RESEARCH

Where the Shells Come From? A New Methodology for Establishing Collection Areas Applied to Upper Palaeolithic and Mesolithic Shell Middens From Northern Iberia

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Abstract

Shellfishing was a common activity among prehistoric hunter-gatherers living in coastal areas in Iberia. Interpreting shellfish collection strategies is crucial to understand the lifeways of these coastal hunter-gatherers. Among collection strategies, the estimation of collection areas is essential for interpretation of mobility and subsistence strategies. In this paper we present a new methodological procedure to identify mollusc collection areas using a Technical Scoring Matrix (TSM). A TSM is a qualitative tool that infers the origin of one or more objects based on probability categories that can be quantified using a scoring system. First, a TSM must be built for a given area, including the range of mollusc species identified in archaeological sites, and considering the type of coastline, substrate and the littoral zone where they currently live. The scoring system is then applied to archaeological molluscs recovered from shell middens to establish collection areas. The application of a TSM to Upper Palaeolithic, Epipaleolithic and Mesolithic shell middens from northern Iberia showed that mollusc collection was focused on rocky substrates of exposed and sheltered coastlines during the Magdalenian and the Azilian, with an increase in diversification of collection areas through time, including important shellfishing activity in soft-bottom areas, such as estuaries, during the Mesolithic. From the Azilian onwards, the lower mesolittoral replaced the upper mesolittoral as the most heavily harvested zone. Higher diversification in collection areas and larger collection in the lower zones over time suggest that intensification started at least in the Magdalenian and increased in the Mesolithic, which aligns with previous interpretations based on the decrease in shell size.

Keywords Marine molluscs · Shellfish · Hunter-gatherers · Palaeolithic · Mesolithic

Introduction

The relationship of hunter-gatherer groups with the sea is reflected in the presence of settlements close to the coast and the evidence of fishing and shellfishing as important activities for their survival (Erlandson, 2001). Among coastal resources, mollusc consumption has been constantly linked to the evolution of our genus, with exploitation since the Middle Pleistocene, around 300,000 years ago (Colonese *et al*., 2011; Ramos-Muñoz *et al*., 2016). Large accumulations of shells, indicating collection, processing, consumption, and various other uses have been recorded all around the world (*e.g*., Álvarez *et al*., 2011; Colonese *et al*., 2011; Gutiérrez-Zugasti *et al*., 2011; Thompson *et al*., 2016). These large shell accumulations are usually known as shell middens, although other terms like "shell mounds" or "shell bearing" sites are also used depending on the characteristics of the accumulations (Claassen, 1991). From a regional perspective, some specific terms have been used to name shell accumulations, such as for example, sambaquis in Brasil (Wagner *et al*., 2011) and køkkenmøddinger in Denmark (Andersen, 2007). Here, we use the term shell midden in a broad sense to include stratigraphic levels with considerable amounts of shells.

The good preservation of shells is of great sedimentological, palaeontological, and archaeological interest in fossil and subfossil records (Gordillo & Boretto, 2020). Consequently, archaeological shell middens are important because: (i) the identification of mollusc species can be used in stratigraphic series to address palaeoenvironmental reconstructions; (ii) they provide information on trends in mollusc consumption and changes in human diet; (iii) they contain information on material culture through the different utilization of the shells (ornamentation, offerings, tools, *etc*.); and iv) they give information on human subsistence strategies and settlement patterns related to the use of molluscs (*e.g*. collection areas and techniques, seasonality). Therefore, shells can be used as proxies for studying past environments, climate changes and human behaviour.

In recent decades there have been important methodological advances in the estimation of indices of abundance (Gutiérrez-Zugasti, 2011a; Harris *et al*., 2015), the seasonality of collection (Mannino *et al*., 2003; García-Escárzaga *et al*., 2019) and the identification of collection areas (Bailey and Craighead, 2003; Gutiérrez-Zugasti, 2009). The last point offers insights into mobility patterns and, in addition, could be indicative of the use of different collection strategies and the effort made in mollusc collection (Gutiérrez-Zugasti, 2009). Therefore, the estimation of collection areas is essential for interpretation of the subsistence strategies of the hunter-gatherer groups that formed the shell middens and justifies the effort made by many researchers to obtain an adequate estimation methodology (*e.g*. Bailey and Craighead, 2003; Gutiérrez-Zugasti, 2009).

The estimation of shellfishing areas is based on the ecology of species and under the assumption that the species found in archaeological sites occupied the same habitats in the past as those currently occupied. Nevertheless, some molluscs are ubiquitous and can occupy different types of habitats, making the estimation of collection areas based on ecological parameters less precise. For example, Gutiérrez-Zugasti (2009) created a method to establish collection areas of shell assemblages

based on ecological factors combined with the abundance of each species in the archaeological sites. However, he concluded that the presence of ubiquitous species was a clear limiting factor to get accurate results, and that only species with restricted habitats were useful to differentiate between collection areas, especially in terms of zonation and exposure. Other contributions were based on the analysis of a single species, such as the regression equations proposed by Bailey and Craighead (2003), which used biometric data from present-day communities of *Patella vulgata* in Great Britain to discriminate between shore type and zonation. However, these equations also have some limitations: they can be only used with one species, and they must be tested with a modern reference collection before they are used in other geographical areas. On the other hand, Campbell (2008) described variations in the shape of limpets depending on their position within the tidal range. However, their shape could also vary with humidity and cover at a constant tidal level, so interpreting these shell-shape models is not straightforward.

In this paper we aim to contribute to this debate by presenting a new methodology to establish shell collection areas using a Technical Scoring Matrix (TSM). A TSM is a qualitative tool that infers the origin of one or more objects based on probability categories that can be quantified using a scoring system. As explained by Buceta (2021), a TSM is a tool for field studies and involves a probability approach that should answer the following question: how likely is it that an object type comes from a given source? According to this statement, it can be used in any scenario to calculate the probability that a set of items $(\times 1, \times 2, \times 3, \ldots xn)$ come from one or more sources (origin).

Tudor and Williams (2004) designed a TSM for the determination of the sources of marine litter emissions, currently used by the countries linked to the Convention for the Protection of the Marine Environment of the North-East Atlantic (https://www.ospar.org/convention). They implemented a TSM with six probability categories for each item and a scoring system was assigned (very probable −16 points-, probable −4 points-, possible −2 points-, improbable −1 point-, very improbable −0.25 points- and impossible or absent −0 points-). This method can be used to determine the most likely habitat of origin for a set of archaeological molluscs and thus make an estimate of the collection areas.

Following this approach, we elaborated a TSM for the marine molluscs of the Cantabrian coast (northern Iberia, Atlantic Europe) considering their current habitats, and then we applied this TSM to shell assemblages from different prehistoric shell middens (*sensu lato*) formed from the Lower Magdalenian (Upper Palaeolithic) to the Mesolithic in the Cantabrian region. We discuss the methodological advance provided by the application of the TSM, and the changes in collection areas in the region during the Pleistocene-Holocene transition.

Study Area

The coastline of central northern Iberia is made up of exposed rocky coasts interrupted by the presence of narrow estuaries. The area between the coastline and the foothills of the Cantabrian Mountains (up to 2,600 masl) consists of Upper

Palaeozoic limestones near the town of Llanes and Cretaceous limestones with rudists and *Orbitolina* near the city of Santander (Fig. 1). The remarkable development of karst processes and fluvial erosion has led to the development of steep-sided valleys where caves and rock shelters are abundant. Many of them show human occupation levels dating back to the Upper Palaeolithic and the Mesolithic.

Archaeological shell middens are always found in caves and rock shelters in northern Iberia (Fig. 1). These shell middens are very abundant in this zone and their study began in the famous Altamira cave at the end of the nineteenth century (Sanz de Sautuola, 1880). However, it was not until the second half of the twentieth century that there was a notable expansion of research on this type of settlement (*e.g.* Arias, 1991; González-Morales, 1982; Straus, 1985).

Shell middens are characterised by the predominance of mollusc shells over other archaeological remains. The oldest accumulations of shells in archaeological sites of northern Iberia are dated to the Middle and Upper Palaeolithic, although the larger shell middens were formed during the Mesolithic. Despite the lack of specific studies on the characteristics and morphology of shell accumulations in the region, shell deposits in Middle-Upper Palaeolithic and Epipalaeolithic (Azilian) sites have been usually considered shell layers, while Mesolithic accumulations have been considered proper shell middens containing several layers where shells are the most abundant component (Gutiérrez-Zugasti *et al.*, 2011). As stated in the introduction, we will use the term shell midden to refer indistinctively to both type of deposits through the manuscript. During the Palaeolithic, limpets (*P. vulgata*) and periwinkles (*Littorina littorea*) were the most consumed molluscs in this region, while in the Mesolithic, the limpets *Patella depressa* and *P. vulgata*, the topshell *Phorcus*

Fig. 1 Location of the selected sites in northern Iberia

lineatus and the mussel *Mytilus galloprovincialis* were the main exploited species (Gutiérrez-Zugasti and Cuenca-Solana 2014).

The distance travelled to capture these species depended on the variation in sea level, which was around −120 m during the coldest peak of the Late Glacial Maximum around 26–23.5 kys cal BP (Andersen *et al*., 2004). Subsequent melting caused a gradual rise in sea level and the flooding of the current estuaries during the Holocene transgression, around 8–3 kys BP (Leorri & Cearreta, 2004).

Material and Methods

Materials

Fourteen sites, located in northern Iberia and containing shell layers and shell middens, were selected for analysis: Cualventi and Las Aguas (Muñoz Fernández & Ruiz Cobo, 2016); Altamira (Álvarez-Fernández, 2009); El Juyo (Madariaga & Fernández, 1987); La Riera (Ortea, 1986); Peña del Perro (Moreno, 1995); La Garma A (Álvarez-Fernández, 2016); La Pila (Gutiérrez-Zugasti, 2009); El Toral III (Arniz-Mateos *et al*., 2024); El Mazo (García-Escárzaga *et al*., 2022a); El Truchiro (Álvarez-Fernández *et al*., 2013); El Carabión (Pérez-Bartolomé *et al*., 2016); La Chora (León-Cristóbal *et al*., 2024); and J3 (Álvarez-Fernández *et al*., 2014) (Fig. 1). All of them were excavated using modern techniques and their shell assemblages have been studied and published. The chronology of the sites ranges from ca. 20,000 to ca. 7,500 cal BP, including the Lower and Upper Magdalenian, the Azilian and the Mesolithic (Table 1). Stratigraphic levels belonging to the same chronocultural period were grouped for analysis.

TSM and Shell Middens

To estimate collection areas, a matrix is used to relate each shell species (columns) with all the parameters that make up a marine habitat (rows), but unlike the information used from the conventional method (absence/presence), probability categories are assigned in each case. Secondly, to transform this matrix into a TSM, these categories are replaced by the scoring system proposed by Tudor and Williams (2004). The designed matrix is then used to calculate the percentages of representation of each parameter and to identify, in probabilistic terms, the habitats of origin. The matrix only includes taxa determined at specific level, as different species of a genus may live preferentially in different environments. This is, for example, the case for the lagoon cockle *Cerastoderma glaucum* (usually in brackish lagoons) and the common cockle *Cerastoderma edule* (usually in estuaries and the adjacent infralittoral zone) (Dabouineau & Ponsero, 2009; Derbali *et al*., 2009; Paradas & Molares, 2008).

The six categories of probability detailed by Tudor and Williams (2004) need to be adapted to the case study of the shell middens, assessing the relationship of molluscs with different habitat parameters. The six modified presence/absence

Table 1 List of selected shell middens and age. Radiocarbon calibrations were carried out using OxCal v. 4.4 software (Bronk Ramsey, 2009) and the IntCal20 (Reimer *et al*., 2020) and Marine20 (Heaton *et al*., 2020) calibration curves. Corrections for marine radiocarbon reservoir effects (ΔR) in shell samples from Holocene and Pleistocene deposits in northern Iberia followed the recommendations of García-Escárzaga *et al*. (2022b) and Soares *et al*. (2016)

Site	Level	Age cal BP	Period	
La Riera	18–20	20,875–17,865	Lower Magdalenian	Upper Palaeolithic
Cualventi	E	19,515–17,480		
Altamira	2	18,870–18,365		
Las Aguas	B	18,230–17,375		
El Juyo	4–6–7–8–9	18,145–16,165		
La Riera	21–24	16,480–13,880	Upper Magdalenian	
La Garma A	N–O	15,230–13,615		
Peña del Perro	2c	14,860–13,605		
La Pila	III.1-III.3	13,725–13,405	Azilian	
La Riera	27–28	12,825–12,100		
Peña del Perro	2a/b	12,450–11,320		
Peña del Perro	1	10,725–10,225	Mesolithic	
La Riera	29–30	10,510–6,945		
El Toral III	10–17-18–19-20–21–22	10,020–7,200		
J3	D-F	9,455–7,860		
La Garma A	Q	9,400–7,915		
El Mazo	100–120	9,270–7,480		
El Carabión	I	8,720–8425		
La Chora	102	7,750–7,590		
El Truchiro	II	7,560–7260		

categories are, from highest to lowest probability: i) facies-forming species (16 points), which have the highest probability of being present in a parameter; ii) characteristic species (4 points), not as abundant as the previous ones but are always present in a parameter; iii) common species (2 points), which normally occupies a habitat, but may be absent; iv) rare species (1 point), whose occurrence is unusual; v) very rare species (0.25 points), the presence of which is highly improbable; and vi) absent species (0 points), if its presence is not possible in a parameter (Table 2). Finally, the TSM to estimate the collection areas of a shell assemblage is obtained by assigning these values to the presence/absence categories. The scoring system of Tudor and Williams (2004) is still valid for this matrix, as the values depend on the number of categories and not on the type of category used.

The TSM includes three types of parameters: i) coastline: exposed, protected or estuary ii) zonation: supralittoral, upper mesolittoral, lower mesolittoral, shallow infralittoral, deep infralittoral and circalittoral; and iii) substrate: mud, sandy mud, muddy sand, sand, gravelly sand, gravels and bioclasts, phanerogams and rock. The type of coastline is linked to hydrodynamics and therefore to water movements due

Table 2 Application of the TSM to a hypothetical shell midden with four mollusc species

PARAMETER		Mollusc A	Mollusc B	Mollusc C	Mollusc D	TOTAL	%
Coastline	Exposed	Common	Common	Common	Common	8	34.78
	Protected	Common	Common	Characteristic	Common	10	43.48
	Estuary	Absent	Rare	Characteristic	Absent	5	21.74
Zoning	Supralittoral	Absent	Absent	Absent	Absent	0	0
	Upper mesolittoral	Absent	Absent	Absent	Absent	0	0
	Lower mesolittoral	Rare	Absent	Facies	Absent	17	39.53
	Shallow infralittoral	Common	Common	Characteristic	Common	10	23.26
	Deep infralittoral	Common	Common	Characteristic	Common	10	23.26
	Circalittoral	Common	Common	Absent	Common	6	13.95
Substrate	Mud	Common	Absent	Characteristic	Absent	6	19.35
	Sandy mud and muddy sand	Common	Absent	Characteristic	Rare	7	22.58
	Sand	Common	Absent	Absent	Rare	3	9.68
	Gravelly sand	Absent	Common	Absent	Absent	2	6.45
	Gravels and bioclasts	Absent	Absent	Absent	Absent	0	0
	Phanerogams	Absent	Common	Characteristic	Absent	6	19.35
	Rock	Absent	Common	Characteristic	Rare	7	22.58

to currents and waves. Exposed coastlines are directly impacted by wave action (*e.g.* cliffs, rocky promontories, beaches, *etc.*), while protected coastlines include ancient glacial flooded valleys, inland lagoons, inlets and harbours. Estuaries are protected coasts, but with a very particular nature and biota and should be treated as a separate type of coastline.

Table 2 includes an example of the application of TSM to a hypothetical shell midden where four mollusc species have been identified (named from A to D). Results indicate more focused catches on protected (43.5%) and exposed (34.8%) coasts than in estuaries (21.7%), while the collection area was concentrated in the lower mesolittoral zone (39.5%) and the entire infralittoral zone (46,6%). Collection was carried out on a wide range of substrates and especially on rocks (22.6%), sandy-muddy sediments (22.6%), mud (19.4%) and phanerogams (19.4%).

In this paper the categories of facies-forming and characteristic species refer to the Interpretative Guide of the Spanish Inventory of Marine Habitats and Species (Templado *et al*., 2012), where explicit reference is made to the North Atlantic coast of Iberia. For those species that do not appear in this guide we have used different specialized bibliography (*e.g.* Chambers, 2009; Gofas *et al*., 2011; Gómez, 2017; Poppe & Goto, 1991; Rolan, 1983; Tebble, 1976; Trigo *et al*., 2018) and our own observations on the Cantabrian coast.

To build the Matrix, all the identified species in the shell midden were initially considered (edible and others, regardless as to whether they are occasional catches represented by a few specimens or systematic collections represented by thousands of shells), but only the species that we positively know that have been collected by humans were included. To make this selection, species present from the supralittoral

to the shallow infralittoral were considered potentially harvestable. Shallow infralittoral species can be caught at low spring tides or washed ashore by currents or waves. However, species exclusive to the deep infralittoral or circalittoral cannot be collected from the shore during low tides and their presence in the shell middens is explained by the collection of empty shells from beach thanatocoenosis. Other species present in the shell middens should be discarded for the TSM, as: i) they do not belong to the study area, since they have been dragged by currents (*e.g.* wood-boring bivalves or gastropods); ii) or they derive from possible exchanges with human groups from other geographical areas (*e.g.* Mediterranean species found in Atlantic coastal sites).

Results and Discussion

Marine Molluscs in Archaeological Sites From Northern Iberia

Fifty-three taxa were identified in the twenty archaeological sites studied, including thirty gastropods, twenty-one bivalves and two scaphopods (Supplementary Material 1). The total number of taxa is slightly higher in the Upper Palaeolithic and the Epipalaeolithic (40) than in the Mesolithic (36). The maximum number of taxa is nineteen in three sites, El Juyo, Peña del Perro (level 1) and El Mazo, while only five taxa have been determined in Cualventi and La Riera (levels 21–24).

The groups with the widest spatial and temporal distributions are the rock-associated species, such as periwinkles (*L. littorea*, *Littorina obtusata*, *Littorina saxatilis*), limpets (*P. depressa*, *P. vulgata*), the topshell *P. lineatus* and the mussel *M. galloprovincialis*. Six gastropods (*Buccinum undatum*, *Tritia mutabilis, Turritellinella tricarinata*, *Aporrhais pespelecani*, *Semicassis saburon* and *Trivia arctica*), five bivalves (*Acanthocardia tuberculata*, *Arctica islandica*, *Pecten maximus*, *Mimachlamys varia* and *Teredo navalis*) and the scaphopod *Antalis vulgaris* have only been reported in the Lower Magdalenian, while seven bivalves (*Ruditapes decussatus*, *Irus irus*, *Striarca lactea, Hiatella arctica, Eastonia rugosa*, *Scrobicularia plana* and *Solen marginatus*) have been collected mainly from the easternmost Mesolithic shells middens. The main taxa used for food in northern Iberia during the study period are included in Fig. 2.

Some species were discarded from the TSM as they come from beach thanatocoenoses or from different geographic areas. The gastropods *S. saburon* and *T. tricarinata* are characteristic of the circalittoral environment, at depths greater than 70 m, where *T. tricarinata* can be the dominant species with hundreds of individuals per square metre (Liu *et al*., 2023; Rolan, 1983; Templado *et al*., 2012). The scallop *P. maximus* is especially abundant in the deep infralittoral and circalittoral sandy muds (Mason, 1983; Templado *et al*., 2012), while the scaphopod *Antalis novemcostata* prefers sandy substrates at depths usually greater than 20 m (Steiner, 1997). The bathymetric distribution of these taxa indicates that their shells come from beach thanatocoenoses. The presence of these species shows that the shells were collected dead for manufacturing ornaments and tools or for other unknown reasons.
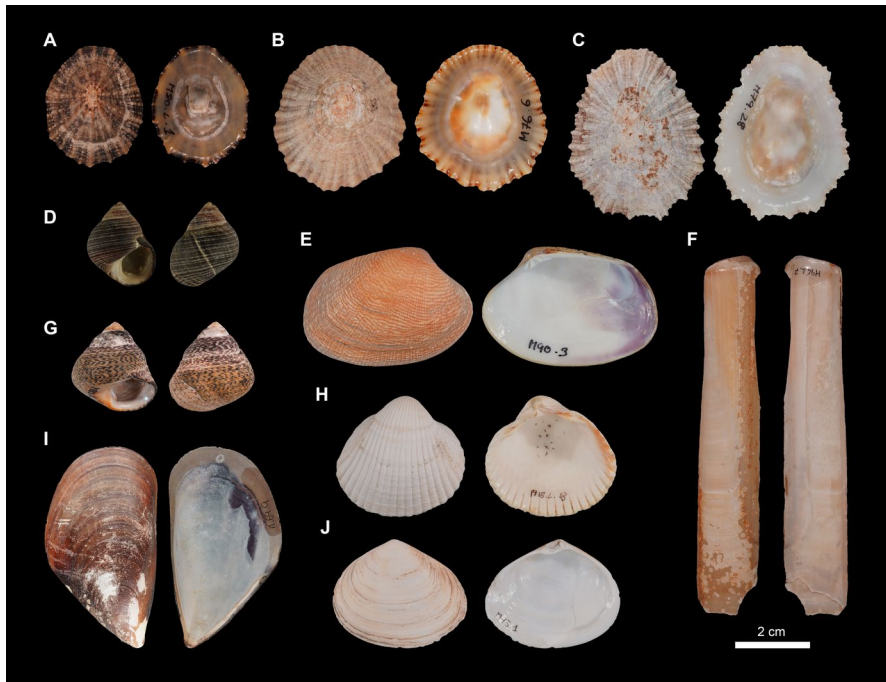
Fig. 2 Main taxa used for food in northern Iberia during the study period. A: *Patella vulgata*; B: *Patella depressa*; C: *Patella ulyssiponensis*; D: *Littorina littorea*; E: *Ruditapes decussatus*; F: *Solen marginatus*; G: *Phorcus lineatus*; H: *Cerastoderma edule*; I: *Mytilus galloprovincialis*; J: *Scrobicularia plana*

Other species were discarded because they come from other regions due to high human mobility or exchanges with other human groups. For example, *T. mutabilis* is a small Mediterranean gastropod whose presence in Atlantic shell middens is due to exchanges with other human groups (Tarriño *et al*., 2021), since its Atlantic distribution is limited to the Strait of Gibraltar and adjacent areas. On the other hand, the shipworm *T. navalis* is a bivalve not included in the TSM because it is a wood borer (Culha, 2010) and it could have reached the shore on driftwood from a distant origin.

The presence of some taxa generates some controversy but their presence in the archaeological deposits must be interpreted considering different past climates. For example, the presence of *A. islandica* is indicative of cold waters as this species is currently distributed from the North Sea to the English Channel (Witbaard & Bergman, 2003). The remains of this bivalve have been found in the Lower Magdalenian levels of El Juyo, during the concurrence of two Heinrich events (H0 and H1), which represented a significant cooling of the Iberian coastal waters (Jiménez & Camuera, 2024). On the contrary, the bivalve *E. rugosa* is distributed from the Strait of Gibraltar to Guinea, including the Canary Islands and Cape Verde and expanding towards the Mediterranean (Soriano *et al*., 2010). It is a thermophilic species (Atich & Soler, 1986) so its presence in shell middens from northern Iberia suggests the occurrence of warmer conditions. We found remains of this species

in level 1 of El Carabión, corresponding to the Mesolithic and coinciding with a Holocene transgressive process that entailed rapid flooding on the Cantabrian coast (Millán & Valcarlos, 2010). A third controversial species is the gastropod *Stramonita haemastoma*, which is distributed in tropical and temperate waters, but is currently present in the Cantabrian Sea (Souto *et al.*, 2008). This species has been found in La Riera, levels 27–28 (end of the Azilian) and 29–30 (Mesolithic), and in El Toral III (Mesolithic).

TSM For the North Coast of the Iberian Peninsula

After discarding one taxon at the family level (Solenidae) and two taxa at the generic level (*Patella* sp. and *Cerastoderma* sp.) and the six species coming from beach thanatocoenoses, forty-four mollusc species have been selected for the application of the TSM, including gastropods (Table 3), bivalves and scaphopods (Table 4). This list includes twenty-six gastropods, most of which (72.4%) are common or characteristic in rocky substrates located mainly in supralittoral to shallow infralittoral zones of exposed coastlines. The best represented genera are *Littorina* (*L. fabalis, L. obtusata*, *L. littorea*, *L. saxatilis*) and *Patella* (*P. depressa*, *P. ulyssiponensis*, *P. vulgata*).

The selected molluscs are completed by seventeen bivalves and one scaphopod (Table 4). Among them, there are seven rock-associated bivalve species mainly characteristic of lower mesolittoral to deep infralittoral zones, of which *M. galloprovincialis* and *O. edulis* are the most abundant in the studied shell middens (Fig. 3). The presence of species that form estuarine facies or are characteristic of estuaries (*S. plana, R. decussatus* and *S. marginatus*) is mostly restricted to the eastern Mesolithic shell middens. The exception is the cockle (*C. edule*), which is widely distributed since it is also a characteristic species of protected coasts.

Application of TSM to Shell Middens in Northern Iberia

During the Lower Magdalenian, molluscs were mainly collected from exposed and sheltered coastlines (mean probability 41% and 47%, respectively), with estuaries as secondary collection areas (12%) (Supplementary Material 2). The mollusc record of this period is mainly composed of species typical of the mesolittoral zone (57%), and especially the upper mesolittoral (35%). They are dominant over taxa of supralittoral (15%) and shallow infralittoral (11%) zones. All shell middens are clearly dominated by species from rocky substrate (72%), but one of them (El Juyo) also includes appreciable proportions of species typical of mixed sandy-muddy substrates (50%) and estuaries (23%). Besides, this site has the highest scores for species from shallow infralittoral to circalittoral zones (44%).

The exploitation of both sheltered and exposed coastlines presents similar percentages in most levels of the Upper Magdalenian (44%—45%), except in Peña del Perro, where the presence of estuarine species increases notably (28%). As a result, the average probability in this period for exposed and protected coasts is 39% and

Table 3 TSM for the north coast of Iberia: gastropods

PARAMETER/SPECIES		Aporrhais pespelecani	Bittium latreillii	Bittium reticulatum	Buccinum undatum	Calliostoma zizyphinum	Charonia lampas	Haliotis tuberculata	Littorina fabalis	Littorina littorea	Littorina obtusata	Littorina saxatilis	Melarhaphe neritoides	Nucella lapillus
Coastline	Exposed	Common	Common	Common	Common	Characteristic	Characteristic	Characteristic	Common	Absent	Characteristic	Characteristic	Characteristic	Common
	Protected	Common	Common	Characteristic	Common	Characteristic	Common	Characteristic	Common	Characteristic	Characteristic	Characteristic	Characteristic	Characteristic
	Estuary	Absent	Rare	Characteristic	Absent	Absent	Absent	Absent	Absent	Common	Absent	Absent	Absent	Absent
Zoning	Supralittoral	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Characteristic	Absent	Characteristic	Characteristic	Absent
	Upper mesolittoral	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Common	Characteristic	Characteristic	Characteristic	Absent	Characteristic
	Lower mesolittoral	Rare	Absent	Characteristic	Absent	Common	Absent	Characteristic	Common	Common	Common	Common	Absent	Common
	Shallow infralittoral	Common	Common	Characteristic	Common	Characteristic	Characteristic	Characteristic	Rare	Absent	Absent	Absent	Absent	Absent
	Deep infralittoral	Common	Common	Characteristic	Common	Characteristic	Characteristic	Common	Absent	Absent	Absent	Absent	Absent	Absent
	Circalittoral	Common	Common	Absent	Common	Absent	Common	Absent	Absent	Absent	Absent	Absent	Absent	Absent

Table 3 (continued)

PARAMETER/SPECIES		Aporrhais pespelecani	Bittium latreillii	Bittium reticulatum	Buccinum undatum	Calliostoma zizyphinum	Charonia lampas	Haliotis tuberculata	Littorina fabalis	Littorina littorea	Littorina obtusata	Littorina saxatilis	Melarhaphe neritoides	Nucella lapillus
Substrate	Mud	Common	Absent	Characteristic	Absnet	Absent	Common	Absent	Absent	Absent	Absent	Absent	Absent	Absent
	Sandy mud and muddy sand	Common	Absent	Characteristic	Rare	Absent	Common	Absent	Absent	Absent	Absent	Absent	Absent	Absent
	Sand	Common	Absent	Absent	Rare	Absent	Common	Absent	Absent	Absent	Absent	Absent	Absent	Absent
	Gravelly sand	Absent	Common	Absent	Absent	Absent	Common	Absent	Absent	Absent	Absent	Absent	Absent	Absent
	Gravels and bioclasts	Absent	Absent	Absent	Absent	Absent	Common	Characteristic	Absent	Absent	Absent	Absent	Absent	Absent
	Phanerogams	Absent	Common	Characteristic	Absent	Absent	Common	Absent	Absent	Absent	Absent	Absent	Absent	Absent
	Rock	Absent	Common	Characteristic	Rare	Characteristic	Characteristic	Characteristic	Common	Characteristic	Characteristic	Characteristic	Characteristic	Characteristic

PARAMETER/SPECIES	Ocenebra erinaceus	Ocinebrina aciculata	Patella depressa	Patella ulyssiponensis	Patella vulgata	Phorcus lineatus	Steromphala umbilicalis	Stramonita haemastoma	Tricolia pullus	Tritia incrassata	Tritia reticulata	Trivia arctica	Trivia monacha

Table 3 (continued)

PARAMETER/ SPECIES		Aporrhais pespelecani	Bittium latreillii	Bittium reticulatum	Buccinum undatum	Caliostoma zizyphinum	Charonia lampas	Haliotis tuberculata	Littorina fabalis	Littorina littorea	Littorina obtusata	Littorina saxatilis	Melarhaphe neritoides	Nucella lapillus
Coastline	Exposed	Common	Common	Characteristic	Characteristic	Characteristic	Characteristic	Characteristic	Characteristic	Common	Common	Common	Characteristic	Characteristic
	Protected	Common	Common	Common	Rare	Characteristic	Characteristic	Characteristic	Common	Common	Common	Characteristic	Common	Common
Zoning	Estuary	Absent	Absent	Absent	Absent	Common	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
	Supralittoral	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
	Upper mesolittoral	Absent	Absent	Characteristic	Rare	Characteristic	Characteristic	Characteristic	Absent	Absent	Absent	Absent	Absent	Absent
	Lower mesolittoral	Common	Common	Common	Characteristic	Common	Absent	Rare	Rare	Common	Common	Common	Very rare	Rare
	Shallow infralittoral	Common	Common	Absent	Absent	Absent	Absent	Absent	Characteristic	Common	Common	Characteristic	Characteristic	Characteristic
	Deep infralittoral	Common	Common	Absent	Absent	Absent	Absent	Absent	Characteristic	Rare	Common	Common	Characteristic	Characteristic
	Circalittoral	Common	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Common	Absent	Common	Absent

Table 3 (continued)

PARAMETER/ SPECIES		Aporrhais pespelecani	Bittium latreillii	Bittium reticulatum	Buccinum undatum	Calliostoma zizyphinum	Charonia lampas	Haliotis tuberculata	Littorina fabalis	Littorina littorea	Littorina obtusata	Littorina saxatilis	Melarhaphe neritoides	Nucella lapillus
Substrate	Mud	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
	Sandy mud and muddy sand	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Common	Common	Common
	Sand	Common	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Common	Common	Absent	Absent
	Gravelly sand	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
	Gravels and bioclasts	Common	Common	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Common
	Phanerogams	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Characteristic	Absent	Absent
	Rock	Common	Common	Characteristic	Characteristic	Characteristic	Characteristic	Characteristic	Characteristic	Common	Common	Absent	Characteristic	Characteristic

Table 4 TSM for the north coast of Iberia: bivalves and scaphopod

PARAMETER/SPECIES		Acanthocardia tuberculata	Anomia ephippium	Arctica islandica	Callista chione	Cerastoderma edule	Eastonia rugosa	Hiatella arctica	Irus irus	Mimachlamys varia
Coastline	Exposed	Common	Common	Common	Characteristic	Absent	Common	Common	Characteristic	Characteristic
	Protected	Common	Common	Rare	Common	Characteristic	Common	Characteristic	Absent	Absent
Zoning	Estuary	Absent	Absent	Absent	Absent	Facies	Absent	Absent	Absent	Absent
	Supralittoral	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
	Upper mesolittoral	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
	Lower mesolittoral	Absent	Common	Common	Absent	Facies	Common	Absent	Common	Common
	Shallow infralittoral	Common	Common	Common	Characteristic	Characteristic	Common	Characteristic	Common	Common
	Deep infralittoral	Common	Common	Common	Characteristic	Absent	Common	Common	Characteristic	Characteristic
	Circalittoral	Absent	Common	Common	Common	Absent	Common	Common	Common	Common

Table 4 (continued)

PARAMETER/SPECIES		Acanthocardia tuberculata	Anomia ephippium	Arctica islandica	Callista chione	Cerastoderma edule	Eastonia rugosa	Hiatella arctica	Irus irus	Mimachlamys varia
Substrate	Mud	Absent	Absent	Ausente	Ausente	Absent	Absent	Absent	Absent	Absent
	Sandy mud and muddy sand	Common	Absent	Common	Characteristic	Characteristic	Absent	Absent	Absent	Absent
	Sand	Common	Absent	Common	Characteristic	Facies	Common	Absent	Absent	Absent
	Gravelly sand	Common	Absent	Absent	Absent	Absent	Common	Absent	Absent	Absent
	Gravels and bioclasts	Absent	Común	Absent	Characteristic	Absent	Absent	Rare	Absent	Absent
	Phanerogams	Absent	Absent	Absent	Absent	Characteristic	Absent	Absent	Absent	Absent
	Rock	Absent	Común	Absent	Absent	Absent	Absent	Characteristic	Characteristic	Characteristic

PARAMETER/SPECIES		Mytilus galloprovincialis	Ostrea edulis	Petricola lithophaga	Pholas dactylus	Raditapes decussatus	Scrobicularia plana	Solen marginatus	Striarca lactea	Antalis vulgaris
Coastline	Exposed	Characteristic	Common	Characteristic	Common	Absent	Rare	Common	Characteristic	Common
	Protected	Characteristic	Common	Absent	Common	Common	Common	Common	Absent	Common
	Estuary	Characteristic	Absent	Absent	Common	Characteristic	Facies	Characteristic	Absent	Absent

Table 4 (continued)

PARAMETER/SPECIES		Acanthocardia tuberculata	Anomia ephippium	Arctica islandica	Callista chione	Cerastoderma edule	Eastonia rugosa	Hiatella arctica	Irus irus	Mimachlamys varia
Zoning	Supralittoral	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
	Upper mesolittoral	Common	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
	Lower mesolittoral	Characteristic	Common	Common	Common	Characteristic	Facies	Characteristic	Común	Absent
	Shallow infralittoral	Characteristic	Common	Common	Common	Common	Common	Common	Characteristic	Common
	Deep infralittoral	Absent	Common	Characteristic	Absent	Absent	Common	Common	Characteristic	Common
	Circalittoral	Absent	Common	Common	Absent	Absent	Rare	Absent	Common	Rare
Substrate	Mud	Absent	Absent	Absent	Absent	Ausente	Facies	Absent	Absent	Absent
	Sandy mud and muddy sand	Absent	Absent	Absent	Absent	Characteristic	Common	Characteristic	Absent	Common
	Sand	Absent	Absent	Absent	Absent	Characteristic	Absent	Characteristic	Absent	Absent
	Gravelly sand	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
	Gravels and bioclasts	Rare	Common	Absent	Absent	Absent	Absent	Absent	Absent	Common
	Phanerogams	Absent	Absent	Absent	Absent	Characteristic	Characteristic	Absent	Common	Common
	Rock	Characteristic	Common	Characteristic	Characteristic	Absent	Absent	Absent	Characteristic	Absent
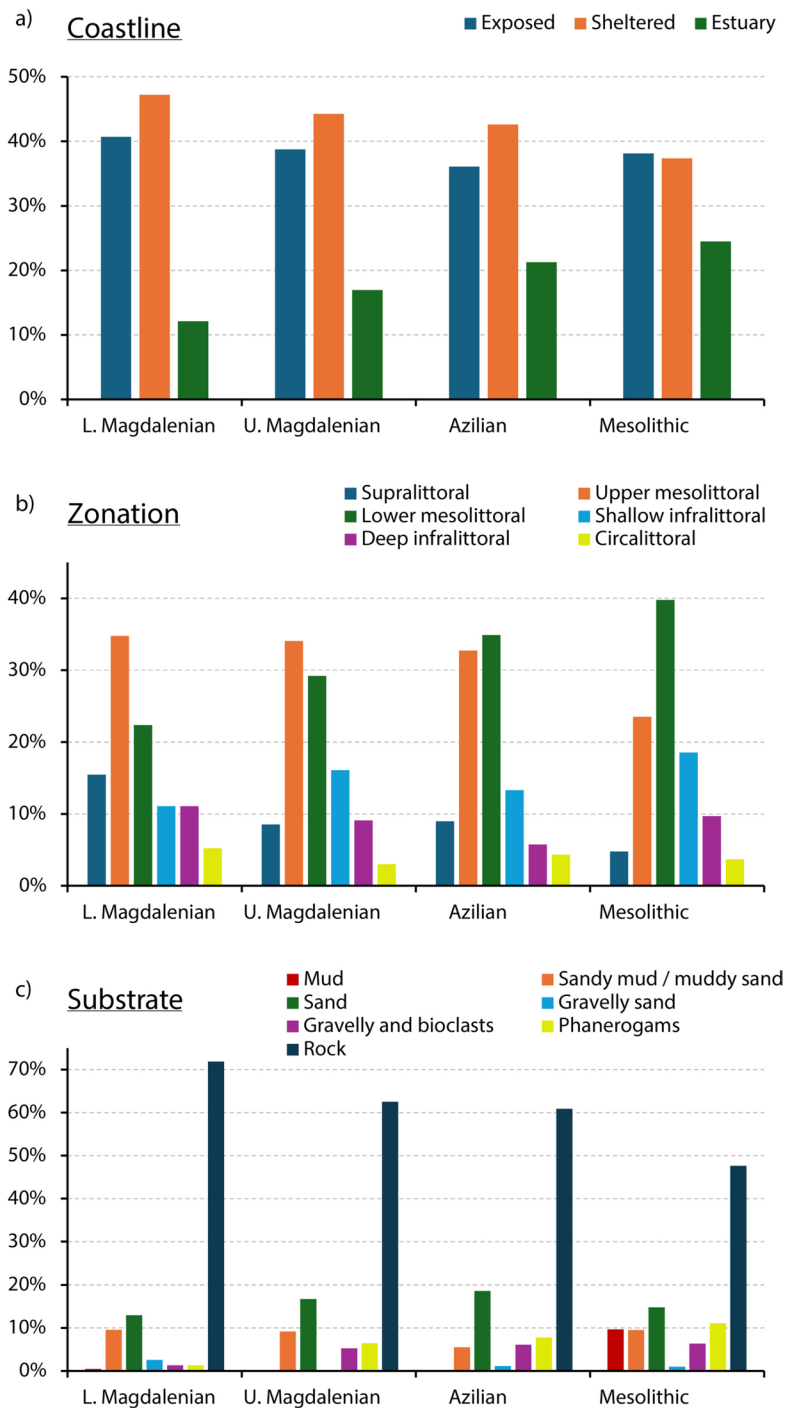
Fig. 3 Collection areas from the Lower Magdalenian to the Mesolithic in northern Iberia. a) type of coastline, b) zonation, c) substrate

44%, respectively. As in the Lower Magdalenian, the collection of molluscs was predominantly carried out in the mesolittoral zone (63%), while the average contribution of shallow infralittoral species increased slightly compared to the previous period (16%). Rocky shores continue to be the dominant substrate (62%). However, the percentages vary from 43% in Peña del Perro to 83% in La Riera, which presents the lowest percentages of taxa associated with sandy-muddy substrates in this period (16%) (Supplementary Material 2).

Sheltered coastlines remain the most heavily exploited environments during the Azilian (43%) compared to the most exposed coastlines (36%), while estuaries increase their importance (21%) in relation to the Lower and Upper Magdalenian (15% and 17%, respectively). The contribution of estuarine species reaches 26%−28% in La Riera and Peña del Perro, respectively. Some additional differences were detected in the zonation, as collection in the lower mesolittoral zone (35%) increased appreciably compared to the previous stages. Rock-associated species remain dominant (61%).

During the Mesolithic exposed and protected coasts were exploited in a similar way (38% and 37%, respectively), while collection in estuaries increased slightly (24%). The representation of the lower mesolittoral (40%) and the shallow infralittoral (19%) also increased, with both strips together showing almost 60% probability as a common shellfishing zone. In this period the representation of rocky substrates (48%) becomes lower than the set of sedimentary substrates, exhibiting a noticeable increase in the diversity of collection environments. Thus, an increase in the exploitation of muddy substrates (10%) and phanerogam meadows (11%) is observed, compared to previous periods. Moreover, two groups of Mesolithic shell middens are distinguished: one group including the sites located to the west (La Riera, El Mazo, El Toral III) and a second group with eastern sites (Peña del Perro, La Garma, J3, El Carabión, La Chora and El Truchiro). In the eastern group there is a greater representation of estuaries as collection areas (28%), compared to the westernmost group (17%). Furthermore, in the eastern shell middens there is a predominance of the lower mesolittoral zone (44%) compared to the western ones (32%). Finally, the westernmost group shows higher percentages of rocky substrate (54%) compared to the eastern shell middens (44%). This reduction in the presence of rocky substrate is due to a notable increase in muddy substrates (12%, compared to 4% in the western locations). In the Upper Magdalenian and Azilian there is no representation of muddy substrate, and in the Lower Magdalenian its presence is testimonial (0.36%).

Estuaries As Collection Areas

The increase in mollusc collection from sandy and muddy substrates in the Mesolithic is related to the flooding process of the current estuaries that started in the region around 8–7 kys cal BP due to stabilisation of sea level rise (Leorri *et al*., 2012). For the Upper Palaeolithic there is no available information about the occurrence of estuaries in the region or about their characteristics. Nevertheless, the limited presence of estuarine species, especially those inhabiting muddy or sandy substrates, suggests that: i) estuarine environments were different to the current

ones with less presence of muddy substrate or ii) human populations did not target those environments when collecting shells. The first hypothesis introduces significant environmental implications, suggesting the existence of differences in coastal morphology through time due to the climate changes that occurred during the Pleistocene-Holocene transition in the region. The second hypothesis has important implications for the interpretation of collection strategies through time, suggesting that human populations diversified the collection areas during the Mesolithic. This diversification has been previously related to the intensification in the use of coastal resources in the region during the Mesolithic (García-Escárzaga *et al*., 2022a; Gutiérrez-Zugasti, 2011b). The geographical variability in collection areas during the Mesolithic is due to the different coastal morphology in the studied areas. In western locations, selected archaeological sites are mainly located in open coast areas dominated by rocky substrates (*e.g*. the classical Asturian area, represented here by sites as La Riera, El Mazo and El Toral III), while some of the sites located in eastern locations are closer to estuarine environments (*e.g*. El Carabión and La Chora, located around 4–5 km from the upper estuary of the Asón river).

The high productivity of estuarine areas could be used by human groups to cover greater food demand in response to demographic increase in the region, especially after 8 kys cal BP (Clark & Barton, 2022; Fernández-López de Pablo, 2019). This would explain the consolidation of these new gathering areas linked to the evolutionary history of coastal settlements (Stiner *et al*., 1999).

The presence of estuarine species in shell middens implies an important technological advance as their biology is very different from those of rocky environments and they require different shellfishing techniques. Estuarine environments are characterized by the abundance of molluscs among the endofauna, mainly bivalves that live buried in muddy substratum, such as such as *Ruditapes decussatus, Scrobicularia plana* and *Solen marginatus*. The collection of these species is linked to technical advancement, as tools are needed for digging (*e.g*. hoes, rakes or shovels). Besides, their collection requires a better knowledge of the environment, including the identification of the marks left by some species in the sand-mud, such as the shape of grooved razor shell burrows.

Reassessing Collection Areas As Indicators of Intensification

The increase in mollusc collection from the lower mesolittoral of exposed shores has been previously related to the intensification of coastal resource exploitation during the Mesolithic (Gutiérrez-Zugasti, 2011b). Regarding this question, the use of TSM for the analysis of collection areas has provided more accurate results than previous methods, helping to clarify some aspects of the collection strategies. In terms of zonation, previous studies using methodologies based on ecological factors combined with the abundance of each species (Gutiérrez-Zugasti, 2009) identified larger collection in the upper mesolittoral from the Late Magdalenian to the Mesolithic, with a slight increase of collection in the lower mesolittoral during the latter period (Gutiérrez-Zugasti, 2009). However, the TSM revealed a gradual increase over time in the use of the lower mesolittoral, with a predominance of collection in this zone

during the Azilian, and especially during the Mesolithic, suggesting that intensification was a strategy that started, at least, in the Upper Palaeolithic. Data on Length/Height ratios from the limpet *P. vulgata* showed a similar pattern (Gutiérrez-Zugasti, 2009). Regarding the type of coastline, previous studies in northern Iberia have proposed an increase in the use of exposed shores over time based on the results of regression equations applied to *P. vulgata*. According to these studies, during the Late Magdalenian and the Azilian exposed and sheltered coasts were equally exploited, while during the Mesolithic *P. vulgata* was mostly collected in exposed shores, suggesting intensification in the collection of this species (Gutiérrez-Zugasti, 2009). However, when results from the TSM are considered, exposed shores were exploited in a similar way over the whole study period. Although it is possible that Mesolithic hunter-gatherer groups used varied collection strategies, targeting some species in specific environments (as in the case of *P. vulgata*, mainly collected from exposed shores), and others in more sheltered areas, these results might be biased by uncertainties related to the use of the regression equations in northern Iberia, as they were constructed using data from modern shells collected in Great Britain. In fact, when the exposure equation was tested with modern specimens of *P. vulgata* from northern Iberia, only 65% of the shells collected in exposed shores were correctly assigned to that type of shores (Gutiérrez-Zugasti, 2009). These results suggest that new methods should be implemented to establish a more accurate provenance of single mollusc species, such as *P. vulgata*, at least in terms of coastal exposure. New technologies, such as geometric morphometrics and artificial intelligence may be helpful for this task (Márquez & Espinosa, 2023; Zhang *et al*., 2019).

Potentials and Limitations of TSM

The highest potential of the Technical Scoring Matrices is their world-wide applicability, simply by adapting the matrix to the biogeographic region of interest. This is possible because molluscs are present in all coastal ecosystems and their ecology is well known. For this reason, they are used to characterise marine communities together with other organisms. The matrices need to be adapted to specific biogeographic regions for several reasons. First, because some species can be ubiquitous, showing different degrees of occupation for different habitats according to their affinity to the type of coastline, zonation and the type of substrate (occupation categories). In addition, each biogeographic region has a characteristic fauna with a specific ecology, although some species (ubiquists and non- ubiquitous) can occupy large areas that include different biogeographic regions with different ecological preferences for the same species. Thus, the affinity of molluscs for their reference habitats may vary in each region. For example, an amphi-Atlantic species may have a different bathymetric distribution on both sides of the Atlantic, or the zonation of the same species may vary depending on the tidal amplitude between a meso-tidal (*e.g.* Cantabrian Region) or micro-tidal (*e.g.* Mediterranean) coast.

Among the limitations, it is necessary to discriminate those species present in an archaeological shell assemblage that come from distant regions and therefore are not

representative of the collection area. This is the case of non-native species coming from exchange of goods or from the thanatocoenosis of shells washed ashore. To differentiate these shells, it is necessary to rely on the geographical distribution of the species, the palaeoecological information and the taphonomic analysis.

The state of preservation is usually an important limiting factor when analyzing archaeological shells. The TSM is a qualitative tool that exclusively uses data on the presence/absence of molluscs and converts this data into probability values. Therefore, an important strength of this methodology is that it can be applied to highly fragmented shell assemblages. Besides, this new method does not use abundance indices or morphometric values since the estimation of collection areas is based on the ecology of the species. However, it must be considered that shell fragments must be taxonomically identified to species level, which can be critical, especially in highly fragmented assemblages. Besides, certain taphonomic processes, such as abrasion, carbonization, biodegradation or bioerosion can also hinder taxonomic identification. Finally, it must be also noted that the independence of the method with respect to abundance indices and morphometric data facilitates and simplifies the estimation of collection areas with respect to other methods.

Conclusions

1. The Technical Scoring Matrix (TSM) is a powerful tool for the estimation of marine mollusc collection areas based on the identification of their source habitats. This identification is possible by assigning probability values to the possible habitats of each species. Compared to the previous methods, this new methodology provides a more precise characterisation of shellfishing areas based on the definition of habitat categories from the mollusc species identified in archaeological sites.

2. The new methodology presented here can be applied in any biogeographic region and over an extensive period of time, but each TSM must refer to a specific geographical area, since the biology of the same species can vary according to the region of study. The design of these matrices requires a solid knowledge of molluscs ecology, but once designed, its use is very simple and the same matrix can be applied to all the shell middens in the same region. In addition, as the process of speciation or extinction in molluscs lasts between one and five million years (Gofas *et al.*, 2011), it would be possible to extend this methodology to older shells, up to the early Pliocene.

3. Regarding collection areas from the Lower Magdalenian to the Mesolithic in northern Iberia, shellfishing on exposed coasts was similar throughout the study period, while a gradual decrease in the exploitation of sheltered coasts is observed. On the contrary, collection in estuaries increased gradually throughout the sequence, reaching its maximum in the Mesolithic. As for the zonation, the upper mesolittoral predominated as a collection zone during the Lower and Upper Magdalenian, while from the Azilian onwards, and especially during the Mesolithic, the harvesting in the lower mesolittoral predominated. The rest of the areas were exploited in a similar way throughout the sequence, although with slight variations. As for the substratum, rocky zones predominated in all periods, although a decrease is observed over time. The rest of the substrates have been frequented in a similar way in all

periods, although the appearance of mud zones during the Mesolithic is noteworthy, as a result of the formation and exploitation of the estuaries. Higher diversification in collection areas and larger collection in lower shores over time suggest that intensification started in the Upper Palaeolithic and increased in the Mesolithic.

4. Estuaries are highly productive environments (Hofrichter, 2004 and Pérez, 2014), so they can provide a large volume of resources. Moreover, their incorporation into the collection areas imply the appearance of new species and explains the diversification of marine mollusc collection during the Mesolithic. Besides, tools are needed for collection of these new species from sandy and muddy substrates, suggesting the introduction of new collection technologies.

5. TSM and other methodologies showed some discrepancies, especially with data from collection areas established for a single species, such as *P. vulgata*. These results suggest that new species-specific methods should be implemented to establish collection areas.

Declarations

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