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Journal of Marine Systems 163 (2016) 43–60

Contents lists available at ScienceDirect

Journal of Marine Systems

journal homepage: www.elsevier.com/locate/jmarsys

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ARTICLE INFO

Article history:
Received 3 February 2016
Received in revised form 5 May 2016
Accepted 22 June 2016
Available online 24 June 2016

Keywords:
Crustaceans
Portugal shelf
Western Mediterranean
Northeast Atlantic
North African
Macaronesian

ABSTRACT

This study analyzed the crustacean diversity, distribution and relationship with environmental factors in the western and the southern Portuguese continental shelf, between 10 and 200 m depth. A total of 10,639 specimens belonging to 242 taxa from 90 families were identified, mostly amphipods (55.8% of the total taxa). The mysid *Gastrosaccus spinifer* and the amphipods *Socarnes erythrophthalmus* and *Cheirocratus sundevallii* were the most abundant and the amphipods *Ampelisca brevicornis*, *Leucothoe incisa* and *Autonoe spiniventris* were the most frequent species. The highest abundance and diversity was found in coarser sediments with up to 306 individuals per 0.1 m^2. Alpha diversity ranged from 1 to 28 sp./0.1 m^2. Moreover, this study confirmed six previously doubtful first records and added an additional 19 new records to the Portuguese fauna. The results also confirmed the Portuguese coast as a transition zone of mixed Atlantic and Mediterranean faunas and exposed a noticeable North African and Macaronesian influence. A multivariate analysis based on the abundance of crustaceans revealed six affinity groups characterized by: (a) *C. sundevallii*, *Guernea* (*Guernea*) *coalita* and *Sarsinebalia cristoboi* on very coarse sands; (b) *G. spinifer*, *Nototropis falcatus* and *Pontocrates arenarius* on coarse sands; (c) *Othomaera othonis*, *Processa modica modica* and *Animoceradocus semiserratus* on heterogeneous medium sands; (d) *A. brevicornis*, *Urothoe pulchella* and *Necalianassa truncata* on fine sands; (e) *Ampelisca pectenata*, *Bodotria scorpioides* and *Astacilla dilatata* on heterogeneous fine sands and (f) *Callianassa subterranea*, *Ampelisca tenuicornis* and *Ampelisca typica* on muddy fine sands. Sediment grain-size and depth were the variables best related to the benthic crustacean spatial distribution patterns along the Portuguese continental shelf.

1. Introduction

Crustacea represent a large group of segmented body animals with exoskeleton and characteristic double pair of antennae, mostly marine although also including a few freshwater and terrestrial species. The vast majority belong to the class Malacostraca which comprises 75% of all known crustaceans. Over 50,000 marine crustacean species have been described and accepted by marine taxonomists up to date, although many more are expected to be discovered (Appeltans et al., 2012), which makes it the largest and most diverse group of animals within the marine benthic communities (Ruppert and Barnes, 1994). Coastal shelf benthic communities' diversity and distribution have been studied in the past decades and multiple environmental factors were shown to affect them, namely sediment type, latitudinal gradients, organic matter content, nutrients, pH, temperature, depth (Dauvin, 2015; Dolbeth et al., 2007; Hily et al., 2008; Levin and Gage, 1998). The importance of these studies for the marine environment conservation and global biodiversity preservation is paramount as they continuously provide an historical record to monitor environmental impact and species diversity (Muñoz et al., 2008). Benthic communities change as they adapt to the prevailing situations and diverse communities show more plasticity thus additional resilience to environmental impacts (Hily et al., 2008).

Present day knowledge of the Portuguese coast macrobenthic communities is well established for estuaries (Moreira et al., 1993; Rodrigues and Quintino, 1993; Rodrigues et al., 2006, 2011, 2012), lagoons (Quintino et al., 1987, 1989) rocky shores (Araújo et al., 2005; Pereira et al., 2006; Saldanha, 1997) sandy beaches (Dexter, 1988; Vale et al., 2010), but less so for submarine canyons (Cunha et al., 2011; Cúrdia et al., 2004) or the continental shelf (Freitas et al., 2011; Marques and Bellan-Santini, 1991, 1993) where the most comprehensive studies are very recent (Martins et al., 2013a, 2013b, 2014). The Portuguese continental shelf, located in the Western Iberian coast, is a region of contact between cold waters from the North Atlantic and warm waters from northern Africa and the Mediterranean Sea. The

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http://dx.doi.org/10.1016/j.jmarsys.2016.06.011
0924-7963/

western Portuguese shelf is dominated by an energetic regime of waves and tides and a complex current system, while the southern shelf is affected by warmer waters and characterized by a lower energy hydrodynamic regime, where the Atlantic inflow to the Mediterranean imposes eastward-directed current patterns (Fiúza, 1983). In terms of hydrodynamic regime, the Portuguese coast has been divided in three broad areas: mesotidal exposed Atlantic coast, from the northern Portuguese border to Cape Carvoeiro west coast, mesotidal moderately exposed Atlantic coast, from Cape Carvoeiro to Ponta da Piedade south coast and mesotidal sheltered Atlantic coast, from Ponta da Piedade to Vila Real de Santo António, the remaining southern coast (Bettencourt et al., 2004). This different regime along the coast affects the sedimentary cover of the Portuguese shelf, where coarser sediments characterize the northwestern shelf, muddy sands dominate the remaining western shelf and muds are mostly present in the sheltered southern shelf (Martins et al., 2012). The Portuguese shelf is also fractured by submarine canyons (depth range: ~50–5000 m), of which the most outstanding are Nazaré, Cascais/Lisboa, Setúbal, and S. Vicente, which cause morphological, sedimentary and hydrological boundaries (Oliveira et al., 2007).

The aim of this study was to characterize the diversity and distribution of the crustacean fauna along the western and southern Portuguese continental shelf and discuss the relationships between the biological and environmental data.

2. Study site

This study comprises data collected in sampling campaigns conducted on the entire Portuguese continental shelf. The study area extends from Caminha on the Northwest (41°51.8′N, 9°15.6′W) to Vila Real de Santo António on the Southeast (36°56.1′N, 7°24.7′W). The survey was more detailed from Porto to the North of Nazaré Canyon, where the coastal shelf is the widest (Fig. 1) and soft sediments dominate the seascape. The detailed results from grain-size analysis and the spatial distribution of superficial sediments are given in Mamede et al. (2015) and Martins et al. (2012). The shallow and mid depth northwestern shelf and areas located close to the major submarine canyons are characterized by coarser sediments with low fines and organic matter content, whereas the southwestern and the deep northwestern shelf are

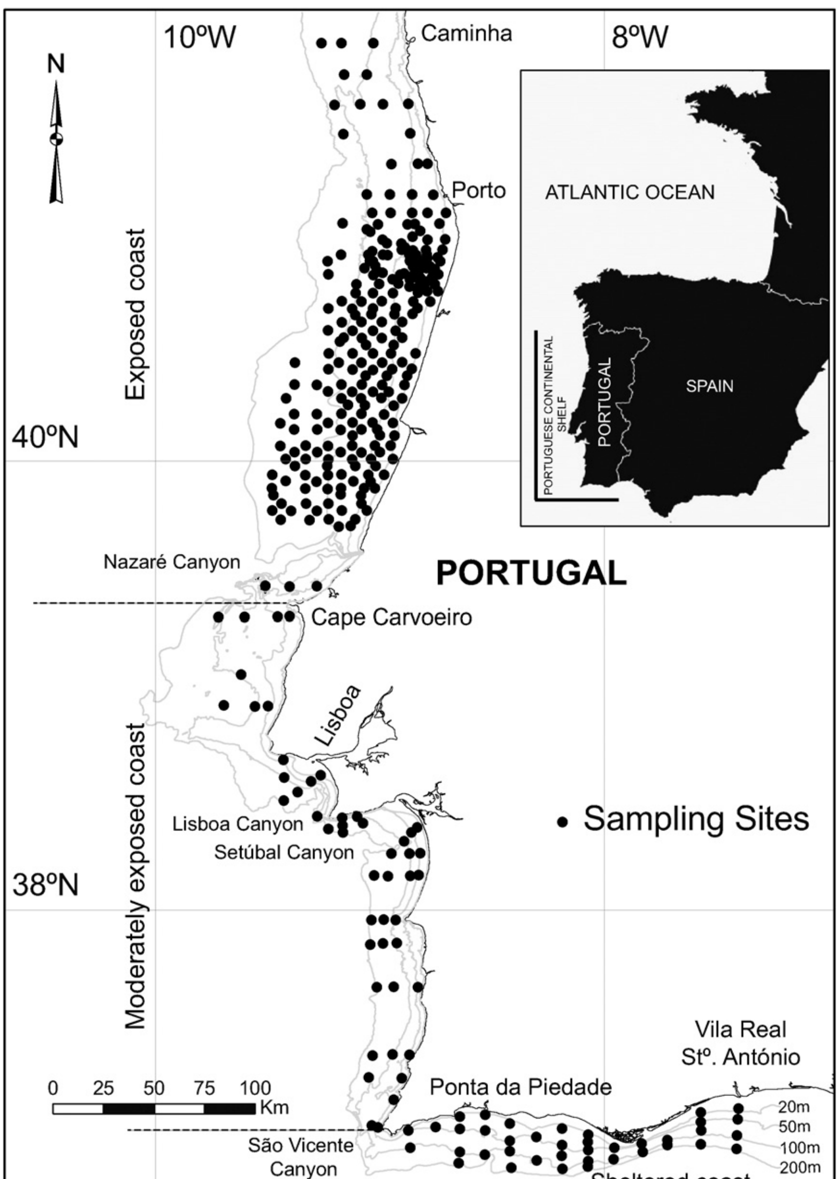

Fig. 1. Study area: the Portuguese continental shelf (Western Iberia) showing the positioning of the sampling sites (circles) and the hydrodynamic regime subdivisions according to Bettencourt et al. (2004).

dominated by fine sands with moderate fines and organic matter content. The western part of the southern shelf is very heterogeneous while muds predominate off the major Portuguese rivers, the Tagus (Lisbon) and the Douro (Porto) on the west and the Guadiana (Vila Real Santo de António), on the south coast (Mamede et al., 2015; Martins et al., 2012).

3. Sampling

A total of 326 sites were visited, distributed in perpendicular lines to the coastline, and with depth ranging from 10 to 200 m (cf. Fig. 1). At each site, two sediment samples were collected with a 0.1 m^2 Smith–McIntyre grab, one to study the macrofauna and the other for grain-size analysis. Macrofauna samples were sieved on board over 1 mm mesh size and the residue fixed in neutralized formalin (4%) and stained with rose Bengal. In the laboratory, macrofauna samples were rinsed with water, hand sorted and the fauna preserved in ethyl alcohol (70%). Crustaceans were identified to the lowest possible taxonomic level, whenever possible, following the faunas of Allen (1967); Bellan-Santini et al. (1982, 1989, 1993); Bouvier (1940); Gurriarán and Méndez (1985); Holdich and Jones (1983); Ingle (1983); Ingle (1993); Ingle and Christiansen (2004); Jones (1976); Lincoln (1979); Mauchline (1984); Moreira et al. (2009); Naylor (1972); Nilsson-Cantell (1978); Smaldon (1979); Tattersall and Tattersall (1951); Zariquiey Alvarez (1968), and specialized papers on crustacean systematic and specimens were counted under a binocular stereomicroscope. Scientific names are in accordance with the World Register of Marine Species (WoRMS – http://www.marinespecies.org).

4. Data analysis

Abundance, species richness and diversity measurements were calculated per sampling site and mean values were obtained per sediment type, depth classes (<30 m, 30–60 m, 60–100 m and >100 m), hydrodynamic regime areas (exposed = 1; moderately exposed = 2; sheltered = 3), latitudinal degree on the western shelf and longitudinal degree on the southern shelf, and major shelf areas (western, southern and the entire shelf). Alpha diversity corresponds to the total quantity of species per sampling unit (0.1 m^2). Beta or turnover diversity corresponds to the extent of biotic change or species replacement along an environmental gradient (Gray, 2000; Whittaker, 1960) and was calculated for all the above categories, except per sampling site. It was obtained by dividing the mean alpha diversity per sample in a given category, by the total number of species found in that same category (Whittaker, 1960). As an example, beta diversity for the whole Portuguese shelf corresponded to the ratio between the mean alpha diversity of the whole set of samples and the total number of species recorded in this study. Other diversity indices were also calculated per site, to complement and comprehend the spatial variation of the diversity along the Portuguese shelf, namely, Shannon–Wiener diversity (H'; $\log_2$), Margalef richness (d), Pielou evenness (J'), and Simpson diversity ($1 - \lambda'$) (Clarke and Gorley, 2006).

The data matrix with the macrofauna abundance per site was fourth root transformed to lower the influence of the most abundant species on the Bray–Curtis similarity calculated between sites. The similarity matrix was analyzed in PRIMER v.6 (Clarke and Gorley, 2006) using agglomerative hierarchical clustering, with the un-weighted pair-group mean average algorithm (UPGMA), to define the similarity between a pair of samples through a simple average, and ordination analysis, with non-metric multidimensional scaling (NMDS). These techniques were used for the identification of the biological affinity groups, also named assemblages throughout the text. The biological groups were characterized according to their mean abundance, species richness, alpha and beta diversity, Shannon–Wiener diversity ($\log_2$), Pielou evenness, Margalef richness, Simpson index, sediment baseline data, number of exclusive species and characteristic species. The characteristic species of each assemblage were obtained following their constancy (C) and fidelity (F) in the assemblage. The constancy corresponds to a sampling frequency and is given by the number of sites where the species was sampled expressed as a percentage of the total number of sites in the assemblage (Dajoz, 1971). The fidelity corresponds to the ratio between the species constancy in a given assemblage and the sum of the constancies of the same species in all the assemblages where it exists (Retière, 1979). For constancy, species were classified into constant ($C > 50.0\%$), common ($50.0 \geq C > 25.0\%$), occasional ($25.0 \geq C > 12.5\%$) and rare ($C \leq 12.5\%$), and for fidelity into elective ($F > 90.0\%$), preferential ($90 \geq F > 66.6\%$), indifferent ($66.6 \geq F > 33.3\%$), accessory ($33.3 \geq F > 10.0\%$) and accidental ($F \leq 10.0\%$). The characteristic species per affinity group were selected following the highest product between the constancy and fidelity indices.

The relationship between the biological and the environmental data was analyzed with the BIOENV procedure using the Spearman correlation coefficient (Clarke and Gorley, 2006) and considering the environmental variables depth, median grain-size, gravel, sand, fines, hydrodynamic regime and latitude. The environmental data was obtained from Mamede et al. (2015) and Martins et al. (2012). The abundance, alpha diversity, Shannon–Wiener diversity and Pielou evenness per site, and the representation of the affinity groups were plotted with ArcGis 10 in a GIS environment.

5. Results

5.1. Abundance and diversity gradients

A total of 10,639 specimens of crustacea were identified corresponding to 90 families and 242 taxa: 135 Amphipoda, 45 Decapoda, 25 Isopoda, 15 Cumacea, 11 Mysida and 11 miscellanea taxa (Euphausiacea, Lophogastrida, Cirripedia, Leptostraca, Ostracoda and Tanaidacea). The most abundant families were Mysidae, Ampeliscidae, Lysianassidae, Maeridae and Cheirocratidae (1407, 1235, 697, 584, 492 total specimens, respectively) and those with the highest number of species were Ampeliscidae, Mysidae, Lyssianassidae, Oedicerotidae, Bathyporeiidae and Bodotridae (19, 11, 10, 9, 8, 8 species respectively).

The most abundant species were the mysid *Gastrosaccus spinifer* (8.7% of total abundance, A_T), then the amphipods *Socarnes erythrophthalmus* ($A_T = 5.0\%$), *C. sundevalli* ($A_T = 4.6\%$), *Ampelisca brevicornis* ($A_T = 4.0\%$) and *O. othonis* ($A_T = 4.0\%$). The most frequent species (F, expressed in percentage and given by the ratio between the number of sites where the species was sampled and the total number of sites) were the amphipods *A. brevicornis* ($F = 26.1\%$), *Leucothoe incisa* ($F = 22.7\%$), *A. spiniventris* ($F = 20.3\%$), *C. sundevalli* ($F = 18.2\%$), *Guernea coalita* ($F = 16.1\%$) and *O. othonis* ($F = 16.1\%$). The number of rare species was high: 25.6% of the species were represented by only 1–2 specimens and 34.3% were confined to 1–2 sites.

Abundance ranged from 0 (in four mud sites) to 306 (one site in medium sand) specimens per site (0.1 m^2, Fig. 2A). The highest mean abundances (Table 1) were obtained in gravel (89.4 ind./0.1 m^2), at mid depth (30–60 m water depth; 56.0 ind./0.1 m^2) and in the northern latitudes (latitude 40–41°N, 41.7 ind./0.1 m^2). The lowest mean abundances (Table 1) were found in the central region (latitude 38°–39°, 7.8 ind./0.1 m^2), in the deep shelf (>100 m; 8.9 ind./0.1 m^2) and in mud sediments (9.5 ind./0.1 m^2). Overall, the crustacean abundance decreased from coarser to finer sediments, from shallow to deeper areas, from the north to the south in the western shelf and from west to east in the southern shelf.

Alpha diversity (Fig. 2B) ranged from 1 to 28 spp./0.1 m^2 (Fig. 2B). The highest mean alpha diversity (Table 1) was found in gravel (14.7 spp./0.1 m^2), in the southwestern sheltered shelf (longitude 8°–8.99°W; 12.4 spp./0.1 m^2) and at mid depth (30–60 m water depth; 11.7 spp./0.1 m^2). The lower values of mean alpha diversity (Table 1) were obtained in mud (4.5 spp./0.1 m^2), in the deep shelf (>100 m; 5.1 spp./0.1 m^2) and in the central region (latitude 38°–39°, 5.3 spp./0.1 m^2) (Table 1).

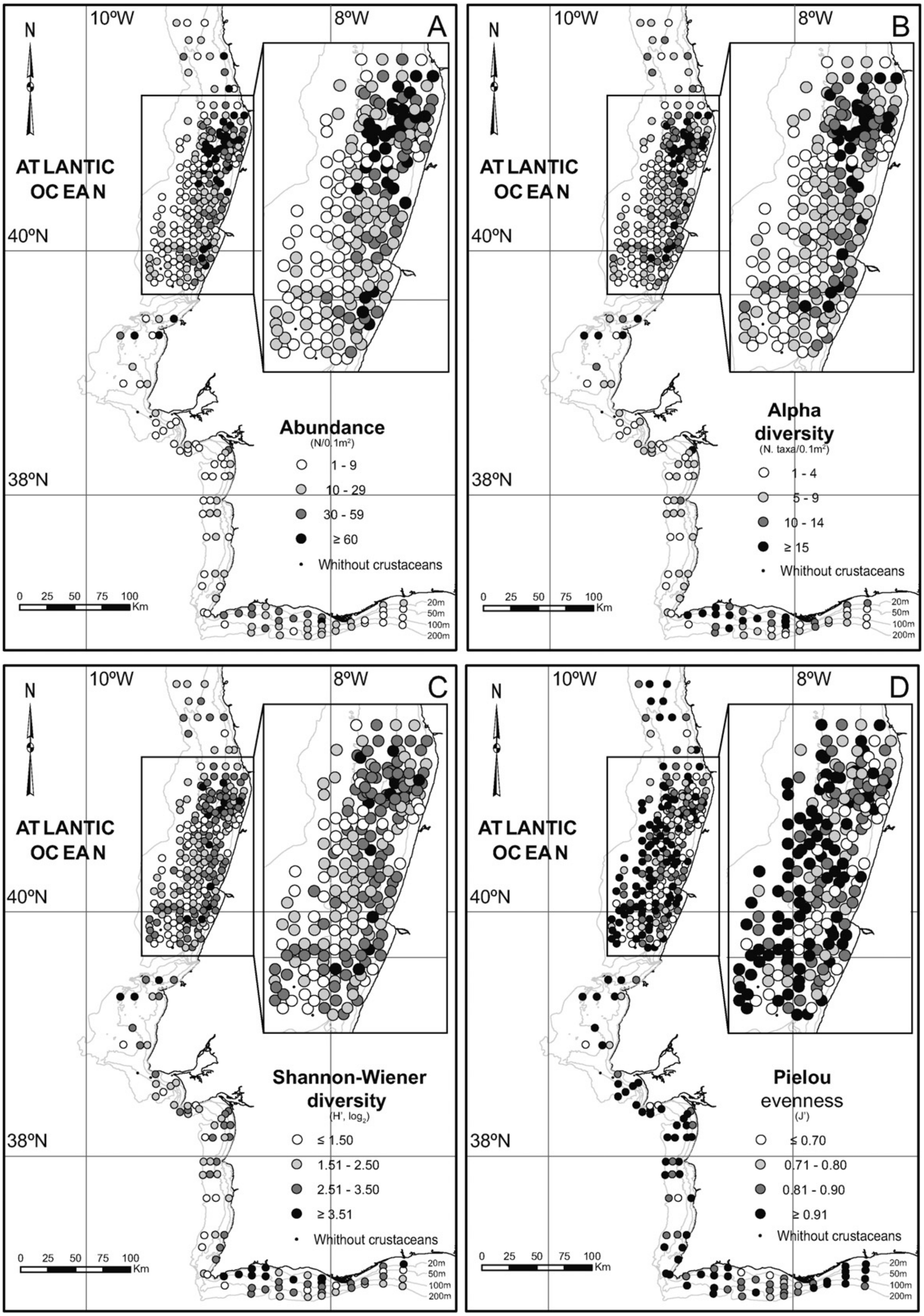

Fig. 2. Spatial distribution of crustacean abundance (A), Alpha diversity (B), Shannon-Wiener diversity (C) and Pielou evenness (D) in the Portuguese continental shelf.

The lowest mean beta diversity (spatial turnover; cf. Table 1) was found in gravel ($\beta = 7.2$), in the southern latitudes (latitude 37°–38°N; $\beta = 9.3$) and in the southwestern sheltered shelf (longitude 8°–8.99°W; $\beta = 9.3$), while the highest mean beta diversity (Table 1) was found in the deep shelf ($\beta = 23.6$), in the exposed shelf ($\beta = 23.1$) and in the latitude 40–41°N ($\beta = 20.3$).

The highest values of the diversity indices [Shannon-Wiener ($H' > 3.5$, Fig. 2C) and Margalef richness ($d > 4.0$)] were obtained in

Table 1
Highest (+) and lowest (−) mean values of diversity measures per environmental factor, indicating the respective class range or type. Ind/0.1 m^2 = individuals per 0.1 m^2. Spp/0.1 m^2 = species per 0.1 m^2.

		Hydrodynamic regime	Sediment type	Depth	Latitude	Longitude
Abundance (ind/0.1 m^2)	+	Exposed 37.8	Gravel 89.4	30–59 m 56.4	40–41°N 41.7	8°–8.99°W 28.9
	−	Moderately exposed 13.6	Silt 9.5	100–195 m 8.9	38–39°N 7.8	7°–7.99°W 11.6
Alpha diversity (spp/0.1 m^2)	+	Sheltered 10.2	Gravel 14.7	30–59 m 11.7	41–42°N 9.2	8°–8.99°W 12.4
	−	Moderately exposed 6.5	Silt 4.5	100–195 m 5.1	38–39°N 5.3	7°–7.99°W 6.7
Beta diversity	+	Exposed 23.1	Fine sand 19.8	100–195 m 23.6	40–41°N 20.3	7°–7.99°W 8.3
	−	Sheltered 11.4	Gravel 7.2	0–29 m 11.0	37–38°N 9.3	8°–8.99°W 8.2
Margalef (d)	+	Sheltered 3.0	Gravel 3.3	30–59 m 2.9	39–40°N 2.7	8°–8.99°W 3.4
	−	Moderately exposed 2.4	Silt 2.0	100–195 m 2.1	37–38°N 2.0	7°–7.99°W 2.4
Pielou's evenness (J′)	+	Moderately exposed 0.93	Silt 0.90	100–195 m 0.92	38–39°N 0.94	7°–7.99°W 0.92
	−	Exposed 0.83	Coarse sand 0.81	0–29 m 0.79	40–41°N 0.83	8°–8.99°W 0.86
Shannon-Wiener (H′, log2)	+	Sheltered 2.7	Gravel 3.0	30–59 m 2.7	41–42°N 2.5	8°–8.99°W 2.9
	−	Exposed 2.3	Silt 1.7	100–195 m 2.0	37–38°N 2.1	7°–7.99°W 2.3
Simpson (1 − λ′)	+	Moderately exposed 0.87	Gravel 0.84	100–195 m 0.84	38–39°N 0.87	7°–7.99°W 0.86
	−	Exposed 0.80	Coarse sand 0.75	0–29 m 0.75	40–41°N 0.79	8°–8.99°W 0.85

shallow depth areas (in the southwestern shelf, off Sesimbra, off Peniche and in the northernmost sector) with coarse sediments and in the western part of the southern shelf. Low diversity values were found far from the coast in muds and sands and deeper areas. High values of Pielou's evenness (J′ > 0.95, Fig. 2D) and Simpson (>0.95) were recorded in muds and fine sands at deep depths (off Sesimbra and Peniche and in the southern shelf).

5.2. Multivariate analysis

The multivariate analysis of the abundance data is shown in Fig. 3 and the spatial representation of the affinity groups in Fig. 4. Six crustacean assemblages were identified: A, B1, B2, C1, C2, and C3, obtained at a level of similarity of 6.5%. Ten sites appeared isolated due to their particular species composition and low abundance and were removed from the final analysis. The NMDS horizontal dimension was high correlated with the sediment fines content and median and the hydrodynamic regime areas (Spearman rho = −0.85, −0.85 and −0.70, respectively, Fig. 3). It separated coarser from finer sediment sites (groups A and B *vs* group C). The NMDS vertical dimension separated groups A and C1 from groups B1 and B2 with C2. This axis discriminated the nearshore coarse sediments from the deeper sandier sites and presented high correlation with gravel, sand content and longitude (0.72, −0.65 and 0.60, respectively).

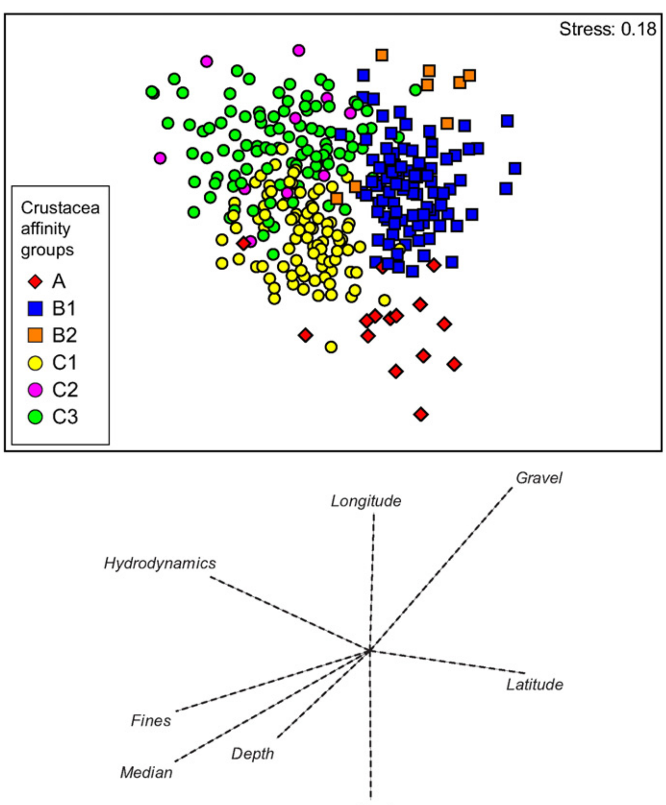

Fig. 3. Ordination diagram (NMDS) based on the abundance of crustaceans.

The biological and environmental characterization of the six crustacean assemblages is summarized in Tables 2 and 3. Group A presented the lowest alpha diversity (4.4 spp./0.1 m^2) and the highest mean abundance (61 ind/0.1 m^2). The most abundant and characteristic species was *G. spinifer* (mean N = 46.0 ind/0.1 m^2, C = 80.0%, F = 85.9%, Tables 2 and 3). *Haustorius arenarius* was the only exclusive species found in this group, comprising 15 sites located mainly in nearshore coarser sediments of the mid-western shelf (Fig. 4).

Group B1 included 93 sites located mainly in moderate depth distributed throughout the continental shelf and characterized by the highest gravel content (34.0%) and very low fines (2.0%). It exhibited very high abundance (60 ind/0.1 m^2) and the highest alpha diversity (12.0 spp./0.1 m^2) and exclusive species count (29 spp., cf. Table 2). *S. erythrophthalmus* (mean N = 5.4 ind/0.1 m^2, cf. Table 3) and *C. sundevalli* (C = 58.1%, F = 72.5%) were the most abundant and characteristic species, respectively.

Group B2 showed low mean abundance (11 ind/0.1 m^2) and alpha diversity (5.9 spp./0.1 m^2). The most characteristic species was *O. othonis* (C = 88.9%, F = 57.5%) and the most abundant was *A. serratus* (mean N = 1.3 ind/0.1 m^2, cf. Table 3). The number of exclusive species was also low (3 spp., cf. Table 2). This group comprised 9 sites located mainly in the mid shelf area, characterized by heterogeneous sediment composition.

Group C1 included 88 sites located mainly in fine sand (75% of the sites), in the mid-western shelf area. It presented relatively high species richness (151 spp.) and moderate mean abundance (29 ind/0.1 m^2), with 25 exclusive species (cf. Table 2). *A. brevicornis* (mean N = 4.4 ind/0.1 m^2, C = 77.3%, F = 58.4%, Tables 2 and 3) was the most characteristic and abundant species.

Group C2 presented very low mean abundance (11 ind/0.1 m^2) and species richness (40 spp.) and 2 exclusive species (Tables 2 and 3). *Ampelisca pectenata* (mean N = 1.2 ind/0.1 m^2, C = 70.0%, F = 82.9%, Tables 2 and 3) was the most characteristic and abundant. The group comprised 10 sites located deeper and mainly in the southwestern shelf, characterized by moderate percentage of fines (19.7%) and very low gravel content (3.1%).

Group C3 gathered 101 sites distributed throughout the continental shelf, mostly over fine and very fine sand and mud, characterized by the highest percentage of fines (34.7%) and a high mean depth (103.0 m). It exhibited high species richness (147 spp., mostly in finer sands) with

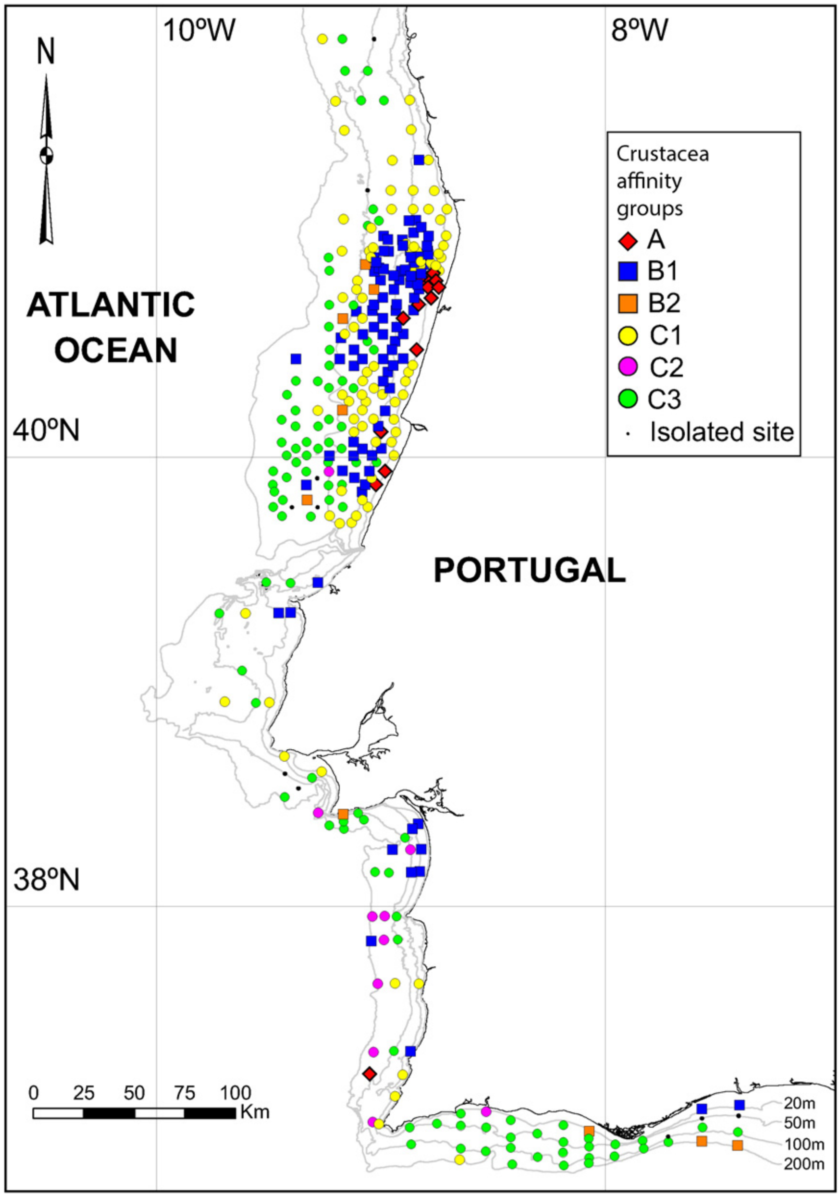

Fig. 4. Spatial distribution of the crustacean communities in the Portuguese continental shelf.

low mean abundance (14 ind/0.1 m^2). *Callianassa subterranea* (C = 33.7%, F = 78.7%) and *Ampelisca tenuicornis* (mean N = 1.6 ind/ 0.1 m^2, cf. Table 3) were the most characteristic and abundant. The number of exclusive species was close to 20% of the total species richness (27 spp., cf. Table 2).

The environmental variables best related to the biological data were depth, sediment median, gravel and fines content (BIOENV, rho = 0.316).

Fig. 5 shows the abundance distribution of selected species, chosen among the two most characteristic within each assemblage (cf. section 3.2) and with the highest abundance and/or frequency. With the exception of *G. spinifer* (up to 306 ind/0.1 m^2, Fig. 5D) and *Apherusa bispinosa* (up to 71 ind/0.1 m^2) inhabiting coarser sediments in the northwestern area (up to latitude 40°N), the majority of the most frequent and abundant species occurred along most of the entire shelf (at least up to latitude 38°N). *Cheirocratus sundevalli* (up to 43 ind/0.1 m^2, Fig. 5C), *Megamphopus cornutus* (up to 15 ind/0.1 m^2), *O. othonis* (up to 37 ind/ 0.1 m^2, Fig. 5F) and *S. erythrophthalmus* (up to 261 ind/0.1 m^2) were recorded in coarse sediments throughout the entire shelf. *Galathea intermedia* (up to 37 ind/0.1 m^2), *G. coalita* (up to 45 ind/0.1 m^2, Fig. 5H), *Haplostylus normani* (up to 194 ind/0.1 m^2), *Psammogammarus caecus* (up to 16 ind/0.1 m^2) and *S. cristoboi* (up to 81 ind/0.1 m^2) were more abundant in very coarse sand and gravel in the northwestern and central areas. *Ampelisca brevicornis* (up to 37 ind/0.1 m^2, Fig. 5A), *A. tenuicornis* (up to 28 ind/0.1 m^2, Fig. 5B), *Diastylis bradyi* (up to 35 ind/0.1 m^2), *N. truncata* (up to 26 ind/0.1 m^2), *Pariambus typicus* (up to 53 ind/0.1 m^2) and *Urothoe pulchella* (up to 20 ind/0.1 m^2, Fig. 5E) were more abundant in finer sediments along the entire shelf, with the exception of the southern sector where *P. typicus* was not record. *Autonoe spiniventris* (up to 6 ind/0.1 m^2), *Bodotria scorpioides* (up to 77 ind/0.1 m^2, Fig. 5G) and *L. incisa* (up to 12 ind/0.1 m^2) showed preference for very fine, fine and very coarse sand, distributed troughout the shelf.

6. Discussion and conclusion

6.1. Diversity and distribution patterns

This study revealed a high diversity of crustaceans in the Portuguese soft bottom continental shelf (10 to 200 m depth), comprising 242 taxa and >10.000 specimens, corresponding approximately to 26% and 9% of

Table 2
Crustacean affinity groups characterization. Mean values are reported to the unit sampling area (0.1 m^2). 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 = preferencial, I = Indifferent, A = accessory; * = Exclusive species in each group.

Affinity groups	A	B1	B2	C1	C2	C3
Nr. of sampling sites	15	93	9	88	10	101
Main sediment type	Coarse sand	Very coarse sand	Medium sand	Fine sand	Fine sand	Fine sand
Sites median agreement	CS(8), MS(5), G(1), FS(1)	VCS(51), G(21), CS(10), FS(4), MS(1)	VCS(3), MS(3), CS(2), FS(1)	FS(66), VFS(7), VCS(4), G(3), CS(3), MS(3), M(2)	FS(4), CS(2), MS(2), VFS(2)	FS(34), VFS(26), M(25), VCS(6), CS(3), G(2)
Gravel content (mean, %)	11.3	34.0	11.2	3.7	3.1	3.9
Sand content (mean, %)	87.8	64.0	65.2	89.3	77.1	61.4
Fines content (mean, %)	1.0	2.0	23.6	7.1	19.7	34.7
Depth (mean, m)	35.4	61.5	99.1	63.8	120.3	103.0
Abundance (mean)	61	60	11	29	11	14
Total species richness	30	151	36	132	40	147
Alpha diversity (mean)	4.4	12.0	5.9	8.4	6.5	7.5
Beta diversity (within the group)	6.8	12.6	6.1	15.7	6.2	19.7
Shannon-Wiener (mean; H′, log2)	1.2	2.8	1.8	2.4	2.3	2.3
Pielou's evenness (mean; J′)	0.6	0.8	0.9	0.8	0.9	0.9
Margalef (mean; d)	1.1	3.0	2.4	2.4	2.3	2.6
Simpson (mean; $1 - \lambda'$)	0.5	0.8	0.8	0.8	0.9	0.9
Nr. of exclusive species	1	29	3	25	2	27
Characteristic species (with Constancy and Fidelity indications)	*Gastrosaccus spinifer* (Cn/P)	*Cheirocratus sundevalli* (Cn/P)	*Othomaera othonis* (Cn/I)	*Ampelisca brevicornis* (Cn/I)	*Ampelisca pectenata* (Cn/P)	*Callianassa subterranea* (C/P)
	Nototropis falcatus (Cn/P)	*Guernea* (*Guernea*) *coalita* (Cn/P)	*Processa modica modica* (C/P)	*Urothoe pulchella* (C/P)	*Bodotria scorpioides* (Cn/P)	*Ampelisca tenuicornis* (C/P)
	Pontocrates arenarius (C/I)	*Sarsinebalia cristoboi* (C/E)	*Animoceradocus semiserratus* (C/I)	*Necallianassa truncata* (C/P)	*Ampelisca pseudosarsi* (C/I)	*Ampelisca typica* (O/I)
	Perioculodes longimanus (C/I)	*Eurydice naylori* (C/P)	*Liocarcinus navigator* (O/E)	*Bathyporeia tenuipes* (O/E)*	*Astacilla dilatata* (0/P)	*Harpinia antennaria* (C/I)
	Monoculodes carinatus (C/I)	*Megamphopus cornutus* (C/P)	*Ampithoe gammaroides* (R/E)*	*Megaluropus agilis* (O/I)	*Ampelisca* sp. (O/P)	*Goneplax rhomboides* (R/E)
	Amphilochus spencebatei (O/P)	*Apherusa bispinosa* (C/P)	*Dexamine* sp. (R/E)*	*Diastylis bradyi* (C/I)	*Ampelisca spinifer* (O/P)	*Anapagurus laevis* (O/I)
	Pontocrates altamarinus (O/I)	*Leucothoe incisa* (C/I)	*Xantho pilipes* (R/E)*	*Leucothoe incisa* (C/I)	*Apseudes talpa* (C/I)	*Gnathia oxyuraea* (O/I)
	Haustorius arenarius (R/E)*	*Haplostylus normani* (C/P)	*Iphinoe tenella* (R/E)	*Ampelisca spinimana* (O/P)	*Westwoodilla caecula* (O/I)	*Ampelisca armoricana* (O/I)
	Natatolana gallica (O/I)	*Galathea intermedia* (C/I)	*Macropodia linaresi* (R/E)	*Bathyporeia elegans* (R/E)*	*Erythrops elegans* (R/E)*	*Autonoe spiniventris* (C/A)
	Diogenes pugilator (O/I)	*Leptocheirus pectinatus* (C/P)	*Processa edulis crassipes* (R/E)	*Perioculodes longimanus* (C/I)	*Tmetonyx similis* (R/E)*	*Diastylis bradyi* (O/I)
	Liocarcinus holsatus (R/P)	*Psammogammarus caecus* (C/I)	*Ampelisca pseudospinimana* (R/E)	*Pariambus typicus* (O/I)	*Iphinoe serrata* (O/I)	*Urothoe elegans* (R/P)
	Astacilla sp. (R/P)	*Microjaera anisopoda* (O/E)*	*Semibalanus balanoides* (R/E)	*Hippomedon denticulatus* (O/I)	*Ampelisca provincialis* (R/P)	*Iphinoe trispinosa* (O/I)
	Megaluropus agilis (O/A)	*Eurydice spinigera* (O/P)	*Ampelisca verga* (R/P)	*Idunella longirostris* (R/E)*	*Ampelisca remora* (R/P)	*Alpheus glaber* (O/I)
	Gastrosaccus sanctus (R/I)	*Socarnes erythrophthalmus* (C/I)	*Thia scutellata* (R/P)	*Urothoe grimaldii* (0/P)	*Idunella picta* (R/P)	*Eurynome spinosa* (R/P)
	Gammaropsis sophiae (R/I)	*Caprella lilliput* (O/E)*	*Isaea montagui* (R/P)	*Abludomelita obtusata* (R/P)	*Nebalia troncosoi* (R/P)	*Kupellonura* sp. (R/E)*

the total macrofauna species richness and abundance (Martins et al., 2013a and unpublished data). Similar species ratios were found in other studies in the Atlantic (Ellingsen and Gray, 2002; Martínez et al., 2007; Rees et al., 1999) and the Mediterranean (Karakassis and Eleftheriou, 1997) continental shelves with differences related to the sampling effort and accuracy of sampling protocols (Gentil and Dauvin, 1988). Higher crustacean abundance ratios have been reported elsewhere (e.g. Martínez et al., 2007), whereas polychaetes dominate in the Portuguese continental shelf (Martins et al., 2013a, 2013b). Furthermore, the ratio between crustacean plus mollusc species to annelids was 1.04 confirming the expected values for temperate areas (Reise, 1991), which was namely also reported for the Tagus basin, the largest Iberian estuary (Rodrigues et al., 2006). The diversity and/or the distribution of species among the various crustacean groups were similar to other North Atlantic large scale benthic studies (Brandt, 1995; Ellingsen et al., 2005; Lyubina et al., 2014; Stransky and Brandt, 2010). Moreover, the percentage of rare species was comparable to similar diversity studies (Aslan-Cihangir and Pancucci-Papadopoulou, 2011; Ellingsen and Gray, 2002; Moulaert et al., 2007). Overall, nearly 90% of the Portuguese crustacean fauna found in this study has also been recorded in the British, French, Spanish or Mediterranean faunas, while an overlap with the Macaronesian/West African fauna approaching 70% (Table 4). Over 60% of the species here reported are shared by all the mentioned faunas when considered together and this percentage rises to 80% when only North Atlantic and Mediterranean are involved (Table 4). This confirmed the Atlantic-Mediterranean status of the Portuguese amphipod fauna denoted by Marques and Bellan-Santini (1991), but also revealed a noticeable subtropical influence. Previously,

Table 3
Distribution of the species per affinity groups according to the mean abundance. Dark gray = the 3 exclusive species with the highest abundance, whenever possible. Light gray = the 10 species with the highest mean abundance in the group, whenever possible. * = Mean abundance below 0.05 individuals/0.1 m^2.

Species	A	B1	B2	C1	C2	C3
Haustorius arenarius (Slabber, 1769)	0.1					
Gastrosaccus spinifer (Goës, 1864)	46.0	2.3		0.2		*
Gastrosaccus sanctus (Van Beneden, 1861)	7.1	0.1		*		*
Nototropis falcatus (Metzger, 1871)	1.3	*		0.1		
Pontocrates arenarius (Bate, 1858)	1.0	0.3	0.2	0.1		
Perioculodes longimanus (Bate and Westwood, 1868)	0.9	0.2		0.5	0.1	*
Monoculodes carinatus (Bate, 1857)	0.7	0.3				*
Pontocrates altamarinus (Bate and Westwood, 1862)	0.6	0.1		0.1		
Diogenes pugilator (Roux, 1829)	0.5			0.4		*
Caprella lilliput Krapp-Schickel and Ruffo, 1987		1.2				
Orchomene similis (Chevreux, 1912)		0.5				
Tryphosella sarsi Bonnier, 1893		0.4				
Socarnes erythrophthalmus Robertson, 1892	0.1	5.4		0.3		*
Cheirocratus sundevallii (Rathke, 1843)	0.1	5.2	0.1	*		*
Apherusa bispinosa (Bate, 1857)		4.1		0.2		
Sarsinebalia cristoboi Moreira, Gestoso and Troncoso, 2003		3.8		0.1		*
Othomaera othonis (Milne-Edwards, 1830)		3.6	3.4	0.4	0.9	0.2
Haplostylus normani (Sars G.O., 1877)	0.2	3.4		0.1		0.1
Guernea (*Guernea*) *coalita* (Norman, 1868)	0.1	2.9		*		*
Galathea intermedia Liljeborg, 1851		2.6	0.1	*		0.2
Ampithoe gammaroides (Bate, 1856)			0.1			
Dexamine sp. Leach, 1814			0.1			
Xantho pilipes A. Milne-Edwards, 1867			0.1			
Animoceradocus semiserratus (Bate, 1862)		0,9	1.3			0.1
Processa modica modica Williamson *in* Williamson and Rochanaburanon, 1979	0.1	*	0.4	*		*
Liocarcinus navigator (Herbst, 1794)			0.4			*
Phtisica marina Slabber, 1769		*	0.3	0.1		0.1
Alpheus glaber (Olivi, 1792)			0.2	*		0.2
Ampelisca pseudospinimana Bellan-Santini and Kaim-Malka, 1977		*	0.2			
Processa edulis crassipes Nouvel andHolthuis, 1957			0.2			*
Bathyporeia tenuipes Meinert, 1877				0.4		
Bathyporeia elegans Watkin, 1938				0.3		
Bathyporeia gracillis Sars, 1891				0.3		
Ampelisca brevicornis (Costa, 1853)		*	0.4	4.4	1.0	0.3
Urothoe pulchella (Costa, 1853)			0.3	2.7		
Necallianassa truncata (Giard andBonnier, 1890)		*		2.0		0.2
Diastylis bradyi Norman, 1879		*		1.7		0.3
Leucothoe incisa (Robertson, 1892)		0.9		1.4		*
Bodotria scorpioides (Montagu, 1804)		*		1.3	0.8	0.1
Pariambus typicus (Krøyer, 1884)	0.1	0.7		1.3		*
Ampelisca spinimana Chevreux, 1900				1.3		*
Megaluropus agilis Hoeck, 1889	0.5	*		0.6		*
Erythrops elegans (Sars G.O., 1863)					0.1	
Tmetonyx similis (Sars, 1891)					0.1	
Ampelisca pectenata Reid, 1951		*		0.1	1.2	0.2
Ampelisca pseudosarsi Bellan-Santini and Kaim-Malka, 1977		*		0.1	0.7	0.1
Ampelisca provincialis Bellan-Santini andKaim-Malka, 1977					0.4	*
Cirolana cranchii Leach, 1818						0.1
Kupellonura sp. Barnard, 1925						0.1
Ericthonius punctatus (Bate, 1857)						*
Ampelisca tenuicornis Liljeborg, 1855				0.1	0.3	1.6
Apseudes talpa (Montagu, 1808)		*	0.2		0.6	0.9
Harpinia antennaria Meinert, 1890	0.1	0.1	0.1	0.3	0.3	0.8
Callianassa subterranea (Montagu, 1808)				0.2		0.6
Ampelisca armoricana Bellan-Santini and Dauvin, 1981		*		0.5	0.1	0.6
Autonoe spiniventris Della Valle, 1893		0.4	0.4	0.4	0.1	0.5
Ampelisca spinipes Boeck, 1861		0.4		0.3	0.2	0.5
Ampelisca typica (Bate, 1856)		*		0.5		0.5
Anapagurus laevis (Bell, 1846)	0.2	0.1		*	0.2	0.3

Cunha et al. (1997) reported, off Aveiro, about 80% resemblance to the northern Atlantic species of amphipods, cumaceans and decapods, which is now nearly 10% higher. The ongoing update of the crustacean checklists by new taxonomy studies and reviews contribute to enhance this resemblance. Nevertheless, the species found in this study comprise just 6% of the 4150 known north Atlantic and Mediterranean crustacean species collected from the intertidal to the deep sea (Costello et al., 2006).

Most of the species sampled in this study were previously recorded in the Portuguese shelf (Cunha et al., 1997; Freitas et al., 2011; Marques, 1989; Marques and Bellan-Santini, 1991, 1993; Martins et al., 2013a). This study confirmed the first record for the Portuguese coast of the amphipods *Dulichia* sp., *Medicorophium minimum*, *Megamphopus brevidactylus* and *Normanion sarsi*, and the cumaceans *Diastyloides serratus* and *Eocuma dimorphum* stated by Martins et al. (2013a). *Diastyloides serratus* and *E. dimorphum* distribution extends from France to West Africa and includes now the Portuguese coast. For the Mediterranean species *M. minimum* and *M. brevidactylus*, the northwestern limit is now set in the southern Portuguese coast, the Algarve. The North Atlantic amphipods *Dulichia* sp. and *N. sarsi* have now the southern limit set off Aveiro (Costa de Prata) and the Nazaré Canyon, respectively.

Acidostoma obesum, *Ampelisca verga*, *A. spiniventris*, *Caprella lilliput*, *Harpinia truncata*, *Idunella excavata*, *Melita* cf. *valesi*, *Metopella* sp., *Orchemene similis* and *Pseudolirius kroyeri* (amphipoda), *Michelopagurus atlanticus* (decapoda), *A. dilatata*, *Cortezura* sp., *Gnathia oxyuracea*, *Kupellonura* sp. and *Microjaera anisopoda* (isopoda), *Nebalia troncosoi*, *S. cristoboi* and *Sarsinebalia urgorii* (leptostraca) are 19 new records for the Portuguese coast. From these, the amphipods *A. obesum*, *A. spiniventris*, *H. truncata*, *Orchomene similis* and *P. kroyeri* and the isopods *A. dilatata*, *G. oxyuracea* and *M. anisopoda* have previously been reported for the Mediterranean and the Atlantic Spanish and/or French coasts (Bachelet et al., 2003; Bellan-Santini et al., 1982, 1989, 1993; Dauvin and Bellan-Santini, 2002; Junoy and Castelló, 2003; Vanquickelberghe, 2004) and are now also reported for the Portuguese continental shelf area, filling this gap in their distributions.

For some species, this study expanded their reported distribution range to northern latitudes, namely the amphipods *C. lilliput* and *Inquilina excavata*, previously considered endemic to the Mediterranean (Bellan-Santini et al., 1989, 1993) but found here off Aveiro (Costa de Prata). Another endemic, *M.* cf. *valesi*, reported here for the first time outside the Mediterranean, was collected off Vila do Conde (Costa Verde). However, this finding must be viewed with caution since there are slight differences from the type species, especially in the antennae morphology (antenna 1 peduncle article 1 reaches the end of antenna 2 peduncle article 4) and in the uropod spines thickness (Bellan-Santini et al., 1982). The isopod *Kupellonura* sp. found in this study in the western coast off Peniche and in the southern coast is also distinct from the Mediterranean species *K. flexibilis* reported from the Baleares islands (Junoy and Castelló, 2003). Ferreira (2009) reported a *Kupellonura* sp. from the Nazaré Cannyon but it remains to determine if it is the same species as reported here. The Western African amphipod *A. verga*, a species originally described as a variety of *Ampelisca aequicornis* by Reid (1951) off Dakar, Senegal, and later confirmed as a true species (Dauvin and Bellan-Santini, 1985) is here firstly recorded in the Algarve coast, the northmost known location.

Anapagurus pusillus and *M. atlanticus* (Decapoda) originally described for the Azores have now extended their distribution eastwards. *Anapagurus pusillus* was first reported outside the Azores in the Algarve coast (cf. Ingle, 1993 and references therein) while this study establishes a new northeastern limit for the species off Figueira da Foz, Costa de Prata. Moreover, *M. atlanticus* was found off Aveiro, Costa de Prata, in shallow depth (41 m), previously reported at 1250 m in the Azores (cf. Ingle, 1993 and references therein). The isopod *Cortezura* sp., a genus reported to Venezuela and North America (Poore and Schotte, 2015), was found in this study off Aveiro, Setúbal, Sines and in the Algarve coast and was identified using the key provided by Poore (2001).

Some boreal species like the amphipod *Metopella* sp. and the cumacean *Brachydiastylis resima* are first records for the Portuguese coast and have established a new southern limit off Figueira da Foz and Marinha Grande (Costa de Prata), respectively. Species from cold waters (e.g. *Apherusa cirrus*, *Argissa hamatipes*; Marques, 1989) are usually also found off the Portuguese coast due to upwelling events (López-Jamar et al., 1992; Nascimento et al., 2012; Ospina-Alvarez et al., 2010). However, *Metopella* sp. reported in this study is distinct from *M. nasuta* reported in British waters by Lincoln (1979) but it is distinguishable from other Sthenothoidae by their narrowed pereopod 6–7 basis. This study also confirmed a new southern limit for the leptostracans *N. troncosoi* (off Figueira da Foz, Costa de Prata), *S. cristoboi* (off Aljezur, Algarve) and *S. urgorii* (off Aveiro, Costa de Prata), formerly ascribed to Galiza, Spain (Moreira et al., 2009).

6.2. Benthic crustacea communities

Soft bottom Atlantic and Mediterranean benthic communities were described by Glémarec (1973); Pérès and Picard (1964), and Thorson (1957), among others. The coarse sands assemblage described in this study (group A) can be linked to the biocoenosis of coarse sands and fine gravels under swell influence identified by Pérès and Picard (1964) in the Mediterranean. This assemblage is characterized by a great abundance of the mysid *G. spinifer* and a low species richness reflecting the shallow water high energy environment. Freitas et al. (2003) reported a very similar assemblage in the shallow waters off Aveiro, populated by *G. spinifer* and *N. falcatus*, and in the north of Spain a similar group, characterized by *G. spinifer* as constant and elective species, was associated to medium sands in Ría de Aldán (Lourido et al., 2008).

The very coarse sands described here (group B1) shared some species with the previous assemblage but were mainly characterized by the highest species richness among all the affinity groups. This assemblage has a good correspondence with the biocoenosis of coarse sands and fine gravels under the influence of bottom currents identified in the Mediterranean by Pérès and Picard (1964) and the *Branchiostoma lanceolatus-Venus fasciata* community recognized in European coasts (Thorson, 1957). Guernea (*Guernea*) *coalita*, *S. erythrophthalmus*, *Haplostylus* sp. and *Eurydice* sp. were also encountered among the coarse sandy sediments in Ría de Aldán (Lourido et al., 2008). Martins and co-workers were unable to separate these two assemblages, when considering the whole macrofauna (Martins et al., 2013a), or the assemblages defined by annelids or molluscs alone (Martins et al., 2013b, 2014), surely due to a much smaller sampling effort than that here considered.

The heterogeneous medium sands assemblage (group B2) was quite different from the two previous affinity groups and characterized by low richness and the dominance of decapod species. This assemblage was observed in deeper waters and has no close resemblance with other Atlantic and Mediterranean communities but shares a few species, namely *O. othonis*, *Dexamine* sp. and other related decapods, with the maërl bottom communities described by Jacquotte (1962) and to some extent resembles the biocoenosis of coastal detritic bottoms defined by Pérès and Picard (1964). This crustacean community is accompanied by some non-crustacean species recognized in the macrofauna southern muddy sand community (Martins et al., 2013a) and the polychaete southern shelf assemblage (Martins et al., 2013b).

The fine sands assemblage (group C1), characterized by *A. brevicornis* and *U. pulchella*, corresponds to the *Venus gallina* community (Thorson, 1957), the fine sands with *V. gallina* and *Mactra corallina* in the infralittoral of the North Gascony continental shelf (Glémarec, 1973) or the well sorted fine sands biocenosis in French Mediterranean (Pérès and Picard, 1964). A similar community was documented in Freitas et al. (2006); Quintino et al. (2001) and Reis et al. (1982).

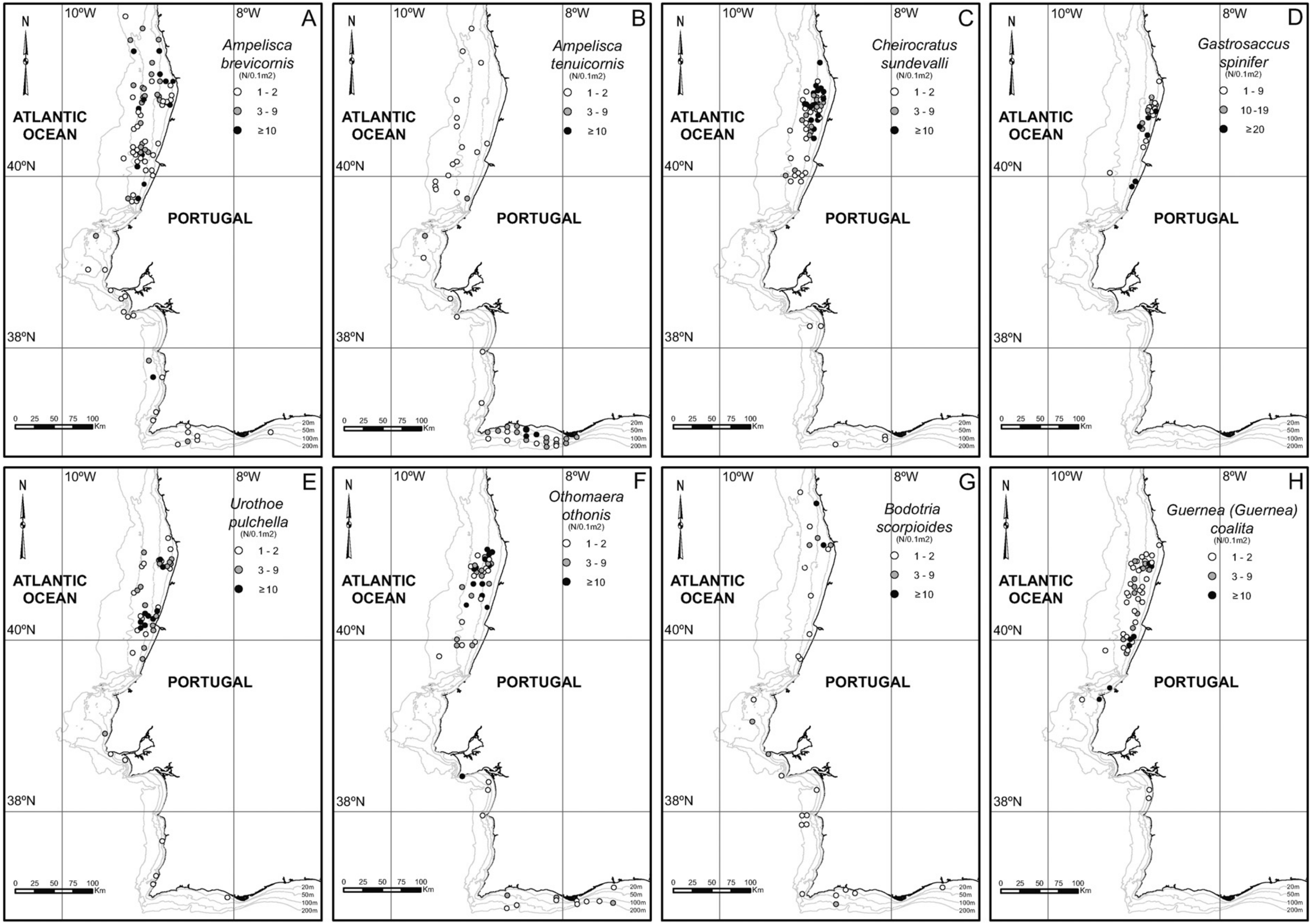

Fig. 5. Abundance distribution patterns of selected crustacean species in the Portuguese continental shelf.

Table 4
Crustacean species total abundance (A), total frequency (F), sedimentary preferences (CS, FS, M) and depth range in this study and their distribution among the European and West Africa faunas. CS = coarse sediment (gravel and coarser sands); FS = finer sands; M = mud; + ≤ 10%; ++ = 10–24%; +++ = 25–49%; ++++ = ≥50%; x = species presence; a = only present in the Atlantic Ocean, m = only present in the Mediterranean Sea. References consulted: Allen, 1967; Almeida, 2008; Bachelet et al., 2003; Bellan-Santini et al., 1982; Bellan-Santini et al., 1989; Bellan-Santini et al., 1993; Borges et al., 2010; Bouvier, 1940; Cacabelos et al., 2010; Cartes et al., 2011; Carvalho et al., 2012; Conradi and López-González, 1999; Corbera, 1995; Costa, 2012; Costello et al., 1989; Cunha et al., 1997; Cunha, 1999; Dauvin, 1999; Dauvin and Bellan-Santini, 2002; Dauvin et al., 2010; Dos Santos and González-Gordillo, 2004; Ferreira, 2009; Godet et al., 2010; Gomes, 2014; Guerra-García et al., 2013; Grimes, 2010; Gurriarán and Méndez, 1985; Holdich and Jones, 1983; Howson and Picton, 1997; Ingle and Christiansen, 2004; Ingle, 1983; Ingle, 1993; Jones, 1976; Junoy and Castelló, 2003; Lagardère, 1973; Lincoln, 1979; Marco-Herrero et al., 2015; Marques, 1989; Marques and Bellan-Santini, 1991; Marques and Bellan-Santini, 1993; Martínez et al., 2007; Martins et al., 2013a; Mauchline, 1984; Menioui, 1998; Montaudouin and Sauriau, 2000; Moreira et al., 2003; Moreira et al., 2009; Munilla and San Vicente, 2005; Naylor, 1972; Neves, 1967; Neves, 1990; Petryashov, 2009; Reis et al., 1982; Smaldon, 1979; Serrano et al., 2006; Tattersall and Tattersall, 1951; Udekem d'Acoz, 1999; Vanquickelberghe, 2004; Zariquiey Alvarez, 1968.

Species	This study						Literature					
	A	F	CS	FS	M	Depth range (meters)	Portugal	Britain	France	Spain	Mediterranean	West Africa and Macaronesia
Amphipoda												
Abludomelita gladiosa (Bate, 1862)	11	3	++++			46–70	x	x	x	x (m)	x	x
Abludomelita obtusata (Montagu, 1813)	15	9	++	++++		23–55	x	x	x	x	x	x
Acidostoma obesum (Bate & Westwood, 1861)	2	1		++++		48		x	x	x	x	
Ampelisca armoricana Bellan-Santini & Dauvin, 1981	106	36	++	++++	++	16–145	x	x	x (a)	x (a)		x
Ampelisca brevicornis (Costa, 1853)	429	86	++	++++	+	17–190	x	x	x	x	x	x
Ampelisca calypsonis Bellan-Santini & Kaim-Malka, 1977	7	5	+++	++++		49–168	x				x	
Ampelisca dalmatina Karaman, 1975	12	7	++++	++	++	53–103	x	x	x (m)	x (m)	x	
Ampelisca diadema (Costa, 1853)	9	9	++	++++	++	31–126	x	x	x	x	x	x
Ampelisca heterodactyla Schellenberg, 1925	13	4	+++	++++		38–58	x	x		x (a)		
Ampelisca pectenata Reid, 1951	37	21	++	++++		46–182	x	x	x (a)	x (a)		
Ampelisca provincialis Bellan-Santini & Kaim-Malka, 1977	8	3	+++	+++	+++	26–53	x	x			x	
Ampelisca pseudosarsi Bellan-Santini & Kaim-Malka, 1977	29	17	++	++++		26–140	x				x	
Ampelisca pseudospinimana Bellan-Santini & Kaim-Malka, 1977	3	2	++++			16–25	x		x (m)		x	
Ampelisca remora Bellan-Santini & Dauvin, 1986	6	4	+++	++++	+++	26–99	x			x (a)		
Ampelisca ruffoi Bellan-Santini & Kaim-Malka, 1977	39	19		++++	++	97–136	x		x (m)		x	
Ampelisca sarsi Chevreux, 1888	10	8		++++		17–117	x	x	x	x	x	x
Ampelisca spinifer Reid, 1951	15	10		++++	++	53–147	x	x	x	x	x	x
Ampelisca spinimana Chevreux, 1900	124	20	++	++++	+++	23–118	x		x	x	x	x
Ampelisca spinipes Boeck, 1861	112	48	++++	+++	+	26–179	x	x	x	x	x	x
Ampelisca tenuicornis Liljeborg, 1855	172	45	++	++++	++	24–190	x	x	x	x	x	x
Ampelisca typica Bate, 1856	92	40	++	++++	+++	16–174	x	x	x	x	x	x
Ampelisca verga Reid, 1951	4	3	++++	+++		25–94						x
Amphilochus spencebatei (Stebbing, 1876)	4	4	++++	+++		27–38	x	x	x	x	x	x
Ampithoe gammaroides (Bate, 1856)	1	1		++++		100	x	x	x	x	x	x
Animoceradocus semiserratus (Bate, 1862)	111	28	++++		+	25–159	x	x	x	x	x	
Aora spinicornis Afonso, 1976	9	5	++++	++		45–69	x	x	x	x	x	x
Apherusa bispinosa (Bate, 1857)	396	41	++++	++	+	33–103	x	x	x	x	x	x
Apherusa cirrus (Bate, 1862)	1	1	++++			48	x	x	x (a)			
Apherusa jurinei Milne-Edwards, 1830	12	7	++++			37–76	x	x	x	x	x	x
Apolochus neapolitanus (Della Valle, 1893)	3	2	++++	++++		33–37	x	x	x	x	x	x
Argissa hamatipes (Norman, 1869)	8	7	++++	+++		23–62	x	x	x	x	x	x
Atylus vedlomensis (Bate & Westwood, 1862)	73	34	++++	++	+	14–190	x	x	x	x	x	x
Autonoe spiniventris Della Valle, 1893	124	67	+++	+++	+	16–195			x	x	x	
Bathyporeia elegans Watkin, 1938	26	10	++	++++		25–69	x	x	x (a)	x (a)		x
Bathyporeia gracilis Sars, 1891	25	5	++	++++		38–50	x	x	x (a)			
Bathyporeia guilliamsoniana (Bate, 1857)	9	4		++++		21–26	x	x	x	x	x	x
Bathyporeia nana Toulmond, 1966	1	1		++++		25	x	x	x	x	x	
Bathyporeia pelagica (Bate, 1856)	9	1		++++		41	x	x	x (a)	x (a)		x
Bathyporeia pilosa Lindström, 1855	7	1		++++		26	x	x	x	x	x	x
Bathyporeia sarsi Watkin, 1938	19	8		++++		17–69	x	x	x	x	x	
Bathyporeia tenuipes Meinert, 1877	36	17	+	++++		21–91	x	x	x (a)	x (a)		
Caprella lilliput Krapp-Schickel & Ruffo, 1987	111	15	++++			33–85	x				x	
Caprella penantis Leach, 1814	1	1	++++			53	x	x	x	x	x	x
Cheirocratus assimilis (Lilljeborg, 1852)	6	2	++++			69–87	x	x	x		x	
Cheirocratus sundevallii (Rathke, 1843)	486	60	++++	+		34–179	x	x	x	x	x	
Deflexilodes subnudus (Norman, 1889)	1	1		++++		48	x	x	x		x	
Dexamine sp. Leach, 1814	1	1			++++	148	x	x	x	x	x	x
Dulichia sp. Krøyer, 1845	3	2	++++			45–69	x	x				
Ericthonius punctatus (Bate, 1857)	5	1			++++	129	x	x	x	x	x	x
Eusirus longipes Boeck, 1861	2	2		++++	++++	93–133	x	x	x	x	x	x
Gammarella fucicola (Leach, 1814)	23	5	++++	++		49–84	x	x	x	x	x	x
Gammaropsis maculata (Johnston, 1828)	24	13	++++	++		25–91	x	x	x	x	x	x
Gammaropsis nitida (Stimpson, 1853)	1	1	++++			45	x	x	x (a)			
Gammaropsis sophiae (Boeck, 1861)	10	7	+++	++++		37–74	x	x	x	x	x	x
Guernea (*Guernea*) *coalita* (Norman, 1868)	276	53	++++	+		23–122	x	x	x	x	x	x

(continued on next page)

Table 4 (*continued*)

Species	This study						Literature					
	A	F	CS	FS	M	Depth range (meters)	Portugal	Britain	France	Spain	Mediterranean	West Africa and Macaronesia
Harpinia antennaria Meinert, 1890	119	46	++	++++	+++	29–174	x	x	x	x	x	x
Harpinia pectinata Sars, 1891	19	9		+++	++++	33–130	x	x	x	x	x	x
Harpinia truncata Sars, 1891	7	6	+++	++++		45–160		x	x	x (m)	x	
Haustorius arenarius (Slabber, 1769)	1	1	++++			15	x	x	x	x	x	x
Hippomedon denticulatus (Bate, 1857)	50	36	+++	++++	+	17–144	x	x	x	x	x	x
Hyperia sp. Latreille, 1823	3	3	++++			41–76	x	x	x	x	x	x
Ichnopus spinicornis Boeck, 1861	1	1	++++			195	x	x	x	x	x	x
Idunella excavata (Schecke, 1973)	31	8	++++			38–55					x	x
Idunella longirostris (Chevreux, 1920)	12	8		++++		21–33	x	x	x (a)	x (a)		
Idunella picta (Norman, 1889)	7	4	++++	++++		38–103	x	x	x	x	x	x
Iphimedia minuta G.O. Sars, 1882	1	1		++++		52	x	x	x	x (m)	x	x
Isaea montagui Milne-Edwards, 1830	6	5	++++		++	66–195	x	x	x		x	
Jassa falcata (Montagu, 1808)	6	5	++++	++		53–106	x	x	x	x	x	x
Lepidepecreum longicornis (Bate & Westwood, 1862)	5	3	++++	+++		37–50	x	x	x	x	x	x
Leptocheirus hirsutimanus (Bate, 1862)	71	16	++++	+		16–103	x	x	x	x (m)	x	
Leptocheirus pectinatus (Norman, 1869)	89	30	++++	++		25–122	x	x	x	x (m)	x	x
Leptocheirus tricristatus (Chevreux, 1887)	7	6	++++	++++		33–85	x	x	x	x (m)	x	
Leucothoe incisa (Robertson, 1892)	211	75	++++	+++	+	14–135	x	x	x	x	x	x
Leucothoe lilljeborgi Boeck, 1861	9	7		++++		38–91	x	x	x	x	x	x
Leucothoe procera Bate, 1857	6	6	+++	++++		37–145	x	x	x	x	x	x
Liljeborgia pallida (Bate, 1857)	2	2	++++	++++		82–131	x	x	x	x	x	x
Lysianassa insperata (Lincoln, 1979)	10	9	++++	++		25–62	x	x	x	x	x	
Lysianassa plumosa Boeck, 1871	2	1		++++		48	x	x	x	x (m)	x	x
Maera grossimana (Montagu, 1808)	44	5	++++			37–179	x	x	x	x	x	x
Maera inaequipes (Costa, 1857)	1	1	++++			102	x	x	x	x	x	x
Maerella tenuimana (Bate, 1862)	6	6	++++			14–179	x	x	x	x	x	
Medicorophium minimum (Schiecke, 1978)	7	6	++	+++	++++	14–100	x				x	
Medicorophium runcicorne (Della Valle, 1893)	1	1		++++		48	x			x	x	x
Megaluropus agilis Hoeck, 1889	65	27	+++	++++	+	17–58	x	x	x	x	x	x
Megamphopus brevidactylus Myers, 1976	3	2		++++		38–49	x				x	
Megamphopus cornutus Norman, 1869	165	49	++++	++		14–100	x	x	x	x	x	x
Melita cf. *valesi* Karaman, 1955	34	4	++++	+++		43–69				x (m)	x	
Melphidippella macra (Norman, 1869)	1	1	++++			99	x	x	x	x (m)	x	x
Metaphoxus fultoni (Scott, 1890)	54	18	++++	+		31–99	x	x	x	x (m)	x	x
Metaphoxus pectinatus (Walker, 1896)	1	1	++++			111	x	x	x	x	x	x
Metopella sp. Stebbing, 1906	58	14	++++	+		44–85		x				
Microdeutopus armatus Chevreux, 1886	41	14	++++	++	+	29–87	x	x	x	x	x	
Microdeutopus chelifer (Bate, 1862)	6	4	++++			57–102	x	x	x	x	x	x
Microdeutopus versiculatus (Bate, 1856)	4	1		++++		38	x	x	x	x	x	x
Microprotopus longimanus Chevreux, 1887	1	1	++++			55	x	x	x	x (m)	x	
Monocorophium acherusicum (Costa, 1853)	3	3	+++	+++	+++	50–72	x	x	x	x	x	x
Monoculodes carinatus (Bate, 1857)	40	26	++++	++		20–124	x	x	x	x	x	
Normanion sarsi Stebbing, 1906	3	1	++++			99	x	x				
Nototropis falcatus (Metzger, 1871)	35	19	++++	+++		21–42	x	x	x	x	x	x
Nototropis swammerdamei (Milne-Edwards, 1830)	4	4	++++	++++		23–52	x	x	x	x	x	x
Oedicerotidae n.i. Lilljeborg, 1865	2	2	++++			74–99	–	–	–	–	–	–
Orchomene massiliensis Ledoyer, 1977	1	1		++++		38	x		x (m)		x	
Orchomene similis (Chevreux, 1912)	48	7	++++			41–71		x	x		x	
Othomaera othonis (Milne-Edwards, 1830)	422	53	++++	++	+	14–179	x	x	x	x	x	x
Pariambus typicus (Krøyer, 1884)	179	26	+++	++++		21–101	x	x	x	x	x	
Peltocoxa brevirostris (Scott & Scott, 1893)	1	1	++++			99	x	x	x (a)	x (a)		
Perioculodes longimanus (Bate & Westwood, 1868)	88	49	+++	++++	+	23–135	x	x	x	x	x	x
Perrierella audouiniana (Bate, 1857)	4	2		++++		47–48	x	x	x	x	x	x
Photis longicaudata (Bate & Westwood, 1862)	20	11	++	++++	++	38–190	x	x	x	x	x	x
Photis longipes (Della Valle, 1893)	11	5	++++		++	14–98	x		x (m)	x	x	x
Phtisica marina Slabber, 1769	27	18	++	++++	++	25–190	x	x	x	x	x	x
Pontocrates altamarinus (Bate & Westwood, 1862)	26	9	+++	++++		15–44	x	x	x	x	x	x
Pontocrates arenarius (Bate, 1858)	51	25	++++	+++		25–100	x	x	x	x	x	x
Psammogammarus caecus Karaman, 1955	157	37	++++	+	++	33–137	x		x (m)		x	
Pseudolirius kroyeri (Haller, 1897)	1	1	++++			57		x	x	x (m)	x	
Pseudoprotella phasma Montagu, 1804	1	1	++++			36	x	x	x	x	x	x
Siphonoecetes (*Centraloecetes*) *striatus* Myers & McGrath, 1979	5	4	+++	++++		31–100	x	x	x	x	x	
Socarnes erythrophthalmus Robertson, 1892	536	36	++++	+++	+	20–128	x	x	x	x	x	x
Stenothoe marina (Bate, 1856)	35	11	++++	+++		24–94	x	x	x	x	x	x
Stenothoe valida Dana, 1852	2	1	++++			33	x	x	x		x	x
Synchelidium haplocheles (Grube, 1864)	1	1		++++		91	x	x	x	x	x	x
Synchelidium maculatum Stebbing, 1906	10	10	++	++++		21–122	x	x	x	x	x	x
Syrrhoites pusilla Enequist, 1949	3	2	++++	++++		50–133	x	x	x	x (m)	x	

Table 4 (*continued*)

Species	This study						Literature					
	A	F	CS	FS	M	Depth range (meters)	Portugal	Britain	France	Spain	Mediterranean	West Africa and Macaronesia
Tmetonyx similis (Sars, 1891)	1	1	++++			103	x	x	x	x (m)	x	
Tryphosa nana (Krøyer, 1846)	2	2	++++	++++		58–124	x	x	x	x	x	x
Tryphosella sarsi Bonnier, 1893	36	6	++++			52–76	x	x	x		x	
Tryphosites longipes (Bate & Westwood, 1861)	7	3	+++	++++		23–57	x	x	x	x	x	x
Unciola crenatipalma (Bate, 1862)	9	5	++	++++		62–128	x	x	x	x	x	
Urothoe brevicornis Bate, 1862	16	2		++++		25–40	x	x	x (a)	x		
Urothoe elegans (Bate, 1857)	23	12		++++		20–144	x	x	x	x	x	x
Urothoe grimaldii Chevreux, 1895	36	16	+++	++++		33–100	x		x	x	x	x
Urothoe marina (Bate, 1857)	24	8	++++			25–140	x	x	x	x	x	x
Urothoe poseidonis Reibish, 1905	6	5	++	++++		21–58	x	x	x	x	x	
Urothoe pulchella (Costa, 1853)	237	44	++	++++		17–101	x	x	x	x	x	x
Westwoodilla caecula (Bate, 1857)	16	14	+	++++	+++	48–147	x	x	x	x	x	x
Cumacea												
Bodotria arenosa Goodsir, 1843	1	1	++++			38	x	x	x	x	x	
Bodotria scorpioides (Montagu, 1804)	137	28	+++	++++	+	14–195	x	x	x	x	x	
Brachydiastylis resima (Krøyer, 1846)	2	2		++++		134–139	x	x				
Campylaspis glabra Sars, 1878	100	16	++++			33–99	x	x	x	x	x	x
Diastylis bradyi Norman, 1879	180	49	++	++++	++	17–190	x	x	x	x	x	
Diastylis rugosa Sars, 1865	2	1	++++			16	x	x	x	x	x	
Diastyloides serratus (Sars G.O., 1865)	1	1			++++	94	x	x	x	x	x	
Eocuma dimorphum Fage, 1928	3	2		++++		45–49	x		x (a)	x(a)		x
Eocuma dolffusii Calman, 1907	2	2		++++		17–49	x	x	x	x	x	x
Iphinoe serrata Norman, 1867	25	19	++	++++	++	14–190	x	x	x	x	x	x
Iphinoe tenella Sars, 1878	3	2	++++	++++		25–47	x	x	x	x	x	x
Iphinoe trispinosa (Goodsir, 1843)	84	29	++	++++	++	21–145	x	x	x	x	x	x
Pseudocuma (*Pseudocuma*) *longicorne* (Bate, 1858)	1	1		++++		93	x	x	x	x	x	x
Pseudocuma simile G.O. Sars, 1900	2	1	++++			80	x	x	x	x	x	
Vaunthompsonia cristata Bate, 1858	2	1			++++	73	x	x	x	x	x	x
Decapoda												
Alpheus glaber (Olivi, 1792)	20	16	++	+++	+++	46–148	x	x	x	x	x	x
Anapagurus hyndmanni (Bell, 1846)	37	18	++++	+++	+	29–94	x	x	x	x	x	x
Anapagurus laevis (Bell, 1846)	46	34	+++	+++	+	29–179	x	x	x	x	x	x
Anapagurus pusillus Henderson, 1888	10	10	+++	++++	++	25–120	x			x (a)		x
Atelecyclus rotundatus (Olivi, 1792)	9	8	++++	+++		21–69	x	x	x	x	x	x
Athanas nitescens (Leach, 1813 [in Leach, 1813–1814])	8	6		+++	++++	62–138	x	x	x	x	x	x
Callianassa subterranea (Montagu, 1808)	81	42	+	++++	++	46–145	x	x	x	x	x	x
Corystes cassivelaunus (Pennant, 1777)	2	2		++++		50–68	x	x	x	x	x	x
Crangon crangon (Linnaeus, 1758)	8	5	++++	+++		36–72	x	x	x	x	x	x
Diogenes pugilator (Roux, 1829)	46	17	++	++++		17–124	x	x	x	x	x	x
Ebalia granulosa H. Milne Edwards, 1837	7	7	++++	+++		57–139	x	x	x	x	x	x
Ebalia nux A. Milne-Edwards, 1883	17	13	+++	++++	+	57–134	x	x	x	x	x	x
Ebalia tuberosa (Pennant, 1777)	2	2	++++			57–111	x	x	x	x	x	x
Ebalia tumefacta (Montagu, 1808)	11	8	++++	+++		29–131	x	x	x	x	x	x
Eualus cranchii (Leach, 1817 [in Leach, 1815–1875])	3	2	++++	++++		41–47	x	x	x	x	x	x
Eurynome spinosa Hailstone, 1835	8	8		++++	++	38–160	x	x	x	x	x	x
Galathea intermedia Liljeborg, 1851	267	49	++++	++	+	111	x	x	x	x	x	x
Galathea strigosa (Linnaeus, 1761)	1	1		++++		134	x	x	x	x	x	x
Goneplax rhomboides (Linnaeus, 1758)	20	16		++++	+++	54–140	x	x	x	x	x	x
Jaxea nocturna Nardo, 1847	3	3		++++		81–136	x	x	x	x	x	x
Liocarcinus holsatus (Fabricius, 1798)	2	2	++++			34–52	x	x	x	x	x	x
Liocarcinus navigator (Herbst, 1794)	5	3		+++	++++	31–159	x	x	x	x	x	x
Liocarcinus pusillus (Leach, 1816)	37	26	++++	+++		23–103	x	x	x	x	x	x
Macropodia linaresi Forest & Zariquiey Alvarez, 1964	2	2	++++	++++		34–46	x	x	x	x	x	x
Michelopagurus atlanticus (Bouvier, 1922)	1	1		++++		41						x
Munida tenuimana Sars, 1872	1	1		++++		48	x	x	x	x	x	x
Necallianassa truncata (Giard & Bonnier, 1890)	204	48	++	++++	+	21–134	x	x	x	x	x	x
Nepinnotheres pinnotheres (Linnaeus, 1758)	1	1			++++	110	x	x	x	x	x	x
Pagurus chevreuxi (Bouvier, 1896)	8	7	+++	++++		25–50	x	x	x	x	x	x
Pagurus cuanensis Bell, 1846	2	2	++++	++++		31–91	x	x	x	x	x	x
Pagurus excavatus (Herbst, 1791)	2	2	++++	++++		82–90	x		x	x	x	x
Pandolina brevirostris (Rathke, 1843)	7	7	++++	++		44–140	x	x	x	x	x	x
Philocheras bispinosus bispinosus (Hailstone, 1835a)	55	28	+++	+++	++	24–118	x	x	x	x	x	x
Philocheras sculptus (Bell, 1847 [in Bell, 1844–1853])	4	4	++++	+++		43–179	x	x	x	x	x	x
Philocheras trispinosus (Hailstone in Hailstone &	8	6		++++		21–49	x	x	x	x	x	x

(*continued on next page*)

Table 4 (*continued*)

Species	This study						Literature					
	A	F	CS	FS	M	Depth range (meters)	Portugal	Britain	France	Spain	Mediterranean	West Africa and Macaronesia
Westwood, 1835)												
Pisidia longicornis (Linnaeus, 1767)	8	2	++++			37–46	x	x	x	x	x	x
Polybius henslowii Leach, 1820	9	8	++++	+++		14–52	x	x	x	x	x	x
Portumnus latipes (Pennant, 1777)	3	2	++++			44–47	x	x	x	x	x	x
Processa edulis crassipes Nouvel & Holthuis, 1957	3	2	++++	++++		25–31	x	x	x	x	x	x
Processa modica modica Williamson in Williamson & Rochanaburanon, 1979	11	11	++++	+++	+	25–134	x	x	x	x	x	x
Processa nouveli holthuisi Al-Adhub & Williamson, 1975	56	29	++++	+++	+	25–179	x	x	x	x	x	x
Thia scutellata (Fabricius, 1793)	3	3	++++			44–121	x	x	x	x	x	x
Upogebia deltaura (Leach, 1815)	12	7	++++	+++	++	48–133	x	x	x	x	x	x
Upogebia pusilla (Petagna, 1792)	3	3		++++		49–139	x	x	x	x	x	x
Xantho pilipes A. Milne-Edwards, 1867	1	1	++++			25	x	x	x	x	x	x
Isopoda												
Anthuridae n.i. Leach, 1814	20	4	++++			25–88	–	–	–	–	–	–
Astacilla dilatata Sars, 1882	10	6	++++	++++		26–131		x	x	x	x	
Astacilla sp. Cordiner, 1793	3	3	++++			33–69	x	x	x	x	x	
Bopyridae n.i. Rafinesque, 1815	1	1		++++		128	–	–	–	–	–	–
Cirolana cranchii Leach, 1818	13	1		++++		38	x	x		x	x	x
Conilera cylindracea (Montagu, 1804)	83	13	++++	++		14–99	x	x	x	x	x	
Cortezura sp. Schultz, 1977	15	9	++++	++		26–111						
Cymodoce truncata Leach, 1814	83	23	++++	+		100	x	x	x	x	x	x
Entoniscidade n.i. Kossmann, 1881	1	1		++++		78	–	–	–	–	–	–
Eurydice naylori Jones & Pierpoint, 1997	117	39	++++	+		37–142	x			x	x	
Eurydice pulchra Leach, 1815	29	14	++++	+		14–99	x	x	x	x	x	x
Eurydice spinigera Hansen, 1890	57	19	++++	+		25–195	x	x	x	x	x	x
Gnathia oxyuraea (Lilljeborg, 1855)	32	21	+++	++++		29–160		x	x	x	x	
Hyssuridae n.i. Wägele, 1981	1	1		++++		29	–	–	–	–	–	–
Ianiropsis breviremis (Sars, 1883)	10	5	++++			33–52	x	x		x	x	x
Jaera sp. Leach, 1814	2	2	++++	++++		97–99	x	x	x	x	x	x
Janira maculosa Leach, 1814	3	2	++++			36–52	x	x	x	x	x	x
Janiridae n.i. Sars, 1897	2	1	++++			99	–	–	–	–	–	–
Kupellonura sp. Barnard, 1925	13	6	++	++++		29–99	x			x (m)	x	
Leptanthura sp. Sars, 1897	1	1	++++			99	x	x	x	x	x	
Microjaera anisopoda Bocquet & Levi, 1955	108	18	++++	+	+	25–122		x		x	x	x
Munna kroyeri Goodsir, 1842	1	1	++++			53	x	x	x	x	x	
Natatolana gallica (Hansen, 1905)	9	7	++++	++		15–133	x	x	x	x	x	x
Natatolana sp. Bruce, 1981	15	12	+++	++++		26–160	x	x	x	x	x	x
Rocinela dumerilii (Lucas, 1849)	1	1		++++		48	x	x		x (m)	x	
Mysida												
Acanthomysis longicornis (Milne-Edwards, 1837)	4	4	+++	++++		33–100	x	x	x	x	x	
Anchialina agilis (Sars G.O., 1877)	19	11	++++	++	+	16–133	x	x	x	x	x	x
Erythrops elegans (Sars G.O., 1863)	1	1	++++			101	x	x	x	x	x	x
Gastrosaccus sanctus (Van Beneden, 1861)	114	5	+++	++++		17–69	x	x	x	x	x	x
Gastrosaccus spinifer (Goës, 1864)	922	24	++++	++		15–111	x	x	x	x	x	x
Haplostylus normani (Sars G.O., 1877)	330	41	++++	++		14–142	x	x	x	x	x	x
Heteromysis norvegica G.O. Sars, 1882	2	1	++++			50	x	x	x	x	x	
Leptomysis gracilis (Sars G.O., 1864)	4	4	++++	+++	+++	48–122	x	x	x	x	x	x
Lophogaster typicus M. Sars, 1857	4	4		++++		103–139	x	x	x	x	x	x
Mysides insignis (Sars G.O., 1864)	1	1		++++		78	x	x	x (a)	x (a)		
Schistomysis ornata (Sars G.O., 1864)	8	5	+++	+++	++	23–103	x	x	x (a)	x (a)		
Schistomysis spiritus (Norman, 1860)	2	2	++++	++++		17–48	x	x	x (a)	x (a)		x
Other taxa												
Apseudes talpa (Montagu, 1808)	99	18	+++	++++	++	16–168	x	x	x	x	x	x
Apseudopsis latreillii (Milne-Edwards, 1828)	30	15		++++		37–140	x	x	x	x	x	x
Meganyctiphanes norvegica (M. Sars, 1857)	12	10	++	++++	++	35–190	x	x		x	x	x
Nebalia troncosoi Moreira, Cacabelos & Dominguez, 2003	12	4	++++	+++	+++	23–103		x		x (a)		
Ostracoda n.i. Latreille, 1802	34	19	++++	+++		38–139	–	–	–	–	–	–
Sarsinebalia cristoboi Moreira, Gestoso, Troncoso, 2003	359	43	++++	+		25–97		x		x (a)		
Sarsinebalia urgorii Moreira, Gestoso, Troncoso, 2003	1	1	++++			85		x		x (a)		
Scalpellum scalpellum (Linnaeus, 1767)	1	1			++++	94	x	x	x	x	x	x
Semibalanus balanoides (Linnaeus, 1767)	2	2		++++		90–100	x	x	x	x	x	x
Tanaidacea n.i. Dana, 1849	66	19	++++	++	+	25–100	–	–	–	–	–	–

Lourido et al. (2008) found a similar assemblage with *Bathyporeia elegans*, exclusive and *A. brevicornis*, constant, in the fine sands of Ría de Aldán. This assemblage is also accompanied by other non-crustacean species linked to the macrofauna nearshore hydrodynamic exposed fine sands assemblage (Martins et al., 2013a), the polychaete nearshore shelf fine sands group (Martins et al., 2013b) and the molluscan *Angulus fabula* community (Martins et al., 2014).

The affinity group C2 corresponds to the heterogeneous fine sands deep assemblage with *A. pectenata* and *B. scorpioides*, characterized by low richness and abundance. This assemblage shows no clear resemblance with other known marine biocoenoses. Zenetos et al. (1997) also classified a complex assemblage from a similar heterogeneous circalitoral environment in the Mediterranean which also included the bivalve *Timoclea ovata*, characterized by a doubtful biocoenotic identity, and other species tolerant to mixed sediments. This assemblage corresponds to the macrofauna southwestern deep shelf assemblage described by Martins et al. (2013a), to the polychaete southwestern deep shelf assemblage (Martins et al., 2013b) or the molluscan *Saccella commutata* community (Martins et al., 2014).

Finally, the deep muddy sands assemblage (group C3) showed high species richness and shared some species with the Northern Europe *Abra alba* community described by Glémarec (1973) and Thorson (1957). This assemblage seems to represent a mix of two important Mediterranean deep communities described by Pérès and Picard (1964), the terrigeneous coastal muds and the bathyal muds biocoenoses, characterized by decapods such as *Alpheus glaber*, *Anapagurus laevis*, *C. subterranea* and *Goneplax rhomboides*. Zavodnik et al. (2005) described a similar assemblage in the North Adriatic Sea, colonized by the silt-tolerant axiid *C. subterranea* and associated to a mixed faunal composition of species characteristic of coastal terrigeneous ooze and bathyal silt biocoenoses. This community is found associated to the macrofauna mud community (Martins et al., 2013a), to the polychaete mud assemblage (Martins et al., 2013b), and the *Tellina compressa-Abra alba* community (Martins et al., 2014), described for the Portuguese coast.

6.3. Environmental-biological relationships

Benthic studies have confirmed a relationship between the distribution of soft bottom benthic macrofauna and abiotic factors, such as sediment grain-size, oxygen availability, organic matter, depth, and hydrodynamics (among others, Coll et al., 2010; Dauvin, 2015; Dolbeth et al., 2007; Hily et al., 2008; Levin and Gage, 1998; Lourido et al., 2008). Sediment grain-size is probably the major determinant of the macrobenthic communities' composition (Basford et al., 1990). The Portuguese shelf crustacean assemblages confirmed this and corresponded well to a range of sediment types: coarse sediments (groups A and B1), heterogeneous medium or fine sediments (B2 and C2), fine sands (C1), and muddy sands (C3). Other studies have also suggested this primary response for sediment grain-size, namely in the continental shelves of Crete (Karakassis and Eleftheriou, 1997), North Bay of Biscay (Hily et al., 2008), Ría de Aldán (Lourido et al., 2008), Bay of Banyuls-sur-mer (northwestern Mediterranean Sea; Grémare et al., 1998), Bay of Veys (English Channel; Dauvin et al., 2004), to mention a few. The distribution of the sediments and associated organic content along the Portuguese shelf reflects their origin and the intensity of the hydrodynamics on the coast (Martins et al., 2012). The coarser sediments in the northwestern exposed shelf provide several interstitial microhabitats for small-sized organisms, good oxygen penetration and topographic relieves suitable for several crustacean species. As a result, the interstitial space between the grains of sediment and the surface relief can support a high abundance and diversity of crustacean species (Rees et al., 1999). In this study, the crustacea abundance was six to seven times higher in gravel or coarser sand than in mud, and the alpha diversity was 3 times higher in gravel than in mud. The impoverished finer sediments are prevalent in the sheltered southern coast and off the major rivers which contribute to an input of terrigenous particles and urban and industrial residuals (Martins et al., 2012). The decrease of abundance and diversity in shelf mud sediments had already been reported and potencially related to historic contamination originated inland (Martins et al., 2012; Quintino et al., 2001; Silva et al., 2004). Moreover, in areas where upwelling is intense, oxygen can drop to minimal levels, in less permeable fine sediments, and also influence the macrofauna distribution, particularly of molluscs and crustaceans (Levin and Gage, 1998; Weston, 1988).

Depth (or associated descriptors) is also related to the distribution of the benthic macrofauna in the Portuguese shelf (Cunha et al., 1997; Dolbeth et al., 2007; Freitas et al., 2011; Martins et al., 2013a, 2013b, 2014), as well as in other continental shelves (Basford et al., 1990; Moulaert et al., 2007). This study highlighted the decrease of crustacean alpha diversity and abundance with increasing depth, as already denoted in other benthic groups in the region (Cunha et al., 1997; Martins et al., 2013a, 2013b, 2014) or among other Mediterranean and Western Atlantic benthic communities (Coll et al., 2010; Bergen et al., 2001). Reduced food availability and nutritional quality with increasing depth can contribute to such abundance and diversity decline (Karakassis and Eleftheriou, 1997), among other factors. Regarding some low abundance and diversity observed in the near shore shelf community in this study, this should be mainly due to its exposure to a high energy environment with possibly strong bottom currents and not to depth itself, as was also indicated by Dolbeth et al. (2007); Martins et al. (2013a, 2013b, 2014); Reis et al. (1982) or Rodrigues and Quintino (1987). Overall, the literature shows different relationships across areas between depth and both macrofaunal diversity and abundance (Brooks et al., 2006 and references therein). While some of these differences can be explained by physico-chemical factors, one needs to take into account possible biological interactions that can influence diversity and how they vary from one region to another (Gooday et al., 2010).

Latitude was also related to the distribution of the crustacean assemblages along the Portuguese shelf with diversity increasing with increasing latitude (except for northernmost latitudes), a pattern shown along the North Atlantic for nematodes (Lambshead et al., 2000) and polychaetes (Dauvin et al., 1994) or in benthic communities of Italian transitional waters (Munari and Mistri, 2008). An opposite trend to that shown in many studies where a benthic diversity decline with increasing latitude is observed, diminishing towards high latitudes in both southern and northern hemispheres (e.g. Roy et al., 1998, 2004; Witman et al., 2004). In this study, the pattern could be related to an extension of species' range edges, particularly of southern species, due to water temperature increase as a result of climate warming (Bates et al., 2014). The diversity increases in the range edges as cold and warm species coexist. On the other end, in the northernmost latitudes, one would expect a diversity decrease as cold species' range edges contract and conditions are still harsh for warmer species to shift northerly (Bates et al., 2014). Hence, the co-occurrence in the Portuguese continental shelf of species from different biogeographic provinces can be explained by the latitudinal gradient, the species climate-mediated range shifts and the geographical context: Temperate cold and/or Arctic-Boreal (e.g. *Apherusa cirrus*, *Argissa hamatipes*, *Brachydiastylis resima*), Lusitanean (e.g. *Ampelisca remora*, *Sarsinebalia cristoboi*, *Urothoe brevicornis*), Mediterranean (*Caprella lilliput*, *Idunella excavata*, *Medicorophium minimum*), Macaronesian and/or West African (e.g. *Ampelisca verga*, *Anapagurus pusillus*, *Michelopagurus atlanticus*). A high diversity and the co-occurrence of northern and southern species show that the Portuguese coast is a transitional zone with high ecological and biogeographic importance (Marques and Bellan-Santini, 1991; Martins et al., 2013a, 2013b, 2014). The prevalence of a complex current system along the Portuguese shelf, where subtropical warm waters from Africa and the Mediterranean Sea and Northern cold waters meet (Fiúza, 1983) is essential to sustain such diversity. Geological modifications on the coast morphology, such as the presence of canyons or other morphological barriers can also influence the latitudinal distribution of species (Cunha et al., 2011; Spalding et al., 2007). Along the western Portuguese shelf major submarine canyons (Nazaré, Lisboa and S. Vicente) may slow down the progression of colder species further south and southern species further north by acting as barriers and limiting the spatial distribution of those species (Martins et al., 2013a, 2013b, 2014).

In conclusion, the Portuguese continental shelf reunites favorable environmental conditions to support diverse benthic crustacean communities from Atlantic, Mediterranean, Macaronesian and West African origins acting as an important transition zone between regions and enhancing European species richness.

Acknowledgements

Leandro Sampaio benefited from a Post-doc grant (SFRH/BPD/72997/2010), Renato Mamede benefited from a Ph.D. grant (SFRH/BD/74312/2010) and Roberto Martins benefited from a Ph.D. grant (SFRH/BD/44231/2008), all awarded by the Portuguese Foundation for Science and Technology (FCT — Fundação para a Ciência e Tecnologia). This investigation was supported by the research projects "ACOSHELF" (POCI/MAR/56441/2004–PPCDT/MAR/56441/2004), "Monitorização Ambiental do Emissário Submarino e da ETAR da Guia do Sistema de Saneamento da Costa do Estoril", funded by SANEST, S.A. and "MeshAtlantic" (with the support of the European Union ERDF–Atlantic Area Program 2009-1/110). Thanks are due, for the financial support to CESAM (UID/AMB/50017/2013), to FCT/MEC through national funds, and the co-funding by the FEDER, within the PT2020 Partnership Agreement and Compete 2020.

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