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THE MOLLUSCAN EPIFAUNA OF THE ALGA *HALOPTERIS SCOPARIA* IN SOUTHERN SPAIN AS A BIOINDICATOR OF COASTAL ENVIRONMENTAL CONDITIONS

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ABSTRACT

The effects of certain environmental factors on spatial variation of the mollusc community associated with the alga *Halopteris scoparia* in Algeciras Bay (southern Spain), located in the Strait of Gibraltar, are studied. Environmental gradients from the exterior to the interior of the bay have been detected, related above all to water movements, solids in suspension, organic content of sediments, and structural complexity of plants. These gradients are seen as differences in the composition of the mollusc communities of the outer zones (Isla de Las Palomas, San García, and Cucareo) and inner ones (Guadarranque and Crinavis). Although the conditions of the inner zone restrict the growth of some groups such as crustaceans and polychaetes, mollusc populations have developed well there in both number and diversity. Species are found exclusively at the exterior of the Bay (include *Cingula amabilis, Pisinna glabrata*, and *Nodulus contortus*) and for the interior (*Alvania montagui, Alvania rudis*, and *Rissoa similis*), the latter being the most discriminating between the two major zones of the bay. The environmental parameters having the greatest effect on the molluscs associated with *Halopteris scoparia* are water movement, the morphological characteristics of the substrate, and most importantly the availability of food.

INTRODUCTION

Environmental differences along the coast of southern Spain are reflected in the composition of the various benthic communities, e.g. sponges, ascidians, crustaceans (Carballo, Sánchez-Moyano & García-Gómez, 1994; Carballo, Naranjo & García-Gómez, 1996; Naranjo, Carballo & García-Gómez, 1996; Conradi, López-González & García-Gómez, 1997; Naranjo, Carballo & García-Gómez, 1998; Sánchez-Moyano & García-Gómez, 1998), the structure of infaunal communities (Estacio, García-Adiego, Fa, García-Gómez, Daza, Hortas & Gómez-Ariza, 1997; Estacio, García-Adiego, Carballo, Sánchez-Moyano & García-Gómez, 1999), and epiphytic communities (Sánchez-Moyano, 1996).

Of the macrophyte-associated fauna, the molluscs, together with the crustaceans and polychaetes, comprise one of the predominant groups (Hagerman, 1966; Allen & Griffiths, 1981; Edgar, 1983; Taylor & Cole, 1994). Descriptions of these communities have been made (e.g. Idato, Fresi & Russo, 1983; Templado, 1984; Boronat, Acuña & Fresneda, 1985; Ros, 1985), with more detailed studies of population dynamics (Southgate, 1982a and b; Robertson & Mann, 1982; Borja, 1986a and b, 1987, 1988), or the effect of certain environmental parameters (e.g. water movement—Fretter & Manly, 1977; Russo, Fresi, Vinci & Chessa, 1983, 1984a and b; Russo, Fresi, Buia & Vinci, 1985; Russo, Chessa, Vinci & Fresi, 1991–; sedimentation rate—Southgate, 1982 a and b; habitat complexity—Robertson & Mann, 1982; Gunnill, 1983;). In addition there has been much work on plant-animal grazing interactions (e.g. Black, 1986; Thomas & Page, 1983; Johnson & Mann, 1986; Clark & Defreese, 1987; Mazella & Russo, 1989; Trowbridge, 1992, 1993).

Halopteris scoparia (L.) Sauvageau (Phaeophyta, Sphacelariales) is one of the most abundant and widely distributed algal species on the Mediterranean and Atlantic coasts (Seoane-Camba, 1965; Meñez & Mathieson, 1981;

Novaczek, Breeman & van den Hoek, 1989) being very common in Algeciras bay. It is a much ramified alga that encloses very small spaces. These provide a large number of microhabitats, so that the abundance of individuals is high, and they are a good trap of sediment and epiphytes (especially diatoms that are the diet of most of the epifauna—Orth & Van Montfrans, 1984). At the same time, they restrict the size of the organisms. Such characteristics, and a great environmental versatility, make the alga a good medium for an abundant and interesting epiphytic community (Sánchez-Moyano, 1996).

The aim of this study is to analyze compositional variation in the community of molluscs associated with the alga *Halopteris scoparia* in relation to the environmental conditions of Algeciras Bay (southern Spain), especially human impacts, and then, to determine the usefulness of molluscs as bioindicators of the environmental quality of coastal waters.

MATERIAL AND METHODS

Algeciras Bay is located in the eastern-most zone of the Strait of Gibraltar. Despite being relatively small (approximately 30 km in length with a width of 8 km at the mouth), it provides a series of very different media with diverse environmental conditions. It is a deep submarine canyon (reaching depths of more than 500 metres) of varied topography and with a narrow platform bounded by the bathymetric contour of 30 metres with a width not exceeding 2 km. Its great mass of water and the intense hydrologic regimen of the Strait of Gibraltar, with circulation of waters from the Atlantic and Mediterranean, means a high circulation. However, the large industrial complex on its coast, and the busy port activity, have resulted in construction of seawalls, breakwaters, and fills that have caused alterations in the natural currents, and the appearance of pocketing. This has been heightened by the presence of a large population (around 300,000 inhabitants), little treatment of waste waters, and the contribution of nutrients and sediments from the two rivers flowing into the bay (Palmones and Guadarranque).

In five areas distributed along the coast of Algeciras Bay and encompassing the greatest range of different environmental conditions thirteen sampling stations were chosen (Figure 1). The areas were Isla de las Palomas (IP), a well illuminated rock zone; Punta de San García (SG), with a shaded environment at lesser depth (in both areas, the stations were established on a transect 200 metres long and at depths of 5, 8, and 10 metres); Cucareo inlet (CU), the area nearest to Algeciras port, is located on a wide platform ranging between 3 and 5 metres in depth (stations were established on a transect of 200 metres); Los Rocadillos (Guadarranque) (GU) is located in the internal zone of the bay, near the mouth of the Guadarranque River, on a strip of natural rock running along the coast between 3 and 5 metres in depth; Crinavis (CR), located in the internal zone, is an artificial substrate in a disused shipyard (stations were located along a breakwater to a depth of 5 metres).

Four replicate samples were taken at each station on five sampling occasions during one year (September 92, December 92, March 93, June 93, and September 93). Each replicate sample consisted of an algal specimen bagged *in situ* and extracted from the bottom by SCUBA diving. The samples were sieved through a 0.5-mm mesh. The date for abundance have been expressed as number of individuals per 100 grams (dry weight) of alga. Abundance was used to calculate the Shannon-Wiener diversity (Shannon & Weaver, 1963).

A series of parameters was calculated for each alga: maximum height, diameter, volume, and dry weight. The theoretical volume was calculated assuming that, in the environment, *H. scoparia* adopts a geometric form akin to a paraboloid. Deducting the real volume from the theoretical one gives the interstitial volume, which represents the living space. The ratio between theoretical and real volumes (Index of Compactness) gives an idea of the level of compactness of the alga—the closer to unity, the more compact the alga (Sánchez-Moyano & García-Gómez, 1998).

In order to establish what parameters affect the composition of the molluscan communities, modules (frameworks with concrete bases and three vertical plastic bars a metre above the bottom) were sited along the arc of Algeciras Bay (Figure 2). Samples were made monthly from November 1992 until November 1993. The variables measured were the following: water movement, sedimentation rate, % of organic matter in the sediments, and solid and % organic matter in suspension. The possible spatial variations of these variables were tested using one-way ANOVA, after verifying variances approximated to normality (Kolmogorov-Smirnov test) and homogeneity (Barlett test). Homogeneous groups were separated by the Tukey test.

Water movement was calculated by the method of 'plaster dissolution' described by Muus (1968) and modified by Gambi, Buia, Casola & Scardi (1989). It is measured as 'water speed equivalents' (V) (Bailey-Brock, 1979). The sedimentation rate was measured by placing sediment traps (six bottles of one-litre capacity in our case). Part of the sedimentation was used to calculate the % of organic matter by combustion at 500°C. The data are expressed as $Kg/m^2/$month. The solids and organic matter in suspension were measured according to the method of Strickland & Parson (1960).

Affinities between stations were established using an MDS (non-metric multidimensional scaling) analysis for each sampling occasion. The goodness of the ranking was tested using the stress coefficient of Kruskal (Kruskal & Wish, 1978). The abundance data was transformed by the fourth root ($\sqrt[4]{x}$).

To determine what environmental variables are affecting the composition of the community, we

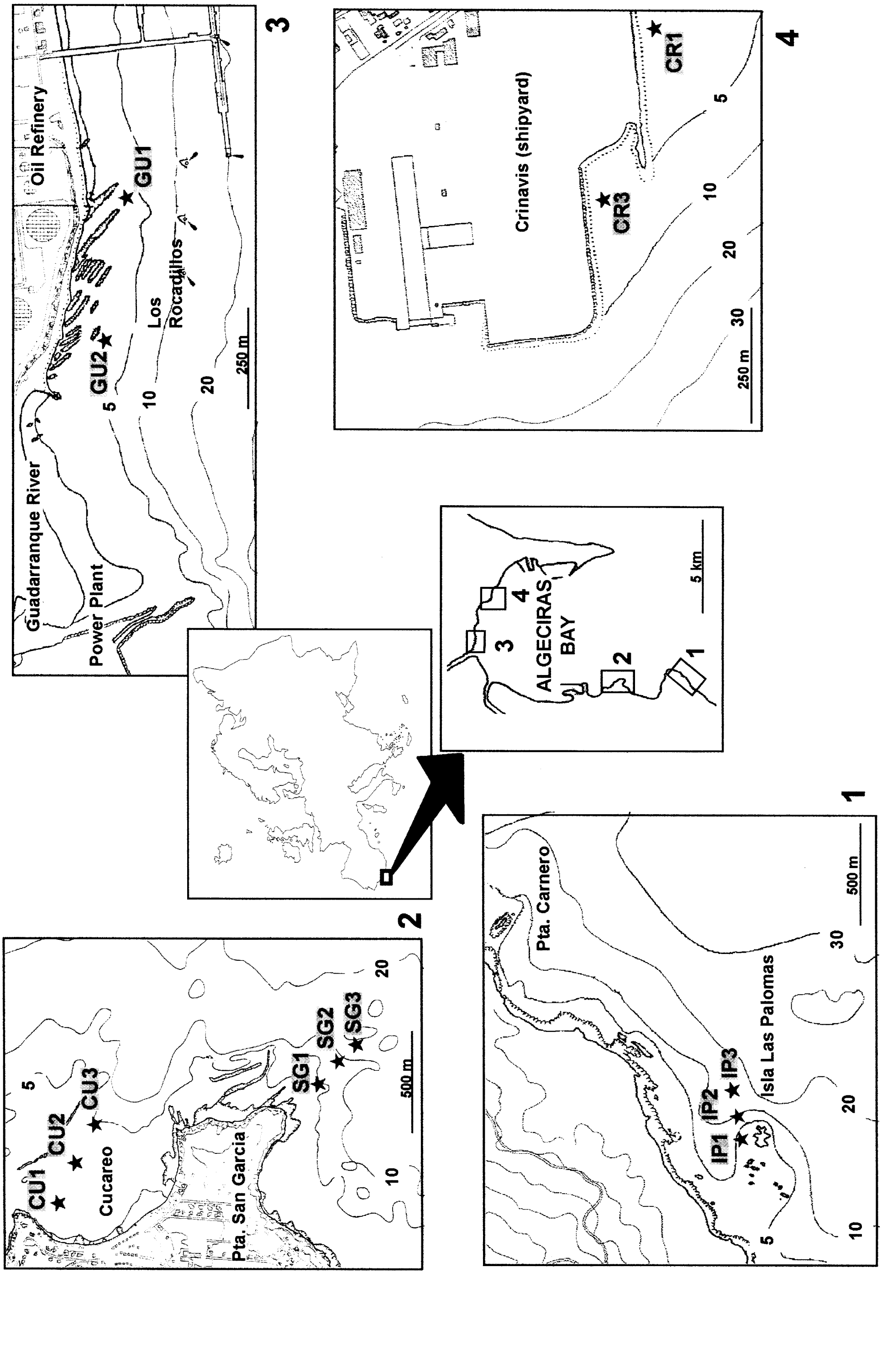

Figure 1. Location of the sampling stations in Algeciras Bay.

applied canonical correspondence analysis (CCA). This is a direct gradient technique, so that the resulting station ranking is related directly to the values of the environmental factors (Ter Braak, 1986, 1990). In order to avoid analytical distortion caused by rare species, these were downweighted. The statistical significance of the analysis was verified using the test of Monte-Carlo for the first axis.

Species responsible for the groupings were determined using the analysis of percentages of similarity or SIMPER (PRIMER package), which calculates the contribution of each species to the dissimilarity between different groups (discriminating species).

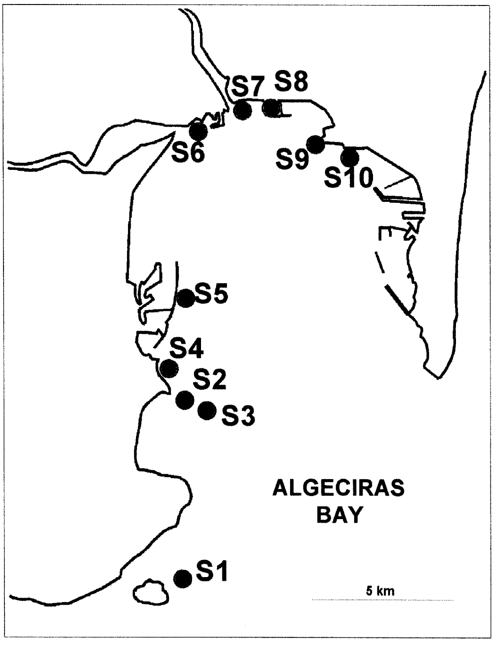

Figure 2. Location of the sampling stations of environmental variables.

Differences in community composition were tested using the ANOSIM non-parametric test of the PRIMER package (Clarke & Green, 1988). This analysis tests the differences from the different abundance of the species at each station.

RESULTS

Environmental variables

The general trend for the different abiotic variables throughout the bay is shown in Table 1 and significant differences are detailed in Table 2. Thus, the most external zones of the bay have greater water movement, with a clearly decreasing trend towards the interior, rising again in the area of Crinavis (S9 and S10) as a result of the bay's tidal current regime. The sedimentation rate is generally higher in the innermost zones, especially those situated in areas influenced by the mouths of the Rivers Palmones (S6) and Guadarranque (S7). In the case of the Cucareo inlet (S4), the sedimentation rate is combined with a great resuspension of substrate due to the shallow depth (5–3 m) and the effect of waves caused by the strong prevailing east winds. The solids in suspension behave similarly (with non-significant differences), tending to increase towards the interior and with a marked effect from the closeness to the rivers (S6 and S7) and urban wastes.

The morphological characteristics of the algae (Figure 3) show a trend to greater interstitial volume (direct measurement of useful vital space, considering both the frond surface and the interfrond spaces) and compactness in the external zone (Isla de Las Palomas, San García, and Cucareo stations) with a gradual ecrease towards the interior of the bay (Guadarranque

Table 1. Average values of the environmental variables in the different stations. Units: rate of sedimentation (kg/m2/month); organic matter of sediments; water movement (V); solids in suspension (mg/l); organic matter in suspension (mg/l).

Stations	Sedimentation rate	Organic content of sediments	Water movement	Solids in suspension	Organic matter in suspension
S1	1.88	14.26	5.80	13.10	3.29
S2	6.18	11.03	5.13	11.31	3.27
S3	8.63	11.78	5.29	12.42	3.40
S4	9.94	11.93	4.51	10.75	3.36
S5	6.00	10.83	4.44	15.61	3.77
S6	59.19	8.08	6.05	15.04	3.20
S7	14.60	10.56	3.22	13.49	3.38
S8	4.13	11.25	5.72	11.46	3.37
S9	2.31	12.97	8.11	9.36	3.07
S10	7.33	11.00	7.46	11.03	3.44

Table 2. Results of the one-way ANOVA for the environmental variables. df: degrees of freedom; MS: squared of the average; F: statistic; *: P < 0,001; **: P < 0,05; ns: not significant. The homogeneous group according to the Tukey test (P < 0,05) are indicated with a continuous line (station keys in Figure 2).

	df	MS	F	Homogeneous groups
Water movement	0	0.307	29,66*	S10 S9 S1 S2 S3 S6 S4 S5 S8 S7
Sedimentation rate	9	80,211	171,97*	S1 S2 S3 S5 S10 S9 S8 S7 S4 S6
Organic matter of sediment	9	23,607	2,54**	S6 S1 S2 S3 S4 S5 S10 S9 S8 S7
Solids in suspension	9	45,185	1,09ns	
Organic matter in suspension	9	0.016	0,08ns	

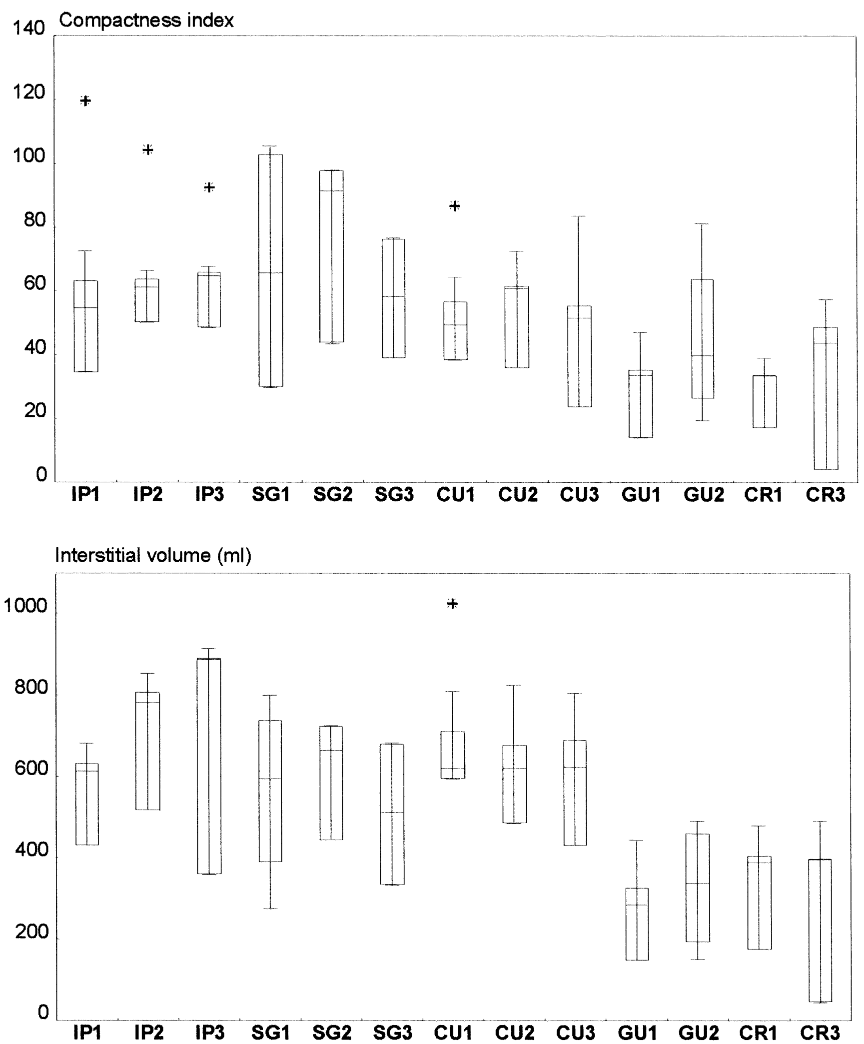

Figure 3. Plots of compactness index and interstitial volume. The thick line corresponds to the median; the rectangles contain 50% of the values, between 1st and 3rd quartile; the thin lines connect the extreme values, unless located at a distance superior to 3 times the height of the rectangle than they are indicated by an asterisk.

and Crinavis). The differences between external and internal stations are greater for interstitial volume.

Faunal analysis

The 13 stations provided a total of 98 taxa, of which 13 were bivalves, 55 prosobranchs gastropods and 30 opisthobranchs. Table 3 shows the overall mean dominance in the study period. Some species were widely distributed throughout the bay, such as the bivalves *Musculus costulatus* and *Parvicardium vroomi*, the prosobranchs *Bittium reticulatum, Alvania scabra, Pusillina radiata* and *Skeneopsis planorbis*, and opisthobranchs *Haminaea exigua, Runcina coronata, Aplysia parvula* and *Odostomia* spp. The dominant species was *Rissoella opalina*, particularly in the outermost stations (Isla de Las Palomas, San García, and Cucareo), where it exceeded 50% of total dominance. At the inner stations (Guadarranque and Crinavis), the percentage of dominance was shared among a higher number of species, such as *Jujubinus ruscurianus, Bittium reticulatum, Rissoa guerinii, Rissoa similis, Alvania montagui* and *Modiolula phaseolina*, together with *Rissoella opalina*. Certain species were exclusive to the outer stations: *Gibbula tingitana, Nodulus contortus, Gibberula jansseni, Pisinna glabrata, Cingula amabilis*, and *Odostomia nivosa*; but most of the best-represented species of the inner sites were also found in the outer sites, although in lesser numbers. Table 4 shows the results for number of species and individuals and for Shannon diversity at each station and in each sampling. In general, there was a predominance of a higher number of individuals inwards from the Guadarranque stations, with the number of species being very similar at all the stations. Diversity showed highest values (above 2) at the inner stations, with minima in the outermost zones of the bay. This is an obvious reflection of the high quantitative dominance of *Rissoella opalina* at the outer stations and the greater sharing at the inner ones, as observed in Table 3.

Multivariate analysis

MDS analysis of the stations according to abundance of the different species in each sampling (Figure 4) separates the stations into two groups, throughout practically the whole sampling period. One comprises the outer stations of the bay (Isla de las Palomas, San García, and Cucareo), and the other the inner ones (Guadarranque and Crinavis). Within the second group, there is a certain dissimilarity between the two areas, with the mouth of the River Guadarranque being distinctive. Similarly, in the outer group, the Isla de Las Palomas stations are also distinct. These are located closer to the Strait, and have a series of exclusive species. The differences are more marked during favourable periods for most of the organisms, such as September ’92 and ’93 and June ’93. In the winter, there is a tendency towards greater uniformity in community composition.

Spatial differences for each sampling were tested using one-way ANOSIM (Table 5). In general, and as in the MDS analysis, the differences between outer and inner stations are very marked. However, within the two groups of stations, especially the outer ones, the situations differ through the sampling period. In September ’92, there was great uniformity in the Cucareo stations, and in those of San García on one hand and Isla de las Palomas on the other, while the differences between them were maintained. Nor were differences observed for the two stations of Guadarranque (GU1 and GU2). However, starting from the samples made in winter (December ’92), there was a greater uniformity in the faunal composition of the various stations, above all in the outer zone.

A canonical correspondence analysis was made to determine whether the measured variables represent an environmental gradient through Algeciras Bay. Figure 5 shows the rankings obtained for stations and total species. The station ranking shows the outer stations to be grouped, and a sharp separation between the two inner areas revealed by the MDS. Table 6 demonstrates an outward rising gradient for compactness index and organic matter of the sedimentation. There is another gradient for the second axis, especially for water movement towards the positive side (with the Crinavis stations at the end) and for the solids and organic matter in suspension towards the negative side (occupied by the Guadarranque stations). These factors are clearly defining the position of the different stations. Sedimentation rate does not seem to have a great direct effect on the communities.

Distribution of a species generally depends on its quantitative and qualitative importance in each zone. The outer groups comprises those that are practically exclusive to the Isla de las Palomas, such as *Cingula amabilis, Vexillum tricolor, Vexillum ebenus, Nodulus contortus, Pisinna glabrata*, and *Eatonina fulgida*, all gen-

Table 3. List of species found and their annual average dominance (%).

	Species	IP1	IP2	IP3	SG1	SG2	SG3	CU1	CU2	CU3	GU1	GU2	CR1	CR3
	BIVALVIA													
1	Indeterm													
2	*Modiolula phaseolina* (Philippi, 1844)													
3	*Musculus costulatus* (Tisso, 1826)													
4	*Anomia ephippium* (L., 1758)													
5	*Limaria loscombii* (Sowerby, 1820)													
6	*Chlamys* sp (juv.)													
7	*Hiatella arctica* (L., 1767)													
8	*Parvicardium vroomi* (Deshayes, 1854)													
9	*Cardita calyculata* (L., 1758)													
10	*Glans aculeata* (Poli, 1795)													
11	*Mysella bidentata* (Montagu, 1803)													
12	*Abra* sp. (juv.)													
13	*Venerupis* sp. (juv.)													
	PROSOBRANCHIA													
14	Juveniles													
15	*Tricolia entomochelia* (Gofas, 1994)													
16	*Tricolia pullus* (L., 1758)													
17	*Tricolia tingitana* Gofas, 1982													
18	*Calliostoma laugieri* (Payraudeau, 1826)													
19	*Clanculus jussieui* (Payraudeau, 1826)													
20	*Dikoleps* sp.													
21	*Gibbula tingitana* Pallary, 1902													
22	*Jujubinus ruscurianus* (Weinkauff, 1868)													
23	*Cerithiopsis tubercularis* (Montagu, 1803)													
24	*Melanella lubrica* (Monterosato, 1890)													
25	*Vitreolina philippii* (Rayneval & Ponzi, 1854)													
26	*Triphora* sp.													
27	*Barleia rubra* (Montagu, 1803)													
28	*Nodulus contortus* (Jeffreys, 1884)													
29	*Chauvetia minima* (Montagu, 1803) (juv.)													
30	*Calyptraea chinensis* (L. 1758)													
31	*Bittium latreillii* (Payraudeau, 1826)													
32	*Bittium reticulatum* (Da Costa, 1778)													

Table 3. (*Continued*)

	Species	IP1	IP2	IP3	SG1	SG2	SG3	CU1	CU2	CU3	GU1	GU2	CR1	CR3
33	*Cerithidium submamillatum* (Rayneval & Ponzi, 1854)													
34	*Cerithium vulgatum* (Bruguière, 1792)													
35	*Vexillum ebenus* (Lamarck, 1811)													
36	*Vexillum tricolor* (Gmelin, 1790)													
37	*Mitrella maldonadoi* Luque, 1984													
38	*Mitrella* sp.													
39	*Eatonina fulgida* (Adams, 1797)													
40	*Fusinus cf. pulchellus* (Philippi, 1844)													
41	*Gibberula cf. caelata* (Monterosato, 1877)													
42	*Gibberula cf. philippii* (Monterosato, 1878)													
43	*Gibberula jansseni* Van Aartsen, Menkhorst & Gittenberger, 1984													
44	*Gibberula* sp.													
45	*Hexaplex trunculus* (L. 1758)													
46	*Ocinebrina aciculata* (Lamarck, 1822)													
47	*Ocinebrina edwarsii* (Payraudeau, 1826)													
48	*Amyclina corniculum* (Olivi, 1792)													
49	*Nassarius cuvierii* (Payraudeau, 1826)													
50	*Nassarius incrassatus* (Ström, 1768)													
51	*Rissoella diaphana* (Alder, 1848)													
52	*Rissoella opalina* (Jeffreys, 1848)			58		50.5	59.2	67.4	74.4	58.9				
53	*Alvania montagui* (Payraudeau, 1826)													
54	*Alvania parvula* (Jeffreys, 1884)													
55	*Alvania rudis* (Philippi, 1844)													
56	*Alvania scabra* (Philippi, 1844)													
57	*Alvania spinosa* (Monterosato, 1890)													
58	*Cingula amabilis* Locard, 1886													
59	*Cingula cf. bruggeni* Verduin, 1984													
60	*Cingula pulcherrima* (Jeffreys, 1848)													
61	*Pisinna glabrata* (Von Mühlfeld, 1824)													
62	*Pusillina radiata* (Philippi, 1836)													
63	*Rissoa cf. parva* (da Costa, 1778)													
64	*Rissoa guerinii* Récluz, 1848													
65	*Rissoa lilacina* (Récluz, 1843)													

66 *Rissoa similis* (Scacchi, 1836)										2–5	5–15	0–2	2–5
67 *Skeneopsis planorbis* (O. Fabricius, 1780)	0–2	0–2	0–2	0–2	0–2		0–2	0–2	0–2	5–15	2–5	0–2	0–2
68 *Mitrolumna wilheminae* Van Aartsen, Menkhorst & Gittenberger, 1984		0–2	0–2			0–2	0–2						
OPISTHOBRANCHIA													
69 *Haminea exigua* Schaefer, 1992	0–2	0–2	0–2	2–5	2–5	0–2	0–2	0–2	0–2	0–2	0–2	0–2	0–2
70 *Philine* sp							0–2						0–2
71 *Retusa truncatella* Locard, 1886	0–2	0–2	0–2			0–2	0–2	0–2	0–2	0–2	0–2	0–2	0–2
72 *Runcina cf. bahiensis* Cervera, García-Gómez & García, 1991	0–2												
73 *Runcina coronata* (Quatrefages, 1844)	0–2	2–5	0–2	5–15	0–2	0–2	2–5	2–5	2–5	2–5	2–5	0–2	0–2
74 *Runcina ferruginea* Kress, 1977	0–2	0–2	0–2	0–2	0–2	0–2	0–2	0–2	0–2			0–2	0–2
75 *Aplysia parvula* Guilding in Moerch, 1863	2–5	2–5	2–5	5–15	5–15	2–5	0–2	0–2	2–5	0–2	0–2	2–5	0–2
76 *Aplysia punctata* (Cuvier, 1803)						0–2		0–2					
77 Doridacea sp											0–2		
78 *Doto* sp										0–2		0–2	
79 *Eubranchus* sp		0–2	0–2	0–2		0–2		0–2	0–2	0–2	0–2	0–2	0–2
80 *Facelina* sp													0–2
81 *Favorinus branchialis* (Rathke, 1806)	0–2	0–2	0–2	0–2		0–2					0–2	0–2	0–2
82 *Coryphella pedata* (Montagu, 1804)										0–2			
83 *Goniodoris castanea* Alder & Hancock, 1845										0–2		0–2	
84 *Limacia clavigera* (Müller, 1776)			0–2										
85 *Polycera* sp			0–2	0–2	0–2	0–2			0–2	0–2	0–2	0–2	0–2
86 *Cuthona* sp1				0–2	0–2					0–2	0–2		
87 *Cuthona* sp2	0–2											0–2	0–2
88 *Cuthona* sp3				0–2								0–2	
89 *Chrysallida* sp.	0–2	0–2	0–2	0–2	0–2	0–2	0–2	0–2	0–2	0–2	2–5	2–5	2–5
90 *Odostomia erjaveciana* Brusina, 1869	0–2		0–2	0–2			0–2			0–2	0–2	0–2	
91 *Odostomia kromi* Van Aartsen, Menkhorst & Gittenberger, 1984	0–2	0–2	0–2	0–2	0–2	2–5	0–2	0–2	0–2	0–2		0–2	
92 *Odostomia lukisii* Jeffreys, 1859			0–2		0–2	0–2	0–2	0–2	0–2	0–2	0–2	0–2	0–2
93 *Odostomia nivosa* (Montagu, 1803)	0–2	0–2	0–2	0–2	0–2		0–2	0–2					
94 *Odostomia striolata* Forbes & Hanley, 1850	0–2	2–5	2–5	2–5	5–15	5–15	0–2	0–2	0–2	0–2	0–2	2–5	0–2
95 *Turbonilla innovata* Monterosato, 1884							0–2	0–2	0–2				
96 *Elysia viridis* Montagu, 1810	0–2	0–2		0–2	0–2		0–2	0–2	0–2	0–2	0–2	0–2	
97 *Hermaea* sp							0–2	0–2					
98 *Placida verticillata* Ortea, 1981							0–2	0–2			0–2	0–2	

☐ 0–2; ☐ 2–5; ☐ 5–15; ☐ 15–25; ■ 25–50; ☐ >50

Table 4. Changes innumber of species and abundance (nº indiv/100 g dry weight of alga) and diversity (H') during the sampling period.

	SEP92			DEC92			MAR93			JUN93			SEP93		
	Nº sp	Nº ind	H'	Nº sp	Nº ind	H'	Nº sp	Nº ind	H'	Nº sp	Nº ind	H'	Nº sp	Nº ind	H'
IP1	29	6340	1.50	10	1500	1.48	15	4370	1.64	29	5970	1.92	22	2780	1.43
IP2	32	7850	1.86	19	5940	0.96	22	2130	2.33	28	2770	1.67	29	4260	1.38
IP3	33	9180	1.76	23	2960	1.69	21	1140	2.47	35	7890	1.34	24	5210	0.93
SG1	35	4600	1.71	16	1040	2.36	16	2040	2.32				23	1789	2.61
SG2	33	6680	1.58	23	2170	2.59	16	1540	2.13						
SG3	40	5550	1.49	17	1270	2.42									
CU1	27	5350	1.52	26	2030	2.05	19	1800	1.35	33	7060	1.67	35	4630	1.14
CU2	23	4650	1.27	15	1150	1.94	21	5140	0.92	28	5150	1.40	26	4570	1.18
CU3	21	2810	1.48	20	1080	2.37	27	3010	1.99	33	6230	1.76	29	4260	1.24
GU1	34	9030	2.41	27	18900	1.95	30	7520	2.39	35	22400	2.32	29	4910	2.45
GU2	34	12600	2.67	28	4410	2.49	23	2640	2.51	34	7310	1.95			
CR1	40	8530	2.88	27	1460	2.70	24	1940	2.29	33	7040	2.45	25	997	2.61
CR3	30	7000	2.45	12	2870	1.82	19	5900	1.96	31	8740	2.28	30	3850	2.88

erally scarce. More centrally are those species typical of the outer area, such as *Gibbula tingitana, Cingula bruggeni, Mitrella maldonadoi, Tricolia entomochelia, Aplysia parvula*, and *Rissoella opalina* (although distributed throughout the bay, its populations are at their largest in this part). At the opposite extreme, in the zone of influence of Crinavis, are species such as *Alvania montagui, Tricolia pullus, Fusinus cf. pulchellus*, and *Jujubinus ruscurianus*, and in that of Guadarranque, very abundant species such as *Cingula pulcherrima, Rissoa similis*, and *Alvania rudis*, and the bivalves *Modiolula phaseolina* and *Cardita calyculata* among others, very much affected by the amount of organic matter in suspension, which in principle should favour filtering organisms. Nevertheless, there is a large group of species in the zone where supposedly the measured parameters reach mean values (although with a certain trend towards more internal stations where we find a greater quantitative growth of the populations). These species seem to have lower requirements and have wider distributions, such as *Bittium reticulatum, Rissoa guerinii, Alvania scabra, Odostomia lukisii, Pusillina radiata, Skeneopsis planorbis, Musculus costulatus, Hiatella arctica*, and *Anomia ephippium*, among others.

The Monte-Carlo test confirmed that the ranking obtained was significant for the first axis ($F = 3.00$, $P = 0.01$). The percentage of similarity analysis (SIMPER) can be used to determine the discriminant species of a group. The technique reveals the extent and consistency of the contribution of a species to the total dissimilarity. Table 7 lists the species contributing most to the differences between inner and outer stations of the bay. Of these, *Tricolia pullus, Rissoa similis* and *Rissoa guerinii* stand out—all being more abundant in the inner zones. Apart from *Rissoella opalina*, all the species are more abundant in the areas of Guadarranque and Crinavis.

DISCUSSION

Two groups of factors as responsible for the composition of the epifauna associated to macroalgae: those related with the physical medium, and those related with the physical characteristics of the plant (Hagerman, 1966). According to Moore (1972) the main factors are water movement, sedimentation rate, turbidity (measured as solids in suspension), levels of nutrients, and plant morphology. Thus the structural complexity of a habitat affects the abundance,

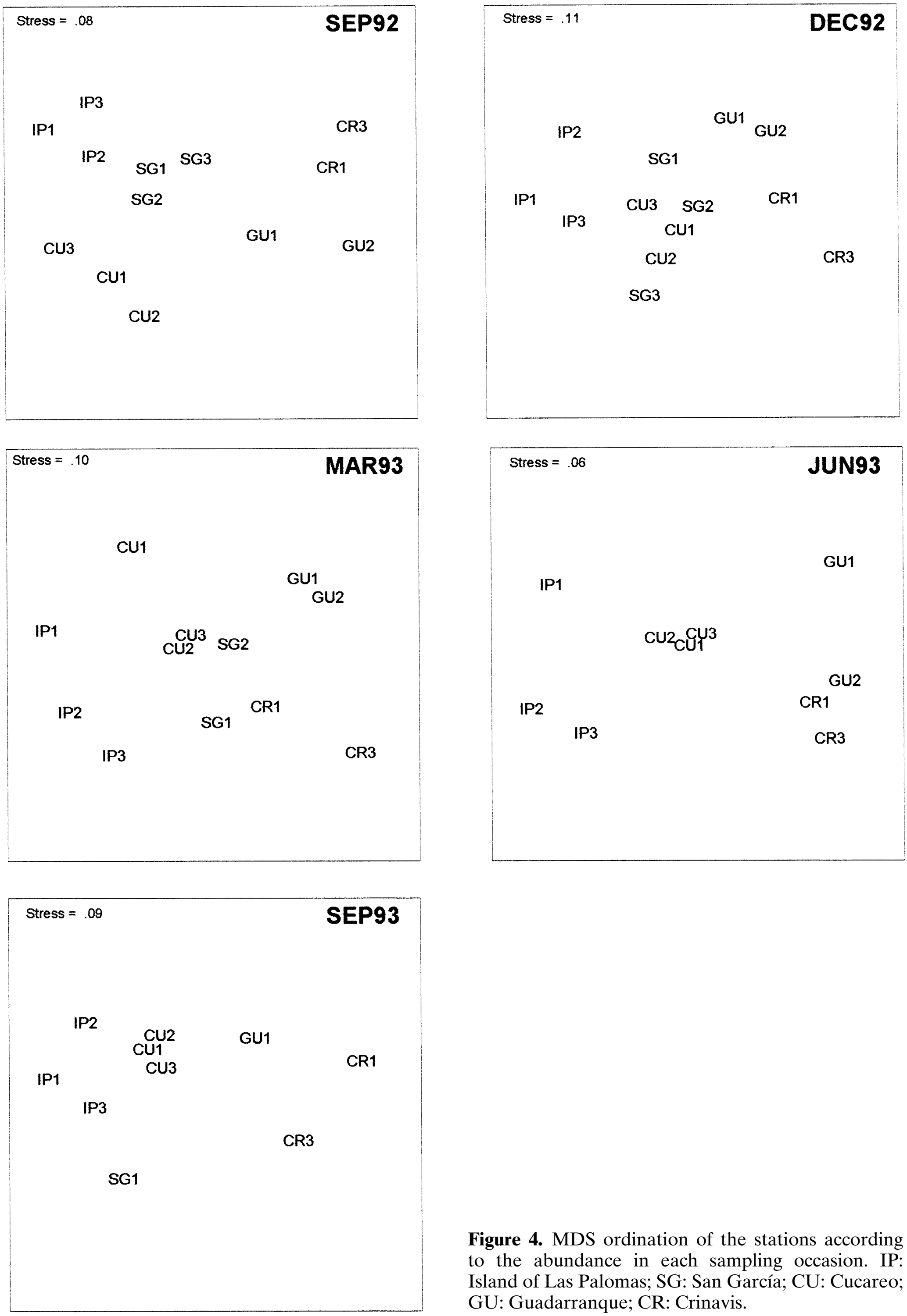

Figure 4. MDS ordination of the stations according to the abundance in each sampling occasion. IP: Island of Las Palomas; SG: San García; CU: Cucareo; GU: Guadarranque; CR: Crinavis.

Table 5. Values of the statistic R (ANOSIM) between the different stations during the period of study. $P < 0.05$; *: not significant. I: Island of Las Palomas; S: San García; C: Cucareo; G: Guadarranque; CR: Crinavis.

Station pairs	SEP92	DEC92	MAR93	JUN93	SEP93	Station pairs	SEP92	DEC92	MAR93	JUN93	SEP93
(I1–I2)	0.33*	0.23*	0.42	0.47	0.51	(S1–G2)	0.98	0.86	0.74*		
(I1–I3)	0.20*	0.18*	0.54	0.73	0.55	(S1–CR1)	1.00	0.93	0.21*		0.98
(I1–S1)	0.85	0.79	0.68		0.61	(S1–CR3)	1.00	0.99	0.70		0.96
(I1–S2)	0.62*	0.80	0.60			(S2–S3)	0.53*	−0.05*			
(I1–S3)	0.90	0.93				(S2–C1)	0.52	0.32*	0.52		
(I1–C1)	0.82	0.99	0.82	1.00	1.00	(S2–C2)	0.47	0.26*	0.28*		
(I1–C2)	0.53	0.77	0.90	0.74	0.94	(S2–C3)	0.65	0.47	0.30*		
(I1–C3)	0.65	0.87	0.94	0.97	0.63	(S2–G1)	0.77	0.70	0.58		
(I1–G1)	0.86	1.00	1.00	1.00	1.00	(S2–G2)	0.99	0.78	0.48*		
(I1–G2)	0.99	1.00	0.97	0.98		(S2–CR1)	0.99	0.70	0.11*		
(I1–CR1)	0.96	1.00	0.99	1.00	1.00	(S2–CR3)	1.00	0.76	0.77		
(I1–CR3)	0.99	1.00	0.99	0.90*	1.00	(S4–C1)	0.93	0.83			
(I2–I3)	0.56	0.06*	0.22*	0.23*	0.24*	(S3–C2)	0.64	0.27*			
(I2–S1)	0.91	0.91	0.46		0.52	(S3–C3)	0.96	0.68			
(I2–S2)	0.81	0.79	0.48			(S3–G1)	0.82	0.99			
(I2–S3)	1.00	0.93				(S3–G2)	1.00	1.00			
(I2–C1)	0.80	0.97	0.74	0.66	0.35*	(S3–CR1)	0.96	1.00			
(I2–C2)	0.67	0.73	0.81	0.52	0.58	(S3–CR3)	0.98	0.94			
(I2–C3)	0.69	0.91	0.67	0.71	0.20*	(C1–C2)	0.02*	0.31*	0.54	0.00*	0.25*
(I2–G1)	0.75	1.00	0.90	0.94	0.05	(C1–C3)	0.16*	0.08*	0.86	−0.22*	0.24*
(I2–G2)	0.96	1.00	0.92	0.90		(C1–G1)	0.74	0.95	1.00	1.00	1.00
(I2–CR1)	1.00	1.00	0.81	0.94	1.00	(C1–G2)	1.00	1.00	1.00	0.98	
(I2–CR3)	1.00	1.00	1.00	0.87*	1.00	(C1–CR1)	1.00	1.00	0.65	0.87	1.00
(I3–S1)	0.89	0.79	0.30*		0.50	(C1–CR3)	0.99	1.00	0.97	0.86*	1.00
(I3–S2)	0.66	0.64	0.34*			(C2–C3)	0.21*	0.55	0.58	0.00*	0.27*
(I3–S2)	0.86	0.94				(C2–G1)	0.56	0.92	0.84	0.91	0.96
(I3–C1)	0.71	0.93	0.60	0.75	0.61	(C2–G2)	0.78*	0.96	0.90	0.91	
(I3–C2)	0.60	0.80	0.61	0.35	0.59	(C2–CR1)	0.82	0.99	0.46	0.90	1.00
(I3–C3)	0.80	0.80	0.56	0.77	0.27*	(C2–CR3)	0.84	1.00	0.94	0.92*	1.00
(I3–G1)	0.81	1.00	0.83	1.00	0.99	(C3–G1)	0.75	0.96	0.97	1.00	0.79
(I3–G2)	0.97	1.00	0.83	0.98		(C3–G2)	0.98	0.99	0.98	0.96	
(I3–CR1)	1.00	1.00	0.54	0.99	0.99	(C3–CR1)	1.00	0.99	0.84	0.85	0.99
(I3–CR3)	1.00	1.00	0.96	0.90*	0.90	(C3–CR3)	1.00	1.00	1.00	0.86*	0.94
(S1–S2)	0.25*	0.19*	−0.33*			(G1–G2)	0.13*	0.55	0.49	0.89	
(S1–S3)	0.97	0.33*				(G1–CR1)	0.59	0.99	0.79	0.76	1.00
(S1–C1)	0.56	0.59	0.47*		0.66	(G1–CR3)	0.67	1.00	1.00	0.86*	1.00
(S1–C2)	0.51	0.47	0.44		0.63	(G2–CR1)	0.90	0.90	0.81	0.52*	
(S1–C3)	0.61	0.53	0.36		0.52	(G2–CR3)	0.95	1.00	0.97	0.35*	
(S1–G1)	0.75	0.83	0.72		0.81	(CR1–CR3)	0.67	0.65	0.71	0.17*	0.96

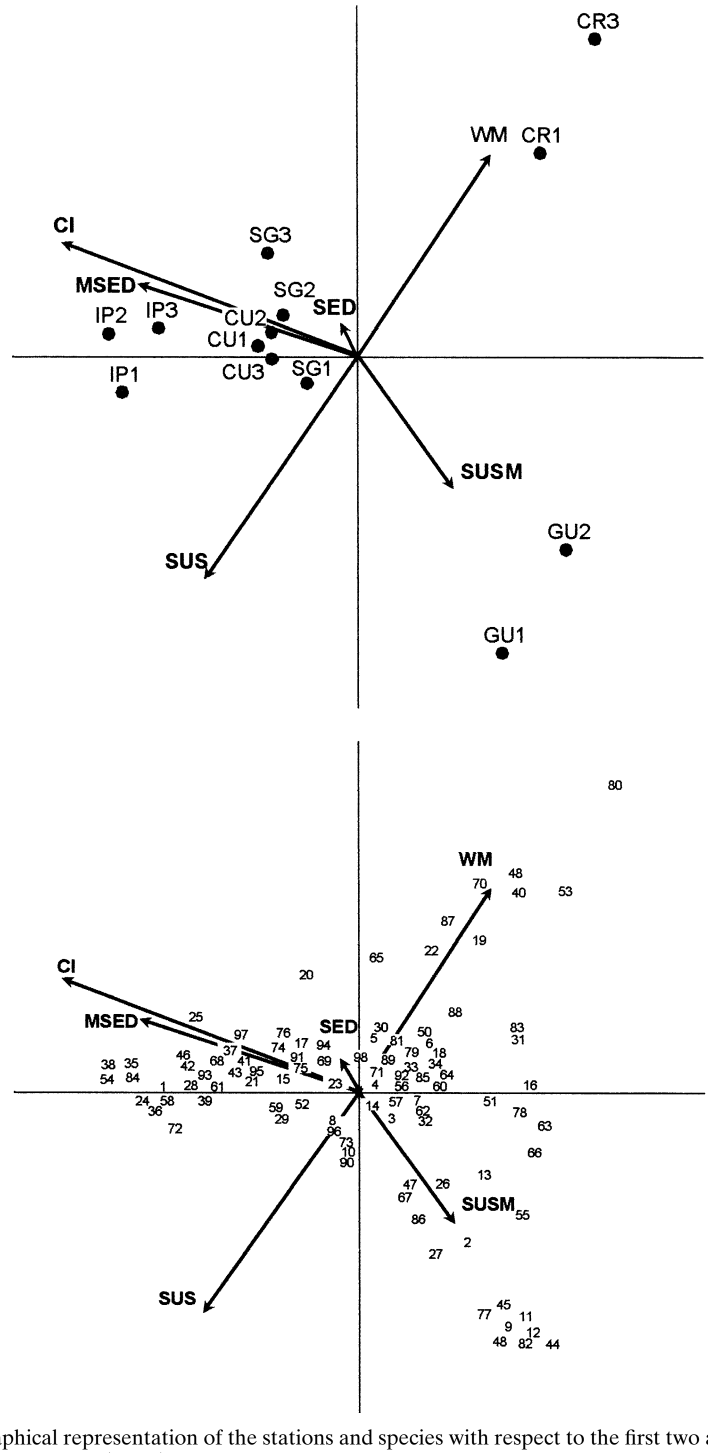

Figure 5. Graphical representation of the stations and species with respect to the first two axes of the canonical correspondence analysis (CCA). The stations and/or species are shown by points and the environmental factors by arrows. WM: water movement; SUS: solid in suspension; SUSM: organic matter in suspension; SED: sedimentation rate: MSED: organic matter of the sediments; CI: compactness. (Species key in Table 3).

Table 6. Results of the canonical correspondence analysis for the stations.

	Intraset values		
	AXIS1	AXIS2	Inflation
Sedimentation rate	−0.045	0.088	1.7368
Organic content of sediment	−0.637	0.205	2.1428
Solids in suspension	−0.451	−0.634	1.8051
Organic content in suspension	0.279	−0.374	1.8146
Water movement	0.387	0.582	1.4863
Compactness	−0.855	0.321	2.3687

	Axis1	Axis2
species-environment correl.	0.863	0.980
cumulative % variance of species data	33.4	49.1
of species-environment relation	42.9	63.2

Table 7. Average abundance of the most relevant species of the stations located in the internal (B) and external areas (A). Species are listed in decreasing order according to their contribution to the average of the disimilarity (Av. Dis.) between the two groups until 45% of the accumulated total disimilarity (Cum. Dis%). The total average disimilarity between the stations is 43.9%.

SPECIES	Abund. B	Abund. A	Av.Dis.	Ratio	Dis.%	Cum.Dis.%
Rissoa similis	293.11	0.00	1.69	4.97	3.85	3.85
Eatonina fulgida	1.42	494.90	1.59	2.39	3.62	7.47
Alvania montagui	329.82	0.00	1.53	2.05	3.48	10.95
Bittium reticulatum	1363.88	95.41	1.25	2.58	2.84	13.79
Rissoa guerinii	399.58	20.32	1.02	4.45	2.33	16.13
Rissoella diaphana	88.36	2.78	1.00	2.75	2.29	18.42
Modiolula phaseolina	329.81	3.73	1.00	1.36	2.29	20.70
Rissoella opalina	1105.17	2074.82	0.96	2.28	2.20	22.90
Jujubinus ruscurianus	327.47	27.24	0.96	1.58	2.18	25.08
Cingula pulcherrima	218.21	21.46	0.92	1.63	2.09	27.17
Venerupis sp	52.29	0.92	0.87	2.27	1.98	29.15
Skeneopsis planorbis	364.59	22.39	0.76	1.19	1.73	30.88
Pusillina radiata	187.45	18.95	0.73	2.78	1.66	32.55
Gibbula tingitana	0.00	25.35	0.73	1.57	1.65	34.20
Cingula amabilis	0.00	82.38	0.72	1.02	1.64	35.84
Barleeia rubra	223.97	4.37	0.70	1.00	1.59	37.44
Nodulus contortus	0.00	18.71	0.68	1.85	1.55	38.98
Cerithidium submamillatum	38.01	6.36	0.66	1.61	1.52	40.50
Clanculus jussieui	33.30	1.70	0.64	1.41	1.47	41.97
Tricolia pullus	5.19	0.00	0.63	5.80	1.43	43.40
Pisinna glabrata	0.00	15.19	0.62	1.53	1.40	44.81

diversity, and distribution of its associated fauna (Heck & Wetstone, 1977; Crowder & Cooper, 1982; Coull & Wells, 1983; Edgar, 1983; Stoner & Lewis, 1985; Dean & Connell, 1987; Russo, 1989; Brown, 1991).

In Algeciras Bay, we have detected a series of environmental gradients based above all on water movement, solids in suspension, and the structural complexity of the plant. In the outer zone, prevailing conditions were high water movement, low sedimentation rate, and high percentage of organic matter in the sedimentation, although slight differences were detected between the three areas depending on their physical and geographical characteristics. Thus, Isla de las Palomas and San García are two great natural rocky sites exposed to the tidal currents of the Strait of Gibraltar and far from the population and industrial nuclei, while Cucareo is an area more sheltered from the tidal currents and is affected by the neighbouring Saladillo inlet, one of the most heavily urban-polluted points of the whole Bay (Estacio *et al*, 1997). In the inner zones, solids in suspension predominate, while water movement differs (low in Guadarranque and among the highest in Crinavis, a zone where two branches of the tidal ebb currents of the Strait of Gibraltar converge (García, 1986)). This is seen in the composition of the mollusc communities at the different points studied, and demonstrated by the MDS and CCA analyses, with a marked separation between the outer areas (Isla de Las Palomas, San García, and Cucareo) and the inner ones (Guadarranque and Crinavis).

Although Ros (1985) considered that food presence, type, and availability have the greatest effect on the distribution and relative abundance of the different mollusc species, above all for those inhabiting hard bottoms, the most important factor in their distribution is water movement, together with the relation with depth (Robertson & Mann, 1982; Idato *et al*, 1983; Russo *et al*, 1984a and b; Russo *et al*, 1991). In fact, canonical correspondence analysis (CCA) showed water movement and solids in suspension (which are perhaps most closely related with food availability and type) to be two of the most-determinant factors. The trophic requirements of the species discriminating the two groups of stations (mainly the inner ones) are detritivorous, as in the case of *Bittium reticulatum, Rissoa similis, Rissoa guerinii*, and *Barleeia rubra*. Moreover, all these are located preferentially on algae with a lower compactness index, that is, with smaller interfrond spaces. Sediment remains on the alga, presumably because the hydrodynamic forces are not strong enough to 'clean' the substrate in this area of Algeciras Bay, especially in Guadarranque, where the high sedimentation from the river almost completely covers the algae, restricting their growth. In Crinavis, strong pressure from large populations of sea urchins restricts the size and distribution of the algae. This area also showed a marked epiphytism on the part of the alga *Asparagopsis armata* Harvey (particularly during spring and early summer), causing loss of ramification in the specimens of *H. scoparia. A. armata* is a great problem at some Mediterranean sites because of its overpowering competition for the substrate with other macroalgae and phanerogams (Verlaque, 1994).

The same CCA analysis shows how these environmental conditions affect the location of most of the mollusc species. Numerous studies have demonstrated the positive correlation between the sediment-retentive capacity of a particular substrate and the population density of certain species of prosobranchs, especially the detritivores (Wigham, 1975; Myers & Southgate, 1980; Southgate, 1982a and b; Boronat *e al*, 1985). At the same time, according to Robertson & Mann (1982), the amount of space on the plant controls the number of individuals, so that the partial loss of frondage of *Halopteris scoparia* during the winter months results in reduced mollusc populations, either by reduction of the microhabitat (Schneider & Mann, 1991) or by a decrease in the available retained food (sediment or epiphyte flora) (Borja, 1986a & b). However, the analyses made have not shown a direct effect of sedimentation rate on the communities, although the percentage of sedimentary organic matter and, secondarily, the solids in suspension could be considered a direct consequence of the sedimentation rate. In fact, one of the most important aspects of this parameter regarding its possible effect on the fauna is its quality, above all the granulometric composition and percentage of organic matter (Sánchez-Moyano, 1996).

Another important point is that in the outer zone, the species most characteristic or most abundant are usually small in size (of the order of a few mm), such as *Rissoella opalina, Eatonina fulgida* and *Cingula amabilis*, whereas many of those of the inner zone are notably larger, as are *Bittium reticulatum, Alvania montagui* and *Tricolia pullus*. Strong hydrodynamic stress, as found in the outer zone of Algeciras Bay, should favour certain sizes, depending on plant morphology. The algae collected in this zone are large and have large interfrond spaces, so that larger organisms will be more exposed to the adverse conditions of the medium, while small individuals will find ready shelter. The inner zone has a lower incidence of currents, and other factors, such as food availability, play a role in the final community composition.

Conditions more negative for the growth of many species in other invertebrate groups, such as sponges and ascidians, have been detected in the inner areas, resulting from the presence of the two rivers that discharge into the bay, the closeness to urban and industrial effluents, and a lesser regimen of currents (Carballo *et al*, 1994; Carballo *et al*, 1996; Naranjo *et al*, 1996). In other epiphytic animal groups on *Halopteris scoparia*, such as crustaceans and—to a lesser extent—polychaetes, more-restrictive conditions for their growth have been detected towards the interior of the bay, with a high number of species found exclusively in the outer areas, although most of the inner species are also present in the exterior (Sánchez-Moyano, 1996; Sánchez-Moyano & García-Gómez, 1998). The molluscs, however, achieve their greatest population growth in this zone, both in number and in diversity, with species exclusive to both exterior (*Cingula amabilis, Pisinna glabrata, Nodulus contortus*, among others) and interior (*Alvania montagui, Alvania rudis*, and *Rissoa similis*). The latter is the most discriminatory species of the two great zones of the bay. The different environmental conditions governing each zone of Algeciras Bay are the decisive discriminators in the final composition of the community, with water movement, the morphological characteristics of the substrate, and (above all) food availability having the greatest effect on the malacofauna associated to *Halopteris scoparia*.

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