slow growth rates (Jerardino, 1997). Middle-Late Holocene sea surface temperature records for the south coast of Tierra del Fuego have been obtained from *M. edulis* (Obelic et al., 1998) and *Retrotapes exalbidus* (Gordillo et al., 2015) shells. Lowest average sea surface temperatures are reached at near 6000 BP and from 500 to 100 BP; the last event coincides with the period known as Little Ice Age in the North Hemisphere. Relatively warmer temperatures were recognized at 4500 BP, 2300 BP, and again between 1000 and 500 BP which coincides with the Medieval Climate Optimum. Shellfish gathering at

Heshkaia 35 site took place in this last period and it seems likely that the warmer sea surface temperatures would have affected the growth rate of blue mussel. However, higher shell sizes of mussels have been reported for other archaeological deposits of the region with similar datings (Orquera and Piana, 2000, 2001; see below). Gordillo et al. (2010) have analyzed Holocene mollusk assemblages from the Beagle Channel, assessing richness and taxonomic abundance and various taphonomic attributes. These authors pointed out that the differences between assemblages do not correlate with climate changes that occurred during the Mid-Late Holocene, but reflect local differences due to microhabitat heterogeneity. Although further evaluations between local paleoenvironment information and its relationship to intertidal gathering strategies should be performed in future investigations, there do not appear to occur co-variation between SST and shellfish community along the Holocene. Additional environmental conditions, such as re-configuration of the coastal morphology or changes in water turbidity due to sea level changes, can also influence shellfish growth rates (Jerardino, 1997; Erlandson et al., 2008). However, considering that the chronology of Heshkaia 35 site indicates that occupations occurred during the final Late Holocene, it is not expected that the paleogeographic conditions of the locality have been extremely different from its current setting.

Basing on the assumption that intense predation by humans can reduce the mean size of many mussel species, ancient human impacts on marine shellfish communities have been reported from many parts around the world (e.g., Raab, 1992; Mannino and Thomas, 2002; Erlandson et al., 2008; Jerardino et al., 2008). This brings up the question whether the evidence from Heshkaia 35 would show such a process. Due to the fact that human population growth is one of the most important cause of increased predation pressure and over-exploitation of shellfish, assessing these processes through broad areas and relatively long periods is convenient for understanding this particular case study. Investigations developed by Luis Orquera and Ernesto Piana (1999a, 2000, 2001) report mean shell sizes of blue mussels for several archaeological sites located within 90 km from Heshkaia 35 westward. Average shell sizes of 40.2 mm (Túnel I, Layer D) and 49.3 mm (Imiwaia I) are observed for Middle Holocene contexts, while a broader range of mean shell sizes is recorded for sites of the Late Holocene: Túnel II (32.0 mm) and Shamakush I (40.2 mm) around 1000 BP, and Shamakush X (47.8 mm) and Túnel VII (33.4 mm) between 500 and 100 BP (Orquera and Piana, 2001, Table XIII). Verdún Castelló (2014a) reports a mean shell size of 35.3 mm for blue mussels from the Lanashuaia I site, which is dated in 100 BP. The average shell size reported for Heshkaia 35 (31.6 mm) is equivalent to those observed in some late archaeological contexts of the south coast of Tierra del Fuego. According to this information, small mean shell sizes are only detected during the Late Holocene, but also large blue mussels continue to appear in other archaeological contexts of that same time period. Orquera and Piana (2001) have previously suggested for the Beagle Channel that no temporal trend is observed at a regional scale towards a reduction in sizes of blue mussel shells along the Holocene.

But, if the abundance of larger blue mussels did not virtually decline through time, why did foragers acquire small blue mussels at Heshkaia 35? Archaeological sites at the southeast coasts of Tierra del Fuego appear to increase in density during the late Holocene with an agglutinated pattern, implying a more intensive use of coastal settings by foragers (Zangrando et al., 2009). Although it is difficult to prove archaeologically, the existence of territories in the southeast of Tierra del Fuego is well-documented in the historical sources (e.g., Gusinde, 1990: 397–406). The ethnographic record for the 19th century indicates that the *Haush* society was organized by local territorial areas, thus establishing the exclusive rights for foraging activities of each lineage (Gusinde, 1990: 402).

The boundaries of each territory were fixed by tradition and, though they were not always respected, the transgression of these limits was a major cause of conflict between the different lineages in this society (Gusinde, 1990: 402).

Accordingly to the central-place foraging models, we assume that the location of settlements was chosen to obtain the highest combined return rates from the use of different patches. With the exception of pinniped or seabird colonies, it is not possible to predict the location of hunting preys in the coastal environment of southern Tierra del Fuego. However, it is possible in the case of sessile shellfish, similarly to what occur in case of plants (e.g., Zeanah, 2002, 2004). Thus, if activities at a coastal site were oriented towards the exploitation of shellfish and terrestrial mammals, it is expected that the settlement would be located close to the shore, to reduce the transport distance of the shellfish. Considering mollusks more like plants than animal resources, Whitaker and Byrd (2014) have recently proposed that low-ranked shellfish in archaeological contexts of the California coast should be understood as part of intensified subsistence economies by shrinking foraging territories. This could be an important point for understanding this case study as well.

In the southern of Tierra del Fuego, coastal environments might be seen as “linear routes” along which forager mobility occurred (Zangrando et al., 2009). The subsistence strategies of these human groups might involve the “following” of depleted shellfish beds by switching foraging activities between alternative coastal localities (Yesner, 1987). Considering that blue mussels are capable of reproduction at 30 mm in length, 12 months after growth begins, their populations could recover at fast rates (see Whitaker, 2008). Therefore, it is possible to argue that small shell size represented at Heshkaia 35 could indicate local coastal resource depression in shellfishing, whose cause could be seen as “driven” by periodical movements along coasts within local territories areas and not necessary as part of a long-term overexploitation.

## 8. Summary and conclusion

Predictions based on the post-encounter return rates (Kcal/h) and the likelihood of field processing rates (meat: shell ratio) indicate that limpets (Fissurellidae and Nacellidae) were expected to be highly represented in the archaeological record of Tierra del Fuego. As we have seen, Heshkaia 35 presents a shellfish assemblage dominated by blue mussels, which has the lower post-encounter return rate and a very reduced meat:shell ratio. Overall, the presented data provide good evidence that the exploitation of shellfish was mainly shaped by the differences among taxa in encounter rates, than by their differences in post-encounter return rates.

Blue mussel shell sizes obtained from whole and fragmented shells using Model I show small shell sizes in the sample. Moreover, significant statistical results indicate a decrease in blue mussel size through the archaeological sequence of the site. The overall mean shell size suggests that gathering activities on mussels have performed under a decreased abundance of higher shell size all along the stratigraphical sequence. Relatively warm sea surface temperatures recorded between 1000 and 500 BP would set up conditions of slow growth rates for the region. However, considering that large shell sizes of blue mussels continue to appear in other archaeological contexts of the south coast of Tierra del Fuego during that period, resource depression due to environmental change does not appear presumable. Similarly, in light of information from several other shellfish assemblages already recovered from nearby localities at the Beagle Channel, resource depression due to human growth population is not either decisive. We conclude that the observed small shell size may result from a reduce depression in blue mussels occurred at a local scale related to a more intensive



use of the southeastern coastal space of Tierra del Fuego by foragers. Further comprehensive studies investigating the range of species composition and shell sizes from other archaeological contexts in the Heshkaia locality are however needed to achieve more accurate results and to verify this postulation.

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