



# Stable oxygen isotope analysis of *Phorcus lineatus* (da Costa, 1778) as a proxy for foraging seasonality during the Mesolithic in northern Iberia

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## Abstract

The Mesolithic period in the Cantabrian region, a coastal area located in northern Spain, is characterised by a marked increase in the human use of coastal resources in comparison with previous periods, resulting in the formation of so-called “shell middens”. Archaeological investigations have provided insights into the formation processes of these shell middens, as well as long-term changes in human exploitation of different marine resources and the relationship of foraging strategies to past climate changes. However, efforts to reconstruct the key environmental factor governing coastal subsistence and foraging resilience, the seasonal availability and use of different marine resources, have been limited in the region and, indeed, across coastal Mesolithic Europe more widely. Here, we use stable oxygen isotope analysis of *Phorcus lineatus* (da Costa, 1778), one of the most widespread molluscs in northern Iberian mesolithic coastal sites, in order to determine the season in which humans collected key coastal resources at the site of EL Mazo (Llanes, Asturias). We demonstrate that *P. lineatus* was exclusively collected in late autumn, winter and early spring. An experimental programme, in which modern *P. lineatus* specimens were collected in situ over the course of three years, established that relative meat yield varied within this species throughout the annual cycle, with higher relative meat yield during colder months. We argue that mollusc collection patterns were driven by a cost-benefit principle during the Mesolithic in the Cantabrian region and human populations had intimate knowledge of the seasonal developmental cycles of exploited marine taxa. This also highlights the importance of developing intra-annual records of resource use and climate change if coastal foraging is to be properly understood in prehistory.

**Keywords** Mesolithic · Shell middens · Cantabrian region · Seasonal subsistence · Stable oxygen isotopes · Relative meat yield

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Asier García-Escárzaga and Igor Gutiérrez-Zugasti are co-first authors.

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## Introduction

The Mesolithic period of Europe is renowned for its diversity of hunter-gatherer adaptations, technological strategies and human responses to climatic fluctuations across the Pleistocene–Holocene boundary (Holst 2010; Mannino et al. 2011; Mason 2000; Richards et al. 2003). In particular, one of the main features of the Mesolithic in Atlantic Europe is the observed increase in coastal resource exploitation when compared to previous periods, leading to the formation of often-massive archaeological shell middens near the seashore in Denmark, France, the British Isles and the Iberian Peninsula (Andersen 2007; Dupont et al. 2009; Milner et al. 2007). The Cantabrian region, a coastal area located in northern Iberia (Fig. 1), is one of the littoral areas with a higher density of Mesolithic shell middens (Arias et al. 2015; Fano *in press*; Gutiérrez-Zugasti et al. 2011) in Atlantic Europe. In this region, the Mesolithic is dated between ca. 10,700 and ca. 6,700 cal BP. Cantabrian shell midden sites are mainly composed by four marine gastropod species: *Phorcus lineatus* (da Costa, 1778) and three species of limpets (*Patella vulgata* Linnaeus, 1758, *Patella depressa* Pennant, 1777 and *Patella ulysiponensis* Gmelin, 1791) (Gutiérrez-Zugasti 2009).

Since the beginning of Mesolithic research in the Cantabrian region, in the first decades of the twentieth century (Vega del Sella 1914, 1923), our knowledge of the *modus vivendi* of the last hunter-fisher-gatherers has increased notably (Bailey 1973; Clark 1976; González-Morales 1982; Straus and Clark 1986). In the last decades, new studies have further defined the main characteristics of coastal resource exploitation patterns during the Mesolithic, including variations in the choices of certain taxa, mobility strategies practiced among different foraging groups and the responses of subsistence adaptations to past climate variability (Álvarez-Fernández 2006, 2011; Álvarez-Fernández et al. 2013; Cuenca-Solana 2013, 2015; Fano *in press*; Gutiérrez-Zugasti 2011a, 2011b; Gutiérrez-Zugasti et al. 2016; Rigaud and Gutiérrez-Zugasti 2016). Nevertheless, a key parameter determining the resilience and nature of marine foraging, namely the seasonality of shellfish collection, has been relatively neglected due to a lack of application of appropriate proxies. This is despite the fact that determining seasonal strategies is essential to understand processes of intensification of coastal resource exploitation and management and their relationship to wider climatic dynamics, in a given region.

Stable oxygen isotope analyses of carbonates are being increasingly applied to marine mollusc shells as a means of reconstructing the seasonality of shell collection in coastal locations in Europe and beyond (Colonese et al. 2009; Mannino et al. 2003, 2011; Prendergast et al. 2016). This methodology is based on the fact that molluscs form their shells by precipitating calcium carbonate in (or close to) isotopic equilibrium with the surrounding environment. Under these conditions, the

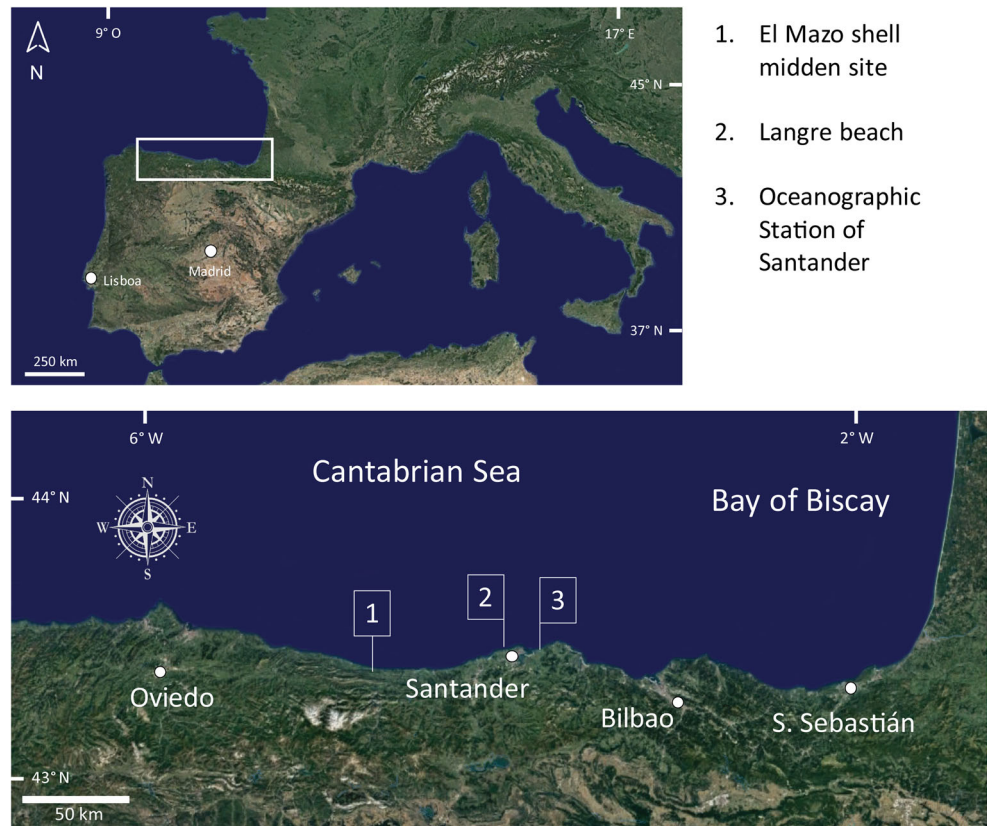
oxygen isotope ratios ( $\delta^{18}\text{O}_{\text{shell}}$ ) are dependent on the sea surface temperature (SST) and the oxygen isotope ratio of the water ( $\delta^{18}\text{O}_{\text{water}}$ ) (Urey 1947; Owen et al. 2002; Wanamaker et al. 2007). Therefore, if  $\delta^{18}\text{O}_{\text{water}}$  values are known, it can be estimated or can be assumed to have not changed significantly during shell growth, and if detailed calibration studies have been performed using modern specimens, the  $\delta^{18}\text{O}_{\text{shell}}$  values can be used to accurately establish past SST during the mollusc life span. With seasonal patterns in temperature established for a given species and region,  $\delta^{18}\text{O}_{\text{shell}}$  data from the final few growth increments leading up to the death of archaeologically deposited shells can reveal the season of shell collection by humans (Andrus 2011). Given a robust sample size, this data provides population-level insights into seasonal marine resource exploitation practiced by humans and their relationship to external changes in marine environments.

Stable oxygen isotope analyses of mollusc remains have been applied to sites in the Cantabrian region since the 1980s, with results suggesting that the  $\delta^{18}\text{O}_{\text{shell}}$  of the mollusc *P. lineatus* reliably records SST and the season of collection (Bailey et al. 1983; Deith 1983; Deith and Shackleton 1986). However, previous archaeological studies have been based on a small number of sub-fossil mollusc specimens, and the archaeological middens studied have lacked robust, well-dated stratigraphic sequences. This has left broader population-level trends in foraging season difficult to discern and has precluded the attainment of information relating to short-term changes (if any) in seasonal coastal resource exploitation over the course of the Mesolithic. Moreover, these isotopic studies were never accompanied by detailed sclerochronological analyses on modern specimens, a key aspect to fully understand the shell growth patterns of this species in the Cantabrian coast as revealed by Gutiérrez-Zugasti et al. (2015) and García-Escárcaga et al. (*in press*). Here, we present the results of stable oxygen isotope analysis of *P. lineatus* recovered from different, accurately radiocarbon dated stratigraphic units at El Mazo shell midden site (Asturias, northern Iberia). The long period of accumulation of this midden (ca. 1,500 years), combined with new experimental insights, yields the opportunity to study prehistoric seasonal variations in mollusc exploitation through time in this part of the world.

## El Mazo shell midden site

El Mazo cave is located in the small town of Andrín in the municipality of Llanes, Asturias (Spain) (Fig. 1). The current distance from the site to the coastline is around 1 km (Fig. 2a). During the Mesolithic, this distance would have varied due to sea level changes. An overall analysis of the Cantabrian coast (Leorri et al. 2012) indicates that this distance would never have been larger than 5 km during the Mesolithic, probably ranging between 3 and 2 km during the time interval of the formation of the El Mazo shell midden (Gutiérrez-Zugasti and

**Fig. 1** Location of the study area in the Cantabrian region, northern Spain (maps modified from Google Earth)

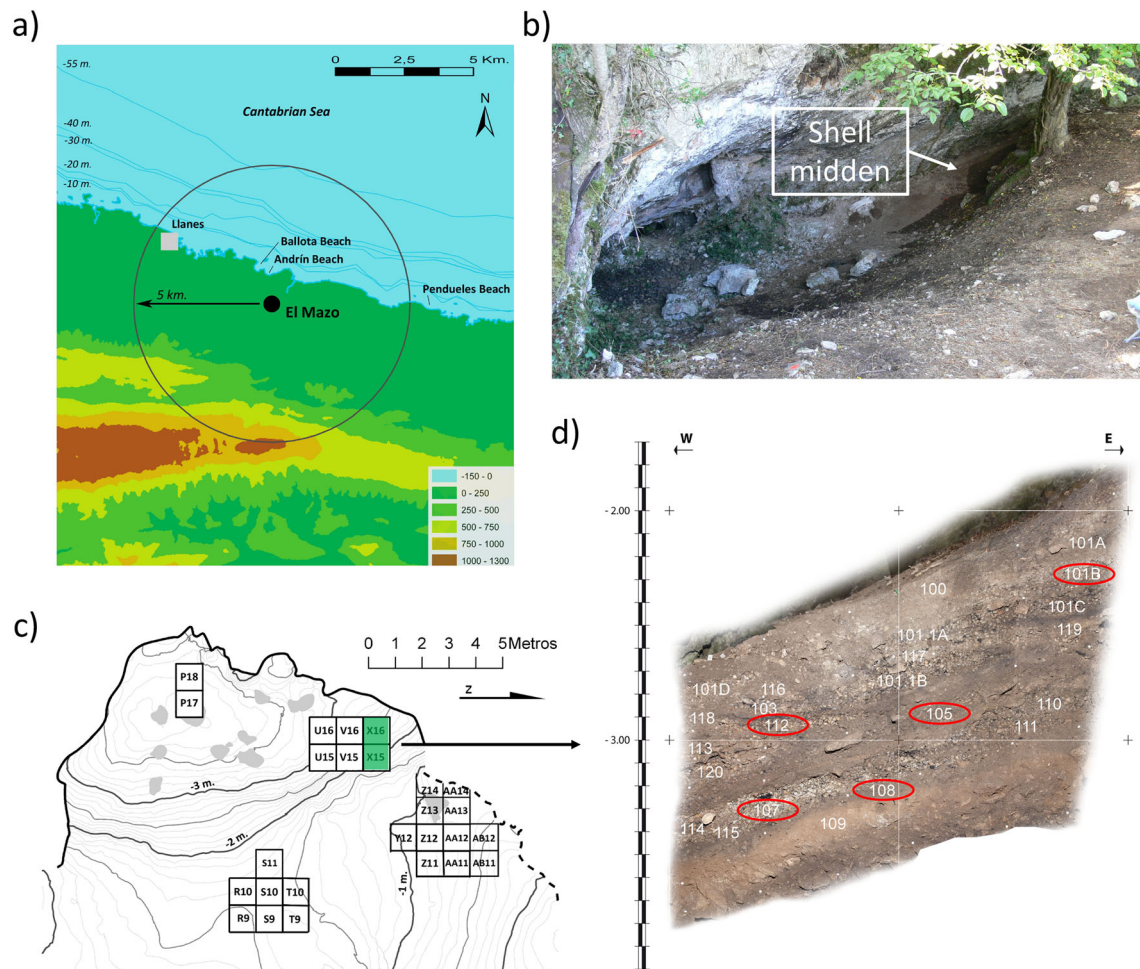


González-Morales 2014; Gutiérrez-Zugasti et al. 2013). The rockshelter that extends from the cave entrance is approximately 18 m wide, 7 m deep and ca. 2 m high (Fig. 2b). Excavations were undertaken inside the rockshelter, close to the walls, in 2009, 2010 and 2012 (Fig. 2c). A 2 × 1 m test pit was opened in 2009–2010 in squares V15 and V16, and the resulting north profile was sampled in 2012 in a limited extension (2 m in the east–west axis × 0.25 m in the north–south axis) of squares X15 and X16 (Fig. 2c). The excavation of the rockshelter area led to the identification of several stratigraphic units (SUs) composed mainly of shell midden deposits: SUs 100 to 108 and 110 to 122. SUs 104, 117 and 122, which are excluded from the analysis, corresponded to combustion structures (hearths) with high densities of charcoal, ash and burnt shells, suggesting that these fire structures were related to shellfish processing. Individual shell midden units were defined by their distinct sediment type and the amount of shells per unit area. In some instances, midden units were composed solely of crust, as a consequence of calcium carbonate precipitation over the shell midden, as was the case for SU 102 and SU 106. The radiocarbon dates place the formation of the shell midden during the Early Holocene, between 9,000 and 7,500 cal BP (García-Escárcaga et al. 2017; Gutiérrez-Zugasti and González-Morales 2014; Gutiérrez-Zugasti et al. 2013, 2018).

## Material and methods

### Material

The specimens of *P. lineatus* studied herein were recovered from the following six stratigraphic units located in the squares X15 and X16 (excavated in 2012): SUs 108, 107, 110, 105, 112C and 101B (Fig. 2d). A total of 130 shells were analysed (Table 1) to decipher shellfish collection patterns, a number that is significantly higher than the standard sample size utilised in similar, existing stable oxygen isotope studies from single sites. The stratigraphic units were selected in order to cover different time intervals of shell midden formation (Fig. 2d). Available radiocarbon dates suggest that the selected units cover a time span of at least ca. 1,000 years in the Early Holocene (Table 2). SU 108, located at the base of the shell midden, formed ca. 8.9 ka cal BP, although the radiocarbon dates suggest that this archaeological level continued accumulating until ca. 8.4 ka cal BP. SUs 107 and 110 are also located at the lower part of the shell midden and formed ca. 8.3 ka cal BP. SUs 105 and 112C, which were dated to ca. 8.2 ka cal BP, are located approximately in the middle part of the sequence. Finally, SU 101B is situated in the upper part of the shell midden and dated to ca. 7.9 ka cal BP.



**Fig. 2** Location of the El Mazo site in the Cantabrian region-general view, topography and stratigraphy of the site. **(a)** Location of El Mazo and distance to the littoral currently and during the Mesolithic (no more than 5 km at Early Holocene); **(b)** external view of the rockshelter; **(c)**

topographic map of the rockshelter showing excavation areas and provenance of the studied samples (shaded squares) and **(d)** stratigraphy of the inner test pit (squares X15 and X16). Shell samples used in this study come from the units indicated by red circles

A total of 20 shell samples were chosen from each stratigraphic unit studied, except for SUs 108 and 105, where 10 and 40 shells were selected, respectively. In the first case (SU 108), this study was performed previously to the other units applying a slightly different, but complementary, sampling procedure. In the second case (SU 105), 20 samples were selected each from squares X15 and X16 in order to observe whether there was any

variation in coastal exploitation patterns between two different spatial portions of the same unit. On the basis of a previous sclerochronological investigation of *P. lineatus* in the Cantabrian region (García-Escárcaga et al. *in press*), only shells smaller than 18 mm in diameter were selected for analysis, in order to avoid shell growth stoppages longer than three months that can occur during the warm season.

**Table 1** Provenance and ID codes of the shell samples analysed in this investigation

Stratigraphic unit (SU)	Spit	Square	Sub-square	N samples studied	Sample ID
101B	2	X15	D	20	MA.101.11 to 30
112C	–	X16	D	20	MA.112.11 to 30
105	2	X15	D	20	MA.105.11 to 30
105	4	X16	D	20	MA.105.31 to 50
110	2	X15	D	20	MA.110.11 to 30
107	2	X16	D	20	MA.107.11 to 30
108	–	X16	C	10	MA.108.02 to 11

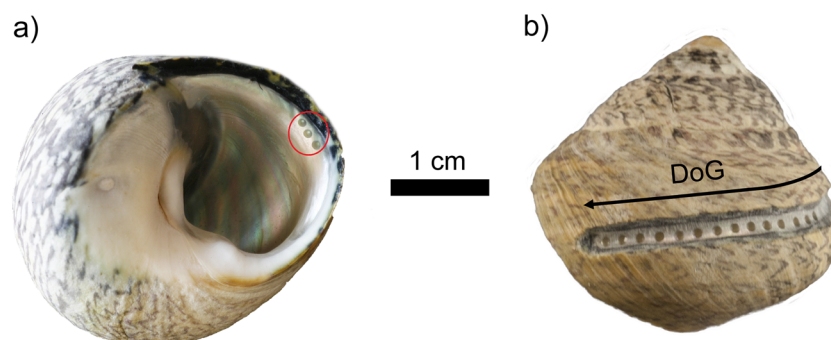
**Table 2** AMS radiocarbon dates for the stratigraphic units studied in this investigation.  $^{14}\text{C}$  ages were calibrated using the IntCal13 and Marine calibration curves (calibration program Oxcal 4.2, Reimer et al. 2013).The reservoir effect was corrected using the  $\Delta\text{R}$  value established for the Holocene in the Cantabrian region by Soares et al. (2016)

Stratigraphic unit (SU)	Square	Date BP	Interval cal BP $2\sigma$	Median cal BP	Material	Lab reference	Reference
101B	X15	7105 $\pm$ 40	8005–7850	7928	Bone	OxA-30780	Soares et al. (2016)
	X15	7310 $\pm$ 40	7970–7772	7871	Shell	OxA-30806	Soares et al. (2016)
112C	X16	7480 $\pm$ 40	8152–7948	8050	Shell	OxA-33173	Unpublished data
105	V15	7640 $\pm$ 30	8517–8384	8451	Charcoal	UGAMS-5408	Gutiérrez-Zugasti et al. (2013)
	X15	7380 $\pm$ 55	8338–8045	8192	Charcoal	OxA-30535	Soares et al. (2016)
	X15	7595 $\pm$ 40	8290–8032	8161	Shell	OxA-30977	Soares et al. (2016)
110	X15	7717 $\pm$ 37	8373–8182	8278	Shell	OxA-28394	Unpublished data
107	X16	7618 $\pm$ 37	8516–8365	8441	Bone	OxA-28408	Unpublished data
108	X15	7935 $\pm$ 35	8586–8396	8491	Shell	OxA-28396	García-Escárzaga et al. (2015)
	X16	8022 $\pm$ 39	9019–8729	8874	Bone	OxA-28411	Soares et al. (2016)
	X16	8222 $\pm$ 36	9008–8730	8869	Shell	OxA-27904	Soares et al. (2016)

### Sampling procedures and stable oxygen isotope analysis

The sampled *P. lineatus* shells were first treated with 30 vol%  $\text{H}_2\text{O}_2$  for 48 h in order to remove organic matter from the shells following a well-established, published methodology (Colonese et al. 2009; García-Escárzaga et al. *in press*; Gutiérrez-Zugasti et al. 2015). The cleaned shells were then air-dried at ambient temperature. Subsequently, calcium carbonate micro-samples were taken sequentially from the shell edge (or lip) following the growth axis, using detailed sclerochronological investigation of *P. lineatus* from previous studies as a guide (García-Escárzaga et al. *in press*). Previous research, using petrographic microscopy, scanning electron microscopy (SEM) and X-ray diffraction (XRD), has demonstrated that *P. lineatus* has an outer calcitic shell layer and an inner aragonitic layer (Gutiérrez-Zugasti et al. 2015; Mannino and Thomas 2007; Mannino et al. 2003). In this study, the outer calcite was removed in order to access the inner aragonite layer using a Dremmel microdrill and a 2-mm drill bit.

Carbonate micro-samples were taken manually on the aragonite layer using a dentist microdrill with a 0.5-mm drill bit coupled to a stereoscopic microscope. The methods applied to take micro-samples are similar to those previously used on this species (Gutiérrez-Zugasti et al. 2015; Mannino and Thomas 2007; Mannino et al. 2003) and on other species of the same genus (Colonese et al. 2009; Mannino et al. 2007, 2008, 2011, 2014; Prendergast et al. 2013, 2016) in order to facilitate comparison between studies. A total of 10 calcium carbonate micro-samples (each 40–60  $\mu\text{g}$ ) were taken from each shell sampled. The only exception was for the shells recovered from SU 108 where a total of 30 samples were taken from the shell edge. This led to a total of 1,500 calcium carbonate micro-samples analysed. In each case, the first micro-sample was taken from inside the edge of the shell aperture (Fig. 3a), with sequential micro-samples being taken every 1 mm from the outside of the shell along the whorl. Therefore, sampling spots were 0.5 mm apart from each other (Fig. 3b).



**Fig. 3** Sampling procedures applied for the extraction of calcium carbonate micro-samples from the aragonite layer. (a) Sampling method used to extract the carbonate from the inner part of the shell aperture. (b)

Sampling method used to extract carbonate samples sequentially along the whorl from the outside of the shell. DoG: direction of growth

Micro-samples taken on the shells recovered from SU 108 ( $n = 300$ ) were analysed using an IRMS Thermo Scientific MAT 253 coupled to Kiel device at the University of Michigan (USA). The instrumental error was better than  $\pm 0.12\text{‰}$ . Micro-samples taken on the specimens recovered from SUs 107, 110, 105, 112C and 101B ( $n = 1,200$ ) were analysed using an IRMS Thermo Scientific MAT 253 coupled to Kiel IV device at the Complutense University of Madrid (Spain). In this case, the instrumental error was better than  $\pm 0.04\text{‰}$ . In both cases, each powder sample was dissolved with concentrated phosphoric acid at  $70\text{ °C}$  and isotopic ratios were calibrated against the international standards NBS-18 and NBS-19. The results are reported as  $\delta^{18}\text{O}$  (‰) relative to the Vienna Pee Dee Belemnite (VPDB) reference standard.

### Determination of *Phorcus lineatus* collection season(s)

The season of collection of *P. lineatus* was investigated using a methodology based in the quartiles system proposed by Mannino et al. (2003, 2007). This approach has been successfully applied by other scholars working on European molluscs in archaeological contexts (Colonese et al. 2009; Kimball et al. 2009; Prendergast et al. 2016). Previous studies on  $\delta^{18}\text{O}$  profiles derived from modern *P. lineatus* samples captured in the Cantabrian region showed that these molluscs experience warm, cooling, cool and warming phases throughout the year (García-Escárzaga et al. *in press*; Gutiérrez-Zugasti et al. 2015). The intra-annual  $\delta^{18}\text{O}$  range and the maximum and minimum  $\delta^{18}\text{O}$  values document the intra-annual SST range and the minimum and maximum SST values, respectively. In order to establish the intra-annual  $\delta^{18}\text{O}$  range of the archaeological shells, long sequences were analysed on eight shells from four separate stratigraphic units (two shells per unit) (SUs 107, 105, 112C and 101).

For these eight shells, a total of 45 carbonate micro-samples were taken from each specimen analysed, following the same sampling procedure explained previously, although the sampling spots were separated by 0.3 mm to obtain a better resolution. Long sequences of  $\delta^{18}\text{O}$  values were not obtained for units 108 and 110 because (a) all mollusc shells recovered from unit 108 were analysed taking long isotopic sequences and (b) unit 110 is chronologically similar to unit 107, and, therefore, the intra-annual SST range (and intra-annual  $\delta^{18}\text{O}$  range) should be very similar for both units. The intra-annual  $\delta^{18}\text{O}$  range for each unit was obtained combining the results from the long and short sequences, since short sequences often offered maxima and minima values higher and lower than those derived from the long sequences.

The intra-annual  $\delta^{18}\text{O}$  range obtained for each unit was divided into four quartiles. Each quartile represents an annual climate season. The upper quartile (i.e. higher values)

represents cool conditions (i.e. winter), and the lower quartile (i.e. lower values) represents warm conditions (i.e. summer). Shell edge  $\delta^{18}\text{O}$  values falling into the upper quartile indicate that the mollusc died (and therefore was collected) in winter. Meanwhile, shell edge  $\delta^{18}\text{O}$  values falling into the lower quartile represent summer collection. The intermediary quartiles represent cooling (i.e. autumn) and warming (i.e. spring) climate seasons and collection. When shell edge  $\delta^{18}\text{O}$  values fall into these quartiles, it is possible to distinguish between collection events that occurred in spring or autumn on the basis of the  $\delta^{18}\text{O}$  trend just before the death of the mollusc (cooling or warming trend). Furthermore, unlike previous studies, in which only three micro-samples were obtained from the shell edge, in this investigation 10 micro-samples were taken. This novel approach facilitates more accurate seasonal placement since the sequences obtained cover, at least, the last four months of shell growth.

## Results

### Shell $\delta^{18}\text{O}$ values

Both short and long sequences obtained from sub-fossil samples demonstrate a sinusoidal pattern along the shell growth axis, covering a variable time span between ca. six months and more than three years in the case of some of the long sequences (see [Supplementary Material](#)). The maximum and minimum  $\delta^{18}\text{O}$  values obtained for all shells studied were 2.85 and  $-0.79\text{‰}$ , respectively. Nevertheless, the maxima and minima, and therefore also the intra-annual  $\delta^{18}\text{O}$  range resulting from the datasets, were different between individuals and stratigraphic units (Table 3). The maxima and minima values obtained for each level fluctuate between 2.85 and 2.37‰ and  $-0.09$  and  $-0.79\text{‰}$ , respectively. Thus, intra-annual ranges for each stratigraphic unit vary between 3.18 and 2.94‰. These values were used to calculate the four quartiles for each unit (Table 3), which were applied to accurately decipher the season(s) when molluscs were collected by Mesolithic populations.

### Season of collection of *Phorcus lineatus* from El Mazo

Our data show a consistently marked seasonality in the collection of *P. lineatus* at El Mazo (Fig. 4). This species was harvested preferably in late autumn ( $n = 35$  samples assigned to this season; 26.9%) and winter ( $n = 87$ ; 66.9%), while collection was limited in early spring ( $n = 7$ ; 5.4%) and was highly residual in summer ( $n = 1$ ; 0.8%). Few changes can be observed throughout the shell midden sequence. In this sense, winter is the most represented season in all units (107 = 90%; 110 = 75%; 105 = 52.5%; 112C = 80% and 101B = 75%), except in the case of unit 108, in which autumn (and more

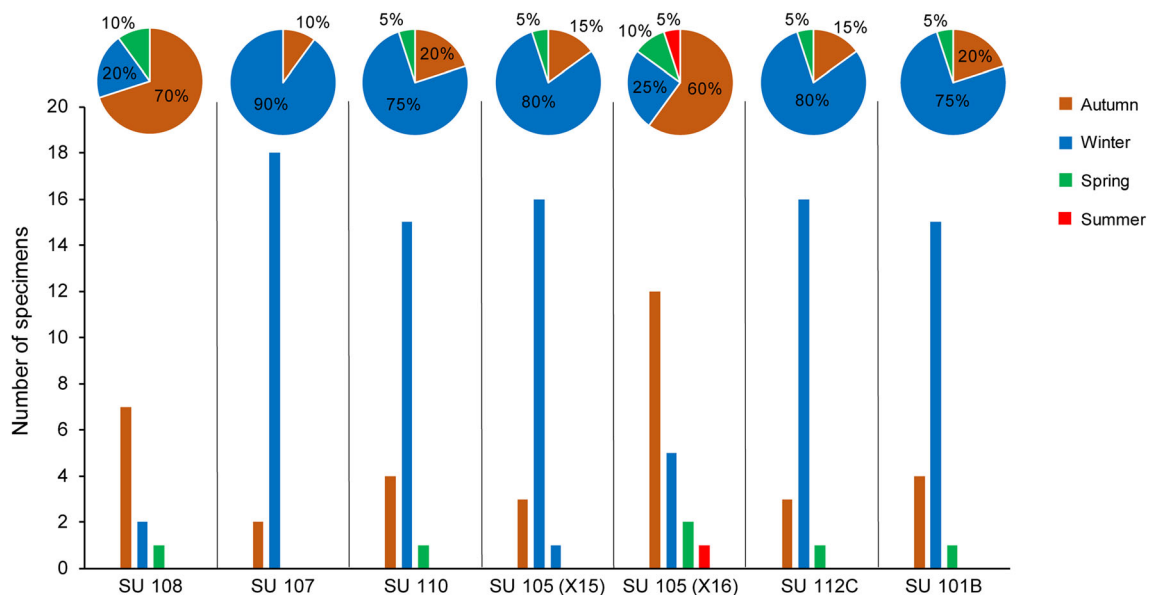
**Table 3** Maxima and minima values from short and long sequences obtained in this study. Intra-annual  $\delta^{18}\text{O}$  range for each stratigraphic unit (SU) was calculated using the maximum and minimum values from each

SU. The four quartiles were estimated from the intra-annual  $\delta^{18}\text{O}$  range following the methods described in the “[Determination of \*Phorcus lineatus\* collection season\(s\)](#)” section

Stratigraphic units (SU)	Sample ID	Maximum $\delta^{18}\text{O}$ value	Minimum $\delta^{18}\text{O}$ value	Intra-annual $\delta^{18}\text{O}$ range	1st quartile	2nd and 3rd quartiles	4th quartile
101B	MA.101.1	2.08	-0.23	2.31			
	MA.101.2	1.75	-0.48	2.23			
	MA.101. 11–30	2.37	-0.79	3.16			
<b>Total SU</b>		<b>2.37</b>	<b>-0.79</b>	<b>3.16</b>	<b>2.37–1.58</b>	<b>1.58–0.00</b>	<b>0.00–-0.79</b>
112C	MA.112.1	2.08	0.17	1.91			
	MA.112.2	2.10	-0.16	2.26			
	MA.112. 11–30	2.53	-0.65	3.18			
<b>Total SU</b>		<b>2.53</b>	<b>-0.65</b>	<b>3.18</b>	<b>2.53–1.73</b>	<b>1.73–0.14</b>	<b>0.14–-0.65</b>
105	MA.105.1	2.08	-0.27	2.35			
	MA.105.2	1.70	0.09	1.61			
	MA.105. 11–50	2.58	-0.59	3.17			
<b>Total SU</b>		<b>2.58</b>	<b>-0.59</b>	<b>3.17</b>	<b>2.58–1.79</b>	<b>1.79–0.20</b>	<b>0.20–-0.59</b>
107–110	MA.107.1	2.08	-0.42	2.50			
	MA.107.2	2.00	-0.26	2.26			
	MA.107. 11–30	2.64	-0.03	2.67			
	MA.110. 11–30	2.39	-0.29	2.68			
<b>Total SUs</b>		<b>2.64</b>	<b>-0.42</b>	<b>3.06</b>	<b>2.64–1.88</b>	<b>1.88–0.35</b>	<b>0.35–-0.42</b>
108	MA.108.02–11	2.85	-0.09	2.94			
<b>Total SU</b>		<b>2.85</b>	<b>-0.09</b>	<b>2.94</b>	<b>2.85–2.11</b>	<b>2.11–0.64</b>	<b>0.64–-0.09</b>

specifically late autumn) is the period of the year with higher representation (70%). In addition, in the case of the spatial divisions within SU 105, samples from square X15 showed a dominance of winter collection while those from X16

showed a dominance of late autumn collection (60%) for *P. lineatus*. In any case, early spring is very scarce in all units studied ( $\leq 10\%$ ), while a summer season of collection was only identified in one of the 130 shells analysed.



**Fig. 4** Seasonality of *Phorcus lineatus* collection by stratigraphic unit (SU). The figure shows the absolute number (bars) and the percentage (pies) of samples assigned to each season. In the case of SU 105, the

results have been represented distinguishing spatially between the squares X15 and X16

## Discussion

### The exploitation of topshells during Mesolithic in the Cantabrian region

Stable oxygen isotope data demonstrates that *P. lineatus* was collected preferentially in winter and, also, in late autumn. The results from the El Mazo shell midden are very similar to those previously obtained during the 1980s from other three Mesolithic shell midden sites (El Penicil, Mazaculos II and La Riera), also located in the western Cantabrian region (Bailey et al. 1983; Deith 1983; Deith and Shackleton 1986). This marked seasonal exploitation pattern has also been documented in other places along the Atlantic façade of Europe. This includes the Mesolithic site of Culverwell (UK), where season(s) of death information indicated a predominance of autumn and winter collection (Mannino et al. 2003; Mannino and Thomas 2007). Stable isotope analyses performed on another *Phorcus* species report similar conclusions. The dataset obtained from *Phorcus turbinatus* (Born, 1778) in different parts of the Mediterranean area (especially in southern Italy but also in Libya) has shown that this species was harvested preferentially during colder months (Colonese et al. 2009; Mannino et al. 2007, 2011, 2014; Prendergast et al. 2016), although, in some cases, minimal summer exploitation was also observed during the Mesolithic (Mannino et al. 2007; Prendergast et al. 2016). As a result, Mesolithic hunter-gatherers demonstrated a remarkably consistent focus on the autumn and winter collection of key molluscan resources across space and across time in Atlantic and Mediterranean Europe.

### Seasonality of subsistence strategies and human behaviour

In the context of the Cantabrian region, Deith (1983) proposed different hypotheses in order to explain the markedly seasonal pattern of Mesolithic molluscan exploitation (Bailey et al. 1983; Deith 1983; Deith and Shackleton 1986). This includes the argument that human settlement was limited in coastal areas during the warmer seasons, leading to a general lack of mollusc consumption in the summer. By contrast, coastal occupation and use occurred primarily during the colder parts of the year. Other scholars have also proposed this for other coastal areas (Mannino et al. 2003; Mannino et al. 2011). Nevertheless, mammals recovered at the Mesolithic shell midden sites of Mazaculos II (Marín-Arroyo and González-Morales 2009), El Toral III and El Mazo (Andreu-Alarcón 2013) demonstrate that coastal areas were also occupied during the summer. Similarly, a sclerochronological study conducted on *P. vulgata* from La Riera cave, a site located close to El Mazo, documented year-round collection of this limpet species (Bailey and Craighead 2003; Craighead 1995).

These results demonstrate that shell collection and hunting also took place in summer months, with molluscs being transported and consumed at the sites during this part of the year. Therefore, an exclusive in situ (on the beach) summer consumption of *P. lineatus*, as proposed by Deith (1983) to explain the appearance of this species at the site only in winter, seems improbable.

Deith (1983) also proposed a high Mesolithic human mobility along the Cantabrian coast throughout the annual cycle in order to explain why shell midden sites located in the western Cantabrian region did not show *P. lineatus* consumption during summer. In addition to the consumption of terrestrial and marine resources during summer months in sites located in the western area (Bailey and Craighead 2003; Marín-Arroyo and González-Morales 2009), a demographic increase (Marín-Arroyo 2013; Straus 2017, 2018; Straus and Clark 1986) and a reduction of human mobility (Arias 2006; González-Morales 1982) have been documented in the Cantabrian region during the Mesolithic. Therefore, according to the available evidence, arguments for a limited settlement in coastal areas during the warmer season and/or the high mobility along the coast cannot be considered as valid arguments to explain *P. lineatus* collection patterns.

The scarcity of other sources of nutrition during colder months has also been argued to be a possible explanation for the focus on *P. lineatus* collection during the colder months in the Cantabrian region (Deith 1983). Similar arguments have been made for an explicit seasonal focus on *P. turbinatus* at Mesolithic sites in the Mediterranean (Mannino et al. 2011; Prendergast et al. 2016). This hypothesis considers intertidal resources as a simple emergency or fallback food (Moss 2013). Nevertheless, the data obtained so far document the presence of mammals during the winter in coastal areas, as a consequence of annual migration mobility (Bailey 1973; Clark 1976). This would suggest that there was not such scarcity of resources during winter. Furthermore, as noted previously, limpets were collected year-round (Bailey and Craighead 2003), which means that a range of molluscs was consistently available for collection on the intertidal areas. The role of fish is practically unknown in the Cantabrian Mesolithic record and, although some evidence has been found (Adán et al. 2009; Fano et al. 2013), seasonality studies are lacking. Finally, the use of a diversity of nuts and other plant foods during autumn and winter months has been documented in the Cantabrian region. For example, hazelnut shells, which have a high energy return (Prado-Nóvoa et al. 2017), have been recorded at El Mazo (López-Dóriga 2015). As a result, the necessity of utilising *P. lineatus* as a fallback food during the colder periods of the year also seems unlikely.

A more “social” explanation for seasonal variation in mollusc exploitation seen at particular sites has been put forward by Mannino et al. (2011) who suggest that shell middens represent an accumulation of feasts or ritual episodes.



The occurrence of feasts, in which social and ritual activities were carried out, has also been proposed for the site of El Mazo on the basis of unusually high densities of the sea urchin *Paracentrotus lividus* (Lamarck, 1816) in the older shell midden units (Gutiérrez-Zugasti et al. 2016), although further studies are still required to corroborate this preliminary hypothesis. Determining if the collection of *P. lineatus* was also conditioned by ritual behaviour is difficult to ascertain on the basis of the available data, although this ceremonial hypothesis seems relatively unlikely. The isotopic results obtained herein suggest that topshells were mainly consumed throughout four months during every year, lacking a signal of highly short-term events that could be identified as feasts. In the same way, other cultural hypotheses previously proposed by other scholars to explain the seasonal pattern in shellfish exploitation such as (a) religious and cultural proscriptions (Milner 2005), (b) a better taste during the coldest months (Mannino et al. 2014) or (c) that people involved in mollusc harvesting were conducting other tasks in summer (Mannino et al. 2011) are very difficult to corroborate with the available data and must be considered as hypotheses for further investigation. Indeed, it is also possible that a more simplistic, economic explanation may be driving these trends in seasonal collection.

### Annual relative meat yield variations in *P. lineatus*

The sclerochronological investigation conducted by Bailey and Craighead (2003) showed that *P. vulgata* was collected year-round, suggesting different exploitation patterns for this species and *P. lineatus* despite them both inhabiting the same littoral area. As a result, Bailey and Craighead (2003) argued that differential exploitation patterns may be linked to different ecological and biological characteristics of these two taxa. They proposed that the relative meat yield obtained from *P. lineatus* was not homogeneous throughout the year and that gonadal development occurring during colder months might be responsible for higher relative meat yield during this part of the annual cycle. In order to test this hypothesis, we performed an experimental programme in which modern *P. lineatus* specimens were collected during three annual cycles.

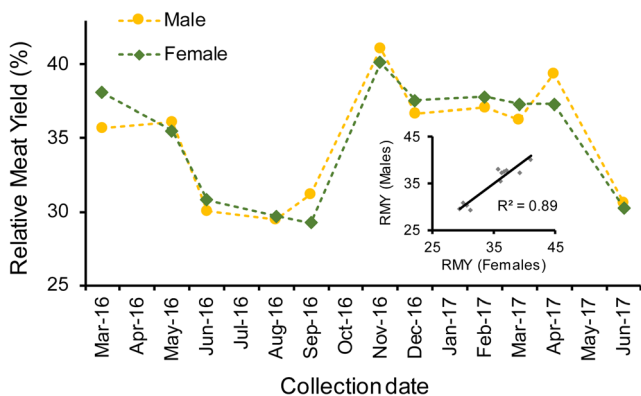
Modern specimens of *P. lineatus* were collected from Langre Beach (Ribamontán al Mar, Cantabria) in northern Iberia (Fig. 1). This location has oceanographic conditions very similar to the coastal areas located near the El Mazo shell midden. The topshells were collected at the start and middle portions of each season throughout three different years (from August 2014 to June 2016), resulting in a total of 24 collection events. Throughout the duration of the study, 40 topshells were captured for each collection event. The mollusc meat was weighed after immersion of each specimen in boiling water for 1 min. To determine the relative meat yield of each individual, a similar methodology to the one published by Thomas and Mannino (2017) was applied. A ratio between

meat and shell weight was calculated, with the result obtained being multiplied by 100 to estimate the meat weight extracted per 100 g of shell. Following previous studies, we identified male and female specimens during a total of 11 collection events using the different coloration of the soft parts (Crothers 2001; Desai 1966). The results showed that the relative meat yield of males and females collected during each collection event was almost the same, exhibiting a strong correlation (Fig. 5;  $R^2 = 0.89$ ;  $p < 0.0001$ ).

The relative meat yield, expressed as weight of meat per 100 g of shell, varied between specimens. Moreover, the average relative meat yield of molluscs captured during each visit to Langre beach demonstrated that the profitability of this species changed through time (Fig. 6). The profiles of the average relative meat yield for each collection event exhibited robust annual variation with a marked sinusoidal pattern, which repeated consistently across the three years of the experimental programme. During the three annual cycles, a lower relative meat yield was obtained during summer and early autumn. By contrast, a higher relative meat yield was recorded in late autumn, winter and spring. The period of maximum relative meat yield varied during the time frame considered in this study, with maxima occurring in early winter in 2014, in early spring in 2015 and in late autumn in 2016. Relative meat yield profiles exhibited a significant correlation with sea surface temperature variations throughout the three annual cycles (Fig. 6;  $R^2 = 0.68$ ,  $p < 0.0001$ ), suggesting that colder months are more profitable for collection of topshells.

As previously described, Bailey and Craighead (2003) proposed that the sexual cycle could drive mollusc relative meat yield variations. Gametogenesis (or gonadal development stage) and spawning (or breeding stage) in *P. lineatus* have been reported to occur in the Cantabrian coast, from November to May and from June/July to September, respectively (Bode et al. 1986; Lombas et al. 1984). Therefore, results from the experimental programme show a strong correlation between relative meat yield variations and sexual cycle in the case of *P. lineatus* in the Cantabrian region, since the period of highest profitability matches well with gonadal development stage (Fig. 6). Previous investigations on oyster molluscs recovered in Atlantic Europe (Berthelin et al. 2000) and the Mediterranean Sea (Dridi et al. 2007) have suggested that in some taxa the accumulation of protein could increase during the stage of gonadal development. Perhaps a similar process occurred in the case of *P. lineatus*, which would explain the higher profitability of this species during gametogenesis, although further studies are necessary to corroborate this hypothesis, including energetic and chemical analyses.

The pattern of higher profitability of *P. lineatus* during the colder times of the year shows a high correlation with the months when *P. lineatus* was collected during the Mesolithic period of the Cantabrian region, but also in other places of



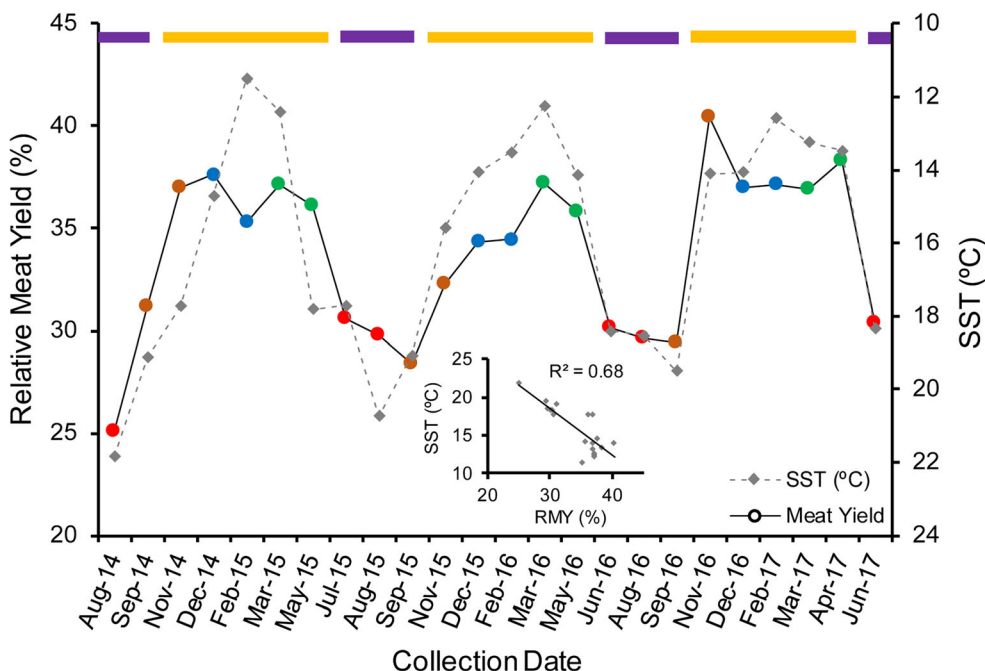
**Fig. 5** *Phorcus lineatus* relative meat yield (RMY) variations during a total of 11 collection events, distinguishing between male and female specimens and showing the correlation ( $R^2$ ) between profiles obtained from both sexes

Atlantic Europe (Mannino et al. 2003), where gonadal stage also occurs during colder months (Underwood 1972). Furthermore, this pattern is coincident with those observed in topshells from sites located in the south of Italy (Colonese et al. 2009; Mannino et al. 2007), since shell collection took place during the period of gonadal development (Mannino et al. 2008). In summary, results derived from this study suggest that (a) human decisions were driven by cost–benefit principles, (b) Mesolithic populations had a close working knowledge of mollusc biology and (c) Mesolithic groups practiced clear strategies of resource management. Moreover, these results suggest that the last hunter–fisher–gatherers developed a schedule to exploit different resources during different

seasons. Nevertheless, further analyses on other abundant mollusc species in the Cantabrian shell middens (e.g. limpets *P. vulgata* and *P. depressa*) are necessary to better understand shellfish exploitation patterns during the annual cycle.

### Coastal resource intensification through Mesolithic

Determining changes in seasonal resource exploitation through time is crucial not only for accurately deciphering changes in mobility strategies, settlement patterns, site use and resource management but also for better understanding the intensification processes in littoral resource exploitation seen in many parts of Europe during the Mesolithic. Increased consumption of coastal resources in Mesolithic Europe, in comparison with previous periods, has traditionally been linked with a higher intensification in shellfish exploitation as a result of population growth and increasingly sedentary occupations (Straus and Clark 1986). According to this interpretation, intensification of molluscan exploitation can be inferred from a clear decrease in shell size through time (Ortea 1986; Vega del Sella 1916). Bailey and Craighead (2003) proposed that decreased shell sizes were instead induced by changes in climatic and environmental conditions. Nevertheless, Gutiérrez-Zugasti (2011a) addressed this topic by studying size and age distributions of marine gastropods (limpets and topshells) from Upper Palaeolithic and Mesolithic sites in northern Iberia. Results revealed a decrease in the mean size and age of these species. Although these data



**Fig. 6** Annual relative meat yield (RMY) variations in *Phorcus lineatus* (circles) and sea surface temperature (SST) (diamonds) and correlation ( $R^2$ ) between the two variables. The colours in the meat yield profiles

represent the season of collection (red = summer; brown = autumn; blue = winter; green = spring). Upper bars show the sexual activity of the mollusc throughout the year (yellow = gametogenesis; purple = spawning)

demonstrated that molluscs were exploited with high intensity at least from the Azilian (c. 12.5 kys cal BP), information on changes (if any) in intensification processes throughout the Mesolithic is still very limited.

Stable oxygen isotope analyses conducted in this investigation have shown that the topshell *P. lineatus* was collected in late autumn, winter, and, to some extent, early spring. In spite of the changes in mollusc percentages assigned to each season throughout the shell midden sequence, the results do not exhibit any pattern of collection biased towards the months when topshells showed lower relative meat yield (i.e. summer and early autumn), a hypothetical scenario that would have suggested a higher human pressure operating on littoral resources. Instead, the absence of collection events during lower profitability periods suggests a recurrent and resilient resource management strategy. However, this information is not enough to refute the existence of intensification in coastal resource exploitation through the Mesolithic, since both processes (i.e. management and intensification) could be independent. Further isotopic and biometric studies from shell assemblages from El Mazo and other Mesolithic sites will be crucial in order to provide new, more detailed insights into resource intensification during this important phase of European prehistory.

## Conclusions

Combining (a) a stable oxygen isotope analyses in order to determine the seasonality of *P. lineatus* collection during the Mesolithic and (b) an experimental programme to decipher relative molluscan meat yield throughout the year has been crucial to better understand not only littoral exploitation patterns in the past but also human behaviour. Our isotopic results demonstrate that *P. lineatus* was exclusively gathered during colder months. Collection patterns are in agreement with previous data obtained for this species in the Cantabrian region and, also, in other coastal areas of Atlantic Europe. The arguments previously published to explain the *P. lineatus* exploitation pattern (limited human settlement in coastal areas during the warmer season, scarcity of food supply during colder months, feasting, etc.) do not agree with existing contextual archaeological information as well as the novel experimental data presented herein. This study demonstrates that the maximum relative meat yield for *P. lineatus* occurred between late autumn and early spring, probably due to gonadal development, suggesting that collection patterns during the Mesolithic were driven by human knowledge of changes in relative meat yield and resource profitability during these times of the year. This information is key for understanding how human populations interacted with the surrounding environment, practiced a consistent resource management strategy by human groups and annually scheduled their resource use patterns and

subsistence strategies. This also highlights the importance of developing intra-annual records of resource use and climate change if coastal foraging among the last hunter-fisher-gatherers of Europe is to be properly understood.

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