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Evolution of a decapod community (Crustacea) of shallow soft bottoms with seaweeds from southern Europe

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The qualitative and quantitative monthly composition and the annual temporal changes in a shallow (3.3–6.3 m) community of Crustacea: Decapoda associated with soft bottoms (very fine–muddy sand) and the seaweed *Caulerpa prolifera* in the south of Spain (Valdelagrana Beach in the Bay of Cadiz) has been studied for two years from February 1994 to January 1996. This community showed a similar pattern in both analysed cycles and could be characterized by a change or succession in the abundances of two groups of species: in autumn–winter *Hippolyte inermis* and *Hippolyte varians* (species associated with seaweeds); and in spring–summer: *Philocheras monacanthus*, *Diogenes pugilator* (characteristic of sandy bottoms) and *Macropodia parva*. The results of the ordination analysis of monthly samples is related to the absence or abundance of these dominant species although it does not define the two seasonal groups. The analysis of monthly richness, equitability, diversity and k-dominance curves, during the two years, showed a stable and rich community (with more than 6100 specimens caught belonging to 49 species) despite the human influence and the proximity of the Guadalete River.

INTRODUCTION

In the Atlantic European waters of the Gulf of Cadiz, the shallow decapod fauna of the infralittoral zone is insufficiently known. Only a few general studies (Arias, 1976; Drake et al., 1997; Sanchéz-Moyano & García Gómez, 1998) and several specific papers on decapods (mainly on fauna and taxonomy, see references in Manjón-Cabeza & García Raso, 1998, 2000) have been made. Of these only one (Manjón-Cabeza & García Raso, 1998) analysed the structure of a decapod community. Conversely, the circalittoral and deep-water decapod fauna (from 100 m in depth) is relatively well known, mainly as results of large surveys made in the nineteenth century and in the first half of the twentieth (see review in García Raso, 1996; and López de la Rosa, 1997).

However, the available knowledge on the structure and temporal evolution of the decapod communities of the area, and from the different biotopes, is very scanty. Only the studies on the macroinvertebrate community of the tidal channels in the Bay of Cadiz (Drake et al., 1997) and on the decapod community of soft bottoms (detritic) under the influence of tidal currents from Barbate (Manjón-Cabeza & García Raso, 1998).

Also, the Bay of Cadiz (in the south-east margin of the Gulf of Cadiz) is in the south-west of the Iberian Peninsula, in the confluence of two biogeographical regions (Atlantic and Mediterranean), which determine the physico-chemical characteristics of the waters and the faunistic composition. This, together with the tidal and coastal currents, the influence of the freshwater from the hydrographical basins of the Guadalquivir River and more specifically of the Guadalete River, which have an influence on salinity, temperature, food resources and larval dispersion (Seoane-Camba, 1965; Rodriguez, 1986), and together with the aquaculture activities (Arias & Drake, 1994; Drake & Arias, 1997) existing in the zone, are determinant factors in the structure and dynamics of the communities.

The aim of this study is to increase the information on these topics and particularly the knowledge of the structure and temporal evolution of the community of shallow very fine–muddy sand with seaweed. A companion paper (Rueda et al., 2001) considered the same questions regarding the molluscan community in this area.

MATERIALS AND METHODS

The sampling site was located off Valdelagrana Beach, at 36°34′N 06°14′W, in the outer part of the Bay of Cadiz (Figure 1), close to the Guadalete River. This area has a relatively high human influence by the proximity of urban areas of Cadiz and Puerto de Santa María. The substratum is dominated by fine–muddy sands with presence of seaweeds, mainly *Caulerpa prolifera* and very small patches of sea grasses.

The monthly samples were collected over the two years, from February 1994 to January 1996, in the morning (normally between 0930 and 1030 h) and between 3.3 and 6.3 m (depending of the tidal coefficient), by towing a semi-circular dredge with a fishing boat, for 10 min at a speed of 1 knot. The estimated sampling area was $\sim 300\,\mathrm{m}^2$. The dredge has a mouth length of 1 m, a height of 60 cm and a net with a mesh of 1-cm (we attempted to use a smaller mesh size, but this was not very feasible due to clogging by the muddy sediment).

In the laboratory the samples were washed over a column of sieves to separate specimens.

The importance of the species in the community was estimated by the presence or constancy (Ci) (Mora, 1980)

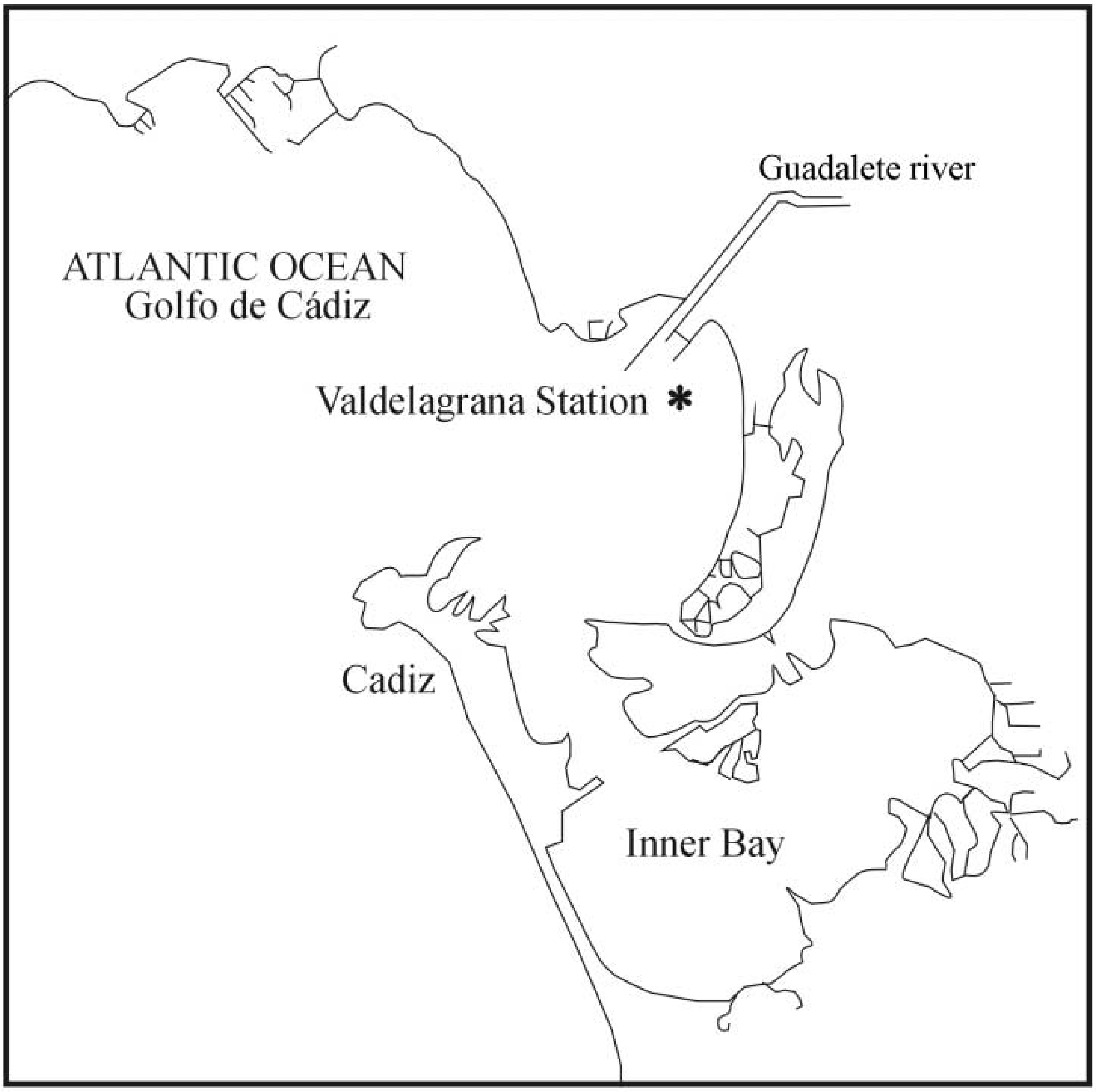

Figure 1. Studied zone: Cadiz Bay (Spain). The sampling area, in Valdelagrana Beach, is indicated as (36°34′N 06°14′W).

and dominance (Di, relative total abundance in percentage) (Glémarec, 1969) indices and the value resulting of Ci×Di (García Raso & Fernández Muñoz, 1987; Manjón-Cabeza & García Raso, 1998).

For analysis of the structure of the community, the programme PRIMER (Plymouth Routines In Multivariate Ecological Research) (Clarke & Warwick, 1994) was used, for calculating the values of the diversity of Shannon index (Shannon & Weaver, 1963; Krebs, 1989) and evenness index (Pielou, 1969) (program DIVERSE), the k-dominance curves (Gray & Pearson, 1982) (program GEOPLOT), to classify the samples, with the Bray–Curtis similarity index (program CLUSTER) and to make an ordination analysis (program MDS).

RESULTS

The physical characteristics of the sampling site were: (i) sediment dominated by very fine–muddy sands (0.125–0.063 mm); (ii) range of percentage of organic carbon between 0.13 and 0.58% (average: 0.30%); and (iii) superficial water temperature between 13.7°C (winter: January) and 25.1°C (summer: July).

The monthly data on the species and specimens collected, and on the presence of ovigerous females, are given in Table 1. The absence of data in December 1995 was a consequence of the very rough sea conditions, which made sampling impossible and caused the disappearance of the vegetal cover.

Over the two years a total 6177 specimens, belonging to 49 species, was captured, which represents an average density of 0.89 specimens m^{-2} with a σ_{n-1}=0.66 (Table 1).

Philocheras monacanthus, *Sicyonia carinata*, *Hippolyte varians*, *Diogenes pugilator* and *Macropodia parva* could be considered as permanent species ($\mathrm{Ci} > 75\%$) and *Hippolyte inermis*, *Thoralus cranchii*, *Hippolyte leptocerus–H. garciarasoi*, *Processa edulis*, *Pisidia longipes*, *Ilia nucleus*, *Liocarcinus vernalis* are very common ($75\% > \mathrm{Ci} > 50\%$). Of these, the more important and characteristic species in the community (values Ci×Di %>5) are *Philocheras monacanthus*, *H. inermis*, *H. varians*, *D. pugilator*, *M. parva* and *Processa edulis* which are responsible for the structure of the

Table 1. *Monthly number of specimens of the different species during the studied period (February 1994 to January 1996).*

Species	F94	M94	A94	M94	J94	J94	A94	S94	O94	N94	D94	J95	F95	M95	A95	M95	J95	J95	A95	S95	O95	N95	J96	Ni	Di	Ci	Ci×Di
Philocheras monacanthus (Holthuis, 1961)	76*	68*	337*	202*	12*	94*	26*	165	3*	13*	2*	14*	8*	24*	56*	81*	120*	19*	3*	1*	4*	3*		1331	21.55	0.96	20.61
Hippolyte inermis Leach, 1815				2*			2	43*	84*	225*	197*	123*	223*	4*	2	20*	5*	110*	26*	32*	136*	146*		1380	22.34	0.74	16.51
Hippolyte varians Leach, 1814				3*			4*	12	121*	122*	149*	97*	88*	10*	5*	11*	1*	7*	20*	11*	64*	47*	1	773	12.51	0.78	9.79
Diogenes pugilator (Roux, 1829)	15	8*	25*	5	17*	78*	23*	13*	2	5*	1	2*	1	35*	40*	66*	57*	16*	5	1			5*	420	6.8	0.91	6.21
Macropodia parva Van Noort & Adema, 1985	6	7*	39*	99*	15*	34*	4*	89*	21*	15*	15*	19*	41*	13	22*	38*	55*	41*	32*	6*	9	1	5*	626	10.13	0.57	5.73
Processa edulis (Risso, 1816)						1				1	2		8*		1*		2	9*	4	9	619*		1*	657	10.64	0.43	4.62
Sicyonia carinata (Brünnich, 1768)	13*	18	14	7			3	20	3	3	13	5	14	41	10	21	3	15	19	6	55	6	18	307	4.97	0.91	4.54
Thoralus cranchii (Leach, 1817)				1*	3		1	1*	12*		5*	2*	64*		1*	1*	11*	3*	4		2*	10*		121	1.96	0.65	1.28
Hippolyte leptocerus (+)(Heller, 1863)				2	2		3	23	12	1	9		3*				3	33*	2*	2	8	4		107	1.73	0.61	1.05
Liocarcinus vernalis (Risso, 1827)	11*	37*	17	8		3		2			4	1	1			1	2		1	1	2		1	92	1.49	0.65	0.97
Pisidia longimana (Risso, 1816) *for. longicornis* (++)		4	4	7*	11*	4		14	3	4	9	1	9*				8*	2		3	6			89	1.44	0.65	0.94
Ilia nucleus (Linnaeus, 1758)	1	2	3	2		3*	2	1		1	1					3*	1*	2			1		1	24	0.39	0.61	0.24
Athanas nitescens (Leach, 1814)			2				1	1			3		7	1			1				9	1		26	0.42	0.39	0.16
Processa macrodactyla Holthuis, 1952	15*												1								25			41	0.66	0.17	0.12
Ethusa mascarone (Herbst, 1785)		1	11*	1				1	1									3					1	19	0.31	0.3	0.09
Palaemon serratus (Pennant, 1777)										1	1	1	2						2	4	3			14	0.23	0.3	0.07
Pilumnus villosissimus (Rafinesque, 1814)								3			9	1		1			1			1				16	0.26	0.26	0.07
Philocheras fasciatus (Risso, 1816)													7*	6*	1*			1*				1		16	0.26	0.22	0.06
Philocheras trispinosus (Hailstone, 1835)		2*											1	8	2									13	0.21	0.17	0.04

(continued)

Table 1. (*Continued*).

Species	F94	M94	A94	M94	J94	J94	A94	S94	O94	N94	D94	J95	F95	M95	A95	M95	J95	J95	A95	S95	O95	N95	J96	Ni	Di	Ci	Ci×Di
Liocarcinus arcuatus (Leach, 1814)											1			1		2*		1		2	1		1	9	0.15	0.3	0.04
Parthenope angulifrons Latreille, 1825			2					2						1				1		2			1*	9	0.15	0.26	0.04
Acanthonyx lunulatus (Risso, 1816)								2					1			3*					1			7	0.11	0.17	0.02
Melicertus kerathurus (Forskål, 1775)	1						2												3					6	0.1	0.13	0.01
Eualus occultus (Lebour, 1936)				1*						4*														5	0.08	0.09	0.01
Processa robusta Nouvel & Holthuis, 1957								1					1					4						6	0.1	0.13	0.01
Processa modica Williamson & Rochanaburanon, 1979	7*							1																8	0.13	0.09	0.01
Ogyrides rarispina Holthuis, 1951		2	1			1									1									5	0.08	0.17	0.01
Upogebia pusilla (Petagna, 1792)																1			2		1			4	0.06	0.13	0.01
Pilumnus hirtellus (Linnaeus, 1761)		1																			3		1*	5	0.08	0.13	0.01
Pilumnus inermis A. Milne Edwards & Bouvier, 1894								1										1	2					4	0.06	0.13	0.01
Brachynotus atlanticus Forest, 1957		1*	1*		1																1			4	0.06	0.17	0.01
Brachynotus sexdentatus (Risso, 1827)						1						1											3*	5	0.08	0.13	0.01
Hippolyte cf *lagarderi* (+++) d'Udekem d'Acoz, 1995																		7						7	0.11	0.04	0
Processa elegantula Nouvel & Holthuis, 1957								1																1	0.02	0.04	0
Palaemon longirostris H. Milne Edwards, 1837																	1							1	0.02	0.04	0
Palaemonetes varians (Leach, 1814)													2											2	0.03	0.04	0
Crangon crangon (Linnaeus, 1758)			2*	1																				3	0.05	0.09	0
Gourretia denticulata (Lutze, 1937)																							1	1	0.02	0.04	0

Spiropagurus elegans Miers, 1881			1				1																	2	0.03	0.09	0
Galathea intermedia Lilljeborg, 1851																1								1	0.02	0.04	0
Atelecyclus undecimdentatus (Herbst, 1783)							1																	1	0.02	0.04	0
Pirimela denticulata (Montagu, 1808)			1																					1	0.02	0.04	0
Pilumnus spinifer H. Milne Edwards, 1834													1											1	0.02	0.04	0
Neopinnotheres pinnotheres (Linnaeus, 1758)						1																		1	0.02	0.04	0
Afropinnothres sp.																				1				1	0.02	0.04	0
Achaeus cranchii Leach, 1817				1																				1	0.02	0.04	0
Pisa armata (Latreille, 1803)				2																				2	0.03	0.04	0
Inachus thoracicus Roux, 1830																							1	1	0.02	0.04	0
Macropodia czerniavskii (Brandt, 1880)																1*								1	0.02	0.04	0
No. specimens	145	151	460	344	61	220	73	396	262	395	421	267	483	145	141	250	271	275	125	82	950	219	41	6177			
Density/M2	0.48	0.50	1.53	1.15	0.20	0.73	0.24	1.32	0.87	1.32	1.40	0.89	1.61	0.48	0.47	0.83	0.90	0.92	0.42	0.27	3.17	0.73	0.14				
No. species	9	12	15	16	7	10	13	20	10	12	16	12	20	12	11	14	15	18	14	15	19	9	14				

Ni, total number of specimens; Di and Ci, total dominance or relative abundance and presence or constancy of the different species, respectively. *, presence of ovigerous females. (+), this population shows a high morphological variation, there are specimens morphologically intermediates between *Hippolyte leptocerus* and *H. garciarasoi* d'Udekem d'Acoz, (1996); (++) specific complex (see García Raso et al., 1987); (+++), juvenile specimens.

community and represent 83.9% of the total abundance. However, the latter is usually scarce during the day and has a high score only as consequence of a sporadic abundance in October of the second cycle. The above species are followed by *S. carinata*, *T. cranchi*, and *H. leptocerus–H. garciarasoi* ($5 > \mathrm{Ci} \times \mathrm{Di}\% > 1$) (Table 1). All these mentioned species represent more than 92% of the total specimens caught.

A seasonal pattern or trend in the monthly evolution of the total number of specimens was not apparent, because there are changes in the relative abundance of the species in the same months between years. However, the total abundance of each year is very similar.

In relation to the dominant species a similar pattern seems to exist between years. This shows a change in the dominances within the year, in autumn and winter the most abundant species are *H. inermis* and *H. varians* which are replaced in spring and summer by *Philocheras monacanthus*, *D. pugilator* and *M. parva* (this last with less weight) (Figure 2; Table 1). The only difference between cycles is the existence of monthly displacements.

The presence and dominance of *Processa edulis* however show a strong increase in the second cycle (25–73% and 0.13–21.9% respectively), with an anomalous maximum in October.

The results of the last month, January 1996, were atypical, and were a consequence of the rough sea conditions of December 1995, which caused the total disappearance of the vegetal cover. So, the structure of the community was modified, with a large decrease in the

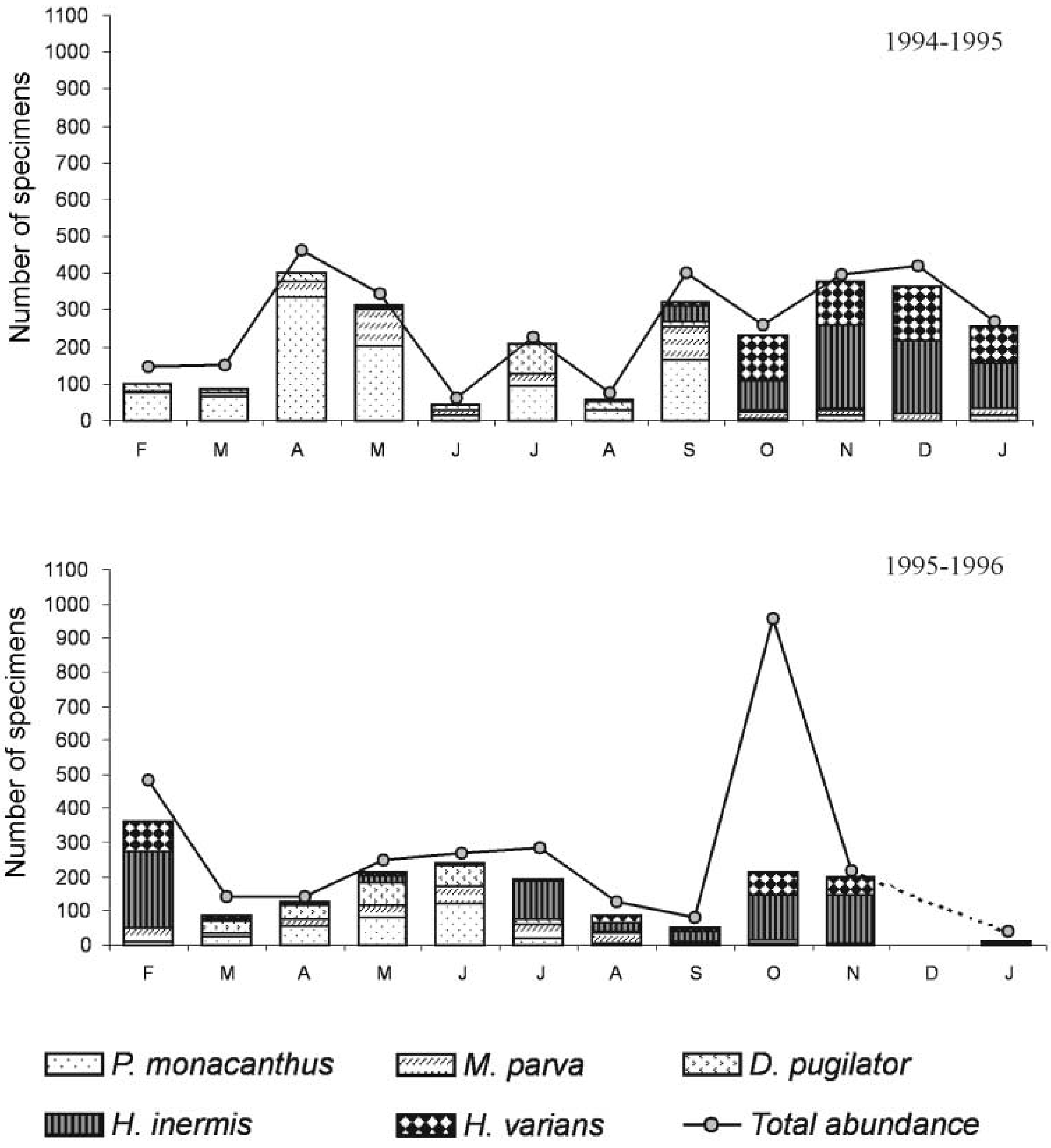

Figure 2. Monthly evolution of the total number of specimens and of the abundance of the dominant species during the two analysed years.

number of specimens, no high values of dominances and the practical disappearance of the species associated with the seaweed such as *H. inermis* or *H. varians*.

The evolution of the diversity, evenness and richness are shown in Figure 3. The average value of monthly species richness is 13.7 with σ_{n-1}=3.6; the fluctuations are a consequence of the presence of rare species or of species with low population densities. The diversity and evenness curves follow a similar evolution. The evenness shows fewer fluctuations and presents an average value of 0.62 (0.59 and 0.66 in both cycles respectively) with a minimum of 0.41 and a maximum of 0.85. The evolution of the diversity follows a pattern more closely related to the evenness than to the richness (more fluctuating); its values ranges between 1.05 and 2.09, with a minimum in November as a consequence of the dominance of the species associated with the seaweed (*H. inermis* and *H. varians*) and perhaps also of the storms, common in this period; there is another minimum (mainly in the first year) in the beginning of spring (April) as a consequence of the dominances of the species of sandy bottoms (*Philocheras monacanthus* and *D. pugilator*). The abnormal result of January 1996, previously cited, generates an increase in the diversity and evenness indexes.

In general, the k-dominance curve of the species by geometrical classes shows that the structure of the

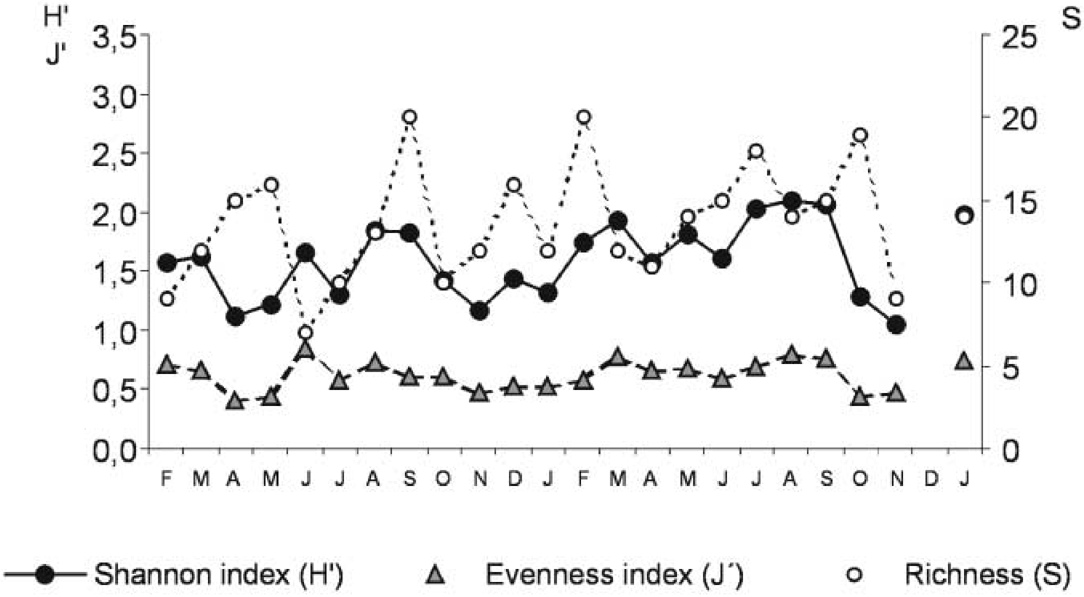

Figure 3. Monthly evolution of the values of the Shannon index (H′), evenness index (J′) and richness (S) during the two analysed years.

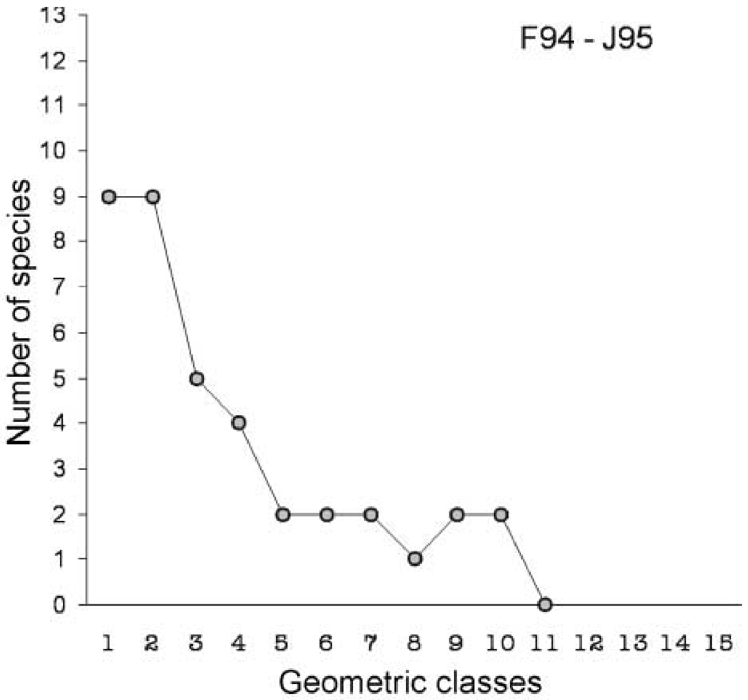

Figure 4. General k-dominance curve by geometrical classes.

community is little disturbed (Figure 4), with exceptions in particular months (e.g. February and June 1994) (Figure 5).

The ordination analysis MDS (based on the Bray–Curtis index) (Figure 6) shows the existence, with a 50% of similarity, of two groups A1 and B1 and two detached samples (June 1994 and January 1996) (stress=0.17, useful two-dimensional picture). The A1 group (on the right side of the axis I) is formed by the samples of the first cycle in which the dominant species associated with the seaweed (*Hippolyte* genus) are absent and there is a strong dominance of the *P. monacanthus*. The B1 group enclosed the

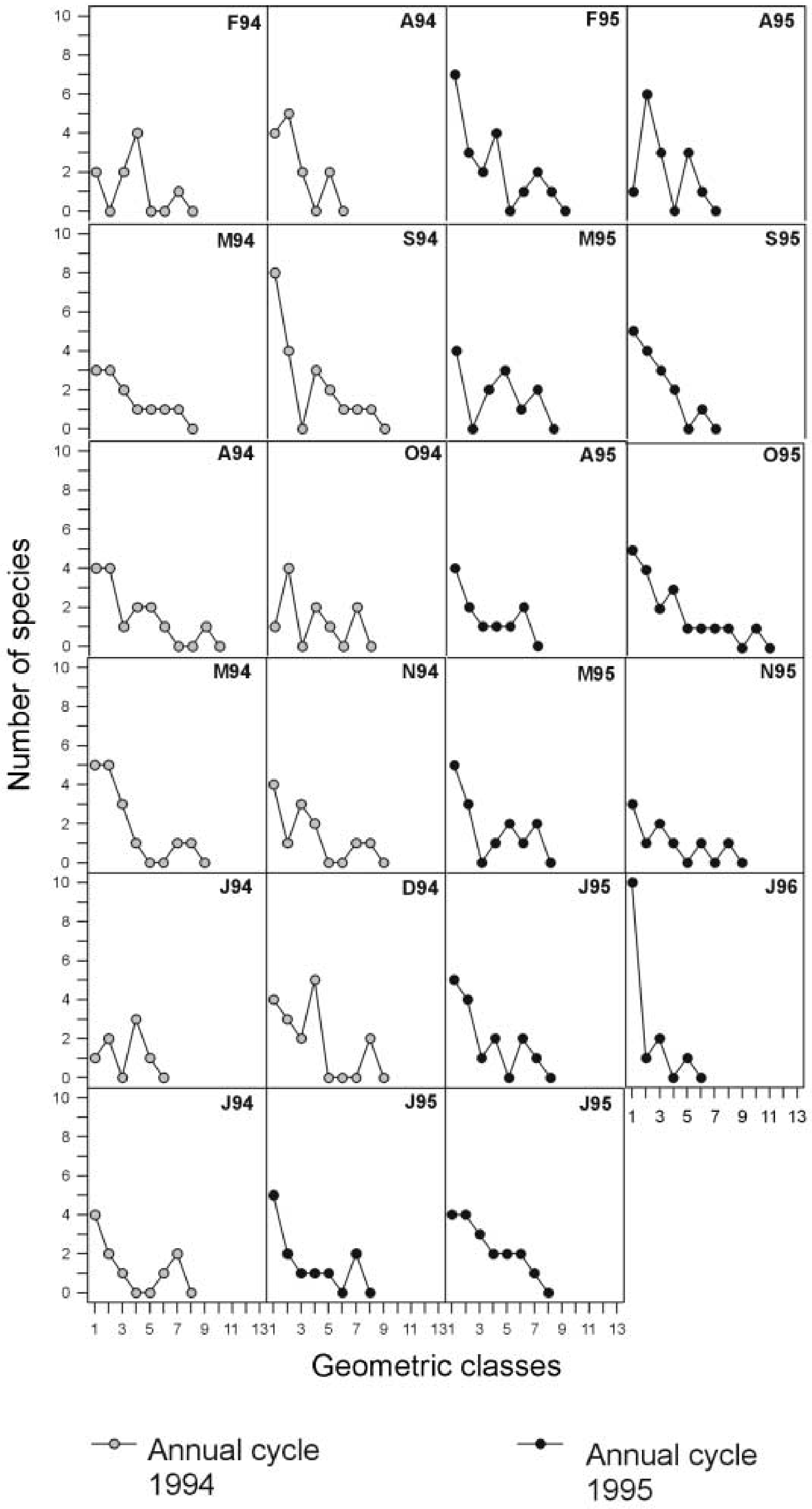

Figure 5. Monthly evolution of the k-dominance curves by geometrical classes during the two analysed years (February 1994 (F94) to January 1996 (J96)).

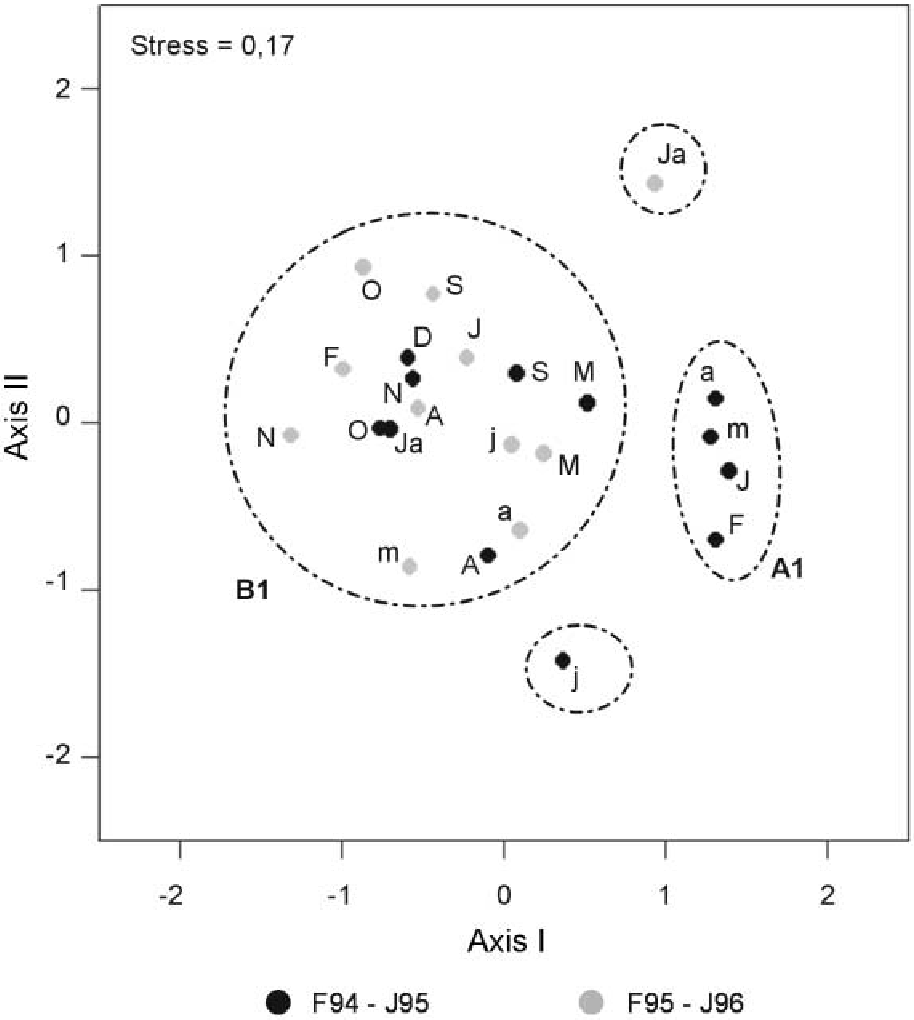

Figure 6. Ordination analysis (MDS) of the monthly samples (grey points: February 1994 to January 1995, black points February 1995 to January 1996). a, April; A, August; m, March; M, May; j, June, J, July; Ja, January.

other samples. In general, the samples with more specimens of *Hippolyte* species are located on the left side of axis I. The two detached samples are very poor and atypical, with a minimum number of specimens. June 1994 has the lower richness and January 1996 shows the strong disturbances previously mentioned (also a species, *Gourretia denticulada*, (Lutze, 1937) never found before in European waters, was caught (López de la Rosa, 1999)).

DISCUSSION

Several studies developed on shallow soft bottoms demonstrate that the seaweed and/or sea grass cover (in addition with the type–size of the sediments) is one of the most important factors for the characterization of the structure of the benthic communities, being responsible for the species composition and abundances (Thorhaug & Roessler, 1977; Gore et al., 1981; Baden & Pihl, 1984; Möller et al., 1984; Pihl, 1986; Isaksson & Pihl, 1992; Manjón-Cabeza & García Raso, 1998).

During the studied period (February 1994–November 1995) there is a vegetal cover in the area, and the structure of the community, dominated by caridean species, could be characterized by a change or successions in the dominance of two groups of species: (i) *Philocheras monacanthus*, *Diogenes pugilator* and *Macropodia parva*; and (ii) *Hippolyte inermis* and *H. varians*, the first group with species of fine sandy–mud sand bottoms and the second with species characteristic of soft bottoms with seaweeds or sea grasses (García Raso, 1982, 1987, 1990; Guillen & Pérez-Ruzafa, 1993; Zupo, 1994). Both are dominant in two different periods, spring–summer and autumn–winter respectively, which shows the existence of a more or less seasonal pattern (Figure 2). These changes in abundance are due to recruitments and movements. Similarly, Zupo (1994) found that *H. inermis* showed a zonation with depth according to age and sexes, with monthly differences. He also noticed a marked recruitment in autumn and a strong decrease of specimens in spring, which are in accordance with our results.

The ordination study of the samples, with the total of the species caught, defines two principal groups which do not show a seasonality, but they are structured and related to the absence and abundance of the two groups of species previously cited, mainly *Hippolyte* spp. and *P. monacanthus*.

A comparable change in the structure of the community during the annual cycle, associated with the presence of seaweed was observed in Barbate (littoral of Cadiz), close to the studied area, by Manjón-Cabeza & García Raso (1998), but not in other communities of sea grass (rhizome stratum of *Posidonia*) and calcareous algae (García Raso, 1990; García Raso & Fernández Muñoz, 1987).

Changes of macrobenthic assemblages are not unusual in shallow waters. Dörjes et al. (1986) analysing the sublittoral macrozoobentos, near the island of Norderney (1976–1985), found changes in the species composition, where many appear sporadically and others only develop large populations in certain years, disappearing completely or decreasing their abundance in others. Fromentin et al. (1997), in the study of the *Abra alba* community in muddy fine sand of the north-west coast of France, found important changes in species composition, with rapid successions of distinct groups of species.

In comparison with other studies from adjacent areas and biotopes, the data show a higher diversity (López de la Rosa et al., 1998) and corroborate that the vegetal cover induces an increase in the structural heterogeneity, giving a three-dimensional scale to the area (Isaksson & Pihl, 1992). The seaweeds make more ecological niches available to be used by different species, which provide an increase in the complexity of the structure of the community (Gray, 1977).

This higher complexity and diversity as consequence of the seaweed cover is also supported by the low richness values obtained after December 1995, when the seaweeds disappeared. Samples taken every three months during a later period (1996 and 1997) showed a modification of the substratum with the total absence of seaweed and lower diversity values (Lopez de la Rosa, 1999), with a decrease in the general abundance of specimens and changes in the species dominances (the more important were *Crangon crangon* and *D. pugilator*) (López de la Rosa et al., 1998).

The disappearance of the seaweed cover in the study area in the last samples and its later absence (see above) was caused, at least in part, by the storms of winter 1995–1996. These storms are determinant factors in environmental control, increasing the hydrodynamism and modifying the granulometric composition and the amount of organic matter in the sediment (Warwick et al., 1991). So, the Bay of Cadiz shows a granulometric variability which is a clear demonstration of the energetic perturbations existing in the different zones of this area (Ligero et al., 1998).

The stability of a community could be recognized by three numerical scales: the total abundance, the position of the species in relation to its abundance and the presence or absence of these, which allow the establishment of a hierarchy (Rahel, 1990). This community could be considered stable, considering the presences–absences and the values of abundance (the two groups are constant in the two years); and it shows a higher equitability than in adjacent biotopes (López de la Rosa et al., 1998).

The very strange peak of abundance of the species *Processa edulis* in the diurnal sample of October could be related to the freshwater flow of the Guadalete River (very close to the sampling area) which, as happens with the storms, modifies the abiotic and biotic factors, directly or indirectly through the actuation of load of substances (including pollutants?), because this species normally remains buried during the day and emerges during the night (Ledoyer, 1966, 1968).

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REFERENCES

Arias, A.M., 1976. Contribución al conocimiento de la fauna bentónica de la Bahía de Cádiz. *Investigación Pesquera. Barcelona*, **40**, 355–386.

Arias, A.M. & Drake, P., 1994. Structure and production of the benthic macroinvertebrate community in a shallow lagoon in the Bay of Cadiz. *Marine Ecology Progress Series*, **115**, 151–167.

Baden, S. & Pihl, L., 1984. Abundance, biomass and production of mobile epibenthic fauna in *Zostera marina* (L.) meadows, western Sweden. *Ophelia*, **23**, 65–90.

Clarke, K.R. & Warwick, R.M., 1994. *Change in marine communities: an approach to statistical and interpretation*. Plymouth: Natural Environment Research Council.

Dörjes, J., Michaelis, H. & Rhode, R., 1986. Long-term studies of macrozoobenthos in intertidal and shallow subtidal habitats near the island of Norderney (East Friesian coast, Germany). *Hydrobiologia*, **142**, 217–232.

Drake, P. & Arias, A., 1997. The effect of the aquaculture practices on the benthic macroinvertebrate community of a lagoon system in the Bay of Cadiz, Spain. *Estuaries*, **20**, 677–688.

Drake, P., Arias, A. & Conradi, M., 1997. Aportación al conocimiento de la macrofauna supra y epibentónica de los caños mareales de la Bahía de Cádiz (España). *Publicaciones Especiales Instituto Español de Oceanografía*, **23**, 133–141.

Fromentin, J.M., Ibañez, F., Dauvin, J.-C., Dewarumez, J.M. & Elkaim, B., 1997. Long-term changes of four macrobenthic assemblages from 1978 to 1992. *Journal of the Marine Biological Association of the United Kingdom*, **77**, 287–310.

García Raso, J.E., 1982. Contribución al estudio de los Pagúridos (Crustacea, Decapoda, Anomura) en el litoral sudmediterráneo español. *Investigación Pesquera. Barcelona*, **46**, 493–508.

García Raso, J.E., 1987. Contribución al conocimiento de los Crustáceos Decápodos de fondos blandos del sur de España. *Graellsia*, **43**, 153–169.

García Raso, J.E., 1990. Study of a Crustacea Decapoda taxocoenosis of *Posidonia oceanica* beds from the southeast of Spain. *P.S.Z.N.I: Marine Ecology*, **11**, 309–326.

García Raso, J.E., 1996. Crustacea Decapoda (excl. Sergestidae) from Ibero-Moroccan waters. Results of Balgim-84 Expedition. *Bulletin of Marine Science*, **58**, 730–752.

García Raso, J.E. & Fernández Muñoz, R., 1987. Estudio de una comunidad de Crustáceos decápodos de fondos 'coralígenos' del alga calcárea *Mesophyllum lichenoides* del sur de España. *Investigación Pesquera. Barcelona*, **51**, (Supplement 1), 301–322.

García Raso, J.E., González-Gurriarán, E. & Sardá, F., 1987. Estudio comparativo de la fauna de crustáceos decápodos braquiuros de tres áreas de la Península Ibérica (Galicia, Málaga, Cataluña). *Investigación Pesquera. Barcelona*, **51**, (Supplement 1), 43–55.

Glémarec, M., 1969. *Les peuplements benthiques du plateau continental Nord-Gascogne*. PhD thesis, University of Paris, France.

Gore, R.H., Gallaher, E.E., Scotto, L.E. & Wilson, K.A., 1981. Studies on the Decapod Crustacea from the Indian River region of Florida. XI. Community composition, structure, biomass and species area relationships of sea grass and drift algae-association macrocrustaceans. *Estuarine, Coastal and Shelf Science*, **12**, 485–508.

Gray, J.S., 1977. The stability of benthic ecosystems. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **30**, 427–444.

Gray, J.S. & Pearson, T.H., 1982. Objective selection of sensitive species indicative of pollution-induced change in benthic communities. I. Comparative methodology. *Marine Ecology Progress Series*, **9**, 11–119.

Guillen, J.E. & Pérez-Ruzafa, A., 1993. Composición estructura y dinámica de los poblamientos de Crustáceos Decápodos asociados a las comunidades arenosas en el SE ibérico. *Publicaciones Especiales del Instituto Español de Oceanografía*, **11**, 175–183.

Isaksson, I. & Pihl, L., 1992. Structural changes in benthic macrovegetation and associated epibenthic faunal communities. *Netherlands Journal of Sea Research*, **30**, 131–140.

Krebs, C.J., 1989. *Ecological methodology.* New York: Harper & Row.

Ledoyer, M., 1966. Écologie de la faune vagile des biotopes méditerranéens accessibles en scaphandre autonome (région de Marseille principalement). II. Données analytiques sur les herbiers de phanérogames. *Recueil des Travaux de la Station Marine d'Endoume*, **57**, 135–164.

Ledoyer, M., 1968. Écologie de la faune vagile des biotopes méditerranéens accessibles en scaphandre autonome (région de Marseille principalement). IV. Synthèse de létude écologique. *Recueil des Travaux de la Station Marine d'Endoume*, **60**, 125–295.

Ligero, R.A., Sales, D., López Agüayo, F., Casas Ruiz, M., García León, M., García Tenorio, R. & Barrera Izquierdo, M., 1998. *Datación de sedimentos en la Bahía de Cádiz. Estudio histórico del impacto industrial*. Universidad de Cádiz—Consejería de Medio Ambiente de la Junta de Andalucía. Informe Técnico, 1–187.

López de la Rosa, I., 1997. Crustáceos decápodos capturados durante las campañas del IEO ARSA 0393 y ARSA 1093 en el Golfo de Cádiz: distribución batimétrica. *Publicaciones Especiales del Instituto Español de Oceanografía*, **23**, 199–206.

López de la Rosa, I., 1999. *Crustáceos decápodos de la bahía de Cádiz (sur de España).* PhD thesis, University of Málaga, Spain.

López de la Rosa, I., González Gordillo, J.I. & Rodríguez, A., 1998. *Crustáceos decápodos como indicadores biológicos en la Bahía de Cádiz.* Instituto de Ciencias Marinas de Andalucía—Consejería de Medio Ambiente de la Junta de Andalucía. Informe Técnico, 1–104.

Manjón-Cabeza, M.E. & García Raso, J.E., 1998. Structure and evolution of decapod crustacean community from the coastal detritic bottoms of Barbate (Cadiz, southern Spain). *Journal of Natural History*, **32**, 1619–1630.

Manjón-Cabeza, M.E. & García Raso, J.E., 2000. Reproductive aspects of the females of the hermit crab *Diogenes pugilator* (Crustacea: Decapoda: Anomura) from southern Spain. *Journal of the Marine Biological Association of the United Kingdom*, **80**, 85–93.

Möller, P., Pihl, L. & Rosenberg, R., 1984. Fish and bottom fauna in Swedish shallow waters in the Skagerrak and Kattegat. In *Biological assessment of swedish shallow marine areas: fish and bottom fauna* (ed. R. Rosenberg), pp. 1–384. Swedish Environmental Protection Board, PM 1911.

Mora, J., 1980. *Poblaciones bénticas de la Ría de Arosa.* PhD thesis, Universidad de Santiago de Compostela, Spain.

Pielou, E.C., 1969. *An introduction to mathematical ecology.* New York: Wiley-Interscience.

Pihl, L., 1986. Exposure, vegetation and sediment as primary factors for mobile epibenthic faunal community structure and production in shallow marine soft bottom areas. *Netherlands Journal of Sea Research*, **20**, 75–83.

Rahel, F.J., 1990. The hierarchical nature of community persistence: a problem of scale. *American Naturalist*, **136**, 328–344.

Rodríguez, A., 1986. Biología del langostino *Penaeus kerathurus* (Forskål, 1775) del golfo de Cádiz. II. Distribución y estructura de la población. *Investigación Pesquera. Barcelona*, **50**, 187–202.

Rueda, J.L., Fernández-Casado, M., Salas, C. & Gofas, S., 2001. Seasonality in a taxocoenosis of molluscs from soft bottoms in the Bay of Cádiz (southern Spain). *Journal of the Marine Biological Association of the United Kingdom*, **81**, 903–912.

Sanchéz-Moyano, J.E. & García Gómez, J.C., 1998. The arthropod community, especially Crustacea, as bioindicador in Algeciras Bay (southern Spain) based on a spatial distribution. *Journal of Coastal Research*, **14**, 1119–1133.

Seoane-Camba, J., 1965. Estudios sobre las algas bentónicas en la costa sur de la Península Ibérica (litoral de Cádiz). *Investigación Pesquera. Barcelona*, **29**, 3–216.

Shannon, C.E. & Weaver, W., 1963. *The mathematical theory of communication.* Urbana: University of Illinois Press.

Thorhaug, A. & Roessler, M.A., 1977. Seagrass community dynamics in a subtropical estuarines lagoon. *Aquaculture*, **12**, 253–277.

Udekem d'Acoz, C. d', 1996. The genus *Hippolyte* Leach, 1814 (Crustacea: Decapoda: Caridea: Hippolytidae) in the east Atlantic Ocean and the Mediterranean Sea, with a checklist of all species in the genus. *Zoologische Verhandelingen*, **303**, 1–133.

Warwick, R.M., Goss-Custard, J.D., Kirby, R., George, C.L., Pope, N.D. & Rowden, A.A., 1991. Static and dynamic enviromental factors determining the community structure of estuarine macrobenthos in SW Britain: why is the Severn Estuary different? *Journal of Applied Ecology*, **28**, 329–345.

Zupo, V., 1994. Strategies of sexual inversion in *Hippolyte inermis* Leach (Crustacea, Decapoda) from a Mediterranean seagrass meadow. *Journal of Experimental Marine Biology and Ecology*, **178**, 131–145.

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