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Seasonality of shellgathering from δ^{18}O analysis and the role of marine molluscs in Mesolithic coastal economies of Atlantic Europe

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ABSTRACT

The role of marine molluscs in Mesolithic subsistence strategies has long been debated, with many studies suggesting that they were of minor significance, used during times of scarcity or as supplementary food sources. However, recent work has challenged this view. This study introduces new seasonal and sub-annual data derived from oxygen-isotope ratios ($\delta^{18}O_{shell}$) of *Patella vulgata* Linnaeus, 1758 and *Phorcus lineatus* (da Costa, 1778) at the archaeological shell midden sites of El Perro, Mazaculos II, Arenillas and El Toral III in the Cantabrian region (northern Iberia, Atlantic Europe). The results provide high-resolution data on the timing of mollusc shell collection for these species and sites over a time span of 4730 years. We compare these results with seasonality studies of terrestrial fauna and previous analyses of molluscs from other sites, and integrate them with other sources of the subsistence economy. We demonstrate that some mollusc harvesting took place in all seasons, with a greater concentration in certain ones, and that this seasonal concentration differed as between species and sites. We conclude that molluscs were part of a coordinated strategy that systematically targeted different species according to their optimal food yield and according to seasons when other food resources were in shorter supply, making a substantial contribution to the viability of the overall palaeoeconomy. The coastal region as a whole was the focus of year-round settlement, but with the use of different sites in different seasons or for different functions, and evidence of extensive movement of individuals between coast and interior.

1. Introduction

Mesolithic shell middens – shell-matrix sites in which shells of edible marine molluscs collected as food are the dominant visible constituent of the deposit (Claassen, 1999; Rick, 2024) – are widely, if patchily, distributed around the coastlines of Atlantic Europe, and to a much lesser degree the Mediterranean (Milner et al., 2007; Colonese et al., 2011; Gutiérrez-Zugasti et al., 2011). The best-known examples occur in concentrated clusters, notably in south-west Portugal, the Cantabrian coast of northern Spain, the Brittany coast of north-west France, the British Isles (mainly Scotland) and the inner straits of Denmark. They pose a number of questions that have been widely debated, notably questions about the palaeodietary significance of the marine molluscs, seasonality of collection, the ways in which their exploitation was integrated with other resources, the role of the shell middens in wider patterns of coastal settlement and mobility, and the question of whether their proliferation in the Mesolithic period represents an overall intensification in the use of marine resources or, more simply, the increased

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visibility of shorelines and coastal settlements following the cessation of postglacial sea-level rise, or some combination of these processes (Bailey and Craighead, 2003; Bailey and Flemming, 2008; Bailey and Milner, 2008; Gutiérrez-Zugasti, 2011; Rick, 2024, and references therein).

In this paper we concentrate on the Cantabrian coastline of northern Spain. The shell middens of this region are of particular interest. They represent one of the largest concentrations in Atlantic Europe, with more than a hundred sites identified and some of the earliest in date, ranging from 11,430 (11.4 ka) cal BP to 6700 (6.7 ka) cal BP (González-Morales, 1982; Straus and Clark, 1986; Bailey and Craighead, 2003; Fano, 2007, 2019; Gutiérrez-Zugasti et al., 2011). They are mostly associated with the Asturian cultural tradition, characterised by the so-called Asturian pick, a flaked pebble tool rather like a small handaxe, thought to be well-suited to removing limpets from the rocks, microlithic flint tools, and regionally distinct lithic industries. The midden deposits are found in caves and rock shelters close to the modern shoreline, usually elevated above it, and sometimes as much as 5 km inland, features which account for the unusually early dates of some of the middens because of their protection from the final stages of postglacial sea-level rise. Deeper layers of Late Pleistocene or Terminal Pleistocene age are stratified beneath midden deposit at some sites and contain marine shells, though in smaller quantities that do not qualify as shell-matrix deposits. Many of the shell-midden deposits were eroded in antiquity, leaving only cemented fragments attached to the cave walls and ceiling, or were dug out by excavation in the early 20th century (Vega del Sella, 1923). However, a number of well-preserved deposits have been discovered and excavated with modern recovery methods in more recent decades. The shell component is dominated by rocky-shore gastropod species, principally limpets, *Patella* spp. and topshells, *Phorcus lineatus* (da Costa, 1778), previously referred to in the literature by the genus names *Monodonta* or *Osilinus* (García-Escárzaga et al., 2022; Arniz-Mateos et al., 2024). Other food remains include bones of terrestrial mammals such as deer, wild boar, and goat (Marín-Arroyo and González-Morales, 2009; Andreu-Alarcón, 2013; Arenas-Sorriqueta et al., 2024), bones of fish (Álvarez-Fernández et al., 2011; Fano et al., 2013) and wild fruits and nuts (López-Dóriga, 2016; Núñez de la Fuente, 2018).

Data on seasonality of mollusc collection are central to the investigation of questions about the palaeodietary contribution of molluscs and the role of shell middens in wider patterns of settlement and mobility. Oxygen-isotope ratios from shell carbonates ($\delta^{18}O_{shell}$) have become a well-established method for reconstructing past sea-surface temperatures (SST) and the seasonality of shellfood collection (Goodwin et al., 2003; Schöne et al., 2004; Burmanl and Schmitz, 2005; Fenger et al., 2007; Schöne, 2008). In northern Iberia, a number of oxygen isotope seasonality studies have been carried out, including pioneering work in the 1980s, resulting in seasonal determinations of improving number, reliability and precision on limpets (*Patella vulgata* Linnaeus, 1758, *Patella depressa* Pennant, 1777), topshells (*P. lineatus*) and mussels (*Mytilus galloprovincialis* Lamarck, 1819) (Bailey et al., 1983; Deith, 1983; Deith and Shackleton, 1986; Gutiérrez-Zugasti et al., 2015; 2017; García-Escárzaga et al., 2019a; 2019b; Milano et al., 2022; García-Escárzaga et al., 2024a; 2025). However, the interpretation of these results has been limited by analytical costs, small sample sizes, or application to individual molluscan taxa or individual midden deposits that may not be representative of wider patterns of palaeoeconomy and site use.

Our aim in this paper is to present a larger set of oxygen isotope seasonality determinations from a variety of midden deposits of varied date and location, and for the two principal species, *P. vulgata* and *P. lineatus*, and to integrate their interpretation with other sources of evidence of palaeodiet, subsistence economy and seasonality, including previous seasonality studies of these and other species at other shell middens in the region. We present stable oxygen isotope analyses from four shell-midden deposits that have been discovered and excavated in recent years in varied locations, namely El Perro, Mazaculos II, Arenillas and El Toral III (Fig. 1), with dates ranging from 11.4 to 6.7 ka cal BP. We present details of these sites and the shell samples selected for analysis and our methods of analysis. We present the resulting seasonality determinations and compare them with previous studies of seasonality, and we discuss their interpretation in relation to questions about the significance of marine molluscs in the Mesolithic

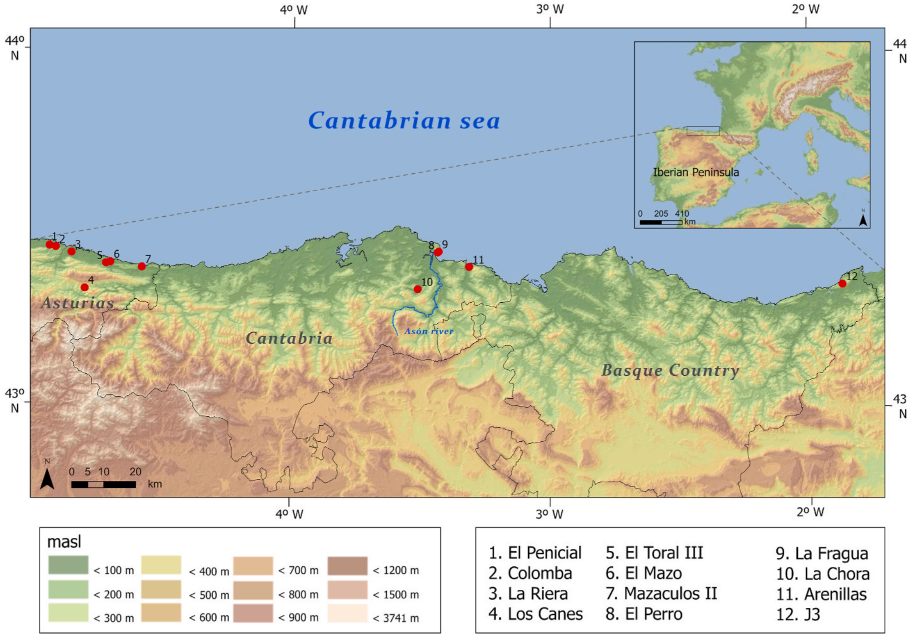


Fig. 1. Map of the Cantabrian coast in northern Iberia, Spain, with the location of the principal archaeological sites discussed in the text. Site numbers 1 to 7 are located on the coastline of Asturias autonomous community, where shell midden deposits were first investigated in the early 20th century, hence the label 'Asturian' for the Mesolithic culture of the region. Sites 8 to 11 are in the autonomous community of Cantabria, and 12 in the province of Guipúzcoa (autonomous community of the Basque Country). The site of La Chora (site 10) is unusually far inland, about 10 km from the open coastline, but its molluscan assemblage is dominated by *Scrobicularia plana* (da Costa, 1778), a brackish water bivalve of estuarine habitat, and the nearest source would have been in the Asón River about 5 km distant. Masl: metres above sea level.

palaeoeconomy, and wider patterns of settlement and mobility in the Cantabrian coastal zone.

2. Materials and methods

2.1. Materials

2.1.1. Archaeological sites

The four sites selected for study are summarised below (see Supplementary Information 1 [SI 1] for further details). El Perro is a rockshelter located in Santoña (Cantabria) on the southeastern slope of Mount Buciero. The site preserves a shell midden along the western wall, with deposits extending up to 2 m above the current ground level. The Mesolithic deposits correspond to Level 1, subdivided into five sublevels (1.1–1.5), and are dated to 11.4–10.2 ka cal BP.

Mazaculos II is a cave situated near the Cabra River (Asturias) at 35 m above sea level, approximately 400 m from the present coastline. Excavations were carried out in Sector 1 (outer rock shelter) and Sector 3 (interior chamber). The Mesolithic occupation is represented by Levels 1, 2 and 3 of Sector 1, which are subdivided into several shell-rich sublevels, including habitation floors in Level 3. Level 1.3, from which the material was analysed, is dated to 9.3–8.4 ka cal BP.

Arenillas is a small cave located on the slopes of Mount Cerredo (Cantabria), at approximately 20 m above sea level. The Mesolithic occupation is represented by Level 0, a shell midden dated to 8–7.1 ka cal BP. This deposit, preserved in a small chamber at the rear of the vestibule, consists mainly of marine molluscs.

El Toral III is a rockshelter located in San Roque del Acebal (Asturias), about 1 km from the present coastline, within the Toral-Pellunarices karst system. Excavations in Area B revealed two vertical stratigraphic sequences: units 17–19 and 20–22, both analysed in this study. These shell midden deposits are dated to 8–6.7 ka cal BP and contained mollusc shells, bones of fish and terrestrial macrofauna, charcoal, seeds, and human remains.

2.1.2. Shell remains

The shells selected for isotope analysis were limited by the species available from excavation, the condition of the shell material, and the analytical costs of isotope measurement. Only limpets (*P. vulgata*) were available for analysis from El Perro, Mazaculos II and Arenillas. From El Toral III, both limpets and topshells (*P. lineatus*) were available. Our target numbers selected for analysis were 10 whole shells from each stratigraphic unit and for each species, as follows: 10 *P. vulgata* specimens from stratigraphic units (SU) 1.4 at El Perro (11.4–10.2 ka cal BP), 1.3 at Mazaculos II (9.3–8.4 ka cal BP) and the shell midden unit (SU 0) at Arenillas (8–7.1 ka cal BP); and 10 shells each of *P. vulgata* and *P. lineatus* from each of five stratigraphic units at El Toral III in Area B (SUs 17, 19 and 20–22, 8–6.7 ka cal BP), resulting in a total of 130 shells (see S1–S3 for details of radiocarbon dates and the shells selected for study).

The target of 10 shells per species per stratigraphic unit was determined by the fact that a large amount of the shell material in these midden deposits is fragmented or otherwise unsuitable for stable isotope analysis, the need for whole shells and multiple isotope analyses from individual shells to establish the edge values and their relationship to the preceding cycle of isotope values along the growth axis of the shell, the need for comparability between the data from the various sites and stratigraphic units, and the limitations on numbers of analyses imposed by analytical costs and labour time. In selecting shells suitable for isotope analysis, we avoided specimens with significant taphonomic alterations, such as fragmentation, post-depositional alteration of the shell carbonate, or bioerosion. We also avoided limpet shells >40 mm in length and topshells >18 mm in width, because these larger shells are typically older specimens in which growth rates are much reduced towards the growing edge of the shell, resulting in poorly resolved growth increments unsuitable for seasonality determinations (Gutiérrez-Zugasti et al., 2017; García-Escárzaga et al., 2019a).

A standard sample size calculation for estimating proportions (Cochran, 1977) has established that the total sample of 130 shells is representative of the total number of molluscs recovered from all sites at the 95 % confidence level, with a margin of error of 9 %, which we consider acceptable. The calculation is based on the formula:

$$n = \frac{z^2 \cdot p \cdot (1 - p)}{E^2} \tag{1}$$

Where $z = 1.96$ (for 95 % confidence), $p = 0.5$ (expected proportion, a conservative estimate of 0.5 is used when this value is unknown), and $E = 0.09$ (margin of error). This yields a minimum required sample size of approximately 119; our sample of 130 exceeds this threshold. When the calculation is performed at the level of individual stratigraphic units, the margin of error increases to around 30 %, since smaller population sizes require proportionately larger sample sizes to achieve a representative result. Given the constraints on the number of isotope measurements and the consistency of the overall dataset, we consider the sample size to be sufficiently robust for identifying significant seasonal patterns and for comparisons between stratigraphic units and sites at the regional scale.

2.2. Methods

Limpets and topshells were cleaned with deionised water for 48 h to remove adhered sediment and then air-dried. Calcium carbonate ($CaCO_3$) micro-samples were extracted using two different methods, depending on shell morphology.

For *P. vulgata*, two thick sections, each 3.5 mm in thickness and oriented parallel to the maximum growth axis, were prepared to analyse the inner m+2 layer (Fenger et al., 2007). To prevent fracturing during cutting, the shells were coated with epoxy resin. The shell sections were mounted on glass slides and polished using silicon carbide (SiC) powder with 600 and 800 grit for 10 min each, followed by final polishing with 1 μm aluminium oxide (Al_2O_3) for as long as necessary to achieve a smooth and clean surface. One of the sections was stained with Mutvei's solution to enhance the visibility of growth lines (Schöne et al., 2005), while the other was used for $CaCO_3$ micro-sampling from the m+2 calcite layer (Fenger et al., 2007) (Fig. 2a). $CaCO_3$ micro-samples were collected from the shell edge to the apex, following the direction of the growth lines, in accordance with established methodologies (Fenger et al., 2007; Gutiérrez-Zugasti et al., 2017; Garcia-Escárzaga et al., 2024a). A New Wave Research computer-controlled microdrill, equipped with a 1 mm conical SiC dental drill bit, was used for limpets recovered from El Perro, Mazaculos II, and Arenillas. For limpets from El Toral III, $CaCO_3$ micro-samples were extracted using a Minimo drill, equipped with a 1 mm conical SiC dental drill bit and coupled with a digital microscope. The number of micro-samples per specimen varied. In eight out of ten shells per stratigraphic unit, a short sequence of 10 $CaCO_3$ micro-samples was taken, sufficient to show the trend of isotope values towards the growing edge, whereas in the remaining two individuals per unit, two long sequences, ranging from 31 to 104 micro-samples, were milled and collected to show the range of isotope values through at least one year's full growth cycle, resulting in a total of 1818 measurements.

For *P. lineatus*, prior to sampling, the outer periostracum and calcite layers were removed to expose the inner aragonite layer, from which $CaCO_3$ micro-samples were extracted using a manual microdrill equipped with a 0.5 mm tungsten drill bit at 1 mm intervals along the mollusc shell growth axis (Gutiérrez-Zugasti et al., 2015; García-Escárzaga et al., 2019b, 2024b, 2025) (Fig. 2b). As described for limpets, in eight out of ten topshells per stratigraphic unit, a short sequence of ten micro-samples was taken, and in two topshells per unit, two long sequences ranging from 36 to 52 micro-samples. The first micro-samples were obtained from the inner part of the shell aperture, and the remaining micro-samples were taken from the outer part of the shell,

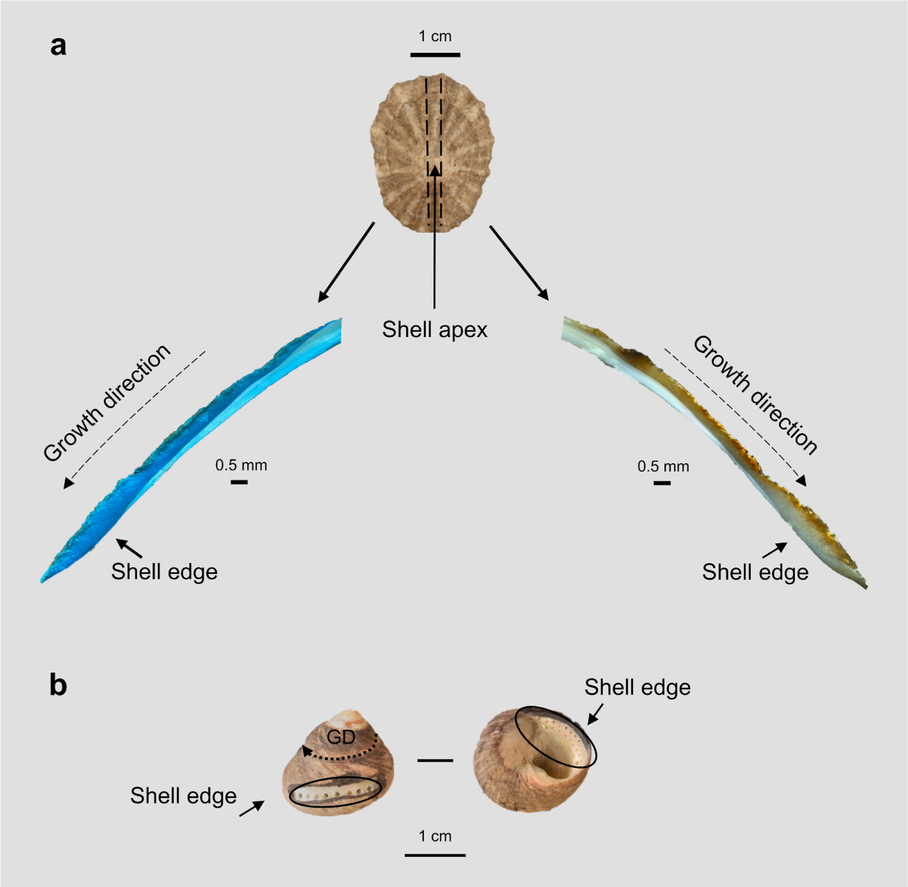


Fig. 2. (a) *P. vulgata* specimen. The dashed lines indicate the cutting axis for the two thick shell sections: one treated with Mutvei's solution and the other designated for $CaCO_3$ sampling. (b) *P. lineatus* specimen micro-samples collected from the outer and inner parts of the shell edge, following the growth direction (GD).

resulting in a total of 832 measurements.

Micro-samples from El Perro were analysed at the Isotope Laboratory of the Instituto de Geociencias (CSIC-UCM, Madrid, Spain), using a Thermo Scientific Mat 235 isotope ratio mass spectrometer (IRMS) coupled to a Thermo Kiel IV device. Standards included NBS18 (−23.2 ‰ VPDB) and NBS19 (−2.20 ‰ VPDB). Analytical replicates were conducted every 10 samples to confirm analytical precision, with an uncertainty of ±0.1 ‰. For Mazaculos II and Arenillas, $\delta^{18}O_{shell}$ measurements were performed at the University of Bradford (UK) using a Thermo GasBench 2 preparation system, coupled to a Thermo Delta V Advantage IRMS. Calibration employed NBS18 and NBS19 standards, achieving a precision better than ±0.1 ‰. Finally, micro-samples from El Toral III were measured at the University of Burgos (Spain) using a Delta V Plus mass spectrometer, coupled to a Gas Bench II. Calibration was performed using international standards IAEA-603 (−2.37 ‰ VPDB) and NBS18. The precision of these analyses was ±0.1 ‰.

To determine the season of collection, we used the quartile method proposed by Mannino et al. (2003, 2007) and routinely employed by other similar studies (Colonese et al., 2009, 2012; Hausmann and Meredith-Williams, 2017; Prendergast et al., 2017; García-Escárzaga et al., 2019b, 2024a, 2024b; Branscombe et al., 2020). The range of measured $\delta^{18}O_{shell}$ values for each individual stratigraphic unit was estimated using the maximum and minimum $\delta^{18}O_{shell}$ values obtained from both long and short sub-sample sequences. The measured $\delta^{18}O_{shell}$ range for each unit was determined separately for each taxon and subsequently divided into four quartiles. The upper and lower quartiles correspond to winter and summer, respectively, while the intermediate quartiles represent spring and autumn. Finally, the mollusc shell edge $\delta^{18}O_{shell}$ values from all individual shell micro-sampling series were assigned to one of these quartiles to determine the season of collection for each mollusc individual. If the shell edge $\delta^{18}O_{shell}$ value fell within either of the intermediate quartiles, the $\delta^{18}O_{shell}$ trend prior to harvesting of the organism was examined to identify the season of capture. An increasing $\delta^{18}O_{shell}$ trend indicated autumn collection, whereas a decreasing trend suggested spring harvesting.

Although the quartile method assumes broadly comparable seasonal representation along the shell growth axis, modern sclerochronological studies in the Cantabrian region indicate that growth-rate variability in *P. vulgata* and *P. lineatus* does not compromise seasonal interpretation. In *P. vulgata*, seasonal growth cessations or reduced growth are limited in duration and do not exceed three months (Gutiérrez-Zugasti et al., 2017), whereas *P. lineatus* exhibits largely continuous growth throughout the year, effectively recording all four seasons (Gutiérrez-Zugasti et al., 2015). Therefore, we consider the quartile method a viable approach for determining the season of shell collection in these taxa within the methodological framework applied here.

3. Results

3.1. Shell oxygen isotope ratios

The isotopic analysis of *P. vulgata* from El Perro, Mazaculos II, Arenillas and El Toral III reveals sinusoidal profiles indicative of cyclical annual patterns along the shell growth axis. The long sequences reflect at least two to three annual cycles, while the shorter sequences range from several months to approximately one year, depending on the specimen (Fig. 3a) (SI 4). The values obtained range from 2.54 ‰ to −0.58 ‰ (Table 1).

The $\delta^{18}O_{shell}$ values of *P. lineatus* at El Toral III also show profiles with a sinusoidal pattern, identifying a variable number of annual

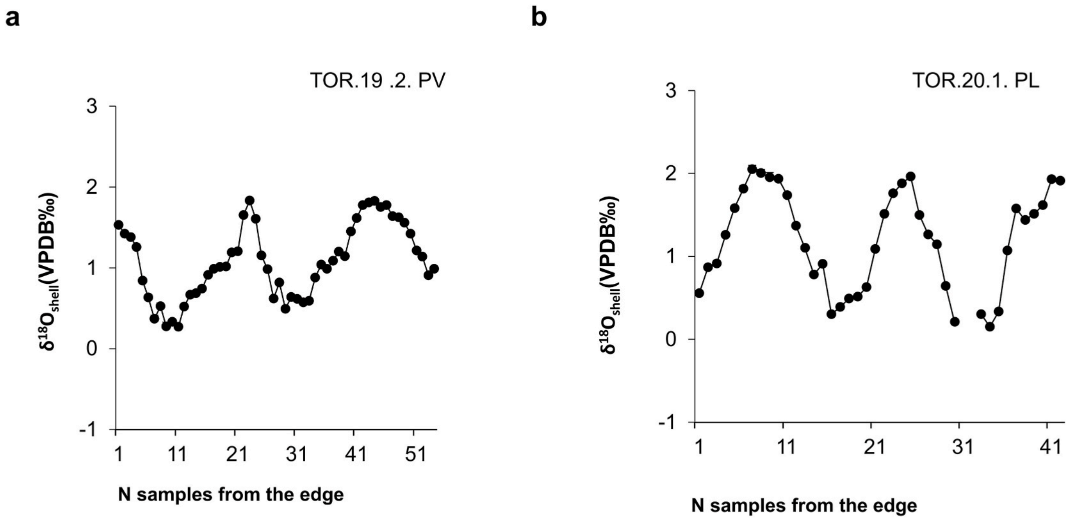


Fig. 3. (a). Example of *P. vulgata* long isotope sequence from El Toral III. (b). Example of *P. lineatus* long isotope sequence from El Toral III. The rest of the sequences can be found in SI4.

Table 1
Maximum and minimum $\delta^{18}O_{shell}$ values from short and long sequences for each stratigraphic unit for *P. vulgata* from each archaeological site analysed in this study expressed in ‰ relative to VPDB standard.

Archaeological site	Stratigraphic unit (s)	Shell code	Max. $\delta^{18}O_{shell}$ value	Min. $\delta^{18}O_{shell}$ value	$\delta^{18}O_{shell}$ range	Q1	Q2-Q3	**Q4**
El Perro	1.4	PR.1.01	2.21	0.34	1.87			
		PR.1.12	2.44	0.09	2.35			
		PR.1,02,04–07,09–011	2.2	0.35	1.85			
	TOTAL		2.44	0.09	2.35	2.44–1.85	1.84–0.68	0.67–0.09
Mazaculos II	1.3	MZ.9	2.37	0.37	1.99			
		MZ.11	2.19	0.54	1.64			
		MZ.1.3.1,3,4–6,11–13,15	2.28	0.26	2.03			
	TOTAL		2.37	0.26	2.11	2.37–1.84	1.83–0.79	0.78–0.26
Arenillas	0	AR.C.4	2.05	−0.25	2.3			
		AR.C.10	1.93	−0.58	2.51			
		AR.C.1,3,5,9,11,13–15	1.94	−0.35	2.28			
	TOTAL		2.05	−0.58	2.64	2.05–1.39	1.38–0.08	0.07 to −0.58
El Toral III	22	TOR.22.1.PV	1.37	−0.53	1.9			
		TOR.22.2. PV	1.65	−0.1	1.75			
		TOR.22.3. PV–TOR.22.10. PV	2.29	0.35	1.94			
	TOTAL		2.29	−0.53	2.82	2.29–1.59	1.58–0.19	0.18 to −0.53
	19	TOR.19.1.PV	2.19	−0.16	2.35			
		TOR.19.2. PV	1.83	0.27	1.56			
		TOR.19.3. PV–TOR.19.10. PV	2.21	0.31	1.90			
	TOTAL		2.21	−0.16	2.37	2.21–1.62	1.61–0.43	0.42 to −0.16
	21	TOR.21.1.PV	1.55	−0.14	1.69			
		TOR.21.2. PV	2.11	0.21	1.90			
		TOR.21.3. PV–TOR.21.10. PV	2.26	−0.33	2.58			
	TOTAL		2.26	−0.33	2.58	2.26–1.61	1.60–0.32	0.31 to −0.33
	20	TOR.20.1.PV	2.17	0.34	1.83			
		TOR.20.2. PV	1.69	0.35	1.34			
		TOR.20.3. PV–TOR.20.10. PV	2.00	0.41	1.86			
	TOTAL		2.17	0.34	1.83	2.17–1.71	1.70–0.8	0.7–0.34
	17	TOR.17.1.PV	1.47	−0.11	1.58			
		TOR.17.2. PV	1.79	−0.20	1.98			
		TOR.17.3. PV–TOR.17.10. PV	2.54	0.29	2.25			
	TOTAL		2.54	−0.20	2.74	2.54—1.86	1.85—0.48	0.47 to −0.2

Maximum and minimum δ18Oshell values from short and long sequences for each stratigraphic unit for P. vulgata from each archaeological site analysed in this study expressed in ‰ relative to VPDB standard.

cycles. Longer sequences represent at least two annual cycles, while shorter ones cover periods ranging from several months to approximately one year, depending on the specimen (Fig. 3b) (Supplementary Information 4). The values obtained range from 2.77 ‰ to −0.15 ‰ (Table 2).

3.2. *Seasonality of shell collection*

The four archaeological sites exhibit a broad temporal range of limpet collection throughout the year, though with variations in the preference for specific periods (Fig. 4). At least three seasons are consistently represented. In the early Mesolithic, in unit 1.4 from El Perro, spring accounts for half of the collected specimens, while autumn and winter are also represented, with no evidence of summer collection. In later periods, unit 1.3 of Mazaculos II exhibits a similar pattern, with spring dominating, but in this case followed by summer and autumn, while winter is absent. The late Mesolithic sequence of Arenillas (unit 0), exhibits a seasonal pattern with a predominant collection in summer, followed by early autumn, winter and spring. Finally, at El Toral III, winter collection remains relatively consistent throughout the sequence, except in unit 20, where its representation is lower. Autumn follows a similar pattern, with consistent values except in unit 20, where it increases significantly at the expense of winter. Spring gradually declines, while summer is recorded in comparable proportions only at the beginning and end of the sequence.

Specimens of *P. lineatus* from El Toral III show a harvesting pattern that differs from the limpets. Harvesting mainly took place during winter/late autumn, while representation of other seasons is limited (Fig. 5). Winter is the dominant season throughout the sequence, similar to *P. vulgata* from the same site. Units 19 and 17 reflect collection in winter and autumn, whereas units 22 and 21 also record collections in the spring period. Overall, a consistent pattern is observed throughout the sequence, except for unit 20, which has evidence of summer collection but only from a single shell.

4. Discussion

4.1. *Seasonality of shellfish collection*

Very little seasonality data has previously been obtained from *P. vulgata* shells because of irregularities in growth patterns, diagenetic alteration of shell carbonate and relatively coarse techniques for sampling along the growth axis of the shell. Deith and Shackleton (1986) produced edge values for 25 shells from the Asturian levels of La Riera, suggesting emphasis on winter or autumn, with possible hints of summer collection compromised by potential diagenetic contamination. Analysis of aragonite/calcite ratios in incremental growth structures at La Riera was later shown to provide seasonality information, with evidence of collection in all seasons of the year throughout the *ca.* 16,000-year sequence of this site (Bailey and Craighead, 2003). However, the assignment to season involved quite a large margin of uncertainty, and the sample size was very small, with only one shell per stratigraphic unit, and just two limpet shells from the upper Mesolithic (Asturian) levels, both showing collection in autumn or winter. The new seasonality data presented here are therefore significant in providing the first substantial data set for *P. vulgata* seasonality in the Cantabrian region and an improved seasonal resolution compared with previous results. Moreover, with the larger sample size available, the results demonstrate that limpets were exploited in all seasons of the year in all of our sites and stratigraphic units, albeit with differences of seasonal emphasis at different sites or in different periods. Spring collection dominated at El Perro and Mazaculos II, summer at Arenillas, and mostly winter or autumn at El Toral III, without any obvious time trend throughout the 4730-year sequence represented by our four sites.

The new data on *P. lineatus* from El Toral III reveal contrasting results, with a consistent focus on winter harvesting throughout the sequence, a lower representation of autumn and spring, and rare summer collection. These findings agree with the seasonality records from previous investigations of other Mesolithic sites in the Cantabrian region, including El Mazo (units 108, 107, 110, 105, 112C and 101B) (García-Escárzaga et al., 2019b), La Riera (unit 29) (Deith and Shackleton, 1986), El Penicial (Deith, 1983), Mazaculos II (unit 1.1, 1.3, 2, 2.2 and 3.3) (Deith, 1983), and J3 (unit D) (García-Escárzaga et al., 2025) (Fig. 6). El Mazo provides the most comprehensive dataset and reveals striking similarities in seasonality patterns with El Toral III, indicating a broadly consistent exploitation strategy. Winter season predominates at both sites, while summer harvesting remains minimal, further reinforcing the overall trend of collection in the colder months. Expanding the comparison to other regional sites emphasises the dominance of winter harvesting. At J3, more than half of the shells analysed were collected in winter, more than the combined total for autumn and spring. At La Riera, isotopic results indicate collection primarily in spring and autumn (Deith and Shackleton, 1986). Mazaculos II and El Penicial show a wider distribution across seasons, although harvesting still occurred predominantly in the colder months (Deith, 1983; Deith and Shackleton, 1986).

Table 2
Maximum and minimum $\delta^{18}O_{shell}$ values from short and long sequences for each stratigraphic unit from El Toral III for *P. lineatus* analysed in this study expressed in ‰ relative to VPDB standard.

Stratigraphic unit (s)	Shell code	Max. $\delta^{18}O$ value	Min. $\delta^{18}O$ value	$\delta^{18}O$ range	Q1	Q2-Q3	Q4
22	TOR.22.1.PL	2.31	0.49	1.82			
	TOR.22.2. PL	2.55	0.20	2.36			
	TOR.22.3. PL–TOR.22.10.PL	2.77	0.23	2.54			
TOTAL		2.77	0.20	2.57	2.77–2.13	2.12–0.84	0.83–0.20
19	TOR.19.1.PL	2.30	0.38	1.93			
	TOR.19.2. PL	2.37	0.17	2.19			
	TOR.19.3. PL–TOR.19.10.PL	2.26	0.13	2.13			
TOTAL		2.37	0.13	2.23	2.37–1.81	1.80–0.69	0.68–0.13
21	TOR.21.1.PL	2.68	0.19	2.49			
	TOR.21.2. PL	2.67	0.49	2.17			
	TOR.21.3. P–TOR.21.10.PL	2.68	0.31	2.37			
TOTAL		2.68	0.19	2.50	2.68–2.06	2.05–0.81	0.80–0.19
20	TOR.20.1.PL	2.05	0.15	1.90			
	TOR.20.2. PL	2.48	0.33	2.15			
	TOR.20.3. PL–TOR.20.10.PL	2.40	0.23	2.16			
TOTAL		2.48	0.15	2.33	2.48–1.90	1.89–0.73	0.72–0.15
17	TOR.17.1.PL	2.19	0.12	2.07			
	TOR.17.2. PL	2.30	0.39	1.91			
	TOR.17.3. PL–TOR.17.10.PL	2.28	−0.15	2.42			
TOTAL		2.30	−0.15	2.45	2.30–1.69	1.68–0.46	0.45 to −0.15

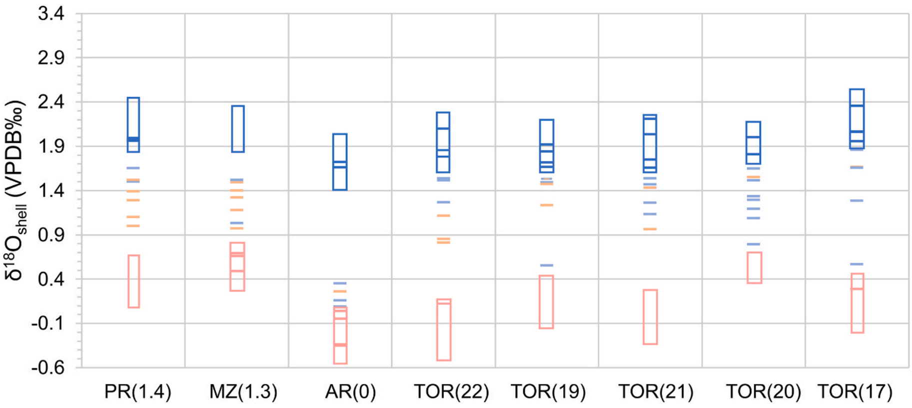


Fig. 4. $\delta^{18}O_{shell}$ edge values from each specimen of *P. vulgata* per stratigraphic unit from El Perro (PR), Mazaculos II (MZ), Arenillas (AR) and El Toral III (TOR) are represented by a dark line, with blue and pink rectangles indicating the maximum and minimum $\delta^{18}O_{shell}$ values of winter and summer. Seasons are colour-coded as follows: winter (dark blue), spring (orange), summer (pink) and autumn (light blue).

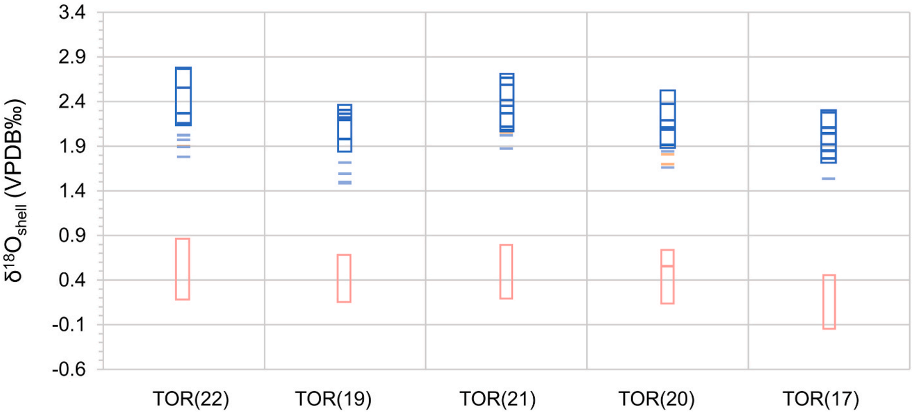


Fig. 5. $\delta^{18}O_{shell}$ edge values from each specimen of *P. lineatus* per stratigraphic unit from El Toral III are represented by a dark line, with blue and pink rectangles indicating the maximum and minimum $\delta^{18}O_{shell}$ values of winter and summer. Seasons are colour-coded as follows: winter (dark blue), spring (orange), summer (pink) and autumn (light blue).

This pattern has been recorded in other areas of the Atlantic façade, such as the Mesolithic site of Culverwell, located in the south of England (Mannino et al., 2003; Mannino and Thomas, 2007). The results for *Phorcus turbinatus* (Born, 1778)*,* a spiral gastropod of the same genus in the Mediterranean, show a similar pattern at the Mesolithic sites of Grotta della Serratura, Grotta di Cala Mancina, Grotta d'Oriente, Grotta del Uzzo and Grotta delle Uccerie in SW Italy and Sicily, with harvesting periods primarily during winter and autumn (Mannino et al., 2007; Colonese et al., 2009, 2018).

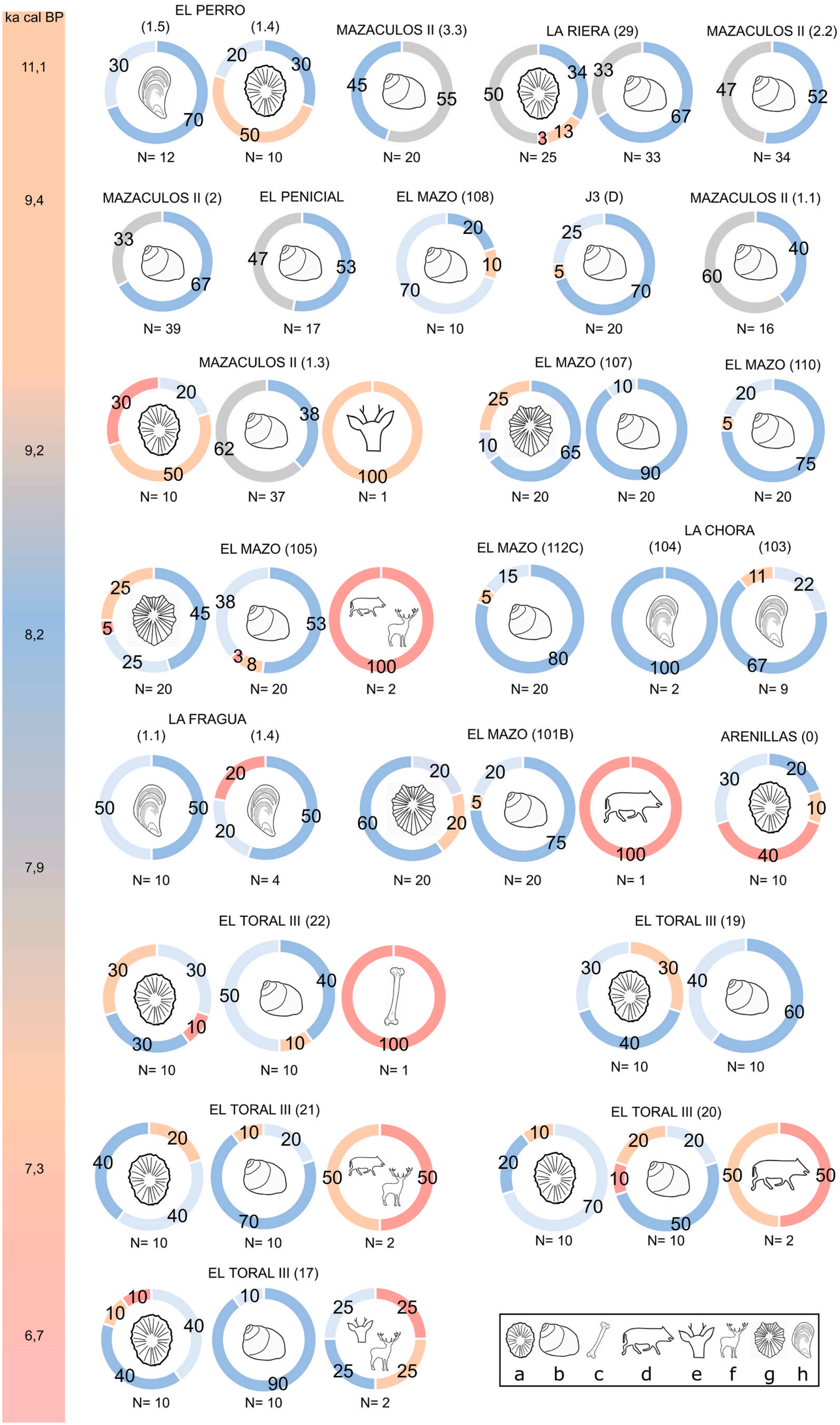
Other species that are less well represented in terms of isotopic data, such as the limpet *P. depressa*, also show a cold-season exploitation pattern, notably at El Mazo, where half the shells were collected in winter, followed by spring and autumn (García-Escárzaga et al., 2024a, Fig. 6). Finally, seasonality data for the bivalve *M. galloprovincialis* in several Cantabrian Mesolithic sites also reveal variations in seasonal harvesting patterns, predominantly in the colder months at El Perro and La Chora, with evidence of year-round harvesting at La Fragua (Milano et al., 2022; León-Cristóbal et al., 2024, Fig. 6).

4.2. Differences in the seasonal patterns of shell collection and the palaeodietary significance of shellfood

We begin with the seasonality evidence for *P. lineatus*, which has the largest number of seasonality determinations from the widest range of sites, and which shows a consistent predominance of collection in the colder months of the year. One hypothesis for this seasonal concentration is that the shell middens were seasonal occupations, only used in the autumn-winter-spring period by people who dispersed inland during the summer months following the seasonal movement of ungulates such as red deer (Bailey, 1973; Deith, 1983). The small number of isotope values originally available for topshells and limpets also seemed to be consistent with this. However, this hypothesis is now definitively ruled out in light of subsequent data. Our new results confirm the predominance of winter collection for *P. lineatus* shells, but demonstrate that *P. vulgata* shells were collected in all seasons, although with a general emphasis on winter and spring, except at Arenillas. Here summer was the dominant season of collection, and some summer collection is also recorded at Mazaculos II and El Toral III.

Season of death information is also available from some of the mammal remains, notably at El Mazo, Mazaculos II and El Toral III (Fig. 6). At El Mazo, juvenile and infant specimens of deer and wild boar, recovered in units 100/101, 103, 103.1, and 105, show that hunting events took place at the end of spring and during the summer, specifically between May and August (Andreu-Alarcón, 2013). At Mazaculos II, hunting of ungulates was restricted to the late spring months, possibly due to a more sporadic use of the site (Marín-Arroyo and González-Morales, 2009). At El Toral III there is evidence of hunting in spring in the earliest level, progressing to spring and summer in later levels, and hunting in all seasons at the end of the sequence (Andreu-Alarcón, 2013).

The above data demonstrate that both limpets and ungulates were exploited in the spring and summer. Other resources were also available



(caption on next page)

Fig. 6. Seasonality patterns of foraging by $\delta^{18}O_{shell}$ edge values, represented as percentages and number of specimens (N), for archaeological sites and their stratigraphic units (in parentheses for those that include this information) organised by chronology on the vertical axis. Seasons are colour-coded as follows: winter (dark blue), spring (orange), summer (pink), autumn (light blue), and autumn/spring (grey) for La Riera, El Penicial, and topshells from Mazaculos II, where these seasons are not distinguished. The different species in the legend correspond to: (a) *P. vulgata,* (b) *P. lineatus*, (c) undetermined infant ungulate bone, (d) *Sus scrofa* Linnaeus, 1758, (e) *Capreolus capreolus* (Linnaeus, 1758), (f) *Cervus elaphus* Linnaeus, 1758, (g) *P. depressa* and (h) *M. galloprovincialis*.

and were likely harvested at different seasons of the year. Marine fish bones have been identified at several Mesolithic sites in the Cantabrian region, including sea bream (*Diplodus* sp.) at Colomba, specimens of the *Serranidae* family at Águila C and Poza l'Egua, and sole (*Soleidae*) at La Riera and Santa Catalina (Álvarez-Fernández, 2011). Fish remains (still under study) are also present at El Mazo and El Toral III. No seasonality data are at present available, but fish would have added to the variety of resources capable of sustaining human settlements in the coastal zone. Plant foods, though notoriously under-represented because of poor preservation, were also likely available and evidence of hazelnuts (*Corylus avellana* L.), indicating autumn collection, is present at El Toral III, Mazaculos II, Arangas, El Carabión and El Mazo (López-Dóriga, 2016; Núñez de la Fuente, 2018). Remains of figs (*Ficus carica* L.) and fruits of rowan trees (*Sorbus* sp.), with their fruiting periods typically occurring in late summer and autumn, have also been identified at El Toral III (López-Dóriga, 2016).

Finally, palaeodietary analysis of stable isotopes $\delta^{13}C$ and $\delta^{14}N$ in human bones from Mesolithic burials at the inland site of Cueva de Los Canes, a site over 10 km inland in the foothills of the Picos de Europa mountain range, indicates a diet dominated by terrestrial foods, with scarcely any trace of marine protein (Arias, 2006, 2013) which suggests that inland populations did not move to the coast during the colder months. This contrasts with stable isotope evidence from human bones in the coastal shell middens of Colomba and J3, which show a strong marine palaeodietary signal.

In summary, varied sources of seasonality evidence demonstrate year-round settlement of Mesolithic populations in the coastal zone and separate populations in the interior (especially in the eastern area of the Cantabrian region, currently known as the autonomous community of Asturias), although the presence of small numbers of marine shells associated with the burials at Los Canes indicates that there were movements of people or contacts between the two zones.

This evidence of year-round settlement raises more acutely the question of why *P. lineatus* shells were restricted to such a narrow and concentrated season of exploitation, and additionally why limpets, though collected over a wider range of seasons, were also collected predominantly in the colder months. This leads to a second hypothesis originally suggested by Deith (1983, p. 76), namely that other resources were more easily available during the summer, making the collection of molluscs less economically viable. The further implication of this is that molluscs in general and *P. lineatus* in particular, are low-ranked resources of marginal significance, only resorted to as emergency foods during periods of food shortage, a view widely canvassed both in relation to Cantabrian Spain and elsewhere (Madariaga, 1976; Osborn, 1977; Arias, 1992; Marín-Arroyo, 2013; Schöne et al., 2025). This view is influenced by the low ratio of meat content to shell and the presumed high labour costs of collection and transport, especially where rocky shore species such as limpets or other gastropods are involved, mollusc species deemed to be unpalatable or unavailable except in small quantities, in contrast to bivalves such as oysters and mussels. It is also influenced by the likely over-representation of bivalves in the food debris of archaeological deposits because of the vast quantity and bulk of the discarded shells, and their greater resistance to taphonomic processes of loss or destruction, compared to animal bones and plant remains.

However, a variety of ethnographic observations and nutritional considerations contradict this concept of molluscs as marginal foods, highlighting their value as an easily available source of fresh protein, one that can be accessed by weaker members of the community and a resource that is regularly available even when other foods are in short supply (Meehan, 1982; Erlandson, 1988). In addition, marine molluscs, like many marine foods more generally, are rich in fatty acids such as arachidonic acid (AA) and docosahexaenoic acid (DHA), both of which are crucial for growth and optimal brain development (Broadhurst et al., 2002; Carlson and Kingston, 2007). Transport costs only become significant if the un-shelled molluscs have to be carried in quantity far from the shoreline. Processing costs may be a relevant variable but are difficult to evaluate in comparing the cost-benefit ratio of scooping the raw meat out of limpet shells, extracting meat from inside topshells likely requiring heating, or the preparation and cooking of meat from animal carcases, or of plant foods.

Turning to the Cantabrian evidence, it is true that the seasonality evidence refers predominantly to the colder months of the year, and this would be the time of year when other food resources were in shortest supply, especially in late winter and early spring. From this, it would be easy to infer that molluscs were second-rate resources, too much trouble to bother with for most of the time and only resorted to when other food was scarce or unavailable. However, this is a misconception. Molluscs are almost always easily available and may be collected at any time of year; our seasonality data demonstrate that point. The fact that they were collected in greater abundance at periods of the year when other resources were likely more scarce demonstrates their central significance rather than their marginality. Meehan's (1982) ethnoarchaeological study of Anbarra shellgathering activities in northern Australia provides an apt analogy. Here, marine molluscs were a valued day-to-day source of fresh food, especially for women and children, and were gathered on over half the days of the year and in all seasons, even though their relative contribution to the annual diet was no more than about 10 % in terms of calories and 26 % in terms of protein. During the wet season, when most other foods were inaccessible, shellgathering intensified in frequency, and people would have suffered real hardship without the availability of the molluscs.

Moreover, detailed quantitative comparison of the meat weight represented by mollusc shells versus bones of terrestrial mammals in Cantabrian shell middens suggests that the mollusc contribution has been consistently under-represented. Revised calculations taking account of taphonomic factors and other biases show that the molluscs could have contributed at least 20 % of the meat weight represented at El Mazo in comparison with the yield from the terrestrial fauna represented at the site, and perhaps more, with similar figures from other Mesolithic sites in the region (García-Escárzaga and Gutiérrez-Zugasti, 2021). These figures are open to debate, depending on how the ungulate meat contribution is calculated, whether using Minimum Number of Individuals (MNI) statistics in which a single bone can stand for a whole carcase, or weights of bone (see also Portero et al., 2022). However, these variables were carefully evaluated in the El Mazo study and the general order of magnitude indicated is in line with results obtained from ethnographic and archaeological studies elsewhere, notably Meehan's (1982) study of the Anbarra. The shellfood contribution could only be reduced to a much lower percentage in the Cantabrian case by assuming that the shell midden deposits contain only a fraction of the remains of ungulates or other non-molluscan food resources originally consumed, and that the bulk of the processing or consumption of these other food resources took place elsewhere at other locations that have not been preserved, for example outside the immediate perimeter of the caves and rockshelters where the shell middens were accumulated, or at more distant open-air locations. However, there is no easy way of testing that assumption, except perhaps by estimating the potential abundance of molluscs and ungulate resources within the foraging radius of the shell midden deposits.

An interesting byproduct of the El Mazo analysis is figures demonstrating that the flesh weight of topshells and their ratio of flesh weight to shell weight is lower than for limpets, indicating that within the molluscan category topshells are less productive than limpets (García-Escárzaga and Gutiérrez-Zugasti, 2021, p. 13). This might account for the narrower seasonal range of topshell collection – because they were resorted to less often than limpets and only in more extreme conditions of general food shortage such as might be expected in the depths of winter.

A third hypothesis is that the patterns of seasonality are related to seasonal variations in the meat yield of the molluscs, collection concentrating in those seasons that ensured the best return of food. The highest yield of meat from topshells is from mid-autumn to mid-spring, coinciding with gamete formation (November–May/June), with a lower yield during the summer and early autumn (June/July–September), when spawning reduces the condition of the meat (Bode et al., 1986; García-Escárzaga and Gutiérrez-Zugasti, 2021). This is consistent with the relatively concentrated seasonal range of topshell collection. Spring collection, however, is rare in our seasonality data for this species, although meat yields would predict this as an optimum collecting season (García-Escárzaga et al., 2019b), perhaps because of other factors discussed above. Shells of *P. depressa* produce their highest meat yield in late winter and early spring, coinciding with gonad maturation, and this is consistent with the cold-season harvesting practices documented for this species at El Mazo (García-Escárzaga et al., 2024a). In contrast, *P. vulgata* does not show seasonal variability in meat yields (García-Escárzaga, 2020), which is consistent with the seasonality evidence that they were harvested at all times of the year.

This hypothesis offers quite a good fit with our seasonality data, but not a perfect fit, because, if true, it would lead us to expect more harvesting of *P. lineatus* shells in spring, and a more even seasonal spread of *P. vulgata* collection throughout the year. The best fit is with both hypotheses presented here, targeting of specific shell species during seasons of optimal food yield, and nested within that constraint, intensification during periods when other food supplies were less abundant or less easily available. This combination of evidence demonstrates that marine molluscs were not exploited at random at any time of year according to the needs of the moment or as emergency rations, but were part of a coordinated subsistence strategy that targeted them according to their optimal season of productivity in relation to seasonal variations in the availability of other food resources. Evidence from size and age analysis of the mollusc shells indicates that they were subjected to sustained predation pressure and in some cases evidence of increasing pressure over time (Gutiérrez-Zugasti, 2011; Arniz-Mateos et al., 2024), which is consistent with the hypothesis that they were resources that played a vital role in the success of the overall subsistence economy.

Several other subsidiary influences on variability in patterns of shellfood collection should be mentioned, namely aggregation events for ritual or ceremonial purposes involving feasting (Milner, 2005), or perceptions of taste and division of labour (Mannino et al., 2011).

Feasting events might be expected to result in aggregations of larger numbers of people at certain times of year for ritual or ceremonial purposes, resulting in an intensification of shellgathering activity to feed a larger temporary demand, as described, for example in one of the sites studied by Meehan (1982), and an unusually large accumulation of mollusc shells. However, such events would be quite difficult to distinguish amongst the general trends identifiable from the types of archaeological deposits available in Mesolithic Cantabria, especially given their limited chronological resolution and the limited comparative data on the volume of deposits and quantity of shells accumulated at different sites. An additional problem would be the difficulty of determining whether evidence of such a concentration of shellgathering was the result of a temporary increase in the local population or a decrease in the availability of other food supplies. The concentration of shellgathering in certain seasons, for example the summer pattern at Arenillas, might conceivably qualify for an interpretation as a feasting event, but the evidence is equally consistent with the use of different sites at different seasons as part of the normal seasonal round by the local resident population, without any temporary aggregation of people drawn from a wider area. In any case, we might suppose that feasting events, if dependent on mollusc food, would occur at times of year when the molluscs were in best condition. Although feasting events by Mesolithic populations may well have occurred, we consider that they would be very difficult to detect, and we see no aberrations in the currently available patterns of seasonality data that would require us to invoke feasting as an additional explanatory factor.

Variations in shellgathering because of cultural or personal differences in the perception of taste, or other such culturally determined preferences or taboos, are equally problematic, not least because the question of such differences is a subjective matter. It is also a variable that is almost impossible to test in a prehistoric archaeological context except by elimination of the alternatives. Limpets are often regarded as the least palatable of the molluscs because the flesh weight is dominated by a relatively large and rubbery foot. We have also drawn attention to seasonal variations in the meat yield of some shell species, which would most likely have been apparent as seasonal variations in palatability. However, even if some species of molluscs exploited as food were low in the ranking because of taste or other cultural or subjective factors, there is nothing in our evidence to suggest that they were habitually avoided, or that they were not incorporated into the overall subsistence strategy according to the variables we have already discussed in terms of meat yields and availability of alternative food supplies. In general, we can see no evidence that a preference for or against particular molluscs because of subjective or cultural motivations needs to be invoked to explain the seasonal patterns we have identified.

Similar comments apply to the division of labour. Mannino et al. (2011) have suggested that the complete absence of shellgathering in summer in the Mesolithic sites of Sicily, based on oxygen isotope analysis of the topshell (*P. turbinatus*), could have been due in part to the fact that the women and children most likely to have been involved in shellgathering were too busy engaged in other subsistence tasks in the summer months. However, Mannino et al. ultimately reject that hypothesis in favour of other explanations. As we have already noted, and as is widely discussed in the ethnographic literature (e.g., Waselkov, 1987; Meehan, 1982; Moss, 1983), it is often the women who collect shellfood rather than the men, along with children and older members of the community, but not exclusively so, as Moss (1993) emphasises. There is some limited grave-good evidence in the Cantabrian Mesolithic for a division of labour, notably the male Azilian burial associated with a harpoon at Los Azules and the Mesolithic female burial with Asturian picks at Molino de Gasparín (Straus, 1992). Madariaga (1976) and Cuenca-Solana et al. (2018) have also suggested that some of the Asturian picks are so small that they make better sense as implements used by women or children. On the other hand, the admittedly limited palaeodietary evidence from the human burials at the site of Los Canes does not show any significant differences based on age or sex (Arias, 2006). Overall, we doubt that division of labour would have been so rigidly applied that women and children would have avoided collecting molluscs in summer if they were available. In any case, our results show that significant numbers of molluscs were collected in summer, mostly limpets, but also, more rarely, topshells.

4.3. *Patterns of settlement and mobility*

As already demonstrated above, our seasonality results provide strong evidence that human populations were present throughout the year in the Cantabrian coastal zone. This process of ‘settling in’ to the coastal landscape appears to have been associated with population growth, with evidence for increased predation pressure on limpets and some ungulate resources (Gutiérrez-Zugasti, 2011; Andreu-Alarcón, 2013; Arenas-Sorriqueta et al., 2024; Arniz-Mateos et al., 2024). This population growth was presumably initiated by general climate warming and increased diversity and abundance of resources across the Late Pleistocene–Holocene boundary, and perhaps further amplified over time by influx of populations from outside the region (Clark, 1995; Fernández-López de Pablo et al., 2019; Clark and Barton, 2022; González-Rabanal, 2022). This leaves open the question of how individual sites fitted into this general pattern of year-round settlement.

As is widely recorded in ethnographic evidence of hunter-gatherer settlement in heavily populated coastal regions with abundance and diversity of food resources and year-round settlement, such as the Northwest coast of North America or Australia, people use a variety of sites for different purposes and on different occasions within the annual cycle, only some of which are residential bases, and even these may be occupied on a seasonal basis (e.g., Murdock, 1967; Kelly, 2013). Year-round settlement of a region does not necessarily mean permanent year-round occupation of individual sites. Meehan (1982), for example, describes how the Anbarra community of northern Australia moved between three major residential bases during the course of a single year and used over 20 other locations for local consumption or processing of shellfood. The principal motivation for this pattern was to maintain proximity to the least transportable resources – freshwater and shellfood, respectively. Freshwater wells were a significant limiting factor during the dry season of this semi-arid environment, while the foraging radius for molluscs was generally as short as possible, generally within 1–2 km. Molluscs were sometimes transported over greater distances, the maximum being 12 km, but the frequency of shellgathering dropped sharply with increasing distance (Meehan, 1982, pp. 64–67; see also Metcalfe and Barlow, 1992; Bettinger et al., 1997; Bird and Bliege Bird, 1997; Bird et al., 2002).

This Anbarra example, suitably adapted for a temperate environment, suggests an appropriate model for the Cantabrian Mesolithic, in which the principal determinants of site location are shelter, especially in cold weather, and therefore a preference for the many caves and south facing rockshelters present in this limestone region, and proximity to molluscs on the shoreline. The importance of shelter is demonstrated by the fact that all known shell deposits are within caves or rockshelters, and the largest number and the largest deposits appear to be within 1–3 km of the shoreline, often quite close to each other along the same stretch of shoreline. Some are at a greater distance inland, the furthest site from the shoreline with deposits containing marine molluscs being the Cave of La Chora, where some shells (limpets and topshells) were brought in from the nearest shoreline at least 10 km away (Milano et al., 2022; León-Cristobal et al., 2024). The quantities of these shells here are relatively few, and the site was used primarily for collection of oysters, clams and mussels, collected in the nearby estuary. In any case, the presence of species inhabiting the open coast at La Chora, demonstrates the occurrence of mobility between locations on the coast and in the coastal hinterland.

The importance of caves and rockshelters does of course raise the possibility of a systematic bias in our seasonality data. The predominance of seasonal shell collection in the colder months may reflect the fact that these are the periods of the year when people would be most likely to resort to caves and rockshelters, whereas during summer processing and consumption of shellfood could be carried out more conveniently in open-air locations closer to the shoreline, locations where the chances of archaeological preservation are much lower or non-existent. Our seasonality data show evidence of some summer collection of shells, but we cannot rule out the possibility that the summer season is under-represented in our data because of this factor. We cannot at present test for this possibility and can only work with the variation present in those shell middens that have been preserved.

On our proposed model, some of the shell middens might represent residential bases used on a permanent or seasonal basis for a variety of subsistence activities, while many other deposits might represent more short-lived sites used on a temporary or seasonal basis to maintain proximity to the supply of shellfood, resulting in frequent site moves and more specialised deposits dominated by mollusc shells. There are some hints of this variability, both in our seasonality results and in other archaeological information. For example, residential areas identified as habitation floors have been documented at Mazaculos II (González-Morales, 1982), while postholes suggest possible domestic structures at El Toral III (Noval, 2013). Other deposits have significant representation of other food resources such as bones of vertebrates or plant remains. The presence of these features could be an indicator of prolonged occupations, distinguishing these sites from short-term or seasonal occupations. Our seasonality data also suggest that some sites were used over a longer period of the year than others, perhaps reflecting a difference between residential bases and specialist shellfood or processing sites. The diversification of seasonal indicators in the most recent layers at El Toral III (Fig. 5) might indicate increased predation pressure on the resource base (e.g., Arenas-Sorriqueta et al., 2024), but it might equally well indicate a change in site function from a specialised or seasonally occupied cave site to a residential base used over longer periods of the year. However, the resolution of our data is not at present good enough to discriminate between these alternative interpretations, or to determine whether multiple seasons of shell collecting at a given site are the result of a single community in residence over a large part of the year, or the result of shorter visits by different groups at different seasons primarily for the collection of shellfood.

One consequence of this model of transportation costs of live shellfood is that the large number of shell middens recorded along the Cantabrian coastline is not in itself sufficient evidence of a larger regional population, as compared with the smaller number of sites from earlier periods. Rather, it could reflect the more frequent moves over short distances required to maintain easy access to shorelines with molluscs in a subsistence economy where the molluscs provided a vital resource, resulting in a large number of shell-middens, many of which were short-lived specialist camps used for shell collection, or residential bases that moved periodically to maintain proximity to shellfood resources.

Finally, within this pattern of year-round coastal settlement and short distance moves of habitations and campsites along or close to the shoreline, there is evidence for widening contacts over large areas that must have involved long-distance travel by some individuals. These moves occurred both along a west–east axis in the coastal region over distances of 250 km for the provision of sought-after raw materials for lithic manufacture, as evidenced at the site of El Mazo (Herrero-Alonso et al., 2025), and on a coast-interior axis. The most dramatic example of the latter is the evidence at the site of La Braña of human skeletal material which has yielded palaeodietary isotope results with an elevated nitrogen value indicating a significant marine element (González-Rabanal, 2022). This is a site that is over 60 km inland from the shoreline and south of the mountain watershed that separates the coastal region of Cantabria from the Iberian interior. How often such long-distance travels occurred, and how many people were involved, is not clear, but this appears to be part of a wider pattern of long-distance contacts, and may have been stimulated in part by a more general influx of new populations into the coastal zone from the Iberian interior (Clark and Barton, 2022).

5. Conclusions

The main conclusions of this study are as follows.

1. With a larger data set of oxygen isotope values on season of shell collection than previously available, and information from a variety of sites and molluscan species, we have been able to confirm some existing results from previous studies, notably the dominance of the winter season in the harvesting of topshells (*P. lineatus*).
2. We have also identified new patterns, most importantly widespread evidence for the collection of limpets of the *P. vulgata* species in all

seasons of the year. Overall, the seasonality results are dominated by evidence of autumn, winter and spring shell collecting. We cannot definitively rule out the possibility that summer collection of shells is systematically under-represented. Collection and consumption of shells in the summer months could have taken place at open air locations which have left no archaeological trace, without the need to use caves and rockshelters for protection from the weather. Given that all Mesolithic shell middens on the Cantabrian coast are in caves or rockshelters, this possibility of systematic bias should be recognised. However, we note that some shell-midden deposits are dominated by summer-collected limpets, and others contain summer-collected shells in lesser quantity. We therefore interpret these results as evidence of year-round settlement within the Cantabrian coastal zone. At the same time, we note evidence for contacts over more extensive regions for provision of raw materials, or palaeodietary isotope evidence for long-distance individual movements between coast and interior.

3. We also demonstrate that the general concentration of evidence in the colder months of the year and evidence of inter-specific variations in seasonal collection are most simply explained by a coordinated subsistence strategy that targeted different mollusc species according to the season of their maximum meat yield and to seasonal variations in the supply of other food resources.
4. We conclude that molluscs played a vital role in sustaining the overall economy over the yearly cycle and cannot be dismissed as minor resources treated in an opportunistic or intermittent manner or resorted to only as an emergency food resource.
5. Our results also provide some information about variations in seasonality of site use and site function. We draw on a model of shell midden location that emphasises the transportation costs of live molluscs in the shell and the need to locate the processing or consumption of the molluscs as close as possible to the source of supply on the shoreline, subject to other constraints such as the need for shelter in bad weather and access to other food supplies. This leads to the expectation that intensive shellgathering should result in large numbers of quite closely spaced shell middens, some of which may be residential bases, while many others are specialised sites used mainly for the collection of molluscs. We see some hints of this variation in our seasonality data and other archaeological features and food remains present at some shell middens.
6. We note that existing data currently lack the chronological and stratigraphic resolution to discriminate reliably between residential settlements and specialist shellgathering sites, or between sites repeatedly visited for short stays by small groups of individuals in different seasons and sites used as residential bases over longer periods of the year, or to identify sites that were used in different ways and for different purposes over longer time spans.

6. Future research

One of the great virtues of mollusc shells is their good preservation, large number and easy availability in archaeological deposits, the detailed growth structures contained within the axis of shell growth that facilitate climatic and seasonality determinations, their amenability to direct radiometric dating of the shell material, and the specific habitats of different species that enable their source of origin to be pinpointed with considerable accuracy. However, these virtues also highlight one of their greatest drawbacks, and that is the sampling challenge presented by the huge numbers of shells typically present in shell midden deposits. The total number of individual mollusc shells represented by all the known Mesolithic shell middens in Cantabrian Spain is not recorded, but it can reliably be estimated, from rough estimates of midden volumes and numbers of shells per unit volume, to run into hundreds of thousands, if not millions.

The main limitation of oxygen isotope analysis is the labour time involved in drilling micro samples from each shell, the costs of machine time for the analyses, and the relatively small sample of shells that can be used. One of the most promising developments for the future is the use of Laser-induced Breakdown Spectroscopy (LIBS) to measure magnesium/calcium (Mg/Ca) ratios in shell growth structure (García-Escárzaga et al., 2015; Hausmann et al., 2017, 2018; Martínez-Minchero et al., 2023; Mirapeix et al., 2025). The Mg/Ca ratio has been shown to be a sensitive proxy of temperature change, and the LIBS technique is capable of taking large numbers of measurements of micro-growth structures across the axis of shell growth at minimal cost, opening up the prospect of taking numbers of measurements orders of magnitude larger than with conventional oxygen isotope analysis. With such new applications, combined with new field data, it should be possible to greatly expand and refine understanding of the Cantabrian Mesolithic, with wider implications for the study and interpretation of shell middens elsewhere on Atlantic coastlines of Europe, and beyond.

Fuller integration of evidence from non-molluscan food remains, especially plant-based food sources, which remain poorly documented in the Cantabrian Mesolithic, excavation of more sites and deposits, larger samples of vertebrate faunal remains and radiocarbon dates, and above all seasonality analyses of more shells from more deposits, are all potential avenues of future investigation.

CRediT authorship contribution statement

Rosa Arniz-Mateos: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization.

Asier García-Escárzaga: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization.

Roberto Suárez-Revilla: Methodology, Investigation, Validation.

Leon J. Clarke: Writing – review, Validation, Resources.

Manuel R. González-Morales: Writing – review, Validation, Funding acquisition.

Geoffrey N. Bailey: Writing – original draft, review and editing, Validation, Resources, Funding acquisition.

Igor Gutiérrez-Zugasti: Writing – original draft, Methodology, Investigation, Formal analysis, Validation, Supervision, Resources, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2026.109812.

Data availability

All data and/or code is contained within the submission.

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