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Species characterization of soft bottom habitats by depth and sediment particle size on the Catalan coast (NW Mediterranean): unexpected species composition of the assemblages

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Abstract

The aim of the study is to describe the macrofaunal composition of marine soft bottom habitats on the Catalan coast between a depth of 3 and 35 meters, considering all groups of macroinvertebrates. The study also aims to compare our data with previous studies focused on the NW Mediterranean and to define the variables that drive assemblage composition. Depending on the species composition and the structure of the assemblages, six different habitats, mainly defined by depth and sediment granulometry, are described. Shallow (<20 m) and deep (>20 m) habitats are easily distinguished and are subdivided in three habitats each: (1) very coarse and coarse sediments (coarse sediments); (2) medium, fine and very fine sands (fine sediments); and (3) muddy sediments. Fine sediments in both shallow and deep waters have emerged as the most common and extensive habitats along the coast up to a depth of 35 meters. Neither coarse nor muddy habitats are frequent. The characterization of shallow habitats produced some unexpected results with respect to previous studies: *Spisula subtruncata* and *Lucinella divaricata* were dominant, while neither *Ditrupa arietina* nor *Owenia fusiformis*, previously mentioned as dominant polychaetes in shallow fine sand habitats, were common. Polychaetes were, in general, the dominant group (both in species richness and abundance) in the six habitats, except in shallow fine sediments, which were dominated by mollusks. The study is a benchmark for future monitoring of soft bottom habitats on the Catalan coast to a depth of 35 meters.

Keywords: soft bottom; macroinvertebrates; habitat types; Mediterranean Sea.

Introduction

The characterization of marine benthic assemblages is critical to identify habitats, propose new protected areas and establish management tools for a better use of these habitats (Gogina & Zettler, 2010). In non-isolated marine ecosystems susceptible to the influence of human activities, such as coastal and estuarine environments, the importance of studies on large spatial scales for improved management of habitats and resources, and especially for the development of the relatively new ecosystem-based approach and the establishment of marine protected area networks (Desroy *et al.*, 2002; Ysebaert & Herman, 2002; Fraschetti *et al.*, 2011) has recently been recognized. Moreover, inadequate knowledge of the assemblages makes it difficult to understand the origin and control of changes due to human activities such as fishing, pollution, habitat destruction, and climate change.

Soft substrates cover the vast majority of oceans bottoms. Soft bottom macrobenthic assemblages along the French coast of the NW Mediterranean Sea were described between 1960 and 1970s (Pérès & Picard, 1964; Guille, 1970; 1971; Massé, 1972), and this knowledge has more recently been updated (Grémare *et al.*, 1998a; Labrune *et al.*, 2008; Bonifácio *et al.*, 2018). The northern Catalan coast was also studied in the 1970s by Desbruyéres *et al.* (1972-73), including all groups of macroinvertebrates. More recent studies have focused on detailed groups of macroinvertebrates, or specific areas or habitats. Polychaete assemblages alone or with bivalves (Sardá, 1986; Pinedo *et al.*, 1996; 1997; Pinedo, 1998; Cardell *et al.*, 1999; Sardá *et al.*, 1999; 2000; 2014) and, to a lesser extent cumaceans (Corbera & Cardell, 1995), have been described on the Catalan coast. Although focusing only on polychaetes, other studies have been carried out along both the French and Spanish Catalan coasts (Sardá *et al.*, 2014). Seasonality of soft bottom assemblages has also been described in specific areas (Pinedo *et al.*, 1996; 1997; Sardá *et al.*, 1995; 1999; Cardell, 1996). Moreover, several studies have been performed on the Ebre Delta continental shelf and in the Ebre Delta Bays (Martin, 1991; Martin *et al.*, 2000; De Juan & Cartes, 2011;

Jordana *et al.*, 2015). All these studies have contributed to a better understanding of the structure and seasonality of soft bottom assemblages and their relationships with environmental variables.

Following Guille (1970; 1971), five benthic "communities" (terminology of the author) can be identified along the French-Catalan coast: (1) the *Spisula subtruncata* community, associated with fine sands; (2) the *Nephtys hombergii* community, associated with muddy sands; (3) the *Scoloplos armiger* community, associated with sandy muds; (4) the *Nucula sulcata* community, associated with pure muds; and (5) the *Venus ovata* (currently named *Timoclea ovata*) community, associated with heterogeneous muds. However, Picard (1965) had previously proposed a different classification for the coast of Provence: (1) the Well Sorted Fine Sands community, associated with fine sands; (2) the Coastal Detritic and Muddy Detritic communities, associated with muddy sands; and (3) the Terrigenous Coastal Muds community, associated with pure muds. More recently, Labrune *et al.* (2007a) made the correspondence between the communities identified by Guille (1971) and Picard (1965), together with the communities found during their study carried out between the French-Spanish border and at the mouth of the Rhône River, based on polychaete assemblages. Labrune *et al.* (2007a) concluded that three different polychaete assemblages associated with depth and sediment granulometry could be identified in the Gulf of Lions (NW Mediterranean): (1) Littoral Fine Sands assemblages at 10-20 meters depth; (2) Littoral Sandy Muds assemblages at 30 meters depth; and (3) Terrigenous Coastal Muds assemblages at 40-50 meters depth. Another assemblage, again based on the study of polychaetes, was recently added to these 3 assemblages: Detritic Sands at 30-50 meters depth (Sardá *et al.*, 2014).

For a long time, shallow soft bottom non-vegetated areas of the Catalan coast were commonly described as inhabited by medium to fine sand assemblages of *S. subtruncata*, which colonizes exposed to semi-exposed sublittoral habitats down to 30 meters depth (Pinedo *et al.*, 1996; Pinedo, 1998; Cardell *et al.*, 1999; Sardá *et al.*, 1999; 2014). Studies on biodiversity and macrofaunal composition changes in the Gulf of Lions (NW Mediterranean) between depths of 10 and 50 meters (Labrune *et al.*, 2008; Dauvin *et al.*, 2017; Bonifácio *et al.*, 2018) have emphasized the importance of crustaceans and mollusks (together with polychaetes). However, none of these studies is based on all groups of macroinvertebrates inhabiting the soft bottom sediments to assess the species richness and to describe the species composition and abundances, the habitat, and the structure of soft bottom assemblages along the entire Catalan coast (NW Mediterranean Sea).

This paper aims to (1) describe the macroinfaunal assemblages and habitats based on macroinvertebrates that inhabit soft bottom sediments on the Catalan coast between depths of 3 and 35 meters; (2) identify the relationships between macrobenthic assemblages and sediment features; and (3) compare the observed habitats with those previously described (Pérès & Picard, 1964; Picard, 1965; Guille, 1970; 1971; Debruyères *et al.*, 1972-73; Labrune *et al.*, 2007a).

Fig. 1: Locations sampled between 2002 and 2010 along the Catalan coast (NW Mediterranean Sea) in shallow (left) and deep (right) bottoms.

Material and Methods

Study area

The Catalan coast (NW Mediterranean Sea; Fig. 1) is a densely populated area, with sections of it affected by high urban and industrial development, coastal modification, agriculture, and tourism (Pinedo *et al.*, 2007; 2014). Several major rivers (Besòs, Llobregat and Ebre) discharge along the Catalan coast, with important human activity in the basin. The commercial harbors of Barcelona and Tarragona are sources of intense shipping traffic in the area. The dominant current along the Catalan coast is from north to south and the continental shelf is characterized by several intersecting canyons (Palanques *et al.*, 2008). The fluvial waters of the Rhône River initially flow out northwest-southeast and are subsequently diverted to the southwest by the Liguro-Provenço-Catalan current, which controls water circulation in the NW Mediterranean basin (Millot, 1990).

Data series

As part of an environmental monitoring program, sediment samples were collected along the Catalan coast in the months of June and July for biological and sedimentological analysis. Sampling was performed in 2002, 2003, 2007, 2009, and 2010, with a total of 328 samples collected at less than 20 meters depth (called shallow samples hereafter) and 79 samples at more than 20 meters depth (called deep samples hereafter) (Fig. 1). Following Pinedo *et al.* (2016), this set of samples corresponded to a total of 204 undisturbed sites, some of them revisited in the different years.

Two replicates were collected at each location using a van Veen grab (600 cm^2), the penetration of which was commonly 10-15 cm. Sediments were sieved through a 0.5 mm sized mesh and preserved in a 4 % buffered formaldehyde solution with Rose Bengal. The fauna was sorted and identified to species level (or higher taxonomic ranks if not possible) in the laboratory. Scientific names follow the WoRMS database. Abundances (number of individuals per sample) were counted for each taxon to characterize the assemblages.

For each grab, two additional subsamples were obtained, one to determine the grain particle size and organic matter content, and the other to analyze heavy metal concentrations. The subsamples were stored at -20 ºC until processed. Sediment was submitted to the standard dry-sediment procedure for granulometric analysis (Golterman *et al.*, 1983). Seven categories were considered, following Wentworth (1922). Median Particle Diameter (MPD) and percentage of Silt-Clay (SC, sediment <63 µm) were used to characterize the sediments. Organic Matter content (OM) of sediment was estimated as loss of weight after ashing for 5 hours at 450 °C. Metal concentrations (Zn, Cu, Pb, V, Cd and Hg) were determined by weighing amounts of around 0.1 g of freeze-dried sediment, following the methodological procedure described in Pinedo *et al.* (2014).

Data analysis

To identify possible sources of variability in environmental variables between samples, a Principal Component Analysis (PCA) was conducted on log-transformed and normalized sedimentological data, including MPD, SC, OM, Zn, Cu, Pb, V, Cd and Hg. Non-metric multidimensional scaling (n-MDS) ordinations based on the macrofaunal composition (square root transformed abundance data; Bray-Curtis dissimilarity, average link grouping) were used to find associations of soft bottom samples. ANOSIM analysis was used to test the differences between groups of samples. The similarity percentage procedure (SIMPER) was used to identify the taxa most responsible for similarities and dissimilarities within and between groups.

Using a one-way model in PERMANOVA add-on (Anderson *et al.*, 2008), the null hypothesis of no significant differences among the habitats identified (n-MDS and ANOSIM analysis) was tested for the fixed factors that mostly determined the sampling groups. The significance in the main and pairwise tests was obtained following unrestricted permutation of the raw data (999 permutations) and the calculation of type III sum of squares. The matching of biotic and environmental patterns in combinations of environmental variables was tested using the BIOENV procedure. Distance-based redundancy plots (dbRDA) were used to facilitate the visualization of the relationships between biological and environmental variables. PRIMER v6 software with PERMANOVA add-on software was used to run the analysis.

Results

Environmental variables

The first two components of the PCA for environmental data accounted for 72.9 % of the total variance (58.7 % and 14.2 %, components 1 and 2, respectively). Samples from shallow bottoms (right side) remained mostly separate from those from deep bottoms, which were placed on the left side of the PCA (Fig. 2; ANOSIM R=0.526, p<0.001). The first component indicated a gradient of OM and metal concentrations (highest values on the left, deep samples), while the second component was related to MPD and SC.

The global information on the sedimentological variables (granulometric features, OM, and heavy metal concentrations) for shallow and deep bottoms in the area has already been included in previous works (Pinedo *et al.*, 2014; 2016). Although the average value of MPD for the shallow and deep samples was similar (Table 1), the variation range was much higher in the shallow ones. The average SC was 22 % in the deep samples, but only 6 % in the shallow ones (Table 1). The OM varied from sediments without organic enrichment in shallow bottoms to maximum values close to 7 % in deep bottoms (Table 1). The heavy metal concentrations also showed much higher values in the deep samples than in the shallow ones.

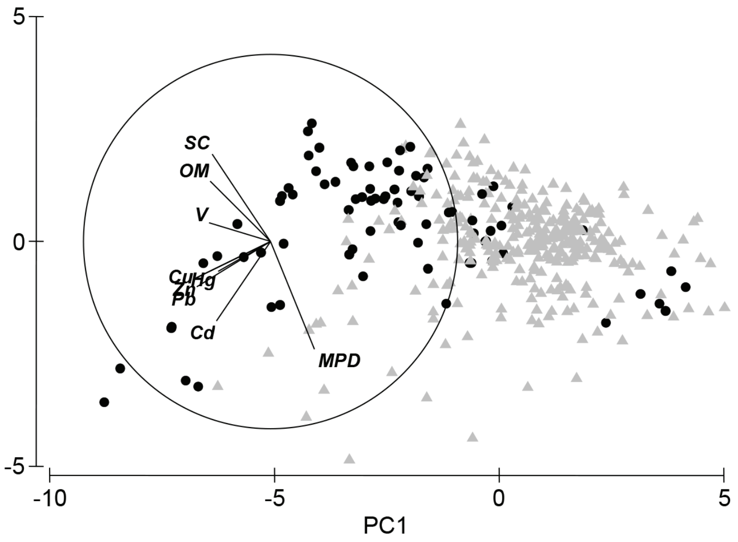

Fig. 2: Projection of samples (▲, shallow and ●, deep) on the first plane of PCA based on percentage of silt-clay (SC), mean particle diameter (MPD), organic matter content (OM), and heavy metal concentrations (Zn, Cu, Pb, Cd, V and Hg). Vectors of the linear correlations with individual variables are superimposed on the graph.

Table 1. Average, minimum, and maximum values of depth and sedimentological features of shallow and deep samples: depth (m), percentage of silt-clay (SC, %), median particle diameter (MPD, μm), percentage of organic matter content (OM, %), and heavy metal concentrations (μg g^{-1}).

	Shallow			**Deep**		
	Average	**Minimum**	**Maximum**	**Average**	**Minimum**	**Maximum**
depth	9.5	2.8	19.0	25.5	20.0	35.0
SC	6.3	0.0	75.7	21.9	0.1	61.7
MPD	167.6	56.6	1,258.9	154.0	23.1	794.3
OM	1.1	0.3	3.7	3.1	0.6	6.8
Zn	42.7	4.5	305.3	94.5	7.6	448.4
Cu	7.8	0.4	63.2	20.2	1.2	89.3
Pb	14.2	2.1	114.7	31.3	2.8	134.1
V	23.3	5.6	76.2	35.0	12.4	86.5
Cd	0.14	0.01	2.31	0.24	0.00	1.40
Hg	0.07	0.00	1.99	0.31	0.00	1.83

Macrofaunal assemblages

Structural characteristics

A total of 154,780 individuals belonging to 788 taxa were sorted and identified, including 310 annelid polychaetes, 224 crustaceans, 209 mollusks, and 22 echinoderms. Several organisms from other taxonomic groups accounted for the remaining taxa. Two main assemblages were identified in the n-MDS analysis (ANOSIM, R=0.769, p<0.001), the shallow samples placed on the left, and the deep samples on the right (Fig. 3). Thus, shallow and deep samples showed differences in species composition and abundances.

The average dissimilarity in species composition between the shallow and deep habitats was 89.8 % (SIMPER analysis; Table S1). The bivalves *Lucinella divaricata* and *S. subtruncata* contributed to the highest dissimilarity between the two groups. These species were very abundant in shallow samples, reaching more than 17 % of cumulative similarity (Table S2). These bivalves, together with the polychaetes *Paradoneis armata* and *Spio decorata*, the bivalve family Mactridae (the named taxon Mactridae, composed mainly of juveniles of *S. subtruncata,* although some juvenile individuals of *Mactra stultorum* can be included), and other bivalves such as *Fabulina fabula* and *Thracia phaseolina* and the tanaidacean *Apseudopsis bacescui*, contributed to more than 40 % of the cumulative similarity in the shallow samples. The deep samples were characterized by the polychaetes *Kirkegaardia heterochaeta*, *Levinsenia gracilis*, *Aponuphis bilineata*, *Lumbrineris* sp.1, *Magelona minuta*, *Mediomastus fragilis,* and *Goniadella galaica*, and the tanaidacean *A. bacescui* as the most domi-

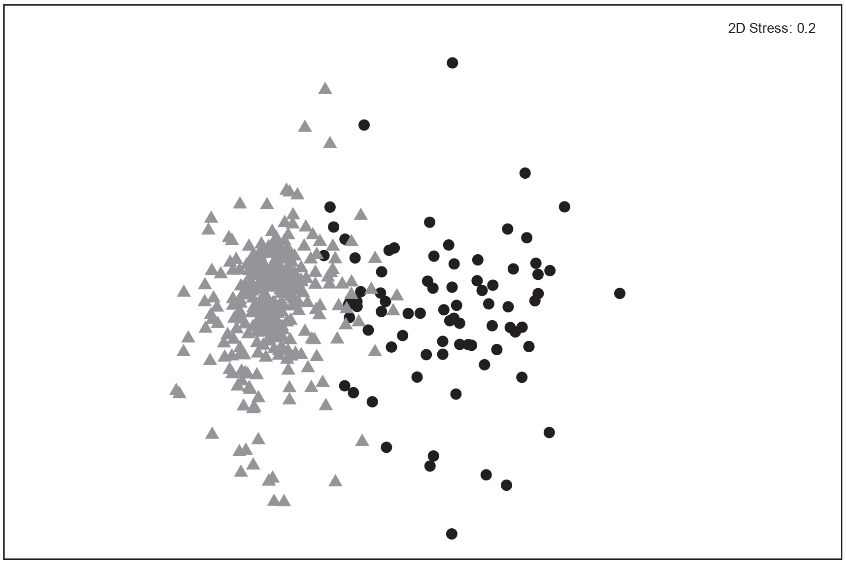

Fig. 3: MDS analysis based on square root transformed macrofaunal abundance for shallow (▲) and deep (●) samples from 2002 to 2010.

nant and frequent species (41 % of cumulative similarity; Table S3). Following these results, the shallow and deep samples were analyzed separately to characterize other potential assemblages in each group of samples.

The contribution of the three major groups, polychaetes, crustaceans, and mollusks, to the richness was almost equal in the shallow and deep habitats (Fig. 4A). Polychaeta was the major taxonomic group contributing to the richness, while crustaceans and mollusks contributed with the same relative values. The contribution of the major taxonomic groups was very different when abundance values were considered (Fig. 4B). While Polychaeta (61 % of the total abundance) was the most abundant group in the deep bottoms, Mollusca (47 %) dominated in the shallow ones (Fig. 4B). The contribution of Crustacea to the total abundance was slightly higher in the shallow bottoms. Other taxa reached almost the same percentage. However, the composition of macroinvertebrates included in the other group differed. In terms of relative values (1) Nemertea contributed similarly to the shallow and deep habitats; (2) Nematoda were more abundant in the shallow habitats; and 3) Sipunculida were a very abundant group in the deep habitats, achieving 3 % of the total abundance, while contributing with only 0.2 % in the shallow ones. In terms of absolute values, the total abundance of lancelets *Branchiostoma lanceolatum*, the phoronid *Phoronis psammophila*, Platyhelminthes and Oligochaeta was high in the shallow habitats, while scarce in the deep ones.

Shallow habitats

The different composition of the shallow samples was mainly driven by MPD (ANOSIM, R=0.271, p<0.001). Pairwise tests enabled the distinction of three groups of samples: 1) very coarse and coarse sand sediments (hereafter shallow coarse sediments); 2) medium to fine and very fine sand sediments (hereafter shallow fine sediments); and 3) muddy sediments (hereafter shallow muddy sediments). SC did not segregate samples (ANOSIM, R=0.080).

The characterization of the shallow habitats is compiled in Table 2. The number of individuals registered in the shallow coarse sediment samples was 7,070, belonging to 164 taxa. Nematoda were present in the overall coarse samples, reaching 35 % of the total abundance, although Oligochaeta (8 % of the total abundance) and the polychaetes *Aonides paucibranchiata* and *Protodorvillea kefersteini* were also dominant (each reaching 6 %) and

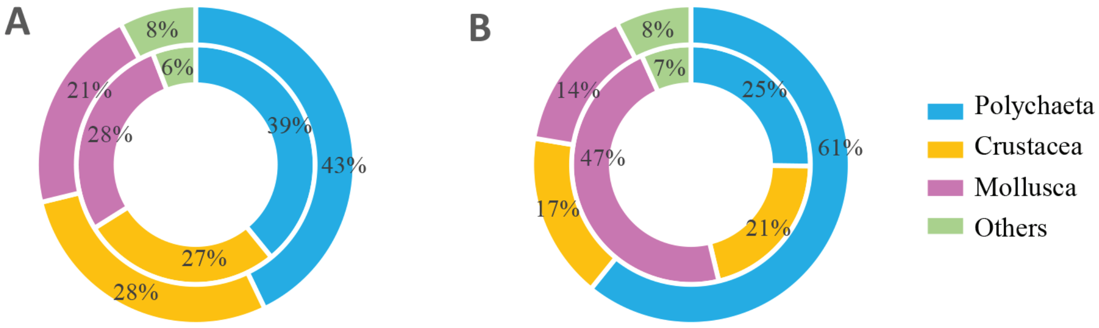

Fig. 4: Contributions of the three major taxonomic groups to the richness (A) and abundance (B) of the total macrofauna within the shallow (inside) and deep (outside) habitats identified in the Catalan coast.

Table 2. List of the ten most abundant taxa for the characterization of each habitat. Other relevant taxa mentioned in the text are included. Total abundance, frequency (in brackets), and the dominance order (in bold) of each taxon are included. pol, polychaete; mol, mollusk; tan, tanaidacean; amp, amphipod; pro, prochordata.

	Shallow						Deep					
Taxa	**Coarse**		**Fine**		**Mud**		**Coarse**		**Fine**		**Mud**	
NEMATODA	2,459 (13)	**1**										
OLIGOCHAETA	541 (8)	**2**										
Aonides paucibranchiata (pol)	453 (9)	**3**										
Protodorvillea kefersteini (pol)	422 (11)	**4**										
Goniadella galaica (pol)	246 (10)	**5**										
Mediomastus fragilis (pol)	230 (2)	**6**			47 (3)	**4**			520 (37)	**1**		
Glycera tesselata (pol)	203 (11)	**7**										
Syllis hialina (pol)	194 (8)	**8**										
VENERIDAE (mol)	175 (8)	**9**										
Lumbrinerides acuta (pol)	172 (11)	**10**										
Lucinella divaricata (mol)	3 (2)	**85**	19,005 (271)	**1**	9 (4)	**37**	9 (1)	**4**	107 (24)	**23**	1 (1)	**101**
Spisula subtruncata (mol)	37 (6)	**27**	13,424 (289)	**2**	125 (4)	**1**			108 (26)	**22**	2 (1)	**64**
Mactridae (mol)			7,806 (241)	**3**								
Donax trunculus (mol)			6,454 (98)	**4**								
Paradoneis armata (pol)			5,330 (282)	**5**								
Apseudopsis bacescui (tan)			4,202 (224)	**6**	32 (5)	**7**	4 (1)	**10**				
Fabulina fabula (mol)			3,223 (230)	**7**								
Loripes orbiculatus (mol)			2,979 (160)	**8**								
Thracia phaseolina (mol)			2,703 (220)	**9**			11 (3)	**3**				
Centroloecetes dellavallei (amp)			2,476 (180)	**10**					220 (24)	**7**		
Rubifabriciola tonerella (pol)					74 (5)	**2**			209 (6)	**8**		
Lumbrineris sp.1 (pol)					64 (5)	**3**			191 (31)	**9**	49 (6)	**3**
Branchiostoma lanceolatum (pro)					42 (3)	**5**						
Galathowenia oculata (pol)					35 (4)	**6**						
Kirkegaardia heterochaeta (pol)					28 (2)	**8**			260 (40)	**3**	48 (8)	**4**
Micronephthys longicornis (pol)					25 (5)	**9**						
Cerapopsis longipes (amp)					24 (5)	**10**	14 (3)	**2**				
Aspidosiphon muelleri (sip)							21 (4)	**1**				
Schistomeringos neglecta (pol)							6 (1)	**5**				
Glycera oxycephala (pol)							6 (2)	**6**				
Aponuphis bilineata (pol)							5 (2)	**7**				
Chone duneri (pol)							4 (3)	**8**				
Euthalenessa oculata (pol)							4 (3)	**9**				
Magelona minuta (pol)									332 (37)	**2**		
Ditrupa arietina (pol)			393 (48)	**54**	1 (1)	**133**	2 (1)	**16**	253 (26)	**4**		
Paradoneis ilvana (pol)									249 (7)	**5**		
Levinsenia gracilis (pol)									227 (42)	**6**	35 (6)	**5**
Notomastus latericeus (pol)									161 (20)	**10**		
Apseudopsis annabensis (tan)											73 (6)	**1**
Aricidea claudiae (pol)											52 (3)	**2**
Thyasira flexuosa (mol)											31 (4)	**6**
Paralacydonia paradoxa (pol)											30 (7)	**7**
Cossura soyeri (pol)											25 (6)	**8**
Nucula hanleyi (mol)											23 (8)	**9**
LUCINIDAE (mol)											22 (3)	**10**
Owenia fusiformis (pol)			648 (121)	**41**	19 (5)	**18**			80 (18)	**33**	1 (1)	**72**
Nº of samples (600 cm^2)	13		309		6		5		65		9	
Nº of taxa	164		680		182		64		421		110	
Nº of taxa accounting 80 % of total abundance	15		49		58		32		87		31	
Total abundance	7,070		136,585		1,337		164		8,868		756	

frequent (Table 2). The bivalve family Veneridae (mostly composed of juveniles of *Polititapes* spp. and *Ruditapes* spp.) and *Modiolula phaseolina* were the most frequent bivalves. Nemertea and the polychaetes *Hesionura serrata* and *Pisione remota* were also very frequent organisms, although not abundant. Several species were exclusively observed in shallow coarse sediments: *Syllis hyalina*, *H. serrata*, *Palposyllis prosostoma*, *Polygordius* spp. and *Saccocirrus* spp., although some of them had occasionally been sampled in the shallow fine sediments but with very low abundances. In fact, the species composition in the shallow fine sediments was quite different. The number of individuals reached 136,585 with 680 taxa (Table 2), while only 49 taxa accounted for 80 % of the total abundance. The bivalves *L. divaricata* and *S. subtruncata* were the most abundant species (each accounting for around 14 % and 10 % of the total abundance, respectively), followed by the family Mactridae (almost 6 % of the total abundance), the bivalve *Donax trunculus* (5 %), which exclusively inhabited this habitat, the polychaete *P. armata* (4 %), and *A. bacescui* (3 %). The rest of the taxa contributed with less than 3 % to the total abundance. Although not very abundant, Nemertea were again frequent in shallow fine sediments. Some others of the most exclusive species in this habitat were the polychaetes *Magelona johnstoni* and *Sigalion squamosus,* the bivalve *Chamelea gallina*, the crustaceans *Ampelisca brevicornis*, *Lembos* sp. 2, *Bathyporeia phaiophthalma*, *Urothoe poseidonis,* and ostracods. Last, samples from shallow muddy sediments were composed of 1,337 individuals belonging to 182 taxa. *S. subtruncata* and the polychaetes *Rubifabriciola tonerella*, *Lumbrineris* sp.1, and *M. fragilis* accounted for 23 % of the total abundance (Table 2). Together with Nemertea, the polychaete *Scolaricia typica* was frequent but not abundant. The low abundance of *L. divaricata* in this habitat is noteworthy.

There were no notable differences to the overall pattern (Fig. 5A) in terms of the contributions to the richness values for each shallow habitat, as shown in Table 2. The number of taxa of mollusks was lower in coarse sediments. However, there were clear differences in the contribution to the abundance of major taxonomic groups (Fig. 6A). The highest contribution to the total abundance in coarse sediments was equally divided between Polychaeta and the "others" group, represented mainly by nematodes. The observed pattern for fine sediments followed the general one (Fig. 4B), where Mollusca dominated. Last, Polychaeta was the dominant group in muddy sediments. Furthermore, the low abundance of crustaceans (3 %) in shallow coarse sediments compared with the other habitats was noteworthy (Fig. 6A).

Deep habitats

The distribution of the deep samples was related to the SC (ANOSIM, R=0.339, p<0.001), while MPD did not clearly separate groups of samples (ANOSIM, R=0.130,

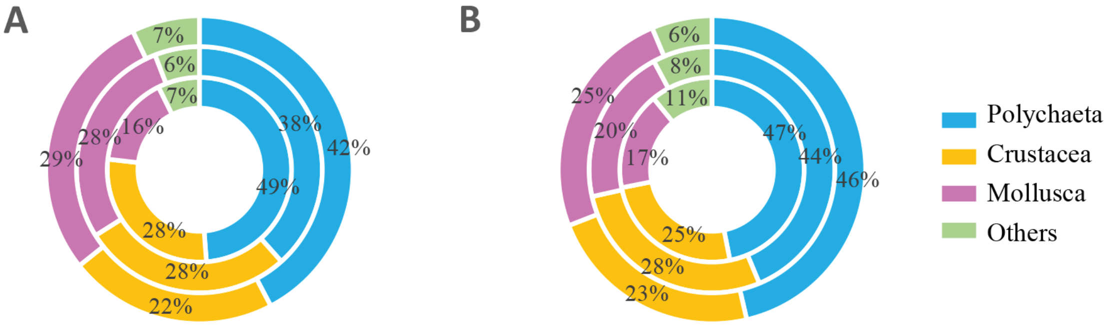

Fig. 5: Contributions of the three major taxonomic groups to the richness of the total macrofauna within the six different habitats identified: coarse (inside), fine (middle) and muddy (outside) sediments at shallow (A) and deep (B) habitats in the Catalan coast.

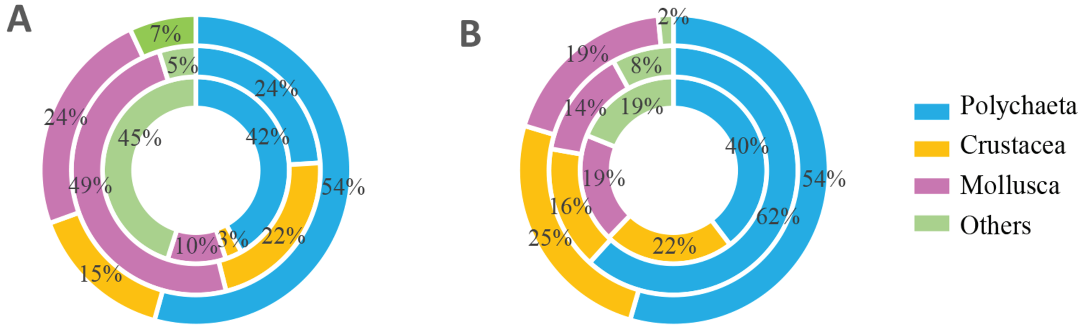

Fig. 6: Contributions of the three major taxonomic groups to the abundance of the total macrofauna within the six different habitats identified: coarse (inside), fine (middle) and muddy (outside) sediments at shallow (A) and deep (B) habitats in the Catalan coast.

p=0.036). However, pairwise tests differed between very coarse and coarse sediments from medium, fine, very fine sediments and muddy samples (0.523≤R≤0.994, p<0.05). Based on the results, and on the species composition from the dataset, three different deep habitats were considered: (1) deep coarse sediments; (2) deep fine sediments; and (3) deep muddy sediments.

The characterization of the deep habitats is shown in Table 2. Only 5 samples in the entire dataset characterized the deep coarse sediments, including 64 taxa and 164 individuals. The sipunculid *Aspidosiphon muelleri*, the crustacean *Cerapopsis longipes*, and the bivalves *T. phaseolina* and *L. divaricata* were the dominant species, accounting for 35 % of the total abundance. However, *L. divaricata*, while abundant was observed in only one sample. Other frequent but not as abundant species were the polychaetes *Chone duneri* and *Euthalenessa oculata*. The latter was exclusively observed in deep coarse sediments. Deep fine sediment samples grouped 421 taxa and 8,868 individuals. Dominance was shared by several species as 87 taxa accounted for 80 % of the total abundance. The polychaetes *M. fragilis*, *M. minuta*, *K. heterochaeta*, *Ditrupa arietina*, *Paradoneis ilvana* and *L. gracilis* dominated the abundance ranking list. There were no bivalves among the ten most abundant and frequent species in this habitat, although *L. divaricata* and *S. subtruncata* were present. Last, deep muddy sediment samples contained 110 taxa with 756 individuals. The tanaidacean *Apseudopsis annabensis* and the polychaetes *Aricidea claudiae*, *Lumbrineris* sp.1 and *K. heterochaeta* dominated, accounting for 29 % of the total abundance. Among the bivalves *Thyasira flexuosa* and *Nucula hanleyi* were frequent and abundant.

The richness values calculated for each deep habitat considered in Table 2 (Fig. 5B) showed that the contributions were nearly the same as those observed in Fig. 4A. However, while the number of taxa of mollusks was lower in coarse sediments, crustacean richness was lower in muddy sediments. Other taxa were more represented (11 %) in deep coarse sediments. Some differences arose when analyzing the contribution to the abundance of major taxonomic groups (Fig. 6B). Polychaeta dominated in fine and muddy bottoms, while the total abundance was more equally distributed within the groups in coarse sediments.

Relationship between macrofaunal assemblages and sediment features

The mean values of the environmental variables that mostly defined the habitats (MPD, SC, OM) are presented in Table 3. The null hypotheses of no significant differences among the habitats were all rejected at p<0.01 (Table S4). Pairwise comparisons indicated that coarse, fine, and muddy habitats differed between themselves both in the shallow and the deep habitats for MPD and SC. However, no significant differences were observed for MPD (pseudo-F=1.4159; p=0.219) and SC (pseudo-F=3.3926; p=0.064) values when comparing the habitats displaying the same granulometry between shallow and deep bottoms. Thus, the MPD and SC did not differ between shallow coarse and deep coarse sediments. The same results were obtained for fine and muddy sediments. Although no statistically significant differences were observed, MPD mean values were always higher in shallow habitats than in their corresponding deep ones, while SC showed opposite results, with higher values in deep sediments both in fine and muddy bottoms. With regards to OM, few significant differences were registered among habitats, but values were always higher in deep habitats than in their equivalent shallow ones.

Similar relationships between macrofaunal assemblages and sediment features have been obtained for shallow and deep habitats, but the combinations of variables were different. Two variables (MPD and OM) obtained the maximum coefficient (BIOENV, ρ=0.421) in shallow habitats. The coarser sediments on the right of the cluster and the finer organic enriched samples on the left were defined by the first axis (Fig. 7A). The second axis was mainly related to the SC. The combination of two environmental variables, SC and OM, was required to maximize the matching coefficient (ρ=0.577, BIOENV) between the environmental variables and the biological data in deep habitats. Muddy samples were located on the left side of the figure, opposite to coarse sediments in the dbRDA ordination in deep sediments (Fig. 7B). The first axis was mainly defined by SC and OM, as finer and organically enriched sediments were located on the left. Last, the granulometric characteristics (MPD and/or SC) and OM drove the species composition and structure of the soft-bottom assemblages determining the different habitat types on the Catalan coast.

Table 3. Mean values of environmental variables in the six habitats identified. Minimum and maximum values in brackets.

	Shallow			**Deep**		
	Coarse	**Fine**	**Mud**	**Coarse**	**Fine**	**Mud**
SC (%)	1.2 (0.1-6.3)	5.4 (0-54.4)	40.4 (12.9-75.7)	0.2 (0.1-0.3)	19.2 (0.5-46.9)	53.5 (34.5-61.7)
MPD (μm)	753 (501-1259)	145 (66-446)	59 (57-62)	693 (537-794)	128 (65-479)	46 (23-62)
OM (%)	0.46 (0.25-0.88)	1.05 (0.33-3.66)	2.08 (1.49-2.89)	0.62 (0.58-0.64)	3.25 (0.62-6.80)	3.30 (2.20-4.30)

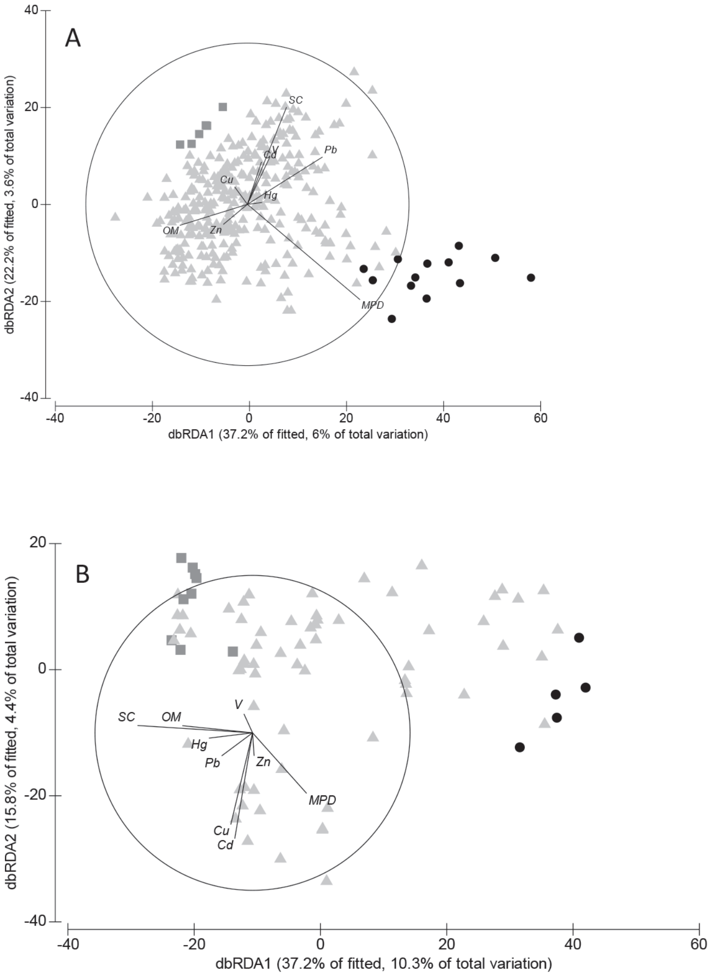

Fig. 7: Distance-based redundancy analysis (dbRDA) plot showing relationships between macrofauna abundance and environmental variables: percentage of silt-clay (SC), mean particle diameter (MPD), organic matter content (OM), and heavy metals concentration (Zn, Cu, Pb, Cd, Hg and V). A. Shallow samples. B. Deep samples. ● coarse sediments; ▲ fine sediments; ■ muddy sediments.

Discussion

Six main different habitats were identified between depths of 3 and 35 meters in sedimentary bottoms along the Catalan coast. Depth and granulometric features were central to explaining the distribution and identification of the habitats. Heavy metals content, however, was not high enough to display any influence on the identification of habitats. While MPD and SC have already been mentioned as the main factors driving the assemblages composition in the soft bottom environments (Pearson & Rosenberg, 1978; Gray, 1981; Pinedo *et al.*, 1996; Dauvin *et al.*, 2004; Simonini *et al.*, 2004; Currie & Small, 2005; Labrune *et al.*, 2007a; Bolam *et al.*, 2008; Cosentino & Giacobbe, 2008; Hily *et al.*, 2008; Dutertre *et al.*, 2013; Martins *et al.*, 2013), along the Catalan coast the combination of depth and granulometric features is pivotal for habitats characterization. Coarse, fine, and muddy sediments harbor very different assemblages, depending on depth. Moreover, the present work describes in detail these six habitats on the Catalan coast considering all macroinvertebrates, unlike the last study carried on 1998-1999, which only addressed the polychaetes (Sardá *et al.*, 2014).

Shallow habitats

In shallow sediments we distinguished three habitats, according to the MPD. The habitat of shallow fine sediments would correspond to the "Littoral Fine Sands" (LFS) *sensu* Labrune *et al.* (2007a), dominated by *L. divaricata* and *S. subtruncata* on the Catalan coast. The low abundance of the polychaetes *D. arietina* and *Owenia fusiformis* in this habitat is noteworthy. Both species were highly abundant in the LFS assemblage described by Labrune *et al.* (2007a; 2008) in the 1998 sampling and in several sites along the Catalan and French coast until 1999 (Grémare *et al.*, 1998a, b; Massé, 2000; Sardá *et al.*, 2014; Dauvin *et al.*, 2017). However, a study in 2003 carried out on the same sites showed that the abundance of both *O. fusiformis* and *D. arietina* had decreased (Labrune *et al.*, 2007b). Later, in 2010, low abundances of *D. arietina* were also observed (Bonifácio *et al.*, 2018) in the same area studied by Labrune *et al.* (2007a). In fact, the LFS assemblage without *Ditrupa* had already been identified on the Spanish littoral coast by Sardá *et al.* (2014) during surveys carried out in 1998-1999. Another study carried out along both the French and Spanish Catalan coasts in 1996 (Grémare *et al.*, 1998b) indicated that *D. arietina* abundance had increased, but the dynamic of the species was shown to be unstable as it was highly sensitive to the presence of fine sediments (Grémare *et al.*, 1998b; Charles *et al.*, 2003). Moreover, this species has classically been associated with the transient "unstable soft bottom community" as described by Picard (1965) and Pérès & Picard (1957). The polychaete *O. fusiformis* was neither abundant nor frequent in our surveys (see Table 2). Only 748 individuals were found in 36 % of the samples, mostly in shallow fine sediments, but it did not characterize the habitat. The high densities of *O. fusiformis* registered in June-July (more than 30,000 ind*m^{-2} in 1994) in the Bay of Blanes (Sardá *et al.*, 1999) contrast with our results. No individuals were sampled during the 2007 survey in the Bay of Blanes and its density was only 33 ind*m^{-2} in July 2010. Moreover, Sardá *et al.* (2014) found high abundances of this species along the Catalan coast during a survey carried out in 1999. This species showed a clear seasonal pattern with a marked and abundant recruitment in spring and a sharp decrease at the beginning of summer, when it could even disappear (Pinedo, 1998; Sardá *et al.*, 1999; Pinedo *et al.*, 2000). Although our samplings were carried out during the drop period of its seasonal cycle, the low abundance could also be due to a severe general decline of the species on the Catalan coast. A decrease of *O. fusiformis* between 1994 and 2003 in the Gulf of Lions was observed (Labrune *et al.*, 2007b), and later a long-term study confirmed that the figure of 16 % of the total abundance in 1998 had reduced to just 2 % in the same area in 2010 (Bonifácio *et al.*, 2018). The population dynamics of this species appears to be rather unstable (Dauvin & Gillet, 1991; Pinedo *et al.*, 2000), which would explain the virtual disappearance of the species on the Catalan coast at least since 2000s. Other factors explaining the distribution of this species are OM and SC content (Pinedo *et al.*, 2000). OM may enhance larval settlement, juvenile survival, and juvenile growth rates of *O. fusiformis* (Pinedo *et al.*, 2000). However, the OM in sediments of the Bay of Blanes in our surveys (Pinedo *et al.*, 2014) was comparable to that registered in 1992-1994 (Pinedo, 1998). The influence of fine fractions in the sediments in structuring *O. fusiformis* populations has been also demonstrated (Pinedo *et al.*, 2000; Serrano, 2012). However, the SC content in the Bay of Blanes has not experienced significant changes since the 90s (Pinedo *et al.*, 1997; Pinedo, 1998; Pinedo et al., 2014). Other factors may be driving the decrease of *O. fusiformis*, which nowadays does not characterize any habitat on the Catalan coast.

The comparison of the composition of assemblages from the Catalan coast and the benthic communities proposed in previous works (Pérès & Picard, 1964; Guille, 1970; 1971; Desbruyères *et al.*, 1972-73), showed that the shallow fine sediments are closely related to the *S. subtruncata* community (Guille, 1970; 1971; Desbruyères *et al.*, 1972-73) and to the Well Sorted Fine Sands community described by Pérès & Picard (1964). The major discrepancy in terms of species composition was the high abundance of the bivalve *L. divaricata* in shallow fine sediments found during the present study, with this species not mentioned in the previous works or in Labrune *et al.* (2007a). Neither was this bivalve a key species pointed out in the most recent studies of French shallow fine sediments located close to Catalonia (Grémare *et al.*, 1998a; Labrune *et al.*, 2008). Only very few individuals of *L. divaricata* at 11 meters depth in Bandol Bay have been observed (Massé, 1970). More recently, in 2010, its presence as a characteristic species in the LFS (*sensu* Labrune *et al.*, 2007a) in the Gulf of Lions has been pointed out (Bonifácio *et al.*, 2018). The first records of *L. divaricata* with abundances similar to those registered for *S. subtruncata* in shallow fine sediments, come from surveys made in the Bay of Blanes between 1992 and 1995 (Pinedo *et al.*, 1996; Pinedo, 1998; Sardá *et al.*, 1999; 2000). Moreover, Sardá *et al.* (1999) pointed out that the population of *L. divaricata* in the Bay of Blanes increased between 1992 and 1995. The presence of *L. divaricata* has been associated with subtidal *Zostera marina* beds (Rueda & Salas, 2008) and other seagrass environments (Büyükmeriç *et al.*, 2016), but it has never been described as co-dominant with *S. subtruncata* in shallow fine sediments. The most relevant difference between our study and those made in the 60s and 70s is the mesh size. Sediments were filtered using a 1 mm mesh size in all the studies without *L. divaricata* -only Massé (1970; 1972) filtered using 0.7 mm- while a mesh of 0.5 mm was used in all the studies that sampled this species abundantly. Moreover, in the Eastern Ligurian Sea (Albertelli *et al.*, 1999), *L. divaricata* dominated the 0.5-1 mm macrofauna at a depth of 5 meters but was absent in the > 1 mm macrobenthos where *S. subtruncata* was present. One could conclude that *L. divaricata* is only present when a 0.5 mm mesh size is used during the sieving process. However, our observations noted that *L. divaricata* specimens were bigger than 1 mm on the Catalan coast, so they should have been retained by the 1 mm mesh. Neither did most recent studies focusing on the macrobenthic assemblages of the littoral zone in the Western Mediterranean, the Adriatic, and the Tyrrhenian Sea (Occhipinti-Ambrogi *et al.*, 2005; Cosentino & Giacobbe, 2008; Hermand *et al.*, 2008; Labrune *et al.*, 2008; Bertasi *et al.*, 2009; Peharda *et al.*, 2010) reveal the presence of this species. The presence of this species among the top 20 in the Western Mediterranean (Dauvin *et al.*, 2017) is only mentioned in several studies carried out in the Bay of Blanes (Pinedo *et al.*, 1996; Pinedo, 1998; Sardá *et al.*, 1999; 2000). A possible explanation for the widespread absence of *L. divaricata* is its misidentification and confusion with *L. orbiculatus*, although the latter has never been found in such high densities as *L. divaricata* in the Northwestern Mediterranean Sea (Guille, 1971; Pinedo *et al.*, 1996; Grémare *et al.*, 1998a; Sardá *et al.*, 1999). The presence of *L. orbiculatus* has been reported as a prevalent species in the Gulf of Baratti (Biagi & Corselli, 1984) and among the ten dominant bivalves at <5 meters depth in Prado Bay (Massé, 1971; 1972; 1998), whose sediments were influenced by waters with high organic matter content due to sewage. In fact, *L. orbiculatus* has usually been associated with high organic matter content in sediments, unlike *L. divaricata* (Pinedo *et al.*, 1996; Pinedo, 1998). Thus, the causes of the recent abundance (since the 90s) of this species along the Catalan coast remain unknown.

The presence of the two characteristic bivalves of shallow fine sediments, *L. divaricata* and *S. subtruncata*, varied over time in our study, changing their contribution to the total abundance. While *S. subtruncata* dominated in 2002, *L. divaricata* did in 2007. Similar values for the two species were found in 2010. Recruitment events could vary in density, time, and space (Pinedo, 1998; Sardá *et al.*, 1999), and moreover, it could be considered that the recruitment of one species hinders the settlement or recruitment of the other. Climatic oscillations could explain changes in the species composition and abundance, thus influencing the success of recruitment of several species (Bonifácio *et al.*, 2018). Furthermore, the presence of many new recruits in the samples can also lead to a biased result, especially if the species is very abundant in the assemblage and shows large mortalities after settlement, such as *S. subtruncata* (Pinedo *et al.*, 1996; Pinedo, 1998; Sardá *et al.*, 1999). *L. divaricata*, however, maintained a stable population during autumn and winter in the Bay of Blanes (Sardá *et al.*, 1999), with higher densities than *S. subtruncata*, which almost disappeared. Although the sampling period for our study was selected to avoid the collection of recruits, this was not always achieved. In fact, the family Mactridae, composed mainly by young recruits of *S. subtruncata,* reached more than 5,000 individuals in 2002, almost 1,500 in 2007 and just over 1,000 in 2010 in shallow fine sediments. The contribution of the mollusks to the total abundance would have decreased in part if the specimens > 1 mm were considered for some of the most abundant and frequent bivalves. Other studies (Cattaneo & Massé, 1983; Ambrogi & Occhipinti-Ambrogi, 1987; Fraschetti *et al.*, 1997) have already evidenced a different scenario, considering the exclusion of new recruits in the calculations of the contribution of some bivalve species to the total abundance.

Although most of the samples collected at shallow depths on the Catalan coast corresponded to fine sands (94 %), coarse and muddy sediments were also present in shallow bottoms. The shallow muddy sediments also dominated by *S. subtruncata* would be a transitional assemblage between the shallow fine sediments dominated by the bivalves *L. divaricata* and *S. subtruncata*, and deep habitats. The presence of some species such as *R. tonerella* and *M. fragilis* that are tolerant to organic matter accumulation -which is enhanced in deep habitats- supports this hypothesis. The polychaete *Lumbrineris* sp.1 is also a dominant and frequent species in shallow muddy sediments. Last, shallow coarse sediments -observed neither in Labrune *et al.* (2007a; 2008) nor in Sardá *et al.* (2014)- would correspond to the coarse sands subjected to high hydrodynamism, following previous authors (Pérès & Picard, 1964). Neither did Desbruyères *et al.* (1972-73) record the presence of coarse littoral sediments with *B. lanceolatum* ("*Amphioxus* sands"). Although "*Amphioxus* sands" themselves were not found during our surveys, the presence of *B. lanceolatum* was widespread. *B. lanceolatum* inhabits sandy bottoms with fragmented shells and gravels across the Mediterranean Sea (Pérès & Picard, 1964; Dauvin, 1988a; Konsulova, 1992; Riisgård & Svane, 1999; Antoniadou *et al.*, 2004; Chintiroglou *et al.*, 2004; Rota *et al.*, 2009). However, contradictory results were observed during our surveys. In 2002 and 2003, the species was mainly observed in coarse and fine sediments. Later, in 2007, the distribution and abundance of *B. lanceolatum* changed, showing low densities and present mainly in fine sediments with high SC content. The highest densities (up to 258 ind·m^{-2}) were reached in 2010 in very fine sands with around 20 % of SC (Pinedo *et al.*, 2014). Thus, the species seems to recruit in a wide granulometrical range of sediments, although it does not always structure stable populations. Our results demonstrate that *B. lanceolatum* does not discriminate muddy sediments and, moreover, muddy sands do not reduce its abundance, as suggested by other authors (Konsulova, 1992; Gans, 1996; Antoniadou *et al.*, 2004). Konsulova (1992) attributed the dramatic reduction of *B. lanceolatum* along the Bulgarian Black Sea coast to the expansion of muddy areas with high organic content, which decreases sediment permeability. Our results relatively reject this hypothesis as the species was found in sediments with high SC but low organic matter content. Thus, it seems that the organic matter content could be more relevant than the SC in the distribution of this species. Last, we cannot confirm the suggested decline of *B. lanceolatum* on the Catalan coast since the number of individuals was similar in 2002 and 2010, although its distribution changed. Moreover, Sardá *et al.* (1999) recorded that *B. lanceolatum* showed a contrasting seasonal pattern compared to other macroinfaunal species, reaching peak abundance in autumn and winter in coarse sediments from the Bay of Blanes. Therefore, the abundance values along the Catalan coast may have been higher if sampling had been carried out at another time of year.

Deep habitats

The deep sediments (20-35 m) from the Catalan coast also make up three different habitats. The deep muddy sediments would correspond to the "Littoral Sandy Muds" (LSM) *sensu* Labrune *et al.* (2007a), and are dominated by *A. annabensis*, *A. claudiae* and *Lumbrineris* sp.1, with the presence of the bivalves *N. hanleyi* and juveniles of the Lucinidae family. This habitat would also correspond to the *N. hombergii* community, as defined previously (Guille, 1970; 1971; Desbruyères *et al.*, 1972-73), although this species was nearly absent and substituted by *Nephtys kersivalensis*. Although the amphipod *Ampelisca diadema* was usually mentioned in previous studies (Guille, 1970; 1971; Desbruyères *et al.*, 1972-73) as a constant species in these assemblages, we did not find it significant in any of the muddy habitats or in the other surveyed habitats excluding shallow fine sediments, where it turned out to be quite abundant.

However, this habitat is not the most frequent in deep waters, with fine sediments again much more commonly found (82 % of the samples). The deep fine sediments showed a higher average SC than the shallow fine sediments and were dominated by several species of polychaetes, as opposed to mollusks. The presence of *D. arietina* in this habitat is noteworthy, both in terms of abundance (253 individuals) and frequency (45 % of samples). The presence of the polychaetes *M. fragilis* and *K. heterochaeta,* together with other species that only appeared in deep fine sediments, such as *M. minuta*, *P. ilvana* and *Notomastus latericeus,* means that this habitat resembled that of the *N. hombergii* community described by Desbruyères *et al.* (1972-73). However, the presence of the bivalves *L. divaricata* and *S. subtruncata* among the first twenty-five species characterizing the assemblage suggests that the sediments sampled from the Catalan coast show a greater sand component than those hosting the *N. hombergii* community.

Last, the deep coarse sediments were very different from the other habitats. The dominant species, the sipunculid *A. muelleri*, was only found as an abundant and frequent species in this habitat. However, it was mentioned in the LSM assemblage described in Labrune *et al.* (2008), but with low contribution to the total abundance, while it was the dominant species in the same area in 2010 (Bonifácio *et al.*, 2018). The different distribution of this species on the Catalan coast than that recorded in the Gulf of Lions (Labrune *et al.*, 2008; Bonifácio *et al.*, 2018) agrees with Ferrero-Vicente *et al.* (2013), who observed that *A. muelleri* does not show any significant preference for muddy or sandy sediments, although it preferentially lives in *D. arietina* tubes.

Other remarks

Crustacea is among the most diverse and abundant group in soft-bottom macrofauna (Fage, 1951; Guille, 1970; 1971; Desbruyères *et al.*, 1972-73; Pinedo, 1998; Dauvin *et al.*, 1994; Prato & Biandolino, 2005; Lourido *et al.*, 2008; Sánchez-Moyano & García-Asensio, 2010). However, this group is usually left out of most studies dealing with the characterization of assemblages, despite being an important source of food for other benthic organisms and fishes (Dauvin, 1988b; Thomas, 1993; de-la-Ossa-Carretero *et al.*, 2011) in littoral habitats and having been recognized as one of the most sensitive to changes in environmental conditions (Sánchez-Moyano & García-Asensio, 2010; de-la-Ossa-Carretero *et al.*, 2011). Furthermore, peracarid crustaceans, which mostly lack a pelagic larval stage, show specific habitat requirements, thus making them excellent candidates for distributional and ecological studies (Thomas, 1993; Corbera & Cardell, 1995). Our research is the only study since the 1970s to consider crustaceans in the specific characterization of soft-bottom assemblages along the Catalan coast. The contribution of this group reached 17 % and 21 % of the total abundance in deep and shallow habitats, respectively. Along the Catalan and Catalan-French coastlines at the beginning of the 1970s (Guille, 1970, 1971; Desbruyères *et al.*, 1972-73), some species of crustaceans were classified among the 10 most important species characterizing *S. subtruncata* and *N. hombergii* communities: *Centraloecetes dellavallei*, *A. brevicornis*, *A. diadema*, *Apseudopsis latreillii*, *Bathyporeia guilliamsoniana*, *Urothoe grimaldii, Urothoe brevicornis* and *Urothoe pulchella*. Nowadays, the most characteristic species of crustaceans along the Catalan coast are almost the same. *A. bacescui* is the most common and frequent crustacean, and moreover *A. annabensis* dominates deep muddy sediments. Both species would correspond to *A. latreillii* described in previous studies. We consider that this species could have previously been misidentified. Meanwhile, *C. longipes* characterizes deep coarse sediments, while *C. dellavallei* characterizes deep fine sediments. In the shallow sediments, *A. bacescui* is the most common and abundant crustacean in fine (together with *C. dellavallei*) and muddy (together with *C. longipes*) bottoms, while none of these species is among the top ten in coarse sediments. Although several crustaceans do not characterize the habitats recognized along the Catalan coast, *Lembos* sp.1, *B. guilliamsoniana*, *A. brevicornis*, *Urothoe intermedia* and *Perioculodes longimanus* are both very common and abundant in shallow sediments. According to our data, no changes seem to have occurred in the last 40 years in terms of the dominant species of soft-bottom crustacean populations along the Catalan coast.

Conclusions

In this study, we showed that the species composition of soft bottom assemblages and habitat types off the Catalan coast are mainly defined according to depth and granulometry. MPD, SC and OM were important to characterize the environmental features of the habitats. Fine sediments both in shallow and deep waters emerged as the most common and extensive habitats along the entire coast down to a depth of 35 meters. Neither the coarse nor the muddy habitats are frequently found. However, the distribution of assemblages is associated with a gradient of environmental variables that act at a small scale in coastal areas (Hewitt & Thrush, 2009). The limits between habitats are not well defined, as highlighted by the ordination analysis, with species composition changing gradually. Thus, muddy sediments in shallow habitats act as a transitional assemblage to deep habitats.

The six assemblages are not clearly separate entities, but they form a particular habitat based on a combination of species, sediment, and depth features. The assemblages described in this study do not always fit with previous descriptions of soft bottom assemblages from the same or nearby areas, probably due to differences in the geographical distribution of the dominant species or to slight long-term changes in their abundances, related to global change (Bonifácio *et al.*, 2018) and other unknown factors. Last, the data obtained in this study can be used as a baseline of soft bottom assemblages at a regional level down to a depth of 35 meters. This information is essential for appropriate management of the marine environment and this knowledge will allow a better assessment of future foreseeable changes due to both natural causes and human activities.

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Supplementary Data

The following supplementary information is available online for the article:

Table S1. Results of the dissimilarity analysis (SIMPER) between shallow and deep samples. The taxa contributing to 50 % of dissimilarity are included.

Table S2. Contribution and average abundance of taxa responsible for most of the similarity (SIMPER analysis) in shallow samples. The taxa contributing to 50 % of the similarity are included.

Table S3. Contribution and average abundance of taxa responsible for most of the similarity (SIMPER analysis) in deep samples. The taxa contributing to 50 % of the similarity are included.

Table S4. Results of the PERMANOVA main test for environmental variable differences among the six soft bottom habitats identified.