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RESEARCH

Mobility and the use of littoral resources in the Late Mesolithic of Northern Spain: the case of La Chora cave (Voto, Cantabria, N Spain)

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Abstract
Littoral resources have been consumed by humans since at least the Middle Palaeolithic. Examples of the use of molluscs have been documented along the shores of Europe during that period but it was not until many millennia later that European hunter-fisher-gatherer societies exploited those resources intensively—see the case of Nerja cave during the Younger Dryas. This economic activity caused the accumulation of shells at archaeological sites during the Mesolithic, resulting in the formation of the so-called shell middens, a very common type of deposit along the Atlantic seaboard of Europe. Despite the large number of research projects that have studied the exploitation of coastal environments and the way of life of Mesolithic populations, questions such as the relationship between human mobility and mollusc exploitation patterns still remain. The archaeomalacological study of the shell midden in La Chora cave (Cantabria, Spain) confirms that people foraged for shellfish at several places along the coast, mainly in the estuary of the River Asón. The main difference between La Chora and other Mesolithic sites is its longer shellfish collection radius as the inhabitants travelled over 10 km to the open coast to collect shellfish. This study has expanded the available data about the subsistence strategies of Mesolithic groups in a little-studied area and improved our knowledge of mobility patterns among Mesolithic societies in the northern Iberian Peninsula.

Keywords Holocene · Littoral resources · Shell middens · Cantabrian Region · Human mobility · Collection areas

Introduction

Research carried out in recent decades regarding the Mesolithic in the Iberian Peninsula has significantly increased information about the way of life and the subsistence strategies of the last hunter-fisher-gatherer populations in southern Europe (Bicho et al. 2013; Gibaja et al. 2015; Fano 2019; Román and Domingo, 2022; Román et al. 2022). This increase in the available data has been especially notable in coastal areas, where the population density was higher (Fernández-López de Pablo et al. 2019). Two aspects that have often been considered about those groups prior to neolithization are the exploitation patterns of the marine environment and the importance of littoral resources in their subsistence strategies (Gutiérrez-Zugasti, 2009, 2011a; Álvarez-Fernández et al. 2011; Fano et al. 2013; Fernández-López de Pablo and Gabriel, 2016; Jordá et al., 2016; Aura et al. 2009, 2016; Fano 2019; García-Escárzaga 2020; Portero et al. 2022; Román et al. 2022). The number of studies of marine resource remains found in archaeological deposits, mainly molluscs but also echinoids, crustaceans and fish, has been particularly high in northern Iberia, partly because of the long tradition of this type of study in the area (Madariaga 1963; Ortea 1986) and especially because of the abundant Mesolithic shell middens that have been documented on the northern coast (Arias et al. 2015; Fano 2019). Other areas of Iberia,

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such as the Mediterranean coast, have received less attention, for a variety of reasons (cf. Colonese et al. 2011).

Studies carried out in the Cantabrian region have shown that coastal resources were frequently consumed by Mesolithic groups and played a significant role in their economy (Fano et al. 2013; García-Escárzaga and Gutiérrez-Zugasti 2021). The quantification of the mollusc species found in the deposits and the temporal and spatial changes in the proportions of the different taxa, have shown the importance of shellfish in the Mesolithic diet and their exploitation patterns. They have also contributed information about the palaeoenvironmental conditions in northern Iberia in the Early Holocene (Gutiérrez-Zugasti, 2009; Álvarez-Fernández 2011; Gutiérrez-Zugasti and Cuenca-Solana 2014; García-Escárzaga 2020; García-Escárzaga and Gutiérrez-Zugasti 2021; García-Escárzaga et al. 2022a, 2022b).

Changes in shell sizes over time have also provided significant information about the intensity of the exploitation of the marine environment, as both long and short-term variability have been observed (Álvarez-Fernández et al. 2011; García-Escárzaga 2020; García-Escárzaga et al. 2022b; Gutiérrez-Zugasti, 2009, 2011a). Geochemical analyses have recently been systematically applied to marine shells to determine the season in which the molluscs were gathered and/or to fill out available information about palaeoenvironmental change in the Early Holocene (García-Escárzaga 2020; García-Escárzaga et al. 2022b, 2024; Soares et al. 2016). Additionally, the study of malacological remains used as tools or for adornment has significantly increased our understanding of the socioeconomic conditions of the populations studied (Álvarez-Fernández 2006; Cuenca-Solana, 2013, 2014; Cuenca-Solana et al., 2013, 2014; Rigaud and Gutiérrez-Zugasti 2016). Despite this increase in the data about the way of life and subsistence strategies of those forager communities in North Iberia, some aspects still need further investigation, particularly the relationship between hunter-gatherer mobility and mollusc exploitation patterns.

This article presents the results of the archaeomalacological analysis of marine and terrestrial molluscs, and echinoderms and crustaceans, found in stratigraphic unit 102 (Late Mesolithic) in the shell midden in La Chora cave (Voto, Cantabria). It complements previous research on a much smaller sample of remains from more problematic stratigraphic and chronological contexts (Gutiérrez-Zugasti, 2009). The identification, quantification and biometric analyses of mollusc remains provide a better understanding of models of littoral resource exploitation and the mobility of the community that obtained them. Regardless of whether these hunters-gatherers were *foragers* or *collectors*, they coped with variability in the productivity of mollusc resources and their irregular distribution in space by adjusting their flexible mobility strategies (Binford 1980, 1983).

Materials and methods

The site of La Chora (Voto, Cantabria)

The cave of La Chora is in the village of San Pantaleón de Aras, which belongs to the municipality of Voto, in the Autonomous Community of Cantabria (Spain). It is now about 3 km from the head of the estuary of the River Asón, and nearly 10 km from the open coast (Fig. 1). However, those distances must have been longer when the cave was occupied in the Upper Palaeolithic and Mesolithic. It has been estimated that when the upper units in the Mesolithic shell midden were formed (ca. 7.7 ka cal BP), sea level would have been between -10 and -15 m below the current level (Leorri et al. 2012). Bearing in mind the data published in that study and bathymetric information in the BACO application (Gutiérrez-Zugasti, 2009), 8000 years ago La Chora would have been about 5 km from the head of the estuary and 12 km from the open coastline.

La Chora is a small cave with two entrances (Fig. 2) although one of them (Entrance 2) is now partially blocked by sediment (Gutiérrez-Zugasti, 2009). Since it was first excavated in the 1960s in the area inside the entrance, several studies have been carried out, focusing initially on the Pleistocene levels (González-Echegaray et al., 1963; González-Echegaray, 1972–1973). The little information that existed about the Mesolithic in the central and eastern part of Cantabrian Spain in the late twentieth century (Fano 2004) led to new archaeological fieldwork in the Asón valley to document sites with Early Holocene occupations. At La Chora, one of the field sites (González-Morales et al., 2000), a shell midden was identified in one of the cave passages during sampling. A radiocarbon date from a charcoal sample placed it in the Late Mesolithic (6360 ± 38 BP; 7420 – 7170 cal BP) (calibration with the OxCal 4.4 programme and the terrestrial IntCal20 curve: Bronk-Ramsey 2009; Reimer et al. 2020).

The documentation of this shell midden has motivated several archaeological studies, including an archaeomalacological analysis (Gutiérrez-Zugasti, 2009). The 2017 excavation only affected two 0.5 × 0.5 m sub-squares, i.e. a total area of 0.5 m^2 (Fig. 2b). Several shell midden units were documented. In 2021, the excavation was extended to 2 m^2, and seven stratigraphic units (102–108) attributed to the Mesolithic were confirmed (Fig. 2c). The present archaeomalacological analysis concentrates on the remains found in unit 102 in sub-squares C and D in Square N97. They come from a volume of 51 L of sediment (32 L from sub-square C and 19 from sub-square D). A date obtained from a faunal specimen (6843 ± 34 BP; 7750 – 7590 cal BP) (calibration with the OxCal 4.4 programme and the terrestrial IntCal20 curve: Bronk-Ramsey 2009; Reimer et al. 2020) suggests that this level formed in the last millennium of the Mesolithic period (Fano et al. 2015).

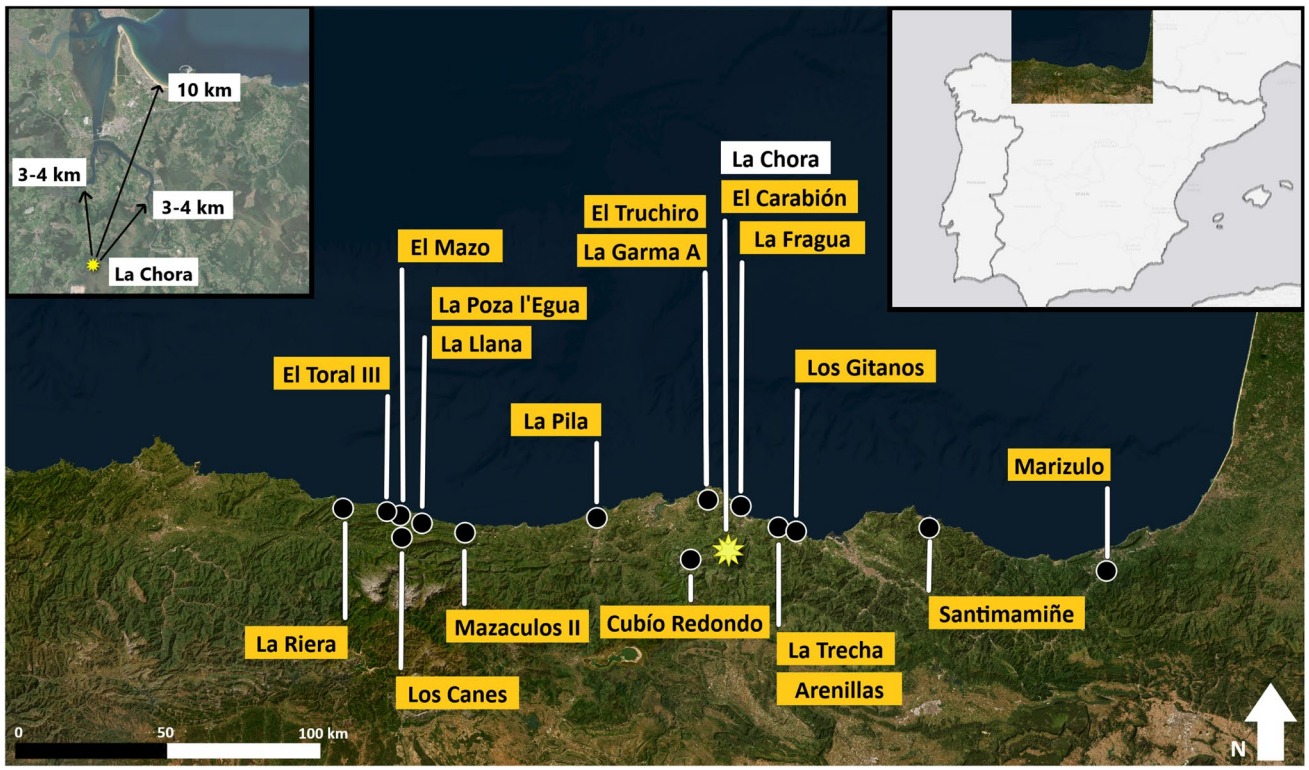

Fig. 1 Location of La Chora cave (Voto, Cantabria) and other archaeological sites whose data have been included or cited in the present study. The present-day distance from La Chora to the estuary of the River Asón and the nearest open coastline are shown in the top left of the figure

Archaeomalacological study

After water-sieving all of the excavated sediment, all mollusc, echinoderm and crustacean remains larger than 2 mm were examined. They were studied and classified following the fragmentation categories developed by R. Moreno (1994) and later added to by I. Gutiérrez-Zugasti (2009, 2011a) for echinoderms and crustaceans. Taxonomic identification was performed with specialised guides (Fechter and Falkner 1993; Palacios and Vega de la Torre 1997) and the comparative collection at the IIIPC (Marín-Arroyo et al. 2015). The taxonomic nomenclature for the marine and terrestrial species follows the proposals of the World Register of Marine Species (WoRMS) and of M. Kerney and R. Cameron (1999), respectively.

The MNI was calculated following the methodology and formulae of Moreno (1994) for molluscs and Gutiérrez-Zugasti (2009, 2011a) for echinoderms and crustaceans. The following abundance estimators are presented in the results: the NR (total number of remains), NR% (percentage of NR in the total sample), MNI% (percentage of MNI of the total sample) and MNI/dm^3 (MNI in each litre of sediment excavated).

The ecological preferences of each species were considered to identify the type of coastal habitats and substrates on which the molluscs were collected (Table 1), based on information published in Gutiérrez-Zugasti (2009) for Cantabrian Spain and new observations derived from subsequent fieldwork on the Cantabrian coast. Following this methodology, the MNI of the species associated with each coastal type (open and/or estuary) and substrate (rocky, sandy, sandy/muddy and muddy) were combined to estimate the percentage importance of each location type.

The biometry of the shells has also been examined for the present study, using measurements presented in Gutiérrez-Zugasti (2009). In the case of spiral gastropods (both marine and terrestrial), the height (or length) and width (or diameter) were measured. For simple gastropods, the length, width and height were recorded, and for bivalves we measured the length and height. Only those shells that preserved at least one of these parameters were measured. The subsequent biometric study only analysed the species for which at least 30 individuals were measured. The hinge was also measured for *Scrobicularia plana* for comparison with specimens from sites in northern Spain where whole shells could not be measured (Gutiérrez-Zugasti 2011b). By comparing the size of each species with the measurements obtained at other sites (Gutiérrez-Zugasti 2011a) and analysing the degree of normality and asymmetry in the distribution of the shell sizes of each species, the intensity of use of the marine environment could be estimated.

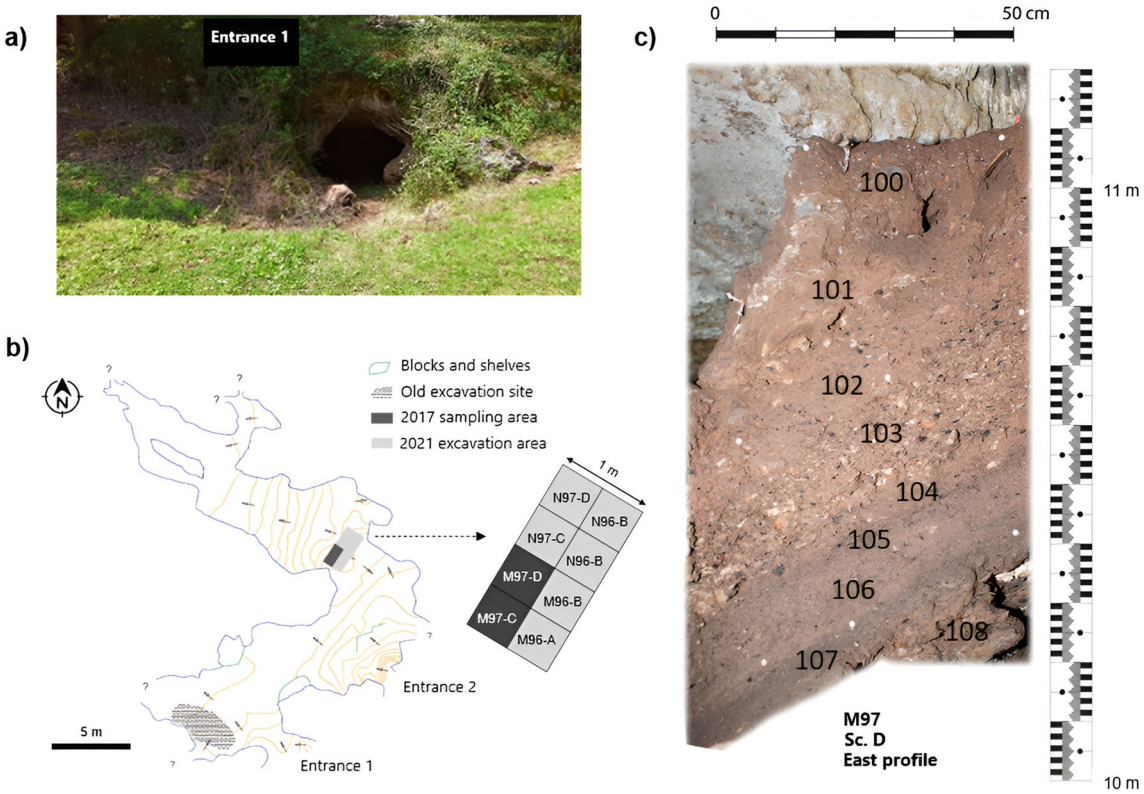

Fig. 2 **a** View of the main entrance of La Chora cave. **b** Plan of the cave, indicating the squares and sub-squares (N97-C and N97-D) studied here and, excavated during the 2017 and 2021 field seasons (modified from Gutiérrez-Zugasti, 2009). **c** Stratigraphic units identified in the east section of Square M97 during the 2021 field season

Table 1. Ecological zonation of the documented mollusc species at the shell-midden of La Chora. Based on the information published in Gutiérrez-Zugasti, 2009, and new observations derived from subsequent fieldworks developed by others for the Cantabrian coasts

Species	OPEN COAST					ESTUARY					Type of substrate
	Supratidal	Intertidal			Subtidal	Supratidal	Intertidal			Subtidal	
		Upper	Middle	Lower			Upper	Middle	Lower		
Mytilus galloprovincialis											Rocky
Ostrea edulis											Rocky
Patella vulgata											Rocky
Patella ulyssiponensis											Rocky
Patella depressa											Rocky
Phorcus lineatus											Rocky
Paracentrotus lividus											Rocky
Ruditapes decussatus											Sandy/Muddy
Solen marginatus											Sandy/Muddy
Scrobicularia plana											Muddy

These measures are used to determine whether specimens were selected based on their size. Average body size has traditionally been used as a measure of the intensity of mollusc exploitation (García-Escárzaga 2020; Gutiérrez-Zugasti, 2009, 2011a). The PAST programme (Hammer et al. 2001) was used to determine the normality of the size distributions. However, as species inhabiting estuaries live in sandy or muddy areas and it is not possible to discriminate their size during their collection, these were not included in the study. Similarly, mussels are not suitable indicators for size selection since they usually cluster in colonies.

Another aspect that provides information about the intensity of the exploitation of the marine environment is the use of the upper or lower intertidal zone in which the molluscs were collected. Here, the biometric data for *Patella depressa*, the Width/Height (W/H) ratio and the threshold value established by García-Escárzaga (2020) for this taxon were used to deduce the intertidal zone in which the specimens of this species were collected. This W/H ratio, initially proposed by Craighead (1995), has been employed in multiple studies to differentiate between the upper or lower intertidal zone (Gutiérrez-Zugasti, 2009). The value 2.53 is used as a

threshold value to distinguish between limpets harvested from low or high intertidal zones. If the resulting value of the equation W/H is lower than this figure, the specimen is assumed to have been collected from the high intertidal zone. Conversely, if the resulting value is higher than 2.53, the specimen would have been collected from the lower intertidal zones.

Results

The total number of mollusc remains from stratigraphic unit 102 in La Chora cave is 39,919, with a MNI of 3,538 (Table 2). In percentage terms, bivalves are the most abundant (76.4%), followed by terrestrial (17.4%) and marine gastropods (6.1%). The best represented species is *S. plana* (53%) (Fig. 3a). Other species are noticeably less frequent: *Mytilus galloprovincialis* (17.4%) (Fig. 3b), *Solen marginatus* (4.0%) (Fig. 3c), *P. depressa* (3.8%) (Fig. 3d), *Patella ulyssiponensis* (0.9%) (Fig. 3e) and *Patella vulgata* (0.7%) (Fig. 3f). *Cepaea nemoralis* (16.4%) is by far the most abundant of the terrestrial gastropods (Fig. 3g). The other species appear in very low frequencies (< 1%). It is necessary to sum the remains of several taxa to reach a percentage of 80% of the total malacological assemblage in the stratigraphic unit.

In terms of the coastal type where the molluscs were gathered, the ecological preferences of the species show that estuaries (73.6%) were exploited more than open coasts (26.4%). Similarly, with regards to the type of substrate, the data reflect a clear preference for muddy areas (61.4%). Resources gathered on rocky shores represent 28.7% of the collection, whereas the use of sandy/muddy and sandy substrates was minimal (4.9%).

The mean length of the individuals of *P. depressa* is 25.3 mm, while the mean height of *M. galloprovincialis* specimens is 41.0 mm. The mean size of the right hinge sizes of *S. plana* is 6.35 mm. The mean diameter of *C. nemoralis* is 23.1 mm (Supplementary Table 1). The normality and asymmetry studies of the populations (Fig. 4) show that the size distribution of *P. depressa* is not normal (or log normal) and the asymmetry is positive, which indicates a selection of larger specimens. Finally, the W/H ratio of *P. depressa*

Table 2. Abundance (NR, MNI and relative frequencies) of the taxa identified and not identified in stratigraphic unit 102 in La Chora cave

Taxon	SU. 102 Quad. N97 Subsq. C and D				
Marine bivalves	**NR**	**NR%**	**MNI**	**MNI%**	**MNI/dm3**
Mytilus galloprovincialis	11358	28.45	617	17.44	12.10
Ostrea edulis	1093	2.74	59	1.67	1.16
Ruditapes decussatus	70	0.18	8	0.23	0.16
Scrobicularia plana	20808	52.13	1875	53.00	36.76
Solen marginatus	1854	4.64	143	4.04	2.80
Total Bivalves	**35183**	**88.14**	**2702**	**76.37**	**52.98**
Marine gastropods	**NR**	**NR%**	**MNI**	**MNI%**	**MNI/dm3**
Patella vulgata	26	0.07	26	0.73	0.51
Patella ulyssiponensis	32	0.08	32	0.90	0.63
Patella depressa	136	0.34	136	3.84	2.67
Patella sp.	294	0.74	18	0.51	0.35
Phorcus lineatus	5	0.013	4	0.11	0.08
Total marine Gastropods	**493**	**1.24**	**216**	**6.11**	**4.24**
Terrestrial gastropods	**NR**	**NR%**	**MNI**	**MNI%**	**MNI/dm3**
Cepaea nemoralis	4176	10.5	582	16.45	11.41
Helicella itala	10	0.03	10	0.28	0.20
Oestophora silvae	4	0.01	4	0.11	0.08
Oestophorella buvinieri	3	0.01	3	0.08	0.06
Orden Pulmonata	13	0.03	13	0.37	0.25
Pomatias elegans	5	0.01	5	0.14	0.10
Total terrestrial Gastropods	**4211**	**10.55**	**617**	**17.44**	**12.10**
Echinoids	**NR**	**NR%**	**MNI**	**MNI%**	**MNI/dm3**
Paracentrotus lividus	8	0.02	1	0.03	0.02
Total Echinoids	**8**	**0.02**	**1**	**0.03**	**0.02**
Crustaceans	**NR**	**NR%**	**MNI**	**MNI%**	**MNI/dm3**
Brachyura order	2	0.01	1	0.03	0.02
Total Crustaceans	**2**	**0.01**	**1**	**0.03**	**0.02**
Indeterminates	**22**	**0.06**	**1**	**0.03**	**0.02**
TOTAL	**39919**	**100**	**3538**	**100**	**69.37**

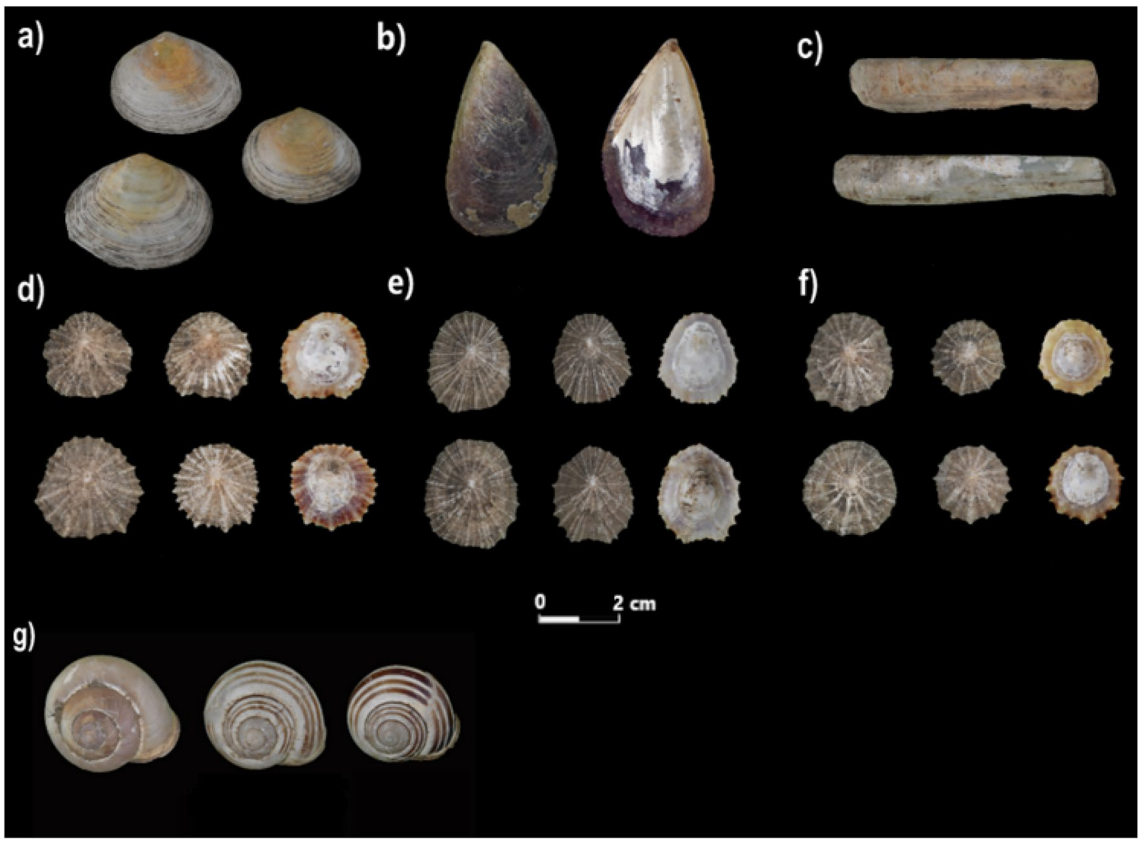

Fig. 3 Photographs of remains from the assemblage in stratigraphic unit 102 in La Chora cave: **a** *S. plana*; **b** *M. galloprovincialis*; **c** *S. marginatus*; **d** *P. depressa*; **e** *P. ulyssiponensis*; **f** *P. vulgata*; **g** *C. nemoralis*. The figure includes well-preserved specimens of the most representative taxa of the shell-midden. Specimens of *Ostrea edulis* are not included, due to their poor conservation

shows that 75.4% of the individuals were gathered in the low intertidal zone (Supplementary Table 2).

Discussion

Taxonomic composition of unit 102 of La Chora and collection areas of littoral resources

The results of the study show that the Late Mesolithic occupants of La Chora cave collected marine resources mainly from intertidal zones of estuarine areas (73.6%) but also from open coasts (26.4%). It is precisely the use of the two coastal environments that explains the diversity of species documented in unit 102, since no one taxa represent more than 55% of the total MNI in the unit. The use of estuaries and open coast in the 8th millennium cal BP had already been observed in a previous study by Gutiérrez-Zugasti (2009). In that case, the results indicated that 71.1% of the individuals were collected in estuaries and the other 28.9% were found on open coasts. Similarly, data

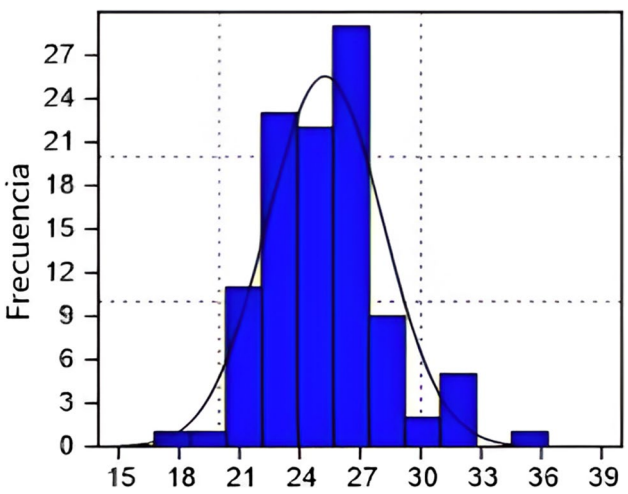

Fig. 4 Statistical representation of the *P. depressa* shell sizes with the PAST programme. The summary statistics are: $N = 103$; Min = 16.8; Max = 36.3; Media = 25.25; Median = 25.25; Skewness = 0.6259192; Shapiro–Wilk W = 0.9676 and p (normal) = 0.01195

from the nearby, coeval site of El Carabión, (7.8 ka cal BP), indicated similar percentages of specimens from these coastal types (75.2% estuary and 24.8% open coast) as those from La Chora (Pérez-Bartolomé et al. 2016). Therefore, the results from these three archaeological levels suggest that the morphology of the coastline in the study area at the start of the Middle Holocene was similar to its present configuration. This means that an estuary had already formed at the mouth of the River Asón in the 8th millennium cal BP, as has also been noted for other parts of the northern Iberian coast (Leorri and Cearreta 2004, 2009).

The results of the taxonomic classification coincide with data published for another Mesolithic unit in the same deposit (Gutiérrez-Zugasti 2009), but with some nuances (Fig. 5), even considering the number of remains in each assemblage (NR in the present study = 39,919, compared with 3,304 in Gutiérrez-Zugasti, 2009). Despite the general similarities between that study and the present one, some noteworthy differences are observed in two species (Fig. 5): *S. plana* (53% in this study and 34.1% in Gutiérrez-Zugasti, 2009) and *Ostrea edulis* (1.7% in this study and 12.8% in Gutiérrez-Zugasti, 2009). The distribution of species in unit 102 in La Chora also resembles the results obtained for the proximate site of El Carabión (Pérez-Bartolomé et al. 2016) (Fig. 5), with a larger sample size (8,288) than in the study by Gutiérrez-Zugasti (2009). However, differences exist in the presence of *S. plana* (53.0% in this study and 21.2% in Pérez-Bartolomé et al. 2016) and of *O. edulis* (1.7% in this study and 21.2% in Pérez-Bartolomé et al. 2016). In addition, the terrestrial gastropods are more abundant than in unit 102 at La Chora (16.4% at La Chora and 37.6% in Pérez-Bartolomé et al. 2016 -see comparisons with other archaeological contexts in Sect. "Exploitation of terrestrial gastropods").

The differences observed in these three archaeological levels do not seem to correspond to changes in the gathering pattern or the distribution of species available on the coast, although the level studied by Gutiérrez-Zugasti (2009) is a little more recent (ca. 7.3 ka cal BP) than those at El Carabión and unit 102 at La Chora (ca. 7.8 ka cal BP and 7.7 ka cal BP, respectively). Changes in the morphology of the estuarine areas between these archaeological assemblages are not expected since they were already formed in this chronology (Leorri and Cearreta 2004, 2009). These small differences in the percentages of the species seem to be due to preferences in the collection of molluscs over time. Nevertheless, the influence of the difference in sample size among these studies cannot be discarded. In any case, despite the slight differences, the data show that the human groups inhabiting the surroundings of La Chora and El Carabión in the last millennium of the Mesolithic mostly gathered bivalves (clams, mussels and oysters).

In accordance with the different representation of some species compared with the study of Gutiérrez-Zugasti (2009), slight variations are also seen in the percentages of the types of substrates where the gathering took place. The new data from La Chora indicate greater importance of muddy substrates (61.4%) in comparison to other types. In contrast, Gutiérrez-Zugasti (2009) found only small differences between shell fishing on rocky shores (48.7%) and in muddy areas (46.2%). The percentages are very similar at El Carabión too (rocky 41.1%; muddy 37.2%). This variation is due to the fewer specimens of *S. plana* and larger number of individuals from rocky substrates, such as *M. galloprovincialis, O. edulis* and *Patella* spp. in the assemblages that were previously studied.

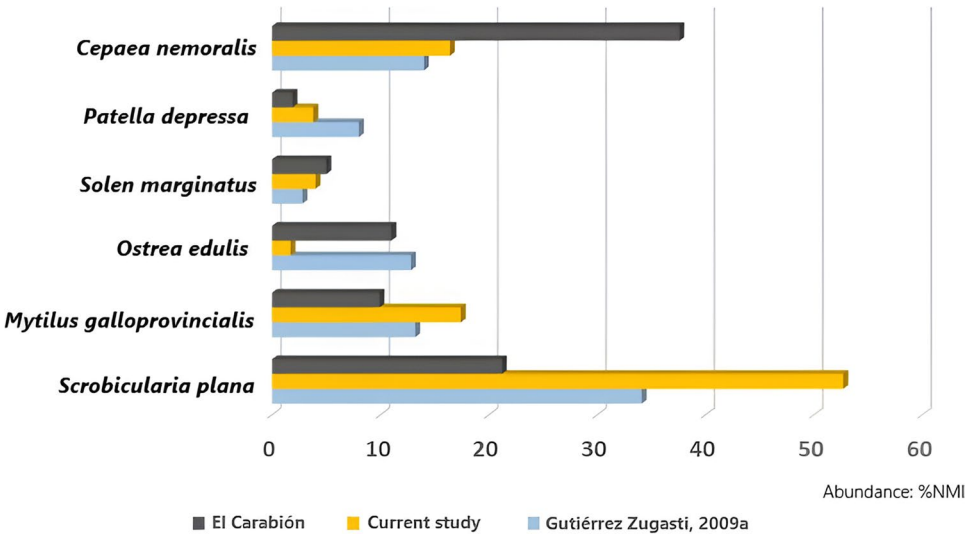

Fig. 5 Comparison of the most abundant taxa identified in the present study, in the previous study at La Chora (Gutiérrez-Zugasti 2009), and at El Carabión (Pérez-Bartolomé et al. 2016). The representation of the different species is expressed in MNI%

The percentages of species from estuary and open coast environments in unit 102 (73.6% estuary and 26.4% open coast) and in the previous research of Gutiérrez-Zugasti (2009) (71.1% estuary and 28.9% open coast) do not differ significantly. Despite the change in the percentage of some species, the importance of the estuary remains similar. This is also the case of El Carabión (75.2% estuary and 24.8% open coast) (Pérez-Bartolomé et al. 2016). The exploitation of those two littoral environments has been observed at other sites relatively close to La Chora, such as La Trecha, Arenillas and La Fragua (Gutiérrez-Zugasti, 2009) (Fig. 1). However, in those cases, the distances to both the estuary and the open coast are very small. La Chora is therefore a relatively unusual case of a shell midden located some distance from the littoral zone, particularly the open coast (> 10 km).

Mobility of human populations in the Late Mesolithic

The mobility of Mesolithic hunter-gatherers in northern Spain has been studied, but the available information is still limited mainly to the western sector of the region and usually lacks a theoretical frame of reference (e.g., Arias 2006; Fano 1998). Generally speaking, lower mobility has traditionally been attributed to Mesolithic populations than to people in previous archaeological periods (Arias et al. 2009; Fano 2004; González-Morales, 1982; Gutiérrez-Zugasti et al. 2011, 2014; Gutiérrez-Zugasti and Cuenca-Solana 2014, among others). Nevertheless, recent lithic raw material studies have determined north–south contacts across the Cantabrian Mountains to the coast (Herrero-Alonso et al., 2020a) and sites like El Mazo have yielded lithic materials from distant or very distant sources (> 120 km). These results challenge the classic paradigm of the Asturian culture (the name given since the early twentieth century to the Mesolithic record in the central-western sector of northern Iberia; cf. Fano 2019), that is to say, that the mobility of these foragers was limited (Herrero-Alonso et al., 2020b, in review).

In the present case, we have shown that the occupants of La Chora, exploited different catchment areas by "journeying" for over 10 km. These large distances covered, to collect and transport shellfish, were not common in the western part of the Cantabrian coast. A large sample in one study (Fano 1998), showed that only 20% of the sites were more than 24 min walking distance from the shore, with seafood being transported for longer than an hour. So, in general, the *Asturian* hunter-gatherer settlement system seems to fit better into a more residential mobility model (cf. Binford 1980), that included travelling multiple kilometres to the coast to procure resources, and then transporting them to caves and rock-shelters inland. Thus, the scale of the mobility of the occupants of La Chora to acquire marine resources is atypical of this region, especially in relation to the distances travelled to obtain open shore resources, with more proximate examples like El Carabión (Pérez-Bartolomé et al. 2016) underscoring that exceptionality. Moreover, it seems that this long shellfish collection radius was maintained over time at La Chora, into the Late Mesolithic, as suggested by the results of the previous archaeomalacological study (Gutiérrez-Zugasti, 2009). The documentation of *M. galloprovincialis* remains also supports long-distance mobility as this resource was collected on the open coast and from different parts of the estuary (Milano et al. 2022). We will have to wait to learn more from other categories of data from La Chora, such as mammalian fauna, but in this case logistical mobility seems to be the most feasible, with the use of sites from which the open coast could be exploited.

Despite the long distances travelled (ca. 12 km to the open coast), the forager groups do not seem to have sought solutions to resolve the problem of transporting the non-edible part of the shellfish (cf. Davidson and Bailey 1984), like those known from ethnography and ethnohistory (Waselkov 1987). The marine resources were transported to La Chora whole. Similar situations are also known from the ethnographic record. For example, the Nguni women in Africa travel 3 to 5 km to the sea and return with the live shellfish to their homes (Waselkov 1987) and Yamana women from South America make baskets to help them gather the shellfish and fish that they obtain by travelling from island to island (Orquera and Piana 2015). These journeys by canoe could cover distances of up to 40 or 50 km although they were usually shorter, between 9 and 17 km.

The transport of shellfish seems to have been a common practice at different times and places throughout history, but we know little about how these resources were carried. Data in historical sources provide valuable information. Castilian chroniclers in the sixteenth and seventeenth century sometimes mention that some Patagonian tribes made baskets of different sizes from plants, such as reeds, to transport both the marine resources they collected and the utensils they used to extract them (De Iriarte 1768; Saletta 2015). Crafts manufactured from plant fibres to make cordage, basketry and textiles for such purposes must have been important in hunter-gatherer societies (Aura-Tortosa et al. 2020). This is evidenced by some traceological studies in northern Iberia; the results obtained at the Mesolithic site of El Toral III are especially significant (Cuenca-Solana, 2013, 2014).

The previous archaeomalacological study (Gutiérrez-Zugasti, 2009) differs very little in the percentage of estuary species. However, greater diversity is seen in open coast species, such as *Hiatella rugosa, Petricola lithophaga* and *Pollicipes pollicipes*, which are absent in unit 102. The presence of a wider range of taxa from the shore, in a sample a tenth of the size of the present one, may indicate more frequent and intense movements to the coast at a slightly later time at the end of the Mesolithic.

Intensity in the use of marine environment in the central sector of Cantabrian Spain

It has been shown that the human groups that inhabited La Chora cave travelled distances of over 10 km to the open coast. However, covering such long distance to collect littoral resources raises some questions. In addition to how the shellfish were transported, this includes how intensively they used these littoral resources. Previous research has approached this aspect through biometric data and shown that the size of marine shells generally decreased from the Late Upper Palaeolithic to the Neolithic (Álvarez-Fernández et al. 2011; Gutiérrez-Zugasti 2011a). Recent studies have confirmed this process in some archaeological sequences, by assessing the main species that were gathered and determining points of increase and decrease in their size during the Mesolithic (García-Escárzaga et al. 2022a). Sufficient data supports the proposition that size reduction over the course of the Mesolithic was related to intensified collection rather than climatic change (Gutiérrez-Zugasti 2011a).

In order to assess the measurements obtained in the present study, they were compared with available biometric information from northern Iberia on three of the most important species at La Chora (i.e., *P. depressa*, *S. plana* and *M. galloprovincialis*). The mean sizes obtained at other sites in the region (Figs. 6a, b and c) were compared with the new and published data. The sites were selected based on the quality of information that they provide, and a well-defined chronology.

For *P. depressa*, 46 units from 10 sites have been included, in chronological order from the Azilian to the Neolithic (Supplementary Table 4). A non-parametric Mann–Whitney pairwise test was applied to those units with more than 30 published samples. Results revealed that the majority of the compared populations are different from one another, indicating statistically significant changes in shell size over time (Supplementary Table 5). The Kruskal–Wallis test also reported meaningful differences between sample size medians. The shell sizes gradually decrease after 9620–9480 cal BP (La Poza l'Egua-2), with lengths dropping under 26 mm, a size from which they never recover (Fig. 6a). According to previous investigations, human pressure on mollusc species was the determining factor in the shell size reduction (García-Escárzaga et al. 2022a; Gutiérrez-Zugasti 2011a). The lengths of *P. depressa* at La Chora are slightly larger than the average specimens from coeval sites and stabilised in the Late Mesolithic and Early Neolithic. This may reflect less intensive use of littoral resources by the occupants of the cave ca. 7800 cal BP. However, it may also correspond to other local factors. The case of La Fragua, located on the present-day mouth of the River Asón, is similar (Fig. 6a). It is possible that the residents of this site collected limpets from areas that were rarely exploited, and thus larger specimens were gathered.

The size distributions and normality of the data obtained for *P. depressa* have also been analysed (Fig. 4). The results confirm that larger specimens tended to be selected as the size distribution is not normal or log-normal, and the asymmetry is positive. These results may suggest, in agreement with previous interpretations (Gutiérrez-Zugasti, 2009, 2010), that the collection of this littoral resource was not particularly intense. Gathering in the intertidal zone may have followed an ecological approach founded on a wide knowledge of the surrounding natural environment. This knowledge would include the rhythm of the tides and the time of reproduction and growth of the species they consumed. From this ecological perspective, the collection of larger individuals would allow the survival and growth of the younger individuals (Gutiérrez-Zugasti, 2010) and enable the regeneration of the life cycle of the shellfish.

Nevertheless, although that interpretation is feasible, another aspect should be considered regarding the gathering of *P. depressa*. The size selection might not be based on ecological knowledge but on the sexual and reproductive condition of *P. depressa*. This limpet is a sequential hermaphrodite; the adult individuals gradually transition from a male to a female sexual function during their life cycle, like such other contemporary species as *Patella ferruginea*, *P. vulgata* and *P. aspera* (Southward and Dodd 1956; Espinosa et al. 2009; Guallart et al. 2013; Borges et al. 2016). This means that if the objective of the human group was to gather the largest individuals, females would have been collected most often. This would affect the reproduction of the species, which would in turn reduce the limpet populations and be incompatible with the sustainable exploitation of the environment. It would be a less profitable subsistence strategy in the long term.

The application of the zonation ratio (W/H) for *P. depressa* has shown that 75.4% of the specimens at La Chora are from the low intertidal zone. Previous research (García-Escárzaga 2020) has applied the same ratio to *P. depressa* populations at the sites of La Llana (W/H ratio indicates that 42% of the individuals are from the low zone) and El Mazo (W/H ratio indicates 40% are from the low zone). These results are very different from those obtained for La Chora, since in those cases the high intertidal zone would have been exploited most (Fig. 7). Consequently, the data from La Chora suggest some intensification in the collection of marine resources as most of the patellids are from lower zones where gathering would be more difficult (Gutiérrez-Zugasti, 2009).

In the case of *P. vulgata*, although the sample from La Chora is too small for a zonation analysis (< 30 individuals), a general view can be obtained through comparison with the data from other sites in northern Iberia. As Fig. 7 shows, most sites indicate that the lower intertidal zone

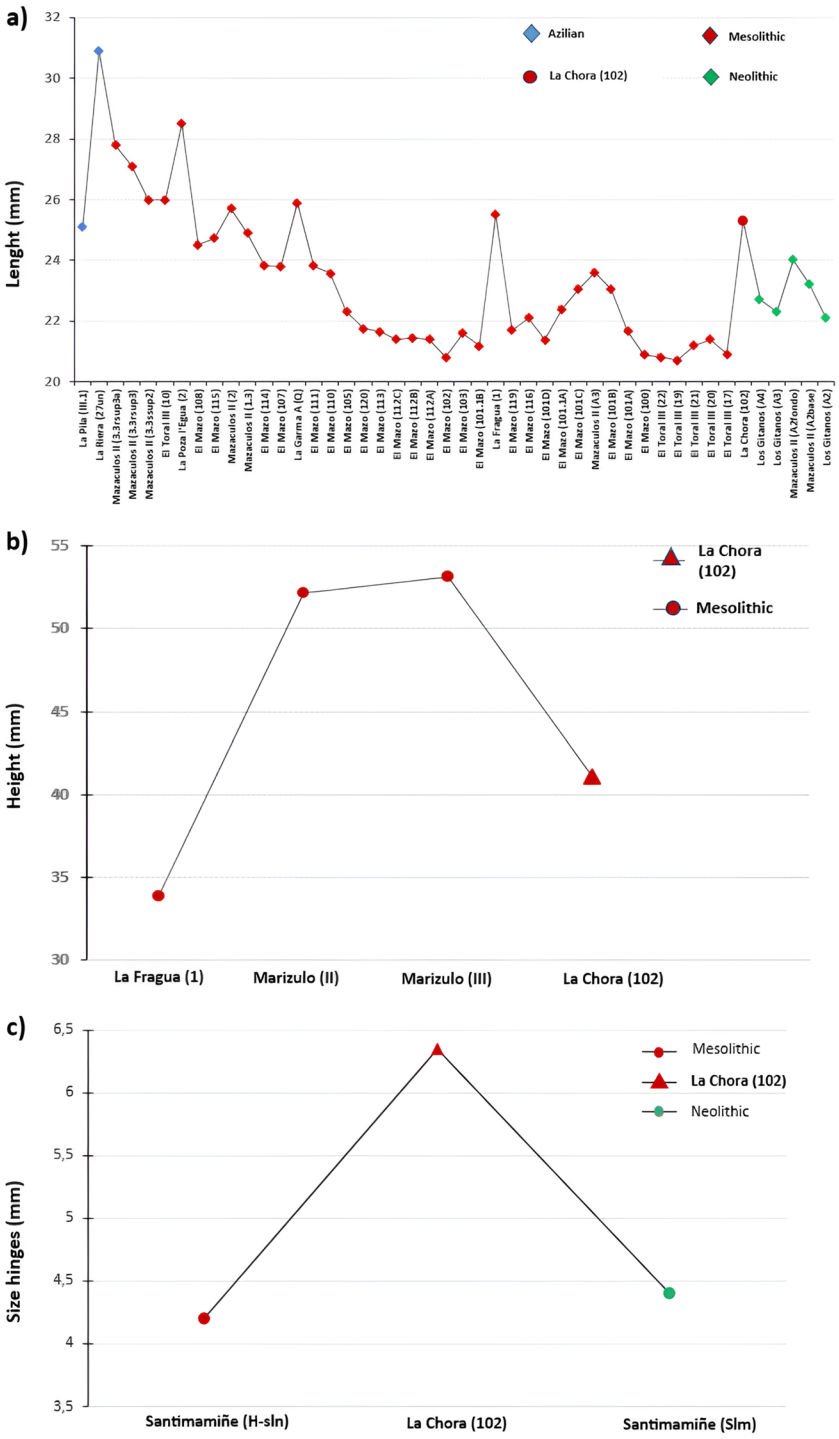

Fig. 6 Biometric data available in northern Iberia for *P. depressa*, *M. galloprovincialis* and *S. plana*. For *P. depressa* (6a), the mean length (in mm) was taken as the point of reference. The sites are presented in chronological order, from the Azilian (blue) to the Neolithic (green). The data comes from the archaeological sites of La Pila (III.1), La Riera (27un), Mazaculos II (3.3rsup3a; 3.3rsup3; 3.3ssup2; 2; 1.3; A3; A2Fondo and A2Base) and La Fragua (1) (Gutiérrez-Zugasti 2011a); La Poza l'Egua (2) (Arias et al. 2007); El Toral III (10) (Arniz-Mateos et al. 2024); El Mazo (108, 115, 114, 107, 111, 110, 105, 120, 113, 112C, 112B, 112A, 102, 103, 101.1B, 119, 116, 101D, 101.1A, 101C, 101B, 101A, 100) (García-Escárzaga 2020); La Garma A (Q) and Los Gitanos (A4, A3, A2) (Álvarez-Fernández et al. 2011); and El Toral III (22, 19, 21, 20, 17) (Arniz-Mateos et al. 2024). For *M. galloprovincialis* (6b) the mean height (in mm) of the right valve was utilised. The sites are in chronological order, from the oldest Mesolithic (red) to the most recent. The data comes from the archaeological sites of La Fragua (1) (Gutiérrez-Zugasti, 2009) and Marizulo (II, III) (Álvarez-Fernández and Altuna, 2013). Finally, for *S. plana* (6c) the mean size of the right hinge (in mm) was used. The sites are ordered chronologically within the Mesolithic period. The data comes from the archaeological site of Santimamiñe (H-sln, Slm) (Gutiérrez-Zugasti 2011b) (Supplementary Table 3)

was exploited most often (between 70 and 85%). As in the case of *P. depressa* at La Chora, gathering took place in the most difficult places to access. Therefore, despite the larger size of the *P. depressa* specimens at La Chora, the intensity of exploitation seems to have been similar and perhaps the peculiarity of this site is a consequence of local factors, as suggested above.

The greater variety of species from a rocky substrate documented in the study by Gutiérrez Zugasti (2009) is another argument in favour of the increasing intensity in the collection of marine gastropods at La Chora in the Late Mesolithic. This would agree with findings at other sites in the region, such as El Mazo (Level 100), where the shell sizes decrease considerably at a slightly earlier time

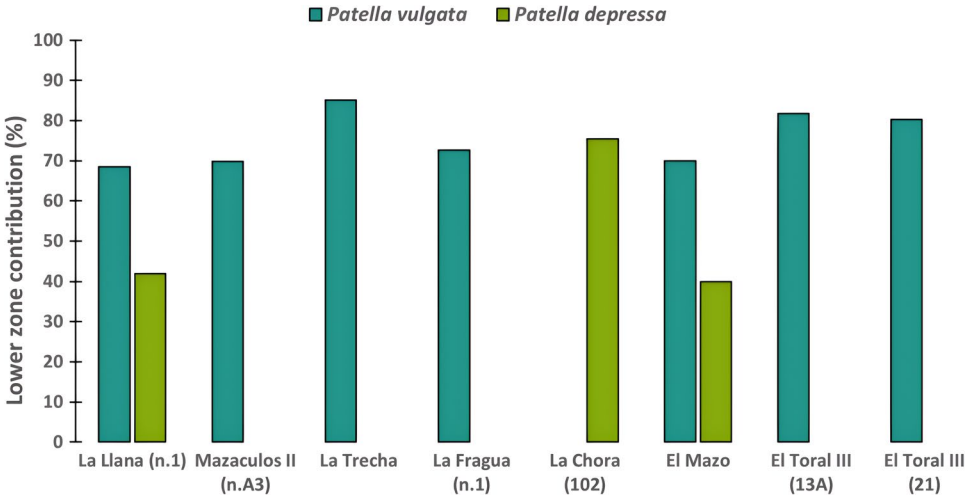

Fig. 7 Zonation of *P. depressa* and *P. vulgata* at sites in northern Spain with available information. For El Mazo, the mean values of all the studied levels have been used. The data comes from the following archaeological sites: La Llana (n.1), Mazaculos II (n.A3) and La Trecha (Gutiérrez-Zugasti, 2009); La Fragua (n.1) (Gutiérrez-Zugasti 2011a); El Mazo (average levels, García-Escárzaga 2020); and El Toral III (13A, 21, Bello-Alonso et al. 2015)

than the decline shown in Level 102 at La Chora (García-Escárzaga 2020).

M. galloprovincialis collections have been studied, from three sites arranged in chronological order from the oldest to the most recent Mesolithic (Fig. 6b). The height (in mm) has been taken as the point of reference. Only right valves were selected (the most numerous). The non-parametric Mann–Whitney and Kruskal–Wallis tests applied on published data for *M. galloprovincialis* indicate that changes in shell sizes over time are statistically significant (Supplementary Table 6). The mean values at La Chora are higher than those at La Fragua and lower than those at Marizulo, and reveal little about the intensity of the collection of those bivalves. However, a recent study (Milano et al. 2022) has shown that, both at La Fragua (Levels 1.1 and 1.4) and in Levels 103 and 104 at La Chora, mussels were collected nearly all year round, in larger or smaller quantities, both in estuaries and on the open coast.

The biometry of *S. plana* has only been compared with the data available for the site of Santimamiñe (Kortezubi, Biscay) (Gutiérrez-Zugasti 2011b). As the length of the hinge was measured for this site, we compare it to the hinge measures from La Chora. In this case, right valves were used because they are the most numerous. As only two sites (three levels) are being compared, it cannot be confirmed that the size of the hinges decreased over time. However, the average size of the hinges at La Chora is larger than in both levels at Santimamiñe (Fig. 6c). According to Mann–Whitney and Kruskal–Wallis tests, the differences between clam sizes obtained from both sites are statistically significant (Supplementary Table 7).

Finally, the biometric data for *C. nemoralis* have been compared with those at the proximate site of La Fragua (Gutiérrez-Zugasti, 2009). The mean size of the gastropods at that site is 24.8 mm, whereas the mean size for La Chora is 17.6 mm, indicating a considerable decrease in size over time. The individuals measured at La Fragua come from Level 3 (Azilian) (13,250–12,590 cal BP). The difference might be related to climate fluctuation (Yanes et al. 2012) because it has been noted that the mean size of *C. nemoralis* individuals was larger during the Pleistocene than in the Late Pleistocene-Early Holocene. This must have been mainly due to the drier conditions in the glacial periods, unlike in the interglacials. This circumstance led to the proposal that the bodies of *C. nemoralis* were considerably larger between 12.1 and 10.9 ka cal BP than between 8.4 and 6.3 ka cal BP because during the drier periods these gastropods consumed a larger amount of limestone to reduce the risk of desiccation. This consumption decreased in more humid periods and therefore also their greater growth.

Exploitation of terrestrial gastropods

Two points of view on the possible consumption of terrestrial gastropods by Mesolithic populations in northern Iberia have been debated. Some authors attribute the presence of *C. nemoralis* in the archaeological record to natural factors (Barandiarán and Madariaga 1989; Straus 1992) whereas others argue that they represent the remains of land snails collected and consumed by humans (González-Morales et al., 2000; Miracle 2001; Lubell 2004a, 2004b; Gutiérrez-Zugasti, 2006, 2009, 2011b). According to this perspective, *C. nemoralis* would have contributed to the diet of Mesolithic populations.

Six terrestrial gastropod species have been identified in unit 102 at La Chora (Table 2). *C. nemoralis* is the most abundant: in fact, it is one of the three most abundant mollusc species in the shell midden, more than double that of the entire marine gastropod assemblage (MNI% = 16.4% vs 6.1%, respectively).

This quantity is noticeably larger than in other Mesolithic sites on the northern Iberian coast, like La Trecha (1.4%) and Santimamiñe (2.5%) (Gutiérrez-Zugasti, 2009, 2011b). However, at other sites in the same period, like El Truchiro, the frequency of *C. nemoralis* is even higher (Álvarez-Fernández et al. 2013). The clearest evidence for the gathering and consumption of these terrestrial gastropods was found in Level 3 at La Fragua, at the present-day mouth of the River Asón and not far from La Chora. In that deposit, the proportion of *C. nemoralis* reaches 94% of mollusc remains (Gutiérrez-Zugasti, 2011c). This consumption has been verified at sites further inland, such as Cubío Redondo, where a shell midden rich in terrestrial gastropods, particularly *C. nemoralis*, was excavated. The accumulation was thought to be anthropic in origin and the snails had been gathered as food (Aparicio 2001). The presence of this species as part of intentional deposits accompanying the dead has also been considered; as in the case of Grave 1, dated in the Mesolithic, in Los Canes cave (Arias 2013).

At La Chora, the volume of land snails found in unit 102 supports the hypothesis that these gastropods were consumed, as proposed in previous studies (Gutiérrez-Zugasti, 2011c). The presence of this resource in archaeological deposits raises questions about how they were gathered and cooked, and their importance in the diet of forager groups. In any case, the available information for the central sector of Cantabrian Spain, where the sites with abundant *C. nemoralis* are located, suggests that their consumption extended over a long period from at least the Azilian onwards.

Conclusions

The new data about the use of the littoral environment by the inhabitants of La Chora cave complement and nuance previous work published from the site, through the analysis of a larger sample with reliable stratigraphy and chronology. The data confirms the practice of shell-fishing in different coastal environments, especially in the estuary of the River Asón. The collection of molluscs in estuaries and the open coast had already been verified at other sites in the central sector of the northern coast, like Arenillas, La Trecha, La Fragua (Gutiérrez-Zugasti, 2009) and La Garma A (Álvarez-Fernández 2013). The location of La Chora is distinguished from other sites because, its residents, travelled a considerable distance to collect shellfish such as *P. depressa* on the open coast (> 10 km) or perhaps temporarily occupied specialized camps to carry out this activity. This indicates the importance of these resources in the diet at that time, although it seems that most gathering took place in the estuary, with shorter distances needed to collect species like *S. plana* (*ca*. 3 km). This agrees with the weight attributed to marine molluscs for human populations on the northern coast (Gutiérrez-Zugasti, 2009, 2011a; García-Escárzaga 2020) and were complemented by the consumption of land snails such as *C. nemoralis*. The distances covered to reach the coast must be considered when investigating the intensity of the exploitation of littoral resources by the inhabitants of La Chora, because these resources would have degraded rapidly (durability/quality) after collection. The increasing variety of taxa from rocky substrates suggests the use of intensive strategies to obtain those resources. However, without more information this hypothesis is still unconfirmed. Biometric measurements also support intensive gathering but in the absence of a study of the complete sequence at the site, it is difficult to confirm this. In contrast, the zonation study confirms more intensive gathering of *P. depressa*, as these limpets were preferentially collected in the lower intertidal zone (75.4% of the studied sample). The sexual circumstances of this marine gastropod clarifies these questions, as females (mainly adults and larger) would have been selected more often than males (mostly juveniles and smaller). In this way the reproducing population would have been depressed, resulting in a long-term negative effect on the size of this species.

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Author Contribution We confirm that all authors have approved the final version of the manuscript and have made substantial contributions. AGE, RAM and IGZ excavated La Chora cave, with IGZ and AGE as directors. ALC carried out the archaeomalacological studies of shellfish remains recovered from the stratigraphic unit 102, subquadrant N97C and the interpretation of the results. JAO carried out the archaeomalacological study of sub-quadrant N97D. MAF wrote part of the original manuscript, provided several revisions and comments on it and included modifications to the manuscript in response to reviewers' comments. JMQ retouched and assisted with the figure of the materials (Fig. 3). All authors wrote and provided comments on the manuscript.

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Declarations

Competing Interests The authors declare no competing interests.

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