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Decapod crustacean assemblages from littoral bottoms of the Alborán Sea (Spain, west Mediterranean Sea): spatial and temporal variability

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SUMMARY: The structure of decapod crustacean assemblages living in shallow waters (5 to 25 m depth) in an area of the Alborán Sea (Mediterranean Sea) neighbouring the Strait of Gibraltar was studied. The relatively high richness found in this area is probably due to the diversity of substrata and the confluence of Atlantic and Mediterranean waters. The most abundant species was the hermit crab *Diogenes pugilator* due to the prevalence of sandy substrate, the shallow depth-range, and the species' life history. The coralligenous bottom showed the highest species richness and diversity values due to the complexity of microhabitats in this type of bottom and probably due to the food flux associated with currents. Conversely, shallow, well calibrated, fine to medium sandy bottoms of 5 m had the lowest values and the maximum densities due to the high abundance of a few well adapted species. The analysis of the different stations showed significant spatial differences according to depth and sedimentary characteristics. Depth is the environmental variable that correlates best with the decapod assemblages, with a particularly significant boundary between 5 m and 15 m. Nevertheless, there was a continuous transition between the assemblages. These results evidence the importance of quantitative studies in differentiating decapod assemblages. Relationships between these assemblages should also be taken into account in coastal management, since altering a substrate could have repercussions for the structure of the communities of neighbouring substrates. No seasonal significant differences were found in the overall analysis of the area, but there were differences between spring and autumn and spring and summer in relation to depth and substrate (crossed analysis). Finally, we present the species which allow us to discriminate the different assemblages according to sediment and depth, as well as the species' contributions.

Keywords: Crustacea Decapoda, biodiversity, structure of assemblages, spatial distributions and relationships, Alborán, Mediterranean.

RESUMEN: LAS COMUNIDADES DE CRUSTÁCEOS DECÁPODOS DE FONDOS LITORALES DEL MAR DE ALBORÁN (ESPAÑA, MEDITERRÁNEO OCCIDENTAL): VARIABILIDAD ESPACIAL Y TEMPORAL. – Se ha analizado la estructura de las comunidades de decápodos de fondos poco profundos (5 a 25 m) de una zona del Mar de Alborán (Mediterráneo) próxima al Estrecho de Gibraltar. La relativamente alta riqueza específica hallada se debe probablemente a la variedad de sustratos y a la confluencia de aguas atlánticas y mediterráneas. La especie más abundante fue *Diogenes pugilator*, debido a la naturaleza del sustrato dominante, el rango batimétrico analizado y la biología de la especie. Los valores más altos de riqueza específica y diversidad se encontraron en fondos coralígenos, como consecuencia de la mayor complejidad de microhábitats y probablemente por el flujo de alimento asociado a corrientes. Contrariamente, los valores más bajos y las mayores densidades se hallaron en los fondos superficiales de arenas finas-medias bien calibradas de 5 m. Esto último es debido a las fuertes dominancias de unas pocas especies bien adaptadas. El análisis de las muestras indicó diferencias espaciales significativas según el tipo de sedimento y profundidad (ésta fue la variable mejor correlacionada con los agrupamientos faunísticos), con una frontera más marcada entre los 5 - 15 metros. En cualquier caso resulta obvia la existencia de una continuidad – relación entre las diferentes comunidades. Estos datos apoyan la importancia de los estudios cuantitativos a la hora de la caracterización de las comunidades de decápodos, pues una actuación sobre un sustrato puede repercutir sobre la estructura de las comunidades de otros fondos colindantes. Por otro lado, no se encontraron diferencias temporales significativas en el conjunto de la comunidad de decápodos de la zona, pero los análisis por profundidades y sustratos mostraron diferencias entre primavera y otoño y primavera y verano. Finalmente, se indican las especies que mejor contribuyen a discriminar los distintos tipos de fondos con sus grados de contribución.

Palabras clave: Crustacea Decapoda, biodiversidad, estructura de las comunidades, distribución y relaciones espaciales, Alborán, Mediterráneo.

INTRODUCTION

The Alborán Sea (southeast Spain) is a biogeographically remarkable area due to its location within the Atlantic-Mediterranean Province (Ekman, 1953) and Lusitanian Province (Briggs, 1974). It is a meeting or confluence point for species from the European Atlantic (Lusitanian region), the African Atlantic (Mauritanian region) and the Mediterranean. The major hydrological features of this sea are the mixture of Atlantic and Mediterranean water masses with different physicochemical characteristics (temperature, salinity), its peculiar hydrodynamic movement (mainly the Alborán Gyre) (Lacombe and Tchernia, 1972; Lanoix, 1974; Parrilla and Kinder, 1987; Tintoré *et al.*, 1991), and the Almeria-Oran semipermanent hydrographic front (Millot, 1987, 1999). Upwelling (Cano, 1977, 1978) supplying nutrient-rich water to the area causes higher plankton richness when compared to other Mediterranean areas (Vives *et al.*, 1975; Greze *et al.*, 1985; Delgado, 1990). All these factors and their temporal variations determine the structure and composition of animal communities and differences in biomass distributions (Rodríguez, 1983; Camiñas, 1983). The Alborán Sea is defined as a specific biogeographical sector for many animal groups and assemblages, such as demersal fish (Gaertner *et al.*, 2005) and epibenthic crustaceans (Abelló *et al.*, 2002), among others. Furthermore, four sectors have been proposed within the Alborán Sea (according to the composition and biomass of fish larvae (Rubín, 1997; Rubín *et al.*, 1997)), and are delimited by the 36°N latitude and 4°W longitude. This longitude coincides with our study area, where it is possible to recognise an Atlantic influence (e.g., in macroalgal composition, Bellon, 1921; Conde and Seoane, 1982; Flores, 1989). This Atlantic influence is also detected in many benthic littoral groups. Thus, within decapod crustaceans some Atlantic (frequently African) species have also been found in the littoral of Malaga and adjacent zones. Some examples are *Scyllarus posteli* Forest, 1963, *Brachynotus atlanticus* Monod, 1957, *Processa macrodactyla* Holthuis, 1952, *Cryptosoma cristatum* Brullé, 1837, *Plesionika ensis* (A. Milne-Edwards, 1881) and *Galathea capillata* Miyake and Baba, 1970 (García Raso, 1981, 1982a, b, 1984, 1993; García Raso and Salas, 1985; García Raso and Manjón Cabeza, 2002a). Some of these species may be present as a consequence of temporary or

accidental introductions resulting from the surface current through the Strait of Gibraltar, as happens with some deep species (Cartes *et al.*, 2000).

In spite of its biogeographical interest, there have been few studies on the structure of decapod assemblages of the different shallow bottoms in the Alborán Sea area (García Raso, 1987, 1990; García Raso *et al.*, 1996, 2006a), and none of them are devoted to the western sector. This is why this study aims to describe the structure of decapod communities (specific composition, richness, diversity, and seasonal and spatial variability according to substrata and depth) in the vicinity of the Strait of Gibraltar, and establish the interactions between the different assemblages. This knowledge will be useful for preserving the European biodiversity in a “hot spot” such as the Alborán Sea, for management studies, and to foresee the effects which an event or human action on a specific substratum could have on the adjacent assemblages and/or the whole area.

MATERIAL AND METHODS

The studied area is located between “Punta de Calaburras” (36°30.4'N 04°38.3'W) in Fuengirola and the marina of Cabo Pino (36°29'N 04°44.3'W) in Marbella (Málaga, Spain), in the surroundings of the Straits of Gibraltar (Fig. 1). This zone is one of the very few natural rocky outcrops existing on the shores of the province of Malaga. The analysed depth range was between 5 and 25 m. The studied zone includes a marine site of community importance (Calahonda: 36°29'1''N 04°42'25''W, code ES6170030, Official Journal of the E.U. of 21.09.2006), which is part of the Natura 2000 network.

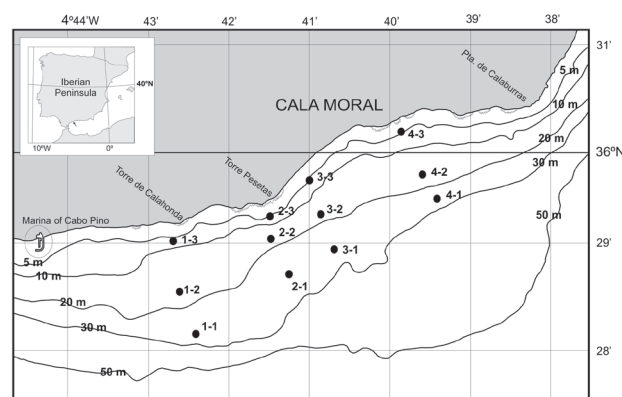


FIG. 1. – Study area and sampling points.

TABLE 1. – Sampling stations. Locations and some observations.

R1. Torre de Calahonda.	
St 1 - 25 m	36°28.0'N - 04°42.3'W. Medium sandy bottoms with bioclasts. "Detritic bottoms".
St 2 - 15 m	36°28.6'N - 04°42.5'W. Bottoms with rocks, abundant gorgonians and bryozoans, with relatively high sedimentation. "Coralligenous bottoms".
St 3 - 05 m.	36°29.1'N - 04°42.7'687W. Shallow fine sandy bottoms. "SFBC".
R2. Torre Pesetas (or Torre Nueva).	
St 1 - 25 m.	36°28.7'N - 04°41.2'W. Coarse sandy bottoms with gravel, clay and bioclasts. "Detritic bottoms".
St 2 - 15 m.	36°29.1'N - 04°41.5'W. Coarse sandy bottoms. "Coarse bottoms"
St 3 - 05 m.	36°29.3'N - 04°41.5'W. Shallow medium sandy bottoms. "SFBC"
R3. West of the river "Cala del Moral".	
St 1 - 25 m.	36°29.0'N - 04°40.8'W. Fine sandy bottoms with clay.
St 2 - 15 m.	36°29.3'N - 04°40.8'W. Fine to very fine sandy bottoms with clay.
St 3 - 05 m.	36°29.7'N - 04°41.0'W. Shallow fine sandy bottoms. "SFBC"
R4. West of "Cabezo del Fraile".	
St 1 - 25 m.	36°29.5'N - 04°39.4'W. Fine sandy bottoms with clay
St 2 - 15 m.	36°29.7'N - 04°39.6'W. Fine sandy bottoms with clay.
St 3 - 05 m.	36°30.2'N - 04°39.8'W. Stones. "Rocky bottoms". - Not sampled -

The bottoms analysed were soft bottoms, some of which had rocky formations. Samples were taken using a small heavy rock dredge, with a rectangular frame of 42 by 22 cm and a mesh size of 4.0 mm knot to knot. Trawling time was 5 minutes for each haul (in the morning, with good sea conditions and at random in the selected locations) at a speed of about 2 knots, which represents a trawling distance of about 300 m or an estimated area of about 130 m², which allowed us to obtain a good representation of specimens.

To study the spatial and temporal variability of the fauna communities, samples from four transects (R1 to R4) were taken perpendicularly to the coast at three different depths, 5, 15 and 25 m (with three replicates from each sample), in summer and autumn 2004 and winter and spring 2005. Sediment samples were also collected using a blind semicircular toothed dredge with a 20 cm mouth. The locations of these sampling-point 'stations' (longitude, latitude and depth) together with some notes (on sediments, some fauna) are given in Table 1 and represented in Figure 1.

In the laboratory the samples were washed over a column of sieves to separate specimens (smallest mesh size: 1 mm). Granulometry followed the Buchanan classification using a column of standard sieves. Organic matter was determined by calcinating the samples and weighting.

A Principal Component Analysis (PCA) with the abiotic parameters (sediment: mean particle diameter (Q_{50}), organic material, clay, gravel and bioclasts, and depths) was used to define sample groups.

PRIMER software (Clarke and Warwick, 1994) was used to study the structure of the communities and their seasonal and spatial variations using qualitative and quantitative data with a fourth root transformation and without standardisation. The data from coralligenous assemblages could be considered semi-quantitative because there are hollows and roughness in this type of bottom which could hide specimens; however, we have considered them as quantitative in order to compare results from different substrates.

Possible significant differences between seasons, stations and assemblages (according to depths and substrates) were assessed using the ANOSIM (non-parametric permutation procedure applied to the similarity matrix) routine of the PRIMER package, since the abundance of zero values could mean that the probability distribution of counts did not approach (multivariate) normality. Furthermore, diversity values of the Shannon index (Shannon and Weaver, 1963; Krebs, 1989), evenness values (Pielou, 1969), Margalef's richness (DIVERSE routine), and k-dominance curves (Gray and Pearson, 1982, GEOPLOT routine) were determined. The similarity matrix (which was calculated using the Bray-Curtis index) was used to construct bivariate MDS plots (MDS routine), in order to determine the relationships between assemblages, together with the contribution levels of the different species (SIMPER routine). Finally, the BIO-ENV routine was used to determine the environmental variables responsible for structuring the assemblages (with normalised Euclidean distance and Spearman correlation).

TABLE 2. – Results of the sediment analysis (according to sizes): <0.063 silts or mud (V), 0.063 - 0.125 very fine sand (VFS), 0.125 - 0.250 fine sand (FS), 0.250 - 0.500 medium sand (MS), 0.50 - 1.0 coarse sand (CS), 1.00 - 2.00 very coarse sand (VCS), >2.00 gravel (G) and organic material (OM%), by radial (R) and depth (D) in meters (sd: standard deviations). Q₅₀: mean particle diameter. In the inferior margin a sketch of sediment distribution by sampling stations; the squares represent different decapod assemblages (*rocky outcrop on sandy bottoms with abundant bryozoans and gorgonian corals).

Meters	Radial	OM%	sd	Sediment	Q ₅₀	Type	%clay (%< 0.063)	%gravel (%> 2.00)	%bioclasts (%> 6.30)
05 m	1	1.26	0.36	0.125 < Q ₅₀ < 0.250	(0.242)	FS↑	2.1	0.1	0.0
	2	1.14	0.28	0.250 < Q ₅₀ < 0.500	(0.320)	MS	1.5	0.0	0.0
	3	0.79	0.47	0.250 < Q ₅₀ < 0.500	(0.326)	MS	1.7	0.1	0.0
	4	-	-	rocks		rocks	-	-	-
15 m	1	-	-	Sand with rocks		Coralligenous (*)	-	-	-
	2	1.24	0.36	0.500 < Q ₅₀ < 1.000	(0.526)	CS↓	5.1	1.2	0.2
	3	1.43	0.51	0.125 < Q ₅₀ < 0.250	(0.133)	FS↓	<u>18.1</u>	0.1	0.0
	4	1.52	0.26	0.125 < Q ₅₀ < 0.250	(0.150)	FS	12.6	0.2	0.0
25 m	1	1.97	0.41	0.250 < Q ₅₀ < 0.500	(0.466)	MS	2.5	8.8	3.5
	2	3.04	0.46	0.500 < Q ₅₀ < 1.000	(1.05)	CS-VCS	11.6	<u>20.1</u>	5.0
	3	1.66	0.42	0.125 < Q ₅₀ < 0.250	(0.132)	FS↓	<u>20.7</u>	0.3	0.1
	4	1.82	0.44	0.125 < Q ₅₀ < 0.250	(0.149)	FS	<u>20.1</u>	3.7	1.5

Radials	1	2	3	4
5 m	FS↑	MS	MS	Rocks
15 m	Sand & rocks*	CS↓	FS↓	FS
25 m	MS	CS-VCS	FS↓	FS

RESULTS

Abiotic factors

The results of the sediment analyses (kinds of sediments: Q50, clay, gravel, bioclasts and organic material) according to radials and depths are indicated in Table 2. The results of the PCA (Fig. 2, Table 3) allow us to group the sampling stations and define the following groups: A) the shallowest bottoms of 5 m, which correspond to the shallow, well calibrated sandy bottoms; B) the 15 and 25 m deep bottoms of

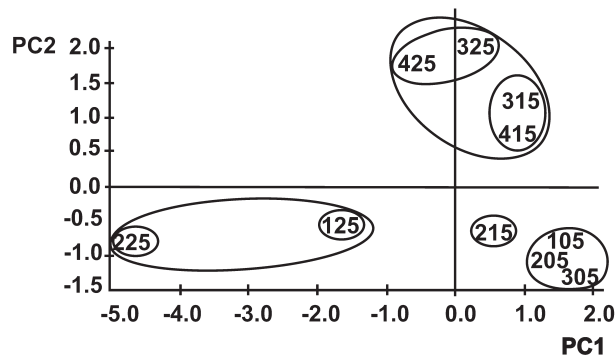


FIG. 2. – Results of the PCA (abiotic parameters included - sediment: Size Q50, organic material, clay, gravel and bioclasts, and depths). The numbers are the sampling stations (examples: 105: radial 1 at 05 m depth, 425: radial 4 at 25 m depth).

TABLE 3. – Results of the Principal Component Analysis.

PC Axis	Eigenvalues	%Variation	Cum. % Variation
1	4.02	67.1	67.1
2	1.62	27.0	94.0
3	0.22	3.6	97.7
4	0.11	1.8	99.5
5	0.03	0.5	100.0

Eigenvectors (Coefficients in the linear combinations of variables making up PC's)					
Variables	PC1	PC2	PC3	PC4	PC5
Q50	-0.392	-0.427	-0.432	-0.649	0.017
Clay	-0.106	0.740	-0.552	-0.015	-0.344
Gravel	-0.485	-0.163	-0.142	0.207	-0.289
Bioclasts	-0.480	-0.133	0.341	0.334	-0.484
Organic material	-0.482	0.128	-0.175	0.392	0.741
Depth	-0.372	0.458	0.584	-0.521	0.121

the two western radials (R3-15, R3-25, R4-15, R4-25), which show the highest values of clay, these bottoms could be considered as muddy fine sand bottoms (if the factor depth is eliminated from the PCA these sampling stations appear more grouped); C) station R2 - 25m with coarse sand and relatively high values of clay and gravel; E) the medium sandy bottom of R1 - 25 m (in these two latter stations there are abundant bioclasts: detritic or detrital bottoms); and D) station R2-15 with coarse sand, between the

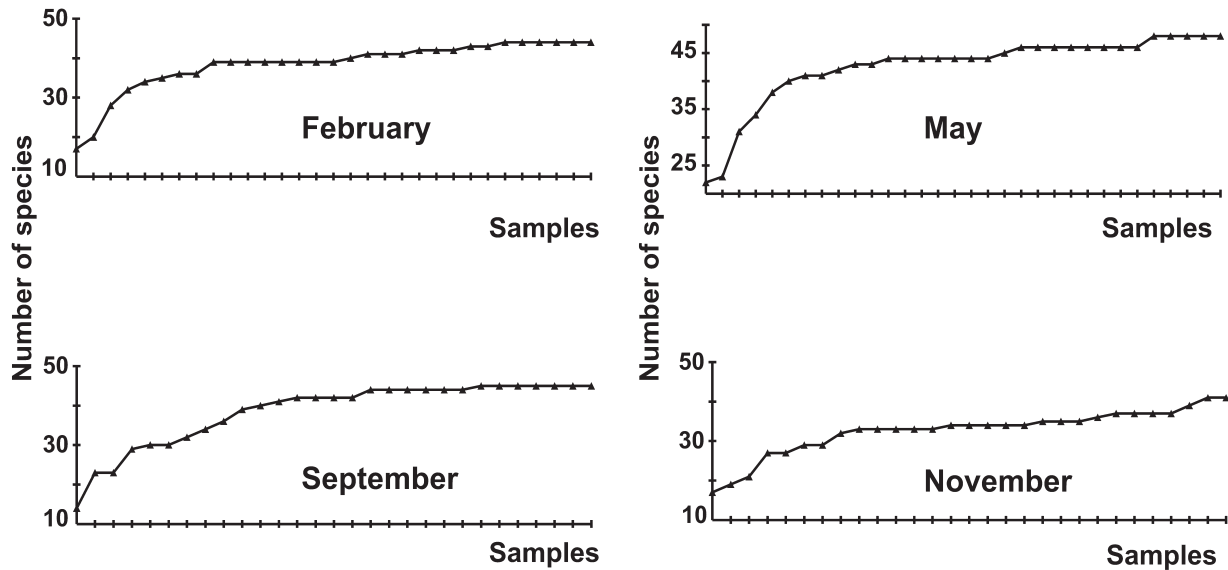


FIG. 3. – Accumulative richness for the whole studied area for the different seasons.

shallow and muddy fine sand bottoms. These results, together with the species composition analysis, allow us to classify the communities into the Pérès and Picard (1964) standards.

Structure of decapod assemblages

A total number of 40309 specimens belonging to 60 species were captured on the soft bottoms of the

TABLE 4. – Total number of specimens (N) per species.

Species	N	%	Species	N	%
<i>Diogenes pugilator</i> (Roux, 1829)	31862	79.044	<i>Spiropagurus elegans</i> Miers, 1881	14	0.035
<i>Anapagurus alboranensis</i> Garcia-Gomez, 1994	1682	4.173	<i>Alpheus glaber</i> (Olivi, 1792)	13	0.032
<i>Anapagurus hyndmanni</i> (Bell, 1845)	835	2.071	<i>Ebalia edwardsii</i> Costa, 1838	13	0.032
<i>Pisidia longicornis</i> (Linnaeus, 1767)	731	1.813	<i>Pagurus anachoretus</i> Risso, 1827	13	0.032
<i>Paguristes eremita</i> (Linnaeus, 1767)	674	1.672	<i>Pilumnus villosissimus</i> (Rafinesque, 1814)	11	0.027
<i>Anapagurus petiti</i> Dechancé & Forest, 1962	626	1.553	<i>Liocarcinus corrugatus</i> (Pennant, 1777)	9	0.022
<i>Pagurus forbesii</i> Bell, 1845	515	1.278	<i>Philocheras sculptus</i> (Bell, 1847)	9	0.022
<i>Philocheras trispinosus</i> (Hailstone, 1835)	494	1.226	<i>Processa macrophthalma</i> Nouvel & Holthuis, 1957	9	0.022
<i>Pagurus cuanensis</i> Bell, 1845	415	1.030	<i>Dardanus calidus</i> (Risso, 1827)	8	0.020
<i>Dardanus arrosor</i> (Herbst, 1796)	401	0.995	<i>Inachus phalangium</i> (Fabricius, 1775)	8	0.020
<i>Calcinus tubularis</i> (Linnaeus, 1767)	293	0.727	<i>Pisa nodipes</i> (Leach, 1815)	8	0.020
<i>Pagurus prideaux</i> Leach, 1815	254	0.630	<i>Cestopagurus timidus</i> (Roux, 1830)	5	0.012
<i>Pagurus excavatus</i> (Herbst, 1791)	251	0.623	<i>Inachus communissimus</i> Rizza, 1839	5	0.012
<i>Galathea intermedia</i> Lilljeborg, 1851	147	0.365	<i>Pandalina brevirostris</i> (Rathke, 1843)	5	0.012
<i>Periclimenes scriptus</i> (Risso, 1822)	145	0.360	<i>Eurynome aspera</i> (Pennant, 1777)	4	0.010
<i>Liocarcinus depurator</i> (Linnaeus, 1758)	122	0.303	<i>Eurynome spinosa</i> Hailstone, 1835	4	0.010
<i>Philocheras monacanthus</i> (Holthuis, 1961)	98	0.243	<i>Inachus dorsettensis</i> (Pennant, 1777)	4	0.010
<i>Ebalia tumefacta</i> (Montagu, 1808)/ <i>E. deshayesi</i> Lucas, 1846	93	0.231	<i>Macropodia longirostris</i> (Fabricius, 1775)	4	0.010
<i>Liocarcinus vernalis</i> (Risso, 1827)	75	0.186	<i>Pisa carinimana</i> Miers, 1879	4	0.010
<i>Eualus occultus</i> (Lebour, 1936)	70	0.174	<i>Ethusa mascarone</i> (Herbst, 1785)	3	0.007
<i>Pinnotheres pisum</i> (Linnaeus, 1767) *	65	0.161	<i>Parthenope angulifrons</i> Latreille, 1825	3	0.007
<i>Pilumnus hirtellus</i> (Linnaeus, 1761)	57	0.141	<i>Sirpus zariquieyi</i> Gordon, 1953	3	0.007
<i>Anapagurus chiroacanthus</i> (Lilljeborg, 1856)	49	0.122	<i>Ebalia tuberosa</i> (Pennant, 1777)	2	0.005
<i>Liocarcinus maculatus</i> (Risso, 1827)	36	0.089	<i>Achaea cranchii</i> Leach, 1817	1	0.002
<i>Ebalia cranchii</i> Leach, 1817	29	0.072	<i>Asthenognathus atlanticus</i> Monod, 1933	1	0.002
<i>Macropodia rostrata</i> (Linnaeus, 1761)	24	0.060	<i>Hippolyte holthuisi</i> Zariquiey-Alvarez, 1953	1	0.002
<i>Parthenope massena</i> (Roux, 1830)	22	0.055	<i>Macropodia longipes</i> (A. Milne-Edw. & Bouvier, 1899)	1	0.002
<i>Atelecyclus rotundatus</i> (Olivi, 1792)	21	0.052	<i>Scyllarus pygmaeus</i> (Bate, 1888)	1	0.002
<i>Thoralus cranchii</i> (Leach, 1817)	21	0.052	<i>Thia scutellata</i> (Fabricius, 1793)	1	0.002
<i>Pilumnus spinifer</i> H. Milne-Edwards, 1834	20	0.050			
<i>Philocheras bispinosus</i> (Hailstone, 1835)	15	0.037	Total	40309	

* Commensal species of *Donax trunculus*. In SFBC community other three species, *Atelecyclus undecimdentatus*, *Portunus latipes* and *Albunea carabus* (more rare), are present in the studied zone but they were not caught during the sampling period and points.

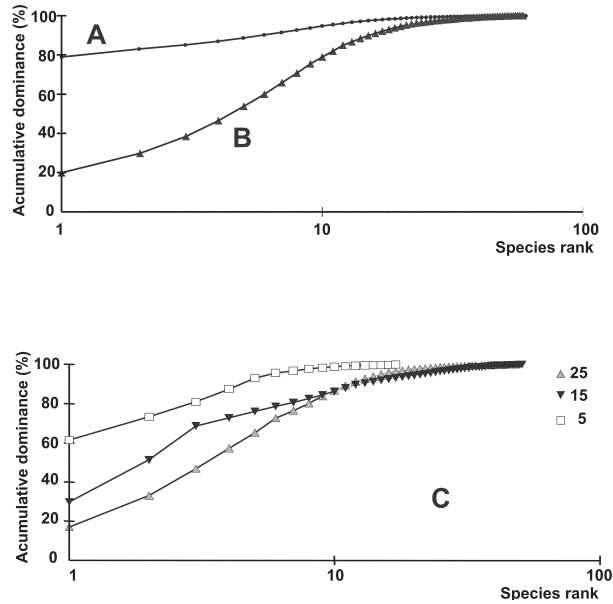


FIG. 4. – Analysis of accumulative abundance. A: of total species, B: without *Diogenes pugilator*, C: without *Diogenes pugilator* according to depth.

study area. However, the 10 most abundant species made up nearly 95% of the total catch (Table 4). The accumulative richness was analysed for the entire study area and showed that at least 80% of the species were seasonally captured with only 9 samples (Fig. 3).

The hermit crab *Diogenes pugilator* was the dominant species, and represented 79% of the total abundance (Table 4). This high dominance could be observed in the accumulative abundance analyses (Fig. 4A) and determines the overall structure of the decapod community, which shows a more or less geometric model. If this species was eliminated from the analysis, equitability increased (Fig. 4B) and curves showed a less geometric model with depth (Fig. 4C).

TABLE 5. – Ranges of values of specific richness (S), equitability (Pielou) (J') and diversity (Shannon) (H') by radials and depths (meters).

Radial depths	S	J'	H'
R1 05 m	03 - 06	0.08 - 0.47	0.11 - 0.80
R1 15 m	12 - 21	0.43 - 0.85	1.20 - 2.58
R1 25 m	12 - 22	0.66 - 0.82	1.72 - 2.26
R2 05 m	02 - 07	0.02 - 0.68	0.01 - 0.83
R2 15 m	03 - 14	0.16 - 0.76	0.38 - 1.88
R2 25 m	11 - 20	0.65 - 0.91	1.71 - 2.39
R3 05 m	02 - 09	0.01 - 0.20	0.02 - 0.27
R3 15 m	04 - 10	0.16 - 0.75	0.22 - 1.20
R3 25 m	03 - 13	0.63 - 1.00	0.80 - 2.01
R4 15 m	05 - 10	0.22 - 0.68	0.35 - 1.48
R4 25 m	07 - 17	0.52 - 0.90	1.25 - 2.23

The specific richness and also, in general, the equitability and diversity values increased with depth (Table 5). Samples from the two western radials (at 15 and 25 m) showed the highest diversity index values ($H' = 2.58, 2.39$), while the lowest values were found in radial 3.

The analyses of each 'station' show that R1 at 25 m, R2 at 25 m (detritic bottoms of medium and coarse sands) and R1 at 15 m (coralligenous) had the highest richness, equitability and diversity values, in opposition to the shallowest medium sandy bottoms (5 m, community of SFBC). Similar results were found if 'stations' were grouped according to substratum and depth (Table 6); only the numerical values changed. Detritic (25 m) and coralligenous bottoms (15 m) in the western part of the study area (R1 and R2), showed the highest richness, equitability and diversity values, in opposition to the shallowest medium sandy bottoms (5 m), in which the maximum density of decapods was found due to the high abundance of *Diogenes pugilator*.

TABLE 6. – Values of Specific richness (S), Margafef's richness (d), total abundances (Nt), density or number of specimens by 100 m² (δ), Pielou's equitability (J'), Shannon's diversity (H') for the different assemblages by sediments (MS: shallow medium and fine sandy bottoms of 5m; FS: fine sandy bottoms with mud (at 15 and 25 m); CS: coarse bottoms at 15 m; C: coralligenous bottoms; D: detritic bottoms at 25 m (of medium sands: DM, and of coarse sands: DC).

Substratum	N° samples	S	d	Nt	δ	J'	H' (log _e)
MS 05 m	36	18	1.68	24821	530	6.45E-2	0.186
C 15 m	8	41	5.72	1095	105	0.56	2.10
D 25 m	19	47	5.48	4428	179	0.65	2.52
DM 25 m	10	37	4.44	3344	257	0.65	2.34
DC 25 m	9	38	5.29	1084	93	0.71	2.57
CS 15 m	11	30	3.97	1496	105	0.29	0.98
FS 15-25 m	37	47	3.98	8469	176	0.33	1.18
FS 25 m	23	29	3.83	1490	50	0.65	2.19
FS 15 m	24	29	3.16	6979	224	0.24	0.82

Study of the temporal variability

No significant differences between seasons (spring, summer, autumn and winter) were found in the complete community analysis (ANOSIM) (samples and replicates were not grouped but studied independently) (pairwise test, $p =$ between 0.10 and 0.75), but the tests for differences between seasonal groups (average across all substrate groups and average across all depth groups) (two-way crossed ANOSIM) showed significant differences between spring and autumn ($p=0.001$, $p=0.001$) and between spring and summer ($p=0.001$, 0.004), and always had low R values (between 0.14 and 0.27).

Study of the spatial variability: Qualitative analysis

The study of samples according to the radial-depth “stations” (ANOSIM) showed no significant differences between the two shallowest western bottoms (R1 at 5 m and R2 at 5 m, $p = 0.70$) and a moderately significant difference to radial 3 (R2 at 5 m and R3 at 5 m, $p = 0.02$). This is probably due to river influence (next to R3), but with a low R value ($R = 0.2$), which confirms that similarities between and within these sites (R2 at 5 m and R3 at 5 m) are the same on average. Moreover, the community composition of all these shallowest bottoms was practically the same and significantly very different from those found in other deeper bottoms (05 – 15 m, $p = 0.001$, $R = 0.65$; 15 – 25 m, $p = 0.001$, $R = 0.19$; 05 – 25 m, $p = 0.001$, $R = 0.89$).

No significant differences were found between samples R3 and R4 both at 15 m, and R3 and R4 both at 25 m ($p = 0.18$ and 0.08 respectively), which are associated with communities of muddy fine sand bottoms. However, there were differences between these two eastern radials depending on depth (R3 at 15 m and 25 m, and R4 at 15 m and 25 m, $p = 0.03$ and 0.02 respectively), but with low R values (0.23 and 0.27), probably related to the strong importance of depth, which has been previously pointed out, and the increase in organic material and clay with depth, mainly in the river sector (Table 2).

Study of the spatial variability: Quantitative analysis

No significant difference was found between radials R1 and R2 ($p = 0.1$), whereas a moderately

significant difference was found between R3 and R4 ($p = 0.02$). The highest significant differences were found between R1 and the two eastern radials (R4 and R5) ($p = 0.01$), which could be related to the different substrata within the radials: in R1 and R2 there are more rocks and detritic substrata and in R3 and R4 muddy fine sands are dominant.

According to depth, assemblages showed clearly significant differences ($P = 0.001$) that were more obvious when depth differences increased (between 5 and 25 m, $R = 0.91$; 5 and 15 m, $R = 0.58$; 15 and 25 m, $R = 0.25$). Furthermore, these R values suggest the existence of a stronger separation between 5 and 15 m.

Analyses of the grouped “stations” according to substratum and depth showed significant differences ($p = 0.001$). The highest differences are between the shallowest medium sandy bottoms (community of SFBC, 5 m) and the other substrata, especially with detritic (stations R1 and R2, at 25 m) and coralligenous (R1, 15 m) stations (R values 1 and 0.99 respectively). However, these results could also be influenced by depth (see results in the previous paragraph). The differentiation between detritic bottoms at 25 m depth into detritic bottoms of medium sand (DM) and detritic bottoms of coarse sand (DC) showed similar results. These differences and groups could also be observed in the MDS analysis (Fig. 5).

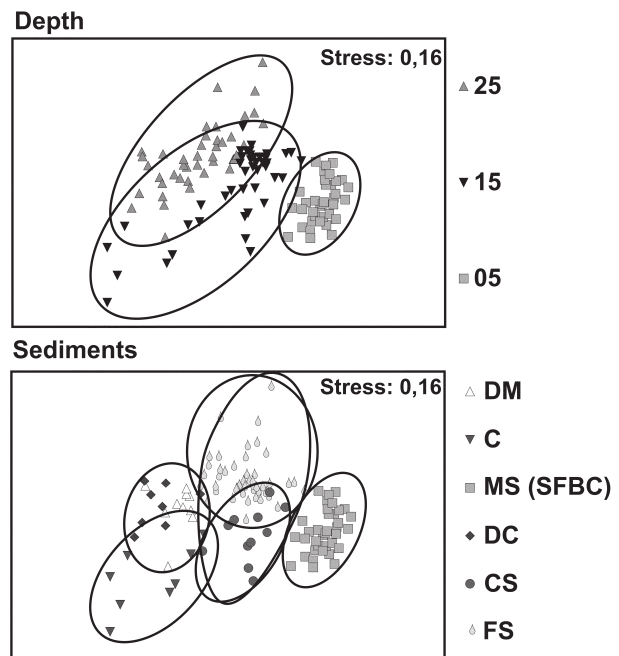


FIG. 5. – MDS analysis of the decapod assemblages according to depth (in meters) and sediments. C: coralligenous, CS: coarse sand, DM detritic of medium sand, DC: detritic of coarse sand, FS: fine sand, and MS: medium sand.

TABLE 7. – Results of the Similarity Percentages - species contributions (SIMPER) of the different assemblages by substrates.

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Medium – fine sandy bottoms. 05 m. Average similarity: 59.60					
<i>Diogenes pugilator</i>	667.44	43.66	4.69	73.25	73.25
<i>Philocheras trispinosus</i>	13.53	5.56	0.66	9.33	82.58
<i>Liocarcinus vernalis</i>	1.67	4.79	0.79	8.04	90.62
Coralligenous bottoms. 15 m. Average similarity: 48.88					
<i>Pisidia longicornis (ana)</i>	71.63	8.32	3.48	17.01	17.01
<i>Anapagurus hyndmanni</i>	5.50	5.69	5.56	11.64	28.66
<i>Calcinus tubularis</i>	11.13	4.72	1.61	9.65	38.31
<i>Pilumnus hirtellus</i>	5.63	3.89	1.64	7.96	46.28
<i>Anapagurus alboranensis</i>	4.88	3.51	1.03	7.19	53.46
<i>Galathea intermedia</i>	6.38	3.26	1.02	6.67	60.13
<i>Eualus occultus</i>	5.88	3.12	1.02	6.38	66.51
<i>Periclimenes scriptus</i>	1.50	2.64	1.02	5.40	71.91
<i>Pilumnus spinifer</i>	2.13	2.07	0.72	4.24	76.15
<i>Pagurus forbesii</i>	1.13	1.67	0.72	3.42	79.58
<i>Alpheus dentipes</i>	1.50	1.67	0.73	3.41	82.99
<i>Diogenes pugilator</i>	4.75	1.63	0.51	3.34	86.33
<i>Pagurus anachoretus</i>	1.38	1.02	0.51	2.09	88.41
<i>Pilumnus villosissimus</i>	1.25	0.95	0.50	1.95	90.36
Detritic bottoms (medium and coarse sands). 25 m. Average similarity: 54.29					
<i>Anapagurus alboranensis</i>	26.42	7.55	4.98	13.90	13.90
<i>Pagurus forbesii</i>	26.26	6.21	4.40	11.45	25.34
<i>Anapagurus hyndmanni</i>	40.95	5.78	2.10	10.65	36.00
<i>Paguristes eremita</i>	33.26	5.42	2.28	9.98	45.98
<i>Diogenes pugilator</i>	31.74	4.10	1.09	7.55	53.52
<i>Pagurus cuanensis</i>	14.58	3.65	1.21	6.72	60.24
<i>Pisidia longicornis (ana)</i>	6.21	3.05	1.13	5.62	65.87
<i>E. tumefacta - deshayesi</i>	3.00	2.88	1.19	5.30	71.17
<i>Pagurus prideaux</i>	5.32	2.75	1.21	5.06	76.23
<i>Dardanus arrosor</i>	16.32	2.40	0.74	4.42	80.65
<i>Pagurus excavatus</i>	1.84	2.28	1.03	4.20	84.85
<i>Galathea intermedia</i>	4.58	1.88	0.75	3.46	88.31
<i>Periclimenes scriptus</i>	2.58	1.55	0.66	2.85	91.16
Coarse bottoms. 15 m. Average similarity: 44.21					
<i>Diogenes pugilator</i>	107.73	22.12	3.25	50.04	50.04
<i>Anapagurus alboranensis</i>	12.18	11.40	1.79	25.78	75.82
<i>Anapagurus petiti</i>	3.36	3.32	0.76	7.52	83.33
<i>Pagurus cuanensis</i>	0.45	1.35	0.32	3.06	86.39
<i>Liocarcinus depurator</i>	1.00	0.91	0.34	2.06	88.45
<i>Anapagurus hyndmanni</i>	1.09	0.85	0.34	1.93	90.38
Fine sandy bottoms with mud. 15 and 25 m. Average similarity: 54.15					
<i>Diogenes pugilator</i>	127.83	17.29	2.58	31.93	31.93
<i>Anapagurus alboranensis</i>	20.98	9.07	1.37	16.75	48.68
<i>Anapagurus petiti</i>	12.09	7.47	1.23	13.80	62.48
<i>Pagurus excavatus</i>	4.53	6.60	1.32	12.18	74.66
<i>Pagurus prideaux</i>	2.81	4.22	1.00	7.80	82.46
<i>Dardanus arrosor</i>	1.83	2.81	0.76	5.18	87.64
<i>Pagurus cuanensis</i>	2.74	2.64	0.66	4.87	92.51

Correlations between station assemblages and environmental variables

The faunal assemblages, according to the BIO-ENV analysis, correlate best with Depth (0.811); Clay and Depth (0.765); Clay, Organic Material and Depth (0.706) and Clay, Bioclasts and Depth (0.704). The correlation values with the environ-

mental variables (considered independently) were Depth: 0.811, Organic Material: 0.407, Clay: 0.326, Bioclasts: 0.211, Gravel: 0.205 and Q5: 0.188.

Discriminating species

According to depth, the species which contributed to the characterisation of the shallowest bot-

toms (5 m) were the following: *Diogenes pugilator*, *Philocheras trispinosus* and *Liocarcinus vernalis* (accumulative contribution: 90.6%). At a depth of 15 m, bottoms were characterised by *D. pugilator*, *Anapagurus alboranensis*, *Anapagurus petiti*, and *Pagurus excavatus* (accumulative contribution: 80.91%), whereas 25 m bottoms were discriminated by *D. pugilator*, *A. alboranensis*, *Pagurus excavatus*, *Pagurus cuanensis*, *Pagurus prideaux*, *Dardanus arrosor*, *Paguristes eremita*, *Liocarcinus depurator* and *Ebalia tumefacta-deshayesi* (with an accumulative contribution of 81.02%). In all cases the average similarity was around 50% and, as shown by the data, deeper assemblages need more species to reach a similar percentage of accumulated contribution. The discriminating species of the different communities and their contributions listed according to substratum and depth are presented in Table 7.

DISCUSSION

The strong dominance of the hermit crab *Diogenes pugilator* in the whole studied area is a consequence of the relatively shallow depth range analysed and the prevailing substrata, which in the entire study area could be considered *sensu lato* as sandy bottoms. *Diogenes pugilator* is the characteristic decapod species of shallow, well calibrated fine sandy bottoms (SFBC) (Pérès and Picard, 1964) or of 'terrigenous' fine sandy bottoms (Ledoyer, 1968), which in our area correspond particularly to shallow fine and medium sandy bottoms at 5 m. Furthermore, this hermit crab could be considered as a generalist species living in many kinds of sandy bottoms within a large depth range (0 m to 162 m; Selbie, 1921), but it usually does not live below 50 m (Forest, 1961). In Spain and the littoral of Malaga it is reported between 0 and 35 m (Zariquiey, 1968; García Raso, 1982c). The species shows an "r" strategy, since ovigerous females are found throughout the year (although with two maxima in winter and summer), and there is continuous recruitment and early sexual maturity (females from 1.32 mm cephalotoracic shield length, males from 1.00 mm) (Manjón-Cabeza and García Raso, 1998a, 2000a, b).

This high dominance significantly affects the diversity and equitability values, which increase with depth as the abundance of *Diogenes* decreases and complex substrata increase, such as coralligenous bottoms. Coralligenous formations provide shelter

to many species (Ballesteros, 2006) and protection against predation risk, which is probably higher in deeper zones due to the presence of more species of different groups (e.g. fishes). It is interesting to note that, due to the high turbidity of the water, this coralligenous bottom is found in very shallow waters (15-20 m), although normally these formations occur between 40-90 m (Harmelin, 1994) or between 20-120 m depth (Ballesteros, 2006). This is also true for the circalittoral coastal detritic or detrital bottoms "Détritiques Côtiers (DC)" present in 20-25 m which are normally found between 30/35 - 90 m depth (Bellan-Santini *et al.*, 1994).

In the eastern English Channel the greatest species richness was recorded for pebble bottoms due to the complexity of microhabitats and the large food flux related to strong currents (Sanvicente-Añorve *et al.*, 2002). Abad *et al.* (2007) showed a significantly higher abundance in Seco de los Olivos seamount (Alborán Sea), which was probably related to higher food availability caused by strong localised currents and upwellings that enhanced primary production. Strong currents are also frequent in our coralligenous bottoms and there are upwellings in the study area (Cano, 1977, 1978). However, in the shallowest bottoms wave disturbances and land influence increase the stress on marine assemblages (Raffaelli and Hawkins, 1996), which reduces the number of species with a density increase of a few well adapted species; so that Guille (1971) found a decrease with depth from 503 specimens/m² in fine littoral sand to 94 specimens in offshore detritic bottoms in the French-Catalan littoral. All these factors explain the lower richness and diversity values found in our shallowest zones and, consequently, the existence of a stronger significant boundary between 5 and 15 m.

The absence of a significant seasonal difference in the whole decapod assemblage of the studied zone could be due, at least in part, to the complexity of biotopes, the interaction between assemblages and species moving between substrates. In addition, the absence of a well developed vegetal community in the analysed substrata could be important, since its life cycle is especially relevant for seasonality in the temporal evolution of the structure of the animal communities. Other factors, such as oceanographic characteristics of the area, could also be determinant. In any case, this absence of a significant seasonal difference in the overall analysis contrasts with the seasonality found when the analyses are focused on specific bottoms or substrates in the study area or in

other areas of the south of Spain (Manjón-Cabeza and García Raso, 1998b; García Raso and Manjón-Cabeza, 2002b; López *et al.*, 2002; López *et al.*, 2006), this is probably because within a substrate the structure of the decapod community is well defined and structured and the reproductive periods of a few, highly dominant species more or less determine seasonality.

The spatial study shows clear, significant differences for the assemblages in terms of substrata and depth (species' composition and abundance). Depth is the abiotic parameter that correlates best. Nevertheless, the ordination analysis showed a continuous transition between decapod assemblages of the different substrata and depths. The relationships and transitions found could be related to factors required by decapods that are present in different habitats, for example micro-refuges (therefore the coralligenous, detritic and coarse sand decapod assemblages are more interrelated). In addition, the high mobility of the group means that many species can be found in several bottoms (a similar ordination analysis for the molluscs of the area shows better defined and separated assemblages (Salas and Gofas, pers. com.)). Probably for these reasons, the assemblage of a coarse sandy bottom (which present high values of organic material) presents practically the same discriminating species (SIMPER) as the neighbouring assemblage of a muddy fine sandy bottom, but with different contribution levels. Consequently, in spite of the existence of a significant difference between them, the former assemblage found at 15 m depth would be considered a transition towards the adjacent community of muddy fine sand rather than a truly different community. A similar consideration could be made for detritic bottoms of medium and coarse sand. The coralligenous assemblage also shows a less intense transition to detritic bottoms. Somaschini *et al.* (1998) found a large complex transition between sandy and muddy communities on circalittoral soft-bottoms of the Ligurian Sea, and Guille (1970) observed many transition zones among these assemblages, so that he recognised only one circalittoral soft-bottom community with many sub-communities or "facies".

These results are in agreement with those found in the PCA of the abiotic factors and define four decapod assemblages or communities: 1) community of well calibrated shallow fine (and medium) sandy bottoms at 5 m (SFBC); 2) community of detritic bottoms (of medium and coarse sandy) at 25 m, with

abundant gravel and bioclasts; 3) coralligenous community at 15 m, and 4) community of muddy fine sandy bottoms at 15-25 m with a high proportion of clay. Sanvicente-Añorve *et al.* (2002) also found a correlation between the spatial heterogeneity of the communities and sedimentary characteristics in the English Channel.

These relationships (transitions) between decapod assemblages from the different soft substrata make quantitative values very important for discriminating communities (sometimes together with several characteristic species), which was also shown in the analysis that compared decapod assemblages living in *Posidonia oceanica* (rhizomes stratum) with those living in calcareous concretions (García Raso *et al.*, 1996). The movements and relationships between the assemblages must be taken into account in coastal management since altering a substrate could have repercussions for the structure of the communities of neighbouring substrates.

The discriminating species found in the shallowest fine sandy bottoms are the same as those mentioned by Pérès and Picard (1964) and Massé (1972), among others. The community of muddy, fine sand is characterised by *Anapagurus alboranensis* which, as shown by the relative abundance data found in the different substrata, prefers 15 m bottoms, although it is more abundant (absolute values) at 25 m, and *A. petiti* which is very abundant at 15 m depth. There is little information on the biology and behaviour of these species: both of them live on soft bottoms but *A. alboranensis* is always more abundant (Manjón-Cabeza and García Raso, 1998b; Macpherson and Raventos, 2004). The species *Paguristes eremita*, *Pagurus forbesii* and *A. hyndmanni* are characteristic of 25 m detritic bottoms, the latter also occurs in coralligenous substrate together with *Pisidia longicornis*, *Calcinus tubularis*, species of the genus *Pilumnus* and *Galathea intermedia*. These species have also been mentioned in maërl, coarse substrate (Pérès and Picard, 1964; Dewarumez and Davoult, 1997) and in coastal detritic bottoms (Ledoyer, 1968; Bellan-Santini *et al.*, 1994; Manjón-Cabeza and García Raso, 1998b, 2002b). The largest hermit crabs of the area, *Dardanus arrosor* and *Pagurus prideaux* are abundant but they are broadly (not specifically) distributed in depth and on soft substrata. In Málaga, *D. arrosor* lives from 1 to 540 (625) m, with maximal abundances at 19-103 m. *P. prideaux* lives between 5 and 279 m, with maximal abundances at 19 to 93 m. *Pagurus excavatus* shows a

similar distribution but is less extensive, between 11 and 93 m, with maximum abundances between 17 and 75 m (García Raso, 1982c). In the present study, *D. arrosor* was found to prefer detritic bottoms, and *P. prideaux* and *P. excavatus* muddy fine sand. All cases always preferred deeper bottoms (25 m).

Finally, we would like to highlight the specific richness found in the study area in the different kinds of bottoms, which is greater than other similar or larger areas in the south of Spain, such as the Natural Park of Cabo de Gata-Níjar (in the eastern part of the Alborán Sea) (García Raso *et al.*, 1992), or the detritic bottoms of Barbate (Cadiz littoral) (Manjón-Cabeza and García Raso, 1998b; García Raso and Manjón-Cabeza, 2002b), and the soft bottoms of Málaga Bay (García Raso, 1987), among others. Moreover, if we include the information from other substrata in the study area, not incorporated in this study, such as *Posidonia oceanica* (this area is the western distribution limit of this habitat in the Mediterranean Sea), *Cymodocea nodosa*, seaweeds, and intertidal rocky bottoms, the total number of species is over a hundred (García Raso *et al.*, 2006b), considering only the depth range between 0 and 35 m. This high specific richness together with the existence of specimens with intermediate morphological forms between those of Atlantic and Mediterranean populations, such as the species *Xantho hydrophilus* (García Raso *et al.*, 1987; Reuschel and Schubart, 2006), and the coexistence of Mediterranean and Atlantic species (see Introduction) confirm the special interest of this area. Similar results have also been found in other groups such as molluscs, with many subtropical African species living in the area and with endemic species from the Strait of Gibraltar (Gofas, 1999; García Raso *et al.*, 2006b). These results justify a protection status for this special biogeographical zone in order to preserve European biodiversity. Thus, knowledge about the structure and relationships of the communities will allow us to foresee the effects of an event (or human action) on a specific substratum and on the neighbouring areas.

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