Cah. Biol. Mar. (2003) 44 : 237-248

Temporal dynamics of molluscan assemblages from soft and bioclastic bottoms in the Strait of Gibraltar

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Abstract: The temporal dynamics of molluscan assemblages of bioclastic gravels and sand bottoms have been studied monthly from October 1993 to September 1995 at four sampling stations in the Bay of Barbate, SW Spain (at the Atlantic entrance of the Strait of Gibraltar), between 18 m and 29 m depth. Species richness per month ranged between 20 and 40, comparable with or greater than those obtained in other studies from soft bottom assemblages of molluscs in European coasts. The strong settlement of the bivalve *Chamelea striatula* during the first studied year, favoured by the effects of dredging in the harbour, decreased the values of diversity of Shannon-Wiener and evenness indices. The values of diversity (Shannon-Wiener) ranged between 2-3 bits for the entire community. According to the ANOVA tests, the ecological indices did not show significant seasonal trend, with and without taking into account the abundance of *C. striatula*. In the same way, the MDS grouped samples without clear seasonal trends. Nevertheless, ANOSIM analyses indicated for both assemblages: (1) significant intra-annual variation between colder (autumn-winter) and warmer (spring-summer) periods for both sampled years and (2) significant inter-annual differences. According to the ANOVA and ANOSIM results, the works in the harbour influenced significantly both assemblages (with and without the data of *C. striatula*). Some species, mainly gastropods with direct development, showed seasonal and cyclical patterns. The absence of seasonality and annual cycles could be explained by (1) the absence of strong seasonal characteristics of the bottom (e.g. seagrass, temperature); (2) the possible influence of strong bottom currents, and (3) anthropogenic impact in the area.

Résumé : *Dynamique temporelle des taxocénoses de mollusques des fonds meubles et bioclastiques dans le Détroit de Gibraltar*. Les taxocénoses de Mollusques de gravelles bioclastiques et de fonds sableux ont été étudiées mensuellement d'octobre 1993 à septembre 1995 sur quatre points d'échantillonnage dans la baie de Barbate (au Sud-Ouest de l'Espagne, à l'entrée atlantique du Détroit de Gibraltar), entre 18 m et 29 m de profondeur. La richesse spécifique pour un mois donné varie entre 20 et 40, comparable ou supérieure à celle obtenue dans d'autres études de mollusques de fonds meubles des côtes européennes. Le recrutement massif du bivalve *Chamelea striatula* pendant la première année d'étude, favorisé par le dragage du port, a fait baisser les valeurs des indices de diversité de Shannon-Wiener et d'équitabilité. Les valeurs de la diversité varient entre 2 et 3 pour l'ensemble de la taxocénose. Les tests d'ANOVA ont montré l'absence de cycles saisonniers dans les taxocénoses de mollusques, que l'on considère ou non les données sur *C. striatula*. De même, dans la plupart des cas, le positionnement multidimensionnel regroupait les échantillons sans faire apparaître une tendance saisonnière. Cependant les analyses d'ANOSIM indiquent pour les deux taxocénoses (1) des changements significatifs intra-annuels entre périodes plus froides (automne-hiver) et plus chaudes (printemps-été) pour les deux années échantillonnées et (2) des

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Reçu le 16 juillet 2002 ; accepté après révision le 9 avril 2003.
Received 16 July 2002; accepted in revised form 9 April 2003.

changements significatifs inter-annuels. Les resultats des tests ANOVA et des analyses ANOSIM indiquent que les travaux dans le port ont eu une influence significative sur les deux taxocénoses (avec et sans les données sur *C. striatula*). Malgré tout, certaines espèces, principalement les gastéropodes à développement direct, montrent des tendances saisonnières et cycliques. L'absence de variations saisonnières et de cycles annuels est expliquée (1) par l'absence de variations saisonnières importantes dans l'environnement (par exemple constance du couvert végétal ou de la température), (2) par la présence de forts courants de fond et (3) par des interventions anthropiques dans les environs.

Introduction

The Strait of Gibraltar is an interesting area for the study of marine fauna, including molluscs, due to the confluence of the Atlantic Ocean and Mediterranean Sea. According to Ekman (1967), the Strait of Gibraltar does not represent an important zoogeographical boundary and the Mediterranean is, therefore, not a distinct faunal unit but enters into a greater one, which includes the neighbouring part of the Atlantic. However, Longhurst (1998), according to oceanographic characteristics, considers a Mediterranean Sea, Black Sea Province (MEDI) and an Eastern (Canary) Coastal Province (CNRY) that comprises the southerly coastal flow of the eastern boundary current of the North Atlantic from Portugal to Senegal. Independently of the hypothesis that we consider, the species richness of marine molluscs in this area is possibly the greatest of the European coasts. In addition, an influence of northern Atlantic and western African fauna is also evident in the southern Iberian Peninsula (Salas, 1996; Rueda & Salas, 1998; Rueda & Gofas, 1999), together with the existence of some endemic species of molluscs from the Strait of Gibraltar (Gofas, 1999).

There are few studies concerning the molluscan fauna in the Strait of Gibraltar. Some of them have only reported faunistic lists (García-Gómez, 1983a; van Aartsen et al., 1984), whereas others included information about molluscan communities (García-Gómez, 1983b; Templado et al., 1993). Moreover, studies on temporal dynamics in molluscan assemblages from the southern coasts of the Iberian Peninsula are also scarce (Salas & Hergueta, 1986; Sánchez-Moyano et al., 2000; Sánchez-Moyano et al., 2001).

Recently, Rueda et al. (2001) studied the dynamics and seasonality of a molluscan assemblage from shallow soft bottoms in the Bay of Cádiz, an eutrophic area with an increase of organic matter due to human activities (e. g. sewage, aquaculture). Within the same research programme, concerning the study of benthic communities in the southern Iberian Peninsule, Rueda et al. (2000) examined the molluscan assemblages from soft bottoms (bioclastic gravels and sand) of the Bay of Barbate, close to the Strait of Gibraltar. A total of 195 living species and 115,164 individuals were recorded over two years and data on biogeographical affinities were included. In spite of the large number of species, the molluscan assemblage was dominated by a small number of species. Results of qualitative and quantitative analyses showed two types of species assemblages. The first, and the most extensive assemblage, inhabited a mixed bottom of bioclastic gravels with fine or coarse sand. In spite of the high species richness, only nine species had dominance values higher than 1%. Some of these species were related with an increase of the mud content of the sediment, such as *Chamelea striatula* (Da Costa, 1778) and *Corbula gibba* (Olivi, 1792), whereas others were associated with typical bioclastic bottoms, such as *Digitaria digitaria* (Linné, 1758), *Calyptrea chinensis* (Linné, 1758), *Tapes rhomboides* (Pennant, 1777) and *Bittium submamillatum* (De Rayneval & Ponzi, 1854). This assemblage was found to be similar to the named «coarse sand and fine gravel under the influence of bottom currents» (SGCF), and to «coastal detritic bottoms» (DC). It is characteristic of deeper bottoms in the Mediterranean Sea, but in the Strait of Gibraltar, an area with the presence of strong coastal currents, it occurs shallower (depth: 21-30 meters). The second species assemblage was found at the shallowest sampling station (depth: 18 meters). There were typical species of shallow sand bottoms displaying high frequency values, such as *Acanthocardia tuberculata* (Linné, 1758), *Nassarius reticulatus* (Linné, 1758), *Nassarius mutabilis* (Linné, 1758), *Nassarius elatus* (Gould, 1845) and *Donax venustus* Poli, 1795. This assemblage was similar to that named as «fine well-sorted sand» (SFBC), but as a result of the strong bottom currents included some bioclastic gravels. During the studied period, frequent dredges in the harbour of Barbate influenced the sampling station, which could be considered as a transitional zone between the bioclastic bottom and the shallow fine sand bottom.

The purpose of this paper is to describe the temporal dynamics of two different molluscan assemblages of the Bay of Barbate (Gibraltar area), under the influence of strong bottom currents and under anthropogenic impacts of the frequent dredging and works in the harbour.

Material and methods

Study site

Samples were collected in the Bay of Barbate, Cádiz, (36° 08' 73"N- 5° 56' 71"W), located on the Atlantic side of the Strait of Gibraltar (Figure 1). The Bay of Barbate is mainly influenced by water masses from the Atlantic Ocean (South Portugal), but its location close to northern Africa also exposes it to African water currents (Rey, 1983). In this bay, Atlantic water currents flow towards the Mediterranean Sea, while Mediterranean water currents flow below 200-250 meters deep in the opposite direction (Vives et al., 1975). Tidal currents can change the direction of the dominant currents, producing local gyres. Mediterranean bottom waters are mixed with opposite Atlantic waters in the area of the Strait of Gibraltar and sometimes can reach the surface level (Stommel et al., 1973). Water temperature within this bay varies from 21° C (summer months) to 14° C (winter months).

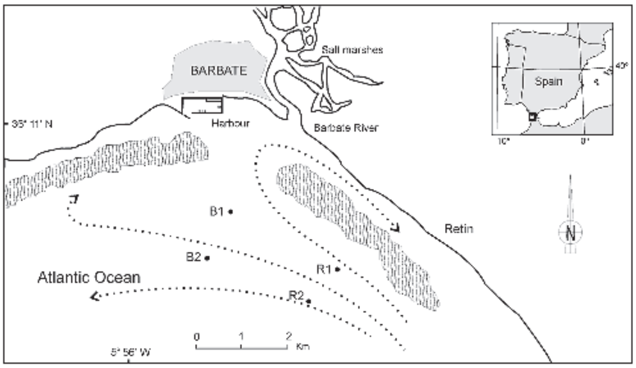


Figure 1. Location of the sampling stations within the Bay of Barbate (southern Spain). The bioclastic assemblage was found in R1, R2 and B2. Rocky bottoms in the bay displayed by lined area, tidal currents represented by dotted line and arrows.

Figure 1. Situation des stations d'échantillonnage dans la Baie de Barbate (Sud de l'Espagne). La taxocénose des bioclastes a été trouvée en R1, R2 et B2. Fonds rocheux dans la baie représentés par des hachures, les courants de marée par des lignes pointillées et des flèches.

Four sampling stations were selected and sampled monthly throughout two years. Sampling stations were positioned on two transects, separated by 2.5 km: one in front of the city of Barbate (B) and the other one further east, in front of Retín (R) (Figure 1). The station B1, the nearest to the harbour and the estuary of the Barbate River, contained high levels of fine sand and a higher percentage of muddy sediment than the other stations. Rocky bottoms are present in the bay as flagstones parallel to the beach (Figure 1), and may play a role in the amplification and channelling of tidal currents in this area.

Over two years of sampling, there were several episodes of dredging (April and May 1994; September to November 1994) and associated works (February 1995 to February 1996) in the harbour of Barbate. These anthropogenic activities have influenced the bottom characteristics of the bay, increasing the percentage of organic matter in the sediment (% OM) (Table 1).

Sampling procedures

Samples were collected monthly from October 1993 to September 1995 using a small, heavy rock dredge, with a rectangular frame of 42 x 22 cm and a double net; the size of the inner mesh was 4.5 mm. In spite of the mesh size, the underestimation of the juvenile abundance was minimized as a result of the usually large amount of the sample collected, which clogged and stretched the double net, reducing the mesh size. The sampled area was ca. 152 m^2 for each sampling station. This research is part of a research program for the study of benthic crustacean and molluscan communities in the littoral of Cádiz (SW Spain). The sampled area considered for this study was established taking into account the data of minimum sample area for the crustaceans. Because of their mobility, this sampling area is greater than the minimum area required for the molluscan taxocoenosis.

Biological samples were sieved onto screens of different mesh sizes (10, 5, 3, and 1mm). Molluscs were separated, determined and quantified in each monthly sample. The granulometric distribution of the sediment was determined by sieving. Wet sieving across a 80 µm sieve separated the mud fraction, and finally the dried sand fraction was sieved in a stacked set of grade sieves. Sediment samples were collected using a bottom grab (width: 20 cm) at the begining (April 1994) and at the end (September 1995) of the harbour works. Determination of % OM in the sediment was obtained by ignition for 2 h at 525° C.

Data analysis

Frequency index (F) (percentage of samples in which the species is present) and Dominance index (D) (percentage of individuals of one particular species from the total) were calculated in order to describe the incidence of the species within the assemblages.

Several ecological indices were calculated monthly, such as: Species richness (S), Diversity of Shannon-Wiener (H') (Krebs, 1989), Evenness (J) (Pielou, 1966) and Heterogeneity (CH) (Margalef, 1956). Comparisons of the monthly ecological indices, according to factors such as sampled years, seasons (autumn, winter, spring and summer), cold (autumn-winter) and warm periods (spring-summer) or before and after the harbour works, were tested using one-way ANOVA, after verifying homogeneity of variances (Barlett test). These statistical procedures were performed using the computer program SYSTAT 9.0.

The relationships amongst monthly samples from each assemblage are graphically represented using non-metric multidimensional scaling (MDS), excluding the data on accidental species (only in one monthly sample). The MDS were calculated quantitatively (species abundance

Table 1. Physical characteristics of the sampling area and list of species with highest dominance and frequency in the assemblages of B1 and bioclasts (BC).

Tableau 1. Caractéristiques physiques des stations d'échantillonage, et listes des espèces ayant les valeurs les plus élevées de dominance et de fréquence pour les taxocénoses de B1 et des fonds bioclastiques (BC).

	B1		**BC**	
Depth (m)	17 – 18		21-29 m	
Sediment	Fine sand with bioclasts		Medium-coarse sand with bioclasts	
Mud (%)	3.5		2.7 – 1.3	
Organic matter (%)	5.9 – 1.2		1.22 – 0.4	
by date	(Ap/94 – S/95)		(Ap/94 – S/95)	
Dominance	*Chamelea striatula*	79.19	*Chamelea striatula*	55.64
	Digitaria digitaria	3.86	*Corbula gibba*	15.41
	Corbula gibba	3.38	*Gouldia minima*	5.05
	Spisula subtruncata	3.07	*Digitaria digitaria*	3.46
	Nuculana pella	1.17	*Calyptraea chinensis*	2.91
	Pandora inaequivalvis	0.98	*Turritella communis*	2.14
	Gouldia minima	0.91	*Tapes rhomboides*	1.19
	Acanthocardia tuberculata	0.85	*Mesalia varia*	1.03
	Nassarius reticulatus	0.84	*Bittium submamillatum*	1.01
	Laevicardium crassum	0.77	*Spisula subtruncata*	0.99
	Nassarius mutabilis	0.74	*Modiolus adriaticus*	0.93
	Nassarius elatus	0.61	*Turritella turbona*	0.87
	Donax venustus	0.38	*Nuculana pella*	0.83
	Bela laevigata	0.36	*Laevicardium crassum*	0.74
	Mesalia varia	0.34	*Gibbula magus*	0.71
	Modiolus adriaticus	0.32	*Pandora inaequivalvis*	0.46
	Calyptraea chinensis	0.31	*Bela laevigata*	0.41
	Callista chione	0.19	*Anomia ephippium*	0.41
	Nassarius pygmaeus	0.18	*Clausinella fasciata*	0.35
	Turritella communis	0.14	*Aporrhais pespelecani*	0.34
Frequency	*Spisula subtruncata*	100	*Chamelea striatula*	100
	Nuculana pella	100	*Corbula gibba*	100
	Acanthocardia tuberculata	100	*Gouldia minima*	100
	Nassarius reticulatus	100	*Digitaria digitaria*	100
	Nassarius mutabilis	100	*Mesalia varia*	100
	Nassarius elatus	100	*Spisula subtruncata*	100
	Digitaria digitaria	91.30	*Nuculana pella*	100
	Mesalia varia	86.96	*Laevicardium crassum*	100
	Corbula gibba	78.26	*Calyptraea chinensis*	95.83
	Laevicardium crassum	78.26	*Turritella communis*	95.83
	Chamelea striatula	73.91	*Bela laevigata*	95.83
	Donax venustus	73.91	*Bolinus brandaris*	95.83
	Pandora inaequivalvis	69.57	*Calliostoma sp.*	95.83
	Callista chione	69.57	*Nassarius pygmaeus*	95.83
	Bela laevigata	65.22	*Ocenebra erinaceus*	95.83

transformed by the fourth root $\sqrt[4]{x}$) and qualitatively (presence/absence) by using the Bray-Curtis similarity coefficient as a meaningful and robust measure (Clarke, 1993). Molluscan assemblages from the different monthly samples were compared, on a time scale, using an analysis of similarities (ANOSIM) which is a non-parametric analogue to a multivariate analysis of variance (MANOVA), without the assumption of multivariate normality. ANOSIM compares ranked similarities between and within groups which were selected according to the considered factors (years, seasons, cold and warm period, harbour works) using a randomization test for significance (Clarke, 1993). One-way ANOSIM analyses use the same matrix of similarities as in the MDS and involved 5000 simulations. Both MDS and One-way ANOSIM were calculated by using the PRIMER package from Plymouth Marine Laboratory, UK.

Results

Temporal variation of the molluscan assemblages

The dynamics of the species richness (S), diversity (H') and evenness (J') of the molluscan assemblages over the studied period are shown in Figures 2 and 3. The dynamics of both assemblages included two sampled years, the first one spanned from October 1993 to September 1994, and the second one from October 1994 to September 1995. Throughout the study period, the trend of the diversity was more similar to the temporal variation in evenness than species richness. In general, the values of diversity and evenness were greater and with less fluctuation during the first year than the second one.

From August 1994, there was a decrease in the values of H' and J', together with a massive recruitment of *C. striatula* (Figures 2a and 3a). As a result of the harbour works, a high amount of mud was deposited in the area, favouring the successful settlement of *Chamelea striatula* in spring 1994. This bivalve was the most dominant species in both assemblages, with abundance values up to 5000 and 13000 individuals per sample (33-86 ind m^{-2}) in some months. Excluding the data of *C. striatula*, the diversity values of these assemblages are greater and more stable in time (Figures 2b and 3b).

In B1, the massive recruitment of *C. striatula* resulted in a strong decrease of H' and J values in August 1994 (Figure 2a). These values remained small during the second year in relation to high dominance of this species. This relationship can be better observed in Figure 2b, in which the H' values for the assemblage without *C. striatula*, are generally greater than those obtained including this species. The values of heterogeneity between samples in B1 (with the data of *C. striatula*) were small (0.22 ± 0.24; Mean value ± standard deviation), except between July and August 1994 (1.13), along with the massive recruitment of *C. striatula* (Figure 2a). After that, the dominance of the latter species remained large during all the second cycle, with low values of heterogeneity. Not considering the individuals of *C. striatula*, the heterogeneity between samples is higher and fluctuates in both cycles (0.37 ± 0.22).

The large abundance of *C. striatula* also influenced the structure and dynamics of the bioclastic assemblage (Figure 3a), and resulted in low diversity values. Without this species, the diversity values were high and very stable in time (Figure 3b). In this case, the fluctuations were related to the large abundance of other mud-living species, such as *C. gibba* or *Turritella communis* Risso, 1826. These species increased their abundance in this assemblage after the dredging of the harbour of Barbate (April-May and October-November 1994). Monthly species richness values were generally higher in the bioclastic assemblage when compared to the one found in B1 (Figures 2a and 3a). In the

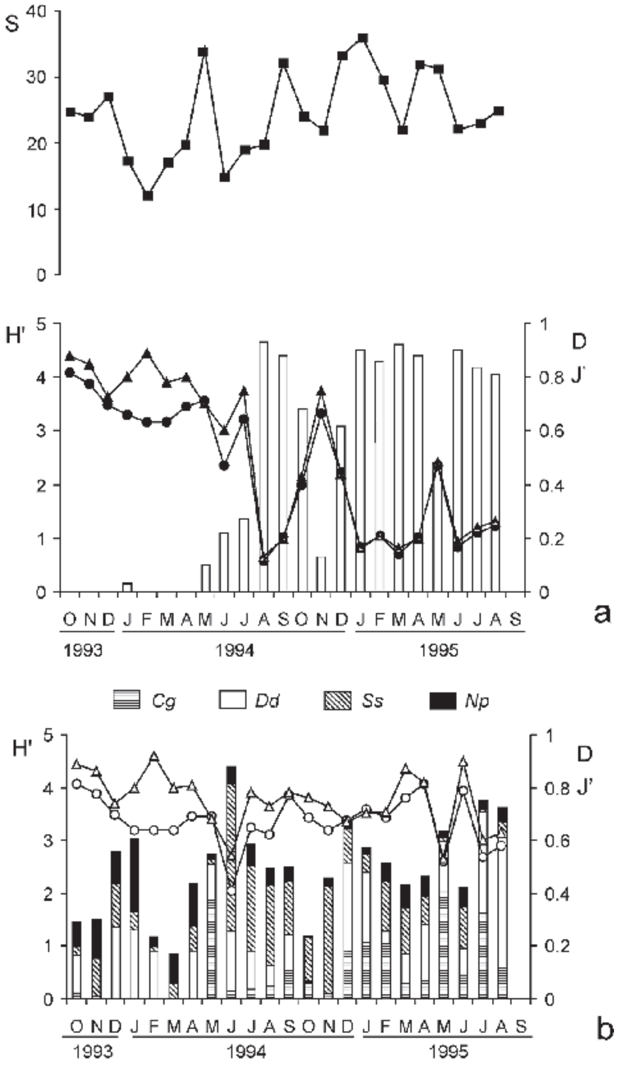


Figure 2. Temporal dynamics of the assemblage of B1. **a.** With the data of *Chamelea striatula*: monthly values of species richness (S) (solid squares), Shannon-Wiener diversity index (H') (solid circles), evenness (J') (solid triangles) and dominance (D) of the bivalve *Chamelea striatula* (bars). **b.** Without the data of *Chamelea striatula*: monthly values of the Shannon-Wiener diversity index (H') (open circles) and evenness (J') (open triangles). Vertical bars represent monthly dominance (without the data of *C. striatula*) of *Corbula gibba* (Cg), *Digitaria digitaria* (Dd), *Spisula subtruncata* (Ss) and *Nuculana pella* (Np).

Figure 2. Dynamique temporelle de l'assemblage de B1. **a.** Avec les données de *Chamelea striatula*: valeurs mensuelles de la richesse spécifique (S) (carrés noirs), indice de diversité de Shannon-Wiener (H') (cercles noirs), équitabilité (J') (triangles noirs) et dominance (D) du bivalve *Chamelea striatula* (barres). **b.** Sans les données de *Chamelea striatula*: valeurs mensuelles de l'indice de diversité de Shannon-Wiener (H') (cercles blancs) de l'équitabilité (J') (triangles blancs). Les barres verticales représentent la dominance mensuelle (sans les données de *C. striatula*) de *Corbula gibba* (Cg), *Digitaria digitaria* (Dd), *Spisula subtruncata* (Ss) et *Nuculana pella* (Np).

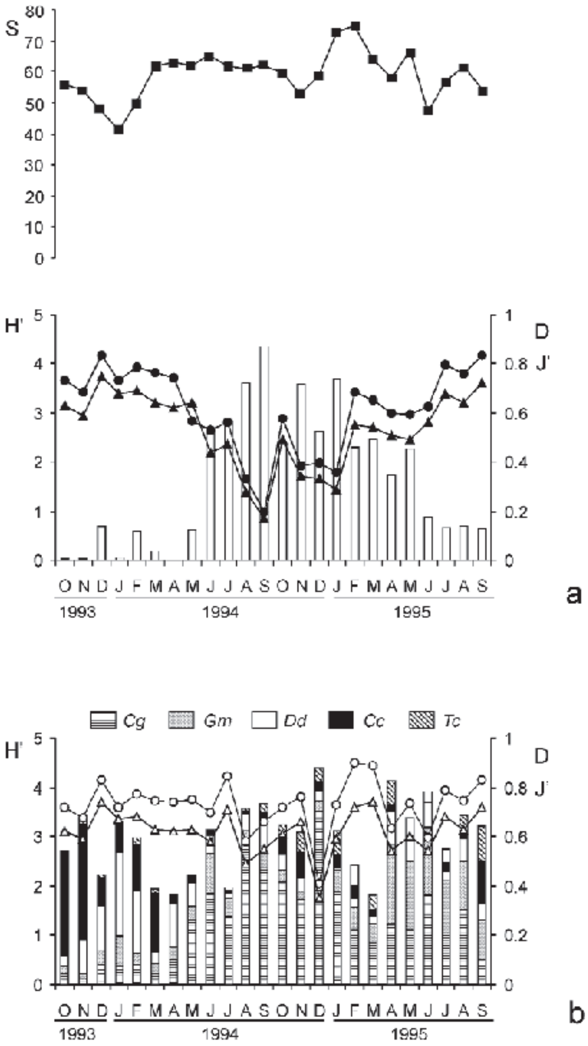


Figure 3. Temporal dynamics of the bioclastic assemblage. **a.** With the data of *Chamelea striatula*: monthly values of the species richness (S) (solid squares), Shannon-Wiener diversity index (H') (solid circles), evenness (J') (solid triangles) and dominance (D) of the bivalve *Chamelea striatula* (bars). **b.** Without the data of *Chamelea striatula*: monthly values of the Shannon-Wiener diversity index (H') (open circles) and evenness (J') (open triangles). Vertical bars represent monthly dominance (without the data of *C. striatula*) of *Corbula gibba* (Cg), *Gouldia minima* (Gm), *Digitaria digitaria* (Dd), *Calyptraea chinensis* (Cc) and *Turritella communis* (Tc).

Figure 3. Dynamique temporelle de l'assemblage des bioclastes. **a.** Avec les données de *Chamelea striatula*: valeurs mensuelles de la richesse spécifique (S) (carrés noirs), indice de diversité de Shannon-Wiener (H') (cercles noirs), équitabilité (J') (triangles noirs) et dominance (D) du bivalve *Chamelea striatula* (barres). **b.** Sans les données de *Chamelea striatula*: valeurs mensuelles de l'indice de diversité de Shannon-Wiener (H') (Cercles blancs) et de l'équitabilité (J') (triangles blancs). Les barres verticales représentent la dominance mensuelle (sans les données de *C. striatula*) de *Corbula gibba* (Cg), *Gouldia minima* (Gm), *Digitaria digitaria* (Dd), *Calyptraea chinensis* (Cc) et *Turritella communis* (Tc).

bioclastic assemblage, the values of the heterogeneity index were small, with (0.17 ± 0.13; Mean value ± standard deviation) and without (0.16 ± 0.12) the individuals of *C. striatula*. The largest heterogeneity occurred between September and October 1994 (0.6), due to the dominance of *C. striatula* in September (with 17144 individuals, ca. 113 individuals m^{-2}). When this species is not included, the largest heterogeneity value appears between November and December 1994 (0.54), as well as a high dominance of *C. gibba* (Figure 3b).

No seasonal trends were found in the temporal dynamics of both assemblages with or without the most dominant species, according to the results of the one-way ANOVA tests (Table 2). In B1, the temporal dynamics of the ecological indices for the first year was significantly different to that of the second year. In the bioclastic assemblage, no significant differences of the ecological indices were found between years, although their pattern was opposite during each year (Figure 3a).

Intra- and inter-annual variation of assemblages

The quantitative MDS ordination of B1 shows that the samples from the second year were grouped without clear seasonal groups (Figure 4). This ordination is related with the persistence of high dominance of *C. striatula*. ANOSIM analysis shows significant differences amongst assemblages (with and without *C. striatula*) from the two different sampled years (Factor year: $p< 0.005$; $p'< 0.05$), but not amongst assemblages from different seasons (autumn, winter, spring, summer) (Factor season: $p> 0.05$; $p'> 0.05$). Intra- and inter-annual differences amongst the assemblages of cold (autumn-winter) and warm (spring-summer) periods were found in both sampled years (with and without *C. striatula* $p < 0.05$ in all cases).

The quantitative MDS ordination for the bioclastic assemblage showed groupings of samples with low (October 1993 - January 1994), medium (February 1994 - May 1994; May 1995 - September 1995) and high abundance of *C. striatula* (June 1994 - April 1995) (Figure 5). Nevertheless, ANOSIM showed that the assemblages of the different years were significantly different (with and without *C. striatula*, Factor year: $p < 0.005$, $p' < 0.005$). The assemblages of cold (autumn-winter) and warm (spring-summer) periods of different years were also significantly different (with and without *C. striatula*, Factor cold season 1 vs. cold season 2: $p < 0.05$, $p' < 0.05$; Factor warm season 1 vs. warm season 2: $p < 0.05$, $p' < 0.05$). Intra-annually, a significant difference was found amongst the assemblages from cold and warm periods in both years (with and without *C. striatula*, Factor cold season vs. warm season: $p < 0.05$, $p' < 0.05$).

Finally, both assemblages of the period October 1993-March 1994, before the first harbour dredging events (April and May 1994), were significantly different to the

Table 2. Results of the one-way ANOVA test for variation of the species richness (S), diversity and evenness with *C. striatula* (H' and J') or without *C. striatula* (H'_2 and J'_2), according to temporal factors such as sampled year (October 1993-September 1994 vs October 1994 - September 1995), season (autumn, winter, spring, summer), colder (autumn-winter) and warmer (spring-summer) periods and harbour works (before and after). df: degrees of freedom; MS: mean square; F: F-statistic; *: $P < 0.05$; **: $P < 0.005$; ns: not significant.

Tableau 2. Résultats du test ANOVA unifactoriel pour la variation de la richesse spécifique (S), de la diversité et de l'équitabilité avec *C. striatula* (H' et J') ou sans *C. striatula* (H'_2 et J'_2), en fonction de facteurs temporels tels que l'année d'échantillonnage (octobre 1993-septembre 1994 vs octobre 1994 - septembre 1995), la saison (automne, hiver, printemps, été), les périodes plus froides (automne-hiver) et plus chaudes (printemps-été) et les travaux portuaires (avant et après). df : degrés de liberté ; MS : carré moyen ; F : statistique F ; * : $P < 0.05$; **: $P < 0.005$; ns : non significatif.

		B1			BC		
Ecological indices	Source of variation	df	MS	F	df	MS	F
S							
	Year	1	169 804	4.644 *	1	77.042	1.269 ns
	Season	3	16.451	0.352 ns	3	43.153	0.672 ns
	Cold-warm	1	3.099	0.070 ns	1	26.042	0.413 ns
	Harbour	1	136.554	3.580 *	1	406.125	8.874 *
H'							
	Year	1	11.690	12.199 **	1	0.039	0.050 ns
	Season	3	2.901	2.385 ns	3	0.181	0.217 ns
	Cold-warm	1	2.959	2.153 ns	1	0.204	0.263 ns
	Harbour	1	12.855	14.239 **	1	4.009	6.660 *
J'							
	Year	1	0.727	14.669 **	1	0.009	0.355 ns
	Season	3	0.121	1.638 ns	3	0.006	0.209 ns
	Cold-warm	1	0.179	2.360 ns	1	0.004	0.150 ns
	Harbour	1	0.811	17.802 **	1	0.140	7.443 *
H'_2							
	Year	1	0.001	0.006 ns	1	0.000	0.000 ns
	Season	3	0.179	0.717 ns	3	0.368	1.402 ns
	Cold-warm	1	0.412	1.777 ns	1	0.075	0.212 ns
	Harbour	1	0.172	0.708 ns	1	0.051	0.179 ns
J'_2							
	Year	1	0.019	1.663 ns	1	0.001	0.086 ns
	Season	3	0.012	1.071 ns	3	0.009	1.214 ns
	Cold-warm	1	0.035	3.318 ns	1	0.004	0.501 ns
	Harbour	1	0.059	6.160 *	1	0.010	1.236 ns

assemblage from April 1994 to August 1995 (all cases, Factor harbour: $p < 0.05$). These significant differences were also obtained without taking into account the abundance of *C. striatula* in the analyses (without *C. striatula*, Factor harbour: $p < 0.05$).

Abundance patterns

The abundance and dominance of bivalve species was greater than that of the gastropods (Table 1), because of the

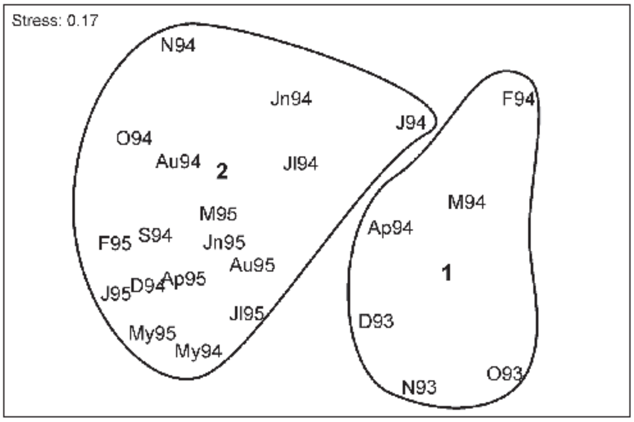


Figure 4. Two-dimensional quantitative MDS ordination plot of the molluscan assemblage of B1 by monthly sample. Encircled points represent sample groups with an average dissimilarity (Bray-Curtis measure) between clusters less than 48.1%. Group 1: samples without *C. striatula.* Group 2: samples with *C. striatula*.

Figure 4. Positionnement multidimensionnel (MDS) en deux dimensions des taxocénoses de Mollusques de la station B1, par échantillon mensuel. Les points entourés représentent des groupes d'échantillons dont la dissimilarité moyenne (mesure de Bray-Curtis) ne dépasse pas 48.1 %. Groupe 1 : échantillons sans *C. striatula.* Groupe 2: échantillons avec *C. striatula*.

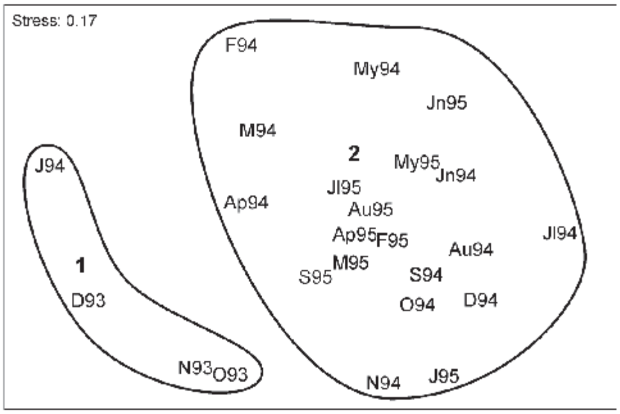


Figure 5. Two-dimensional quantitative MDS ordination plot of the molluscan assemblage of bioclastic bottoms by monthly sample. Encircled points represent sample groups with an average dissimilarity (Bray-Curtis measure) between clusters less than 46.5%. Group 1: samples without *C. striatula.* Group 2: samples with *C. striatula*.

Figure 5. Positionnement multidimensionnel (MDS) en deux dimensions des taxocénoses de Mollusques des fonds bioclastiques (BC) par échantillon mensuel. Les points entourés représentent des groupes d'échantillons dont la dissimilarité moyenne (mesure de Bray-Curtis) ne dépasse pas 46.5 %. Groupe 1 : échantillons sans *C. striatula.* Groupe 2 : échantillons avec *C. striatula*.

clumped distribution presence of bivalves in these soft bottoms. The abundance dynamics of the different species over two years followed different patterns:

1) For most of the species no clear seasonal pattern was found in their monthly abundance.

2) A second pattern was found for species with high values of abundance during winter and autumn months of both years, such as the gastropod *Calyptraea chinensis* (Linné, 1758) (direct larval development) and the bivalve *Anomia ephippium* Linné, 1758 (planktotrophic larval development). Both of these species were associated with the bioclastic component of the sediment (Figure 6).

3) A third pattern occurred for species with maximal abundance during spring and summer months of both years. This group included gastropods with direct larval development, such as the gastropods *Aporrhais pespelecani* (Linné, 1758) and *Bolinus brandaris* (Linné, 1758). Nevertheless, most of these species were bivalves with planktotrophic larval development and associated with bioclastic bottoms, including *Parvicardium scabrum* (Philippi, 1844), *Modiolus adriaticus* (Lamarck, 1819) and *Flexopecten flexuosus* (Poli, 1795) (Figure 7).

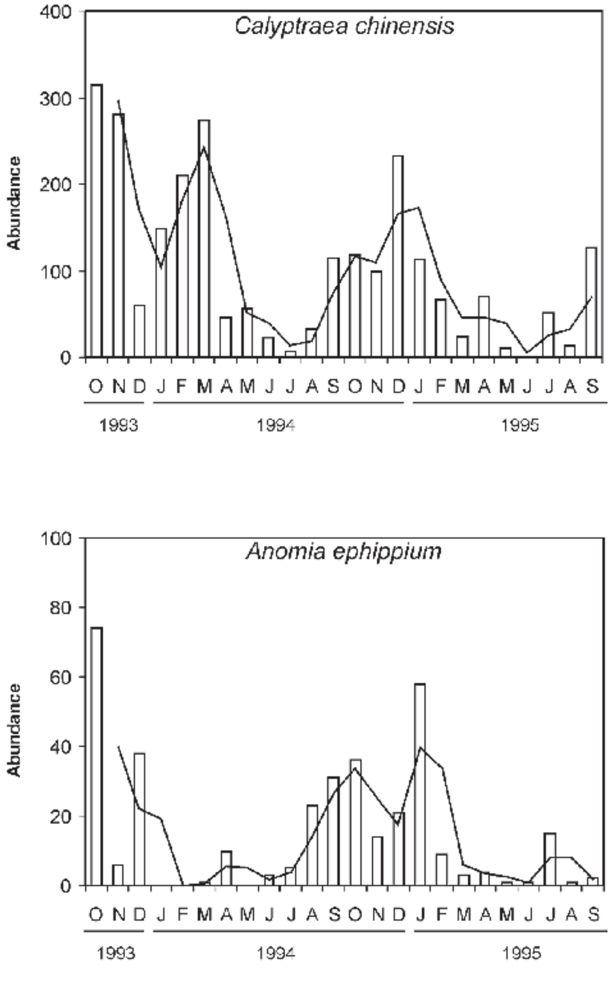


Figure 6. Species showing seasonal pattern with peaks of abundance during autumn-winter in both sampled years for the four sampling stations.

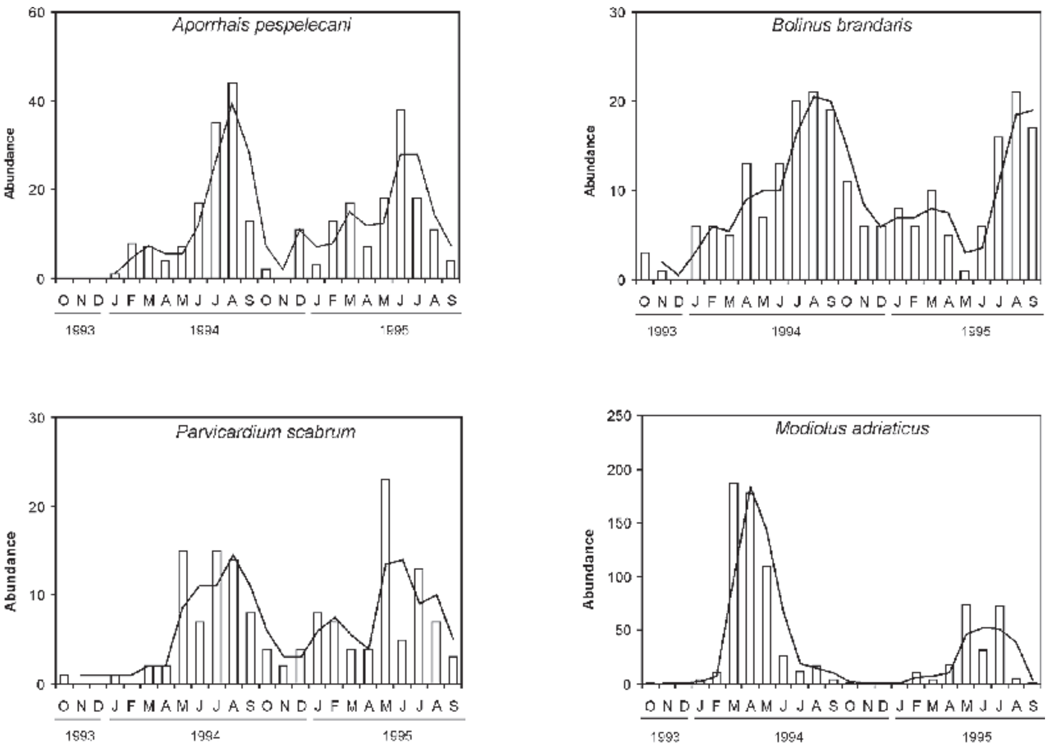
Figure 6. Espèces montrant une tendance saisonnière avec des pics d'abondance en automne-hiver dans les deux années échantillonnées et les quatre stations.

4) A fourth pattern was displayed by species with planktotrophic larval development (Figure 8). In this case, peaks of abundance occurred only during spring-summer months of the first studied year. High abundance was recorded for the bivalves *Pecten maximus* (Linné, 1758) and *Aequipecten opercularis* (Linné, 1758), both species associated with the bioclastic component of the bottom. The recruitment for most bivalves associated with the soft component of the bottom, such as *S. subtruncata* and *Tapes rhomboides* (Pennant, 1777) was higher in the first year than in the second one. Finally, *C. striatula* and *C. gibba*, both associated to muddy bottoms, only showed one recruitment event in the first sampled year.

Discussion

Dynamics of the assemblages

Marine benthic communities have been frequently characterized by the dominance of their different species. However, the presence of a certain species with high dominance may be accidental, during a short time, and in relation with particular circumstances. This has happened in the Bay of Barbate with the massive recruitment of *C. striatula* and *C. gibba*, which has been favoured by several episodes of dredging in the harbour of Barbate. The occurrence of *C. striatula,* as the first dominant species, is related to its massive settlement during the first dredging in the harbour (April-May and September-October, 1994) that resulted in organic matter contents up to 5.9% in the sediments of B1 in April 1994 (Figure 2a). No successful recruitment occurred in the second year and a decrease in the population was observed in the bioclastic assemblage (Figure 3a) together with a decrease of organic matter content in the sediments (Table 1). Ansell (1961) has registered such strong occasional settlement for the same species in the Scottish coasts. In Northern Spain, a subtidal community from soft bottoms registered large fluctuations of the species richness and diversity values, and an increase of organic matter content of the sediment after harbour dredging events (López-Jamar et al., 1986). After this and as a result of these changes, some opportunistic species, such as the bivalve *Thyasira flexuosa* (Montagu, 1803), increased their densities in a short period of time (4 months). According to Dewarumez et al. (1986), some erratic modifications in the community of *Abra alba* in Southern



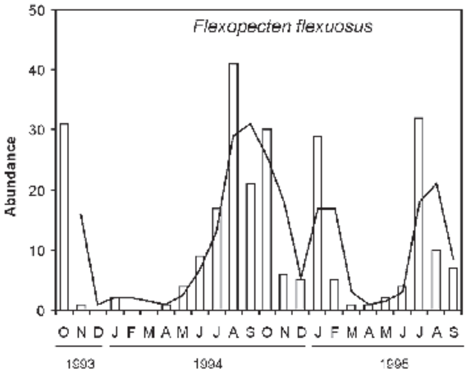


Figure 7. Species showing seasonal pattern with peaks of abundance during spring-summer in both sampled years for the four sampling stations.

Figure 7. Espèces montrant une tendance saisonnière avec des pics d'abondance au printemps et en été dans les deux années échantillonnées et les quatre stations.

Bight of the North Sea were generated by the dominance of one of the main species. These modifications were partly related to larval transport, which occurred parallel to the coast in the form of planktonic patches and, consequently, induced important spatial heterogeneity of the recruitment (Dewarumez et al., 1993). Strong bottom currents, parallel to the coast, influence the hydrodynamics of the Bay of Barbate, with local gyres related to tidal movements, which may be amplified and channelled by the presence of flagstones. These water movements are very important in the larval transport and they have probably also favoured the massive recruitment of *C. striatula*, which is a common bivalve in muddy deep bottoms of this area (Salas, 1996). Its allochthonous origin is confirmed by its absence in most of initial samples and by the progressive decrease of the population with time in the studied area.

The high dominance of *C. striatula* influenced the values of diversity and evenness and resulted in intra- and inter-annual differences in molluscan assemblages (Figures 2a and 3a). The values of the diversity before the settlement of this bivalve, or without taking into account this species (Figures 2b and 3b), are similar to those obtained in assemblages of molluscs from the Mediterranean Sea. These included the molluscan assemblages from *Posidonia oceanica*, seaweed, calcareous algae and rocky bottoms from Spanish coasts (Salas & Hergueta, 1986; Dantart et al., 1990; Hergueta, 1996). A similarity in the ecological indices between years has not been documented in short or long-

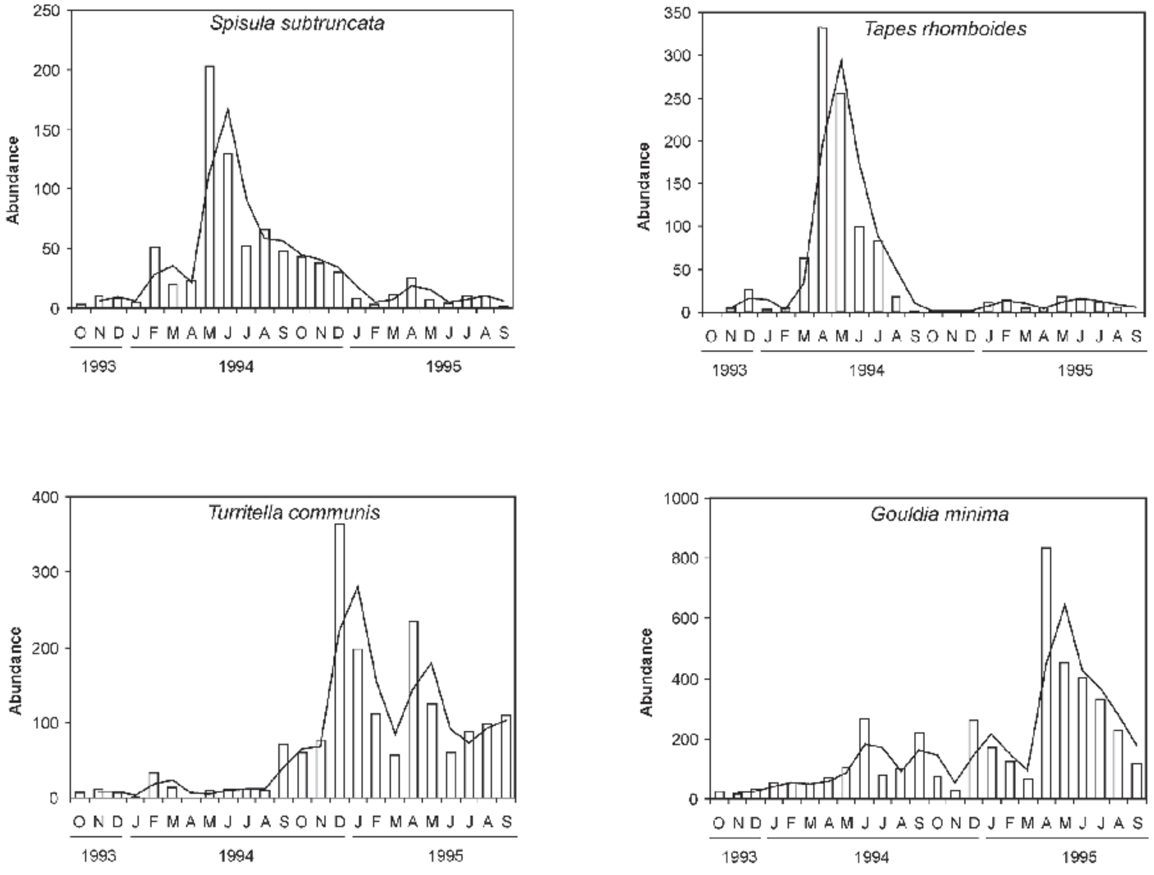


Figure 8. Species with peaks of abundance during the first studied year such as *Spisula subtruncata* and *Tapes rhomboides*, or during the second studied year, such as *Turritella communis* and *Gouldia minima*, for the four sampling stations.

Figure 8. Espèces montrant des pics d'abondance au cours de la première année d'étude, comme *Spisula subtruncata* et *Tapes rhomboides*, ou au cours de la seconde année, comme *Turritella communis* et *Gouldia minima*, pour les quatre stations.

term studies on dynamics of benthic communities from unvegetated soft bottoms (Pearson et al., 1986; Josefson & Rosenberg, 1988; Fromentin et al., 1997).

The temporal dynamics of the diversity of the primary taxocoenosis, without the data of *C. striatula*, showed larger fluctuations in the bioclastic bottoms than in B1, a sampling station close to the harbour of Barbate. This happened in spite of the higher influence of the harbour, fine sediment inputs from the river of Barbate during heavy rain periods and the transport of common species from the assemblage of bioclastic bottoms during winter gales. This would be in accordance to the model of benthic response suggested by Boesch & Rosenberg (1981) who found that communities in less constant environments are generally more resistant to disturbances.

Seasonality in the assemblages

Seasonality in molluscan assemblages, in qualitative and quantitative terms, has been earlier documented in southern Spain, mainly in shallow bottoms such as seagrass beds (Hergueta, 1996), calcareous algae (Salas & Hergueta, 1986) and shallow soft bottoms (Rueda et al., 2001). In all these cases, the seasonal trend was related to seasonal changes of the environment, such as increase of seagrass or algal cover, together with seasonal reproductive events.

The results of the ANOVA tests reflected no seasonal trends in the ecological indices of the molluscan assemblages (with and without *C. striatula*) in the bay of Barbate (Table 2). Inter-annual differences in the indices were registered in the B1 assemblage, whereas no significant differences were found in the bioclastic assemblage. ANOSIM analyses showed intra-annual differences between cold (autumn-winter) and warm (spring-summer) periods in both assemblages. This intra-annual variation could be related to recruitment events, which could be at the origin of inter-annual differences (Figures 6, 7 and 8)**.** The recruitment of many molluscan species is seasonal (mainly spring and summer months) and it can have an indirect influence on the quantitative seasonality of some assemblages (Rueda et al. 2001). According to some authors (Bachelet, 1986; Holland et al., 1987), inter-annual differences in recruitment events, and therefore of abundance, represent sometimes a key factor influencing the presence or absence of seasonal and cyclical trends.

The works in the harbour during all the second year may have amplified inter-annual differences, because of the input of a large amount of muddy sediment, and their inhabiting species, to the bay. This could explain the presence of a higher number of accidental species (with both low dominance and frequency values) during the second year, when compared to the first one. In fact, the results of the ANOVA tests and the ANOSIM analyses show significant differences between the monthly samples before and after the harbour works. In temperate seas, several long term studies in soft bottoms have shown differences in the annual cycles of benthic species and/or benthic communities in relation to climatic factors (Pearson et al., 1986; Fromentin et al., 1997) or anthropogenic impacts (López-Jamar et al., 1986; Dauvin & Ibañez, 1986).

Dredging in the harbour have caused cascade effects in the assemblages from the Bay of Barbate, especially when looking at the successful recruitment of some opportunistic species such as the filter feeders *C. striatula* and *C. gibba*. During the second year, the recruitments of most of the species, with planktotrophic larval development and inhabiting soft sediments, such as *S. subtruncata* or *T. rhomboides,* were less abundant (Figure 8). These inter-annual differences of the recruitment events would be a consequence of the high density of *C. striatula* in the area, which imply predation of larvae by filtration from the water column, and post-settlement competition for the space and food (Olafsson et al., 1994). Therefore, the presence and dominance of *C. striatula* largely influenced the subsequent dynamics of the assemblages. On the other hand, species with direct development (mainly gastropods) or species with planktotrophic development, but associated with bioclasts, had similar number of juveniles in both years (Figures 6 and 7). Their abundance, however, was not high enough to influence a seasonal ordination of the samples.

Longer term studies are needed to detect cyclical trends in these types of molluscan assemblages of the Bay of Barbate. The absence of short term trends, such as seasonality, and the year-to-year variations are a consequence of the complexity of the assemblages containing a high number of species. Other factors such as competition for food between species, their reproductive events or their different response to anthropogenic impacts increase the complexity of these assemblages.

Acknowledgements

The Spanish Government funded this study with the project DGICYT PB92-0415. We are grateful to Serge Gofas (University of Málaga), for his help in the determination of some species and its useful comments, and to Greg Skilleter (University of Queensland) and two anonymous referees for their valuable comments on earlier drafts of the paper. Ana S. López and M.E. Manjón-Clouté (University of Málaga) are thanked for their support during the sampling program. We are indebted to Raimundo Real (University of Málaga) and Jesús Olivero (University of Málaga) for their statistical support.

References

Ansell A. 1961. Reproduction, growth and mortality of *Venus striatula* (Da Costa) in Kames Bay, Millport. *Journal of the Marine Biological Association of the United Kingdom,* **41**: 191-215.

Bachelet G. 1986. Recruitment and year-to-year variability in a population of *Macoma balthica* (L.). *Hydrobiologia,* **142**: 233-248.

Boesch D.F. & Rosenberg R. 1981. Response to stress in marine benthic communities. In: *Stress effect on natural ecosystems* (G. M. Barret & R. Rosenberg eds), pp. 179-200. John Wiley & Sons: New York.

Clarke K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**: 117-143.

Dantart L., Frechilla M. & Ballesteros M. 1990. Fauna malacológica del Estany des Peix (Formentera). *Iberus,* **9**: 111-125.

Dauvin J.C. & Ibanez F. 1986. Variations à long-terme (1977-1985) du peuplement des sables fins de la Pierre Noire (baie de Morlaix, Manche occidentale): analyse statistique de l'évolution structurale. *Hydrobiologia,* **142**: 171-186.

Dewarumez J.M., Quisthoudt C. & Richard A. 1986. Suivi pluriannuel du peuplement à *Abra alba* dans la partie méridionale de la Mer de Nord (région de Dunkerque-France). *Hydrobiologia,* **142**: 187-197.

Dewarumez J.M., Belgrano A., Craeymeersch J.A., Duquesne S., Heip C., Hilde D. & Vincx M. 1993. Influence de la circulation des masses d'eaux dans la dynamique du peuplement à *Abra alba* de la Baie sud de la Mer du Nord. *Journal de Recherche Océanographique,* **18**: 1-4.

Ekman S. 1953. *Zoogeography of the sea.* Sidgwick & Jackson : London. 417 pp.

Fromentin J.M., Ibanez 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-Gómez J.C. 1983 a. Moluscos opistobranquios del Estrecho de Gibraltar y bahía de Algeciras. *Iberus,* **3**: 41-46.

García-Gómez J.C. 1983 b. Estudio comparado de las tanatocenosis y biocenosis malacológicas del Estrecho de Gibraltar y áreas próximas. *Iberus,* **3**: 75-90.

Gofas S. 1999. Marine molluscs with a very small range in the Strait of Gibraltar. *Diversity and Distributions,* **4**: 255-266.

Hergueta E. 1996. *Estudio de las taxocenosis malacológicas asociadas a concrecionamientos de Mesophyllum lichenoides (Ellis) Lemoine y a una pradera de Posidonia oceanica (Linnaeus) Delile del litoral almeriense*. PhD Thesis. University of Málaga, Spain. 860 pp.

Josefson A.B. & Rosenberg R. 1988. Long-term soft bottom faunal changes in three shallow Fjords, West Sweeden. *Netherlands Journal of Sea Research,* **22**: 149-159.

Krebs C.J. 1989. *Ecological Methodology*. Harper & Row Publishers: New York. 654 pp.

López-Jamar E., González G. & Mejuto J. 1986. Temporal changes of community structure and biomass in two subtidal macroinfaunal assemblages in La Coruña bay, NW Spain. *Hydrobiologia*, **142**: 137-150.

Longhurst A. 1998. *Ecological geography of the Sea*. Academic Press: San Diego. 398 pp.

Margalef R. 1956. Informacion y diversidad especifica en las comunidades de organismos. *Investigacion Pesquera,* **3**: 99-106.

Olafsson E.B., Peterson C.H. & Ambrose W.G. Jr. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanography and Marine Biology, an Annual Review,* **32**: 65-109.

Pearson T.H., Duncan G. & Nuttal J. 1986. Long term changes in the benthic communities of loch Linnhe and Loch Eil (Scotland). *Hydrobiologia,* **142**: 113-119.

Pielou E.C. 1966. The measurement of diversity in different types of biological collection. *Journal of Theoretical Biology,* **13**: 131-144.

Rey J.C. 1983. El paso del atún rojo, *Thunnus thynnus* (Linnaeus, 1758), a traves del Estrecho de Gibraltar y su relación con la hidrología. Esquemas de migración. *Boletín del Instituto Español de Oceanografía,* **1**: 85-94.

Rueda J. & Salas C. 1998. *Modiolus lulat* (Dautzenberg, 1891): A Tropical West African bivalve recorded from South European coasts. *Journal of Conchology,* **36**: 80.

Rueda J. & Gofas S. 1999. *Sinum bifasciatum* (Récluz, 1851) (Gastropoda: Naticidae) confirmed in Mediterranean Fauna. *Journal of Conchology,* **36**: 81-82.

Rueda J., Salas C. & Gofas S. 2000. A molluscan community from coastal bioclastic bottoms in the Straits of Gibraltar area. *Iberus,* **18**: 95-123.

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.

Salas C. & Hergueta E. 1986. La fauna de moluscos de las concreciones calcáreas de *Mesophyllum lichenoides* (Ellis) Lemoine. Estudio de la diversidad de un ciclo annual. *Iberus,* **6**: 57-65.

Salas C. 1996. Marine bivalves from off the Southern Iberian Peninsula collected by the Balgim and Fauna 1 expeditions. *Haliotis,* **25**: 33-100.

Sánchez-Moyano J.E., Estacio F.J., García-Adiego E.M. & García-Gómez J.C. 2000. The molluscan epifauna of the alga *Halopteris scoparia* in southern Spain as a bioindicator of coastal environmental conditions. *Journal of Molluscan Studies,* **66**: 431-448.

Sánchez-Moyano J.E., Estacio F.J., García-Adiego E.M. & García-Gómez J.C. 2001. Effect of the vegetative cycle of *Caulerpa prolifera* on the spatio-temporal variation of invertebrate macrofauna. *Aquatic Botany,* **70**: 163-174.

Stommel H., Bryden H. & Mangelsdorf P. 1973. Does some of the Mediterranean outflow come from great depth? *Pure and Applied Geophysics,* **105**: 879-889.

Templado J., Guerra A., Bedoya J., Moreno D., Remon J.M., Maldonado M. & Ramos M.A. 1993. *Fauna marina circalitoral del sur de la Península Ibérica. Resultados de la campaña oceanográfica «Fauna I»*. MNCN-CSIC: Madrid. 160 pp.

van Aartsen J., Menkhorst H.P.M.G. & Gittenberger E. 1984. The marine Mollusca of the Bay of Algeciras, Spain, with general notes on *Mitrella, Marginellidae* and *Turridae*. *Basteria,* suppl. 2: 1-135.

Vives F., Santamaria G. & Trepat J. 1975. El zooplancton de los alrededores del Estrecho de Gibraltar en Junio-Julio de 1972. *Resultados de las expediciones cientificas del B/O Cornide,* **4**: 7-100.