



# Diversity, distribution and ecology of benthic molluscan communities on the Portuguese continental shelf



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## ABSTRACT

The diversity, ecology and distribution patterns of the Portuguese continental shelf malacofauna and its relationship with abiotic factors were studied from samples covering the western and the southern coast. A total of 2544 specimens were identified corresponding to 169 taxa, mostly bivalves (62% of the total taxa). *Abra alba* was the most abundant and the most frequent species. The  $\alpha$  diversity ranged from one species to 21 spp.  $0.1 \text{ m}^{-2}$ . The highest abundance and diversity were obtained in coarser sediments. Multivariate analysis based on the abundance data identified five major malacological groups: (a) *Angulus pygmaeus* and *Thracia villosiuscula* in the coarser sediments of the western inner and mid shelf; (b) *Calyptrea chinensis* and *Leptochiton cancellatus* in the heterogeneous and organically enriched sediments of the southern shelf; (c) *Angulus fabula*, *Spisula subtruncata* and *Pharus legumen* in the near shore exposed fine sands; (d) *A. alba* in muddy fine sands, mainly in the northwestern shelf and (e) *Saccella commutata* in the southwestern deeper shelf. The malacofauna could be used as a proxy for the major benthic communities known to occur in this area, except in muddy patches, where molluscs were absent or low abundant. Median grain-size, gravel content, depth and hydrodynamic regime were the environmental factors best related to the malacofauna spatial distribution patterns. This study sets the first record of *Astarte borealis*, *Leptochiton asellus*, *Mercenaria mercenaria* and *Montacuta phascolionis* in the Portuguese shelf and the most northern limit for *Anadara polii*, *Glycymeris nummaria*, and *Leptochiton algesirensis* along the northwestern shelf. This study also gives new ecological insights for several species, in terms of bathymetric range distribution, as well as habitat type and highlighted the transitional characteristics of the molluscan communities from this particular northeastern Atlantic area where boreal, temperate and subtropical faunas can coexist.

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## 1. Introduction

Studies of macrofaunal benthic communities are relevant to assess the biodiversity and the environmental status of the marine environment (e.g. Cacabelos et al., 2008; Koulouri et al., 2006). Benthic communities are well characterized in Portuguese lagoons (e.g. Quintino et al., 1987, 1989), estuaries (e.g. Moreira et al., 1993; Rodrigues and Quintino, 1993; Rodrigues et al., 2006, 2011), intertidal rocky shores (e.g. Araújo et al., 2005; Pereira et al., 2006; Saldanha, 1995), submarine canyons (e.g. Cunha et al., 2011; Cúrdia et al., 2004) and the continental shelf (e.g. Freitas et al., 2011; Marques, 1987; Martins et al., 2013a, 2013b, 2013c).

Within the benthic community, the phylum Mollusca is one of the most diverse and widespread in the marine environment (Rueda et al., 2009). Several works focused on the study of spatial and temporal malacofauna distribution patterns and used them as a surrogate of the whole benthic community (e.g. Cacabelos et al., 2008; Quintino et al., 1986; Rufino et al., 2008, 2010; Urra et al., 2013; Zenetos, 1996). Coastal molluscs (mostly bivalves) also represent an important economic

resource, being widely exploited in Portugal (Gaspar et al., 2003). Nearly 1600 marine mollusk species are mentioned for the Portuguese coast (Macedo et al., 1999), but no dedicated studies were carried out regarding the diversity of molluscs of the entire Portuguese shelf. This area has a particular ecological and biogeographic interest (Saldanha, 1995), since it corresponds to the majority of the Western and part of the Southwestern Iberian coast, a region of contact between warmer waters from northern Africa and the Mediterranean Sea and colder waters from the North Atlantic (Fiúza, 1983). The area between the latitudes 38° and 40° N mark the transition between two different climatic marine zones (thus, biogeographically distinct), both through the pre-glacial Pliocene, before 3.0 Ma, as well as at the Present-day (Silva et al., 2006, 2010; Monegatti and Raffi, 2007). Furthermore, the Portuguese shelf is dissected by several canyons, important morphological and sedimentary boundaries (Oliveira et al., 2007), and presents a variety of hydrodynamic conditions (Bettencourt et al., 2004) and sediment types (Martins et al., 2012), which increase the probability of occurrence of different faunas.

The scope of the present study was to characterize the diversity and distribution of molluscan communities on the Portuguese continental shelf, to give new insights about the ecology of some mollusk species and to discuss the relationships between the environmental and biological data and its potential use as a surrogate of the overall fauna.

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## 2. Material and methods

### 2.1. Study area

This study was conducted on the entire Portuguese continental shelf, from Caminha (41° 51.8' N, 9° 15.6' W) to Vila Real Santo António (36° 56.1' N, 7° 24.7' W), covering the majority of the Western and the South-western Iberia (Fig. 1). A total of 145 sampling sites were positioned in a regular grid of perpendicular lines to the coastline, separated from each other 10 to 15 km (Fig. 1) and stratified by depth (<50 m, 50 m, 100 m, >100 m), ranging from 13 to 195 m water depth. The sites were

distributed over the entire survey area in order to cover as much as possible the whole range of potential benthic habitats. At each site, two 0.1 m<sup>2</sup> Smith-McIntyre grab samples were collected, one for macrofauna and the other for baseline sediment analyses (grain-size and total organic matter content (TOM)). The samples for macrofaunal analyses were sieved on board over 1 mm mesh size and the residue fixed in neutralized formalin (4%) stained with rose Bengal. The detailed grain-size results and the spatial distribution of superficial sediments were given in Martins et al. (2012). The spatial distribution of the sediment fine content and TOM is shown in Fig. 1. Coarser sediments with less than 5% fines content were dominant in the northwestern inner and mid shelf sector

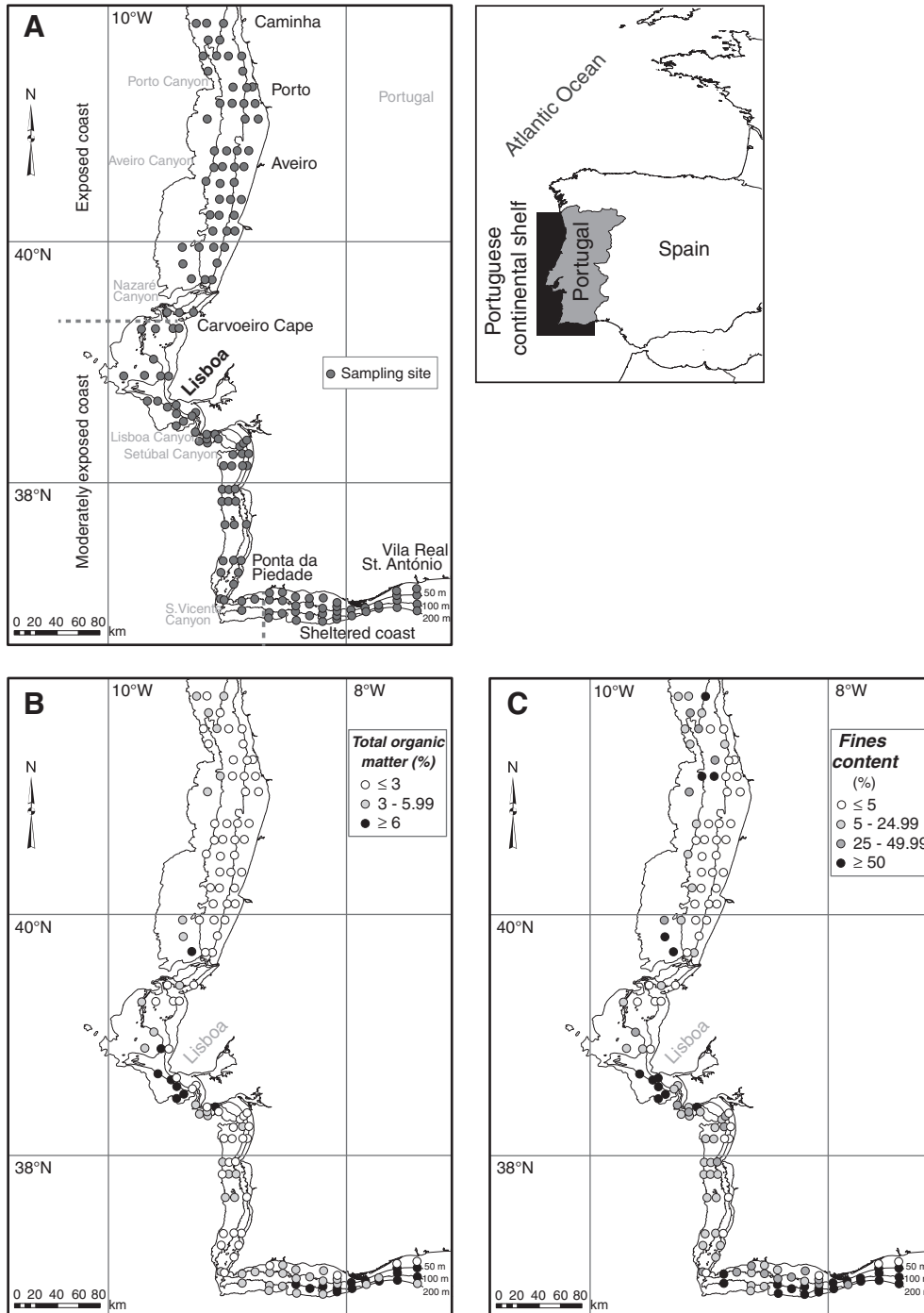


Fig. 1. Study area: the Portuguese continental shelf (Western Iberia) showing the coastal hydrodynamic regime subdivisions according to Bettencourt et al. (2004) (A), and the distribution of sediment total organic matter content (B) and fines content (C).

and immediately south of the Nazaré and Setúbal Canyons. Fine and very fine sands with fine content ranging mainly between 5 and 25% occurred in the southwestern shelf sector and deeper than 80 m in the northwestern shelf. In the southern shelf, fine sands with high fines and organic matter content were prevalent in the western part while an extensive mud patch ruled the eastern part. Muddy areas were also identified in the western coast, on the shelves off the Tagus, Douro and Minho rivers. High correlation was found between total organic matter and sediment fines content (Spearman rho = 0.71).

## 2.2. Laboratory analysis

In the laboratory, the macrofaunal samples were rinsed with water through a 0.5 mm mesh sieve, hand sorted and the specimens preserved in ethyl alcohol (70%). Mollusks were identified to species level, whenever possible, following, namely Graham (1988), Macedo et al. (1999), Tebble (1976), and Thompson (1988). The validity of species name was checked in the WoRMS website (Bouchet and Gofas, 2013) and ecological preferences in those references and others considered suitable (e.g. Antoniadou et al., 2005; Ávila et al., 2008; Bouchet and Gofas, 2013; Duff et al., 2009; Krylova, 2006; Prena et al., 1999; Rodríguez and Sánchez, 1997).

Abundance, total species richness and *alpha* diversity (species richness per unit sampling area) were determined per site and mean values were obtained per sediment type, depth classes (<30 m; 30–60 m; 60–100 m; >100 m), for the western and southern coasts and for the entire coast.

The data matrix with the species abundance per site was square root transformed, and the similarity between sites calculated following the Kulczynski similarity coefficient (K), according to the expression

$$K_{(A,B)} = \frac{1}{2} \left( \frac{W}{A} + \frac{W}{B} \right)$$

where A and B correspond to the total abundance of samples A and B, and W to the sum of the minimum value of abundance of the common species to samples A and B (Legendre and Legendre, 1983). A dummy variable was added in the calculation of the similarity matrix to reduce the influence of samples with very low similarity with the others and therefore increase the redundancy. The resulting similarity matrix was submitted to agglomerative hierarchical clustering, using the unweighted pair-group mean average algorithm (UPGMA) and to ordination analysis using Non-Metric Multidimensional Scaling (NMDS), for the identification of biological affinity groups. These groups were characterized using the mean *alpha* diversity, total species richness, mean abundance, characteristic species, number of exclusive species and the sediment baseline data. The characteristic species were chosen from the set of species with highest product between constancy (sampling frequency) and fidelity (species preference) per affinity group. Constancy (C) classes were used according to Dajoz (1971) (constant, C > 50.0%; common, 50.0 ≥ C > 25.0%; occasional, 25.0 ≥ C > 12.5%; rare, C ≤ 12.5%) and fidelity (F) according to Retière (1979) (elective, F > 90.0%; preferential, 90 ≥ F > 66.6%; indifferent, 66.6 ≥ F > 33.3%; accessory, 33.3 ≥ F > 10.0%; accidental, F ≤ 10.0%). The relationship between the environmental and biological data was examined with the BIOENV procedure (BEST routine) based on the environmental variables (depth, median, gravel, sand, fines, biogenic fraction and TOM contents, hydrodynamic regime and latitude). The hydrodynamic regime categories were defined following the classification proposed for the Portuguese coast by Bettencourt et al. (2004); (1 – sheltered Atlantic coast, from Ponta da Piedade to Vila Real de Santo António, most of the southern coast; 2 – moderately exposed Atlantic coast, from Cape Carvoeiro to Ponta da Piedade, corresponding mostly to the southwestern coast; 3 – exposed Atlantic coast, from the northern Portuguese border to Cape Carvoeiro, in the northwestern coast).

All the multivariate analyses were performed with PRIMER v.6 (Clarke and Gorley, 2006). Abundance and *alpha* diversity of each site, abundance of selected species (*Abra alba*, *Corbula gibba*, *Glycymeris glycymeris*, *Leptochiton cancellatus*, *Nassarius reticulatus*, *Saccella commutata*, *Thracia villosiuscula* and *Thyasira flexuosa*) and biological affinity groups were plotted in a GIS environment using ArcGIS 10 software. The latitudinal distribution of species occurring at least twice in the samples was spatially represented and compared to the literature and worldwide on-line databases (e.g. [www.marinespecies.org](http://www.marinespecies.org), [www.marbef.org](http://www.marbef.org), <http://naturalhistory.museumwales.ac.uk/britishbivalves>).

## 3. Results

### 3.1. Abundance and diversity gradients

A total of 2544 specimens were analyzed corresponding to 169 molluscan taxa: two Aplousobranchia, two Scaphopoda, eight Polyplacophora, 53 Gastropoda and 105 Bivalvia. Abundance ranged from one to 172 specimens per 0.1 m<sup>2</sup> (Fig. 2–A). From the 145 sites sampled, 13 had no mollusks (Fig. 2–A), similar to the results obtained for Arthropods (crustaceans), but much more than Annelids (one site without specimens; Table 1). *Alpha* diversity per sampling site ranged from one to 21 molluscan species (Fig. 2–B), which is lower than arthropods or annelids (Table 1). In terms of sediment types, the highest mean abundance and mean *alpha* diversity was found in gravel (49.6 ind., 11.1 spp. 0.1 m<sup>-2</sup>), the highest total species richness was found in fine sand (89 spp.), while mud presented the lowest values for all measurements (6.7 ind. 0.1 m<sup>-2</sup>, 2.3 spp. 0.1 m<sup>-2</sup>, 37 spp. respectively). Mean *alpha* diversity, mean abundance and total species richness decreased from shallower to deeper bottoms, peaking between 30 and 60 m in the case of abundance and total species richness (25.0 ind. 0.1 m<sup>-2</sup>; 105 spp., respectively), probably associated to the prevalence of coarse sediments in the mid-shelf and fine sands in the near shore shelf. The southern shelf presented half of the mean abundance of the western shelf (9.6 and 20.6 ind. 0.1 m<sup>-2</sup>, respectively) and lower mean *alpha* diversity (5.3 and 6.8 spp. 0.1 m<sup>-2</sup>, respectively). The most abundant species (N > 100 ind. 0.1 m<sup>-2</sup>) were *A. alba*, *T. villosiuscula*, *T. flexuosa*, *Kurtiella bidentata* and *C. gibba*. The most frequent species, occurring at least in 20 sites, were *A. alba*, *C. gibba*, *T. villosiuscula*, *S. commutata*, *Tellina compressa*, *T. flexuosa*, *Angulus pygmaeus*, *Fustiaria rubescens*, *Gouldia minima*, *Dosinia lupinus* and *Tellimya ferruginosa*.

### 3.2. Habitat preferences and abundance spatial distribution patterns

Table 2 summarizes the total abundance, total frequency, sediment types and bathymetric ranges of the mollusk species studied within the scope of this work (only taxa identified to species level were considered here). A total of 37 species was recorded exclusively in coarse sediment, mostly in the near shore and mid-shelf (e.g. *Digitaria digitaria*, *G. glycymeris*), 33 species in fine sand, mostly from the mid and the deepest shelf (e.g. *Bela fuscata*, *Serratina serrata*), three species in mud between 100 and 137 m (*Ecrobia truncata*, *Nassarius ovoideus*, *Ringicula buccinea*), two species in fine sand and mud from the mid-shelf (*Aporrhais pespelecani*, *Chaetopleura* (*Chaetopleura*) *angulata*), and 32 species in both coarse sediment and fine sand in a wide bathymetric range (e.g. *Arca tetragona*, *Clausinella fasciata*; Table 2). The remaining species were found in a variety of sediment types and bathymetric range. Some were more frequent and abundant in deeper finer sediments (e.g. *T. compressa*, *S. commutata*), others in shallower fine sands (e.g. *Angulus fabula*, *Spisula subtruncata*) or in shallower coarse sediments (e.g. *Chamelea striatula*, *Chamelea gallina*) (Table 2). A total of 15 species were recorded in maërl in the eastern part of the southern shelf, at 13 m water depth, being *L. cancellatus* the most abundant. The species *Centrocardita aculeata*, *Chiton* (*Rhyssoplax*) *olivaceus*, *Ocenebra erinaceus*

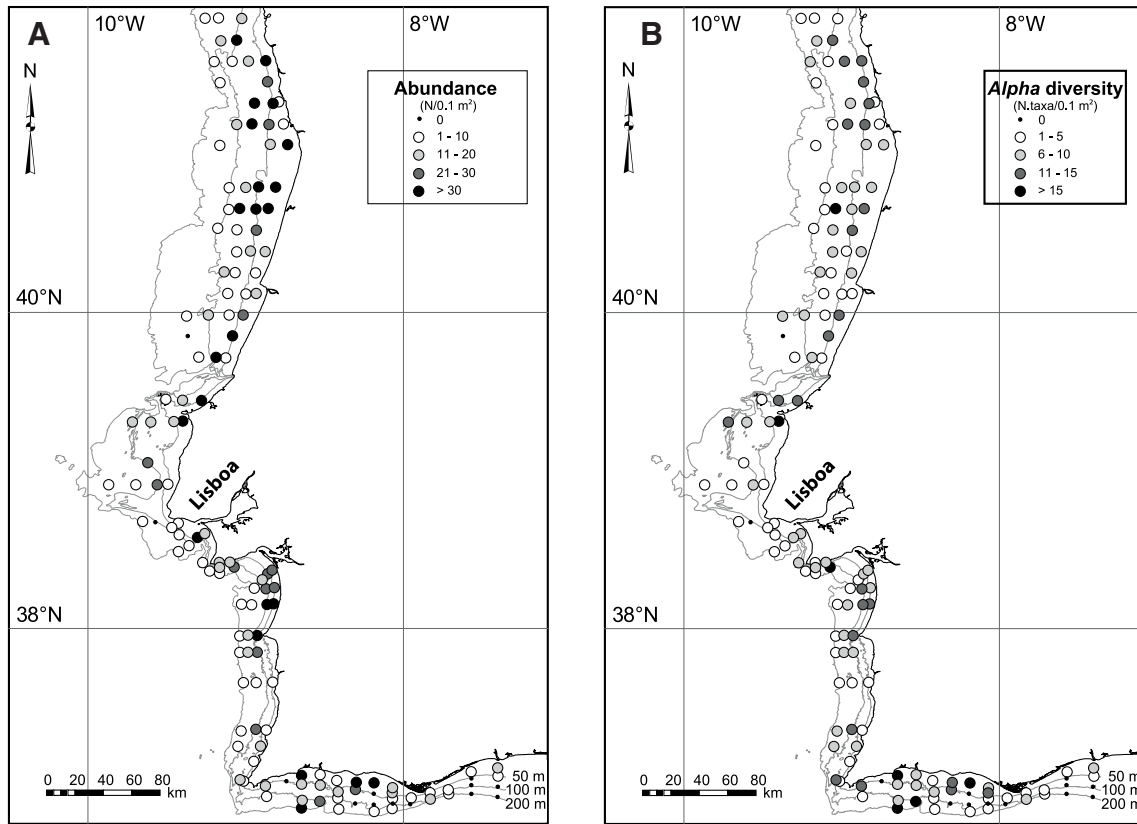


Fig. 2. Spatial distribution of Mollusk abundance (A) and  $\alpha$  diversity (B) in the Portuguese continental shelf.

and *Rocellaria dubia* were exclusively recorded in that type of substrate (Table 2).

The latitudinal distribution range of species that occurred at least twice in the samples is shown in Fig. 3. Fig. 4 shows the abundance spatial distribution of selected species. Overall, the majority of the most frequent species occurred along the entire shelf (Fig. 3) apart from *A. pygmaeus* that occurred exclusively in the coarser sediments of the northwestern shelf and at the head of Setúbal canyon, and *T. ferruginosa* only recorded along the western shelf. Species with wider spatial distribution (Fig. 3) showed however higher abundance values in some specific areas: (a) in the northwestern moderately deep fine sediments (e.g. *T. flexuosa*, Fig. 4–A, *A. alba*, Fig. 4–B, *C. gibba*, Fig. 4–C, up to 43, 36 and 28 ind.  $0.1\text{ m}^{-2}$ , respectively); (b) in the northwestern mid-shelf coarser sediments (e.g. *T. villosiuscula*, Fig. 4–D, up to 20 ind.  $0.1\text{ m}^{-2}$ ); (c) in the northwestern nearshore shelf (e.g. *N. reticulatus*, Fig. 4–E, up to eight ind.  $0.1\text{ m}^{-2}$ ); (d) in the

southwestern deepest shelf (e.g. *S. commutata*, Fig. 4–F, up to 11 ind.  $0.1\text{ m}^{-2}$ ). Other species showed more restricted spatial distributions (Fig. 3): (a) exclusively in the northwestern shelf sector, up to Nazaré or Lisbon canyons (e.g. *G. glycymeris*, Fig. 4–G); (b) in the western shelf sector, from the northern border up to the Setúbal canyon (e.g. *D. digitaria*); (c) exclusively in the southwestern shelf (e.g. *Yoldiella philippiana*); (d) from off Peniche to the southern shelf, but more frequent in the southwestern shelf (e.g. *Aplocophora* sp.); (e) from off Aveiro (e.g. *Leptochiton algesirensis*, Fig. 4–H) or from off north of Lisbon (e.g. *Anadara polii*) to the southern shelf (with higher abundance in this sector); (f) from the Setúbal canyon to the southern shelf (e.g. *Calyptrea chinensis*); (h) exclusively in the southern shelf (e.g. *Glans trapezia* among other 37 species).

### 3.3. Multivariate analysis

The multivariate analysis of the abundance data is shown in Fig. 5 and the spatial representation of the affinity groups in Fig. 6. Five mollusk communities were identified: A, B1, B2.1, B2.2.1 and B2.2.2 (Figs. 5 and 6). Five sites appeared isolated due to their particular species composition and low abundance. NMDS horizontal dimension (Fig. 5–B) opposed the sites from groups B2.2.1 and B2.2.2 to the sites of group A. Axis 1 was high correlated with fines content, median grain-size, depth, total organic matter content, and gravel content (Spearman  $\rho = 0.60, 0.59, 0.58, 0.58,$  and  $-0.49$ , respectively), separating the coarser sediments (group A) from the organically enriched finer sediments (groups B2.2.1 and B2.2.2). NMDS vertical dimension separated B2.1 with B2.2.1 from B1 with B2.2.2. Axis 2 discriminated shallower and other sites located in the northern and exposed shelf sectors, from sites in the southern and sheltered sectors. This axis showed high correlation with hydrodynamic regime areas, latitude and biogenic fraction (Spearman  $\rho = 0.50, 0.48, -0.44$ ). The most correlated species (Spearman  $\rho > 0.35$ ) were represented as vectors in Fig. 5. *T. villosiuscula* and *A. pygmaeus* were the species most correlated

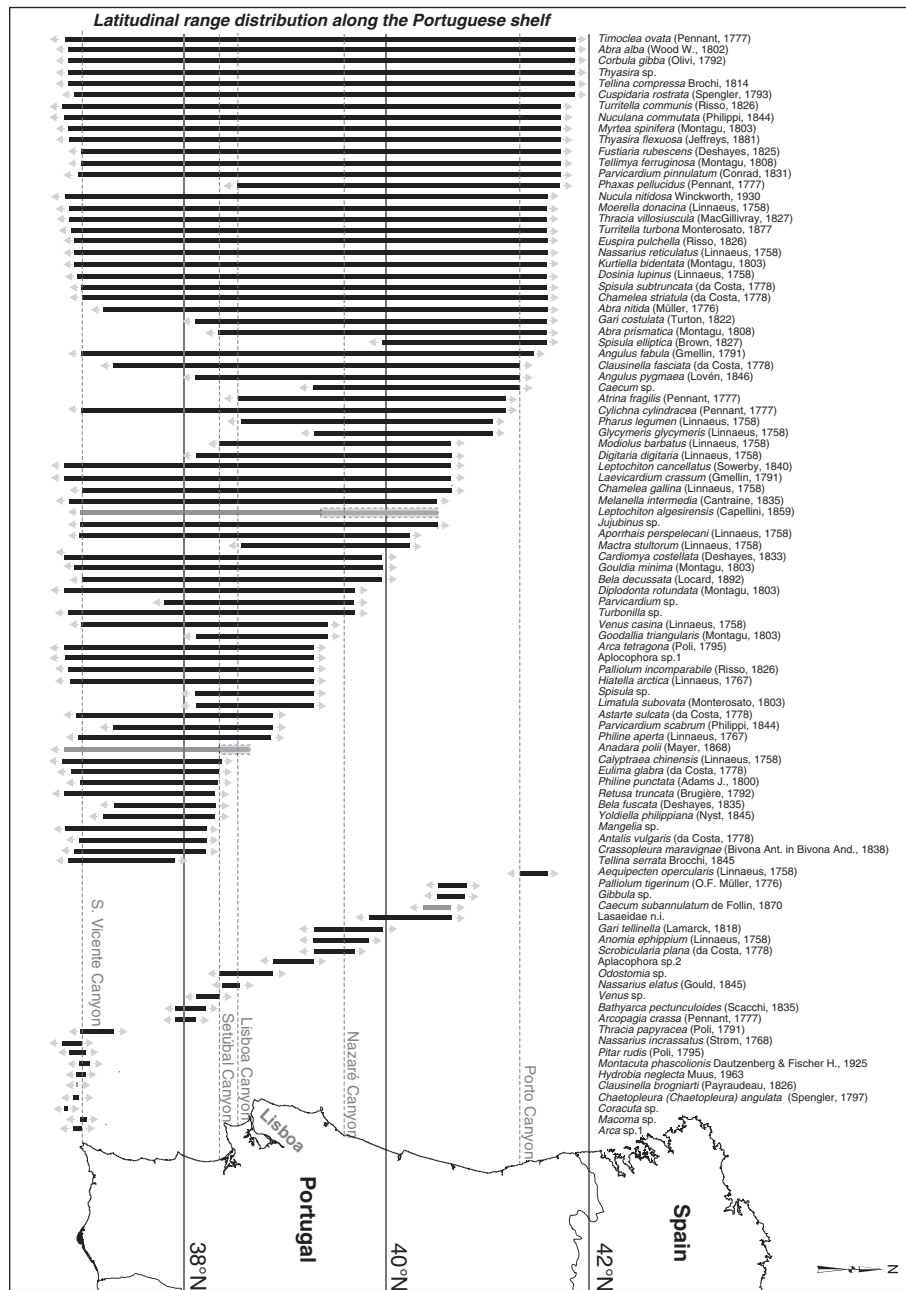
Table 1

Abundance and species richness of the major phyla and the whole benthic macrofauna in the Portuguese continental shelf sediments.

|  | Mollusks   | Annelids               | Arthropods<br>(crustaceans) | Macrofauna<br>(all)    |
|--|------------|------------------------|-----------------------------|------------------------|
| Nr. sites with individuals             | 132        | 144                    | 131                         | 145                    |
| Nr. sites without individuals          | 13         | 1                      | 14                          | 0                      |
| Total abundance                        | 2544       | 20,241                 | 2236                        | 30,008                 |
| Mean abundance/sample                  | 19.3       | 140.6                  | 17.1                        | 207.0                  |
| Range of abundance/sample              | 1–172      | 3–670                  | 1–141                       | 7–1307                 |
| Total species richness                 | 170        | 320                    | 195                         | 737                    |
| Mean $\alpha$ diversity/sample         | 7.0        | 29.4                   | 6.9                         | 45.8                   |
| Range of $\alpha$ diversity/<br>sample | 1–21       | 1–66                   | 1–30                        | 3–96                   |
| Reference                              | This study | Martins et al. (2013b) | This study                  | Martins et al. (2013a) |







**Fig. 3.** Latitudinal range distribution of Mollusk species along the Portuguese continental shelf. Gray arrows signify that the species is known to occur further north (▲) and/or further south (▼). Gray dashed show the proposed northern limit of the worldwide species distribution.

with group A, *S. commutata* and *Aplocophora* sp.1 with group B2.2.2, *T. compressa*, *Phaxas pellucidus* and *A. alba* with B2.2.1, *A. fabula* with B2.1 and *C. chinensis* with B1.

The environmental and biological characterization of the five mollusk communities is summarized in Tables 3 and 4. Group A included 27 sites, located mainly in areas with coarser sediments of the mid-western shelf (Fig. 6), characterized by the highest gravel and biogenic fraction content (Table 3). This group presented the highest mean species richness and mean abundance. The most abundant species was *T. villosiuscula*, while the most characteristic was *A. pygmaeus* (Tables 3 and 4). A total of 31 species were found exclusively here. This group matched community A obtained from the multivariate analysis based on the entire macrofauna dataset and in the polychaetes apart (Table 3).

Group B1 gathered 17 sites located on the southern shelf (Fig. 6), mostly mud and fine and very fine sand, characterized by the highest percentage of fines, TOM and biogenic fraction content (Table 3).

Mean species richness and mean abundance were moderately high (Table 3). *C. chinensis* and *L. cancellatus* were the most characteristic and most abundant species (Tables 3 and 4). The proportion of exclusive species was high (23/67; Table 3). It agreed mostly with group C3 obtained in the macrofauna study and group C2 from the polychaetes study (Table 3).

Group B2.1 comprised 13 sites mainly from the near shore shelf (Fig. 6). Sediments were mainly fine sand, with very high content of sand and very low TOM content (Table 3). Mean abundance was low and the mean species richness was the lowest. *Abra alba* was the most abundant and *Angulus fabula* the most characteristic species (Tables 3 and 4). This group resembled groups B and B1, based on the entire macrofauna and polychaetes only datasets.

Group B2.2.1 corresponded to 38 sites mainly located in the north-western outer shelf (Fig. 6). Fine and very fine sand and muds were the dominant sediments (Table 3). The mean species richness and

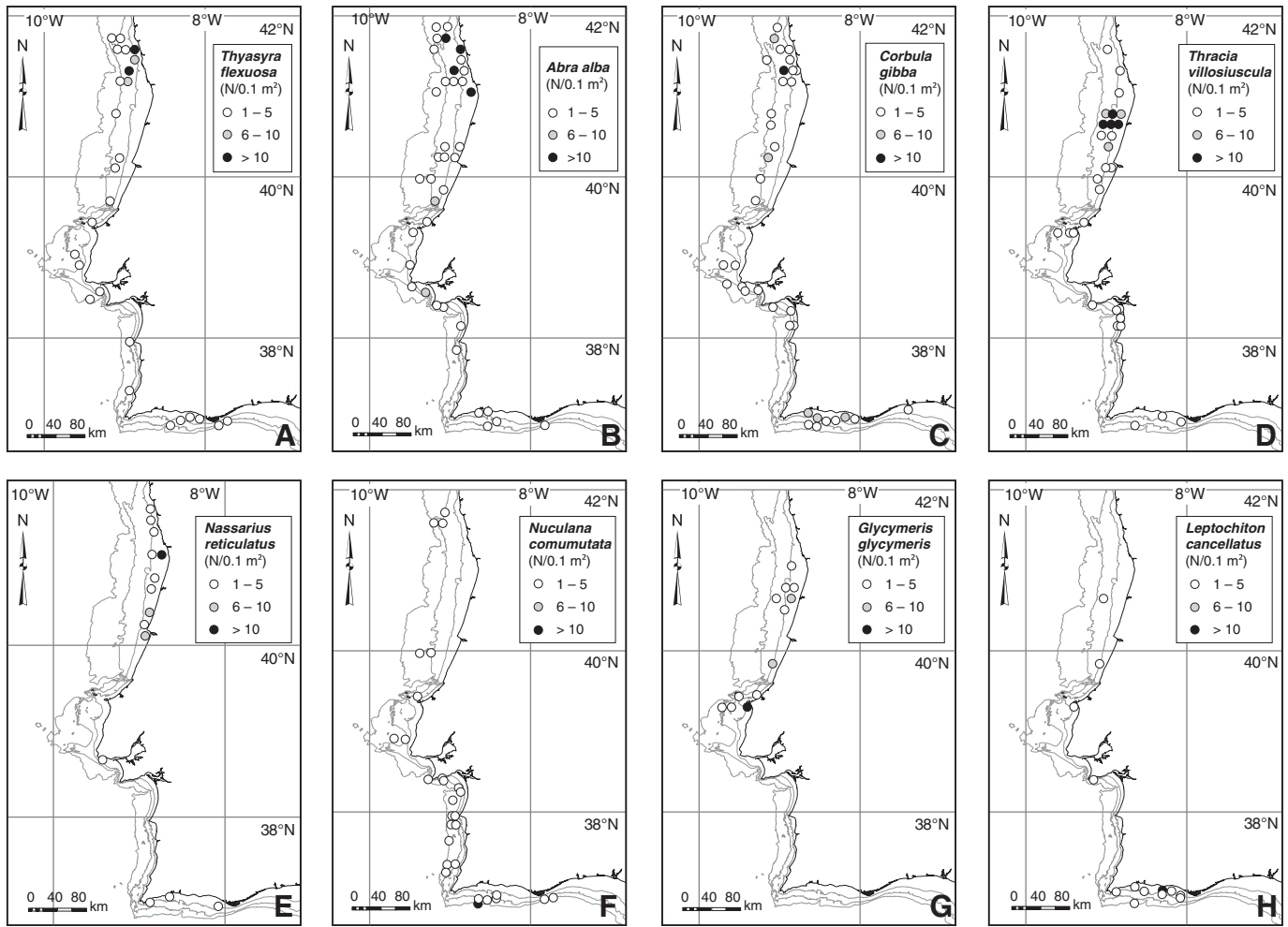


Fig. 4. Abundance spatial distribution patterns of selected species: *Thyasira flexuosa* (A), *Abra alba* (B), *Corbula gibba* (C) *Thracia villosiuscula* (D), *Glycymeris glycymeris* (E), *Nassarius reticulatus* (F), *Saccella commutata* (G) and *Leptochiton cancellatus* (H).

mean abundance were moderate compared to other groups (Table 3). *T. flexuosa* and *K. bidentata* were the most abundant and *T. compressa* and *A. alba* were the most characteristic species. A total of 16 species were exclusively recorded in this group (Table 3). This group was close to all muddy sand and muddy affinity groups found among the macrofauna (C1, C2, D and C3) and polychaetes (B2, C1, C3 and C2).

Group B2.2.2 gathered 32 sites, mostly deep and mainly located in the southwestern shelf (Fig. 6). Sediments were similar to group B2.2.1, mainly fine and very fine sand. Mean alpha diversity and mean abundance were moderate. *S. commutata* was the most abundant and characteristic species (Tables 3 and 4). Nineteen species were exclusively found here (Table 3). This community resembled the muddy sand groups C2 and C1 from macrofauna and polychaetes analyses, respectively.

The environmental variables best related to the biological data were depth, median, gravel content and hydrodynamic regime (BIOENV,  $\rho = 0.319$ ).

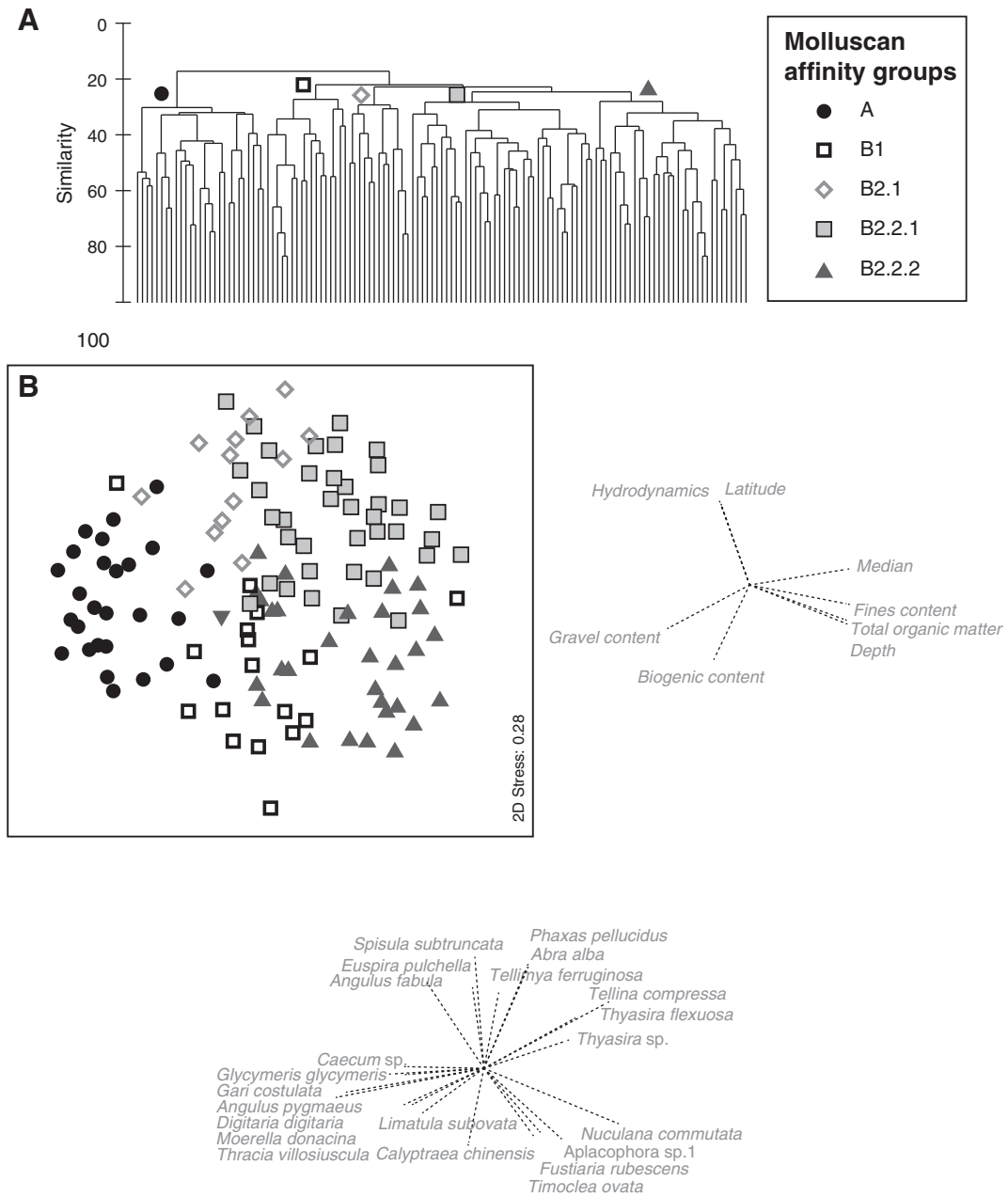
## 4. Discussion

### 4.1. Diversity and distribution patterns

The 169 molluscan taxa identified in the course of this work corresponded to 13% of the Western European malacological fauna (Narayanaswamy et al., 2010). Several studies focused on the molluscan fauna have been carried out in worldwide continental shelves (Table 5). Algae or seagrass meadows, maërl and other hard substrate types tend to be richer in species than soft-bottoms (e.g. Riera et al., 2012; Urra

et al., 2013). The lower species richness recorded in those works compared to the present study, may be related to the area sampled, which was much bigger in this work covering six latitudinal degrees. The species *Astarte borealis*, *Leptochiton asellus*, *Mercenaria mercenaria* and *Montacuta phascolionis*, are here firstly reported for the Portuguese continental shelf (Macedo et al., 1999). This work sets a new meridional distribution limit for *A. borealis* in the northwestern Portuguese shelf, known before for the Arctic and the northern Atlantic and Pacific. Hidalgo (1917) found *L. asellus* occurring on hard substrates in the Setúbal shore (SW Portugal). Nevertheless, Macedo et al. (1999) state that this species was not yet recorded either in the western or in the southern Portuguese coasts. The North American edible quahog clam *M. mercenaria* was introduced in Europe in the 19th Century, firstly in the United Kingdom and then all around Europe, from the British Isles to Morocco and the Mediterranean Sea. Macedo et al. (1999) do not recognized this species in the Portuguese fauna, despite the recent release from the Portuguese Government of the checklist of authorized commercial species, which includes this clam species. *M. phascolionis* is a commensal species well known in northern Europe and in the Mediterranean Sea. In the shallow southern continental shelf it was found in symbiosis with the polychaete *Syllis mercedesae* and the sipunculid *Phascolion (Phascolion) strombus strombus*, in empty gastropod shells. This ecological association may be new for science and was reported in Martins et al. (2013a). According to Macedo et al. (1999), *A. polii*, *Glycymeris nummaria* and *L. algesirensis* are southern species with their northern limit located off Setúbal (SW Portugal), off Portimão (S Portugal) and off Carvoeiro Cape (W Portugal), respectively. This study





**Fig. 5.** Classification (A) and ordination diagrams (NMDS, B) based on the abundance of mollusks. Spearman correlation vectors of environmental data and of the most correlated species ( $\rho > 0.35$ ) are provided as supplementary variables.

shows that these species have wider geographical distributions, being now recorded further north than previously known, in the northwestern shelf. This study also provides new ecological data, such as bathymetric distribution and substrate type preferences, for several species (Table 2). Based in the reports from Graham (1988), Macedo et al. (1999), Tebble (1976), Thompson (1988) among other references, this work sets new maximum depth ranges for 33 species (e.g. *A. alba*, *C. striatula*; full list identified as light gray in the depth column in Table 2) and defines bathymetric ranges for eight species, not given in those references (e.g. *Caecum subannulatum*, *M. phascalionis*; dark gray in the depth column in Table 2). Regarding species substrate preferences, this study gives new information for 17 species (e.g. *Bornia geoffroyi* in coarse sediment, *Ringicula auriculata* in finer sands, *R. buccinea* in mud; dark gray in the sediment types preferences column in Table 2). Sixteen molluscan species which were associated to hard substrate or seaweeds (e.g. Macedo et al., 1999; Tebble, 1976) were here firstly reported in soft bottoms, such as *Caecum subannulatum* in very coarse sand or

*Hanleya hanleyi* in very fine sand (light gray in the sediment types preferences column in Table 2). *Eulima glabra* and *Melanella polita*, living parasite species of echinoderms (Macedo et al., 1999), were found in coarse sediments and fine sands without echinoderms (Table 2). In several cases, the substrate preference range was widened and now several species are also known to live in mud (*Cylichna cylindracea*), in finer sand (e.g. *Jolya martorelli*) or in coarse sediment (e.g. *Philine punctata*; Table 2). No previously published data existed regarding mollusks inhabiting maërl in the Portuguese territory. From the 15 species found in this study (Table 2), two were reported for this substrate for the first time, namely *K. bidentata* and *C. (Rhyssoplax) olivaceus* (e.g. Antoniadou et al., 2005; Grall and Hall-Spencer, 2003; Riera et al., 2012). Maërl beds, which correspond to accumulations of dead and live unattached coralline algae, such as *Phymatolithon calcareum*, supports a highly diverse community having a relevant ecological and economic importance, namely mollusks, which are commercially exploited (Grall and Hall-Spencer, 2003). As it was recognized in the EU Habitats Directive

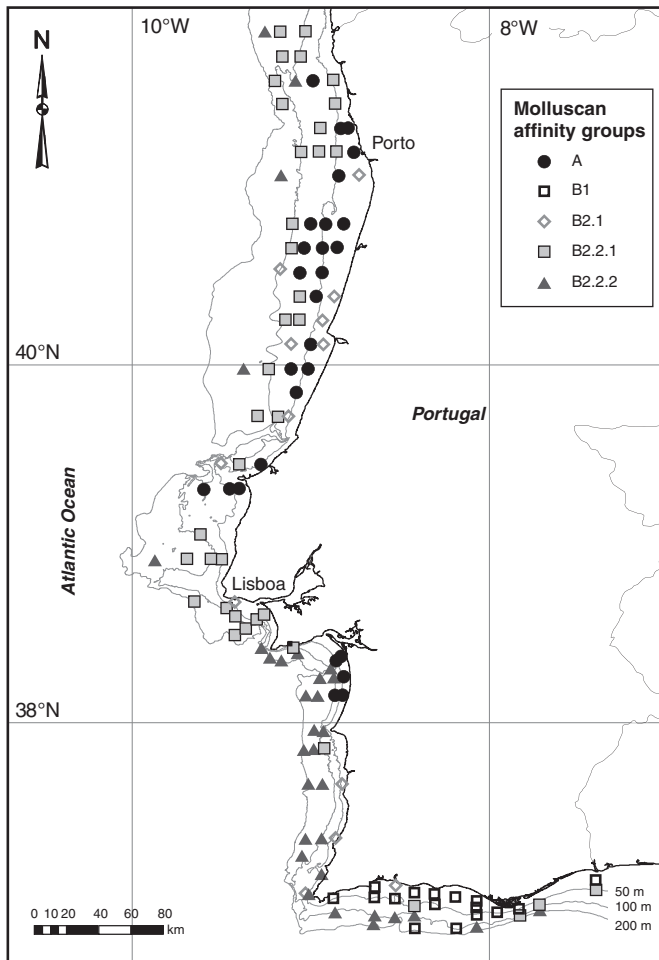


Fig. 6. Spatial distribution of the mollusk communities in the Portuguese continental shelf.

and OSPAR, this is one of the most threatened marine habitats of Europe (Riera et al., 2012).

The highest molluscan diversity and abundance was recorded in the coarse sediments of the western Portuguese shelf. In the northwest (between Porto and south of Aveiro) and the southern Portuguese nearshore coasts, molluscan banks are exploited, mainly the surf clam, *Spisula solida* (Gaspar et al., 2004, 2005). Other species (e.g. *G. glycymeris*) are also occasionally taken for the canning industry (Gaspar et al., 2004, 2005). Bivalve dredge fishing is one of the most important fishing activities undertaken in southern Portugal (Pereira et al., 2007). The Portuguese Fisheries Institute regularly assesses the conservation status of the exploited dredge banks (e.g. Gaspar et al., 2004, 2005), and in the course of this study the following species were identified from the list of the most abundant species occurring there: striped venus (*C. gallina* and *C. striatula*), the Norwegian egg cockle (*Laevicardium crassum*), the mature dosinia (*Dosinia exoleta*), the bean solen (*Pharus legumen*), the big telina (*Arcopagia crassa*), the banded venus (*C. fasciata*) and the dog cockle (*G. glycymeris*).

#### 4.2. Benthic macrofauna communities

This study identified five main molluscan communities. The *A. pygmaeus* community (group A), recorded in coarser sediments, corresponded to a Lusitanian version of the well-known *Venus* community (*Venus fasciata* (now *Clausinella*) – *Spisula elliptica*; Thorson, 1957) or to the French Atlantic gravels of *Astarte sulcata* – *Venus*

*casina* (Glémarec, 1973). These key northern species showed low abundance in this study, being replaced by others with Lusitanian and/or Mediterranean biogeographic preferential affinity (e.g. *A. pygmaeus*, *C. subannulatum*, *C. gallina*, *Gari costulata*, *Gari tellinella*). This community was identified as the western Portuguese shelf coarse sediments, with *Protodorvillea kefersteini*, *Pisone remota*, *A. pygmaeus* and several other interstitial species (Martins et al., 2013b, 2013c).

The *C. chinensis* and *L. cancellatus* community in mud and finer sands of the southern coast (group B1) showed few resemblances with other communities. The most similar could be a sandy mud circalittoral community described in Italy (shared species: *C. chinensis* and *C. gibba*) or the Mediterranean biocenosis of coastal detritic bottoms (shared species: *Pitar rudis*; Picard, 1965), or the coastal and the offshore detritic biocenosis from the southern Portuguese shelf with *C. gibba* or the infralittoral sands biocenosis with *C. chinensis*, described by Marques (1987). The difficulty in matching our communities with others may be due to the reduced spatial resolution used in this study (a more detailed spatial coverage could change the current image) or to seasonal variations. A southern community was also found in previous studies by Martins et al. (2013b, 2013c).

The *A. fabula* community (group B2.1), occurring predominantly in fine sand at shallow depth, corresponded to the Northern European community *Angulus tenuis* and *A. fabula* (formerly *Tellina*) defined by Thorson (1957), to the well sorted fine sands from the French Mediterranean coast (Picard, 1965), and to the recently described Portuguese near shore fine sands with *Magelona johnstoni*, *Urothoe pulchella* and *A. fabula* (Martins et al., 2013b, 2013c). This community presented fewer species and specimens than others herein described, possibly due to the strong influence of waves and currents near the coast, which is in agreement with descriptions of equivalent communities elsewhere (Picard, 1965).

The *T. compressa* and *A. alba* community in the deep northwestern shelf (group B2.2.1) is widely reported for muddy fine sand habitats in Northern European coasts (Cacabelos et al., 2008; Glémarec, 1973; Moulart et al., 2007; Thorson, 1957), corresponding to the *A. alba* (formerly *Syndosmya*) community. It sets the most southern reference of this community in the northeastern Atlantic (e.g. Cacabelos et al., 2008; Moulart et al., 2007). This community however presented lower abundance and diversity than similar communities in northern latitudes. It also reflects a mixture of faunal communities already described in this shelf area, one for muds and other for muddy sands (Martins et al., 2013b, 2013c). The overall lower diversity and abundance of mollusks in finer sediment substrates (e.g. Glémarec, 1973; Picard, 1965) could explain this.

The *S. commutata* community in the deeper southwestern and southern shelf (group B2.2.2) was defined by a set of deep and southern species with others spanning a biogeographic distribution from the Boreal to Western African Transition provinces. This may explain why this community could not be easily ascribed to other European communities. This particular community shared the species *S. commutata* and *Timoclea ovata* with the Atlantic mixed sediments of *Nucula nucleus* and *P. rudis* of the open sea étage, described by Glémarec (1973) and also shared the species *Abra nitida* and *Y. philippiana* with the *Maldane sarsi* and *Ophiura sarsii* muddy community of Petersen (1918) and the Mediterranean biocenoses of the terrigenous coastal and deep muds described by Picard (1965). Martins et al. (2013b, 2013c) also identified a community in the muddy sands of the southwestern deep shelf using the whole benthic macrofauna and the polychaetes apart.

This study showed that mollusks may successfully be used to assess the diversity and composition of the major marine benthic communities that may be expected to occur in a particular area, as previously documented by Koulouri et al. (2006) and Zenetos (1996). However, the low abundance, low diversity or even absence of mollusks in most of the muddy areas, oversimplifies the spatial patterns detected from the study of the whole macrofauna, thereby making it advisable that other groups, such as polychaetes, should preferably be included in these assessments (Martins et al., 2013b, 2013c).

**Table 3**

Molluscan affinity groups characterization. Mean values are reported to the unit sampling area (0.1 m<sup>2</sup>). G = gravel, VCS = very coarse sand, CS = coarse sand, MS = medium sand, FS = fine sand, VFS = very fine sand, M = mud (number of sediment samples within brackets); Constancy: Cn = constant, C = common, O = occasional, R = rare; Fidelity: E = elective, P = preferential, I = indifferent, A = accessory; \* = Exclusive species in each group.

| Affinity groups  | A  | B1  | B2.1  | B2.2.1  | B2.2.2   |
|--|--|---|---|---|--|
| No. of sampling sites  | 27   | 17  | 13  | 38  | 32   |
| Main sediment type   | Coarser sediments  | Finer sands and mud   | Fine sand   | Finer sands and mud   | Finer sands and mud  |
| Sites median agreement   | VCS (12/27),<br>G (8/27), CS (5/27),<br>MS (2/27)  | M (5/17), FS (4/17),<br>VFS (4/17), VCS (2/17),<br>CS (1/17), maerl (1/17)  | FS (9/13), VCS (2/13),<br>MS (1/13), VFS (1/13)   | FS (19/38), M (11/38),<br>VFS(5/38), VCS (1/38),<br>CS (1/38), no data (1/38)   | FS (15/32), VFS (6/32),<br>MS (5/32), M (4/32),<br>CS (1/32), no data (1/32)   |
| Gravel content (mean; %)   | 32.4   | 4.0   | 4.1   | 1.0   | 1.5  |
| Sand content (mean; %)   | 65.2   | 58.9  | 90.2  | 63.5  | 71.8   |
| Fines content (mean; %)  | 2.3  | 37.0  | 5.7   | 35.7  | 26.7   |
| Biogenic fraction (mean; %)  | 3.8  | 4.8   | 1.0   | 1.2   | 2.2  |
| TOM (mean; %)  | 0.7  | 4.2   | 1.6   | 3.7   | 3.8  |
| Depth (mean; m)  | 50.3   | 46.4  | 46.9  | 88.6  | 126.9  |
| Abundance (mean)   | 33   | 14  | 12  | 23  | 11   |
| Total species richness   | 71   | 59  | 30  | 61  | 86   |
| Mean <i>alpha</i> diversity  | 9.1  | 7.7   | 5.2   | 6.5   | 6.1  |
| Nr. of exclusive species   | 31   | 22  | 3   | 16  | 19   |
| Characteristic species<br>(with constancy and<br>fidelity indications) | <i>Angulus pygmaeus</i> (Cn/E)<br><i>Thracia villosiuscula</i> (Cn/P)<br><i>Gari costulata</i> (C/E)<br><i>Caecum</i> sp. (C/E)*<br><i>Glycymeris glycymeris</i> (C/P)<br><i>Digitaria digitaria</i> (C/E)*<br><i>Spisula elliptica</i> (C/E)*<br><i>Limatula subovata</i> (O/E)*<br><i>Moerella donacina</i> (C/I)<br><i>Gari tellinella</i> (O/E)* | <i>Calyptraea chinensis</i> (Cn/E)*<br><i>Leptochiton cancellatus</i> (Cn/P)<br><i>Montacuta phascolionis</i> (C/E)*<br><i>Nucula nitidosa</i> (C/I)<br><i>Gouldia minima</i> (C/I)<br><i>Kurtiella bidentata</i> (C/I)<br><i>Hydrobia acuta neglecta</i> (O/E)*<br><i>Pitar rudis</i> (O/P)<br><i>Myrtea spinifera</i> (C/I)<br><i>Chaetopleura (Chaetopleura) angulata</i> (R/E)* | <i>Angulus fabula</i> (Cn/P)<br><i>Spisula subtruncata</i> (Cn/I)<br><i>Pharus legumen</i> (O/P)<br><i>Cylichna cylindracea</i> (C/I)<br><i>Nassarius reticulatus</i> (C/I)<br><i>Venus casina</i> (O/P)<br><i>Turbonilla</i> sp. (O/P)<br><i>Philine aperta</i> (O/I)<br><i>Phaxas pellucidus</i> (O/I)<br><i>Ensis</i> sp. (R/E)* | <i>Tellina compressa</i> (Cn/I)<br><i>Abra alba</i> (Cn/I)<br><i>Corbula gibba</i> (Cn/I)<br><i>Thyasira</i> sp. (C/P)<br><i>Thyasira flexuosa</i> (C/I)<br><i>Phaxas pellucidus</i> (C/I)<br><i>Tellimya ferruginosa</i> (C/I)<br><i>Saccella commutata</i> (C/A)<br><i>Atrina fragilis</i> (R/E)*<br><i>Nassarius elatus</i> (R/E)* | <i>Saccella commutata</i> (Cn/P)<br><i>Aplacophora</i> sp.1 (C/P)<br><i>Timoclea ovata</i> (C/I)<br><i>Fustiaria rubescens</i> (C/I)<br><i>Parvicardium scabrum</i> (O/E)*<br><i>Yoldiella philippiana</i> (O/E)*<br><i>Cardiomya costellata</i> (O/P)<br><i>Bela fuscata</i> (O/P)<br><i>Pallioium incomparabile</i> (O/P)<br><i>Arca tetragona</i> (R/P) |
| Macrofauna affinity<br>groups agreement<br>(Martins et al., 2013b)     | <b>89%A</b> , 4%C1, 7%O  | <b>59%C3</b> , 24%D, 18%A   | <b>61%B</b> , 23%C1, 8%A, 8%C3  | <b>53%C1</b> , 18%C2, 18%D,<br>5%B, 3%C3, 3%O   | <b>69%C2</b> , 16%C1, 6%B, 6%D, 3%A  |
| Polychaetes affinity<br>groups agreement<br>(Martins et al., 2013c)    | <b>85%A</b> , 7%B2, 7%O  | <b>53%C2</b> , 29%C3, 18%A, 6%C1  | <b>61%B1</b> , 23%B2, 8%A, 8%C2   | <b>37%B2</b> , <b>31%C1</b> , 16%C3, 8%B1,<br>3%O, 3%C2, 3% no group  | <b>69%C1</b> , 9%C2, 9%C3,<br>6%B1, 3%A, 3%B2  |

Values in bold indicate the highest agreement between the Mollusks affinity groups and the affinity groups identified in the analysis of the whole macrofauna data and the Polychaetes alone. The highest agreement corresponded to the group identified in the coarser sediments.

#### 4.3. Environmental–biological relationships

The present study corroborates that the spatial distribution patterns of marine mollusks are influenced by substrate characteristics, depth and hydrodynamics (e.g. Cacabelos et al., 2008; Koulouri et al., 2006; Michel et al., 2011; Quintino et al., 1986; Rufino et al., 2010). It is widely accepted that some organisms are best adapted to specific soft bottom habitats, the species they belong to showing higher abundance and biomass in a particular grain-size range (Hily, 1987). This circumstance also influences their growth rate, burrowing time, foraging effectiveness and metabolic activity (Byrnes et al., 2003; Huz et al., 2002). The variety of the Portuguese shelf sediment types (Martins et al., 2012) supported the high molluscan diversity, some exclusively or abundantly recorded in a specific soft substrate type (e.g. *D. digitaria*) and others found in a broader substrate range (e.g. *A. alba*) (e.g. Byrnes et al., 2003; Cacabelos et al., 2008). However, it is recognized that marine biological distribution patterns are also depth related in several continental shelves (Benkendorfer and Soares-Gomes, 2009; Moulaert et al., 2007). This study documented the decrease of abundance and *alpha* diversity with depth, which can be related to the decrease of the quantity and quality of Chlorophyll a, as it was suggested by Karakassis and Eleftheriou (1997). The occurrence of a fine sands community with fewer species, in shallow waters, may be explained by the harsh hydrodynamic conditions induced by waves and bottom currents rather than the preference for shallower depths (e.g. Glémarec, 1973; Picard, 1965).

Finally, the Portuguese shelf is influenced by a complex current system and seasonal upwelling events that affect productivity and summer and winter Sea Surface Temperatures (SSTs) (Fiúza, 1983; Nascimento et al., 2012). This favors the mixing of subtropical warm and northern cold waters in the Portuguese continental shelf. Colder and nutrient-rich waters over the continental shelf during upwelling periods could,

at least in part, explain the occurrence at these latitudes of colder water species (e.g. *Batharca pectunculoides*, *L. asellus*), while higher mean SST in the southern coast, as well as the downwelling events, could explain the record of several warmer water species, particularly in the south (e.g. *Lioberus agglutinans*, *Turritella turbona*) (Silva et al., 2006). In fact, SST seems to be a key factor in certain species distribution (Silva et al., 2006, 2010; Raffi et al., 1985). Along the Iberian coasts, the minimal reproduction temperature for some thermophilic gastropod species is 20 °C (Silva et al., 2010; Raffi et al., 1985). The medium monthly SST is very variable along the Portuguese shelf, reaching 20 °C in the SW coast (from Nazaré canyon till Cape S. Vincent; 39–37° N). This can contribute to the definition of a transitional faunal break zone, separating northern “Franco–Iberian” colder water communities from southern, “Mediterranean–Moroccan” warmer water communities such as suggested by Silva et al. (2010). Rapid changes in shelf conditions, such as the presence of canyons cannot be discarded in the latitudinal distribution of species (Cunha et al., 2011; Spalding et al., 2007). However, the most relevant shelf morphologies (mainly Nazaré, Lisbon and S. Vicente canyons) are coincident with that transitional faunal shelf zone, being difficult to conclude if those structures affect the mollusks latitudinal distribution along the Portuguese shelf.

#### 5. Conclusions

More than 2500 specimens were identified corresponding to 169 taxa, in the Portuguese continental shelf. The present study showed that the most abundant and frequent species was *Aa alba*. This work sets the first record of *Aa borealis*, *L. asellus*, *M. mercenaria* and *M. phascolionis* in the Portuguese coast and extends the northern limit of *A. polii*, *G. nummaria* and *L. algesirensis* to the northwestern Portuguese shelf. Furthermore, the present study provides new information on

**Table 4**  
Distribution of the species per affinity groups according to mean abundance. Dark gray = exclusive species. Light gray = group where the species presents the highest mean abundance.  
\* = Mean abundance below 0.05 individuals 0.1 m<sup>-2</sup>.

| Species   | A   | B1  | B2.1 | B2.2.1 | B2.2.2 |
|---|-----|-----|------|--------|--------|
| <i>Caecum</i> sp.   | 2.9 |     |      |        |        |
| <i>Limatula subovata</i> (Monterosato, 1875)                      | 2.0 |     |      |        |        |
| <i>Digitaria digitaria</i> (Linnaeus, 1758)                       | 1.9 |     |      |        |        |
| <i>Gari tellinella</i> (Lamarck, 1818)                            | 1.9 |     |      |        |        |
| <i>Goodallia triangularis</i> (Montagu, 1803)                     | 1.2 |     |      |        |        |
| <i>Ervilia castanea</i> (Montagu, 1803)                           | 0.6 |     |      |        |        |
| <i>Gibbula</i> sp.  | 0.6 |     |      |        |        |
| <i>Spisula elliptica</i> (Brown, 1827)                            | 0.4 |     |      |        |        |
| <i>Palliolum tigrinum</i> (O. F. Müller, 1776)                    | 0.3 |     |      |        |        |
| <i>Philine punctata</i> (Adams J., 1800)                          | 0.3 |     |      |        |        |
| <i>Loripes</i> sp.  | 0.3 |     |      |        |        |
| <i>Caecum subannulatum</i> de Folin, 1870                         | 0.2 |     |      |        |        |
| <i>Aequipecten opercularis</i> (Linnaeus, 1758)                   | 0.1 |     |      |        |        |
| <i>Anomia ephippium</i> Linnaeus 1758                             | 0.1 |     |      |        |        |
| <i>Glycymeris nummaria</i> (Linnaeus, 1758)                       | 0.1 |     |      |        |        |
| Lasaeidae n.i.  | 0.1 |     |      |        |        |
| <i>Spisula</i> sp.  | 0.1 |     |      |        |        |
| <i>Tellina distorta</i> Poli, 1791                                | 0.1 |     |      |        |        |
| <i>Melanella frielei</i> (Jordan, 1895)                           | 0.1 |     |      |        |        |
| <i>Thracia villosiuscula</i> (MacGillivray, 1827)                 | 5.1 | 0.2 | 0.2  |        | *      |
| <i>Angulus pygmaeus</i> (Lovén, 1846)                             | 3.5 |     |      |        | *      |
| <i>Glycymeris glycymeris</i> (Linnaeus, 1758)                     | 1.5 |     | 0.1  |        |        |
| <i>Gouldia minima</i> (Montagu, 1803)                             | 1.2 | 0.8 |      | 0.1    | 0.2    |
| <i>Gari costulata</i> (Turton, 1822)                              | 1.0 |     |      | *      |        |
| <i>Dosinia lupinus</i> (Linnaeus, 1758)                           | 0.6 | 0.1 | 0.6  | 0.3    |        |
| <i>Moerella donacina</i> (Linnaeus, 1758)                         | 0.6 | 0.1 | 0.1  |        | *      |
| <i>Clausinella fasciata</i> (da Costa, 1778)                      | 0.4 | 0.2 | 0.2  | 0.1    |        |
| <i>Palliolum incomparabile</i> (Risso, 1826)                      | 0.3 |     |      |        | 0.3    |
| <i>Chamelea gallina</i> (Linnaeus, 1758)                          | 0.2 |     | 0.1  | 0.1    |        |
| <i>Calyptrea chinensis</i> (Linnaeus, 1758)                       |     | 1.0 |      |        |        |
| <i>Montacuta phascolionis</i> Dautzenberg and Fischer H., 1925    |     | 0.4 |      |        |        |
| <i>Hydrobia acuta neglecta</i> Muus, 1963                         |     | 0.2 |      |        |        |
| <i>Nassarius incrassatus</i> (Strøm, 1768)                        |     | 0.2 |      |        |        |
| <i>Musculus subpictus</i> (Cantraine, 1835)                       |     | 0.2 |      |        |        |
| <i>Monophorus perversus</i> (Linnaeus, 1758)                      |     | 0.1 |      |        |        |
| <i>Bornia geoffroyi</i> (Payraudeau, 1826)                        |     | 0.1 |      |        |        |
| <i>Acanthochitona fascicularis</i> (Linnaeus, 1767)               |     | 0.1 |      |        |        |
| <i>Venerupis corrugata</i> (Gmelin, 1791)                         |     | 0.1 |      |        |        |
| <i>Chaetopleura (Chaetopleura) angulata</i> (Spengler, 1797)      |     | 0.1 |      |        |        |
| <i>Macoma balthica</i> (Linnaeus, 1758)                           |     | 0.1 |      |        |        |
| <i>Corbula gibba</i> (Olivi, 1792)                                | 0.4 | 2.1 |      | 1.8    | 0.1    |
| <i>Leptochiton cancellatus</i> (Sowerby, 1840)                    | 0.2 | 1.9 |      |        | 0.1    |
| <i>Myrtea spinifera</i> (Montagu, 1803)                           |     | 0.4 | 0.2  | 0.1    | 0.1    |
| <i>Leptochiton algesirensis</i> (Capellini, 1859)                 | *   | 0.3 |      |        |        |
| <i>Aporrhais pespelecani</i> (Linnaeus, 1758)                     |     | 0.3 |      | *      |        |
| <i>Pitar rudis</i> (Poli, 1795)                                   |     | 0.3 |      |        | 0.1    |
| <i>Crassopleura maravignae</i> (Bivona Ant. in Bivona And., 1838) | *   | 0.1 |      |        |        |
| <i>Antalis vulgaris</i> (da Costa, 1778)                          |     | 0.1 |      |        | *      |
| <i>Hiatella arctica</i> (Linnaeus, 1767)                          |     | 0.1 |      | *      | 0.1    |
| <i>Abra alba</i> (W. Wood, 1802)                                  | 0.2 | 0.2 | 3.1  | 2.5    | 0.2    |
| <i>Spisula subtruncata</i> (da Costa, 1778)                       | *   | 0.1 | 1.5  | 0.6    |        |
| <i>Nassarius reticulatus</i> (Linnaeus, 1758)                     | 0.2 | 0.2 | 1.4  | 0.1    |        |
| <i>Angulus fabula</i> (Gmelin, 1791)                              |     |     | 1.1  | 0.4    | 0.1    |

**Table 4** (continued)

|  |     |     |     |     |     |
|--|-----|-----|-----|-----|-----|
| <i>Pharus legumen</i> (Linnaeus, 1758)                 |     |     | 0.2 | *   |     |
| <i>Venus casina</i> Linnaeus, 1758                     | *   |     | 0.2 |     |     |
| <i>Philine aperta</i> (Linnaeus, 1767)                 |     |     | 0.2 | *   | 0.1 |
| <i>Turbonilla</i> sp.                                  |     |     | 0.2 |     | 0.1 |
| <i>Nassarius elatus</i> (Gould, 1845)                  |     |     |     | 0.2 |     |
| <i>Ecrobia truncata</i> (Vanatta, 1924)                |     |     |     | 0.2 |     |
| <i>Mactra</i> sp.                                      |     |     |     | 0.1 |     |
| <i>Thyasira flexuosa</i> (Montagu, 1803)               | 0.1 | 0.2 | 0.1 | 3.2 | 0.3 |
| <i>Kurtiella bidentata</i> (Montagu, 1803)             | 1.1 | 0.8 |     | 2.1 |     |
| <i>Tellina compressa</i> Brocchi, 1814                 |     | 0.1 | 0.3 | 2.1 | 0.4 |
| <i>Thyasira</i> sp.                                    |     | 0.1 |     | 1.7 | 0.1 |
| <i>Phaxas pellucidus</i> (Pennant, 1777)               |     |     | 0.4 | 1.1 | 0.1 |
| <i>Nucula nitidosa</i> Winckworth, 1930                | *   | 0.7 |     | 0.9 | 0.2 |
| <i>Euspira nitida</i> (Donovan, 1804)                  | 0.7 | 0.1 | 0.5 | 0.7 |     |
| <i>Cyllichna cylindracea</i> (Pennant, 1777)           |     |     | 0.4 | 0.5 | 0.1 |
| <i>Chamelea striatula</i> (da Costa, 1778)             | 0.2 |     | 0.1 | 0.4 |     |
| <i>Tellimya ferruginosa</i> (Montagu, 1808)            | 0.1 |     | 0.2 | 0.4 | 0.2 |
| <i>Turritella turbona</i> Monterosato, 1877            | *   | 0.3 |     | 0.4 | 0.1 |
| <i>Turritella communis</i> Risso, 1826                 | 0.3 | 0.2 | 0.1 | 0.3 |     |
| <i>Aplacophora</i> sp.2                                | *   |     |     | 0.1 |     |
| <i>Abra prismatica</i> (Montagu, 1808)                 | *   |     |     | 0.1 |     |
| <i>Parvicardium scabrum</i> (Philippi, 1844)           |     |     |     |     | 0.3 |
| <i>Bathyarca pectunculoides</i> (Scacchi, 1835)        |     |     |     |     | 0.2 |
| <i>Ringicula auriculata</i> (Ménard de la Groye, 1811) |     |     |     |     | 0.2 |
| <i>Serratina serrata</i> (Brocchi, 1814)               |     |     |     |     | 0.2 |
| <i>Yoldiella philippiana</i> (Nyst, 1845)              |     |     |     |     | 0.2 |
| <i>Venus</i> sp.                                       |     |     |     |     | 0.1 |
| <i>Saccella commutata</i> (Philippi, 1844)             |     |     |     | 0.4 | 1.6 |
| <i>Fustiaria rubescens</i> (Deshayes, 1825)            | 0.2 | 0.4 | 0.1 | 0.2 | 0.9 |
| <i>Aplacophora</i> sp.1                                | 0.1 |     |     | *   | 0.9 |
| <i>Timoclea ovata</i> (Pennant, 1777)                  | 0.2 | 0.1 |     | 0.1 | 0.6 |
| <i>Laevicardium crassum</i> (Gmelin, 1791)             | 0.1 | 0.1 |     |     | 0.3 |
| <i>Arca tetragona</i> Poli, 1795                       | *   |     |     |     | 0.3 |
| <i>Diplodonta rotundata</i> (Montagu, 1803)            | *   |     |     | 0.1 | 0.2 |
| <i>Cardiomya costellata</i> (Deshayes, 1833)           |     |     |     | *   | 0.2 |
| <i>Abra nitida</i> (Müller, 1776)                      |     |     |     | 0.1 | 0.1 |
| <i>Anadara polii</i> (Mayer, 1868)                     |     | 0.1 |     | 0.1 | 0.1 |
| <i>Parvicardium pinnulatum</i> (Conrad, 1831)          |     |     |     | *   | 0.1 |

substrate preferences and bathymetric distribution for several species. Five major benthic molluscan communities were identified, being grain-size, gravel content, depth and hydrodynamic regime the abiotic

factors best related to the molluscan data. This area is an important transitional zone, where elements of boreal, temperate and subtropical molluscan faunas coexist, particularly in the transitional faunal break zone, between Nazaré and S. Vicente canyons, in the western coast.

**Table 5**

Mollusks species richness in worldwide continental shelves.

| Locality                       | Latitude  | Species richness | Reference               |
|--------------------------------|-----------|------------------|-------------------------|
| Bay of Biscay (W France)       | 46–47° N  | 29               | Hily et al. (2008)      |
| Ensenada S. Simon (NW Spain)   | 42° 18' N | 68               | Cacabelos et al. (2008) |
| Portugal                       | 36–42° N  | 170              | <i>This study</i>       |
| Southeastern Portugal          | 36° N     | 89               | Freitas et al. (2011)   |
| Strait of Gibraltar (Spain/UK) | 35.5° N   | 70               | Gofas (1998)            |
| Alboran Sea (SE Spain)         | 36.7° N   | 162              | Rueda et al. (2009)     |
| Uruguay                        | 34–36° S  | 25               | Riestra et al. (2006)   |
| Macaé (Rio de Janeiro–Brazil)  | 22° N     | 152              | Absalão et al. (2006)   |
| Golfe d'Arguin (Mauritania)    | 19–21° N  | 118              | Michel et al. (2011)    |

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