



Feet on the ground: Marine archaeomalacology resources during the Mesolithic-Neolithic transition in the Iberian Peninsula



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ABSTRACT

The Iberian Peninsula is the ideal setting for the study of the use of marine resources in the Mesolithic and Neolithic periods. Previous studies have focused on specific geographical areas and on a single chronological period. Instead, we offer here a synthesis of the peninsula covering a broad period of time, thus allowing a study of the role of marine resources in the Neolithisation process. Published data on the exploitation of marine molluscs from 59 archaeological levels, close to the coast and dated between 10,400 and 4650 cal BP, in the Iberian Peninsula are reviewed in order to examine the change that occurred in the consumption of marine resources following the introduction of domestic plants and animals. The analysis of the composition and diversity of assemblages collected at each site has allowed us to identify specialisation in the management strategy of marine molluscs during the Neolithic. Regional variability in the diversity of species collected, particularly in the Cantabrian region, where there is continuity in the management of molluscs between the Mesolithic and Neolithic periods, could be linked to the pace at which agriculture and animal husbandry were adopted. In short, together with environmental factors, the establishment of farming practices may have had a slight impact on the specialisation in the management of coastal environments.

1. Introduction

The consumption of marine resources and their importance for the subsistence of the last hunter-gatherer and early farming societies in the Iberian Peninsula has been a subject of debate in archaeology in the last two decades. Marine resources are considered an important nutrient for the last hunter-gatherer societies (Stiner, 2002; Aura et al., 2009), based on the presence of abundant archaeomalacological remains in Mesolithic sites, mainly in the Cantabrian and Portuguese regions (González-Morales et al., 2004; Bicho et al., 2010; Gutiérrez-Zugasti et al., 2011; Araújo et al., 2014) and, to a lesser extent, in the Mediterranean region (Román et al., 2022; Ramos et al., 2011). Some researchers argue that the collection of this resource intensified during the Mesolithic and early Neolithic (Fano, 2004; Dean and Carvalho, 2011; Gutiérrez-Zugasti, 2011b; Cortés-Sánchez et al., 2012; Dean et al., 2012; García-Escárraga and Gutiérrez-Zugasti, 2021). This intensification is associated, on the one hand, with a greater availability of marine resources, due to more favourable environmental conditions (Bicho and Haws, 2008; Valente, 2012), and, on the other hand, with the scarcity compared to previous periods of terrestrial resources (particularly

ungulates), considered the main food sources, as suggested for the Cantabrian region (González-Morales et al., 2004) and some Mediterranean island areas (e.g. Grotta dell'Uzzo; Colonese et al., 2011). After the Mesolithic, a period of intensification in the exploitation of marine resources, there was a decrease in the size and quantity of shells (Carvalho, 2008; Nukushina, 2016), a phenomenon that has been interpreted as evidence of the decline in the importance of these foods in the human diet, linked to the Neolithisation process (Anderson, 2007). However, in the Cantabrian region (Gutiérrez-Zugasti et al., 2011; Álvarez-Fernández, 2015), Portugal (Dean and Carvalho, 2011; Valente, 2012), and the Mediterranean region (Aura et al., 2001; Pascual Benito, 2010, 2014), there is some continuity in their consumption with respect to the end of the Upper Pleistocene.

In addition to archaeomalacological studies, isotopic analyses of collagen in human remains also provide information on the origin of proteins consumed during the last years of the individual's life (Salaizar-García et al., 2018). The analysis of C and N isotopes in a sample of 763 individuals of chronologies between the Middle Neolithic and Mesolithic from different Iberian coastal sites has allowed an estimate of the importance of the intake of proteins of marine origin relative to

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terrestrial protein. The results show a relatively lower consumption of marine resources at sites on the Mediterranean coast compared with those on the Atlantic coast, both in the Mesolithic and at the beginning of the Neolithic (3.7% and 0.4% difference with respect to the total contribution of marine carbon to the diet, respectively). A general decline in the consumption of this type of resource is also observed throughout the Neolithic (6.3% of total marine carbon in the Atlantic and 2.9% in the Mediterranean) (Carvalho and Petchey, 2013; Fontanals-Coll et al., 2014; Salazar-García et al., 2018; Cubas et al., 2019; Fernández-Crespo et al., 2020).

Analyses of organic residues on pottery have also provided information on the food and other materials that were processed in these vessels (Breu, 2019; Cubas et al., 2020; Breu et al., 2023). In this case, it should be stressed that this methodological approach is reduced to Neolithic contexts with the presence of pottery, excluding the possibility of comparing them with the contexts of hunter-gatherer societies. The analysis of organic residues shows that, despite the presence of mollusc remains in Neolithic settlements near the coast, no seafood was processed in the ceramic vessels (Cubas et al., 2020). This may be related to the type of preparation these foods require to be consumed, either raw or grilled (over hot stones and ashes or in direct contact with fire) (Aldeias et al., 2019).

Studies on the exploitation of marine resources, focused on the analysis of molluscs, are mainly articulated at regional level (Cantabrian, Portuguese Atlantic, Mediterranean). In this paper we propose an assessment of marine mollusc collection strategies in the different regions to determine their importance and variability between the Mesolithic and the Neolithic. By analysing these three coastal areas together, it will be possible to approach the change and economic implications of the use of marine resources, considering environmental variability and chronological lags in Neolithisation. These areas encompass two coastal environments (Atlantic and Mediterranean) with different biomass and productivity of marine molluscs. The Atlantic Ocean has higher marine productivity due to upwelling processes of nutrient-rich deep waters and a wide tidal range. The Mediterranean Sea is less nutrient rich and the tidal range is narrower, which reduces the biomass of intertidal molluscs (Fa, 2008). The variability in environmental conditions in different regions makes it possible to assess whether or not adaptive strategies differed, based on this characteristic.

With this aim, the published data on the use of marine molluscs at archaeological sites in the Iberian Peninsula, close to the coastal areas and with occupations dated between 10,400 and 4650 cal BP, are reviewed systematically here. The main objective is to offer a synthesis for the peninsula over a broad period that allows us to account for changes in the consumption of these resources coinciding with the introduction and expansion of the farming economy. To this end, the study considers both the variety and the proportion of marine mollusc species that were gathered.

2. Materials and methods

A literature review of early Holocene archaeological sites where archaeomalacological studies are available was carried out and a database was compiled. Since the information in the published material is quite diverse, a series of criteria have been followed to ensure the comparison of data between sites and regions and make a critical evaluation of the existing information. The criteria considered have been, firstly, the application of rigorous protocols for the recovery of remains (use of fine mesh metal sieves, up to 2 mm, to sieve the sediment); secondly, the degree of preservation of remains has been considered, taking into account only those contexts that have allowed taxonomic identification and their quantitative treatment. The sites in the database are located in four different geographical areas: the Cantabrian coast, the Atlantic coast, the Mediterranean coast and the Gulf of Cádiz, with the record in the latter area exclusive to the Neolithic period (Fig. 1). The final sample is made up of 40 sites, of which 25 are in caves, five in

shelters and ten in the open air, where the 69 levels analysed were excavated. On both the Bay of Biscay and the Mediterranean, cave sites are more abundant, while on the Atlantic seaboard (Portuguese coast and Gulf of Cádiz) they are mainly open-air sites (Table 1).

The chronology of the selected contexts covers the transition from the Mesolithic to the Neolithic. For this study we have taken into account levels with radiocarbon dates (C14). The dates have been calibrated with OxCal 4.4 (Ramsey, 2009) and the IntCal20 calibration curves (Reimer et al., 2020). The dates of marine samples have been corrected with the corresponding value of the reservoir effect: Cantabrian coast $\Delta R = -238 \pm 28$ (García-Escárzaga et al., 2022), Atlantic-Portuguese coast $\Delta R = 95 \pm 15$, southern Algarve $\Delta R = 69 \pm 17$ and Gulf of Cádiz $\Delta R = -108 \pm 31$ (Soares, 2015), and Catalan Mediterranean coast $\Delta R = 35 \pm 70$ (Siani et al., 2000) and calibrated with the Marine13 (Reimer et al., 2013) and Marine20 curve, in the case of the Cantabrian region (Heaton et al., 2020). Levels with dates obtained by aspartic acid racemization have been discarded, as they have a standard deviation > 200 years.

Taking into account that, in northern Spain, in contexts exclusively of Mesolithic shell-middens, where the so-called Asturian pick (Vega del Sella, 1923; Fano, 2004) is characteristic, levels with this type of artefact have been included in the database whether or not they have absolute dates.

Once these criteria have been applied, the period studied ranges from 10,400–4650 cal BP. The temporal arrangement of the selected contexts is based on the resource management strategies defined for each site, given that the general objective is to assess the extent to which the adoption of agriculture and livestock farming influenced the exploitation of molluscs. Thus, the first group is made up of sites in which the exclusive practice of hunting, fishing and gathering is documented, corresponding to the last hunter-gatherer societies (between 9700 and 7000 cal BP in the Cantabrian region, 10,500–7900 cal BP on the Atlantic and 10,200–7500 cal BP on the Mediterranean). The second group includes sites with the presence of domesticates and pottery (between 7200 and 4500 cal BP on the Bay of Biscay, 7400–6900 cal BP

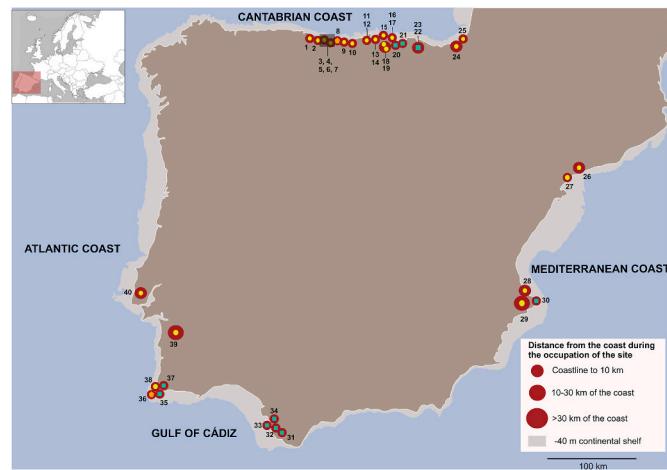


Fig. 1. Location of Mesolithic and Neolithic sites in the Iberian Peninsula (based on the map from Bailey et al., 2020). Information on the distance of the site from the coast at the time of occupation and the extent of the continental shelf is included. Site codes: 1. El Cierro; 2. Cuetu la Hoz; 3. La Poza L'Egua; 4. Colomba; 5. El Alloru; 6. Toral III; 7. La Llana; 8. Mazaculos II; 9. El Pindal; 10. Toralete; 11. Barcenillas; 12. El Mazo; 13. La Garma A; 14. El Truchiro; 15. La Fragua; 16. Arenillas; 17. La Trecha; 18. La Chora; 19. Carabión; 20. Los Gitanos; 21. Pico Ramos; 22. Santimamiñe; 23. Kobaederra; 24. Marizulo; 25. J3; 26. La Cativera; 27. Solà del Pep; 28. Collado; 29. Santa Maira; 30. Les Cendres; 31. La Esparragosa; 32. SET Parralejo; 33. Campo de Hockey; 34. Retamar; 35. Vale Santo; 36. Rocha das Gaviotas; 37. Padrao I; 38. Barranco das Quebradas; 39. Amoreira; 40. Toledo. Chronology of sites: Mesolithic yellow circle, Neolithic blue square, both chronologies orange pentagon.

Table 1

List of analysed sites. Code of the regions: A. the Cantabrian coast, B. Portuguese Atlantic coast, C. Atlantic coast of the Gulf of Cádiz, D. Mediterranean coast. Site type: C cave, AB shelter and AIR free-air. SM: Shell Midden. C14: * and Asturian pick: **.

Cd.	Yacimiento	Tipo	Región	Nivel	Cronología (BP)	Periodo	NMI	Biografía
1	El Cierro	C	A	B	7470 ± 38*, **	M	824	(Álvarez-Fernández et al., 2020)
2	Cuetu la Hoz	C	A	SM	7690 ± 130*	M	255	(Fano Martínez, 2004; Arias-Cabal et al., 2007)
3	La Poza l'Egua	C	A	SM	8550 ± 80*	M	1601	(Arias et al., 2007a; Álvarez-Fernández, 2015; Portero et al., 2022)
4	Colombá	C	A	SM	7020 ± 90*	M	782	(Arias Cabal et al., 2007b)
5	El Allorru	C	A	SM	8360 ± 70*, **	M	2306	(Álvarez-Fernández, 2015; Arias et al., 2016)
6	Toral III	C	A	13A	7000 ± 40*	M	4744	(Bello Alonso et al., 2015)
7	Toral III	C	A	21	7080 ± 30*	M	8063	(Bello Alonso et al., 2015)
8	La Llana	C	A	SM	**	M	6704	(Gutiérrez-Zugasti, 2009)
9	Mazaculos II	C	A	A3	7030 ± 120*, **	M	1074	(Gutiérrez-Zugasti, 2009)
10	El Pindal	C	A	2	7138 ± 35*, **	M	462	(Álvarez-Fernández, 2015)
11	El Toralete	C	A	SM	7890 ± 80*	M	494	(Arias et al., 2007b; Fano, 2008)
12	Barcenillas	AB	A	5	7020 ± 30*	M	234	(Muñoz-Fernández et al., 2013)
13	El Mazo	AB	A	100	7212 ± 35*	M	5151	(García-Escárzaga, 2020)
14	El Mazo	AB	A	101B	7105 ± 40*	M	4504	(Soares et al., 2016; García-Escárzaga, 2020)
15	El Mazo	AB	A	101C	7230 ± 36*	M	1963	(Gutiérrez-Zugasti et al., 2016; García-Escárzaga, 2020)
16	El Mazo	AB	A	101.1A	7357 ± 34*	M	3200	(García-Escárzaga, 2020)
17	El Mazo	AB	A	101.1B	7205 ± 37*	M	6932	(García-Escárzaga, 2020)
18	El Mazo	AB	A	105	7380 ± 55*	M	16362	(Soares et al., 2016; García-Escárzaga, 2020)
19	El Mazo	AB	A	107	7618 ± 37*	M	6432	(García-Escárzaga, 2020)
20	El Mazo	AB	A	108	8022 ± 39*	M	2003	(Soares et al., 2016; García-Escárzaga, 2020)
21	El Mazo	AB	A	113	7212 ± 35*	M	6390	(Soares et al., 2016; García-Escárzaga, 2020)
22	El Mazo	AB	A	114	7990 ± 38*	M	389	(García-Escárzaga et al., 2017)
23	El Mazo	AB	A	115	8004 ± 39*	M	1849	(García-Escárzaga et al., 2017)
24	La Garma A	C	A	Q	7710 ± 90*	M	2578	(Arias and Ontañón, 2008; Álvarez-Fernández, 2016)
25	El Truchiro	C	A	II	8296 ± 31*	M	1136	(Álvarez-Fernández et al., 2013)
26	La Fragua	C	A	1	6860 ± 60*	M	11900	(Gutiérrez-Zugasti, 2009)
27	Arenillas	C	A	SM	7143 ± 36*	M	9240	(Gutiérrez-Zugasti, 2009)
28	La Chora	C	A	SM	6360 ± 80*	M	159	(Gutiérrez-Zugasti, 2009)
29	Carabirón	AB	A	N1	7800 ± 50*	M	760	(Pérez-Bartolomé et al., 2016)
30	La Trecha	C	A	SM	7500 ± 70*	M	1505	(Gutiérrez-Zugasti, 2009)
31	Marizulo	C	A	II	6035 ± 100*	M	278	(Mujika Alustiza and Alday, 1997; Álvarez Fernández and Altuna, 2013)
32	J3	AB	A	D	8300 ± 50*	M	5123	(Iriarte-Chiapusso et al., 2010; Álvarez Fernández et al., 2014)
33	La Cativera	C	D	A	7979 ± 60*	M	465	(Morales-Hidalgo, 2010)
34	La Cativera	C	D	B	8230 ± 40*	M	359	(Morales Hidalgo, 2010)
35	Solà del Pep	C	D	SM	6786 ± 34*	M	233	(Álvarez-Fernández et al., 2022)
36	El Collado	AIR	D	IV	9020 ± 40*	M	359	(Fernández-López de Pablo, 2016; Fernández-López de Pablo and Gabriel, 2016)
37	El Collado	AIR	D	II	7610 ± 30*	M	826	(Fernández-López de Pablo, 2016; Fernández-López de Pablo and Gabriel, 2016)
38	El Collado	AIR	D	I	7660 ± 44*	M	358	(Fernández-López de Pablo, 2016; Fernández-López de Pablo and Gabriel, 2016)
39	Santa Maira	C	D	SM3	8890 ± 50*	M	65	(Aura Tortosa et al., 2006; Morales-Pérez, 2013)
40	Barranco das Quebradas 5	AB	B	SM	8035 ± 80*	M	5277	(Carvalho and Valente, 2005; Valente, 2010)
41	Barranco das Quebradas 4	AB	B	SM	8493 ± 57*	M	4184	(Carvalho and Valente, 2005; Valente, 2010)
42	Barranco das Quebradas 3	AB	B	C-1 higher	7980 ± 85*	M	2897	(Carvalho and Valente, 2005; Valente, 2010)
43	Barranco das Quebradas 3	AB	B	C-1 lower	8400 ± 65*	M	5534	(Carvalho and Valente, 2005; Valente, 2010)
44	Barranco das Quebradas 1	AB	B	Capa 3	9473 ± 54*	M	3836	(Carvalho and Valente, 2005; Valente, 2010)
45	Barranco das Quebradas 1	AB	B	Capa 1-2	9020 ± 70*	M	600	(Carvalho and Valente, 2005; Valente, 2010)
46	Rocha das Gaviotas	AIR	B	2c lower	6821 ± 50*	M	9418	(Carvalho et al., 2010)
47	Rocha das Gaviotas	AIR	B	3	8673 ± 78*	M	3817	(Carvalho and Valente, 2005; Carvalho et al., 2010)
48	Toledo	AIR	B	B	9200 ± 70*	M	3454	((Araújo, 2011; Dupont, 2011))
49	Amoreira	AIR	B	SM	7230 ± 40*	M	8040	(Soares, 2013)
50	Les Cendres	C	D	XI-X	6260 ± 80*	N	4271	(Bernabeu and Molina, 2009)
51	Les Cendres	C	D	IX-VIII	5930 ± 80*	N	3306	(Bernabeu and Molina, 2009)
52	Les Cendres	C	D	VII-VI	5640 ± 80*	N	5696	(Bernabeu and Molina, 2009)
53	Les Cendres	C	D	IV	5000 ± 90*	N	1755	(Bernabeu and Molina, 2009)
54	El Retamar	AIR	C	SM	6370 ± 80*	N	2434	(Ramos and Lazarich, 2002)
55	Campo de Hockey	AIR	C	SM	5650 ± 40*	N	1226	(Vijan de Vila, 2009; Cuenca-Solana et al., 2013)
56	SET Parralejo	AIR	C	SM	4930 ± 50*	N	203	(Cuenca et al., 2013; Villalpando and Montañés, 2016)
57	La Esparragosa	AIR	C	SM	4644 ± 31*	N	1490	(Vijande Vila et al., 2019)
58	Mazaculos II	C	A	A2	5050 ± 120*	N	422	(Gutiérrez-Zugasti, 2009)
59	Los Gitanos	C	A	A4	5490 ± 200*	N	3990	(Ontañón, 2005; Álvarez-Fernández et al., 2014b)
60	Los Gitanos	C	A	A3	5945 ± 55*	N	3706	(Ontañón, 2005; Álvarez-Fernández et al., 2014b)
61	Los Gitanos	C	A	A2	4370 ± 150*	N	9203	(Ontañón, 2005; Álvarez-Fernández et al., 2014b)

(continued on next page)

Table 1 (continued)

Cd.	Yacimiento	Tipo	Región	Nivel	Cronología (BP)	Periodo	NMI	Biografía
62	Pico Ramos	C	A	4	6040 ± 90*	N	2198	(Zapata et al., 2007; Moreno-Nuño, 2017)
63	Kobaederra	C	A	IV	5375 ± 90*	N	521	(Zapata, 2002; Gutiérrez-Zugasti, 2009)
64	Kobaederra	C	A	III	5820 ± 240*	N	803	(Zapata, 2002; Gutiérrez-Zugasti, 2009)
65	Kobaederra	C	A	II	5460 ± 60*	N	191	(Zapata, 2002; Gutiérrez-Zugasti, 2009)
66	Santimamíñe	C	A	Slm	5450 ± 50*	N	1641	(Gutiérrez-Zugasti, 2011; López-Quintana and Guenaga, 2011)
67	Padrao I	AIR	B	Capa 2	6440 ± 60*	N	1429	(Gómez et al., 1987; Callapez and Pimentel, 2018)
68	Rocha das Gaviotas	AIR	B	2c higher	6801 ± 39*	N	1342	(Carvalho et al., 2010)
69	Vale Santo	AIR	B	SM	6245 ± 60*	N	746	(Carvalho and Valente, 2005; Carvalho, 2008)

on the Atlantic, 7400–5500 cal BP on the Mediterranean and 6500–5300 cal BP on the Gulf of Cádiz) (Fig. 2).

2.1. Units of classification, analysis and quantification

For the comparative analysis we used the categories established by Colonese et al. (2011), grouping the marine mollusc shells documented in the different sites according to genus rather than species (Table A.1). This is because the species in the Atlantic Ocean and the Mediterranean Sea are different, which makes it difficult to compare them. This solves the problem of studying large territories, covering areas with different environmental conditions. In addition, a more general category called “others” has been used, which includes species that represent <5% of the minimum number of individuals (MNI). Most of these specimens correspond to molluscs that are consumed, but which are difficult to collect alive, as they live at great depths. They are taxa from the infratidal bed, at 40 m (Mediterranean) and 10–15 m (Atlantic), and the circalittoral, the edge of the continental platform (Templado et al., 2012). The nomenclature used for marine molluscs follows WoRMS (WoRMS Editorial Board, 2017; <http://www.marinespecies.org>).

The publications reviewed show that, depending on the region, different units are used to describe the quantitative importance of marine resources. In the Cantabrian region the Minimum Number of Individuals (MNI) is used, in Portugal the weight of the remains, and in the Mediterranean region the Number of Remains (NR) is more frequent. In this paper we have chosen to articulate the comparative analysis based on the unit of MNI. The MNI provides a real value of the proportion per species as opposed to the NR or weight (gr) (Valente, 2012). The calculation of NR is influenced by the high fragmentation that characterises mollusc shells, potentially causing their over-representation. As for the weight unit, taphonomic agents, which can cause decalcification, crusting or cementation of the remains (Fernández López, 2000), directly interfere with their weight, so the value obtained using this unit is null (Lyman, 2008). For this work, only contexts with a minimum of 100 specimens represented have been taken into account. In addition, the percentages of species are calculated from the MNI of marine mollusks only, which causes differences with the percentages of the original publications where terrestrial mollusks and other invertebrates are included.

2.2. Evaluation of the economic and dietary importance of the taxa and exploitation strategies

The evaluation of the economic and dietary importance of the malacological taxa is based on their quantitative proportion in the samples. The determination of the type of exploitation strategies of these species, by geographical areas and chronological periods, has been carried out by means of diverse biodiversity indices. The characterisation of the community structure of the taxa consumed makes it possible to differentiate between exploitation based on a broad-spectrum strategy and more specialised management, the latter focusing on a limited number

of species. Some indices can be used to measure the dominance, equitability and uniformity of species within a community, which is the basis for establishing the degree of diversity of the sample (Moreno, 2001; Jones, 2004). For this purpose, the indices described below are applied to the data.

Simpson's dominance index measures the relative abundance of species present in an ecosystem and is expressed by the following equation (Eq. 1):

$$D = \sum_{i=1}^S p_i^2$$

in which, S is the number of species and p_i is the relative abundance of species i. This index represents the probability that two individuals chosen at random, within an ecosystem, belong to the same species (Moreno, 2001). The dominance is based on the number of individuals of each taxon and determines whether the sample is concentrated in a few taxa or in several taxa. The value obtained varies between 0 and 1, where higher values indicate greater dominance of a few species. From this value, the inverse of Simpson's index is obtained, which divides 1/D, providing a good indication of diversity (Feinsinger, 2004). This value indicates the species richness of the sample and provides an estimate of the degree of diversity of the sample. The value of this index varies between 1 and the number of species present in the community (S), where higher values are equivalent to higher diversity.

Uniformity in the proportion of species is measured by the Shannon-Weiner index (H'), expressed by the following equation (Eq. 2):

$$H' = - \sum p_i \ln p_i$$

In this, p_i represents the proportional abundance of species i. This index expresses the degree of uncertainty in which a randomly selected individual from the sample corresponds to a given species (Cultid-Medina and Escobar, 2019). In this case, uniformity indicates the proportion of taxa with the same abundance and can establish the diversity of species and their importance in the sample. Values can vary between 0, when all individuals are of the same species, and the logarithm of S (total number of species in the community), when all species are represented by the same number of individuals. From this value, the equity index and the Effective Number of Species are calculated.

Pielou's equity index (J) measures the ratio of observed diversity to the maximum expected diversity (Magurran, 1988). This index is expressed by the following equation (Eq. 3):

$$J = \frac{H'}{\ln(S)}$$

Where H' is the Shannon-Weiner index and S is the number of species present in the community. The index is based on the importance value of each taxon and the total number of species in the sample. Values vary between 0 and 1. The higher the value obtained, the greater the homogeneity of the sample. Therefore, greater homogeneity equals greater

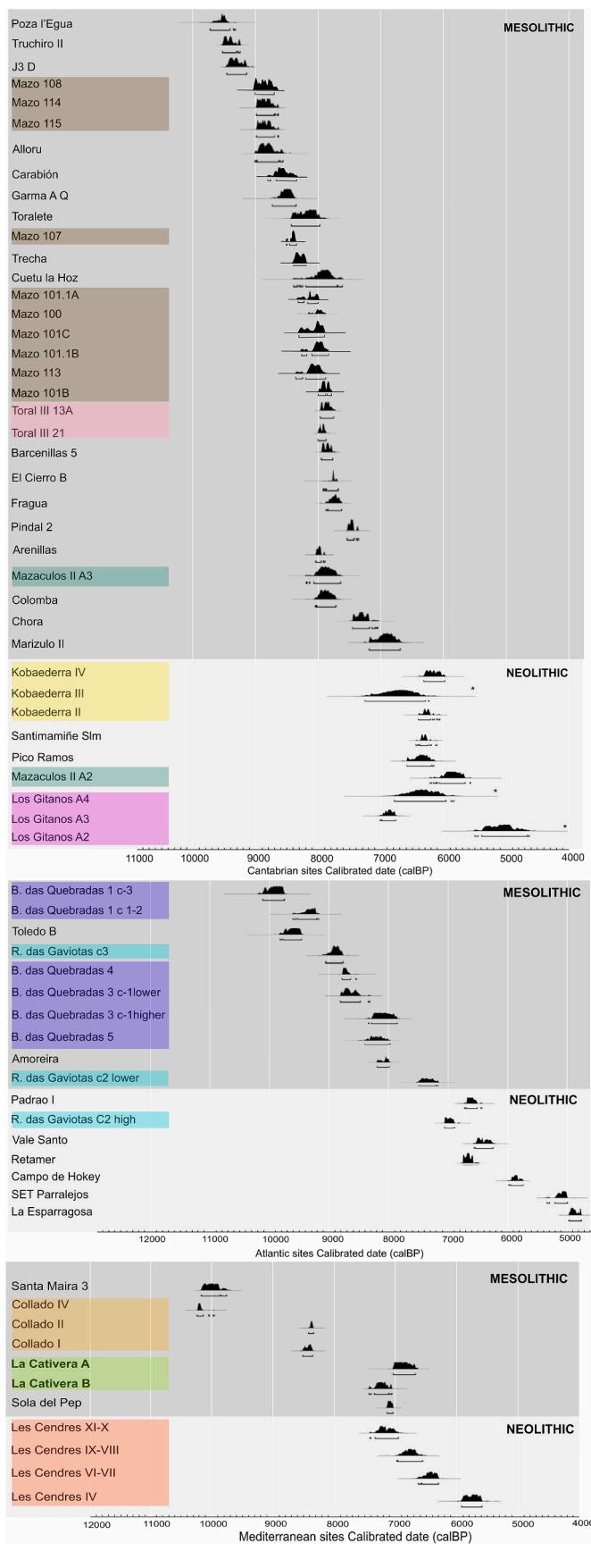


Fig. 2. Radiocarbon dates (cal BP) of all levels analysed by region (Cantabrian, Atlantic and Mediterranean). Calibration has been performed with the IntCal 20 curve and OxCal version 4.4.4 (Bronk Ramsey, 2021). The dates with the largest deviations are highlighted with an asterisk, while archaeological levels at the same site are highlighted with a coloured background. Marine samples have been corrected with the corresponding value of the reservoir effect: Cantabrian coast $\Delta R = -238 \pm 28$ (García-Escárzaga et al., 2022), Atlantic-Portuguese coast $\Delta R = 95 \pm 15$, southern Algarve $\Delta R = 69 \pm 17$ and Gulf of Cádiz $\Delta R = -108 \pm 31$ (Soares, 2015), and Catalan Mediterranean coast $\Delta R = 35 \pm 70$ (Siani et al., 2000) and calibrated with theMarine13 (Reimer et al., 2013) and Marine20 curve (Heaton et al., 2020).

species diversity.

The Effective Number of Species in the different geographical areas has been calculated using the exponential of the Shannon-Weiner index (MacArthur, 1965) (Eq. 4):

$$^qD = \exp \left(- \sum p_i ln p_i \right)$$

This index indicates the effective number of equally common species in an ecosystem and transforms Shannon entropy into a uniform set of mathematical properties that accurately capture the concept of diversity (Jost, 2006). Therefore, this value reflects the effective number of species corresponding to a diversity value of the Shannon index (Moreno et al., 2011).

In order to know the relationship and similarity between the geographical areas studied on the basis of the malacological assemblages, a matrix has been constructed that expresses the values of Simpson's similarity coefficient. To illustrate these relationships graphically, a cluster analysis was carried out using the PAST software (Hernández-Acevedo et al., 2005).

The mollusc collecting areas were determined based on ecological information on the habitat of each species. The vast majority of marine molluscs present in the sites studied come from the intertidal zone (Table A1). This coastal strip is delimited based on the tidal range and presents a vertical zonation of the coastline (Petrakis et al., 2008). It is divided into three zones: (i) supratidal, which corresponds to the wave splash zone that does not become submerged at high tide, (ii) intertidal, the zone between the maximum and minimum tidal range, and (iii) infratidal, which is established between the lower level of low tide, which emerges only at spring tides, and the permanently submerged seabed (Templado et al., 2012). In addition to the zonal distribution, the habitat of molluscs is distinguished by the type of substrate, either rocky or sandy-muddy, found in the different littoral environments (rocky shore, estuaries, coastal lagoons, or mudflats). Thus, molluscs from sandy-muddy environments of coastal lagoons and estuaries, such as the bivalves *Cerastoderma edule/Cerastoderma glaucum*, *Solen* sp. and *Ruditapes decussatus*, would be collected in the intertidal and *Mimachlamys varia* in the upper infratidal of all coastal areas (Templado et al., 2012). In the case of the gastropods *Stramonita haemastoma* and *Hexaplex trunculus*, and the bivalves *Ostrea edulis* and *Mytilus* sp., they would be collected in the rocky lower intertidal or upper infratidal (Suchanek, 1978; Templado et al., 2012). The genera *Patella* and *Phorcus*, however, are collected in different areas of the coast. *Patella rustica* and *Patella caerulea*, endemic to the Mediterranean, are found in the upper and mid intertidal, respectively (Vafidis et al., 2020), while *Patella vulgaris* and *Patella depressa*, characteristic of the Atlantic, are collected in the intermareal zone. *Patella ulyssiponensis* inhabits the lower intertidal and upper infratidal shore of both seas (Casal et al., 2018). The genus *Phorcus* encompasses two species living in the upper and mid intertidal, one from the Mediterranean *Phorcus turbinatus* and the other from the Atlantic *Phorcus lineatus* (Sousa et al., 2017). The species *Scrobicularia plana* inhabits the muddy substrate of the estuaries of the Atlantic coast more frequently.

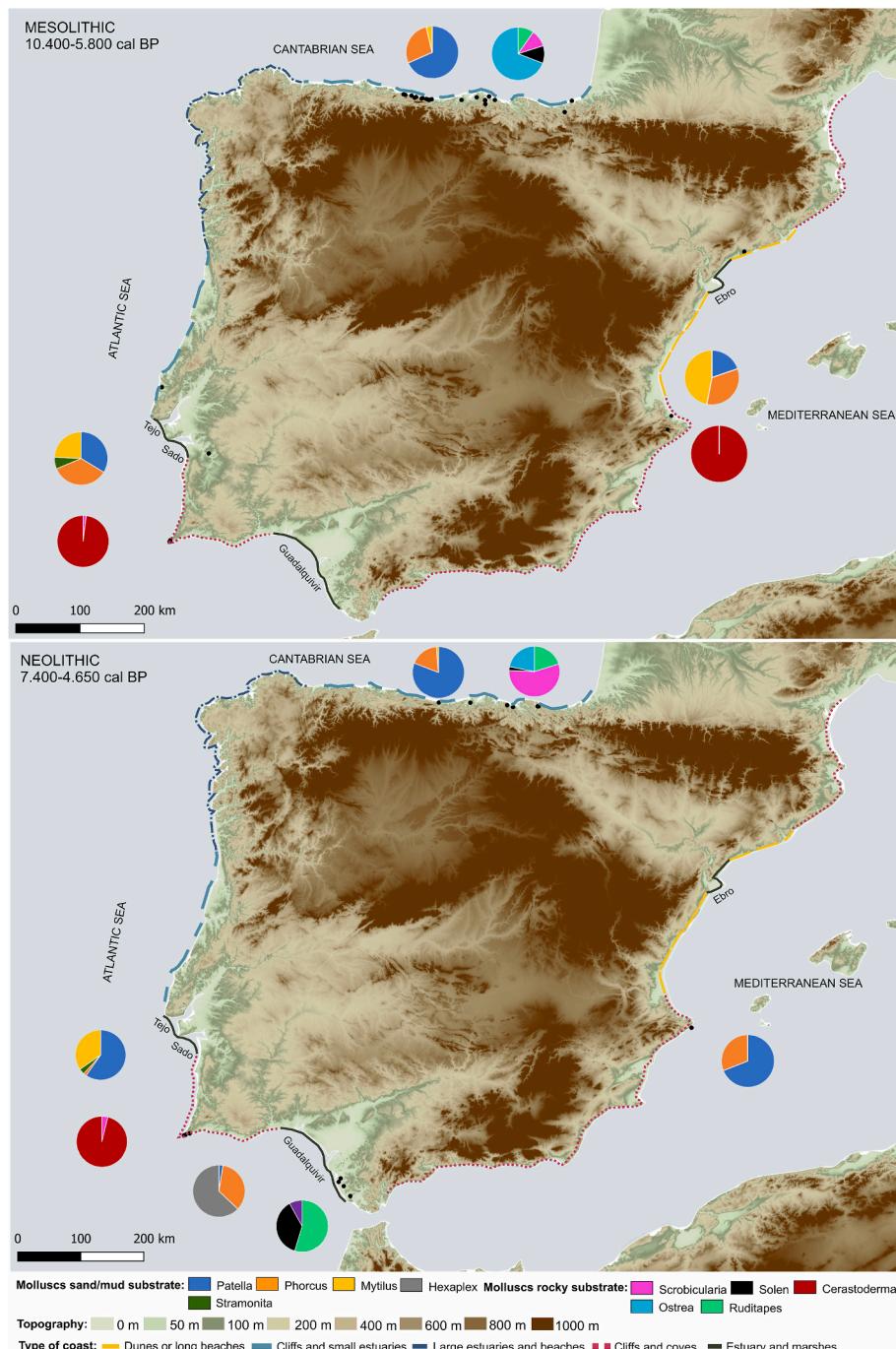


Fig. 3. Map showing the representation of mollusc species exploited during the Mesolithic and Neolithic periods in the Iberian Peninsula.

2.3. Location of sites in relation to the coastline at the beginning of the holocene

The location of the sites in relation to the distance from the coastline at the time of occupation has also been considered to determine whether this is a factor influencing the species composition of the assemblages. In the last Eustatic hemicycle, characterised by global warming and partial melting of the polar ice caps (Ruddiman and McIntyre, 1981), sea levels rose in the different regions of the Iberian Peninsula (García-Artola et al., 2018). Consequently, there is evidence that at the beginning of the Holocene, the extent of coastal territory was reduced and coastal ecosystems were altered. This event influences the visibility of marine resource use, as marine resource consumption usually decreases with distance from the coast (Bailey and Craighead, 2003; Bicho and Haws, 2008). Given the difficulty in determining site distance from the sea with precision in the early millennia of the Holocene, sites have been grouped as follows: (i) sites close to the coast (0–10 km), (ii) sites in the intermediate zone (10–30 km), and (iii) sites inland (>30 km) (Fig. 1). This classification has been established on the basis of whether or not the coastal area is within the theoretical exploitation territory of the populations that inhabited the sites studied. In this case, the 10 km is equivalent to a displacement of approximately 2 h, the maximum travel time that has been calculated to define the catchment area of hunter-gatherer societies (Lee, 1972; Marín-Arroyo, 2009). The 30 km limit for defining inland sites is established in relation to palaeodietary studies, where it is concluded that from 30 to 40 km onwards, repeated consumption of marine resources is unlikely (Salazar-García et al., 2014).

The variation in the proportion of gastropod and bivalve specimens at near-shore and inland sites is represented by box plots, while the proportion of specimens of different genera by region and chronology is represented by pie charts.

3. Results

The malacological assemblages from a total of 40 sites and 69 archaeological levels have been systematised and analysed comparatively. Most of these are located on the Cantabrian coast ($n = 41$), followed by the Atlantic ($n = 17$) and Mediterranean ($n = 11$), and correspond to both the Mesolithic ($n = 49$) and Neolithic ($n = 20$) periods. The results are first presented individually, according to geographic area, and then a comparative synthesis is made, evaluating the possible differential dynamics.

3.1. Cantabrian coastline

For the Mesolithic period, the assemblages from 32 archaeological levels have been analysed. The absolute dates of these levels correspond to three different chronological intervals. The first between 9700 and 9100 cal BP, with five levels (El Cierro level B, La Poza L'Eguia, El Allor, El Truchiro level II and J3 level D); the second between 9000 and 7600 cal BP, with 12 levels (El Pindal 2, El Mazo 100, 101 B, 101C, 101.1 A, 101.1 B, 105, 107, 108, 113, 114 and 115, Toral III level 13 A and 21, El Toralete, Mazaculos II level A3, Colomba, Arenillas, La Garma A, La Trecha, Carabión, Cuetu de la Hoz and Barcenillas level 5); and the third between 7400 and 6600/5700 cal BP, with only three levels (La Chora and Marizulo level II). Therefore, the sample shows a 100-year gap between the first and second intervals, and a 200-year gap between the

second and third intervals. As for the variability in the MNI of molluscs represented, a maximum of 16,362 MNI was found in unit 105 at El Mazo and a minimum of 159 MNI in La Chora. The density of remains per excavated volume, calculated according to the availability of published data, shows a maximum density of 475,77 MNI/dm³ in Level B at El Cierro and a minimum density of 84,14 MNI/dm³ in Level II at El Truchiro.

From a taxonomic point of view, collection of marine molluscs is centred on rocky substrate species (97.4%). *Patella* is the genus that predominates in 32 of the levels analysed, reaching over 90% of specimens in El Pindal level 2, Toral III level 21 and J3 level D. In this case, it is specified at species level, documenting the presence of *Patella depressa* (black-footed limpet), *Patella vulgata* (common limpet) and *Patella ulyssiponensis* (China limpet). In terms of the proportion of these, *P. depressa* is the most collected, although in sites such as El Cierro (27.67%) and the six levels of El Mazo (101.1 B: 35.78%, 105: 27.69%, 108: 26.76%, 113: 44.63%, 114: 22%, 115: 16%) *P. vulgata* dominate. In contrast, *P. ulyssiponensis* is the scarcest species in all levels. The species *P. lineatus* (top shell) predominates only in the Mesolithic sites of El Mazo levels 101 B (49.75%), 101C (52.78%), 101.1 A (57.69%), 107 (64.36%), 114 (55.78%) and 115 (54.08%), Toralete (55.67%) and El Allor (48.8%), while in the rest of the sites it is the second most collected species. *Mytilus* sp. (mussel) is also the most frequent mollusc at the Mesolithic sites of Barcenillas (44.44%), where it is the dominant rocky substrate species. Although to a lesser extent, molluscs are also collected from sandy-muddy substrates (2.6%). The most abundant species is *Scrobicularia plana* (peppery furrow shell), being predominant at La Chora (45.28%) and Carabión (33.95%). The remaining species, except for *Ostrea* sp. (oyster) at La Chora (16.98%), do not exceed 1% of the total MNI. Therefore, based on the malacological composition, exploitation is mainly focused on species from the upper to the lower intertidal strip of the rocky coast, while those from a sandy/muddy substratum are rarely exploited (Table A.2).

From a palaeoecological point of view, the values of 0.56 in Simpson's dominance index (D) and 1.78 in Simpson's diversity index (1/D) indicate that the malacological assemblage has low species diversity, dominated by few taxa. The Effective Number of Species (qD), with a value of 2.39, confirms this low diversity, considering that some levels, such as Arenillas, contained more than 30 different species, including non-food species. As for the relative abundance of the taxa, the Shannon-Weiner index (H'), with a value of 0.87, shows the low uniformity of the assemblage. Likewise, Pielou's equity index (J) indicates low homogeneity in terms of the proportion of each species, with a value of 0.29. This means that most specimens correspond to a few taxa (Table A.3).

Based on the composition and distribution of the abundance of species collected during the Mesolithic in the Cantabrian region, a management strategy for marine molluscs specialising in specific species that inhabit the most accessible areas of the intertidal zone is evident.

The assemblages from nine Neolithic archaeological levels have been analysed. Of these, eight are dated between 7200 and 5500 cal BP (Los Gitanos A4 and A3, Mazaculos II A2, Pico Ramos level 4, Kobaederra levels IV, II and I, and Santimamiñe level SLM) and one (Los Gitanos level A2) between 5450 and 4500 cal BP. In this case, there is a gap of 50 years between the two chronological intervals. The levels contained a maximum of 9203 MNI in Level A2 at Los Gitanos and a minimum of 191 MNI in Level II at Kobaederra. The calculation of the density of remains per excavated volume has only been possible in the Santimamiñe and Kobaederra levels. Maximum densities of 76.32 MNI/dm³ (Santimamiñe

level Slm) and a minimum density of 1.09 MNI/dm³ (Kobaederra level II) were found.

From a taxonomic point of view, the collection of marine molluscs is based on rocky substrate species (86.59%). Most of them belong to the genus *Patella* and constitute more than 80% of the total MNI in Los Gitanos, Mazaculos II and Pico Ramos. Among the three species identified (*P. depressa*, *P. vulgaris* and *P. ulyssiponensis*), *P. depressa* is the most abundant at all levels. Specimens of the genus *Phorcus* do not exceed 22% of the total MNI in any level, being less than 2% of the MNI at Santimamiñe and Kobaederra. *Mytilus* sp. constitutes less than 5% in all levels, with the exception of Pico Ramos (6.92%). In this case, a relative abundance is observed in the collection of sandy-muddy substrate species (10.96%). The most abundant species is *Scrobicularia plana*, which is the predominant mollusc in Santimamiñe (87.45%). In addition, the collection of *Ostrea* sp. is documented in levels III (36.49%) and II (33.51%) at Kobaederra and *Ruditapes decussatus* (Grooved carpet shell) in Kobaederra IV (31.09%). Consequently, both the rocky littoral and estuarine environments were exploited, with a focus on intertidal species (Table A.2).

From a palaeoecological point of view, the value of 0.54 for Simpson's dominance index (D) and the value of 1.87 for Simpson's diversity index (1/D) show that the assemblage displays low species diversity and is dominated by a few taxa. The low Effective Number of Species (qD), with a value of 2.69, confirms this low diversity of the assemblage. The Shannon-Weiner index (H'), with a value of 0.99, indicates low evenness in the relative abundance of each species. This unequal distribution of abundance can also be seen in the low value (J = 0.35) of the Pielou equity index (Table A.3).

In conclusion, the management strategy for marine molluscs during the Neolithic in the Cantabrian region diversifies with the exploitation of new coastal environments such as estuaries, although it continues to be a specialized collection in few taxa. The acquisition of molluscs took place in the most accessible and visible areas of the intertidal zone.

3.2. Atlantic coast

For the Mesolithic period, the assemblages from ten archaeological levels on the Portuguese Atlantic coast have been analysed. Absolute dating places these levels in four chronological intervals. The first, dated between 10,500–10,200 cal BP, with two levels (Barranco das Quebradas 1 layer 3 and Toledo level B); the second between 9800 and 8500 cal BP, with six levels (Barranco das Quebradas 5, 4, 3 upper and lower layer 1 and 1 layer 1–2, and Rocha das Gaviotas 3); the third between 8100 and 7900 cal BP, with one level (Amoreiras); and the fourth between 7700 and 7500 cal BP, with one level (Rocha das Gaviotas 2c-lower). Therefore, there are relatively long intervals without information, of 400 years between the first and the second period, and between the second and the third, and of 200 years between the third and the fourth. A maximum of 9418 MNI is observed in Level 2c-lower at Rocha das Gaviotas and a minimum of 600 MNI in Level c1-2 at Barranco das Quebradas 1. The calculation of the density per excavated volume has been possible only in the levels of Barranco das Quebradas. A maximum density of 234.53 MNI/dm³ (Barranco das Quebradas 5) and a minimum of 120 MNI/dm³ (Barranco das Quebradas 1 layer 1–2) were recorded.

From a taxonomic point of view, mainly rocky substrate molluscs were collected (71.31%). *Phorcus* is the predominant genus in four levels, exceeding 60% of the MNI in three levels at Barranco das Quebradas (BQ4 with 70.89%, BQ1 c3 with 65.09% and BQ1 c1-2 with 62.16%). *Patella* sp. is the most abundant species in Barranco das Quebradas Levels 5 and 3 upper Layer 1 (37.14% and 37%, respectively) and Rocha das Gaviotas 3 (68.71%). *Mytilus* sp. predominates only in Rocha das Gaviotas 2c lower (62.02%), while *Stramonita haemastoma* (red-mouthed rock shell) is present in all levels, although it only exceeds 10% in Barranco das Quebradas 5 (17.38%) and Barranco das Quebradas 4 (10.8%). Among the sandy-muddy substrate species (27.69%), *Cerastoderma edule* (cockle) predominates in the Toledo (83.61%) and

Amoreira (98.25%) sites. Therefore, molluscs are exploited both in the lower intertidal and infratidal strip of estuarine environments, and in the upper intertidal zone of rocky coasts (Table A.4).

From a palaeoecological point of view, the 0.32 value of Simpson's dominance index (D) and the 3.17 value of Simpson's diversity index (1/D) indicate relative diversity in the composition of collected species, where no single taxon is dominant. This is also observed in the value of the Effective Number of Species (qD) which shows a diversity equivalent to 3.67 species. Regarding the uniformity and homogeneity of the analysed assemblage, the value of 1.3 of the Shannon-Weiner index and the value of 0.45 of the Pielou equity index show a more uniform distribution in the relative abundance of the different taxa (Table A.3).

Therefore, during the Mesolithic in the Atlantic region, the management strategy for marine molluscs is relatively diversified, exploiting both the most accessible areas (upper intertidal zones) and the most inaccessible (infratidal floor), thus including all available littoral environments in the catchment.

For the Neolithic period, the assemblages of three archaeological levels in the Portuguese Atlantic region and four archaeological levels in the Bay of Cádiz have been analysed.

In the Portuguese Atlantic, the three levels date between 7400 and 6900 cal BP, corresponding to the first occupations in the Early Neolithic. Regarding the variability of the MNI unit, a maximum value of 1429 MNI is observed in Layer 2 at Padrao I and a minimum value of 746 MNI in the Vale Santo shell midden. In this case, it has not been possible to calculate the density of remains per excavated volume, since the sediment volume of the studied levels is not published.

From a taxonomic point of view, the collection is mainly based on rocky substrate molluscs (89.43%). *Patella* is the most abundant genus in Levels C2 at Padrao I (64.39%) and Level 2c-above at Rocha das Gaviotas (62.59%). *Mytilus* sp. predominates in Vale Santo (70.38%) and is the second most abundant species in the rest of the sites. Likewise, *S. haemastoma* is present in all levels, but does not exceed 5% of the total MNI in any of them. The genus *Phorcus* is only relevant at the Padrao I site (7.7%). Molluscs from sandy-muddy substrata are collected only occasionally (2.99%), with *Cerastoderma* sp. being the most relevant species with 7.07% (Padrao I). This species composition indicates that mollusc exploitation is centred on the upper and lower intertidal strip of the rocky coast (Table A.4).

From a palaeoecological point of view, the 0.38 value of Simpson's dominance index (D) and the 2.63 value of Simpson's diversity index (1/D) indicate relative diversity in species composition, with no dominant taxon. The high value of the Effective Number of Species (qD), with a value of 3.71, confirms this diversity. As for the uniformity of the assemblage, the Shannon-Weiner index (H'), with a value of 1.31, indicates greater homogeneity in the distribution of the relative abundance of the taxa. This can also be observed in the 0.44 value of Pielou's equity index (J) (Table A.3).

Therefore, during the Neolithic in the Atlantic region, the management strategy for marine molluscs focused on the intertidal fringe of rocky coasts. Relative specialisation is documented although without prioritising the gathering of a single species.

In the Gulf of Cádiz, the absolute dates place each level in a different chronological interval. Retamar is dated between 7400 and 7000 cal BP, followed by Campo de Hockey dated between 6500 and 6300 cal BP, and SET Parralejo between 5800 and 5500 cal BP. The most recent level is La Esparragosa, dated between 5400 and 5300 cal BP. They are therefore separated by relatively long-time intervals, such as 500 years between Retamar and Campo de Hockey, and between Campo de Hockey and SET Parralejo. In the case of SET Parralejo and La Esparragosa, there is a gap of 100 years. The MNI of molluscs shows a maximum value of 2434 at the Retamar site and a minimum of 203 at the SET Parralejo site. Although we have not been able to calculate the density of remains per excavated volume, based on the surface area excavated at the four sites, which exceeds 400 m², we would expect a lower density of remains compared to levels in other regions.

From a taxonomic point of view, molluscs from sandy-muddy substrata are most frequently collected (65.95%). Among them, the species *R. decussatus* predominates at SET Parralejo (62.56%) and La Esparragosa (72.45%), while *S. capensis* (razor shell) is the most abundant mollusc in the Retamar site (48.27%). The species *Mimachlamys varia* (variegated scallop) is present in all levels, although it only exceeds 10% of the total MNI in Campo de Hockey (17.02%) and La Esparragosa (13.07%). Rock substrate molluscs represent 15.01% of the total, with *P. lineatus* being the predominant species at Campo de Hockey (20.83%). The presence of the species *Hexaplex trunculus* (banded dye-murex) is significant only in the sites of Retamar (14.38%) and Campo de Hockey (12.64%). The genus *Patella* does not exceed 3% of the total MNI in any of the sites. Therefore, molluscs are exploited both in the intertidal and upper infratidal strip of estuaries and coastal marshes, and in the upper intertidal and, occasionally, in the infratidal zone of rocky coastlines (Table A.5).

From a palaeoecological point of view, the 0.23 value of Simpson's dominance index (D) and the 4.34 value of Simpson's diversity index indicate a faunal assemblage with high diversity in species composition, with no single taxon dominating. The high Effective Number of Species (qD) of 6.95 corroborates the high species diversity of the assemblage. Furthermore, the Shannon-Weiner index (H') value of 1.94 and the Pielou equity index (J) value of 0.58 show high evenness in the relative abundance distribution of the different taxa in the assemblage (Table A.3).

Therefore, a diversified marine mollusc management strategy was carried out in the Gulf of Cádiz during the Neolithic in terms of species composition and coastal environments exploited.

3.3. Mediterranean coast

For the Mesolithic period, the assemblages from seven archaeological levels have been analysed. The absolute dates of the levels correspond to four different chronological intervals. The first between 10,200 and 9700 cal BP, with two levels (El Collado level IV and Santa Maira level 3); the second between 9400 and 8600 cal BP, with two levels (La Cativera level A and B); the third between 8400 and 8300 cal BP, with two levels (El Collado level II and I); and the fourth between 7600 and 7500 cal BP, with a single level (Solà del Pep). This indicates that there are relatively long chronological intervals between the levels studied (300 years, 200 years and 600 years, respectively). A maximum value of 826 MNI is observed in Level II at El Collado and a minimum of 65 MNI in Level 3 at Santa Maira. The density of remains per excavated volume could only be calculated in Santa Maira, El Collado and La Cativera. In this case, the maximum value of density of remains is 116.25 MNI/dm³ in La Cativera level A and the minimum of 0.58 MNI/dm³ in Santa Maira level 3.

From a taxonomic point of view, the collection of marine molluscs is mainly based on sandy-muddy substrate species (66.89%). *Cerastoderma* sp. is the predominant genus in the three levels at El Collado (Level IV 86.91%, Level II 91.65%, and Level I 87.15%) and in Level A at La Cativera (66%). Among the rocky substrate species (33.11%), *Mytilus* sp. is the most frequent in Level B at La Cativera (46%) and in Level 3 at Santa Maira (67%), as well as *Phorcus turbinatus* (top shell) at Solà del Pep (72.96%). Therefore, the faunal composition shows an exploitation of molluscs centred on the mid and lower intertidal strip of coastal lagoons, as well as rocky coasts (Table A.6).

From a palaeoecological point of view, the 0.47 value of Simpson's dominance index (D) and the 2.11 value of Simpson's diversity index (1/D) indicate relative diversity in the composition of collected species,

where no single taxon is dominant. This diversity is also reflected in the Effective Number of Species (qD), with a value of 3.13. In terms of evenness, the Shannon-Weiner index (H') with a value of 1.14 indicates a more even distribution of the relative abundance of each taxon. Pielou's evenness index (J) also shows a more homogeneous assemblage in relation to the proportion of species per taxon (Table A.3).

Therefore, during the Mesolithic, the marine mollusc gathering strategy in the Mediterranean region was diversified, focusing on species from low-lying intertidal zones in different littoral environments.

For the Neolithic period, the assemblages from four archaeological levels have been analysed. These come from a single site, Les Cendres. The absolute dates correspond to three different chronological intervals. The first is dated between 7400 and 6900 cal BP, where Level XI-X is located; the second between 6900 and 6200 cal BP, where both Levels IX-VIII and VII-VI are located; and the third between 5900 and 5500 cal BP, where Level IV is located. In this case, there is an absence of 300 years between the second and third chronological intervals. Regarding the MNI of molluscs, the maximum value is 4271 MNI (Level XI-X) and the minimum is 1755 MNI (Level IV). Likewise, the calculation of density of remains per excavated volume shows a maximum value of 18.37 MNI/dm³ in Level VII-VI and a minimum of 8.26 MNI/dm³ in Level VIII-VII.

From a taxonomic point of view, the collection of molluscs was mainly focused on rocky substrate species (96.61%). *Patella* is the predominant genus in all four levels, exceeding 60% of the total MNI. *Phorcus* is the second most frequent in all levels, while *Mytilus* sp. represents <1% of the total MNI. In this case, sandy-muddy substrate bivalves such as *Cerastoderma* sp. are merely anecdotal (<3%). Therefore, the species composition indicates that mollusc exploitation focused on the upper and mid intertidal fringe of the rocky shore (Table A.6).

From a palaeoecological point of view, Simpson's diversity index (D) shows a value of 0.55 and Simpson's diversity index (1/D) 1.81. This means that it is an assemblage with low species diversity, dominated by few taxa. The low Effective Number of Species (qD), with a value of 2.05, confirms this low diversity, considering that the assemblage is formed by 12 different taxa. Furthermore, the assemblage is characterised by a low evenness and homogeneity in the distribution of the relative abundance of the taxa, as shown by the 0.72 Shannon-Weiner index (H') and the 0.29 Pielou equity index (J) (Table A.3).

Therefore, based on the taxonomic and palaeoecological data, during the Neolithic period at Les Cendres site, the marine mollusc management strategy specialised in a few taxa. Although it is not possible to generalise from a single site, it seems that exploitation was now focused on the most accessible and visible areas of the rocky coastline, the strip of the upper intertidal zones.

3.4. Use of marine molluscs in the Mesolithic and Neolithic periods

Based on the composition and distribution of the relative abundance of mollusc species by period, we can observe a change in the management strategy for this resource in the Iberian Peninsula (Fig. 3). On the one hand, there is a trend towards diversification in the collection of molluscs on the Cantabrian coast during the Neolithic. Despite the continued predominance of mollusc collection from the upper rocky intertidal zone (*Patella depressa* and *Phorcus lineatus*) in both periods, the ecological analysis shows an increase in species diversity in the Neolithic assemblages: 1/D = 1.77 (Mesolithic) and 1.87 (Neolithic); qD = 2.38 (Mesolithic) and 2.69 (Neolithic). This is due to the fact that in the Neolithic period, sites specialised in the exploitation of species from estuarine environments (*Scrobicularia plana*) are documented. In

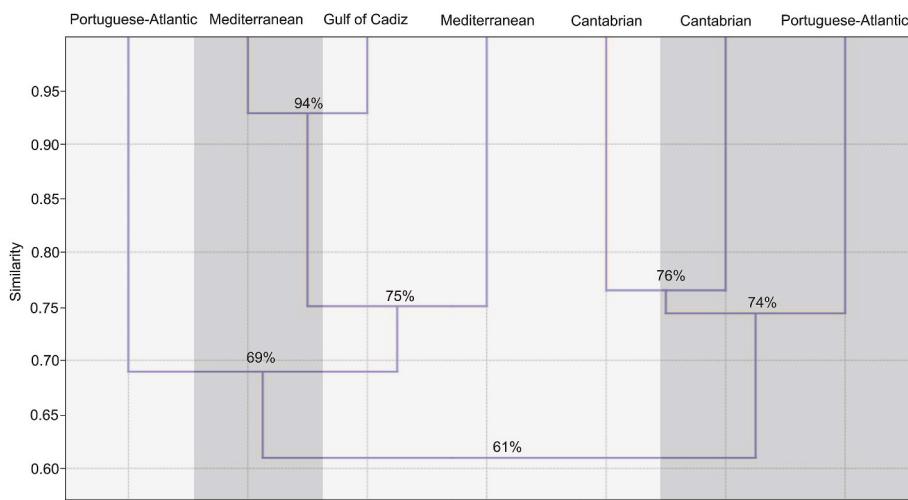


Fig. 4. Cluster chart based on Simpson's similarity index analysing the diversity of mollusc collection in the different geographical areas studied. The light grey background corresponds to the Neolithic period and the dark grey to the Mesolithic period.

contrast, there is a trend towards specialisation in mollusc harvesting on the Atlantic-Portuguese and Mediterranean coasts during the Neolithic. On the Atlantic-Portuguese coast, the collection of molluscs from high rocky intertidal zones predominates during the Mesolithic (*Patella* sp. and *Phorcus lineatus*) and the collection area extends to lower intertidal zones during the Neolithic (*Patella* sp. and *Mytilus* sp.). Data from the ecological analysis indicate a decrease in the diversity of species collected during the Neolithic: $1/D = 3.17$ (Mesolithic) and 2.63 (Neolithic); $qD = 3.67$ (Mesolithic) and 3.66 (Neolithic), linked to a significant decrease in the collection of species from estuarine environments (*Cerastoderma* sp.). On the Mediterranean coast, during the Mesolithic, molluscs were collected in the lower intertidal zone, both in coastal lagoons (*Cerastoderma glaucum*) and on rocky coasts (*Mytilus* sp.) and in the Neolithic, particularly in Cova de Les Cendres, collection centred on the upper zones of the rocky intertidal shore (*Patella* sp. and *Phorcus turbinatus*). The results obtained with the ecological analysis indicate a decrease in the diversity of species collected during the Neolithic: $1/D = 2.11$ (Mesolithic) and 1.81 (Neolithic); $qD = 3.13$ (Mesolithic) and 2.05 (Neolithic). In the case of the Gulf of Cádiz region, mollusc collection centred on the low intertidal areas of the coastal marshes and in the high rocky intertidal areas. The ecological analysis shows a high degree of diversity of collected species ($1/D = 4.34$ and $qD = 6.96$), so that a diversified exploitation of molluscs during the Neolithic period can be observed.

Comparison using Simpson's similarity index of the malacological assemblages from the different coastal areas indicates that there are differences in the diversity of the species collected between regions and chronological periods. In the Mesolithic period, there is greater similarity between the Cantabrian and Atlantic-Portuguese assemblages, with similar ecological characteristics, than those from the Mediterranean coast. However, in the Neolithic period, greater similarity is observed between the assemblages from the Mediterranean coast, the Gulf of Cádiz and the Atlantic-Portuguese coast than with those from the Cantabrian coast. The malacological assemblage from the latter region shows greater similarity with the Mesolithic assemblages on both the Cantabrian and the Portuguese Atlantic (Table A.3 and Fig. 4). This indicates that the collection of molluscs on the Cantabrian coast is practically unchanged between the Mesolithic and Neolithic periods.

Only two of the studied sites contain both Mesolithic and Neolithic occupations. In the case of the Cantabrian region, Mazaculos II Level A3 is dated between 8100 and 7600 cal BP and Level A2 between 6100 and 5500 cal BP. Level A2 ascribed to the Neolithic has a higher number of specimens ($n = 6587$) compared to Level A3 from the Mesolithic ($n = 1074$). In terms of species composition by level, no changes are observed

in either the species collected or their proportions. The diversity indices show a slight decrease in the diversity of the assemblages collected in the Neolithic period: $1/D = 3.92$ (A3) to 3.78 (A2) and $qD = 4.71$ (A3) to 4.6 (A2), indicating a trend towards more specialised management. Therefore, despite slight variations in shellfish management at the local level, there is continuity in shellfish harvesting practices between the Mesolithic and Neolithic periods.

In the Portuguese Atlantic region, Rocha das Gaviotas has two levels dated to the Mesolithic (Level RG 3 dated between 9800 and 9400 cal BP and RG 2c-lower dated between 7700 and 7500 cal BP) and one to the Neolithic (RG 2c-higher dated between 5800 and 5700 cal BP). The oldest level (RG 3 = 4264) is the one with the highest number of specimens, compared to the most recent levels (RG 2c-lower = 1666 and RG 2c-higher = 1342). In terms of species composition by level, a change is observed from the predominance of the species *Mytilus* sp. during the first phase of the Mesolithic to that of *Patella* sp. in the second phase of the Mesolithic, which would be maintained during the Neolithic period. The diversity indices show a slight decrease in the diversity of the assemblages collected between the Mesolithic and Neolithic periods: $1/D = 2.06$ (c3) and $1/D = 2$ (c2 higher). This decline in diversity begins in the later Mesolithic phase: $1/D = 2.06$ (c3) to 1.81 (c2 lower) and $qD = 2.44$ (c3) to 2.09 (c2 lower) and increases slightly in the Neolithic period (level c2 higher). Therefore, regarding the composition of collected species and their management, there is no rupture between the Mesolithic and Neolithic periods.

4. Discussion

The Iberian Peninsula has a significant archaeological record that allows us to study the exploitation of marine resources during the Mesolithic and Neolithic periods and any possible changes. Recent research on this subject shows that there is certain continuity in the exploitation of the coastal environment during the Mesolithic and Neolithic in practically all areas (Pascual Benito, 2014; Ramos et al., 2011; Soares, 2013; Nukushina, 2016; Álvarez-Fernández et al., 2015). The Mediterranean coast, despite a lower biomass than the Atlantic coast, was also inhabited during this time interval by groups whose subsistence was based on marine resources (Fontanals-Coll et al., 2023).

However, the results obtained in the present study indicate that the relative abundance of exploited species and the areas of acquisition of molluscs varied both temporally and regionally. These observations are consistent with data from contemporary sites that have not been included in this study because of insufficient sampling or because the MNI was not used as a unit of quantification. In the case of the

Cantabrian coast, during the Mesolithic, the predominance of limpets and top shells can be observed in Cuesta de la Encina Level A (*Patella* sp.), Cuevas del Mar Level 3 (*Patella* sp. and *P. lineatus*), Cueva de El Mar (*Patella* sp. and *P. lineatus*), La Garma B Level A (*Patella* sp. and *P. lineatus*), Los Canes Level 7 (*Patella* sp.) and Linatzeta Level II (*Patella* sp. and *P. lineatus*) (Álvarez-Fernández, 2015). There is also evidence of the exploitation of estuarine environments during this period, particularly in Level H-Sln at Santimamiñe (*Ostrea* sp. and *S. plana*; Gutiérrez-Zugasti, 2011b).

On the Atlantic-Portuguese coast, the importance of the collection of estuarine species during the Mesolithic is also confirmed at Vale Fraude (*R. decussatus*, Araújo et al., 2014), Pinhal da Fonte (*Cerastoderma* sp., Araújo et al., 2014), Cabeço de Arruda (*Cerastoderma* sp. and *S. plana*, Lentacker, 1986), Cabeço de Amoreira (*Cerastoderma* sp. and *S. plana*, Lentacker, 1986), Barranca do Grilo (*Cerastoderma* sp. and *S. plana*) and Montes de Baixo (*Ostrea* sp. and *Mytilus* sp., Soares, 1996). The number of species gathered from these environments decreased during the Neolithic. In the Gulf of Cádiz, the collection of estuarine and coastal marsh specimens is documented from the Mesolithic at El Embarcadero del Río Palmes (*R. decussatus*, Ramos and Castañeda, 2005) and Cañada Honda (*R. decussatus*, *Lutraria* and *Cerastoderma edule*, Fernández et al., 2023), and it became a recurrent practice during the Neolithic.

On the Mediterranean coast, the predominance of *Cerastoderma* sp. in the Mesolithic assemblages is evident in L'Assut, (*Cerastoderma* sp., Román et al., 2022), Nerja Mina, levels 13 and 12 (*Mytilus* sp., *Cerastoderma* sp. and *R. decussatus* in descent, Jordá-Pardo, 1984), Nerja Vestibule, level 3C (*Mytilus* sp., Jordá-Pardo, 1984) and Bajondillo 3 (*Mytilus* sp. and *Cerastoderma* sp., Cortés-Sánchez et al., 2020). During the Neolithic period, the predominance of limpets and top shells is confirmed at Costamar (*Patella* sp., Carrasco, 2009), Tossal de Basses (*Patella* sp. and *Phorcus* sp., Luján-Navas, 2016), La Vital (*Patella* sp., Pascual-Benito, 2010) and Nerja Mina, levels 10–5 (*Patella* sp., Jordá-Pardo, 1984), with the exception of Barranquet, where *Cerastoderma* sp. predominates (Esquembre et al., 2008).

These diachronic variations in species representation and abundance show the existence of different strategies in the management of marine molluscs between the two periods analysed. From the ecological analysis, based on the distribution of the relative abundance of the species collected by region, a relatively more diversified management strategy is observed during the Mesolithic, while the degree of specialisation increased in the Neolithic. While three to four main species were collected in the Mesolithic, in the Neolithic most of the collected specimens correspond to one or two species. Previous studies of Mesolithic and Neolithic shell middens in Portugal suggest the possibility that this specialisation in mollusc management was due to a decrease in foraging efficiency (Dean and Carvalho, 2011; Dean et al., 2012). In this context, it has been hypothesised that reduced upwelling and increased aridity during the early Holocene reduced the availability of intertidal resources in the Late Mesolithic, affecting their harvesting and consumption (Bicho et al., 2010). Similarly, for the Mediterranean coast, some researchers suggest that the loss of coastal plain and the morphological change from lagoon ecosystem to rocky coast affected the availability of coastal resources, causing a change in the species of molluscs consumed between the Mesolithic and Neolithic (Fernández-López de Pablo and Gabriel, 2016; Brisset and Fernández-López de Pablo, 2022). Likewise,

studies on shell middens in the Cantabrian region suggest that the scarcity of terrestrial resources, such as deer and ibex, and the formation of estuaries during the early Holocene, led to a change in the species consumed and the importance of shellfish gathering at the end of the Mesolithic (Gutiérrez-Zugasti, 2011a; Milano et al., 2022).

In addition to environmental factors, it is possible that the adoption of domesticates at the beginning of the Neolithic could also have influenced the change in the management of marine molluscs. The cluster chart obtained from Simpson's similarity index shows that in the Neolithic the diversity of the malacological assemblages from the Mediterranean and Atlantic-Portuguese coasts changes with respect to the previous period, while on the Cantabrian coast the diversity remains similar to that of Mesolithic assemblages. In this case, the differences observed between the Cantabrian region and the rest of the areas studied during the Neolithic (Fig. 4) could be related to the rhythm of adoption of agriculture and livestock farming, with Neolithisation showing a certain chronological lag in the northern area compared with the rest of the regions (Isern et al., 2014; Cubas et al., 2016; Saña et al., 2020).

The results obtained also show a tendency for the Neolithic to favour the optimal species in productive or energetic terms, practising a more specialised strategy. In this regard, it is documented, for example, that limpets are the most commonly collected molluscs, with the exception of the Gulf of Cádiz, where *R. decussatus* predominates. Limpets and top shells are the most predictable and easy-to-process species in the upper-mid rocky intertidal area (Fa and Fa, 2002; Fa, 2008). In addition, the different limpet species are more profitable in terms of meat yield compared to top shell (García-Escárzaga and Gutiérrez-Zugasti, 2021). *R. decussatus* is also one of the molluscs with the highest biomass and nutritional value that can be acquired in estuarine areas (Fa and Fa, 2002; Fernández et al., 2023). The increased importance of these species during the Neolithic could be an indicator of the need to optimise food acquisition in these littoral areas.

Another significant difference documented in mollusc management strategies is related to the coastline, and in particular with their distance of the site. Sites located >10 km from the coast show a higher proportion of bivalves, while those located <10 km away show a higher proportion of gastropods (Fig. 5). This may be related to several aspects, including the energy cost of transporting the resource, the conservation of the food up to the place of consumption, or the non-bromatological use of some mollusc species. Regarding the cost of transport, the study by Coding et al. (2014) suggests that taxa with a higher proportion of meat than shell that require longer processing times are usually transported with the shell to the site, whereas otherwise they are discarded at the point of acquisition. Thus, specimens of the genera *Halotis* and *Callista* are likely to be processed on shore, while *Mytilus*, *Patella*, *Phorcus* and *Ostrea* are likely to be processed at the site (Fa, 2008; Jazwa et al., 2015). In terms of food preservation, bivalves can close and create an airtight seal between the shells, reducing the variation of relative humidity and temperature inside the shells (Fa, 2008). Limpets are able to close hermetically by adhering to a hard substrate, while in periwinkles their closure will depend on the impermeability of the closure of the operculum (Madariaga and Fernández, 1987). In addition, the presence of certain molluscs in inland sites may be related to non-bromatological use. At La Draga (Girona), a site more than 100 km from the Mediterranean coast, the presence of *Mytilus* sp. and *Callista* sp. shells are linked

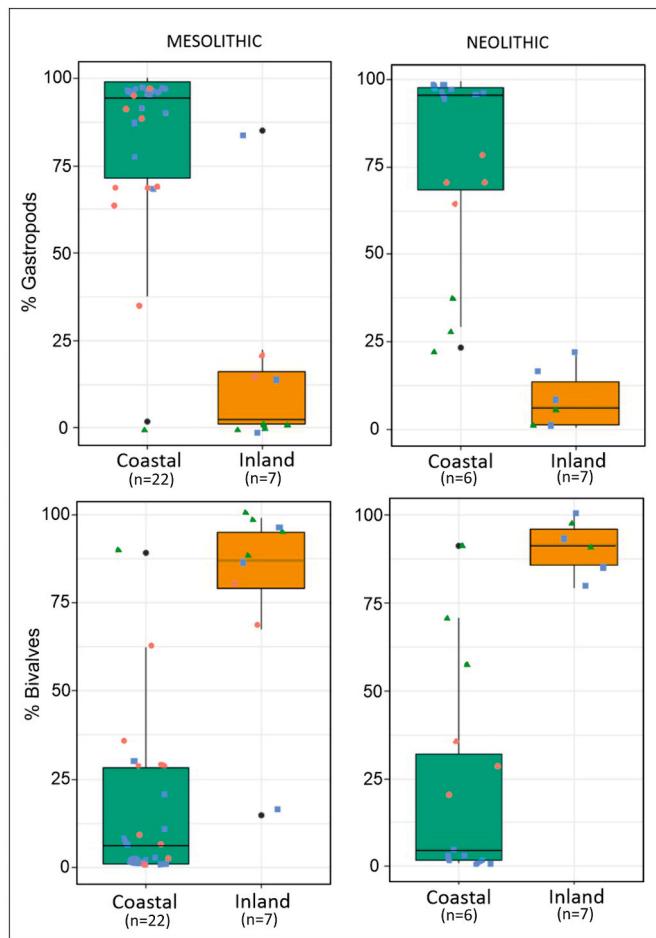


Fig. 5. Bar box plot of the percentage of gastropods versus bivalves in coastal and inland sites during the Mesolithic and Neolithic in the Iberian Peninsula. Type of sites: cave: blue square, shelters: pink circle and open-air: green triangle.

to the production of tools (Clemente-Conte and Cuenca, 2011; Verdún-Castelló et al., 2019). In Santimamiñe (Basque Country), also, *Ruditapes* sp. and *Ostrea* sp. shells were used as tools (Cuenca-Solana, 2015), as well as in another Basque cave, Marizulo, in this case a *Callista chione* shell (Álvarez-Fernández and Altuna, 2013). Finally, the location of the inland sites, closer to the upper part of the estuaries compared to the exposed coast, could explain the greater presence of bivalve species that mainly inhabit these estuarine zones.

These aspects influence the composition of the assemblages and may be the cause of the differences observed in mollusc consumption between inland and coastal sites. In Santa Maira (Alicante), for example, their consumption was combined with that of terrestrial resources, demonstrating the practice of a strategy that integrates territories, coast and inland valleys during the Mesolithic (Aura-Tortosa et al., 2006).

In short, the study shows that there was a change in the management of marine molluscs between the Mesolithic and Neolithic periods in the Iberian Peninsula, except in the Cantabrian region. There was a

specialisation in the exploitation of these resources during the Neolithic, with a reduction in the number of species collected, linked to the processes of Neolithisation that took place in the different regions of the Iberian Peninsula. In addition, the location of the sites in relation to the coast influenced the strategies for collecting marine molluscs, which favoured the collection of species that were transported and preserved better over time, such as bivalves.

5. Conclusions and future prospects

The Iberian Peninsula is the ideal setting for a study of the role played by marine resources in the diets of the last hunter-gatherer societies and the first agricultural societies.

The results obtained in this work, which focuses on marine molluscs, show, firstly, a change in management strategies between the Mesolithic and Neolithic periods. This change consists of a specialisation in shellfishing during the Neolithic, which now focused on a few taxa (different species of limpets, top shells and clams). Despite 65% similarity in the diversity of mollusc harvesting throughout the peninsula during the Neolithic, certain regional variability may be conditioned by economic and social factors as well as ecological ones. Among the former, it should be emphasised that the rate of adoption of domesticated species, with a 500-year lag in the north compared to the rest of the peninsular areas (Saña, 2013; Saña et al., 2020), may have influenced the survival and greater relative importance of the strategies practised at the beginning of the Holocene in the north of the peninsula. Thus, on the Cantabrian coast there is a slight trend towards diversification in the exploitation of marine molluscs. In this case, considering that the morphological change of the coastline had been consolidated by 7000–6000 cal BP (Leorri et al., 2012; Brisset and Fernández-López de Pablo, 2022), it is possible that the adoption of agriculture and livestock farming had a slight impact on the specialisation of the management of coastal environments.

Secondly, and in relation to ecological factors and coastline, it has been shown that when settlements are located more than 10 km from the coastline, they may not represent the total number of mollusc species consumed. This demonstrates the need to evaluate the dietary importance of this type of resource considering the rest of the subsistence strategies practised, integrating the exploited territories in a synchronous manner and, in particular, coastal and inland contexts, thus overcoming the possible biases that can result from studies focused on a single site.

Finally, it is important to point out the need to apply new lines of research to advance our knowledge of the role played by marine resources, and molluscs in particular, in the subsistence strategies of the last hunter-gatherer societies and the first agro-pastoral societies. On the one hand, biometric studies and the analysis of changes in the size of harvested molluscs will allow us to determine whether the pressure exerted by human harvesting could have caused a decrease in the availability of marine resources at the end of the Mesolithic and Neolithic periods (Dean and Carvalho, 2011; Dean et al., 2012; Álvarez-Fernández et al., 2011). Furthermore, studies on the seasonality of collection of these invertebrates will allow us to test the hypothesis of the seasonal nature of their consumption proposed for the Neolithic (Pascual Benito, 2014), and whether or not this documented change in management patterns may be related to the

onset of farming and animal husbandry practices.

Author contributions

Amaia Aguirre-Uribesalgo: Conceptualization, Formal analysis, Data curation, Writing – original draft, Writing – review & editing. Esteban Álvarez-Fernández: Formal analysis, Data curation, Writing – review & editing. María Saña: Formal analysis, Data curation, Writing – review & editing.

Data availability

As this paper represents a review of many sources, the data and references for which can be found within the text and bibliography presented here.

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.

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Appendix

Table A.1

Main species of marine molluscs consumed and their habitat during the Mesolithic and Neolithic in the Iberian Peninsula. For the habitat we follow the classification proposed by the European Union: 1110: Sandbanks that are slightly covered by sea water all the time; 1130: Estuaries; 1150: Coastal lagoons; 1160: Large inlets and shallow bays; 1170: Reefs (source http://ec.europa.eu/environment/nature/natura2000/marine/index_en.htm).

Genus	Species	Substrate	Habitat code	Zonation	Bibliography
Patella (limpets)	<i>P. vulgata</i> Linnaeus, 1758	Rocky	1170	Intertidal (upper to lower)	Casal et al., 2018
	<i>P. dpressa</i> Pennant, 1777	Rocky	1170	Intertidal	Casal et al., 2018
	<i>P. ulyssiponensis</i> Gmelin, 1791	Rocky	1170	Lower intertidal and upper infratidal	Casal et al., 2018
	<i>P. caerulea</i> Linnaeus, 1758	Rocky	1170	Intertidal	Mauro et al., 2003
Phorcus (Top shell)	<i>P. rustica</i> Linnaeus, 1758	Rocky	1170	Upper intertidal	Prusina et al., 2014
	<i>P. lineatus</i> (da Costa, 1778)	Rocky	1170	Upper and mid intertidal	Sousa et al., 2017
	<i>P. turbinatus</i> (Von Born, 1778)	Rocky	1170	Upper and mid intertidal	Sousa et al., 2017
Stramonita (red-mouthed rock shell)	<i>S. haemastoma</i> (Linnaeus, 1767)	Rocky	1170	Lower intertidal and infratidal (5–10 m depth)	Templado et al., 2012
Hexaplex (Banded Dye-murex)	<i>H. truculus</i> Linnaeus, 1758	Rocky	1170, 1150, 1110	Upper infratidal	Templado et al., 2010
Mytilus (mussel)	<i>Mytilus</i> sp. Linnaeus, 1758	Rocky	1170, 1130	Mid intertidal to upper infratidal	Suchanek, 1978
Ostrea (Oyster)	<i>O. edulis</i> Linnaeus, 1758	rocky or sandy/muddy	1170, 1160, 1110	Lower intertidal to upper infratidal	Templado et al., 2012
Cerastoderma (common cockle)	<i>C. edule</i> (Linnaeus, 1758)	sandy/muddy	1160, 1150, 1130, 1110	Intertidal to infratidal (5–20 m depth)	Templado et al., 2012
Ruditapes (Grooved carpet shell)	<i>R. decussatus</i> (Linnaeus, 1758)	sandy/muddy	1160, 1110	Intertidal	Templado et al., 2012
Solen (Razor shell)	<i>S. marginatus</i> Pulteney, 1799	sandy/muddy	1160, 1110	Intertidal to infratidal (5–20 m depth)	Templado et al., 2012
Scrobicularia (Peppery furrow shell)	<i>S. plana</i> (da Costa, 1778)	sandy/muddy	1130, 1110	Intertidal	Templado et al., 2012
Mimachlamys (variegated scallop)	<i>M. varia</i> (Linnaeus, 1758)	sandy/muddy	1170	Infratidal	Templado et al., 2012

Table A.2

Percentages of edible marine mollusc genera documented at Early Holocene sites in the Cantabrian region. Site code: 1. El Cierro (B), 2. Cueto de Hoz, 3. La Poza L'Egua, 4. Colomba, 5. El Alloru, 6. Toral III (13A), 7. Toral III (21), 8. La LLana, 9. Mazaculos II (A3), 10. El Pindal (2), 11. El Toralete, 12. Barcenillas (5), 13. El Mazo (100), 14. El Mazo (101B), 15. El Mazo (101C), 16. El Mazo (101.1A), 17. El Mazo (101.1B), 18. El Mazo (105), 19. El Mazo (107), 20. El Mazo (108), 21. El Mazo (113), 22. El Mazo (114), 23. El Mazo (115), 24. La Garma A (Q), 25. El Truchiro, 26. La Fragua (1), 27. Arenillas, 28. La Chora, 29. Cabirón, 30. La Trecha, 31. Marizulo (II), 32. J3 (D), 38. Mazaculos II (A2), 59. Los Gitanos (A4), 60. Los Gitanos (A3), 61. Los Gitanos (A2), 62. Pico Ramos (4), 63. Kobaederra (IV), 64. Kobaederra (III), 65. Kobaederra (II), 66. Santimamiñe (Slm).

Cd.	Total	Limpet		Top Shell		Mussel		Grooved carpet shell		Peppery furrow shell		Oyster		Others	
		MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
1	824	737	88.90	23	2.19	48	5.82	1	0.12	10	1.21	2	0.24	3	1.52
2	155	112	72.26	34	21.94	8	5.16	0	0.00	0	0.00	0	0.00	1	0.64
3	1601	1327	82.80	267	16.68	7	0.44	0	0.00	0	0.00	0	0.00	0	0.00
4	782	516	66.00	263	33.63	3	0.38	0	0.00	0	0.00	0	0.00	0	0.00
5	2309	1172	51.10	1127	48.80	0	0.00	0	0.00	0	0.00	0	0.00	10	0.43
6	4744	3257	68.65	1431	30.16	44	0.92	0	0.00	0	0.00	0	0.00	12	0.25
7	8063	7578	93.98	346	4.29	127	1.57	0	0.00	0	0.00	0	0.00	12	0.14
8	6704	3506	52.29	3063	45.69	111	1.66	0	0.00	0	0.00	0	0.00	21	0.36
9	1074	925	86.13	128	11.92	12	1.12	1	0.09	1	0.09	3	0.28	4	0.37
10	462	451	97.62	7	1.51	3	0.65	0	0.00	0	0.00	1	0.22	0	0.00
11	494	218	44.13	275	55.67	1	0.20	0	0.00	0	0.00	0	0.00	0	0.00
12	234	98	41.88	26	11.11	104	44.44	1	0.43	2	0.85	1	0.43	1	0.43
13	5151	3551	68.93	1565	30.38	176	3.42	0	0.00	0	0.00	0	0.00	35	0.68
14	4504	2220	49.29	2241	49.75	24	0.53	1	0.02	0	0.00	0	0.00	43	0.95
15	1963	901	45.90	1036	52.78	8	0.41	0	0.00	0	0.00	0	0.00	26	1.32
16	3200	1342	41.94	1846	57.69	16	0.5	0	0.00	0	0.00	0	0.00	12	0.38
17	6932	4747	68.48	2157	31.12	10	0.14	1	0.01	0	0.00	0	0.00	28	0.40
18	16362	10592	64.73	5595	34.19	243	1.48	0	0.00	0	0.00	0	0.00	175	1.07
19	6432	2250	34.98	4140	64.36	57	0.88	0	0.00	0	0.00	0	0.00	42	0.65
20	2003	1656	82.67	329	16.42	12	0.60	0	0.00	0	0.00	0	0.00	18	0.90
21	6390	4760	74.49	1574	24.63	122	1.91	0	0.00	0	0.00	0	0.00	56	0.88
22	389	160	41.43	217	55.78	4	1.03	0	0.00	0	0.00	0	0.00	8	2.06
23	1849	817	44.18	1000	54.08	22	1.19	0	0.00	0	0.00	0	0.00	10	0.54
24	2578	1691	65.59	870	33.75	7	0.27	0	0.00	0	0.00	2	0.08	1	0.12
25	1136	850	74.83	262	23.06	8	0.70	0	0.00	6	0.53	1	0.09	6	0.79
26	11900	10155	85.33	542	4.55	1028	8.64	37	0.34	0	0.00	58	0.49	77	0.65
27	9240	5839	63.19	712	7.71	1627	17.60	77	0.83	43	0.47	755	8.17	156	2.03
28	159	22	13.84	0	0.00	28	17.61	2	1.26	72	45.28	27	16.98	7	5.03
29	760	63	8.29	29	3.82	120	15.79	81	10.66	258	33.95	134	17.63	75	9.87
30	1505	956	63.52	245	16.28	186	12.36	14	0.93	7	0.47	87	5.78	9	0.66
31	278	230	82.74	7	2.52	26	9.35	1	0.36	1	0.36	12	4.32	1	0.35
32	5123	4853	94.73	257	5.02	2	0.04	0	0.00	0	0.00	0	0.00	7	0.21
58	6587	5511	83.66	960	14.57	84	1.27	1	0.03	2	0.03	3	0.04	10	0.40
59	3990	3437	86.14	522	13.08	8	0.20	0	0.00	0	0.00	3	0.08	26	0.50
60	3706	3135	84.59	545	14.71	8	0.22	0	0.00	0	0.00	1	0.03	17	0.45
61	9203	6936	75.37	1988	21.60	18	0.20	0	0.00	0	0.00	0	0.00	20	2.83
62	2198	1248	56.78	500	22.75	152	6.92	126	5.70	0	0.00	131	6.00	17	0.77
63	521	37	7.10	2	0.38	13	2.50	162	31.09	137	26.30	148	28.41	4	1.53
64	803	96	11.96	12	1.49	11	1.37	215	26.77	148	18.43	293	36.49	7	2.12
65	191	36	18.85	4	2.09	4	2.09	42	21.99	31	16.23	64	33.51	2	1.58
66	1641	3	0.18	0	0.00	2	0.12	92	5.61	1435	87.45	50	3.05	4	2.19

Table A.3

Palaeoecological data of selected Mesolithic and Neolithic archaeological levels by geographical areas (A = Cantabrian coast, B=Portuguese coast, C = Gulf of Cádiz, D = Mediterranean coast). MNI = Minimum Number of Individuals, S = number of species, D = Simpson's index, 1/D = inverse of Simpson's index, H' = Shannon-Weiner index, J = Pielou's equality, qD = effective number of species and faunal affinity matrix based on Simpson's similarity index comparing the whole of each geographical area.

Geographical areas	Period	MNI	S	D	1/D	H'	J	qD	A	B	C	D
A	Mesolithic	72746	21	0.563	1.776	0.87	0.286	2.387	A	1	0.72	0.43
		23242	18	0.315	3.170	1.3	0.450	3.669	B	0.72	1	0.57
		2098	14	0.473	2.113	1.14	0.432	3.127	D	0.43	0.57	1
B	Neolithic	29113	17	0.535	1.869	0.99	0.350	2.691	A	1	0.59	0.76
		3203	19	0.380	2.629	1.3	0.443	3.669	B	0.59	1	0.84
		5040	29	0.230	4.339	1.94	0.576	6.959	C	0.76	0.84	1
		14775	12	0.553	1.808	0.72	0.289	2.054	D	0.58	0.58	0.83

Table A.4

Percentages of edible marine mollusc species documented at early Holocene sites on the Atlantic seaboard, Portuguese coast. Site code: 40: Barranco das Quebradas 5, 41 Barranco das Quebradas 4, 42: Barranco das Quebradas 3 (c1 higher), 43: Barranco das Quebradas 3 (c1 lower), 44: Barranco das Quebradas 1 (c3), 45: Barranco das Quebradas 1 (c1-2), 46. Rocha das Gaviotas (2c lower), 47: Rocha das Gaviotas (3), 48: Toledo (B), 49: Amoreira (B), 67: Padrao I (C2), 68: Rochas das Gaviotas (2c higher), 69: Vale Santo.

Cd.	Total	Red-mouthed											
		Limpet		Top shell		Rock shell		Cockle		Mussel		Others	
		MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
40	5277	1960	37.14	893	16.92	917	17.38	0	0.00	1467	27.80	22	0.42
41	4184	510	12.19	2966	70.89	452	10.80	0	0.00	252	6.02	2	0.05
42	2897	1072	37.00	595	20.54	130	4.49	0	0.00	1099	37.94	1	0.03
43	5534	1406	25.41	2504	45.25	264	4.77	0	0.00	1354	24.47	6	0.11
44	3836	993	25.88	2497	65.09	51	1.33	0	0.00	292	7.61	2	0.05
45	600	150	25.00	373	62.16	38	6.33	0	0.00	40	6.66	0	0.00
46	4264	2930	68.71	24	0.56	102	2.39	0	0.00	1206	28.28	2	0.047
47	1666	523	31.29	42	2.52	63	3.78	0	0.00	1034	62.02	4	0.24
48	3459	9	0.26	6	0.17	17	0.49	2892	83.61	119	3.44	349	10.09
49	8040	0	0.00	0	0.00	0	0.00	7899	98.25	0	0.00	141	1.75
67	1415	911	64.39	0	0.00	54	3.82	100	7.07	125	7.28	69	4.87
68	1342	840	62.59	4	0.30	21	1.56	1	0.07	437	35.56	16	1.19
69	746	120	16.09	58	7.77	38	5.09	0	0.00	525	70.38	0	0

Table A.5

Percentages of edible marine mollusc species documented in early Holocene sites on the coast of the Gulf of Cádiz. Site codes: 54. Retamar, 55. Campo de Hockey, 56. SET Parralejos, 57. La Esparragosa.

Cd.	Total	Banded				Grooved				Variegated			
		Limpet	Top shell	Dye-murex	Carpet shell	Razor shell	Scallop	Others					
		MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
54	2434	6	0.25	21	0.86	350	14.38	557	22.88	1175	48.27	7	0.29
55	1234	9	0.73	257	20.83	155	12.64	167	13.53	127	10.29	210	17.02
56	203	5	2.47	0	0.00	1	0.49	127	62.56	9	4.43	15	7.39
57	1492	0	0.00	1	0.07	0	0.00	1081	72.45	10	0.67	52	13.07

Table A.6

Percentages of edible marine mollusc species documented in early Holocene sites on the Mediterranean coast. Site code: 33. La Cativera (A), 34. La Cativera (B), 35. Sola del Pep, 36. El Collado (IV), 37. El Collado (II), 38. El Collado (I), 39. Santa Maira (3), 50. Les Cendres (XI-X), 51. Les Cendres (IX-VIII), 52. Les Cendres (VII-VI), 53. Les Cendres (IV).

Cd.	Limpet		Top shell		Mussel		Cockle		Others		
	Total	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
33	465	65	14.00	9	2.00	56	12.00	307	66.00	5	1.00
34	274	17	6.00	3	1.00	123	46.00	36	13.00	27	10.00
35	233	26	11.16	170	72.96	33	14.16	0	0.00	4	1.72
36	359	0	0.00	0	0.00	0	0.00	312	86.91	8	2.23
37	826	0	0.00	0	0.00	0	0.00	757	91.65	22	2.66
38	358	0	0.00	0	0.00	0	0.00	312	87.15	13	3.63
39	67	0	0.00	0	0.00	45	67.00	3	4.00	16	23.88
50	4279	3074	71.84	936	21.87	12	0.28	5	0.12	76	1.78
51	3311	2078	62.76	1142	34.49	3	0.12	1	3.00	54	1.63
52	5703	3382	59.30	2205	38.66	9	0.16	0	0.00	89	1.56
53	1755	1497	85.25	200	11.39	0	0.00	0	0.00	56	3.19

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