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Strengthening the evidence for seasonal intertidal exploitation in Mesolithic Europe and new insights into Early Holocene environmental conditions in the Bay of Biscay from the oxygen isotope composition of *Phorcus lineatus* (da Costa, 1778) shells

Asier García-Escárzaga [a,*], Alejandro León-Cristóbal [b], Esteban Álvarez-Fernández [c], André C. Colonese [a], Alvaro Arrizabalaga [d], María José Iriarte-Chiapusso [d,e], Eneko Iriarte [f], Miguel Ángel Fano [b,†]

[a] *Department of Prehistory and Institute of Environmental Science and Technology (ICTA-UAB), Universitat Autònoma de Barcelona, Bellaterra, Spain*
[b] *Departamento de Ciencias Humanas, Universidad de La Rioja (UR), Logroño, Spain*
[c] *GIR PREHUSAL, Departamento de Prehistoria, Historia Antigua y Arqueología, Universidad de Salamanca, Spain*
[d] *Departamento de Geografía, Prehistoria y Arqueología, Universidad del País Vasco (UPV-EHU), Vitoria, Spain*
[e] *IKERBASQUE, Basque Foundation for Science, Spain*
[f] *Laboratorio de Evolución Humana-IsoTOPIK Stable Isotope Laboratory, Universidad de Burgos, Burgos, Spain*

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ABSTRACT

Marine molluscs have been exploited by human societies since prehistoric times. Such practices have often resulted in large accumulations of shell remains in archaeological sites that offer unique information on biological, ecological and cultural aspects of human interaction with coastal systems in the past. In this study, stable oxygen isotope ($\delta^{18}O$) analysis was carried out on archaeological shells of *Phorcus lineatus* (da Costa, 1778) from the Mesolithic shell midden site of J3 (northern Iberian coast) to determine the seasonality of intertidal collection. The results indicate a consistent pattern of winter exploitation, supporting the emerging view that collections were governed by cost-benefit and management principles that are now widespread documented in other coastal Mesolithic sites in Europe. The consistent seasonal collections of *P. lineatus* during colder months can be taken as evidence of specie-specific management strategy to optimize yield while preserving local populations for future exploitation. Our results reinforce the view that European hunter-gatherers developed ecological knowledge on specific animal resources that persisted over large geographic areas. Additionally, from a palaeoenvironmental perspective, the sea surface temperatures (SST) inferred from $\delta^{18}O$ values derived from mollusc shells ($SST_{\delta18O}$) indicate that coastal marine waters during the Early Holocene in the southern Bay of Biscay were warmer than those observed today. These environmental conditions are evaluated in relation to changes in insolation and ocean currents over time.

1. Introduction

Hominins have exploited marine resources for food along the European coasts since at least ca. 250–300 ka years ago (Colonese et al., 2011; Cortes-Sánchez et al., 2019; Ramos-Muñoz et al., 2016). However, the littoral food supply apparently did not play a significant role in human subsistence strategies until the Early Holocene, when a noticeable increase in shellfish remain accumulations becomes apparent in coastal archaeological sites (Colonese et al., 2011; Gutiérrez-Zugasti et al., 2011; Milner et al., 2007), representative of a greater protein contribution to human diets (Cubas et al., 2019; Fontanals-Coll et al., 2023; García-Escárzaga and Gutiérrez-Zugasti, 2021). Considering the relevant role acquired by littoral food sources to human subsistence just before adopting agriculture during the Neolithic, determining coastal exploitation strategies by the last European hunter-gatherers is critical for reconstructing their way of life. In this regard, the use of stable

* Corresponding author.
E-mail addresses: asier.garcia@uab.cat, a.garcia.escarzaga@gmail.com (A. García-Escárzaga).
† deceased.

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oxygen isotope ($\delta^{18}O$) values from marine shells are now an established approach for the reconstruction of sea surface temperatures (SST) during the molluscs' lifespan (Leng and Lewis, 2016; Schöne et al., 2004). This information also allows scientists to determine the season when this food supply was harvested by ancient humans, thus shedding light on past resource management, subsistence, and settlement strategies (Andrus, 2011; Thomas, 2015; Hausmann, 2024).

Although these isotopic studies have been carried out elsewhere around the world and have been applied to different chronological contexts (Burchell et al., 2018; Branscombe et al., 2021; Colonese et al., 2018; Leclerc et al., 2023; Mannino et al., 2014; Prendergast et al., 2016), the Cantabrian Region, a coastal area located in the northern Iberian Peninsula (Fig. 1a), has shown unusual research dynamism since the past century (Bailey et al., 1983; Deith, 1983; Deith and Shackleton, 1986) till the present (García-Escárzaga, 2020; García-Escárzaga et al., 2019a, 2024a; Milano et al., 2022). The isotope investigations conducted on marine shells recovered from the Cantabrian sites reported a stronger preference for mollusc consumption in winter by Mesolithic populations (Deith and Shackleton, 1986; García-Escárzaga et al., 2019a). Two recent research papers have proposed that shellfish exploitation was driven by the higher mollusc meat yield return during colder months due to gonadal development, which would indicate that prehistoric communities i) annually scheduled resource use to maximise their energetic returns (García-Escárzaga et al., 2019a, 2024a) and ii) managed resources to ensure their sustainable exploitation, in accordance with the principles of stewardship (Bandiaky-Badji et al., 2023; Jackley et al., 2016). Even though these same winter preference strategies are like those deduced from another Atlantic site, Culverwell in southern Britain (Mannino et al., 2003), new additional information is needed to determine whether this pattern is a local human adaptation or conversely a common strategy developed by prehistoric populations during the Mesolithic.

Given the high density of shell middens (Fano, 2007, 2019) and the high number of oxygen isotope studies published for the northern Iberian Peninsula, this is an exceptional location to test spatial variability in shellfish exploitation patterns. Shell middens are concentrated especially in the western part of the Cantabrian coast. In fact, in less than 50 km of the eastern coast of Asturias, more than 130 deposits have been identified (Fano, 1998, 2019). When considering the entire "Asturian area," which includes the western coast of Cantabria province (Fig. 1a), the number of shell middens increases to ca. 300 (García-Escárzaga, 2013; Fano et al., 2024). However, shell middens become scarcer towards the east of the Cantabrian Region, especially in the Basque Country, an area not rich in this type of archaeological deposit characteristic of the coastal European Mesolithic (Fano, 2019). The information available so far on the seasonality of shellfish collection patterns has been obtained exclusively from the western and central areas of the region. Therefore, understanding how Mesolithic groups who inhabited the eastern littoral area of northern Iberia, where shell midden density is lower, managed the seasonality of littoral resource collection strategies will enable us to better comprehend the way of life of the last forager populations in the entire Cantabrian Region, as well as in Atlantic Europe.

This paper, therefore, presents new isotopic data from the eastern Cantabrian Region, an area previously not considered by scholars. Specifically, we examined the stable oxygen isotope composition ($\delta^{18}O$) of *Phorcus lineatus* (da Costa, 1778) shells from the Mesolithic shell midden site of J3. Our goal was to establish the seasonality of intertidal collection, as *P. lineatus* was a heavily exploited species in prehistoric times in Atlantic Europe (Gutiérrez-Zugasti, 2009; Milner et al., 2007; Thomas and Mannino, 2017). These results contribute to broadening our understanding of the role marine resources played in the evolution of hunter-gatherer societies in the region. Additionally, $\delta^{18}O$ values obtained from *P. lineatus* were used to infer SST in the past, providing new high resolution seasonal insights into Early Holocene marine environmental conditions in the Northeast Atlantic in general and the Bay of Biscay in particular.

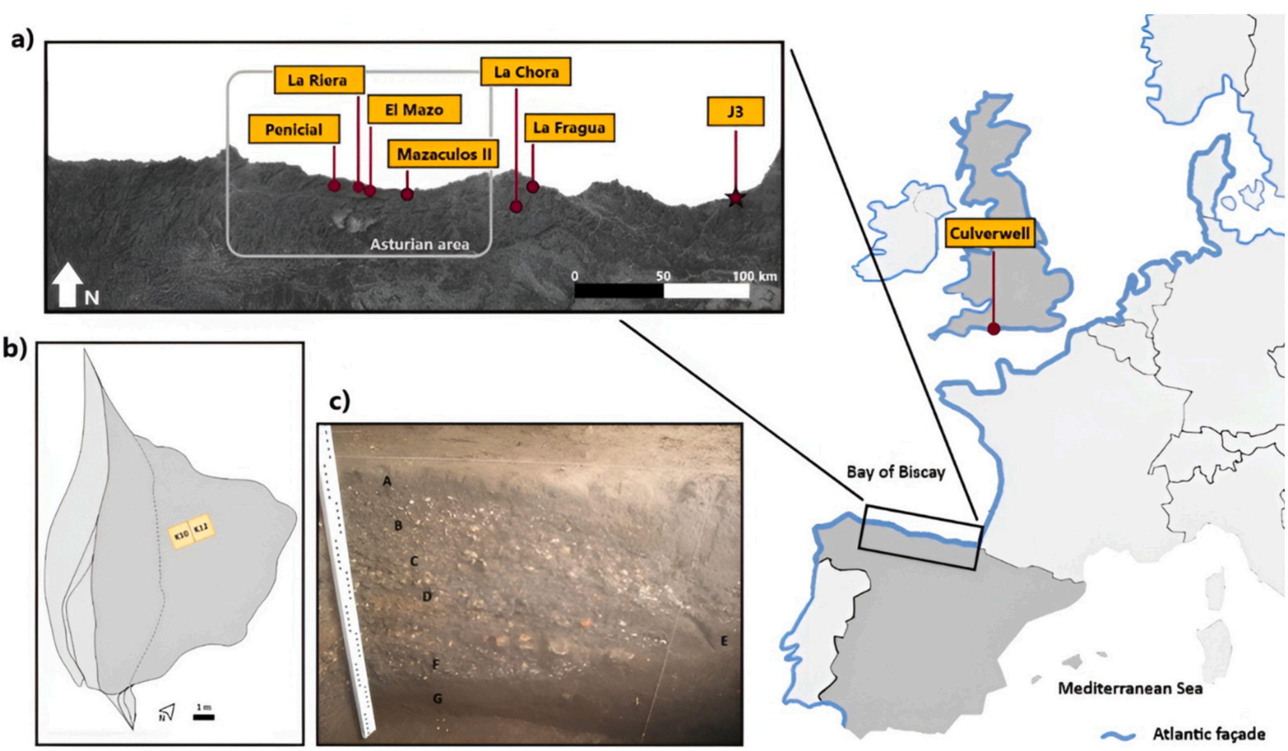

Fig. 1. a) Location of the archaeological sites mentioned in this study along the Cantabrian Region coast, and the images of the b) J3 rockshelter, and c) the stratigraphy of J3 site.

2. Materials and methods

2.1. J3 shell midden site and selection of *P. lineatus* shells

The J3 rock shelter is located in the municipality of Hondarribia (Gipuzkoa, Basque Country, Spain) (Fig. 1a) at a distance from the current intertidal area of ca. 200 m. The excavation in two square meters (Fig. 1b) revealed seven stratigraphic units (Fig. 1c), four of which belonged to a shell midden (units B, C, D and F). In addition, a human burial was documented in the unit D and a male skeleton was recovered (Iriarte-Chiapusso et al., 2010). The radiocarbon dates obtained from J3 placed the shell midden formation during the Mesolithic (ca. 10,700–6700 cal BP) (Fig. 2; Supplementary Table 1). Previous studies on mollusc remains recovered from the four shell midden layers indicated that the limpets *Patella* spp. and the topshells *P. lineatus* represented more than 99 % of the shell remains at the site (Álvarez-Fernández et al., 2010, 2014). The overwhelming presence of these gastropods and the recovery of other littoral taxa, such as goose

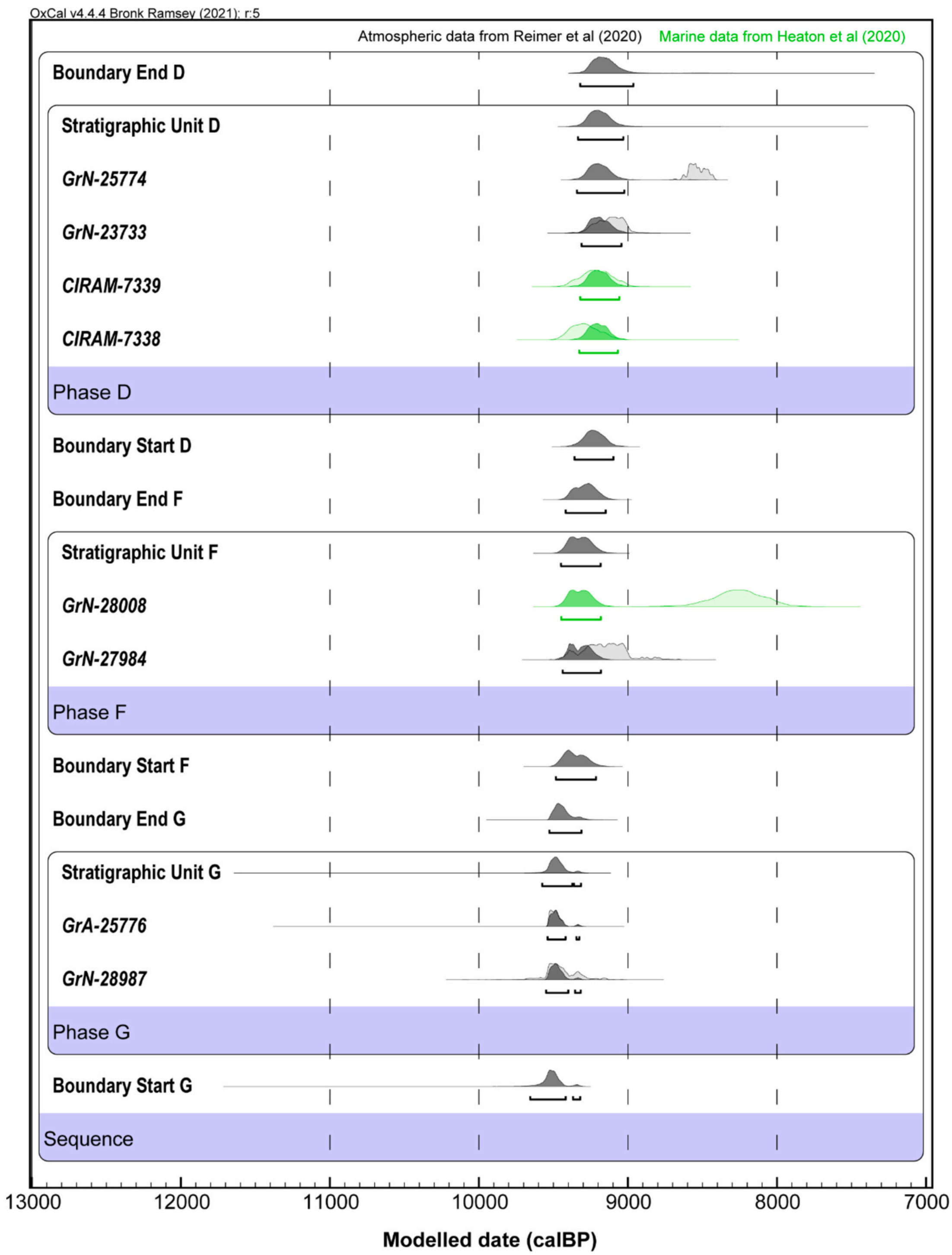

Fig. 2. Bayesian modeling of radiocarbon dates obtained from J3 (Iriarte-Chiapusso et al., 2010; Table 1) calibrated in OxCal v.4.4.2 (Bronk Ramsey, 2009a, 2009b) using IntCal20 (Reimer et al., 2020) and Marine20 (Heaton et al., 2020) curves and the ΔR values previously published by García-Escárzaga et al. (2022a) for the Cantabrian Region.

barnacles, crabs, or *Diplodus* spp., indicate that J3 inhabitants preferentially exploited rocky exposed shore areas with fully marine environmental conditions (Álvarez-Fernández et al., 2014).

The specimens of *P. lineatus* selected for our study were recovered from level D, which reported the highest MNI of this taxon throughout the archaeological sequence ($n = 257$) (Álvarez-Fernández et al., 2014). New two AMS radiocarbon dates obtained from this layer at CIRAM laboratory (France) confirm its deposition during the Early Holocene (Fig. 2; Supplementary Table 1). The results obtained from the Bayesian modeling of radiocarbon dates indicate that unit D was formed between 9400 and 9040 cal BP with a 95 % of credible interval. The high percentage of species adapted to rocky open shores recovered from level D, as well as the total absence of exclusively estuarine adapted taxa (e.g., *Scrobicularia plana*), suggests that the shells analysed here grew under marine conditions, where the stable oxygen isotope composition of the seawater remained relatively stable throughout the year, with no influence from freshwater inputs.

In this investigation, 20 shells of *P. lineatus* were carefully chosen for $\delta^{18}O$ analysis. This taxon was selected based on previous investigations carried out on shells of the same species along Atlantic Europe (Mannino et al., 2003; Mannino and Thomas, 2007), including northern Iberian Peninsula (García-Escárzaga, 2020; García-Escárzaga et al., 2019a, 2019b, 2022b; Gutiérrez-Zugasti et al., 2015), and the same genus in the Mediterranean Basin (Branscombe et al., 2021; Colonese et al., 2009, 2018; Mannino et al., 2007, 2014; Prendergast et al., 2013, 2016), which amply demonstrated that shell $\delta^{18}O$ values of *Phorcus* spp. reflect the SST variations during the mollusc life span.

2.2. Stable oxygen isotope analysis and determination of mollusc collection season(s)

Building on these previous investigations conducted on the *Phorcus* genus, the same sampling methodological approach was applied. Micro-samples of calcium carbonate ($CaCO_3$) were taken every 1 mm from the aragonite layer for $\delta^{18}O$ analysis. Micro-samples were extracted using a dentist microdrill with a 0.5 mm tungsten drill bit. The first two micro-samples were obtained from the inner part of the shell lip (Fig. 3a) before removing the outer calcite layer and the next micro-samples were sequentially extracted in parallel to the direction of shell growth (Fig. 3b). In three shells (J3.14.1, J3.11.1 and J3.11.9) a total of 50 micro-samples were taken, and in the remaining 17 shells, 10 micro-samples from the shell edge to the apex were extracted to get long and short isotope series, respectively. A total of 320 $CaCO_3$ micro-samples obtained were stored within glass vials (1.5 ml) and analysed using a Thermo Scientific DELTA V Plus IRMS coupled to a Gas Bench II Interface at the IsoTOPIK Laboratory at the University of Burgos. The analytical error of the instrument was systematically better than 0.1 ‰. The measured isotopic ratios were normalized against NBS-18 ($\delta^{18}O = -23.2$ ‰), IAEA-603 ($\delta^{18}O = -2.37$ ‰), and IAEA-CO-8 ($\delta^{18}O = -22.7$ ‰) standards, and the results were reported in per mil (‰) relative to the Vienna Pee-Dee Belemnite (VPDB) standard.

To estimate the seasons in which archaeological specimens were collected, the quartiles method proposed by Mannino et al. (2003, 2007), and adopted by other scholars (Colonese et al., 2009, 2018; García-Escárzaga et al., 2019a; 2024b; Prendergast et al., 2016) was used. Shortly, the intra-annual $\delta^{18}O$ range of the stratigraphic unit was divided into four quartiles, each roughly corresponding to a season. The upper quartile reflects cooler conditions (i.e., winter), while the lowest quartile indicates warmer conditions (i.e., summer). $\delta^{18}O$ values at the shell edge within the highest or lowest quartiles suggest the mollusc was collected during winter or summer, respectively. The middle quartiles represent transitional periods (i.e., autumn and spring). If the shell edge $\delta^{18}O$ values fall into these middle quartiles, the season of collection can be determined by considering the $\delta^{18}O$ trend before the mollusc's death. To calculate the intra-annual $\delta^{18}O$ variability and the maximum and minimum $\delta^{18}O$ values, which are required for establishing the $\delta^{18}O$ value range assigned to each quartile, a combination of $\delta^{18}O$ values from both the long and short isotope series obtained was used.

2.3. Estimation of past sea surface temperatures (SST) from shell $\delta^{18}O$values

Following the investigations previously conducted in modern and ancient *P. lineatus* species (García-Escárzaga et al., 2019b, 2022b; Gutiérrez-Zugasti et al., 2015), to estimate the SST from shell $\delta^{18}O$ values ($SST_{\delta 18O}$), the water-aragonite fractionation factor published by Kim et al. (2007) for synthetic aragonite was used:

$$1000 ln\alpha = 17.88^{*} \left(10^{3}/T\right) - 31.14 \quad (1)$$

where T corresponds to SST in Kelvin and α is the fractionation between water and aragonite described by the equation:

$$\alpha = 1000 + \delta^{18}O_{shell}\ (SMOW‰)/1000 + \delta^{18}O_{water}\ (SMOW‰) \quad (2)$$

To reconstruct the $\delta^{18}O_{water}$ values from the past, the correction published by Fairbanks (1989), which was recently applied successfully for this goal in northern Iberian Peninsula (García-Escárzaga et al., 2022b), was used. Fairbanks (1989) suggested a gradual adjustment of +0.011 ‰ for every meter of sea level rise. In this study, the average annual $\delta^{18}O_{water}$ value of 0.90 ‰ (García-Escárzaga et al., 2019b; Gutiérrez-Zugasti et al., 2015) was employed to infer the $\delta^{18}O_{water}$ values for the past. To determine the sea level height during the formation of stratigraphic unit D of J3, radiocarbon dates acquired for this unit were combined with previously published estimates of sea level rise for northern Iberia during the Early Holocene (Leorri et al., 2012).

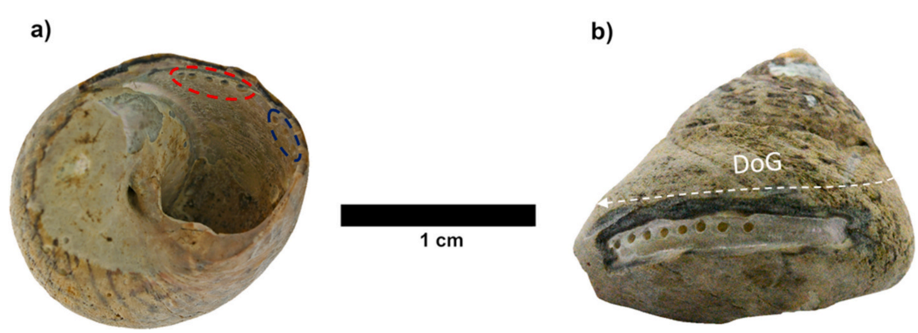

Fig. 3. Sampling methodological approach employed for taking $CaCO_3$ micro-samples from the aragonite layer on *P. lineatus* shells (ID shells: a) J3.11.20; b) J3.11.10). a) Method used to extract the carbonate from the inner part of the shell aperture (dashed red and blue circles show the first and second micro-samples taken near the shell lip, respectively). In the case of these two first samples, several drills were conducted along the same growth lines to reach a minimum powder amount of 200 μg. b) Sampling method applied to extract micro-samples sequentially along the whorl from the outside of the shell (DoG: direction of growth). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

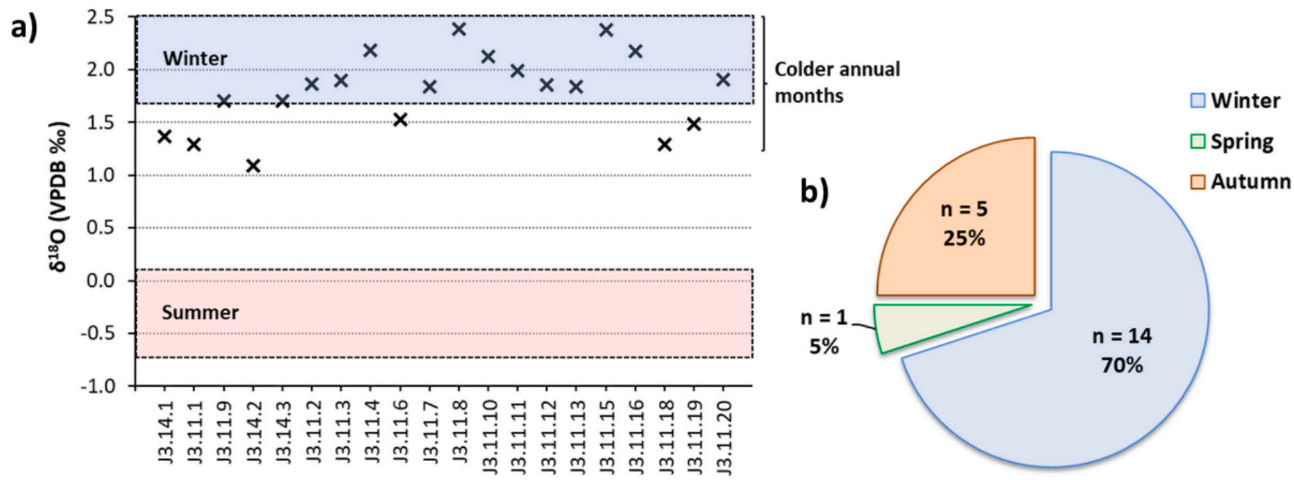

Fig. 4. a) Shell edge δ^{18}O values (each represented with a cross) from the 20 *P. lineatus* specimens analysed in this study. The upper quartile (blue rectangle) represents winter (i.e., the 25 % colder annual temperatures), and the lower quartile (red rectangle) indicates summer (i.e., the 25 % warmer annual temperatures). 70 % of the last shell growth δ^{18}O values were assigned to winter. Among the six individuals attributed to intermediate seasons, five reported δ^{18}O values included in the 37.5 % colder temperatures of the year (a figure that represents the winter quartile values plus a fourth of the colder values of the two intermediate quartiles), suggesting a collection near winter, i.e., late autumn and early spring. b) The percentage (pies) of samples assigned to each season. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

The maximum and minimum δ^{18}O value, which indicate coldest and hottest SST, respectively, obtained are +2.49 and −0.72 ‰, respectively (Supplementary Table 2). Winter and summer quartiles ranged from +2.49 and +1.69 ‰, and +0.08 and −0.72 ‰, respectively. Two intermediate quartiles extend from +1.68 ‰ and +0.09 ‰. The oxygen isotope profiles derived from the 20 shells considered herein followed a sinusoidal pattern along the shell growth axis, clearly reflecting colder and warmer seasons, as well as warming and cooling periods. The sequences obtained reflect a variable time span, ranging from several weeks or a few months in most of the short series (Supplementary Fig. 1) and more than one year in one of the long series (Supplementary Fig. 2).

The δ^{18}O values derived from the shell edge of every specimen, which reflect the SST during the last growth of the mollusc (i.e., prior its collection), show a robust seasonal collection pattern with a strong preference for winter ($N = 14$; 70 %). Autumn ($N = 5$; 25 %) and spring (N = 1; 5 %) seasons are scarcely represented (Fig. 4). No collection in summer has been documented. Regarding the six specimens that died in autumn and spring, five of them yielded shell-edge δ^{18}O values ascribed to the upper fourth of the intermediate quartiles (δ^{18}O value >1.28 ‰). In other words, all specimens analysed herein, except one, were collected from late autumn to early spring.

Finally, the $SST_{\delta 18O}$ estimated from shell δ^{18}O values ranged from 11.04 to 26.32 °C (Supplementary Table 3). While the maximum $SST_{\delta 18O}$ reported by three long isotope series are very similar (J3.14.1: 26.32 °C; J3.11.1: 25.79 °C; J3.11.9: 25.89 °C), the minimum $SST_{\delta 18O}$ show differences between shells (J3.14.1: 12.92 °C; J3.11.1: 15.14 °C; J3.11.9: 13.90 °C). The maximum $SST_{\delta 18O}$ derived from the set of short isotope series (26.01 °C) was remarkably comparable to those reported by long sequences. However, a total of eight short isotope series reported colder temperatures than those obtained from the long isotope sequences (J3.14.2: 12.15 °C; J3.11.4: 11.75 °C; J3.11.8: 11.44 °C; J3.11.10: 12.71 °C; J3.11.11: 12.88 °C; J3.11.15: 11.54 °C; J3.11.16: 12.46 °C; J3.11.20: 11.04 °C).

4. Discussion

4.1. Intertidal resource optimization among Mesolithic hunter-gatherers

The marked seasonal exploitation pattern observed from shells recovered at J3 matches with broad data derived from several Mesolithic sites along the European coast (Branscombe et al., 2021; Colonese et al., 2018; Mannino et al., 2003, 2014; Prendergast et al., 2016), as well as those obtained from shell middens located in the northern Iberian Peninsula (Deith, 1983; Deith and Shackleton, 1986; García-Escárzaga, 2020; García-Escárzaga et al., 2019a, 2024a; Milano et al., 2022). The investigations carried out on shells of *P. lineatus* from the northern Iberian Peninsula reported a strong collection tendency of this species during colder months of the year (i.e., from late autumn to early spring) (Fig. 5). Winter is the season most represented in four out of five archaeological sites, even when both intermediate seasons are considered together, as data published by Deith (1983) and Deith and Shackleton (1986) do not allow us to differentiate between a collection in spring and autumn due to only the micro-samples from the last shells growth were analysed. Solely Mazaculos II reported a higher *P. lineatus* consumption percentage during the intermediate seasons than during winter. However, in all archaeological sites studied so far, between 74 % and 95 % of the shell edge δ^{18}O values were assigned to the colder period of the year, which represents the time span from late autumn to early spring.

Different hypotheses have been proposed to explain this widespread seasonal collection strategy, including the absence of hunter-gatherer populations in coastal areas in summer, the scarcity of terrestrial food sources during colder months, the high human mobility along the coast, and social or religious reasons (Deith, 1983; Mannino et al., 2011). However, none of the previous proposals had been entirely convincing (García-Escárzaga et al., 2019a). Significantly, recent studies show that this is also the period of the year when *P. lineatus* offers the higher meat yield return due to gonadal development stage (García-Escárzaga et al., 2019a). Such an observation is significant because in a context of rapid

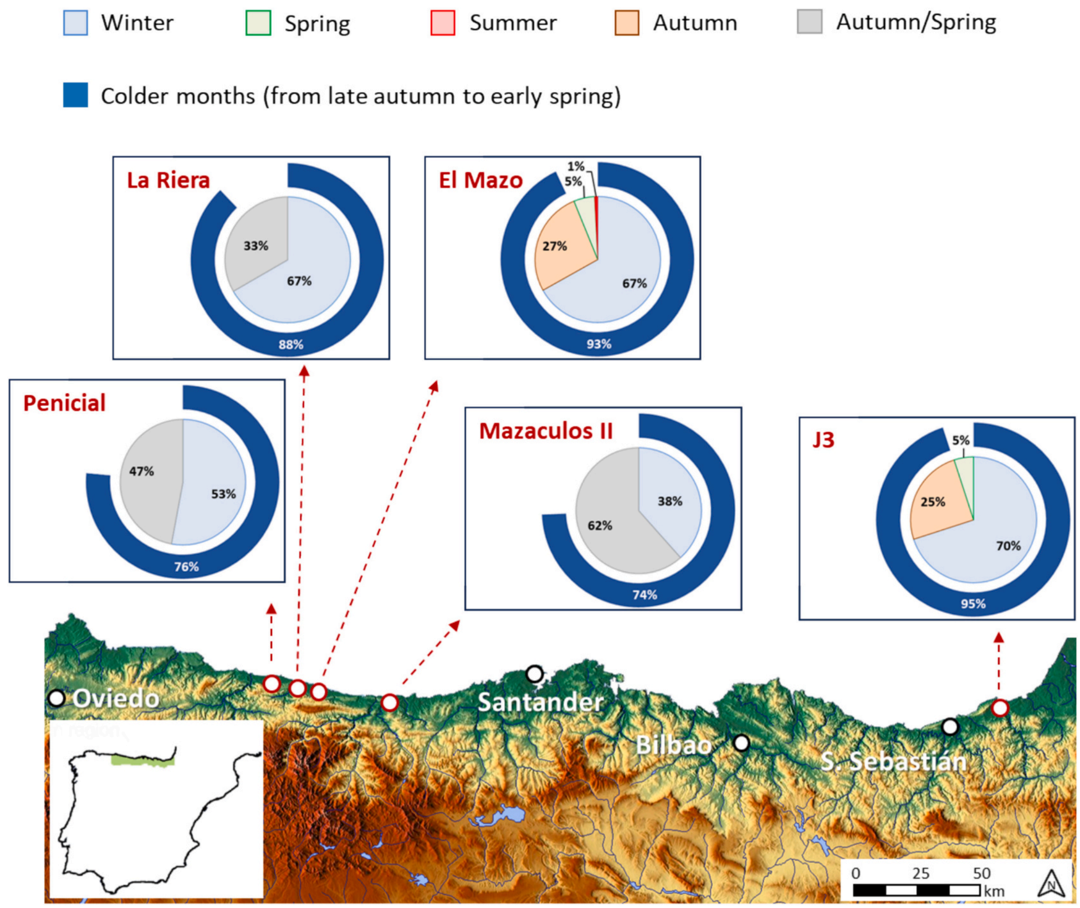

Fig. 5. Summary of the results published on the seasonality of *P. lineatus* collection in the Cantabrian Region (northern Iberian Peninsula). Colder months refer to the period between late autumn and early spring, and its isotope range is defined by the 37.5 % of coldest temperatures of the year. Isotopic data from Penicial, La Riera and Mazaculos II were published by Bailey et al. (1983), Deith (1983) and Deith and Shackleton (1986). Dataset from El Mazo were published by García-Escárzaga et al. (2019a).

human population growth, as during the Early Holocene in Europe (Fernández-López de Pablo et al., 2019; McLaughlin et al., 2021), resource optimization may have been an imperative strategy to face population pressure, territoriality, and resource competition (Belovsky, 1988). Optimization without planning and adequate management, however, may prevent the long-term benefit from localized resources, most notably from stationary animals that are prone to exhaustion if intensively harvested. The fact that *P. lineatus* had been exploited by Mesolithic groups for hundreds to thousands of years, suggests that these groups practiced some form of management to ensure its sustainable exploitation. Such management may have gone beyond restricting collections to specific periods of the years and involved other forms of stewardship such as the establishment of protected areas, which are archaeologically invisible.

The results obtained in this research allow us to bring light on human-marine environment interaction in a coastal area previously not considered along the Atlantic façade of Europe, such as the southeastern Bay of Biscay. The robust similarities in the seasonal collection patterns of *P. lineatus* species developed by last European foragers from southern British Islands (Mannino et al., 2003) to the western Iberian Peninsula confirm that the elucidated intertidal exploitation model does not respond to a local human adaption and suggest that fundamental ecological knowledge on intertidal organisms existed among the last European hunter-gatherers, and that such knowledge seems to have been shared over an extensive geographic areas of the continent. Nevertheless, further investigations are still needed to characterise in detail the role of coastal resources in winter, especially in relation to the scheduling of more profitable subsistence strategies. Likewise, gaining a deeper understanding of the seasonal settlement patterns of the last coastal foragers is necessary to enrich future discussions.

4.2. Reframing the Mesolithic in the Cantabrian Region

This study also provides knowledge of a scientific gap in Mesolithic understanding in the northern Iberian Peninsula. The new data are of particular interest to assess a long-standing debate on the existence or not of “different Mesolithic facies” along the Cantabrian coast: the Asturian culture in the West and the eastern Cantabrian Mesolithic (usually called “Geometric Epipaleolithic”) (Fano et al., 2022). The idea began to be forged in 1920 through Vega del Sella’s observations on the materials recovered by Aranzadi et al. (1931) in Santimamiñe Cave (Basque Country). According to Vega del Sella, the shell midden excavated at this site was “a completely different facies from the Asturian, both in terms of the mollusc species forming it and the lithic assemblage it contains” (Vega del Sella and Conde de la, 1923). The debate in this regard was not favoured, either by the scarce scientific relationship maintained by pioneers who were working on both sides of the northern Iberian Peninsula nor for the recurrent lack of existing information (until the 1980s and 1990s) for the eastern part of the region (Cantabria and Basque Country, essentially). So, for decades, the Asturian and the eastern Mesolithic recorded in Cantabria and the Basque Country were considered independent research objects (Fano et al., 2022).

However, research in recent years has generated evidence that questions the historiographical framework described above, although some authors already supported a greater homogeneity in the archaeological record across the region some decades ago (González-Morales, 1995). Similar subsistence strategies based on the combination of marine and terrestrial resources have been deduced through human bone collagen stable carbon and nitrogen isotope measurements (Cubas et al., 2019). In addition, it has been observed that some Asturian lithic assemblages offered a picture similar to non-Asturian Mesolithic sites in the northern Iberian Peninsula or surrounding regions (Fuertes-Prieto et al., 2021). Similarly, studies of the Asturian lithic raw materials have questioned the paradigm of an "isolated" Asturian, as raw materials of regional and even extra-regional (>120 km away) origin have been identified (Álvarez-Fernández et al., 2020; Herrero-Alonso et al., 2020). At the same time, scientists have confirmed the existence of similar mortuary practices throughout the region. Human burials in shell pits, or levels rich in shells, seem to have been a relatively common practice throughout the region (see, for example, the case of J3 studied here) (Fano, 2019). Although investigations published during the last decades have focused on the similarities between the West and the East of the region, more studies are still needed to address this long-term discussion. Reconstructing the littoral exploitation patterns by Mesolithic communities who inhabited the western and eastern Cantabrian Region could be helpful to understand this enquiry better.

Previous isotope investigation conducted by Milano et al. (2022) on mussels from the Mesolithic sites of La Fragua and La Chora, located in the central area of the Cantabrian Region (Fig. 1a), revealed that forager populations who inhabited out of the traditional Asturian culture area also developed a preferential winter collection pattern, as it was previously deduced from western locations (Fig. 5). However, the annual scheduling pattern developed by Mesolithic populations of the East, where the density of shell middens seems to be notably lower (Iriarte-Chiapusso et al., 2010; Fano, 2019), still needed to be analysed. The results obtained here have demonstrated no difference in coastal resources exploitation by Mesolithic groups along the Cantabrian Region. This contributes to the idea that differences in the archaeological assemblage between western and eastern Cantabrian populations only result from local adaptation rather than profound divergences in their subsistence strategies.

4.3. Environmental conditions in the Early Holocene in the Bay of Biscay (Northeast Atlantic)

Although the warmest $SST_{\delta18O}$ reported by three long isotope series were similar each other (from 25.79 to 26.32 °C), the coldest $SST_{\delta18O}$ derived from these same specimens showed slight differences (from 12.92 to 15.14 °C) (Supplementary Table 3). This could be explained by the fact that, although the long isotope sequences allowed us to track $SST_{\delta18O}$ variations over several months during the mollusc lifespan, specimens J3.11.1 and J3.11.9 did not cover a complete winter season, thereby not recording the minimum annual SST. Despite long isotope series from specimen J3.14.1 showing mollusc growth during the winter prior to collection (at around 31 mm from the shell edge) (Supplementary Fig. 2), minimum $SST_{\delta18O}$ inferred from some short sequences was even colder. The differences in minimum $SST_{\delta18O}$ between specimens could be driven by variations in the coldest SST across different years and/or small growth stoppages during the coldest week of the year due to thermal stress, which has been previously attested to in this same species by sclerochronological investigations conducted on modern samples (García-Escárzaga et al., 2019b).

The estimation of $SST_{\delta18O}$ during the Early Holocene suggests that marine temperatures in the southern Bay of Biscay ranged from 11.04 °C in winter to 26.32 °C in summer at 9400–9040 cal BP (Fig. 6). While the maximum $SST_{\delta18O}$ is reasonably similar to the current maximum values observed in the coastal area where J3 is located (ca. 26 °C), daily SSTs in the southern Bay of Biscay rarely exceed 24 °C (González et al., 2008). This contrasts with our results, as all three shells analysed sequentially reported $SST_{\delta18O}$ values higher than or close to 26 °C. Additionally, four out of five short sequences that cover the summer before the mollusc collection reported $SST_{\delta18O}$ values significantly higher than 24 °C, thus

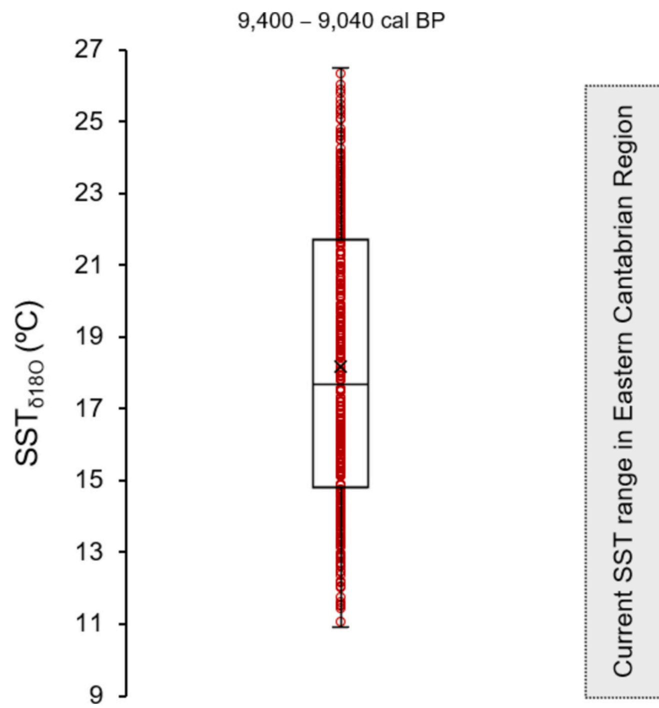

Fig. 6. Calculated SST derived from shell $\delta^{18}O$ values ($SST_{\delta18O}$) obtained from *P. lineatus* shells recovered from the shell midden site of J3. $SST_{\delta18O}$ was estimated using Eqs. (1) and (2). Grey square shows current SST range in Eastern Cantabrian Region in the Southern Bay of Biscay (González et al., 2008).

suggesting that summer temperatures around 9.2 ka cal BP were generally warmer than today. These results align with the data published by Mojtahid et al. (2013) for the same marine location and correspond with the Early Holocene warmer climate phase in the Northern Hemisphere (NH), known as the Holocene Thermal Maximum (HTM), during which warm temperatures were primarily driven by orbital forcing (Berger, 1978; Wanner et al., 2008). During the Early Holocene, NH summer solar insolation was significantly high, causing the HTM from ca. 10 to 6 ka cal BP (Wanner et al., 2008; Renssen et al., 2009; Martin et al., 2020). This increase in summer solar insolation supports our $SST_{\delta18O}$ calculations, warmer than present day temperatures during this season, due to the marked seasonal SST change in the southern part of the Bay of Biscay is mainly related to the seasonal insolation variation and the formation of a seasonal thermocline during spring and summer (Koutsikopoulos and Le Cann, 1996).

The minimum calculated $SST_{\delta18O}$ in the Early Holocene also appears to have been higher than current typical winter values in the southern Bay of Biscay (ca. 9 °C) (González et al., 2008). These warmer winter SSTs at 9.2 ka cal BP are consistent with previous investigations carried out in the Bay of Biscay for this chronology (Mojtahid et al., 2013; Mary et al., 2017). Although shell growth cessations during winter could explain why current temperatures are warmer than those recorded in the analysed specimens, conclusions from a sclerochronological study on modern samples from northern Iberian latitudes (García-Escárzaga et al., 2019b) suggest that growth stoppages are not expected in ontogenetically younger individuals. This lower SST than today may initially appear surprising given that winter insolation was lowest during the Early Holocene, further consideration related to the dynamics of marine currents in the Bay of Biscay is required. The general marine circulation in the Bay of Biscay is characterised by an intermittent poleward slope current, primarily influenced by the interaction between the weak North Atlantic Central Water and Mediterranean Water masses, in the mid-latitude waters along the eastern boundary of the North Atlantic oceanic circulation. The annual cycle of the slope current is driven by seasonal distribution of the wind off the Iberian Peninsula (Durrieu de

Madron et al., 1999). In the southern Bay of Biscay, the summer is characterized by weak upwellings and the development of an equatorward slope current, while the winter is marked by the emergence of a thermohaline poleward slope current due to the weakening of the southward component of wind stress. During winter, surface waters show a maximum poleward transport, and relatively warm water flows along the Atlantic coast of the Iberian Peninsula, forming the so-called Navidad Current (Pingree and Le Cann, 1992; Fernández et al., 1993; Pingree, 1994; Bode et al., 2002). An enhanced Navidad Current scenario has been attributed to an abrupt increase in the strength of the Atlantic Meridional Overturning Circulation (AMOC) at the beginning of the Holocene, which allowed the arrival of subtropically sourced warm subsurface water masses in the southeastern Bay of Biscay (Mojtahid et al., 2013). This resulted in a more intense Navidad Current along the Cantabrian coast and warmer SST during winter, as recorded in the shells analysed in this study.

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CRediT authorship contribution statement

Asier García-Escárzaga: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Alejandro León-Cristóbal:** Writing – original draft, Investigation. **Esteban Álvarez-Fernández:** Writing – review & editing, Validation. **André C. Colonese:** Writing – review & editing, Validation. **Alvaro Arrizabalaga:** Writing – review & editing, Resources. **María José Iriarte-Chiapusso:** Writing – review & editing, Resources. **Eneko Iriarte:** Supervision, Writing – review & editing. **Miguel Ángel Fano:** Writing – original draft, Validation, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All are included in the manuscript and/or in the supplementary material

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2024.112624.

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