

The effect of depth and sediment type on the spatial distribution of shallow soft-bottom amphipods along the southern Portuguese coast

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Abstract The present study provides updated information on amphipod assemblages of the southern Portuguese coast, the most south-western part of continental Europe. The influence of depth and sediment type on the spatial distribution of shallow soft-bottom amphipods was tested by means of univariate and multivariate methods. Samples were collected down to 40 m depth within areas ranging from very fine sand to gravel. The ratio between density and diversity was found to increase with depth and from coarser to finer sediments. Both physical variables tested were found to play a major role in structuring amphipod assemblages. However, some dominance of depth was evident as samples were mainly separated according to this variable. Moreover, while only 15 taxa were common to all depth levels, 35 were collected from all sediment types. Both depth and sediment type may override the potential effects of geographical location, as samples from different areas along the southern Portuguese coast were biologically related. A peculiar habitat was sampled in this study: a maerl bed, which was confirmed to be a hotspot of density. Nevertheless, this habitat did not harbor a distinct amphipod assemblage but some taxa such as *Caprella* spp., *Lembos websteri*, lysianassids and *Gammarella fucicola* were preferentially collected there. The biogeographical analysis

pointed out the occurrence of 8% of Mediterranean endemic species, confirming the influence of the Mediterranean Sea beyond the Strait of Gibraltar, and the Atlantic-Mediterranean feature of the amphipod fauna of this geographically relevant area. The present results support the need to interpret the spatial distribution patterns of marine species in relation to the combined effect of depth and sediment characteristics.

Keywords Benthos · Amphipoda · Soft bottom · Spatial distribution · Depth · Sediment · Biogeography · Southern Portuguese coast

Introduction

Marine soft-bottom communities support a high diversity of species with different ecological characteristics. Depth and sediment type have been pointed out as important factors affecting the distribution of marine macrobenthic communities (Cunha et al. 1997; Hoey et al. 2004; Mackie et al. 1997; Martínez and Adarraga 2001; Snelgrove 1998). Along a depth gradient, species are distributed according to their ability to cope with both physical (e.g., sediment composition, hydrodynamics) and biological factors (e.g., food, competition, predation).

Among the macrobenthic fauna, Amphipoda (Crustacea: Peracarida) represent a major taxonomic component, both in terms of density and diversity, inhabiting marine soft-bottom habitats from polar to tropic areas and from the tidal to the abyssal zone (Marques and Bellan-Santini 1990a). Moreover, amphipods are useful bioindicators of seawater and sediment quality (Conradi et al. 1997; Guerra-García and García-Gómez 2002), reflecting changes in environmental conditions that result from natural or anthropogenic

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disturbances. Therefore, the knowledge of the structure and composition of amphipod assemblages may be of major importance to assess changes in the marine environment as well as for management purposes (e.g., conservation areas).

The continental shelf off the Portuguese south coast is of particular interest due to the combined influence of Atlantic and Mediterranean currents. Nevertheless, few studies have addressed the benthic communities of this area (Monteiro Marques 1979; Sousa Reis et al. 1982). Most studies have focused on the Ria Formosa and Alvor lagoons (e.g., Carvalho et al. 2006b; Carvalho et al. in press; Gamito 1989; Lock and Mees 1999; Marques and Bellan-Santini 1990b; Rodrigues and Dauvin 1987; Sprung 1994). Concerning amphipods, only one major work was undertaken along the southern Portuguese coast (both offshore and inshore) in the 1980s, as part of a general study on amphipods of Portuguese coastal waters (Marques and Bellan-Santini 1985, 1986, 1987, 1990a, b, 1991, 1993). Therefore, there is a lack of updated knowledge concerning this relevant faunal group.

The present work provides updated information on the distribution and ecology of benthic amphipods of shallow coastal areas, increasing our knowledge on the biodiversity of the most south-western part of continental Europe. A biogeographic analysis of the amphipod species was undertaken. Data were also analyzed on the basis of species composition, density and habitat features, namely depth and sediment type. The depth gradient considered comprises both exposed and sheltered zones. The influence of two major physical variables (depth and sediment type) on the spatial distribution of shallow water amphipod assemblages was tested.

Materials and methods

Study area

The study area covers most of the southern Portuguese coast (Fig. 1). Samples were collected in different subtidal

zones from 1 to 37 m depth. For the purpose of the present study, samples were allocated to one of the following three depth levels: <10 m, 10–25 m and >25 m deep, based on Dolbeth et al. (2007).

Data source

The biological material was gathered within the framework of several monitoring projects carried out between 2000 and 2006 along the southern Portuguese coast. Therefore, samples are not evenly distributed along the coast; deeper stations are scarce in the eastern part of the study area (Fig. 1). This is a common handicap already indicated in similar studies (Hoey et al. 2004; Zenetos et al. 2000). Most samples were collected during spring–summer seasons (Table 1). Generally, subtidal samples were collected using a Van Veen grab (0.05 m²) (Table 1). However, some samples from shallow waters (down to 6 m depth) were collected by scuba divers using hand-cores (three core samples as one replicate; combined area of 0.018 m²) (Table 1). Therefore, in order to compare different samples, abundance values were standardized to 1 m² (Zenetos et al. 2000). Regardless of the sampling method, at least three replicates were taken per site in a total of 211 samples. In the laboratory, amphipods were sorted and specimens were identified to the lowest possible taxonomic level and counted under a binocular stereomicroscope. Species' names are in accordance with the World Register of Marine Species—WoRMS (<http://www.marinespecies.org/aphia.php?p=search>).

Sediment samples

The information on sediment classification was gathered from different project reports. Within the study area, sediments ranged from very fine sand to gravel. Fine, medium, and coarse sand were also well represented (Table 1). Sediments were grouped into three types: very fine to fine sands (VF–F), medium sands (M), and coarse sand to gravel (C–G).

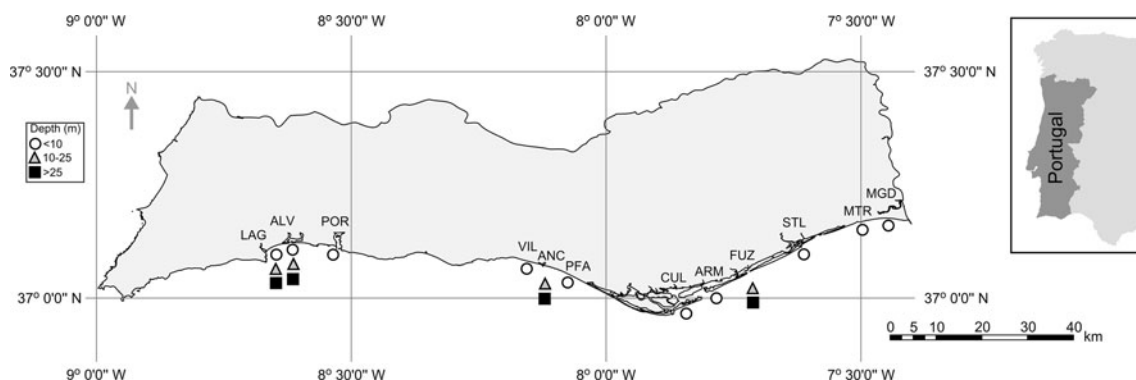


Fig. 1 Southern Portuguese coast; location of sampling stations

Table 1 Information on depth, sediment type, sampling method and date for all sites analyzed in the present study

Site	Depth	Sediment type	Sampling method	Sampling date
LAG4	15	Very coarse sand	Van Veen grab	Spring 2006
LAG5	25	Fine sand	Van Veen grab	Spring 2006
LAG6	30	Fine sand	Van Veen grab	Spring 2006
LAG8	5	Mean sand	Van Veen grab	Spring 2006
LAG12	8	Mean sand	Van Veen grab	Spring 2006
ALV2	24	Very fine sand	Van Veen grab	Spring 2000
ALV3	24	Very fine sand	Van Veen grab	Spring 2000
ALV4	26	Coarse sand	Van Veen grab	Spring 2000
ALV5	12	Mean sand	Van Veen grab	Spring 2000
ALV6	13	Mean sand	Van Veen grab	Spring 2000
ALV7	8	Mean sand	Van Veen grab	Spring 2000
ALV8	4	Coarse sand	Van Veen grab	Spring 2000
ALV9	13	Fine sand	Van Veen grab	Spring 2000
POR1	6	Mean sand	Corer	Spring 2004
POR2	6	Mean sand	Corer	Spring 2004
POR3	6	Mean sand	Corer	Spring 2004
VIL1	6	Coarse sand	Corer	Spring 2004
VIL2	6	Coarse sand	Corer	Spring 2004
VIL3	6	Coarse sand	Corer	Spring 2004
ANC2	13	Fine sand	Van Veen grab	Winter 2001
ANC3	31	Very fine sand	Van Veen grab	Winter 2001
ANC4	32	Very fine sand	Van Veen grab	Winter 2001
ANC5	20	Coarse sand	Van Veen grab	Winter 2001
ANC6	37	Very fine sand	Van Veen grab	Winter 2001
ANC7	21	Coarse sand	Van Veen grab	Winter 2001
ANC8	31	Very fine sand	Van Veen grab	Winter 2001
ANC9	29	Coarse sand	Van Veen grab	Winter 2001
ANC10	34	Mean sand	Van Veen grab	Winter 2001
ANC11	12	Coarse sand	Van Veen grab	Winter 2001
ANC12	15	Coarse sand	Van Veen grab	Winter 2001
ANC13	25	Fine sand	Van Veen grab	Winter 2001
PFA1	6	Fine sand	Corer	Spring 2004
PFA2	6	Fine sand	Corer	Spring 2004
PFA3	6	Fine sand	Corer	Spring 2004
PFA4	1	Fine sand	Van Veen grab	Spring 2004
PFA5	1	Fine sand	Van Veen grab	Spring 2004
PFA6	1	Fine sand	Van Veen grab	Spring 2004
PFA7	1	Mean sand	Van Veen grab	Spring 2004
PFA8	1	Mean sand	Van Veen grab	Spring 2004
PFA9	1	Mean sand	Van Veen grab	Spring 2004
CUL1	6	Mean sand	Corer	Spring 2004
CUL2	6	Mean sand	Corer	Spring 2004
CUL3	6	Mean sand	Corer	Spring 2004
ARM1	6	Fine sand	Corer	Spring 2004
ARM2	6	Fine sand	Corer	Spring 2004
FUZ2	27	Fine sand	Van Veen grab	Summer 2001

Table 1 continued

Site	Depth	Sediment type	Sampling method	Sampling date
FUZ3	23	Fine sand	Van Veen grab	Summer 2001
FUZ4	30	Very fine sand	Van Veen grab	Summer 2001
FUZ5	26	Fine sand	Van Veen grab	Summer 2001
FUZ6	13	Very fine sand	Van Veen grab	Summer 2001
FUZ7	28	Very fine sand	Van Veen grab	Summer 2001
STL1	6	Coarse sand	Corer	Spring 2004
STL2	6	Coarse sand	Corer	Spring 2004
STL3	6	Coarse sand	Corer	Spring 2004
MRT1	6	Coarse sand	Corer	Spring 2004
MRT2	6	Coarse sand	Corer	Spring 2004
MRT3	6	Coarse sand	Corer	Spring 2004
MGD1	6	Coarse sand	Corer	Spring 2004
MGD2	6	Coarse sand	Corer	Spring 2004

Data analysis

Varying sample sizes do not allow for reliable comparisons of species richness across the study area, as this variable will increase with sample size (Magurran 1988). Therefore, rarefaction curves developed by Sanders (1968) and modified by Hurlbert (1971) were used to provide an unbiased estimate of species richness, as the estimated number of species in a sub-sample of 50 individuals [$ES_{(50)}$]. Density (ind. m^{-2}) was calculated and analyzed together with $ES_{(50)}$ in relation to depth and sediment type. Relationships between $ES_{(50)}$ and density as a function of depth and sediment type were established through regression analyses, by fitting a linear function to raw data ($Y = bX$, no intercept in the model, as null number of species implies null density). The degree of association between variables was assessed by the correlation coefficient (r), and the slopes of the linear regressions were compared using a t -test ($H_0: \beta_A = \beta_B$; $H_A: \beta_A \neq \beta_B$) (Zar 1996).

The amphipod community structure was analyzed by a combination of uni- and multivariate techniques included in the PRIMER v5 software (Clarke and Gorley 2001). Faunal relationships were assessed by a hierarchical cluster analysis (CLUSTER) using the Bray-Curtis coefficient and the unweighted pair-group average algorithm. As data were not homogeneously sampled, a presence/absence transformation was chosen in order to remove the effect of varying sample sizes and seasonality (Ysebaert et al. 2002). Correlations between density of the most abundant amphipods with depth and sediment type were performed using the STATISTICA software. Species showing significant correlations were selected, and subsequently, a one-way ANOVA was performed for factors 'depth' (orthogonal, 3 levels: <10 m; 10–25 m; >25 m) and 'sediment' (orthogonal, 3 levels: VF–F; M; C–G).

Species were also assigned to different biogeographic regions adopted from Conradi and López-González (1999). The groups established were the following:

- I. Mediterranean endemic
- II. Atlantic, present in the Mediterranean
- III. Atlantic, absent from the Mediterranean
- IV. Atlantic, present in the Mediterranean and Indo-Pacific Ocean
- V. Atlantic, present in the Indo-Pacific Ocean
- VI. Cosmopolitan

Results

The present data set allowed the identification of 93 taxa belonging to 24 families. The most abundant families were Ampeliscidae (21.9%), Corophiidae (19.8%), Caprellidae (11.6%), Urothoidae (10.6%), and Aoridae (7.5%).

$ES_{(50)}$ and density as a function of depth and sediment type are shown in Fig. 2. Significant relationships were observed for all depth levels. The ratio density/species richness increased with depth (Fig. 2a). The comparison of slopes of the linear regressions showed that significant differences were observed between depth levels (except between all data and the 10–25 m depth level) (Fig. 2a).

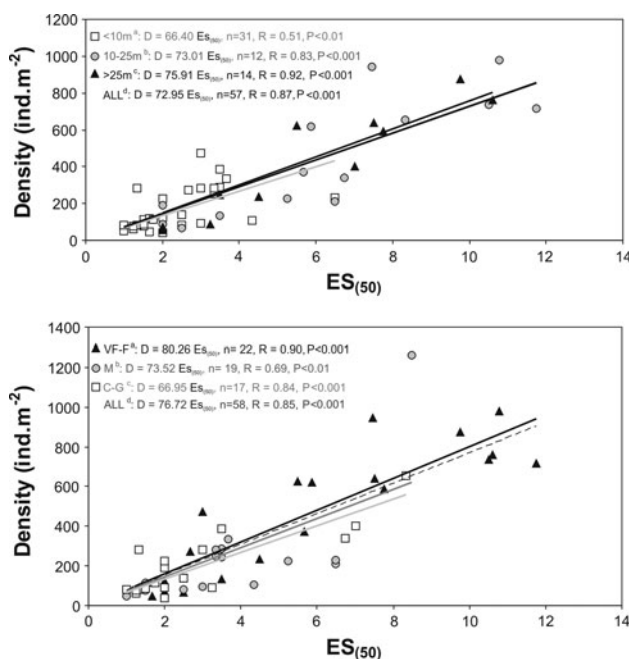


Fig. 2 Relationships between density (D , ind. m⁻²) and diversity ($ES_{(50)}$ = estimated number of amphipod taxa in a subsample of 50 individuals) for different depth levels (above) and sediment types (below). Different superscript letters denote statistically significant differences between slopes of regression lines. ALL = entire depth gradient and all sediment types, respectively; VF–F very fine to fine sand, M medium sand, C–G coarse sand to gravel. For clarity, only average values per station have been plotted

Significant differences were also detected for all sediments considered (Fig. 2b). The ratio density/species richness significantly increased from coarser to finer sediments (Fig. 2b). It is worth noting that some outliers were removed from this analysis, namely samples from a maerl bottom, which turned out to be a hotspot of density. Therefore, benthic assemblages associated with maerl beds were analyzed separately with respect to faunal differences related to sediment type.

Amphipod assemblages

Multivariate analysis performed in order to assess for spatial patterns along the southern Portuguese coast is presented in Fig. 3. Density, estimated number of species, depth, and sediment classification for each site are also presented. Three main clusters were observed (I, II, III). Clusters I and II mainly comprised shallower stations with medium sand to gravel (Fig. 3). Samples of both clusters were characterized by low density and low estimated number of species. Nevertheless, while samples from cluster I presented a slightly higher mean density (cluster I: 162 ± 119 ind. m⁻²; cluster II: 152 ± 108 ind. m⁻²), samples from cluster II showed higher mean species richness (cluster I: 2.0 ± 0.9 ; cluster II: 2.7 ± 0.9) (Fig. 3). In contrast, cluster III (sub-clusters a and b) mainly comprised samples located at depths higher than the 10-m depth contour (Fig. 3). Both clusters, IIIa and IIIb, showed high density and number of species. Cluster IIIa mainly comprised samples located at greater depth (mean depth 25 ± 5 m) and of finer sediments than cluster IIIb (mean depth 12 ± 6 m). Higher species richness was associated with cluster IIIa (cluster IIIa: 8.1 ± 2.1 ; cluster IIIb: 6.2 ± 1.6), while cluster IIIb presented higher density (cluster IIIa: 683 ± 161 ind. m⁻²; cluster IIIb: 780 ± 1111 ind. m⁻²).

Species affinities

Some amphipod taxa showed a preferential distribution to specific depth levels. Fifteen taxa, however, were common to all depth levels: *Atylus vedlomensis* (Bate & Westwood, 1862), *Cheirocratus sundevalli* (Rathke, 1843), *Medicorophium annulatum* (Chevreux, 1908), *Lembos websteri* Bate, 1857, *Leptocheirus pectinatus* (Norman, 1869), *Leucothoe oboa* Karaman, 1971, *Orchomenella nana* (Kroyer, 1846), *Periculodes longimanus* (Bate & Westwood, 1868), *Phtisica marina* Slabber, 1769, *Siphonocetes* (*Centraloecetes*) *dellavallei* Stebbing, 1899 and *Urothoe elegans* (Bate, 1857). *Ampelisca* spp., *Caprella* spp., members of the family Melitidae and *Photis* spp., were also common to all depth levels; these taxa, however, were not identified to species level, and the relationship between their density and depth has thus to be interpreted with caution. The most

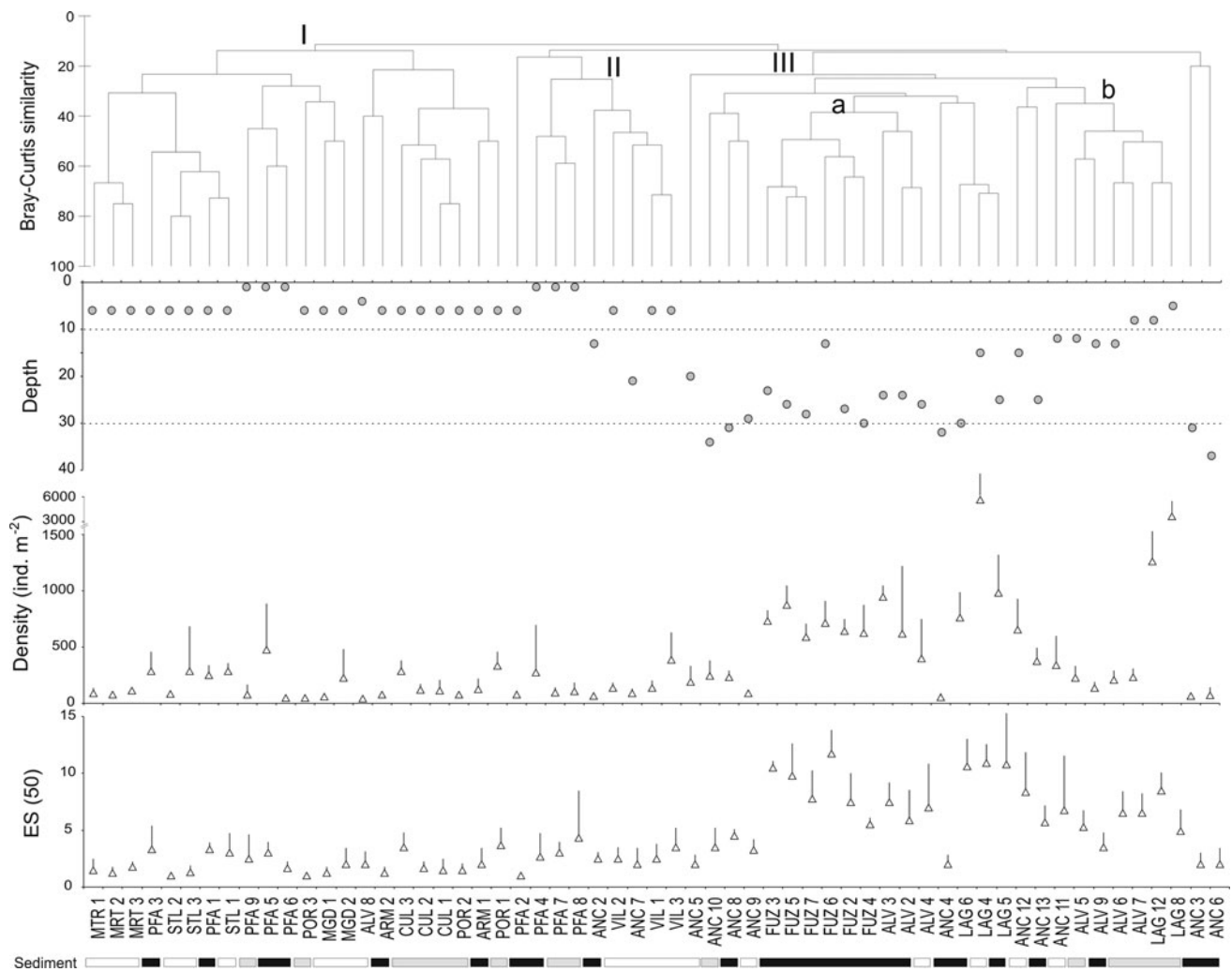


Fig. 3 Cluster diagram of sampling stations with the respective depth, sediment classification, density (+SD) and estimated number of species ($ES_{(50)}$ + SD). Sediment: *black rectangles* = very fine to fine sands; *gray rectangles* = medium sand; *white rectangles* = coarse sand to gravel

abundant taxa as well as taxa which were exclusive to a particular depth level are listed in Table 2. Within the most abundant taxa, the intermediate and the deepest depth level shared the highest number of taxa. Nevertheless, the highest number of exclusive taxa was observed for the two upper depth levels (<10 and 10–25 m). The species of the genus *Siphonoecetes* (*Centraloecetes*) and *Bathyporeia* were particularly abundant above 10 m depth, together with *Urothoe grimaldii* Chevreux, 1895, *Urothoe poseidonis* Reibish, 1905, and *Perioculodes longimanus*. *Urothoe poseidonis* and *Siphonoecetes* (*Centraloecetes*) *kroyeranus* Bate, 1856, were not only abundant but also exclusive of this depth level, together with other species with less expression (Table 2). Although not exclusive, the genera *Ampelisca*, *Caprella*, and *Photis* were well represented between the 10 and 25 m isobaths, as well as *Harpinia antennaria* Meinert, 1890, *Microdeutopus armatus* Chevreux, 1886, *Urothoe elegans*, *Leptocheirus pectinatus*, *Leptocheirus hirsutimanus* (Bate, 1862), *Lembos websteri*,

Leucothoe oboa, *Pariambus typicus* (Krøyer, 1884), and *Megamphopus cornutus* Norman, 1869. At depths greater than 25 m, *Maera grossimana* (Montagu, 1808), *Argissa hamatipes* (Norman, 1869), and members of the Isaeidae were the most characteristic taxa, but only the latter two were exclusively sampled at this depth level.

The most abundant taxa per sediment type and the taxa which were exclusive to a specific sediment type are represented in Table 3. The highest number of exclusive taxa was observed in VF–F sands, while 35 taxa (37%) were common to all sediment types. This latter group comprises taxa common to all depth levels (except Melitidae): *Bathyporeia* spp., *Gammaropsis maculata* (Johnston, 1828), *Gammaropsis* sp., *Harpinia antennaria*, *Lembos* sp.A, *Leptocheirus hirsutimanus*, *Leucothoe incisa* (Robertson, 1892), Lysianassidae, *Maera grossimana*, *Megaluropus agilis* Hoeck, 1889, *Megamphopus cornutus*, *Microdeutopus armatus*, *Microdeutopus gryllotalpa* Costa, 1853, *Microtopus maculatus* Norman, 1867, *Monoculodes*

Table 2 Density (D —no. ind. m^{-2}) of the most abundant taxa in the considered depth levels

<10 m		10–25 m		>25 m	
Taxa	D	Taxa	D	Taxa	D
Most abundant taxa					
<i>Siphonocetes (Centraloecetes) dellavallei</i>	11,140	<i>Ampelisca</i> spp.	13,840	<i>Ampelisca</i> spp.	3,980
<i>Urothoe grimaldii</i>	2,590	<i>Caprella</i> spp.	10,040	<i>Harpinia antennaria</i>	920
<i>Bathyporeia</i> spp.	2,540	<i>Harpinia antennaria</i>	2,620	<i>Microdeutopus armatus</i>	500
<i>Siphonocetes (Centraloecetes) kroyeranus</i>	1,960	<i>Microdeutopus armatus</i>	1,800	<i>Atylus vedlomensis</i>	160
<i>Urothoe poseidonis</i>	1,500	<i>Photis</i> spp.	1,620	<i>Maera grossimana</i>	160
<i>Ampelisca</i> spp.	1,460	<i>Urothoe elegans</i>	1,420	<i>Medicorophium annulatum</i>	140
<i>Medicorophium annulatum</i>	1,300	<i>Leptocheirus pectinatus</i>	1,260	<i>Leucothoe oboa</i>	140
<i>Urothoe cf. hesperiae</i>	1,110	<i>Urothoe cf. hesperiae</i>	1,240		
<i>Atylus vedlomensis</i>	990	<i>Leptocheirus hirsutimanus</i>	980		
<i>Periculodes longimanus</i>	960	<i>Medicorophium annulatum</i>	900		
		<i>Lembos websteri</i>	720		
		<i>Leucothoe oboa</i>	660		
		<i>Urothoe grimaldii</i>	620		
		<i>Pariambus typicus</i>	600		
		<i>Megamphopus cornutus</i>	600		
		<i>Atylus vedlomensis</i>	560		
Exclusive taxa					
<i>Amphilochus tenuimanus</i>		<i>Caprella rapax</i>		<i>Argissa hamatipes</i>	
<i>Monocorophium ascherusicum</i>		<i>Animoceradocus semiserratus</i>		Isaetidae	
<i>Dexamine spinosa</i>		<i>Lepidepcreum longicornis</i>			
<i>Monoculodes subnudus</i>		<i>Metaphoxus pectinatus</i>			
<i>Siphonocetes (Centraloecetes) kroyeranus</i>		<i>Urothoe pulchella</i>			
<i>Urothoe poseidonis</i>		<i>Westwoodilla</i> sp.			

Only taxa accounting for 80% of total density per depth level are shown. Only taxa which occurred in at least two samples from a certain depth level were considered exclusive

carinatus (Bate, 1857), *Pontocrates altamarinus* (Bate & Westwood, 1862), *Siphonocetes (Centraloecetes) neapolitanus* Schiecke, 1979, *Urothoe grimaldii*, *Urothoe cf. hesperiae* Conradi, Lopez-Gonzalez & Bellan-Santini 1995, *Urothoe intermedia* Bellan-Santini & Ruffo, 1986 and *Urothoe pulchella* (Costa, 1853). The taxa *Medicorophium annulatum* and *Bathyporeia* spp. were well represented both in fine and medium sands, while *Photis* spp. presented high densities in both VF–F sand and C–G bottoms. On the other hand, *Urothoe grimaldii* and *Urothoe cf. hesperiae* were common to M and C–G sediments.

A one-way ANOVA was performed for factors ‘depth’ and ‘sediment’ separately for the most abundant taxa (i.e., taxa accounting for more than 80% of abundance per depth level and sediment type). Species showing significant correlations with at least one factor are presented in Figs. 4 and 5. This analysis showed that seven taxa presented significant differences for the factor ‘depth’ and eight for the factor ‘sediment’ (Figs. 4, 5). *Bathyporeia* spp. and *Urothoe grimaldii* were more abundant at the lowest depth level

(Fig. 4). For the former taxa, significant differences were observed between stations located at this depth level and the remaining stations, while for the urothoid, significant differences were only detected for the deepest level. Densities of *Leucothoe oboa*, *Microdeutopus armatus*, and *Urothoe elegans* peaked at the intermediate depth level (10–25 m) but significant differences were only detected between stations located at this level and the shallower stations (<10 m). On the other hand, density of *Ampelisca* spp. and *Harpinia antennaria* was significantly lower at the shallower stations when compared with the remaining stations. As to the factor ‘sediment’, *Ampelisca* spp., *Harpinia antennaria*, and *Microdeutopus armatus* were significantly more abundant in finer sediments than in the remaining sediment types (Fig. 5). On the other hand, *Urothoe cf. hesperiae* and *Urothoe grimaldii* presented significantly higher densities in medium sands than in finer sediments. In contrast to these two species, the congeneric *Urothoe elegans* showed significantly higher densities in very fine to fine sands than in coarse sand to gravel. *Atylus vedlomensis* was significantly

Table 3 Density (D —no. ind. m^{-2}) of the most abundant taxa for the different sediment types

VF–F		M		C–G		Maerl	
Taxa	D	Taxa	D		D	Taxa	D
Most abundant taxa							
<i>Ampelisca</i> spp.	15,740	<i>Siphonoecetes</i> (<i>Centraloecetes</i>) <i>dellavallei</i>	11,160	<i>Ampelisca</i> spp.	1,830	<i>Caprella</i> spp.	9,780
<i>Harpinia antennaria</i>	3,460	<i>Bathyporeia</i> spp.	2,010	<i>Urothoe grimaldii</i>	1,340	<i>Lembos websteri</i>	640
<i>Siphonoecetes</i> (<i>Centraloecetes</i>) <i>kroyeranus</i>	1,940	<i>Ampelisca</i> spp.	1,670	<i>Atylus vedlomensis</i>	1,230	<i>Leptocheirus</i> <i>pectinatus</i>	620
<i>Microdeutopus armatus</i>	1,900	<i>Urothoe grimaldii</i>	1,570	<i>Urothoe poseidonis</i>	1,050	<i>Photis</i> spp.	560
<i>Urothoe elegans</i>	1,340	<i>Urothoe</i> cf. <i>hesperiae</i>	1,380	<i>Urothoe</i> cf. <i>hesperiae</i>	910	Lysianassidae	480
<i>Medicorophium annulatum</i>	900	<i>Mediorophium annulatum</i>	1,200	<i>Periculodes longimanus</i>	780	<i>Cheirocratus</i> <i>sundevalli</i>	360
<i>Photis</i> spp.	750	<i>Pontocrates arenarius</i>	810	<i>Leptocheirus hirsutimanus</i>	540		
<i>Pariambus typicus</i>	620			<i>Leptocheirus pectinatus</i>	450		
<i>Leucothoe oboa</i>	580			<i>Autonoe denticarpus</i>	440		
<i>Bathyporeia</i> spp.	550			<i>Megaluropus agilis</i>	420		
<i>Periculodes longimanus</i>	500			<i>Leucothoe incisa</i>	350		
				<i>Photis</i> spp.	340		
				<i>Abludomelita obtusata</i>	340		
				<i>Phthisica marina</i>	300		
				Melitidae	250		
				<i>Medicorophium annulatum</i>	240		
				<i>Megamphopus cornutus</i>	220		
				<i>Pontocrates altamarinus</i>	200		
Exclusive taxa							
<i>Apherusa bispinosa</i>		<i>Dexamine spinosa</i>		<i>Abludomelita obtusata</i>		<i>Gammarella fucicola</i>	
<i>Apherusa ovalipes</i>							
<i>Argissa hamatipes</i>							
<i>Atylus guttatus</i>							
<i>Caprella rapax</i>							
<i>Medicorophium runcicorne</i>							
<i>Harpinia crenulata</i>							
Isaeidae							
<i>Leucothoe spinicarpa</i>							
<i>Pariambus typicus</i>							
<i>Synchelidium haplocheles</i>							
<i>Westwoodilla rectirostris</i>							
<i>Westwoodilla</i> sp.							

Only taxa accounting for 80% of total density per sediment type are shown. Only taxa which occurred in at least two samples from a certain sediment type were considered exclusive. VF–F very fine to fine sand, M medium sand, C–G coarse sand to gravel

more abundant in the latter sediment type than in medium sands, whereas *Bathyporeia* spp. were preferentially collected in medium sands compared with coarser sediments.

Due to the specificity of maerl substrate, samples from this type of bottom were analyzed separately. In maerl beds, 27 amphipod taxa were collected. Samples were characterized by an extremely high dominance level of caprellids of the genus *Caprella* (62.9% of total density). Only six

taxa accounted for 80% of total abundance, namely (besides *Caprella* spp.) *Lembos websteri*, *Leptocheirus pectinatus*, *Photis* spp., Lysianassidae and *Cheirocratus sundevalli* (Table 3). *Gammarella fucicola* (Leach, 1814) was exclusive to maerl beds.

Species affinities were also assessed by means of cluster analysis (Fig. 6). The results indicated that groups 1, 2, and 3 were separated from groups based on depth differences. Spe-

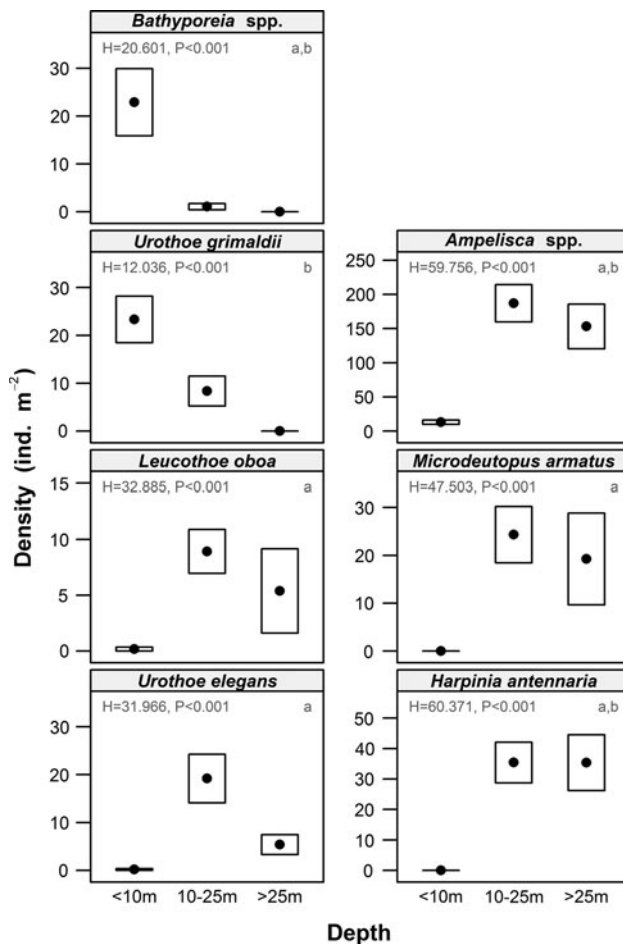


Fig. 4 Boxplots showing mean density and standard error (box) for the amphipod taxa with a significant relationship with depth. a, significant differences between <10 and 10–25 m depth; b, significant differences between <10 and >25 m depth; c, significant differences between 10–25 m and >25 m depth, $P < 0.05$

cies of groups 1, 2, and 3 were mainly associated with samples collected from shallow waters down to 10 m depth, while species of group 4 were chiefly distributed on deeper bottoms. The separation of groups 1, 2, and 3 were less evident. In general, group 3 comprises species especially abundant in medium sands (except *Megaluropus agilis*, dominant in coarse sediments), while *Leucothoe incisa* and *Autonoe denticarpus* (Myers & McGrath, 1978) (group 1) were mainly associated with coarse sand to gravel. The separation of species of group 2 was not clear; two species (*Siphonocetes neapolitanus* and *Urothoe intermedia*) were mainly associated with medium sands, while *Urothoe poseidonis* was more frequent in coarse sediments. Most of the species of group 4 were preferentially distributed between 10 and 25 m depth in very fine to fine sands [*Gammaropsis sophiae* (Boeck, 1861), *Harpinia pectinata* Sars, 1891, *Microdeutopus armatus*, *Ampelisca* spp., *Urothoe elegans*, *Orchomenella nana*] or on maerl bottom (*Gammaropsis* sp., *Cheirocratus sundevalli*, *Leptocheirus pectinatus* and *Caprella* spp.).

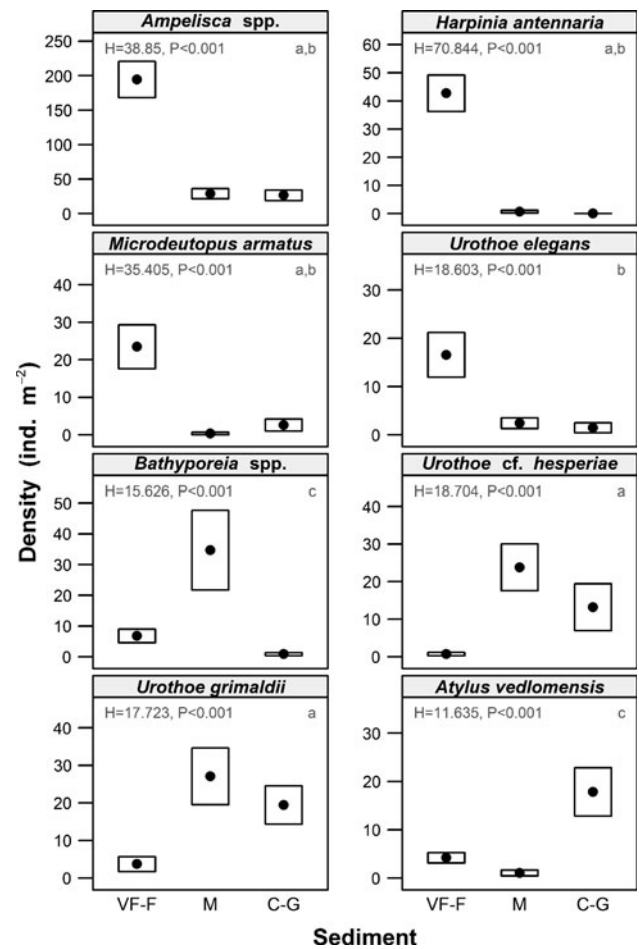


Fig. 5 Boxplots showing mean density and standard error (box) for the amphipod taxa with a significant relationship with sediment type. a, significant differences between VF-F and M; b, significant differences between VF-F and C-G; c, significant differences between M and C-G, $P < 0.05$

Biogeography

Most recorded species have an Atlantic-Mediterranean distribution, corresponding to groups I–II and accounting for 72% of the total number of taxa (Fig. 7). The number of taxa common to the Atlantic, the Mediterranean, and the Indo-Pacific Ocean (group IV) was high (12%), while only 5% of the taxa were exclusive for Atlantic waters (group III).

Discussion

Distribution of amphipod assemblages in relation to depth

The study of amphipod assemblages along the southern Portuguese coast in relation to habitat features (sediment type and bathymetry) showed that depth may be a major physical factor affecting the spatial distribution and composition of

Fig. 6 Cluster diagram of species present in more than 5% of samples based on the Bray-Curtis similarity index

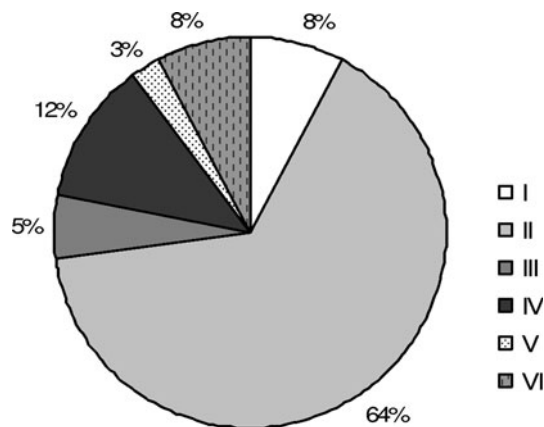
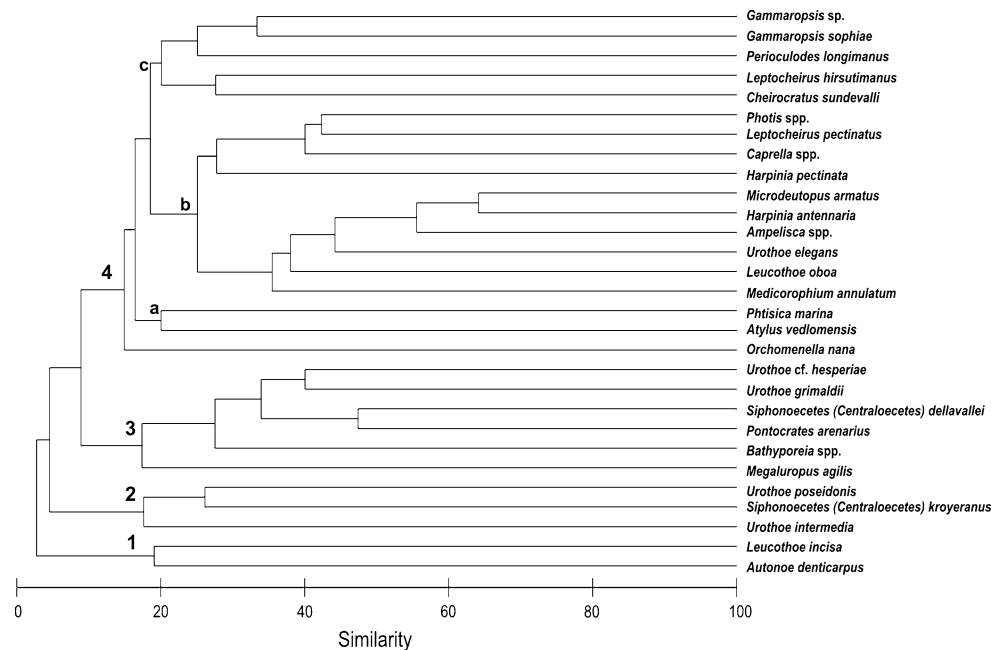


Fig. 7 Percentage of recorded taxa belonging to the following groups of geographical distribution. I—Mediterranean endemic; II—Atlantic, present in the Mediterranean; III—Atlantic, absent from the Mediterranean; IV—Atlantic, present in the Mediterranean and Indo-Pacific Ocean; V—Atlantic, present in the Indo-Pacific Ocean; VI—Cosmopolitan

these crustaceans. Despite the occurrence of different sediment types along the depth profile, biological samples were mainly separated according to depth. The main segregation was observed between samples collected in shallow waters (<10 m) and those from greater depth levels. These two major groups showed distinct community patterns with more diverse and abundant assemblages in sediments deeper than 10 m.

Along the depth profile, changes are observed in several environmental characteristics such as food availability (namely primary productivity), temperature, and bottom stability, the latter being correlated with the influence of waves, wind, and storm events (Hernández-Arana et al.

2003; Snelgrove 1998). In the present study, environment harshness, in terms of wave impact, came along with decreased diversity and density. When analyzing a depth gradient in the central part of the southern Portuguese coast, Dolbeth et al. (2007) also found lower values of these biological variables in the shallower and more hydrodynamic areas. The influence of the hydrodynamics on the distribution of macrobenthic communities was also reported in other studies (Cunha et al. 1997; Janssen and Mulder 2005; Martínez and Adarraga 2001; Munilla and San Vicente 2005; San Vicente and Sorbe 1999). In the present study, the number of exclusive taxa, diversity and density peaked between 10 and 25 m depth. This may reflect an abatement of physical constraints caused namely by waves, allowing for the establishing of a higher number of species. Indeed, for the central part of the southern Portuguese coast, Dolbeth et al. (2007) found that active depths, i.e., depths at which hydrodynamics is higher, can be extended up to 10 m deep. As to the relationship between density and diversity, however, we found increase of density with depth.

Distribution of amphipod assemblages in relation to sediment grain-size

Significant relationships between density/diversity and sediment type were also detected for the amphipod assemblages. Higher diversity and density were observed in finer and medium grain-size sediments, in accordance with amphipod assemblages reported previously for the Portuguese coast (Marques and Bellan-Santini 1990b). Finer sediments usually present higher organic matter content

(Carvalho et al. 2006a; Sousa et al. 2007), which is an important food resource for benthic communities (Rodríguez-Graña et al. 2008). Moreover, the existence of finer sediments also reflects low levels of physical disturbance. Very fine to fine sands mainly occur beyond the depth of closure, i.e., at depths where beach-nearshore profiles display minor vertical change, and limited net sediment transport is expected to occur (Nicholls et al. 1998). Along the central to the eastern part of the south Portuguese coast, this depth was estimated to 6–10 m (Andrade 1990; Ferreira et al. 2000). The depth of closure reflects differences in hydrodynamics, with lower energy conditions seawards this limit (Dolbeth et al. 2007), which is in accordance with the present findings. Therefore, both increased food availability and reduced disturbance may allow for the existence of richer and denser assemblages. In contrast, coarser sediments are known to generally support lower density and richness values (e.g., Hoey et al. 2004), which was also observed for the amphipod assemblages of southern Portugal.

A particular location characterized by maerl presented a peak of density and was not considered for the regression analysis. In terms of sediment particle size analysis, samples were classified as gravel, produced by loosely lying coralline red algae (Rhodophyta, Corallinales) or unattached calcified red algae. These forming algae can be regarded as ‘ecological engineers’ (Steller et al. 2003), creating ecological conditions which allow the establishment of a high number of species with distinct functional traits (De Grave 1999; Sciberras et al. 2009; Steller et al. 2003). Considering the particular features of these habitats, amphipod assemblages of maerl beds may be expected to diverge from those typical of clean sandy areas. To our knowledge, this is the first description of macrobenthic communities of Portuguese maerl beds, and this is particularly relevant as these are priority conservation areas (Barbera et al. 2003; Birkett et al. 1998; Grall and Hall-Spencer 2003; Wilson et al. 2004). Maerl beds serve as nurseries for the juveniles of several commercial species (Kamenos et al. 2004). In Galicia (NW Spain), commercial bivalves (*Pecten maximus*, *Aequipecten opercularis*, *Mimachlamys varia* and *Venerupis* spp.) are also gathered from maerl habitats (Peña and Bárbara 2009). Besides fishing, dredging, eutrophication, and aquaculture are known to threaten these highly diverse habitats (Barbera et al. 2003; Grall and Hall-Spencer 2003; Hall-Spencer and Moore 2000; Hall-Spencer et al. 2006). A study on the crustacean community associated with maerl habitats in Ireland showed that the 48 amphipod taxa collected accounted for more than 95% of the community’s abundance (De Grave 1999). Nevertheless, this dominance of amphipods was not always observed; other studies reported the co-dominance of molluscs,

crustaceans, and annelids (Sciberras et al. 2009). Maerl bottoms are characterized by high species diversity, although most dominant species are not exclusively associated with them (De Grave 1999; Sciberras et al. 2009; and the present study). Rather than the occurrence of exclusive species, it is the overall species assemblage that makes these habitats unique (Sciberras et al. 2009). In some studies, amphipod assemblages of maerl beds were found similar to those of gravel bottoms, which were linked to similar hydrodynamic conditions and the three-dimensional sediment structure in terms of large interstitial cavities (De Grave 1999). The dominance of caprellids, lysianassids, *Leptocheirus pectinatus* (Corophiidae), and *Cheirocratus sundevalli* (Cheirocratidae) had also been reported by De Grave (1999) and Axelsson et al. (2008). Axelsson et al. (2008) also found *Gammarella fucicola* as a dominant species within maerl beds. Although not dominant in the present study, *Gammarella fucicola* was exclusively collected within this area. However, this species is not exclusively associated with maerl, as it was already collected in other distinct habitats, both intertidal (Carvalho et al. 2006b) and subtidal (Carvalho et al. 2007, 2009) areas of the Ria Formosa lagoon (southern Portuguese coast).

Ecological patterns of dominant taxa

In the present study, the ten most abundant taxa accounted for 67.5% of the total density (*Ampelisca* spp., *Siphonoeetes dellavallei*, *Caprella* spp., *Harpinia antennaria*, *Urothoe grimaldii*, *Bathyporeia* spp., *Urothoe* cf. *hesperiae*, *Medicorophium annulatum*, *Microdeutopus armatus* and *Siphonoeetes kroyeranus*). The dominance of *Ampelisca* spp. may be biased by the identification to genus level only. However, the dominance of ampeliscids is common in soft-bottom communities (Marques and Bellan-Santini 1991; Poggiale and Dauvin 2001). Marques and Bellan-Santini (1991) suggested that they have a key role as food for many secondary consumers. Nevertheless, different species of ampeliscids are likely to occur along the depth profile and within areas of different sediment types. From the top ten taxa, only four were present across the depth profile (*Ampelisca* spp., *Siphonoeetes dellavallei*, *Caprella* spp. and *Medicorophium annulatum*). However, they were not equally distributed. *Ampelisca* spp. and *Caprella* spp. were dominant in intermediate depths, while *Siphonoeetes dellavallei* were mainly collected in low depths (<10 m). *Medicorophium annulatum* was abundant until the 25 m isobath. These taxa were also collected from very fine to fine sands to gravel and, except for *Medicorophium annulatum*, were also present in maerl samples. Although this corophiid has been described as typical of mud (Myers 1982), Conradi and López-González (1999) also collected it in a

wide variety of substrata. Therefore, and assuming that depth is an important factor for the spatial distribution of amphipods, the species previously reported may be less specific with respect to environmental conditions, particularly down to 40 m depth.

Bathyporeia spp., *Urothoe grimaldii*, *Urothoe* cf. *hesperiae*, and *Microdeutopus armatus* were also recorded from very fine sand to gravel, but their spatial distribution was limited by depth. *Microdeutopus armatus* was absent from samples collected down to 10 m. The remaining species were only present down to 25 m depth and were especially abundant until 10 m depth or, in the case of *Urothoe* cf. *hesperiae*, evenly distributed until 25 m. *Urothoe* cf. *hesperiae* was also recorded in the Algeciras Bay from 3 to 30 m, while species of the genus *Bathyporeia* and *Urothoe grimaldii* are very typical of shallow water sandy areas (Conradi and López-González 1999; Hoey et al. 2004; Lourido et al. 2008; Marques and Bellan-Santini 1991, 1993; Scipione et al. 2005). Although it did not range among the ten most abundant species, another urothoid was collected in this study (*Urothoe elegans*). While the previous urothoids were mainly observed in medium sands, *Urothoe elegans* was preferentially distributed in fine sands between 10 and 25 m depth. Therefore, three species of the same genus show different ecological traits, which is worth noting when inferring such traits at higher taxonomic levels. *Harpinia antennaria* presented a density peak between 10 and 25 m depth and was absent from the shallowest areas. *Siphon-oecetes kroyeranus* proved to be more habitat-specific, as it was only recorded down to 10 m depth and was absent from the coarsest sediments. This species has been reported as dominant in both Atlantic (Moreira et al. 2008) and Mediterranean (San Vicente and Sorbe 1999) beach sediments, and in fine to medium sandy bottoms of Galician rias (Lourido et al. 2008) which is in accordance with the present findings.

Biogeographic notes

Amphipods are often expected to have an endemic tendency due to their limited dispersal capacity, resulting both from the direct development and from reduced swimming capacity (Marques and Bellan-Santini 1990a). Conradi and López-González (1999) found a typical Mediterranean amphipod community (although with only 18% endemic species, compared to 38% in the Mediterranean) in Algeciras Bay (Strait of Gibraltar), the westernmost part of the Mediterranean Sea. In the present study, Atlantic-Mediterranean amphipods were well represented on the southern Portuguese coast, and the occurrence of 8% of Mediterranean endemic species may reflect the extension of the Mediterranean fauna beyond the Strait of Gibraltar. Previous studies on benthic amphipods (Marques and Bellan-Santini 1990a) and on brachyurans

(Almaça 1985) along the Portuguese coast showed a high affinity with the Mediterranean fauna, highlighting the relevance of this area as a biogeographic transition between Atlantic and Mediterranean. Therefore, the classification of the southern Portuguese benthic fauna as Atlantic-Mediterranean was once more confirmed in the present study. Nevertheless, as amphipods are sensitive to changes in seawater temperature (e.g., Lawrence and Soame 2004), the distribution patterns of amphipod assemblages are also expected to change in a global warming scenario. In this context, the present study may provide valuable baseline information to ascertain potential future impacts of climate change.

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