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Habitat structure and zonation patterns of northwestern Mediterranean shoreline strands

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Summary: We studied the habitat structure (macrofaunal assemblages and bottom types) and zonation patterns of 29 unvegetated shoreline strands along the 900-km coast of Catalonia (NW Mediterranean Sea). Organisms were sampled with grabs, pitfall traps, sticky traps, clam nets and spades to ensure capture of the different proportions of macrofaunal assemblages from the supra-, medio- and infralittoral levels. We collected 211 taxa: 194 animals and 17 algae. The most abundant and dominant organisms collected with van Veen grabs were Nematoda, Oligochaeta and Collembola at the supralittoral level; the polychaetes Saccocirrus spp. and Pisione remota, the amphipod Corophium orientale, Nematoda, and Turbellaria at the mediolittoral level; and Nematoda at the upper infralittoral level. SIMPER analysis revealed great dissimilarity between the organisms inhabiting the supralittoral and the other littoral levels. Regarding the epifauna, the sticky traps used at the supralittoral level mainly collected Collembola, which were nearly absent in pitfall traps. The qualitative study performed with a clam net and a small spade revealed that Nematoda, Saccocirrus spp., Turbellaria, Nemertea and the polychaete P. remota were the most abundant animals at both the medio- and the infralittoral levels and no differences were found between these levels. Different qualitative sampling methodologies showed that in fine sediments the bivalves Donax trunculus and D. semistriatus determined more than 97% of dissimilarity from coarse-sand sites. Richness increased in protected sandy and cobble shores. Littoral level and bottom-type features were only to a certain extent valid indicators of specific biotic components for a specific habitat.

Keywords: macrofauna; zonation patterns; littoral habitats; Catalonia; beach.

Estructura de los hábitats y patrones de zonación en playas del Mediterráneo noroccidental

Resumen: Se ha estudiado la estructura de los hábitats (comunidades de macrofauna y tipos de sedimento) y los patrones de zonación de 29 playas desprovistas de vegetación a lo largo de los 900 km de la costa de Cataluña (Mediterráneo noroccidental). El muestreo de los organismos se realizó mediante dragas, trampas de caída, trampas adhesivas, redes de marisqueo y palas para asegurar una captura exhaustiva de los organismos presentes en las comunidades de macrofauna de los niveles supralitoral, mediolitoral e infralitoral. Se colectaron 211 taxones: 194 animales y 17 algas. Los organismos más abundantes y dominantes recolectados con dragas van Veen fueron: Nematodos, Oligoquetos y Colémbolos en el nivel supralitoral; los poliquetos Saccocirrus spp. y Pisione remota, el antípodo Corophium orientale, Nematodos y Turbelarios en el nivel mediolitoral; y Nematodos en la parte menos profunda del nivel infralitoral. Los análisis SIMPER detectaron grandes diferencias entre los organismos del nivel supralitoral y los de los otros niveles. Respecto a la epifauna, las trampas adhesivas usadas en el nivel supralitoral capturaron principalmente Colémbolos, los cuales estaban ausentes en las trampas de caida. El estudio cualitativo realizado con una red de marisqueo y una pala pequeña reveló que Nematodos, los poliquetos Saccocirrus spp. y Pisione remota, Turbelarios y Nemertinos eran los animales más abundantes tanto en el nivel mediolitoral como en el nivel infralitoral y que no había diferencias entre ambos niveles. Diferentes métodos cualitativos de muestreo revelaron que en los sedimentos finos los bivalvos Donax trunculus y D. semistriatus determinaban más del 97% de la disimilitud con los sedimentos gruesos. La riqueza en especies aumentaba en playas mixtas de arenas y cantos. El nivel y el tipo de sedimento fueron solo hasta cierto punto indicadores válidos de la composición de especies para cada hábitat concreto.

Palabras clave: macrofauna; patrones de zonación; hábitats litorales; Cataluña; playas.

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INTRODUCTION

The distribution of habitats along rocky sea shores has been extensively studied (e.g. Underwood and Denley 1984, Menge et al. 1985, Fraschetti et al. 2005) and shows well-defined patterns of animal and plant assemblages along the vertical axis perpendicular to the shoreline (e.g. Chappuis et al. 2014, Stotz et al. 2016). Similar distributions have been described for sandy beaches (McLachlan and Jaramillo 1995, Pérez-Domingo et al. 2008, Reyes-Martínez et al. 2015), for which clear faunal zonation patterns along the vertical axis are acknowledged (Schlacher and Thompson 2013). On the other hand, shores characterized by the presence of coarse sediments ranging from gravels to large cobbles have been poorly studied as for habitat species compositions (but see Gauci et al. 2005). For such bottoms, the macroscopic features defining the habitats are often provided by the grain size rather than the presence of particular species or species guilds. Altogether, these systems may occupy large portions of the coastlines of many seas (Schlacher and Thompson 2013). Nonetheless, as other authors have long pointed out, these environments, often regarded as marine deserts (see McLachlan 1983), are among the least known because of their biodiversity and the functioning of their communities.

Shoreline strands, and notably sandy beaches, are also well-known for their ecological importance, for the special adaptations of their fauna and flora, and for the tremendous impacts of human activities and natural disturbances (Węslawski et al. 2000, McLachlan and Brown 2006, Bessa et al. 2013). In spite of the existence of several seminal reports (Dahl 1952, McLachlan 1983) and other similar studies from other seas (e.g. Janssen and Mulder 2005, Rodil et al. 2006, Rodil et al. 2014), most research on the macroinvertebrate fauna from shoreline strands of the Mediterranean Sea has focussed on the organisms inhabiting lower infralittoral habitats (Pinedo et al. 1997, Sardá et al. 1999, Labrune et al. 2007). To date, there are a few comprehensive accounts in the literature about the macroinvertebrates from Mediterranean Sea shoreline strands and beaches in general (Deidun et al. 2003, Colombini et al. 2003, Gauci et al. 2005). Mediterranean shoreline strands are inhabited by animals ranging from tiny Collembola and flying insects to large bivalves and crustaceans (Marques et al. 2003, Colombini et al. 2005, Covazzi Harriague and Albertelli 2007). However, very little information is available for the northwestern Mediterranean Sea, where research has only been conducted on small swimming animals, mainly crustaceans (Munilla and San Vicente 2005).

In the last few decades of the twentieth century, the focus of conservation shifted unmistakably from species to habitats. In Europe, the Habitats Directive (92/43/EEC) states that the habitat of a species is an environment defined by specific abiotic and biotic factors, in which the species lives at any stage of its biological cycle.

Many habitat classification schemes often use the classical division of the littoral into three main levels: supra-, medio- and infralittoral. For example, while the European Nature Information System (EUNIS) considers these divisions in some instances (e.g. A.2.25, Mediterranean communities of mediolittoral sands), in other cases the nomenclature does not specify the littoral level to which a habitat is assigned (e.g. Å2.11 Shingle (pebble) and gravel shores). Other classification schemes for the Mediterranean Sea adopt these divisions. In the Lista Patrón de los Hábitats Marinos Presentes en España" (hereafter LPRE, Templado et al. 2012), and to a lesser extent in the original Coordination of the Information of the Environment (CORINE) Biotopes, each habitat is framed within the corresponding littoral level.

The main goal of this study was to characterize sediment grain features and macrofaunal assemblages from 29 unvegetated shoreline strands along the whole coast of Catalonia (NW Mediterranean Sea). The study represents the first descriptive assessment of the zonation patterns of the organisms found from the upper supralittoral level down to the upper infralittoral level (one metre depth). By relating taxon presence and abundance to granulometric features of the strands, we also evaluate whether the EUNIS, CORINE Biotopes (Ballesteros et al. 2014) and LPRE (Templado et al. 2012) habitat classifications, which are based on sediment composition and shore levels, reflect actual differences in species distributions for the area studied.

MATERIALS AND METHODS

Sampling

To avoid the presence of people and beach-cleaning machines, which operate mainly in summer, 29 shoreline strands (Fig. 1) were visited between autumn and winter either in 2010 or 2011. To study habitat structure and species composition, sediment samples for granulometric and biological analysis were collected at each site and for each level (supra-, medio- and upper infralittoral, see Fig. 2).

The sediment was stored in 250-mL plastic pots and taken to the laboratory. Most samples were analysed by sieving the dry sediment through a 2000, 1000, 750, 500, 375, 250, 125 and 63 μ m column of mesh sizes. When very fine grains were found, the samples were analysed using an automatic Mastersizer 2000 (Malvern instruments Ltd., UK).

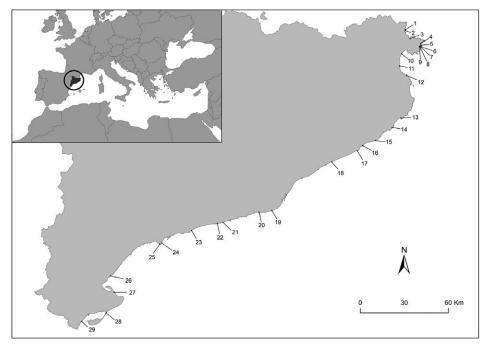
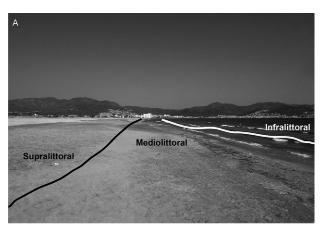


Fig. 1. – Map of the studied coastline. The position of each site is shown (see Tables 1 and 2 for details).



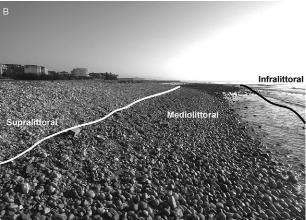


Fig. 2. – The three littoral levels on a sand-dominated (A) and a cobble-dominated (B) strand.

To obtain the most representative organisms characterizing the habitats, samplings were carried out using different devices at 29 sites (Fig. 1). We selected 19 sites as representative of different grain sizes and gen-

eral strand morphology to sample the infauna at each level using a van Veen grab of 600 cm² area (Table 1). At each site, one single grab was used at each littoral level. The van Veen grab is a widely used device and was used in order to facilitate comparison of our data with those from other studies.

To collect the organisms that move over the shore sediment at the supralittoral level (epifauna), pitfall traps and sticky traps were used. Pitfall traps were made of 500-mL plastic pots filled with tap water and a few drops of formaldehyde. Each trap was inserted into the sediment so that the pot mouth was flush with the strand surface. At one side of the pitfall trap, a 66×4.5 cm sticky trap was installed. Both devices were left at dusk and collected the next morning. For several reasons (e.g. broken, missing or flooded traps), data were not available for all the 19 sites (see details in Table 1).

The van Veen grab sampling area of 600 cm² is too small for a representative sampling of large molluscs. To ensure their collection, a clam net (30×15 cm mouth, 0.7 cm mesh size) was used in the medio- and the upper infralittoral levels at nine sites for which previous knowledge about past presence of bivalves existed (Table 1). The clam net was trawled once along an approximately 20-m-long transect parallel to the shore at each site and for each littoral level (see Table 1 for details). A tiny spade (30 cm long, 7 wide) was also used to sample sediments where the clam net was difficult to handle (e.g. around stones). At one particular site on the Ebre River Delta outer beach (site 27, Marquesa Beach) medio- and infralittoral habitats were represented by compacted clays. Since the use of the grab was practically impossible, sampling was done with the tiny spade. At that site, the medio- and infralittoral levels, which were hardly distinguishable, were sampled through a single sedi-

Table 1. – The different methods employed at each site to sample the three littoral levels.

	supralittoral	mediolittoral	infralittoral
1 Borró Gran	grab, pitfall trap, sticky trap	grab	grab
2 Canyelles	pitfall trap, spade (wrack)	_	_
3 Port de la Selva	grab, pitfall trap, sticky trap, spade (wrack)	grab, spade	grab
4 Jonquet	=		spade
5 Portlligat	grab	grab	grab, clam net, spade
6 Confitera	_	clam net, spade	clam net, spade
7 Ros	_	clam net, spade	clam net, spade
3 Llaner	=	clam net, spade	clam net, spade
9 Empuriabrava	grab, pitfall trap, sticky trap	grab	grab
10 Sant Pere Pescador	grab, pitfall trap, sticky trap	grab	grab
11 Montgó	grab, pitfall trap, sticky trap	grab	grab
2 Palamós	_	clam net, spade	clam net, spade
3 Sant Pol	grab, pitfall trap, sticky trap	grab	grab
14 Sant Feliu		clam net, spade	clam net, spade
15 Llevador	grab, pitfall trap, sticky trap	grab	grab
16 Sant Francesc	grab	grab	grab
17 Malgrat	grab, pitfall trap, sticky trap	grab	grab
18 Arenys de Mar	grab, pitfall trap, sticky trap	grab	grab
9 Remolar	grab, pitfall trap, sticky trap	grab	grab
20 Castelldefels	grab	clam net, spade	clam net, spade
21 Delta del Foix	grab, pitfall trap, sticky trap	grab	grab
22 Cubelles		clam net, spade	clam net, spade
23 Torredembarra	grab, pitfall trap, sticky trap	grab	grab
24 Pineda	spade	clam net, spade	clam net, spade
25 Cala Font	grab, pitfall trap, sticky trap	grab	grab
26 Estany Podrit	grab, pitfall trap, sticky trap	grab	grab
27 Marquesa	_	spade	spade
28 Aluet	grab, pitfall trap, sticky trap	grab	grab
29 Martinenca	grab, pitfall trap, sticky trap	grab	grab

Table 2. – The different substrate types found at each site for the three littoral levels.

	supralittoral	mediolittoral	infralittoral
1 Borró Gran	cobbles, gravels, and sand	gravels, cobbles, and sand	gravels and sand
2 Canyelles	P. oceanica wracks	_	_
3 Port de la Selva	cobbles, gravels, and P. oceanica	coarse sands, gravels, and P. oceanica	cobbles and gravels
4.7	wracks	wracks	111 1 1 1 1 1
4 Jonquet	-	_	cobbles, gravels, and <i>C. nodosa</i>
5 Portlligat	cobbles and fine sands	coarse sands and gravels	cobbles
6 Confitera	_	cobbles and gravels	cobbles and gravels
7 Ros	_	coarse sands and gravels	cobbles and gravels
8 Llaner	_	coarse sands and gravels	cobbles and gravels
9 Empuriabrava	gravels	coarse sands and gravels	cobbles, gravels, and coarse sands
10 Sant Pere Pescador	medium sands	gravels and very coarse sands	medium sands
11 Montgó	cobbles and gravels	gravels and cobbles	cobbles and gravels
12 Palamós	_	gravels	gravels and very coarse sands
13 Sant Pol	gravels	gravels and very coarse sands	medium sands
14 Sant Feliu		very coarse sands and gravels	very coarse sands and gravels
15 Llevador	cobbles	cobbles	large cobbles
16 Sant Francesc	very coarse sands and gravels	very coarse sands and gravels	very coarse sands and gravels
17 Malgrat	gravels	gravels and cobbles	cobbles and gravels
18 Arenys de Mar	gravels and cobbles	very coarse sands and gravels	gravels and cobbles
19 Remolar	medium and fine sands	medium sands	fine sands
20 Castelldefels	fine and medium sands	medium sands	fine sands
21 Delta del Foix	cobbles and gravels	gravels and cobbles	large cobbles
22 Cubelles	_	fine sands	fine sands
23 Torredembarra	fine sands	fine and medium sands	fine sands
24 Pineda	fine sands	fine sands	fine sands
25 Cala Font	fine sands	fine sands	fine sands
26 Estany Podrit	cobbles and gravels	cobbles and gravels	fine sands
27 Marquesa	_	compacted clays	compacted clays
28 Aluet	fine sands	fine and medium sands	fine sands
29 Martinenca	fine sands	fine and medium sands	fine and medium sands

ment collection. The sample volume was comparable to that collected for the other sediment types. The spade was also used at Jonquet (site 4) to sample the infralittoral sediment around *Cymodocea nodosa* sheaths and to collect *Posidonia oceanica* wracks at the supralittoral level of two sites: Canyelles (site 2) and Port de la Selva (site 3, Table 1).

All samples were stored in sealed plastic bags with a formalin-seawater solution and taken to the laboratory for sorting and identification of the organisms under the dissecting microscope.

Quantitative data were obtained from the grab, pitfall and sticky trap methodologies. Samples taken with both the net and the spade were qualitatively analysed. The presence of seagrass and seaweeds was also recorded. The sampling tools employed at each study site are detailed in Table 1.

Table 3. – Codes used for the sediment description in the analyses and figures. Only dominant proportions are shown.

		_
Code	Sediment description	
C CG G CoSG MeS FiS CC PO	Large to small cobbles and cobbles with sands Cobbles and gravels Gravels and gravels with sands Coarse to very coarse sands and gravels Medium sands alone or with fine sands Fine sands alone or with medium sands Compacted clays Posidonia oceanica wracks	
PO	Posidonia oceanica wracks	

Data treatment and statistical analysis

Quantitative and qualitative data were analysed separately. Abundance data resulting from grabs (ind m⁻²) and traps (standardized to individuals per hour per trap) were square root transformed for further analysis. All organisms collected with the spade or the clam net were analysed based on their presence or absence in the samples. Non-metric multidimensional scaling (MDS) ordinations based on taxa composition (Bray-Curtis similarity, average link grouping) were done to identify patterns of similarities among sites. An analysis of similarities (ANOSIM) was used to test the differences between groups of samples. Finally, the similarity/dissimilarity percentages analysis (SIMPER) was performed in order to identify the species characterizing each level or group of samples.

PRIMER v6 software with PERMANOVA add-on was used to run the analyses.

RESULTS

The granulometry of the studied shoreline strands ranged from fine sands to large cobbles (Table 2). The sediment type often changed throughout the three shore levels (supra-, medio- and infralittoral). *P. oceanica* wracks (two sites), *C. nodosa* meadows (one site), and compacted clays (one site) were also found (Table 2). Sediment codes used in the analyses and relative figures (see below) and in the Supplementary Material are listed in Table 3.

We distinguished five different habitats at the supralittoral, six at the mediolittoral, and seven at the infralittoral level by their substrate characteristics (see Appendix). These habitats corresponded to different extents to habitats from the LPRE, EUNIS, and CORINE Biotopes nomenclatures (Appendix 1). Correspondences with habitat codes from the three classifications and with the main taxa found in each of the sampled habitats are detailed in the Appendix 1.

Grabs, traps and clam nets allowed us to collect a wide proportion of the organisms inhabiting the strands. A total of 211 taxa were collected, most of them animals (194; Supplementary Material, Table S1) but also some algae (17).

In the supralittoral level, Nematoda and Oligochaeta were the most abundant and frequent taxa collected with the grabs (Table 4). Springtails (Collembola) were the most abundant and dominant organisms in the sticky traps, except at most fine-sand sites, where few organisms were collected with this method (see Supplementary Material, Table S1). Pitfall traps captured few specimens, of which the Collembola and the amphipods Talitrus saltator and Cryptorchestia cavimana were the most abundant ones (Supplementary Material, Table S1). At the mediolittoral level, polychaetes of the genus Saccocirrus were the most abundant organisms captured with the grabs (Table 5), mainly in coarse sediments, followed by the amphipod Corophium orientale, Nematoda, Turbellaria, and the polychaete *Pisione remota* (Table 5). At the infralittoral level, Nematoda were overall the most abundant animals, but Saccocirrus spp. were the most frequent organisms at most northern sites with coarse sediments (Table 5). Some taxa were irregularly very abundant: Polychaetes (Ctenodrilus serratus, Eurydice affinis, Malacoceros fuliginosus, Notomastus latericeus and Salvatoria spp.), amphipods (Hyale perieri and Melita spp.) and the gastropod Neverita josephinia (Table 5).

The qualitative samplings carried out with the clam net and the spade at the medio- and infralittoral levels allowed us to collect some bivalves species that were absent in the samples collected with the grabs. The

Table 4. – Main taxa collected at the supralittoral level with the grab method. Taxa are ordered by their total abundance (ind m⁻²). Only taxa representing up to 70% of the total abundance at each site are included. See Tables 1 and 2 for site numbers. Asterisks indicate widespread taxa that are not included in the 70% of the total abundance at a particular site.

	1	3	5	9	10	11	13	15	16	17	18	19	20	21	23	25	26	28	29
Nematoda			32			*							5					3200	*
Corophium orientale																		800	
Oligochaeta		144	64	4		28	67			46				*				*	
Turbellaria														283					
Collembola		*						33	8		67								
Antalis cf. vulgaris											133								
Siphonoecetes dellavallei															67				
Staphylinidae				8			*												
Leptochelia savignyi					4	*								*					
Coleoptera sp1				4										*					
Formicidae				8		8													
Apocrita					4	8													
Diptera sp. 7																			8
Labidura riparia						8													
Aora gracilis						8													
Platynereis sp.					8														
Ampithoe cf. spuria									4										
Abundance	0	180	96	32	20	84	83	33	16	50	216	0	6	367	83	0	0	4684	12
Richness	0	3	2	6	4	11	2	1	3	2	3	0	2	6	2	0	0	13	2

	$\stackrel{1}{M}_{}}$	Ξ	3 I	S M	П	9 M	I	$^{10}_{\rm M~I}$	11 M		$^{13}_{ m M}$	15 M	I M	16 1 I	M	П	$^{18}_{\rm M}$	19 M	I M	21 [I	23 M I		25 M I	$_{\rm M}^{26}$	28 M	Ι	29 M
Nematoda Saccocirrus spp. Turbellaria Monocorophium insidiosum	* 67 1334	* 1200	* *	233 (233 6017 1883 3534 * * * * 800	* 8 8 3 3.	3534 * 800	50	1111	50 * 33 283	* 133 1	150 * * * * * 133 283 133 10000 350 67	* 350 83 67	*	298		179 * 267 183	400	* * 3267	* 77	~					* *	
Corophium orientale Pisione remota Salvatoria spp. Melita spp. Capitella spp.	*	*	* *			1000	*		Q	200 200		-	* **	* 5516	2666	67	*		1083	33 * 1334	-+				7418 *	* 2901 *	
Ctenodrilus serratus Eurydice affinis Notomastus laterieus Hyale perieri Malacoceros fuliginosus Nemertea Microdeutopus similis Oligochaeta	2367 83		2667 *		* *	* +	* * *	* *	-	*				* *	* *	*	*		* * *	2717	50				*	2851 2434 *	183
Donactula comea Neverita josephinia Hesiomura serrata Dosinia lupinus Jassa ocia Echinogammarus cf. foxi Scolelepis mesnili Donax trunculus Copepoda Synchelidium cf. haplochele Lumbrineris acuta Syllis variegata Bivalvia Amphitoe cf. spuria Amphitoe cf. spuria	2		999		*	÷	· * *	<i>L</i> 9	200				* 33	~	*	99	* 200		71 71	*	17	17 33 17 33 *	50 3 50 17	100	0		33
Kurtiella bidentata Abundance Richness	17 4718 283 1700 4197 233 6983 3944 5884 33 217 217 517 500 150 10050 716 167 6183 4849 300 562 533 433 50 6100 16296 83	1700	4197	233 (5983 3	944 5	1 884 3	17 33 217	217 5	17 500) 150 1	00000	716 16	7 618	3 4849	300 5	562 533	3 433 ;	30 61C	0 1629	6 83	50 67	7 83	17 13	83 17 133 16352 22071 183 167	22071	18

Table 6. – Main taxa collected through the qualitative sampling at the supralittoral (S), mediolittoral (M) and infralittoral (I) levels. Taxa are ordered by their total frequency throughout sites. Only taxa found at more than one site are shown. For the site numbers see Tables 1 and 2.

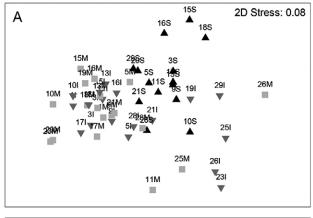
	2		3	4	5	(5	,	7		8	1	2	1	4	2	20	2	2		24		27
	S	S	M	I	I	M	I	M	I	M	I	M	I	M	I	M	I	M	I	S	M	I	M-I
Nematoda				+		+		+		+		+	+	+	+								
Saccocirrus						+			+		+	+	+	+	+	+							
Turbellaria	+		+	+			+		+	+			+	+									
Nemertea								+			+	+	+	+					+				
Pisione remota										+	+	+	+	+	+								
Oligochaeta								+		+	+			+	+								
Donax trunculus																	+	+			+	+	
Portumnus latipes							+										+				+	+	
Donax semistriatus																		+			+	+	
Nereididae	+			+							+												
Scolelepis squamata																			+		+	+	
Capitella spp.							+													+			
Carcinus aestuarii					+		+																
Cerastoderma glaucum					+														+				
Ensis minor																					+	+	
Eurydice affinis																+				+			
Hesionura serrata												+		+									
Naineris laevigata				+													+						
Nassarius mutabilis																		+	+				
Protodrillus sp.									+				+										
Siphonoecetes dellavallei																				+			+
Richness	9	1	1	24	2	2	6	3	3	4	9	5	6	10	4	2	6	3	7	4	5	9	6

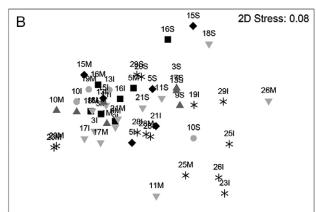
Table 7. – Contributions and average abundances of species responsible for 70% of dissimilarities (SIMPER analysis) between groups (supralittoral (S), mediolittoral (M), and infralittoral (I) levels) based on total macrofaunal composition. Total dissimilarity between groups is included.

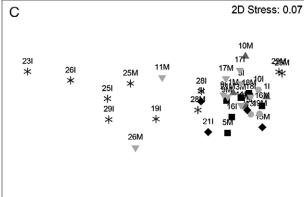
	Taxa	Average abundance	Average abundance	Contribution (%)	Cumulative contribution (%)
Groups M and I (89.20 %)		Group M	Group I		
	Saccocirrus spp.	11.51	6.38	13.93	13.93
	Nematoda	9.84	14.80	11.59	25.52
	Turbelaria	10.13	3.64	8.50	34.03
	Pisione remota	8.98	3.94	8.16	42.19
	Eurydice affinis	4.24	1.37	5.69	47.88
	Nemertea	4.55	2.45	4.65	52.53
	Scolelepis mesnili	0	0.88	2.89	55.42
	Dosinia lupinus	1.01	0.45	2.70	58.12
	Donax trunculus	0	0.94	2.68	60.80
	Melita bulla	1.32	1.98	2.67	63.47
	Hesionura serrata	0.32	1.69	2.62	66.10
	Melita palmata	0	4.36	2.43	68.53
	Ctenodrilus serratus	Ŏ	3.72	2.10	70.63
Groups M and S (97.73 %)		Group M	Group S		, , , , ,
Groups III and B (57176 76)	Saccocirrus spp.	11.51	0	15.01	15.01
	Nematoda	9.84	4.89	12.09	27.09
	Turbelaria	10.13	1.20	9.71	36.81
	Oligochaeta	0.62	3.45	8.42	45.23
	Pisione remota	8.98	0	7.90	53.12
	Eurydice affinis	4.24	Ö	7.55	60.67
	Nemertea	4.55	Ö	4.88	65.55
	Dosinia lupinus	1.01	Ŏ	4.49	70.04
Groups I and S (97.09 %)	2 osinte impinus	Group I	Group S		, 6.6 .
Groups runa B (57.05 %)	Nematoda	14.80	4.89	11.00	11.00
	Saccocirrus spp.	6.38	0	10.57	21.57
	Oligochaeta	2.36	3.45	7.62	29.18
	Turbelaria	3.64	1.20	4.88	34.06
	Scolelepis mesnili	0.88	0.25	4.56	38.63
	Pisione remota	3.94	0.23	4.18	42.81
	Donax trunculus	0.94	Ő	3.98	46.79
	Collembola	0.54	1.60	3.61	50.39
	Hesionura serrata	1.69	0	3.09	53.49
	Melita palmata	4.36	0	2.86	56.35
	Nemertea	2.45	0	2.73	59.08
	Melita bulla	1.98	0	2.73	61.69
	Ctenodrilus serratus	3.72	0	2.31	64.00
	Melita valesi	3.64	0	2.26	66.26
	Scolelepis squamata	0.45	0	2.20	68.28
	Eurydice affinis	1.37	0	1.96	70.24
	Euryaice affinis	1.37	U	1.90	70.24

bivalves *Donax semistriatus*, *D. trunculus* and *Ensis minor* were exclusively present at the southern sites (Table 6). Nematoda, *Saccocirrus* spp. Turbellaria,

Nemertea and the polychaete *P. remota* were the organisms most frequently collected (Table 6) through the qualitative sampling. The maximum numbers of







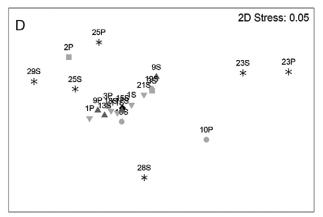


Fig. 3. – MDS plots. A, plot based on macrofauna abundance (ind m^{-2}) of grab samples showing the littoral level: S, supralittoral, dark triangle; M, mediolittoral, quadrat; I, infralittoral, bright triangle. B, plot based on macrofauna abundance (ind m^{-2}) of grab samples showing the sediment type. C, plot based on macrofauna abundance (ind m^{-2}) of the medio- and infralittoral grab samples showing the sediment type. D, plot based on macrofauna collected with traps in the supralittoral, with label indicating the sampling method (P, pitfall; S, sticky). Labels indicate the site number and the littoral level in plots A, B and C. Sediment types (see Table 3 for codes) are plotted as follows: C, rhombus; CG, bright triangle; G, dark triangle; CoSG, quadrat; MeS, circle; FiS, asterisk; PO, quadrat.

taxa (24) were found at the infralittoral level of the shallow meadow of *C. nodosa* (site 4, Table 2 and Supplementary Material, Table S1) and 20 of them were exclusively present at this site. The isopod *Sphaeroma serratum* was exclusively present at Marquesa (site 27, see Supplementary Material, Table S1) and represented a new finding for the Iberian Peninsula.

Erect algae covered the upper surface of the large cobbles of Llevador (site 15) and Delta del Foix (site 21). The green algae Chaetomorpha mediterranea and Cladophora spp., the red algae Polysiphonia tripinnata and Ceramium diaphanum, and the brown alga Dictyota sp. were found at Llevador. Cobbles from Delta del Foix were colonized by the red algae Gelidium pusillum, Haliptilon virgatum, Ceramium gr. strictum, Polysiphonia sertularioides and Corallina elongata and the green alga Cladophora albida. The presence of algae was also observed in the infralittoral fine sands of Aluet (site 28), where the red alga *Chondria cap*illaris and the green alga Ulva curvata were present. The xanthophyte Vaucheria submarina was collected in Cubelles (site 22). Finally, several algae were collected over the compacted clays of Marquesa beach (site 27): the green algae Cladophora vagabunda and Ulva prolifera and the red algae C. diaphanum and Polysiphonia sp.

The MDS analysis with the data collected with the grabs showed that only the supralittoral segregated from the other two levels, which were highly overlapped (Fig. 3A). The ANOSIM test showed that the supralittoral level was significantly different from the medio- and infralittoral levels (p<0.001), but no significant differences were found between these two levels (p>0.05). SIMPER analysis revealed that the average dissimilarity was more than 97% between the organisms inhabiting the supralittoral and those of the medio- and infralittoral levels (Table 7). The presence of Oligochaeta at the supralittoral level and Saccocirrus spp. and Nematoda at the medio- and infralittoral levels determined the dissimilarities between levels. As for the distribution of granulometry across the samples (Fig. 3B), most bottom types were mixed up together (ANOSIM; p>0.05), although fine sands were slightly segregated at the MDS plot. The dissimilarity of fine-sand assemblages from the rest of sediment types was more than 96% (SIMPER analysis). P. remota, Saccocirrus spp. and Turbellaria, which strongly characterized medium to large grain-sized strands at the medio- and infralittoral levels, were in fact negligible in fine sands, where Nematoda, Scolelepis squamata, S. mesnili, D. trunculus and E. affinis dominated.

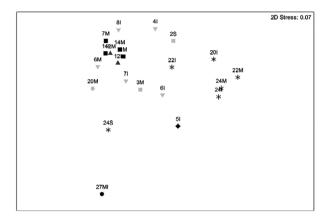


Fig. 4. – MDS plot based on qualitative samples. Labels include the site number (see Table 1) and the littoral level (S, supralittoral; M, mediolittoral; I, infralittoral). Sediment types (see Table 3 for codes) are plotted as follows: C, rhombus; CG, bright triangle; G, dark triangle; CoSG, dark quadrat; MeS, bright circle; FiS, asterisk; CC, dark circle; PO, bright quadrat.

Although medio- and infralittoral samples plotted together when supralittoral samples were excluded from the analyses (Fig. 3C), the infralittoral level of sites 19, 23, 25, 26, and 29 and the mediolittoral level of sites 11, 25 and 26 were segregated. The markedly different position was mainly due to the presence of the abovementioned taxa, which were exclusive of fine sands, and the lack of those characteristic of coarse sediments.

The MDS analyses performed with the supralittoral epifauna captured with traps revealed no clear pattern (Fig. 3D) for either the sample device used (pitfall and sticky traps; ANOSIM, p>0.05) or the bottom type (ANOSIM, p>0.05). However, fine-sand sediments plotted separated from the other bottom types. SIMPER analysis revealed more than 93% dissimilarity between fine-sand assemblages and the other assemblages. Pairwise tests showed a significant difference (p<0.05, R=0.325) between the assemblages of macroinvertebrates inhabiting cobbles and gravels and those found in fine sands. When fine sands were removed from the analyses, the sampling methods (sticky and pitfall traps) were clearly separated (ANOSIM, R=0.420, p<0.05). Sticky traps mainly collected Collembola, which were almost absent in pitfall traps. The species T. saltator was exclusively found in pitfall traps.

The MDS analyses performed with the qualitative samples (Fig. 4) showed noticeable and significant dissimilarities between substrate types (ANOSIM, R=0.443, p<0.05). Fine sands plotted separately from the rest of bottom types (Fig. 4). The presence of the bivalves D. trunculus and D. semistriatus at the fine-sand sites accounted for more than 97% of the dissimilarity (SIMPER analysis) between these sites and those with P. oceanica wracks (R=0.625, p<0.05), cobbles and gravels (R= 0.528, p<0.01), coarse to very coarse sand and gravels (R=0.681, p<0.01), and those dominated by gravels (R=0.536, p<0.05). The high dissimilarities observed were mainly due to the presence of Turbellaria in P. oceanica wracks, cobbles and gravels, to the presence of Saccocirrus spp. in cobble and gravel bottoms, and to the presence of Nematoda, Oligochaeta and the species P. remota at sites dominated by coarse to very coarse

sand and gravels. Those species were never recorded in the qualitative samples from sites dominated by fine sands. Finally, qualitative samples showed no clear pattern as regards the littoral levels (ANOSIM, p>0.05).

DISCUSSION

With the exception of the studies of Munilla et al. (1998) and Munilla and San Vicente (2005) on suprabenthos of Catalan beaches and several studies focussing on a few macrobenthic taxa from vegetated sandy littoral ecosystems (e.g. Colombini et al. 2003), this is to our knowledge the first account of the whole spectrum of macrobenthic fauna and marine flora inhabiting the supra-, medio- and upper infralittoral of shoreline strands from a long (900 km) NW Mediterranean stretch of coast. To achieve this result, various complementary methods were used. None of them alone would have helped collect the entire spectrum of organisms from the studied habitats.

The distance to the shoreline is the main factor driving the different habitats' structure (considered as macrofauna composition) in the strands. The macroinvertebrate assemblages at the supralittoral level were clearly different from those found at the medio- and infralittoral levels. This division between the supralittoral and the two other littoral levels has been observed in northern beaches of Spain (Rodil et al. 2006) and in Tunisia (Pérez-Domingo et al. 2008). Oligochaeta, Nematoda, and Turblellaria may be quantitatively dominant in several Mediterranean beach portions (see Covazzi Harriague et al. 2006) that are comparable to the supra- and mediolittoral levels studied here. Saccocirrus spp. and P. remota have been reported in coarse sediment of medio- and infralittoral beaches from other Mediterranean Sea areas (Villora-Moreno 1997, Covazzi Harriague and Albertelli 2007). The amphipods Monocorophium insidiosum and C. orientale, which were exclusively present in high numbers at sites 21 and 28, respectively, are used for toxicity testing and may prefer brackish waters (Prato et al. 2010). These two sites showed the highest infaunal richness. As regards the substrate types, the sediment classification (bottom type) was the second factor driving the difference in species composition. Fine sands showed distinctively different taxa from the rest of the sediments across the littoral levels. This pattern was even more evident when the supralittoral was excluded from the analyses, mainly because of the absence in fine-sand bottoms of Saccocirrus spp., P. remota, Hesionura serrata and Turbellaria, which were very common taxa in coarse sediments. The polychaete H. serrata, which is probably an alien species in the Mediterranean Sea (Zenetos et al. 2010), has been collected in medium to very coarse sediments in several areas of the NW Mediterranean (Authors, unpublished results). Fine-sand sites were inhabited by Nematoda and the polychaete S. mesnili, which reached 100 ind m⁻² at the infralittoral level of site 26 (Estany Podrit), where it was dominant. S. mesnili is very common in fine-to-medium-sand bottoms in the lower infralittoral of the Mediterranean Sea (e.g. Pérez-Domingo et al. 2008). The cirolanid isopod *E. affinis*, which was captured only at fine-sand sites, is quite a common inhabitant of sandy beaches in the Mediterranean Sea (Dexter 1989, Munilla and San Vicente 2005). Finally, the bivalve *D. trunculus* was only observed in fine sediments (see also below) although its presence has been related to fine to medium sandy bottoms in the Mediterranean Sea (Pérez-Domingo et al. 2008, Weber and Zuschin 2013).

The qualitative samples collected with the clam nets and the spades were, overall, highly similar between the medio- and infralittoral levels. Clam nets proved to be irreplaceable tools for collecting the bivalve fauna from the medio- and infralittoral levels, particularly the species D. trunculus, D. semistriatus and E. minor, which were almost absent in the grab samples. The presence of some species in the qualitative samples was rather unexpected. The polychaete Perinereis sp., which may come from nearby rocky substrates, was not found again in subsequent samplings specifically targeting these organisms (Authors, unpublished research). Although we did not repeat the same samplings at the same site, the dominance of Nematoda, the Polychaeta Saccocirrus spp. and P. remota, Oligochaeta and Nemertea in the qualitative samples support the conclusion that these taxa are the most abundant in the shoreline strands studied. As expected, the compacted clays had a completely different flora and fauna. The bivalve *Pholas dactylus*, whose empty shells were copiously found in the immediate vicinity of the compacted clays, was absent in the qualitative samples. As in the case of the other bivalve species for which the collection of a large volume of sediment was needed for their detection, the spade sampling was possibly inadequate for the collection of this important boring mussel.

Traps (sticky and pitfall traps) collected a different array of organisms compared with the grabs at the supralittoral level, thus demonstrating their importance for properly describing species composition of beaches. Sticky traps were by far the most efficient devices for sampling animals moving over the sediment surface, such as insects. Epifauna abundance and richness in pitfall traps was much lower. Gauci et al. (2005) demonstrated the inefficiency of pitfall traps for capturing organisms on shingle beaches. Low animal abundance was also observed in Malta when pitfall traps were used (Deidun et al. 2003). The most frequent trap captures were Collembola (often representing more than 94% of the organisms at northern sites), Fucellia maritima and other diptera, as observed on other Mediterranean beaches (Colombini et al. 2005). On the other hand, the amphipod T. saltator the only abundant organism in the pitfall traps (Supplementary Material, Table S1)—was not as frequent and abundant as described in other studies (Węslawski et al. 2000, Pérez-Domingo et al. 2008, Reyes-Martínez et al. 2015). This species generally shows low densities in late winter, a rapid increase from early spring to July, and the highest densities in summer (Marques et al. 2003, Gonçalves et al. 2009). Thus, seasonality may be a major cause of the low densities recorded in this study. T. saltator is also known to move to terrestrial habitats and dunes in winter (Gonçalves et al. 2009).

With the obvious exceptions of sites 2 and 3, where the presence of *P. oceanica* wracks led to a distinct faunal composition (Gauci et al. 2005), our results show that there is no clear correspondence between any particular taxon and a specific supralittoral habitat based on substrate types. Most macroinvertebrates that move over supralittoral surfaces show no preference for any particular grain size. However, Collembola, which do not fly, seem to avoid fine sands, possibly because they provide them with no shelter for hiding. Once more, fine sands definitively prove to be different habitats at all the littoral levels studied.

Our results, based upon both epifauna and infauna, support the existence of key differences in the assemblages across the littoral levels and among bottom types. However, these differences were not observed when we focused on either epifauna or macroinfauna separately or on the results from a single sampling methodology. For instance, if we do not consider the infauna, the supralittoral level of unvegetated strands characterized by coarse sands, gravels and cobbles harbours a quite homogeneous assemblage, populated primarily by Collembola and some insect groups. Moreover, the medio- and upper infralittoral levels show very similar habitats, with Nematoda, Turbellaria, the polychaetes P. remota and Saccocirrus spp., the isopod E. affinis, and some bivalves as the principal taxa. However, strands characterized by fine sands are host to very distinct medio- and infralittoral assemblages mainly because of the presence of the bivalves *Donax* spp. and E. minor, which were exclusively collected with the clam net.

Richness may increase on protected sandy shores. By providing a greater surface for colonization, hides and crevices, particularly when cobbles are large or the exposure to water movements is small enough (see Sousa 1979), cobble shores may contain several algae and many macroinvertebrate species.

Variability in the biotic component among beaches has been attributed to a set of different factors in the literature. Shore characteristics such as the presence of vegetation, slope and coastal exposure, human pressures and food availability are among the main factors driving differences in species composition and abundance. Vegetation cover seems to favour high diversity of species because of the higher numbers of microhabitats available (Colombini et al. 2003). In this study, we have not dealt with vegetated strands, which cannot be considered as belonging to the strictly marine supralitoral level. Nevertheless, the proximity of *Salicornia*-dominated salt marshes at site 28 may have played a role in determining the high numbers of observed taxa.

Gentle beach slopes, often accompanied by small grain sizes, on so-called dissipative beaches (low wave exposure) have often been related to higher abundance of species in other seas (see McLachlan 1996, McLachlan and Jaramillo 1995, Rodríguez et al. 2003). Here, despite the lack of strand slope and exposure assessments, the highest numbers of organisms and taxa were found at the more dissipative, gentle steeped sites regardless of the bottom type (i.e. sites 21 and 28). The cobble shore of site 21 (Delta del Foix) has extremely

shallow waters, which protect the strand from the breaking waves (Authors, personal observations). The fine-sand shore at site 28 is confined into a shallow area in the largest bay of the Ebre Delta region.

Trampling and beach cleaning are among many human impacts that affect beaches worldwide (see Moffet et al. 1998, Gheskiere et al. 2005, Bessa et al. 2014). In the study area, mechanical beach cleaning and, especially, human trampling were very reduced or absent in autumn and winter months, when sampling was conducted. This may have helped reduce the potential effects of these activities on the results from the supralittoral and, to some extent, the mediolittoral levels. Site 28, where trampling and cleaning never occur, showed the highest numbers of species and individuals (see Table 5 and Supplementary Material, Table S1). However, other sites, which are very frequented by people in summer (site 9) and where machine beach cleaning is performed, showed similar species abundance and richness (Table 5 and Supplementary Materia, Table S11). Daily and seasonal variability have also been claimed as important factors driving differences in richness and species abundance. However, such variability could not be observed in our study, since most sites were visited on one sampling date. This has been criticized by some authors (see Brazeiro and Defeo 1996). Nevertheless, results from so-called "snapshots" may reveal a shift of some taxa from one shore level to another rather than their complete disappearance (see Brazeiro and Defeo 1996). Moreover, much of the temporal difference has also been attributed to tidal migrations (see McLachlan and Jaramillo 1995), which are negligible because of the absence of tides in the study area. However, because of our winter-based sampling (see above), we ought to assume a bias in the estimations of the actual abundance for at least one species, T. saltator.

European environmental advisory programmes warn that conservation priorities need robust, widely accepted and affordable methods of habitat classification. In this study, we provide a clear assessment in this line, describing habitats in terms of features such as bottom type and the species that inhabit them. It seems that distance to the shoreline, particularly from the upper infralittoral to the mediolittoral level, and the bottom type features are only to a certain extent valid predictors of the presence of specific biotic components. Thus, general habitat divisions based upon littoral level and grain size ought to be accepted with caution. Finally, we provide a comparison between the most used classification schemes (EUNIS, CORINE Biotopes and LPRE nomenclatures; see Appendix 1), which we believe is especially valuable for managing practices.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available through the online version of this article and at the following link: http://scimar.icm.csic.es/scimar/supplm/sm444

Table S1. - A, total abundance values for grabs and traps (ind. m-2 and ind. h-1 trap-1, respectively); and B, total abundance values for qualitative samples (ind. sample-1).

Appendix 1. – Habitats observed, correspondences among Mediterranean habitat classifications, and main taxa encountered; *habitats in the CORINE Biotopes Manual of the Catalan Habitats (see

		B	Ballesteros et al. 2014)	•	
STAGE LEVEL	HABITAT OBSERVED	LPRE CODE (LEVEL) AND HABITAT DESCRIPTION	EUNIS CODE AND HABITAT DESCRIPTION	CORINE CODE AND HABITAT DESCRIPTION	MAIN TAXA
Supralittoral	Supralittoral cobbles alone or accompanied by gravels and sands	01020101 (4) Supralittoral boulders and cobbles		17.11* Supralittoral unvegetated shingle beaches	Collembola, Oligochaeta, Diptera, Coleoptera Staphilindae
Supralittoral	Supralittoral gravels alone or accompanied by coarse sands	01020103 (4) Supralittoral coarse sands		16,111* Supralittoral unvegetated sand beaches	Collembola, Oligochaeta
Supralittoral	Supralitoral medium sands alone or accompanied by fine sands	01020104 (4) Supralittoral medium sands		16,111* Supralittoral unvegetated sand beaches	Collembola, Nematoda
Supralittoral	Supralittoral fine sands	01020105 (4) Supralittoral fine sands		16,111* Supralittoral unvegetated sand beaches	Nematoda, Siphonoecetes dellavallei, Aora spinicornis
Supralittoral	Supralittoral wracks of Posidonia oceanica	0102010502 (5) Wrack mainly composed of leaves of seagrasses in supralittoral sediments	A2.131 Facies of banks of dead leaves of <i>Posidonia oceanica</i> and other phanerogams	16.1111* Suprallittoral banks of leaves and debris of <i>Posidonia oceanica</i> and other seagrasses	Collembola, Fucellia maritima, Talitrus saltator
Mediolittoral	Mediolittoral cobbles alone or accompanied by gravels and sands	02020102 (4) Beaches of cobbles, stones and gravels	A2.11 Shingle (pebble) and gravel shores	17.12* Mediolittoral unvegetated shingle beaches	Turbellaria, Nematoda, Nemertea, Euridice affinis, Pisione remota, Saccocirrus spp.
Mediolittoral	Mediolittoral fine and medium sands in sheltered shores	020202 (3) Mediolittoral sands and muddy sands	A2.25 Mediterranean communities of mediolittoral sands	13.21* Mediolittoral estuarine muddy sands	Corophium orientale, Nematoda, Capitella spp., Salvatoria alvaradoi
Mediolittoral	Mediolittoral gravels alone or accompanied by coarse sands	02020209 (4) Mediolittoral coarse sands	A2.25 Mediterranean communities of mediolittoral sands	16.1121* Mediolittoral unvegetated coarse sands and gravels	Nematoda, Nemertea, Saccocirrus spp., Pisione remota, Turbellaria
Mediolittoral	Mediolittoral medium or fine sands	02020208 (4) Mediolittoral fine and medium sands	A2.25 Mediterranean communities of mediolittoral sands	16.1122* Mediolittoral unvegetated medium and fine sands	Euridice affinis, Saccocirrus spp., Donax trunculus, Donax semistriatus
Mediolittoral	Mediolittoral compacted terrigenous clays	020204 (3) Mediolittoral compacted terrigenous clays		16.132* Mediolittoral compacted terrigenous clays	Caprella dilatata, Jassa ocia, Cladophora vagabunda, Pholas dactilus, Ulva prolifera
Mediolittoral	Mediolittoral wracks of Posidonia oceanica	02020703 (4) Wracks of leaves and rhizomes of <i>Posidonia oceanica</i> and other seagrasses	A2.131 Facies of banks of dead leaves of <i>Posidonia oceanica</i> and other phanerogams	16.1123* Mediolittoral banks of leaves and debris of <i>Posidonia oceanica</i> and other seagrasses	Talitrus saltator, Turbellaria, Hyale cf. schmidti, Guernea cf. coalita
Infralittoral	Infralittoral cobbles alone or accompanied by gravels and sands	03040119 (4) Lower infralittoral cobbles and pebbles of sheltered zones	A5.131 Sparse fauna on highly mobile sublittoral shingles	11.23* Infralittoral cobbles	Monocorophium insidiosum, Hyale perieri, Melita palmata, Microdeutopus similis
Infralittoral	Infralittoral exposed alone or accompanied by gravels and sands	03040118 (4) Infralittoral cobbles and pebbles of exposed zones	A5.131 Sparse fauna on highly mobile sublittoral shingles	11.23* Infralittoral cobbles	Ctenodrilus serratus, Turbellaria, Saccocirrus spp., Melita bulla, Euridice affinis

Appendix 1 (Cont.). – Habitats observed, correspondences among Mediterranean habitat classifications, and main taxa encountered; *habitats in the CORINE Biotopes Manual of the Catalan Habitats (see Ballesteros et al. 2014)

STAGE LEVEL	HABITAT OBSERVED	LPRE CODE (LEVEL) AND HABITAT DESCRIPTION	EUNIS CODE AND HABITAT DESCRIPTION	CORINE CODE AND HABITAT DESCRIPTION	MAIN TAXA
Infralittoral	Infralittoral coarse sands and gravels	03040218 (4) Infralittoral coarse sands and gravels of exposed zones		11.2222* Infralittoral coarse sands and gravels of exposed zones	Melita valesi, Melita palmata, Saccocirrus spp., Pisione remota
Infralittoral	Infralittoral medium or fine sands	03040219 (4) Infralittoral fine and medium sands of exposed zones	A5.236 Mediterranean communitites of well-sorted fine sands	11.2221* Infralittoral fine sands of exposed zones	Scolelepis mesnili, Donax trunculus
Infralittoral	Infralittoral compacted terrigenous clays	030404 (3) Infralittoral and circalittoral compacted terrigenous clays		16.133* Infralittoral compacted terrigenous clays	Caprella dilatata, Jassa ocia, Cladophora vagabunda, Pholas dactilus, Ulva prolifera
Infralittoral	Cymodocea nodosa	0305130104 (5) Seagrass beds on coastal lagoons and bays with <i>Cymodocea nodosa</i>	A5.53132 Association with <i>Cymodocea</i> nodosa on superficial muddy sands in sheltered waters	11.331* Mediterranean shallow beds of <i>Cymodocea nodosa</i>	Nematoda, Heteromastus filiformis, Brania arminii, Loripes lucinalis