RESEARCH

Seasonal exploitation of intertidal resources at El Mazo (N Iberia) reveals optimized human subsistence strategies during the Mesolithic in Atlantic Europe

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Abstract

Over the last few decades, research has significantly enhanced our understanding of the role played by shellfish in human subsistence during the Mesolithic period along the Atlantic coast of Europe. Instrumental to this advance has been the analysis of stable oxygen isotope measurements ($\delta^{18}O$) from mollusc shells, which offers valuable insights into the seasonality of shellfish exploitation. The $\delta^{18}O$ values serve as reliable indicators of past seasonal seawater temperature variations experienced by the molluscs, enabling us to accurately determine the time of year when past humans collected them. Recent studies using this approach have successfully identified seasonal exploitation patterns of the topshell *Phorcus lineatus* (da Costa, 1778) in Atlantic Europe. However, uncertainties remain regarding the exploitation schedule of *Patella depressa* Pennant 1777, one of the most abundantly collected species in Mesolithic sites. Here we used shell $\delta^{18}O$ values of *P. depressa* from the Mesolithic sites of El Mazo (Northern Iberia) to determine its seasonality of exploitation. Our study reveals that *P. depressa* was prevalently exploited during colder months. Modern specimens of the same limpet species were also collected during two annual cycles to assess potential seasonal changes in meat yield return. Results obtained has profound implications for better understanding how last coastal foragers managed available littoral resources throughout the year.

Keywords Shell middens · Atlantic Europe · Cantabrian region · Stable isotopes · Seasonality · Subsistence strategies

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Introduction

Coastal areas and marine resources played a significant role in the subsistence strategies of past hominins around the world (Bicho and Esteves 2022; Colonese et al. 2011; Jerardino and Marean 2010; Ramos-Muñoz et al. 2016). The use of shellfish as a key resource has been argued to have been especially pronounced during periods of adverse climate conditions (García-Escárzaga et al. 2022a; Klein et al. 2021; Marean et al. 2007). During the Mesolithic period, in the first millennia of the Holocene, human populations residing along the coasts of Europe extensively harvested intertidal resources, resulting those in the formation of large shell deposits, mainly in caves and rock shelters, but in open air sites as well (Astrup et al. 2021; Bicho et al. 2010; Gutiérrez-Zugasti et al. 2011; Milner et al. 2007). This kind of archaeological assemblage is particularly abundant in Northern Iberia (Arias et al. 2015; Fano 2007, 2019). Recent

investigations in the Cantabrian region (littoral area located in Northern Iberia), have advanced our understanding of the lifeways of the last foragers along the Atlantic coast of Europe. These studies have highlighted the role of molluscs in the subsistence strategies of Mesolithic human groups (García-Escárzaga and Gutiérrez-Zugasti 2021; Gutiérrez-Zugasti et al. 2016; Portero et al. 2022), the importance of mollusc shells for reconstructing shellfish collection patterns (Álvarez-Fernández 2011; Gutiérrez-Zugasti 2009, 2011; Gutiérrez-Zugasti et al. 2011; García-Escárzaga 2020; García-Escárzaga et al. 2021), as well as the impact of abrupt climate changes, such as the 8.2 ka cal BP cold event, on marine ecology and human populations (García-Escárzaga 2020; García-Escárzaga et al. 2022a). These studies have also been instrumental in determining the technological and symbolics uses of shell remains (Álvarez-Fernández 2006; Cuenca-Solana 2015; Rigaud and Gutiérrez-Zugasti 2016), among other relevant issues.

Analyses of stable oxygen isotope values (δ^{18}O) in marine mollusc shells have been extensively applied to archaeological assemblages to establish the season(s) when molluscs were collected by the past human groups (e.g., Branscombe et al. 2021; Hausman and Meredith-Williams, 2017; Leclerc et al. 2023; Prendergast et al. 2016). For example, studies have shown that Mesolithic groups in the Northern Iberia collected the topshell *Phorcus lineatus* (da Costa, 1778) primarily during the coldest months of the year (Bailey et al. 1983; Deith 1983; Deith and Shackleton 1986; García-Escárzaga et al. 2019). Interestingly, studies around the Mediterranean basin also reached similar conclusions for the topshell *Phorcus turbinatus* (Born, 1778), which was found to have been mostly exploited during the coldest months of the year by distinct Mesolithic populations (Colonese et al. 2018; Mannino et al. 2011; Prendergast et al., 2016). A consensus thus appears to emerge that most intertidal resources were exploited during the colder months of the year. Although different explanations have been proposed (e.g., absence of hunter-gatherers in coastal areas during the warmer seasons, scarcity of food supply during colder months, high mobility along the coast, social or religious reasons, etc.), thus far the driving factor remains unclear based on available data (Deith 1983; Colonese et al. 2009; García-Escárzaga et al. 2019; Mannino et al. 2011). Recently, García-Escárzaga et al. (2019) demonstrated throughout an experimental programme, in which modern live-collected molluscs were harvested, boiled, and weighed, that *P. lineatus* offered higher meat profitability during colder months due to gonadal development, therefore suggesting that cost-benefit principles may have driven seasonal exploitation patterns.

Although we have made significant progress in our understanding of the role of some marine mollusc species in human diets, significant gaps still exist for other taxa that were also abundantly collected in the past. This is the case of the limpet *Patella depressa* Pennant, 1771, an open coast species which dominates shell assemblages in some Late Mesolithic sites in the Southern Atlantic Europe (Bello-Alonso et al. 2015; García-Escárzaga 2020; García-Escárzaga et al. 2021, 2022a; Stiner et al. 2003; Valente 2012). Although a preliminary investigation conducted by Bailey and Craighead (2003) suggested throughout a study of the shell annual growth lines that limpets were harvested year-round during the Mesolithic in Northern Iberia, further evidence are still needed due to the uncertainties of the method used to establish the season of capture. A sclerochronological investigation using live-collected *P. depressa* shells from Northern Iberia has recently highlighted that shell δ^{18}O values of this species accurately reflect seasonal temperature variations year-round, and thus can act as a robust paleothermometer (García-Escárzaga et al. 2020), as well as a proxy for the season of collection by human foragers. Here, we present the results obtained from stable oxygen isotope analyses conducted on sub-fossil *P. depressa* shells recovered from El Mazo (Northern Iberia), a Mesolithic shell midden site in the European Atlantic façade with highly resolved chronological and sedimentary deposits (García-Escárzaga et al. 2022a). These results are combined with those previously obtained from *P. lineatus* topshells recovered from the same archaeological site (García-Escárzaga et al. 2019), which is crucial to understand how last foragers scheduled littoral exploitation annual patterns. In addition to isotopic data, we have also conducted an experimental program involving the collection of modern *P. depressa* samples for two years. By combining these approaches, we are able to explore the principles that drove seasonal mollusc exploitation patterns in this region. The study advances our understanding of forager adaptation to Early Holocene environmental conditions in Western Europe.

Background

El Mazo shell midden site

El Mazo is in the municipality of Llanes (Asturias, Northern Spain) (43° 24′ 4″ N, 4° 42′ 42″ W) (Fig. 1a). Currently, this archaeological site is situated approximately 1 km away from the seashore. Sea level fluctuations during the Mesolithic period would have caused this distance to vary, although previous studies on the Cantabrian region suggest that it would not have been greater than three kilometres over the course of the past 9,000 years (Leorri et al. 2012; Gutiérrez-Zugasti et al. 2013). The shell midden was formed along the 18-meter-long rock shelter, but only
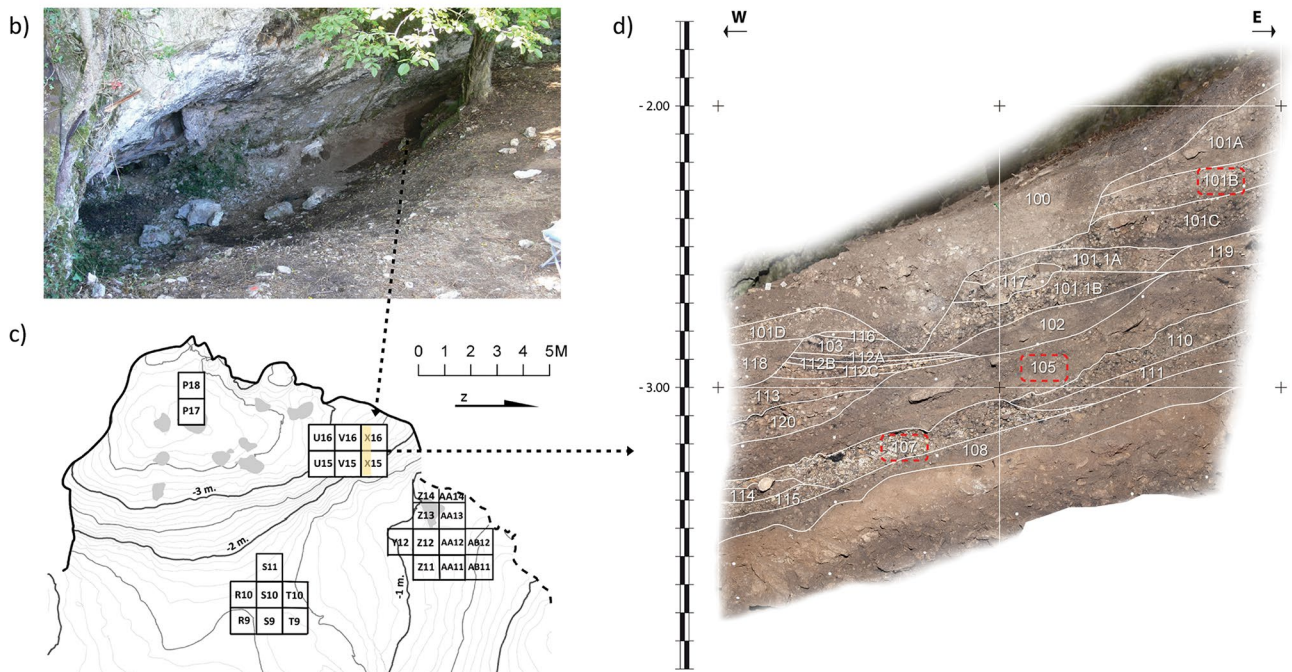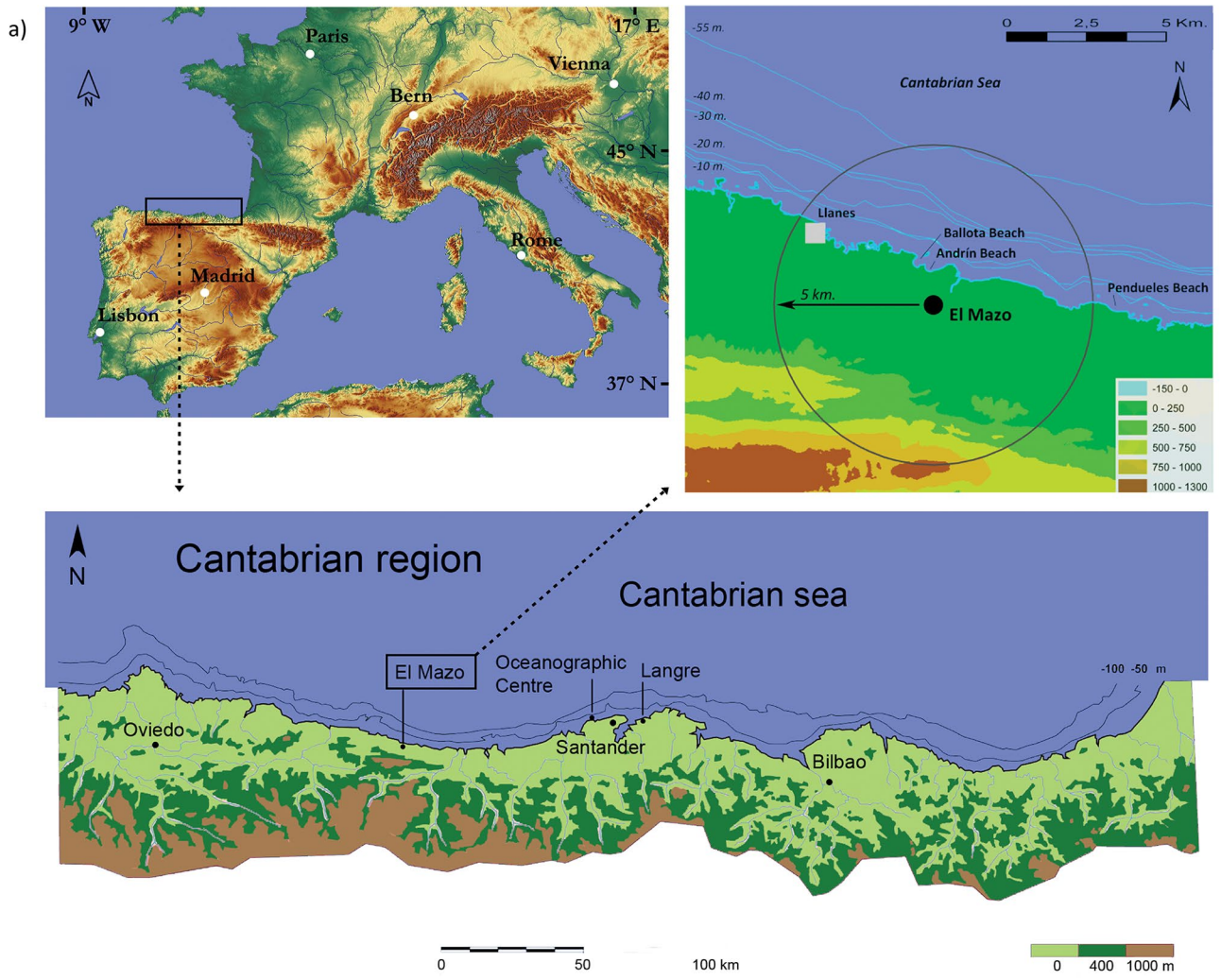
Fig. 1 a) Location of the study area (Cantabrian region, Northern Iberia) and El Mazo shell midden site. **b**) External view of the El Mazo rock-shelter. **c**) Squares excavated during several archaeological campaigns (2009–2017), highlighting in yellow that area sampled during 2012. **d**) Stratigraphy of the inner test pit (squares X15 and X16). Stratigraphic units from which the shell analysed herein were recovered (107, 105 and 101B) are framed by a red square

a small area near the walls has been preserved to this day (Fig. 1b). In 2009 and 2010, a test pit measuring 2 × 1 m was excavated in squares V15 and V16, and the resulting north profile was sampled in a limited area (2 m in the east-west axis x 0.25 m in the north-south axis) in 2012 (squares X15 and X16) (Fig. 1c) (Gutiérrez-Zugasti and González-Morales 2013). A total of 25 stratigraphic units (SUs) were identified in squares X15 and X16 (Fig. 1d), providing important insights into the site's history of occupation. The excavation of the rock shelter area produced several stratigraphic units composed mainly of shell deposits (Gutiérrez-Zugasti and González-Morales 2013). The modelled radiocarbon chronology of the deposit constrained the formation process to the Early and Middle Holocene, between 9.0 and 7.4 ka cal BP (García-Escárzaga et al. 2022a, b) (Fig. 2). This is a critical time interval marked by the abrupt 8.2 ka cal BP cold event (García-Escárzaga et al. 2022a).

Biology and ecology of *Patella depressa* Pennant, 1777

The limpet *P. depressa* (Fig. 3a) is a marine gastropod that geographically extends from Southwestern England and Wales to Northern Africa (Fretter and Graham 1976). A previous study conducted on the Portuguese coast showed that *P. depressa* has a life span of no longer than three years (Guerra and Gaudencio 1986). *P. depressa* is a microphagous herbivore that feeds on microscopic plants and macroalgae by grazing the rocky substrate using a horny tongue (radula) (Moore et al. 2007). The length and morphology of this species varies depending on its position in the intertidal zone. Shells in the upper intertidal zone are usually steeply conical and very thick, whereas at lower intertidal levels, they are polygonal, flattened, and thin (Orton and Southward 1961). Sclerochronological investigations previously conducted on this species using modern samples from the Northern Iberia show that the species grows almost year-round in this middle latitude (ca. 43° N). Despite the observation of short stoppages in summer and winter, because of surpassing its thermal tolerance, these growth cessations were no longer than six weeks and did not prevent correct deduction of the season of mollusc collection (García-Escárzaga et al. 2020). Their spawning and gonadal development stages vary depending on latitude (Orton and Southward 1961; Ribeiro et al. 2009). In Northern Iberia, mature gonads are found all year-round except for the summer months, reaching their maximum prior to the two main spawning events, which occur in January/February and April/June (Fernández et al. 2016).

Materials and methods

Material

Archaeological shells were recovered from three stratigraphic units from squares X15 and X16 (excavated in 2012): SUs 107, 105 and 101B (Fig. 2). These stratigraphic units were selected to cover different time intervals, as well as different environmental conditions before, during and after the 8.2 ka cal BP cold event. The Bayesian model indicates that the selected units covered a time interval of ca. 700 years through the Early and Middle Holocene (Fig. 2) (García-Escárzaga et al. 2022a). SU 107 is in the lower part of the shell midden and was formed between 8,550 and 8,330 cal BP (95% confidence interval). SU 105 is located approximately in the middle part of the sequence and had radiocarbon dated between 8,315 and 8,185 cal BP (95% confidence interval), partially corresponding to the 8.2 ka cold event (García-Escárzaga et al. 2022a). An increase in the percentage of *P. vulgata* shells, a species adapted to cold climate conditions, revealed a significant impact of the 8.2 ka cold event during the stratigraphic unit formation (García-Escárzaga et al. 2022a). In addition, a decrease of mollusc shell sizes in SU 105 also suggests a higher human pressure over the intertidal resources at that time (García-Escárzaga et al. 2022a). Finally, SU 101B is situated in the upper part of the shell midden and was formed at the first centuries of the Middle Holocene, between 7,945 and 7,795 cal BP (95% confidence interval). A total of 20 *P. depressa* shells were analysed per stratigraphic unit (Table 1; Supplementary Table 1) to determine the season(s) when this species was harvested by Mesolithic populations. The amount of *P. depressa* isotopically analysed against the total individuals recovered from each stratigraphic unit is low (SU 107 = 0.5%; SU 105 = 0.4%; SU 101B = 0.9%). However, limpets studied herein were randomly selected from a volume of 2.5 L, and the results from a previous investigation on seasonality of shell collection (García-Escárzaga et al. 2019) were very similar when using shells from different squares of the same unit. Although the variance in length between specimens of the same stratigraphic unit is low (Supplementary Table 1), according to a Kruskall-Wallis test, there are significant differences in mean sizes ($p < 0.01$) between units. However, all of the specimens are smaller
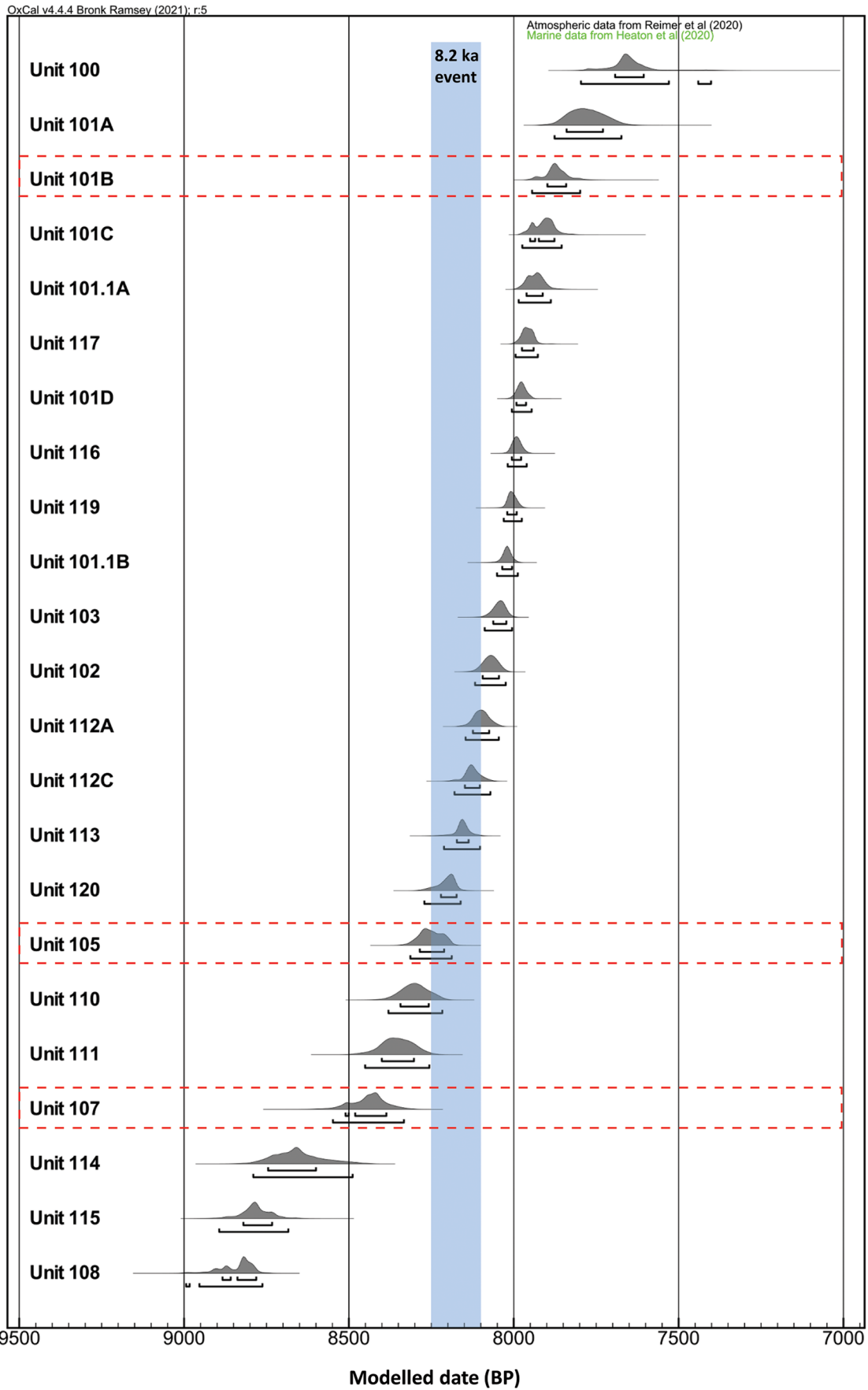
OxCal v4.4.4 Bronk Ramsey (2021); r:5

Atmospheric data from Reimer et al (2020)
Marine data from Heaton et al (2020)

8.2 ka event

Unit 100
Unit 101A
Unit 101B
Unit 101C
Unit 101.1A
Unit 117
Unit 101D
Unit 116
Unit 119
Unit 101.1B
Unit 103
Unit 102
Unit 112A
Unit 112C
Unit 113
Unit 120
Unit 105
Unit 110
Unit 111
Unit 107
Unit 114
Unit 115
Unit 108

9500　　9000　　8500　　8000　　7500　　7000

Modelled date (BP)

Fig. 2 Bayesian modelling of a total of 65 radiocarbon dates obtained from the shell midden site of El Mazo cave (Asturias, N Spain) calibrated in OxCal v.4.4.4 (Bronk Ramsey 2009a, b) using IntCal20 (Reimer et al. 2020) and Marine20 (Heaton et al. 2020) curves and the ΔR values published by García-Escárzaga et al. 2022b for *Patella vul-*

gata Linnaeus, 1758 and *P. lineatus* mollusc species. Figure published by García-Escárzaga et al. 2022a and modified in this study to add red dashed rectangles to indicate the units from which marine samples analysed herein were recovered
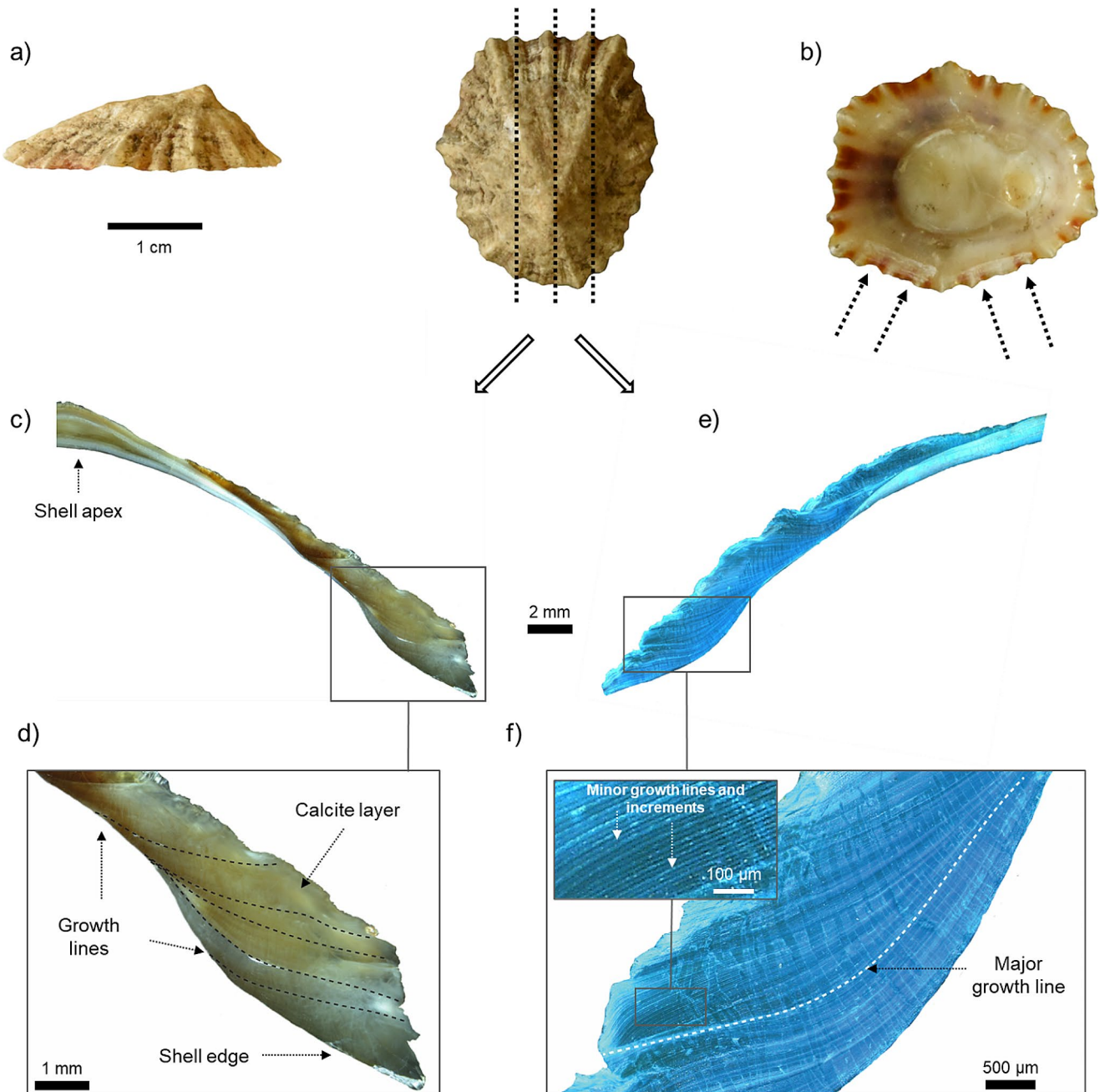

Fig. 3 *P. depressa* from the shell midden site of El Mazo. Dashed lines show the cutting axis from which two think sections (**c** and **e**) were obtained. **b**) Inner side of *P. depressa* shell. Arrows indicate the shell edge area from where the calcium carbonate powder micro-sample representative of the last shell growth were taken. **c**) Thick section of a limpet shell. **d**) Edge portion of a think section showing the visible growth lines and the calcite layer from which calcium carbonate micro-samples were extracted. **e**) Thick section stained with Mutvei's solution. **f**) Mutvei's-stained cross section displaying major and minor growth lines/increments

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

Strati-graphic unit (SU)	Spit	Square	Sub-square	N samples analysed	Sample ID
101B	2	X15	D	20	MA.101B.51 to 70
105	2	X15	D	20	MA.105.51 to 70
107	2	X16	D	20	MA.107.51 to 70

than 30 mm in length, which is the only size criterion that could impact our seasonal estimations following the criteria derived from the sclerochronological investigation recently conducted on modern limpets of this species from the same coastal location (García-Escárzaga et al. 2020). The selection of individuals smaller than 30 mm in length was conducted to limit the effect of an ontogenetic slowing down of shell growth rate.

Sampling and stable oxygen isotope analysis

Building on previous studies on limpets, including *P. depressa*, such as Fenger et al. (2007), García-Escárzaga et al. (2020), Gutiérrez-Zugasti et al. (2017), and Prendergast and Schöne (2017), two complementary methods were employed to obtain calcium carbonate ($CaCO_3$) for stable oxygen isotope analysis. Firstly, a $CaCO_3$ micro-sample was manually taken from the shell edge using a dentist microdrill with a 1 mm diamond drill bit by milling along the perimeter of the innermost part of the shell edge. This was done to prevent loss of the isotope signal corresponding to the last growth of the shell during the next sampling phase in case the limpet margin was broken (Fig. 3b). Secondly, the remaining $CaCO_3$ micro-samples were sequentially taken along the axis of shell growth to obtain $\delta^{18}O$ value profiles across the lifespan of the mollusc. To achieve this, the specimens were partially coated with a metal epoxy resin along the axis of maximum growth, from the anterior to the posterior margin, to prevent shell breakage when sectioned using a Buehler Isomet low speed saw and a diamond wheel. Two thick sections (~3 mm each) were obtained per sample. They were fixed onto a glass microscope slide with metal epoxy resin. The sections were then ground on glass plates using 600 and 800 SiC grit powder and polished with 1 μm diamond suspension grit until the internal growth lines and increments were visible (Fig. 3c). One of these thick sections was used for studying shell growth patterns, and the other was employed for taking $CaCO_3$ micro-samples from the calcite layer using a New Wave MicroMill and a 1 mm diamond drill bit. The sampling was conducted in a direction parallel to the visible

growth increments and from the edge to the apex of the shell (Fig. 3d).

The sampling approach conducted here aimed to obtain long and short isotope series. It involved taking the maximum $CaCO_3$ micro-samples possible ($n = 40–73$) from nine shells (three per stratigraphic unit) (Supplementary Table 1). Additionally, 15 $CaCO_3$ micro-samples of the final stage of shell growth were taken on 17 shells per unit (Supplementary Table 1). Both long and short isotope sequences were used for estimating the maximum and minimum $\delta^{18}O$ values and the intra-annual $\delta^{18}O$ range for each archaeological assemblage and the season when *P. depressa* species were harvested by Mesolithic groups. The width of the sampling paths in both cases was measured using the New Wave MicroMill software. The weight of each carbonate powder sample obtained was more than 200 μg, and they were stored in glass vials. The $\delta^{18}O$ analyses were carried out using a Thermo Fisher Scientific DELTA V IRMS coupled to a Gas Bench II Interface at the Department of Archaeology, Max Planck Institute of Geoanthropology (formerly for Science of Human History) Jena, Germany. Each powder sample was dissolved in 100% concentrated phosphoric acid at 70 °C in helium flished vials. The raw isotopic ratios of the resulting CO_2 gases were normalized using a three-point calibration against international standards NBS-18 (-23.2‰), IAEA-603 (-2.37‰), and IAEA-CO-8 (-22.7‰). The results are reported as $\delta^{18}O$ (‰) relative to the Vienna Pee Dee Belemnite (VPDB) standard. The analytical error of the instrument was determined to be ±0.1‰.

Determination of *Patella depressa* collection season(s)

To determine the season(s) when the molluscs were collected, the quartiles system proposed by Mannino et al. (2003, 2007) was used. This method has been also successfully adopted by other scholars working on other European contexts (Branscombe et al. 2021; Colonese et al. 2009, 2018; Kimball et al. 2009; Prendergast et al. 2016), including Northern Iberia (García-Escárzaga et al. 2019). The maximum and minimum $\delta^{18}O$ values and the intra-annual $\delta^{18}O$ range for each stratigraphic unit were determined by combining the $\delta^{18}O$ values from the long and short isotope sequences. Then, the intra-annual $\delta^{18}O$ range obtained for each unit was divided into four quartiles. Each quartile approximately represents a 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 $\delta^{18}O$ values falling into the upper and lower quartiles indicate that the specimens were collected in winter and summer, respectively. The intermediary quartiles represent cooling (i.e., autumn) and

warming (i.e., spring) periods. When shell edge $\delta^{18}O$ values fall into these quartiles, it is possible to distinguish between collection events that occurred in spring or autumn based on the $\delta^{18}O$ trend just before the death of the mollusc. If $\delta^{18}O$ values increase during the last weeks/months of the shell growth, specimens were collected in a cooling period (i.e., autumn). In contrast, if results report a decrease in $\delta^{18}O$ values before the individual dying, it was harvested in a warming season (i.e., spring).

Shell growth lines/increments study

To accurately estimate the collection season, we examined the shell growth lines and increments, with particular focus on those located near the shell ventral margins, in every shell to determine if $CaCO_3$ precipitation ceased during the final months of the mollusc's lifespan, even if the specimen stopped growing. This information allows for a more precise estimation of the season of collection. To achieve this objective, one of the thick sections obtained from each limpet was polished until the internal growth lines and increments were clearly visible. The sections were then immersed in Mutvei's solution for 20 min at 37–40 ºC to increase the visibility of the growth lines and increments (Schöne et al. 2005) (Fig. 3e). Growth lines and increments were analysed using a sectoral dark-field illumination under a Leica S8APO stereoscopic microscope (8−50x magnification) at the IIIPC – University of Cantabria (Spain), coupled to a Leica MC190HD digital camera (10MP), following identification criteria previously established for this species (García-Escárzaga et al. 2020).

Modern specimens and relative meat yield calculation

To determine variations (if any) in the profitability of *P. depressa*, living specimens were collected every ca. 45 days from Langre Beach (Ribamontán al Mar, Cantabria), in Northern Iberia (Fig. 1a). The area exhibits similar oceanographic conditions to those littoral areas located near the archaeological site where Mesolithic specimens were collected. Shell collection was carried out year-round throughout two non-consecutive years (from August 2014 to July 2015 and from March 2016 to June 2017), in the beginning and during the middle part of each season during a total of 19 collection events (Supplementary Table 2). The collections were suppressed during seven months (from July 2015 to March 2016) to maintain the local population.

During the experimental programme, a total of 950 samples were collected, 50 specimens from both lower and higher intertidal zones per collection event. Their soft parts were extracted from the shell, and the mollusc meat was weighed. Shells were also weighed to obtain a direct comparison between the weight of the shell and the mollusc meat. The relative meat yield (RMY) was estimated following Thomas and Mannino (2017) and García-Escárzaga and Gutiérrez-Zugasti (2021). The results obtained were compared with sea surface temperature (SST) measured from August 2014 to June 2017 by the Aquaculture Facility of Santander's Oceanographic Centre (Cantabria, N Iberia) (Fig. 1a).

Table 2 Maxima and minima $\delta^{18}O$ values from short and long sequences for each stratigraphic unit (SU). Intra-annual $\delta^{18}O$ range of each SU was estimated using the maximum and minimum values obtained from that SU. The four quartiles were calculated from the intra-annual $\delta^{18}O$ range following the method explained above

Stratigraphic Units (SU)	Sample ID	Maximum $\delta^{18}O$ value	Minimum $\delta^{18}O$ value	Intra-annual $\delta^{18}O$ range	1st Quartile			2nd and 3rd Quartiles			4th Quartile		
101B	MA.101B.51	2.99	0.10	2.89									
	MA.101B.52	2.30	0.07	2.23									
	MA.101B.53	2.78	0.68	2.10									
	MA.101B. 54 - 70	2.99	0.18	2.81									
Total SU		**2.99**	**0.07**	**2.92**	2.99	-	2.26	2.25	-	0.81	0.80	-	0.07
105	MA.105.51	2.39	0.05	2.34									
	MA.105.52	2.58	0.07	2.51									
	MA.105.53	2.43	0.35	2.08									
	MA.105. 54 - 70	2.98	−0.17	3.15									
Total SU		**2.98**	**−0.17**	**3.15**	2.98	-	2.19	2.18	-	0.63	0.62	-	−0.17
107	MA.107.51	2.78	0.22	2.56									
	MA.107.52	2.33	0.40	1.93									
	MA.107.53	2.56	−0.05	2.61									
	MA.107. 54 - 70	2.78	−0.12	2.90									
Total SU		**2.78**	**−0.12**	**2.90**	2.78	-	2.06	2.05	-	0.62	0.61	-	−0.12

Results

Shell δ¹⁸O values

Both short and long sequences obtained from sub-fossil samples demonstrate a sinusoidal pattern along the shell growth axis. The time span covered by the isotope series was variable, spanning from a few months to one year in the case of the short sequences (Supplementary Fig. 1) and from one to two years in the case of the long sequences (Supplementary Fig. 2). The maximum and minimum δ^{18}O values were $+2.99‰$ and $-0.17‰$, respectively. The maxima and minima, and therefore also the intra-annual δ^{18}O range resulting from the dataset, differed between individuals and stratigraphic units (Table 2). The maxima and minima values obtained for each stratigraphic unit level ranged between $+2.99‰$ and $+2.78‰$ and $-0.05‰$ and $-0.17‰$, respectively. Thus, intra-annual ranges for each unit vary between 3.15‰ and 2.90‰. These values were used to calculate the four quartiles for each stratigraphic unit (Table 2; Supplementary Fig. 1).

Seasonality of collection

The δ^{18}O profiles obtained from the 60 shells retrieved from the three stratigraphic units demonstrate a consistent collection pattern over time. All specimens were collected between autumn, winter, and spring, except one sample from unit 105 that indicated a death in summer (Fig. 4). Most specimens, however, were collected during the winter season, as evident in the three units under study (SU 101B: $n=12$, 60%; SU 105; $n=9$, 45%; 107: $n=13$, 65%). A detailed study in which lower δ^{18}O values of winter quartiles and δ^{18}O values obtained from the last portion of growth of those shells assigned to autumn and spring were considered allowed us to estimate the moment of the season when molluscs died more precisely. Many of the individuals included in the intermediate seasons were collected at the end of autumn and at the beginning of spring, suggesting that *P. depressa* were predominantly harvested during the colder months of the year. (Supplementary Figs. 1 and 2). Specifically, around 87% of the specimens analysed were gathered between November and April. The number of specimens collected in the warmest period of the year (including late spring and early autumn) was minimal, comprising only three out of 60 shells (5%).

Shell growth cessation and major growth lines

The analysis of growth increments revealed that the species grew almost continuously throughout the year during the Early/Middle Holocene. Only a few specimens exhibited significant growth cessation in the form of major growth lines, which was likely caused by exceeding upper and lower thermal tolerances during summer and winter, respectively. For instance, specimen MA.101B.53 displayed a major growth line located 5.3 mm from the shell edge (Fig. 5a). This distinct line coincided with the
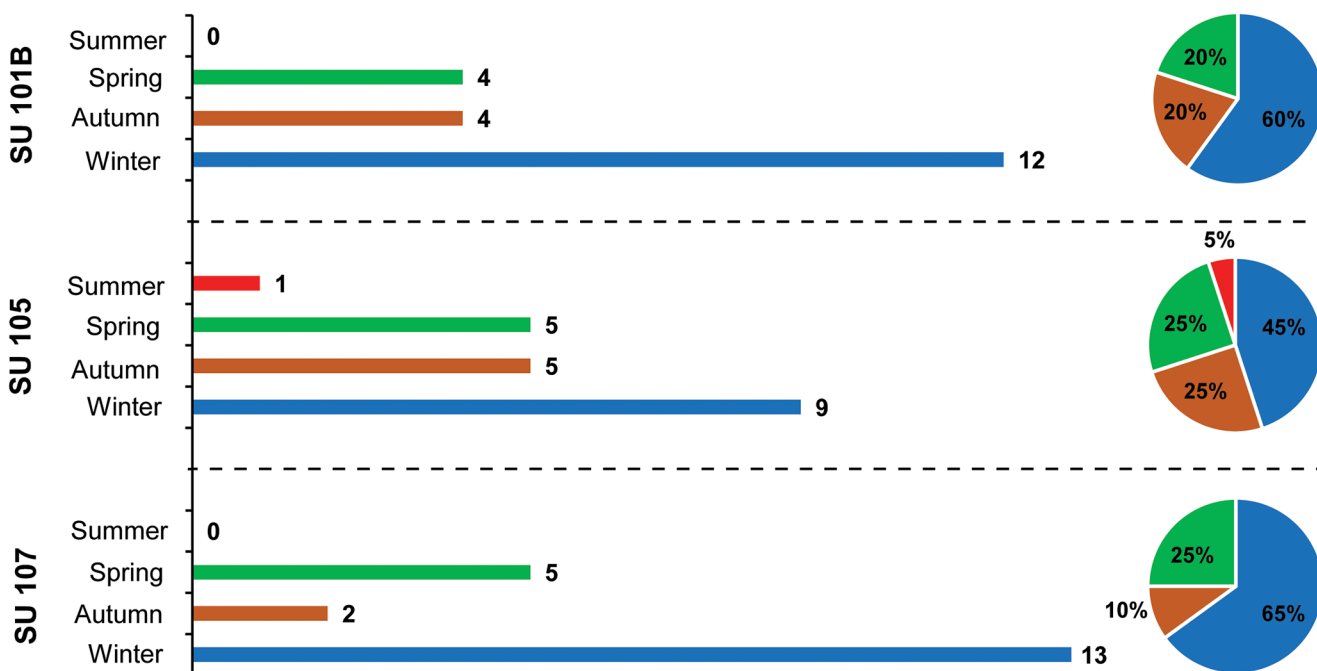

Fig. 4 Seasonality of *P. depressa* by stratigraphic unit (SU). The figure shows the absolute number (bars) and the percentage (pies) of specimens assigned to each season

Fig. 5 Portions of Mutvei's-stained thick section of four *P. depessa* shell recovered from the shell midden site of El Mazo: Dashed white lines indicate growth stoppages and dashed red lines indicate the location throughout the isotope profiles of a shell growth cessation
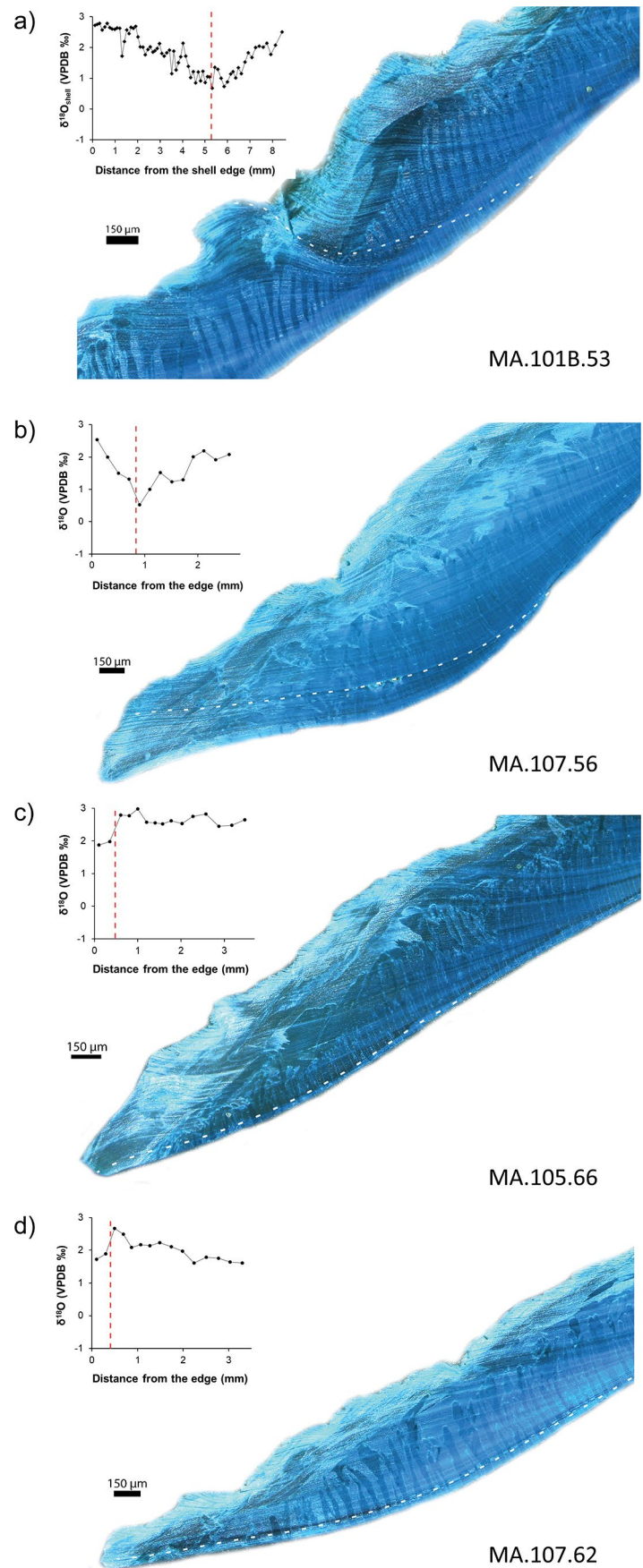
minimum isotope value of the long series (+0.68‰), which was assigned to the summer season based on lower quartile values for unit 101B (−0.07‰ to +0.80‰). Specimen MA.107.56 also showed a growth cessation at 0.9 mm from the ventral margin (Fig. 5b), and similarly the isotope value around the major growth line (+0.52‰) is also assigned to the summer quartile (−0.12‰ to +0.61‰). In both cases, the minimum values of the series are significantly higher than minimum intra-annual $\delta^{18}O$ value estimated for those units, therefore suggesting that there were probably lengthy growth stoppages in these individuals due to exceeding the upper thermal tolerance during summer. Major growth lines were also observed very close to the shell edge (less than 0.4 mm from the margin) on two other specimens (MA.105.66 and MA.107.62), indicating that shell growth ceased a few weeks before the molluscs were collected (Fig. 5c-d). While $\delta^{18}O$ values prior to the shell growth cessation (MA.105.66 = +2.79‰; MA.107.62 = +2.67‰) were clearly assigned to winter quartiles (Table 2), $\delta^{18}O$ values after major growth lines (MA.105.66 = +1.98‰;

MA.107.62 = +1.89‰) were ascribed to intermediary quartiles. These results reported, therefore, a shell growth cessation in the coldest moment of the year because of exceeding the lower thermal tolerance of these two specimens and a resuming of the calcium carbonate deposition in the early spring after the temperature increase.

Relative meat yield (RMY)

Seasonal variation in the average RMY of 950 modern specimens revealed that protein return per unit effort changes throughout the year (Fig. 6). Highest RMY values were always recorded in middle winter (ca. February) and early spring (ca. March). By contrast, the lowest RMY values were always observed in middle summer months (ca. August). Nevertheless, lower RMY were also obtained in late spring, autumn, and even early winter (December 2014). RMY values exhibited a significant correlation with SST variations throughout the three annual cycles ($R^2 = 0.72$, $p < 0.0001$), suggesting that coldest months (ca. from February to April) were more profitable for collecting *P. depressa* limpets.
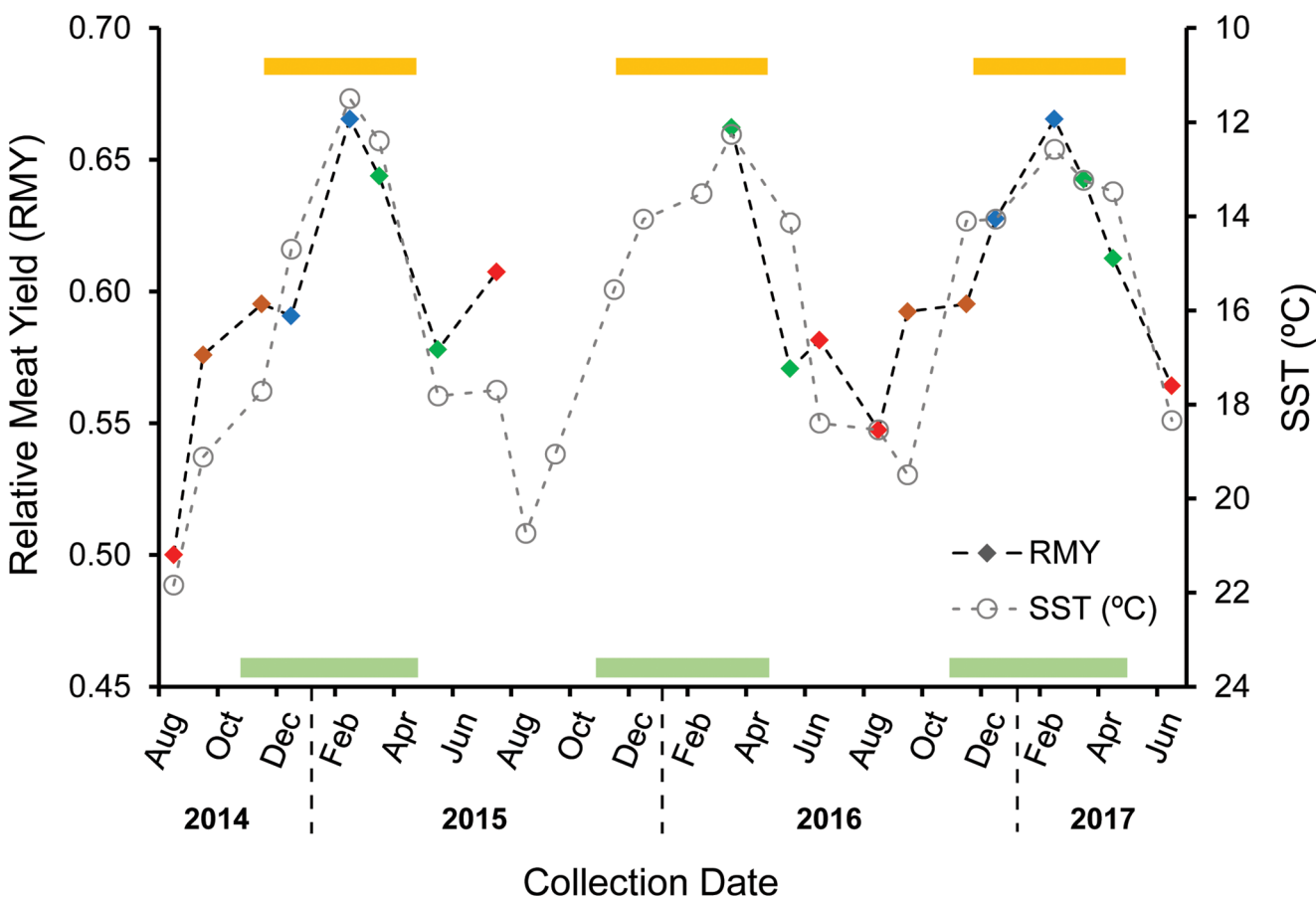

Fig. 6 Variation in annual relative meat yield (RMY) from modern *P. depressa* (diamonds) and current sea surface temperature (SST) (empty grey circles). The colours in the meat yield series represent the season of collection (red = summer; brown = autumn; blue = winter;

green = spring). The upper and lower bars show the period of maximum gonadal development (ca. December to April) (yellow rectangles) and the months when *P. depressa* were primarily collected by the Mesolithic populations in Northern Iberia (green rectangles), respectively

Discussion and conclusion

P. depressa growth patterns in Northern Iberia during the Early and Middle Holocene

A previous study on *P. depressa*, using live-collected specimens in Northern Iberia, suggested that this species grows all year-round but not continuously throughout all seasons (García-Escárzaga et al. 2020). Our results extend these conclusions to archaeological specimens collected during the first millennia of the Holocene (from ca. 9 ka to 7.4 ka cal BP). Prominent major growth lines in specimens MA.101B.53 and MA.107.56 likely indicate shell growth stoppages during the year's warmest months. The position of the minima $\delta^{18}O$ values of these two profiles (Fig. 5a-b) within the summer quartile ranges for each unit (Table 2) suggest that these individuals stopped growing for several weeks during the warmest months of the year. Nevertheless, in both cases, the growth stoppages would not have prevented us from accurately deducing a possible collection in that summer. This is because the last $\delta^{18}O$ values before shell growth cessation could have been assigned to the warmest season quartile (i.e., summer). The same conclusion can be derived from those shells that have reported a growth stoppage during the winter (Fig. 5c-d). Despite shells were not growing during the coldest week of the year and, therefore, recording the minimum annual seawater temperatures, a collection in winter would have been correctly deduced since the last $\delta^{18}O$ value prior to growth stoppages had assigned to the upper quartile (i.e., winter). Furthermore, no analysed shell had reported a growth cessation longer than three months, and all minima and maxima values of all profiles (Supplementary Figs. 1 and 2) are consistent with winter and summer quartiles (Table 2), respectively.

Examining and studying the shell growth patterns near the shell edge was also a very helpful tool for accurately determining the season when the specimens were collected. Mutvei's-stained cross sections revealed major growth lines and short-term stoppages in samples MA.105.66 and MA.107.62 located at 0.35 and 0.30 mm from the shell edge, respectively (Fig. 5c-d). The last $\delta^{18}O$ values before mollusc shell growth stoppages (MA.105.66 = +2.79‰; MA.107.62 = +2.67‰) were ascribed in both specimens to winter. However, $\delta^{18}O$ values after resuming carbonate deposition were assigned to spring. The possibility of deducing a cessation in shell growth close to the edge is crucial for accurately estimating the proper season of mollusc collection. Our observation of a growth stoppage of presumably several weeks because of colder temperatures in MA.105.66 and MA.107.62 has allowed us to read this decrease in $\delta^{18}O$ values as a change of season and not only as a possible short warm event in the middle of the cold

season. These two molluscs stopped shell growth at the end of winter and then resumed it just before their collection by Mesolithic humans during early spring.

Seasonal shellfish collection during the Mesolithic in N Iberia

P. depressa was primarily collected during colder months of the year by Mesolithic populations that inhabited El Mazo from ca. 8.5 ka to 7.8 ka cal BP. This marked seasonal pattern is very similar to that previously observed in Mesolithic occupations in caves and rock shelters along the Northern Iberian coast (Bailey et al. 1983; Deith 1983; Deith and Shackleton 1986), including El Mazo (García-Escárzaga et al. 2019), but also in other places located in Northern Atlantic Europe, such as Great Britain (Mannino et al. 2003). Likewise, a similar seasonality pattern has been documented in the Mediterranean coastal areas (Mannino et al. 2007, 2011, 2014; Colonese et al. 2009, 2018; Prendergast et al. 2016), even though some shellfish exploitation during summer was also observed during the Mesolithic along the Mediterranean coast (Branscombe et al. 2021; Mannino et al. 2007; Prendergast et al. 2016). Our study therefore contributes to the robust body of evidence suggesting that Mesolithic groups that occupied caves and rock shelters in Atlantic Europe and the Mediterranean Basin had a strong preference for consuming intertidal molluscs during the colder months of the year.

Previous studies proposed that such a pattern could reflect low summer human population density along the coast, or scarcity of terrestrial food resources in coastal areas in winter, among others (Deith 1983; Deith and Shackleton 1986; Mannino et al. 2007, 2011; Prendergast et al. 2016). However, the available information so far from the Northern Iberia appears to refute these explanations. Zooarchaeological studies revealed that El Mazo was inhabited year-round (Marín-Arroyo et al. 2020), thus confirming that other prey was available in summer and that humans were locally exploiting them. Traditionally, molluscs have been considered an emergency food supply alternative during periods of scarcity in higher meat return resources (Marín-Arroyo et al., 2013; Moss 2013). However, studies have shown that this may not have always been the case. The role of shellfish in human subsistence strategies along Atlantic Europe has been recently re-evaluated from an approach based on meat yield estimations, concluding that the contribution of this littoral resource to human diets during the Mesolithic could be even higher than terrestrial mammals in some littoral archaeological contexts (García-Escárzaga and Gutiérrez-Zugasti 2021). Moreover, experimental studies demonstrated that winter collections coincide with the period of higher mollusc meat yield, suggesting that winter

Mesolithic collections reflected optimization, based on cost-benefit principles, which does not agree with the idea that shellfish were only an emergency food supply.

Our results from modern *P. depressa* broadly support this optimization argument. The relative meat yield variation year-round confirms that a higher meat yield would have been attained in the late winter and early spring, coinciding with that annual period in which gonads reached their maximum size (Fernández et al. 2016). Although late autumn and early winter did not show maximum meat yield values, they consistently reported a significant increase in relative meat yield compared to summer. This rise in meat yield return that occurs in November probably justified why Mesolithic populations started to collect *P. depressa* limpets again after the summer break at the end of autumn. The results suggest, therefore, that mollusc collection in Southern Europe during the Mesolithic very likely responded to cost-benefit principles supported by a deep human knowledge of local marine ecosystems.

Littoral resource management over time

Previous investigations carried out along the Atlantic façade of Europe have documented an increase in the intensification of littoral resource exploitation patterns from the Palaeolithic to the Late Mesolithic, attending to the evolution of mollusc shell sizes throughout time (Álvarez-Fernández et al. 2011; Gutiérrez-Zugasti 2011; Mannino and Thomas 2001). Biometric analyses conducted from marine shells recovered from El Mazo also revealed short-term changes in the intensification of shellfish collection during the Mesolithic (García-Escárzaga et al. 2022a). Shell sizes and, consequently, the meat grams extracted from each mollusc specimen of the main species represented throughout the El Mazo sequence (García-Escárzaga and Gutiérrez-Zugasti 2021) demonstrated a significant decrease in those stratigraphic units formed around the 8.2 ka cal BP cold event due to higher human pressure on marine resources (García-Escárzaga et al. 2022a). Deciphering seasonality in shellfish collection patterns could also be a helpful tool for inferring how past human managed the use of intertidal resources. For example, Mannino et al. (2007) observed that while molluscs were exclusively harvested during colder months in the Early Mesolithic, their collection expanded to all seasons during the Late Mesolithic. They considered these as a sign of an increase in the intensification of rocky shore mollusc consumption just before of adopting a Neolithic economy.

The results obtained herein showed that *P. depressa* was primarily exploited from late autumn to early spring throughout the sequence (Fig. 4), including during the formation of stratigraphic unit 105, which was dated to during the 8.2 ka cal BP cold event (Fig. 2) and where a significant shell size and meat return decrease has been argued to have been linked to increasing human exploitation of these resources (García-Escárzaga et al. 2022a). These data suggest that despite existing periods of higher anthropic pressure over coastal resources, which provoked a very relevant shell size decrease, this higher intensification in shellfish exploitation did not change the annual subsistence strategies scheduled by Mesolithic populations to mainly collect molluscs during the seasons of higher meat yield return. A conclusion that highlights how last foragers were able to develop and maintain throughout time complex ecological subsistence strategies for not overexploiting available food sources despite periods in which the pressure over marine resources significantly increased, such as during 8.2 ka cal BP cold event.

Author contributions We confirm that all authors have approved the final version of the manuscript and have made substantial contributions. AGE and IGZ designed the isotopic project. AGE, IGZ, DCS and MRGM excavated El Mazo cave. AGE and RAM extracted the calcium carbonate samples from *Patella depressa* shells. AGE, JI and ML conducted the isotopic analyses at the Max Planck Institute for Science of Human History. All authors interpreted the data. All authors wrote and provided comments on the manuscript.

Declarations

Competing interests The authors declare no competing interests.

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