

Seasonal dynamics and structure of soft-bottom assemblages in Blanes Bay (northwest Mediterranean Sea)

S. Pinedo, R. Sardá and D. Martín

Centro de Estudios Avanzados de Blanes (CSIC). Camí de Santa Bàrbara, s/n. 17300 Blanes (Girona), Spain.

Received September 1995. Accepted May 1996.

ABSTRACT

The seasonal dynamics and community structure of the soft-bottom benthic macroinfauna, inhabiting shallow sublittoral habitats in Blanes Bay (northwest Mediterranean Sea), were investigated from March 1992 to March 1993. Macroinfaunal abundance and biomass varied seasonally with a peak during spring, decreasing sharply in summer and reaching low values in winter. Mean annual biomass was higher in the most sheltered and disturbed sediments ($4.5 \text{ g dry weight} \cdot \text{m}^{-2}$). Lower biomass values were obtained at the other two sites ($3.4 \text{ g dry weight} \cdot \text{m}^{-2}$ and $1.7 \text{ g dry weight} \cdot \text{m}^{-2}$). Organic matter content of the sediments showed different patterns among stations and did not explain the variability in abundance and biomass.

Key words: Seasonal dynamics, soft-bottom zoobenthos, northwest Mediterranean.

RESUMEN

Dinámica estacional y estructura de las comunidades de fondos blandos en la bahía de Blanes (Mediterráneo noroccidental)

Se ha estudiado la dinámica estacional y la estructura de la comunidad de la macroinfauna de fondos blandos sublitorales de la bahía de Blanes (mar Mediterráneo noroccidental) entre marzo de 1992 y marzo de 1993. Tanto la abundancia como la biomasa varían estacionalmente, presentando un pico durante la primavera, una disminución brusca durante los meses de verano y valores bajos en otoño e invierno. La biomasa media anual más elevada se obtuvo en la estación más perturbada situada en un área protegida ($4,5 \text{ g de peso seco} \cdot \text{m}^{-2}$). Las otras dos estaciones situadas en zonas más abiertas de la bahía registraron valores más bajos ($3,4 \text{ g de peso seco} \cdot \text{m}^{-2}$ y $1,7 \text{ g de peso seco} \cdot \text{m}^{-2}$). El contenido en materia orgánica del sedimento mostró diferentes patrones estacionales para cada una de las estaciones; sin embargo, este factor no explicó la variabilidad observada para la abundancia y la biomasa.

Palabras clave: Dinámica estacional, zoobentos, fondos blandos, Mediterráneo noroccidental.

INTRODUCTION

Shallow littoral soft-bottoms in the northwest Mediterranean are characterised by sandy sediments. The habitat is highly influenced by storm waves and currents. Although the seagrass meadow of *Posidonia oceanica* (L.) Delile, 1813, is the climax community in the sublittoral zone, sand sediments without vegetation are the most usual communities in the area (Pérès and Picard, 1964; Pérès, 1967; 1982).

Marine habitats are characterised by species populations that are highly variable in space and time. Soft-bottom benthic studies have often focused on descriptions of the spatial distributions of the species. To better understand patterns of organisation, long-term studies are needed to explain the factors affecting species composition change.

Although seasonal dynamics has been intensively studied in temperate areas of the Atlantic Ocean (Sanders, 1960; Pearson, 1971; Dauvin, 1984; Dörjes, Michaelis and Rhode, 1986; Ibanez and Dauvin, 1988), few works have dealt with seasonality of sublittoral soft-bottom communities in the Mediterranean Sea (Guelorget and Michel, 1979a; 1979b; Martín, 1991; Millet and Guelorget, 1994; Sardá *et al.*, 1995).

In this paper we examine seasonal variation of a soft-bottom macrobenthos in sublittoral environments in Blanes Bay (Mediterranean Sea). Three different assemblages were sampled to test whether variation in natural and anthropogenic disturbances affect structure and trophic composition and to correlate the seasonality of the benthic invertebrate fauna (abundance and biomass) with the organic matter content in sediment.

MATERIAL AND METHODS

Three stations were sampled from March 1992 to March 1993 (Sardá *et al.*, 1995). The sampling area is highly influenced by freshwater inputs of the Tordera River, Blanes harbour, the submarine outfall from the city, and the combined action of the dominant east and south winds. Station 1 was located in front of the mouth of the river at a depth of 15 m. Station 2 was situated in the middle of Blanes Bay, at a similar depth, and station 3 was located in the mouth of the Blanes Harbour at a depth of 8 m.

Samples were obtained fortnightly in stations 1 and 2, and monthly in station 3 to estimate the

species density and biomass. We used a Van Veen grab covering an area of 600 cm². At each station, the grab was able to penetrate to different depths (15 cm in station 1, and 12 cm in stations 2 and 3) depending on sediment compaction. No biogenic structures were seen on the bottom of the grab samples, indicating the absence of large burrower organisms. Two replicates were collected at each station on every sampling date. Samples were sieved through a 0.5 mm screen and preserved in formalin seawater stained with rose bengal.

The organisms retained by the sieve were counted and classified to the lowest possible taxonomic level for polychaetes, bivalves, large nematodes and echinoderms. The rest of the taxa were classified only to major groups. The species biomass was determined as dry weight (24 h at 70°C), except for calcified species, where it was obtained by the loss of weight after ashing (5 h at 450°C). Regressions were used to convert length measurements to biomass for the polychaete *Owenia fusiformis* Delle Chiaje, 1842, and the different species of bivalves. Organisms were classified into five trophic groups: (F): filter feeders; (M): mixed (filter and surface-deposit feeders); (S): surface-deposit feeders; (SS): subsurface-deposit feeders; (C): carnivores/omnivores, using information in Fauchald and Jumars (1979) and Dauvin and Ibanez (1986). The bivalve species of the subfamily Tellinoidea and subfamily Nuculoidea were included in the mixed group (Levinton, 1982). The rest of the bivalves were classified as filter feeders. Each species was classified into a single trophic group to avoid overestimating the obtained values.

Small sediment subsamples were collected from the grab for organic content and mechanical granulometric analysis. Organic content of dry sediment was estimated as the loss of weight after ashing. Sediment was submitted to the standard dry-sieved procedure described in Wentworth (1972) for granulometric analysis. Six size classes were used in this study: mud (<63 µm), very fine sand (63 to 120 µm), fine sand (120 to 250 µm), medium sand (250 to 500 µm), coarse sand (500 to 750 µm), and very coarse sand (750 to 1000 µm). Medium grain size (m. g. s.) is used to characterise the sediment.

We used parametric analysis to establish the pattern of seasonal variability in abundance, biomass and organic matter. Abundance data were transformed to meet assumptions of normality and homoscedasticity (as tested by Kolmogorov-Smirnov and Bartlett tests, respectively). One-way analysis of

variance was run with time (month) as a factor within each station. Multiple comparisons among months were calculated by the Tukey test (Tukey, unpublished). A regression analysis (Pearson correlation test) was used to reveal relationships of the variables at each station.

RESULTS

Seasonal dynamics

The seasonal pattern in macroinfaunal abundance at the three sites was characterised by a peak during spring (April-May-June), a sharp decrease

through summer and lower values in autumn and winter (figure 1, top graph). A one-way ANOVA of the abundance seasonal variability revealed significant differences at each station (table I). Multiple comparison tests showed May and June as the most different months at stations 1 and 2, with April and June at station 3. Maximum densities were reached in May (21 106 ind. · m⁻² at station 1, 46 400 ind. · m⁻² at station 2, and 51 600 ind. · m⁻² at station 3). Annual mean abundance of the assemblages is given in tables II, III, and IV.

The seasonal pattern of biomass followed roughly that of abundance (figure 1, bottom graph). Biomass peak was observed in late spring at stations 2 and 3. No significant differences were revealed by

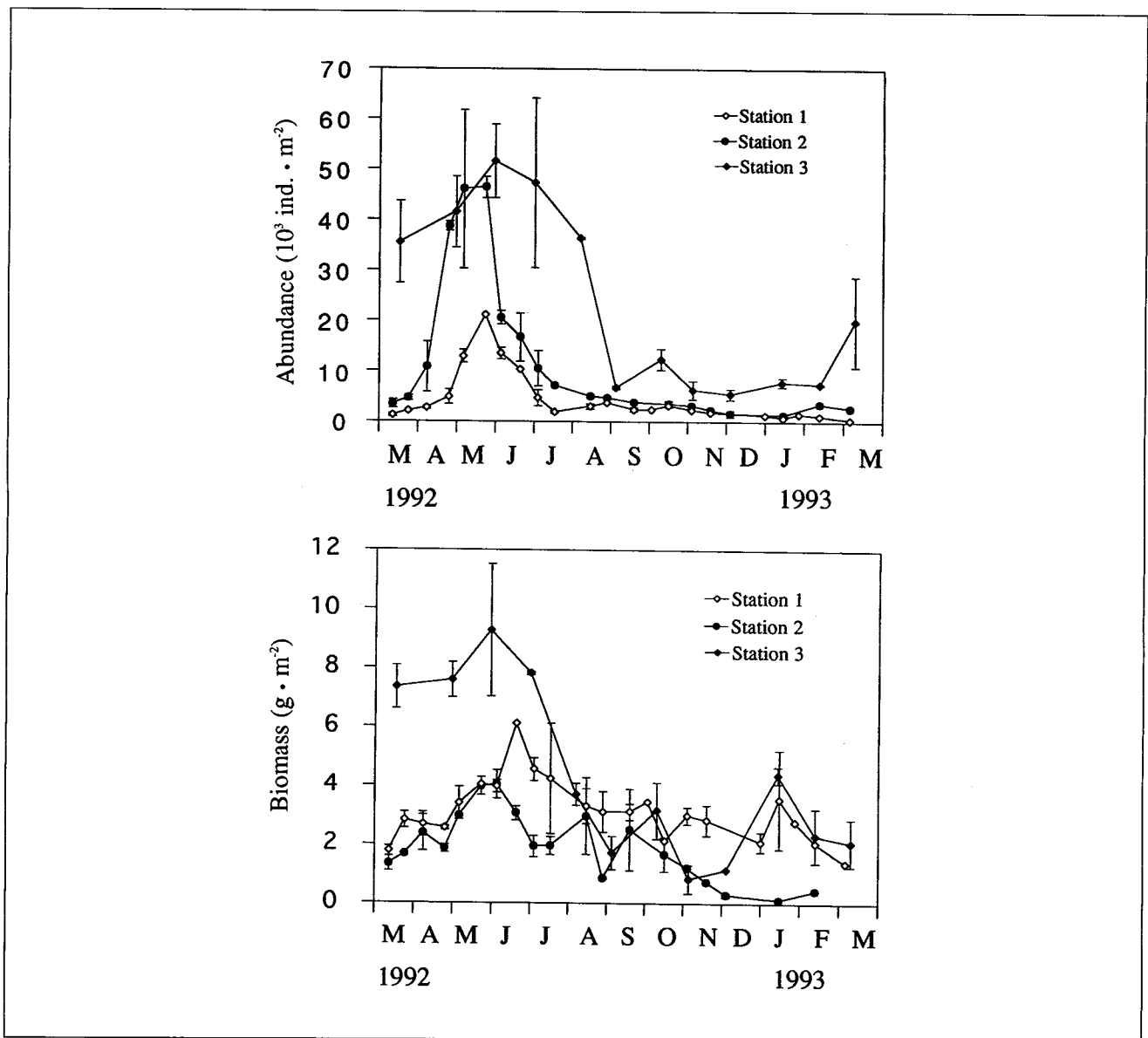


Figure 1. Seasonal variation in abundance and biomass of the three assemblages studied in Blanes Bay. Vertical bars are standard deviations.

the one-way ANOVA of the biomass data at station 1 (table I). Multiple comparisons tests explained the highest variation in May and June at these stations. The peak of biomass values were reached in May ($4.1 \text{ g} \cdot \text{m}^2$ at station 2 and $9.3 \text{ g} \cdot \text{m}^2$ at station 3). Annual mean biomass of the assemblages is given in tables II, III, and IV.

The annual variation of organic matter content of the sediments was different at the three sites (figure 2). According to that observed for biomass, the one-way ANOVA analysis showed significant differences at stations 2 and 3 (table I). Multiple comparisons tests revealed September and November as the most different months at station 2 and June at station 3. The highest values of mean annual organic matter content were found at the most disturbed station in the mouth of the harbour (1.63%), while 0.71% was computed at station 1, and 1.08% at station 2.

Relationships among measured variables are presented in table V. Macroinfaunal abundance was highly related to the biomass values at each studied assemblage. However, abundance was not correlated with organic matter content at station 1 and was negatively correlated at station 2. In the disturbed site, significant relationships were found among organic matter and the other measured variables.

Structure of the benthic assemblages

The assemblages were dominated by polychaetes and bivalves. Echinoderms and crustaceans were

found in lower densities together with other less representative groups. The number of species was similar among sites (70 ± 8 species of polychaetes, 15 ± 1 species of bivalves and 13 different groups).

The macroinfaunal assemblage of station 1 (Tordera River) inhabited coarse sand sediments (m. g. s. = $575 \mu\text{m}$) with low organic content (0.71%). Polychaetes were the most representative group in terms of abundance, and the bivalves in biomass (figure 3). The dominant species were the bivalve *Spisula subtruncata* Da Costa, 1778, and the polychaetes *Ditrupea arietina* (Muller, 1776) and *Owenia fusiformis*. These organisms showed high recruitment in spring, with low values during the rest of the year (table II). Mean annual biomass was calculated as $3.4 \text{ g} \cdot \text{m}^2$. Twelve species accounted for 70% of the biomass (table II). The main contributors were the bivalve *Callista chione* (L., 1758) and the polychaetes *Glycera capitata* Oersted, 1843 and *D. arietina*.

The fine sand sediments (m. g. s. = $148 \mu\text{m}$) of the macroinfaunal assemblage of station 2 (Blanes Bay) showed lower biomass than station 1. Polychaetes were the dominant group in terms of abundance and biomass (figure 3). *Owenia fusiformis* was the most abundant species but was observed only during the recruitment period. Other important species in terms of abundance were the polychaete *Paradoneis armata* Glemarec, 1966 and the bivalves *Spisula subtruncata* and *Loripes lacteus* (L. 1758). Mean annual values of biomass averaged $1.7 \text{ g} \cdot \text{m}^2$. Twenty-three species accounted for 70% of the biomass, with *Echinocardium medi-*

Table I. Summary table of the one-way ANOVA analysis. (*): $p < 0.05$, (**): $p < 0.01$, (***): $p < 0.001$, (n. s.): differences not significant, (DF): degrees of freedom, (MS): mean square and (F): F-ratio.

STATION	VARIABLE	SOURCE	DF	MS	F
1	Abundance	month	11	1.278	24.030 ***
		error	9	0.053	
	Biomass	month	11	1.001	1.448 n. s.
		error	9	0.691	
	Organic Matter	month	11	0.026	3.294 n. s.
		error	7	0.008	
2	Abundance	month	11	2.134	31.579 ***
		error	9	0.068	
	Biomass	month	11	2.081	3.290 *
		error	9	0.633	
	Organic Matter	month	11	0.095	10.735 ***
		error	11	0.009	
3	Abundance	month	11	1.719	22.215 ***
		error	12	0.077	
	Biomass	month	11	16.791	11.866 ***
		error	12	1.415	
	Organic Matter	month	11	0.511	6.305 **
		error	12	0.081	

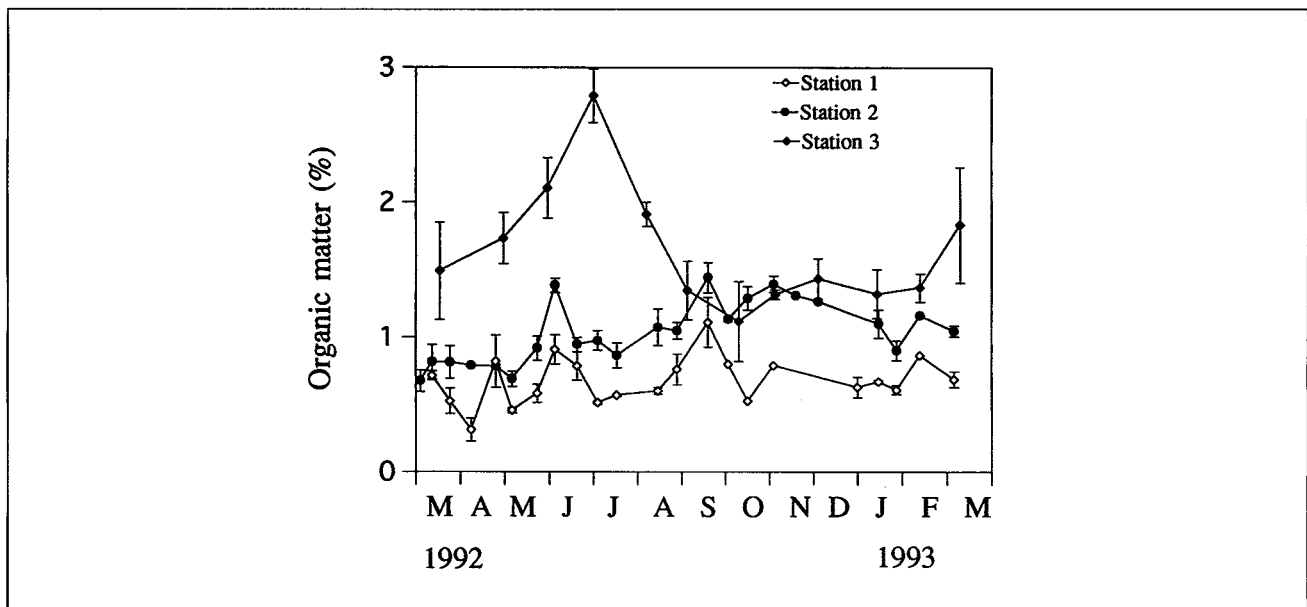


Figure 2. Seasonal variation in organic matter content of the three assemblages studied in Blanes Bay. Vertical bars are standard deviations.

terraneum (Forbes 1844) as the main contributor. Large rare species, such as the polychaetes *Laetmonice hystrix* (Savigny, 1820) and *Amphitrite variabilis* (Risso, 1826), and epifaunal species, such as the echinoderm *Holothuria* sp. and several species of decapods, were not included in the value. These organisms accounted for $1.4 \text{ g} \cdot \text{m}^2$ of mean annual biomass.

The macroinfaunal assemblage of station 3 (Blanes Harbour) was found on fine sand sediments (m. g. s. = $179 \mu\text{m}$) with the highest organic

content (1.63%). Polychaetes were largely the dominant group (figure 3). This site showed the highest values of mean annual biomass of the three studied stations ($4.5 \text{ g} \cdot \text{m}^2$). Seven species accounted for more than 70% of the mean annual abundance and biomass (table IV). The polychaete *Owenia fusiformis* was the most representative species, maintaining a stable population of adults throughout the year. These worms were responsible for the high recruitment of this species in the bay during spring.

Table II. Species composition, abundance (ind. $\cdot \text{m}^{-2}$), biomass ($\text{g} \cdot \text{m}^{-2}$) and percentages of the macroinfaunal assemblage at station 1. 70% of the total biomass is represented. (BIV): Bivalva, (POL): Polychaeta, and (EQU): Equinodermata. Trophic groups: (F): filter feeders, (C): carnivores/omnivores, (S): surface deposit feeders, (M): mixed and (SS): subsurface deposit feeders.

SPECIES	TROPIC GROUP		ABUNDANCE		BIOMASS	
			MEAN	PERCENTAGE	MEAN	PERCENTAGE
<i>Callista chione</i>	BIV	F	16	0.3	1.179	34.6
<i>Glycera capitata</i>	POL	C	351	7.4	0.390	11.4
<i>Ditrupa arietina</i>	POL	F	703	14.9	0.192	5.6
<i>Echinocardium mediterraneum</i>	EQU	S	106	2.2	0.153	4.5
<i>Owenia fusiformis</i>	POL	M	418	8.9	0.119	3.5
<i>Spisula subtruncata</i>	BIV	F	735	15.6	0.096	2.8
<i>Loripes lacteus</i>	BIV	F	41	0.9	0.078	2.3
<i>Lumbrineris acuta</i>	POL	C	78	1.7	0.056	1.6
<i>Dosinia</i> sp.	BIV	F	3	0.1	0.047	1.4
<i>Sigalion squamatum</i>	POL	C	2	0.1	0.038	1.1
<i>Clymenura clypeata</i>	POL	SS	7	0.2	0.031	0.9
<i>Thracia</i> sp.	BIV	F	32	0.7	0.028	0.8
Others			2 220		1.002	
Total			4 712		3.410	

Trophic composition of macroinfauna made it possible to observe a replacement of filter feeder and carnivore/omnivore species by surface deposit feeder and mixed species from the most exposed

station in front of the Tordera River to the most sheltered and disturbed site at the mouth of the harbour (figure 3).

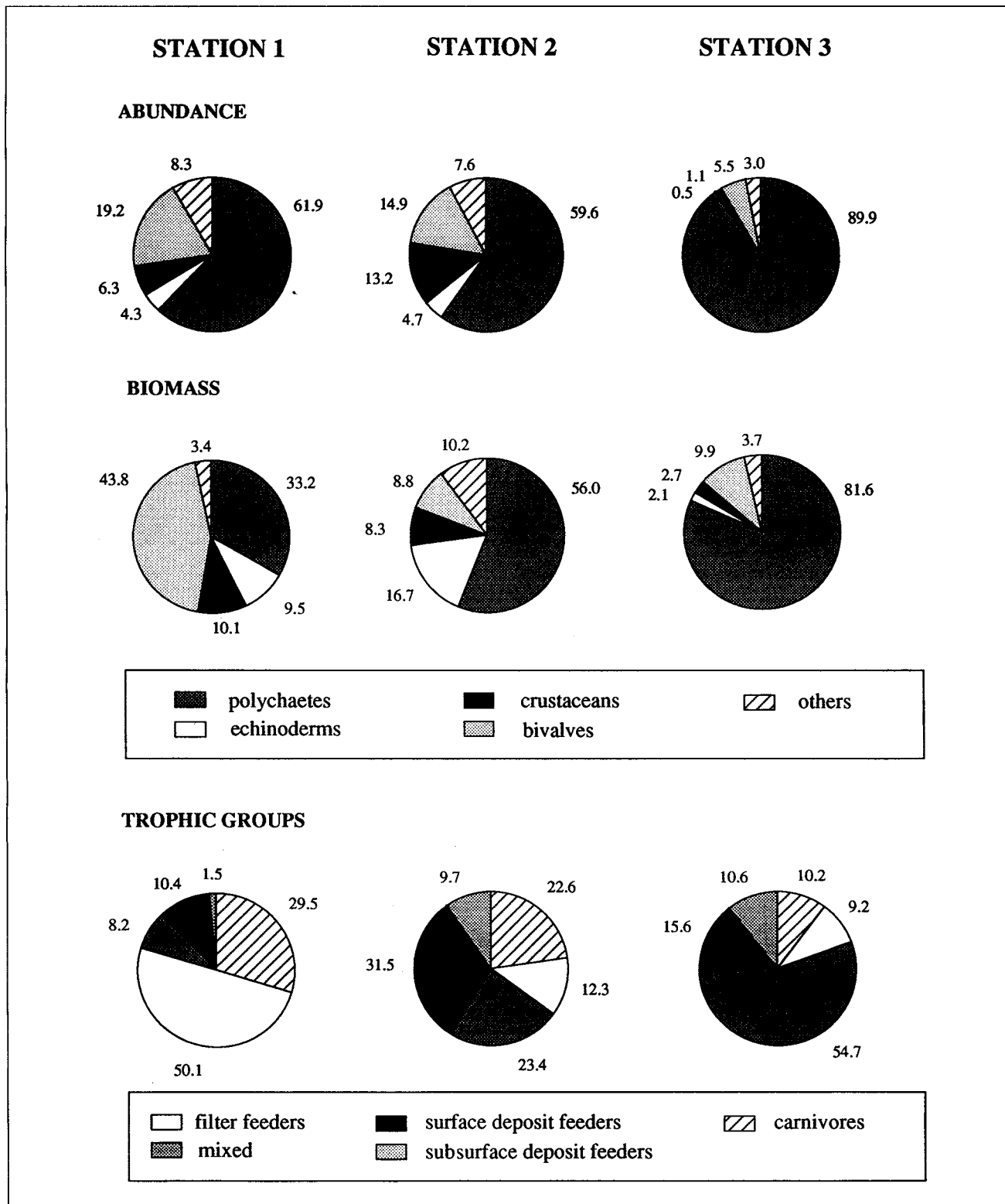


Figure 3. Top graphs: Abundance and biomass distribution of different groups of the three assemblages studied. Bottom graphs: Dominance of the trophic group in the three assemblages studied. Values are expressed on percentages.

Table III. Species composition, abundance (ind. · m⁻²), biomass (g · m⁻²) and percentages of the macroinfaunal assemblage at station 2. 70% of the total biomass is represented. (EQU): Equinodermata, (POL): Polychaeta, and (BIV): Bivalva. Trophic groups: (S): surface deposit feeders, (M): mixed, (SS): subsurface deposit feeders, (F): filter feeders and (C): carnivores/omnivores.

SPECIES	TROPHIC GROUP		ABUNDANCE		BIOMASS	
			MEAN	PERCENTAGE	MEAN	PERCENTAGE
<i>Echinocardium mediterraneum</i>	EQU	S	429	4.2	0.259	15.3
<i>Spiochaetopterus costarum</i>	POL	M	152	1.5	0.176	10.4
<i>Owenia fusiformis</i>	POL	M	3 257	32.2	0.123	7.3
<i>Phylo foetidus</i>	POL	SS	3	0.03	0.102	6.0
<i>Spisula subtruncata</i>	BIV	F	652	6.4	0.065	3.8
<i>Ditrupea arietina</i>	POL	F	8	0.08	0.060	3.6
<i>Paradoneis armata</i>	POL	S	494	4.9	0.059	3.5
<i>Sigalion squamatum</i>	POL	C	10	0.1	0.056	3.3
<i>Loripes lacteus</i>	BIV	F	500	4.9	0.032	1.9
<i>Chone infundibuliformis</i>	POL	M	82	0.8	0.026	1.5
<i>Malacoceros fuliginosus</i>	POL	S	37	0.4	0.025	1.5
<i>Nephtys hombergi</i>	POL	C	2	0.02	0.024	1.4
<i>Myriochele oculata</i>	POL	M	57	0.6	0.021	1.2
<i>Glycera capitata</i>	POL	C	28	0.3	0.021	1.2
<i>Magelona minuta</i>	POL	S	407	4.0	0.021	1.2
<i>Glycera rouxii</i>	POL	C	8	0.08	0.019	1.1
<i>Dosinia</i> sp.	BIV	F	7	0.07	0.018	1.1
<i>Nephtys cirrosa</i>	POL	C	44	0.4	0.017	1.0
<i>Spio decoratus</i>	POL	S	149	1.5	0.015	0.9
<i>Pectinaria koreni</i>	POL	SS	15	0.1	0.013	0.8
<i>Mediomastus fragilis</i>	POL	SS	231	2.2	0.013	0.8
<i>Capitella capitata</i>	POL	SS	256	2.5	0.012	0.7
<i>Hyalinoecia bilineata</i>	POL	C	5	0.05	0.011	0.7
Others			3 289		0.500	
Total			10 122		1.690	

DISCUSSION

Benthic variations observed in sublittoral assemblages of Blanes Bay provided evidence of the seasonal pattern of abundance and biomass. The general trend reveals a spring peak and low values in autumn and winter. This same trend has been commonly observed during the following years (personal observation). Sublittoral soft-bottom environments seem to show biomass trends similar to the mediolittoral ones in the Mediterranean (Sardá *et al.*, 1995). While the species composition of mediolittoral fauna is characterised by low richness through the year and large reproductive periods, sublittoral habitats tend to be structurally complex, showing sporadic appearances of many species and large recruitment of others in short periods of time.

Sublittoral seasonal fluctuations observed in this study differ from those of the Atlantic Ocean (Sanders, 1960; Dauvin, 1984; López-Jamar, González and Mejuto, 1986) and North Sea data (Dörjes, Michaelis and Rhode, 1986; Künitzer, 1992), where a tendency to accumulate density and

biomass in summer periods has been noted. The mean biomass values obtained in Blanes Bay are similar to low ranged values found on coastal Atlantic shores (Sardá *et al.*, 1995). This supports the idea that the Mediterranean benthos is poorer in biomass compared to the similar North Atlantic sea floor (Ketchum, 1983; Ben-Tuvia, 1983).

As no seasonal pattern and relationships were found for organic matter content, other variables may affect the community structure. The faunal composition seems to be related to the hydrodynamic conditions of different sites in the bay. In shallow exposed zones, wave action can be the limiting factor, as has been pointed out by Muus (1967) and Wolff (1973). Water movement prevents organic matter accumulation in sediments and could explain the insignificant relationships between abundance-biomass and organic matter content. In the most sheltered zone (station 3), organic matter peaked following the maximum values of abundance and biomass. This increase may be the result of juvenile mortality after the recruitment period. Nevertheless, the amount of organic content at this site could be the factor main-

Table IV. Species composition, abundance (ind. · m⁻²), biomass (g · m⁻²) and percentages of the macroinfaunal assemblage at station 3. 70 % of the total biomass is represented. (POL): Polychaeta and (BIV): Bivalva. Trophic groups: (M): mixed, (S): surface deposit feeders, and (SS): subsurface deposit feeders.

SPECIES	TROPIC GROUP		ABUNDANCE		BIOMASS	
			MEAN	PERCENTAGE	MEAN	PERCENTAGE
<i>Callista chione</i>	BIV	F	16	0.3	1.179	34.6
<i>Owenia fusiformis</i>	POL	M	4 796	20.4	2.034	45.3
<i>Paradoneis armata</i>	POL	S	2 378	10.1	0.293	6.5
<i>Spiochaetopterus costarum</i>	POL	M	398	1.7	0.260	5.8
<i>Mediomastus fragilis</i>	POL	SS	6 493	27.6	0.258	5.7
<i>Aonides oxycephala</i>	POL	S	791	3.4	0.154	3.4
<i>Capitella capitata</i>	POL	SS	2 155	9.2	0.094	2.1
<i>Abra</i> sp.	BIV	M	318	1.4	0.084	1.9
Others			6 160		1.317	
Total			23 489		4.484	

taining its high biomass and longer-lasting abundance.

In temperate latitudes, population density may change substantially due to the seasonal patterns of reproduction. The abundance and biomass peak detected during May and June coincides with the recruitment of several benthic species, such as: the polychaetes *Owenia fusiformis*, *Ditrupa arietina*, *Magelona minuta* Eliason, 1962 and *Paradoneis armata*, the bivalves *Spisula subtruncata* and *Loripes lacteus*, and the echinoderm *Echinocardium mediterraneum*. The presence of benthic invertebrate larvae in the water column follows the bloom of phytoplankton production observed in late February (Mura *et al.* in this volume). The late winter presence of larvae has been previously described in areas near Blanes Bay (Bhaud, 1987). This agrees with previous observations of the coupling between the pelagic larval phase and phytoplankton blooms (Thorson, 1946; Starr, Himmelman and Therriault, 1990).

The trophic category of organisms can be defined as the complex of the relationships existing between composition and food size, the mechanisms involved in food uptake, and motility. The distribution of trophic guilds was related to gradients of environmental factors. The dominance of filter feeders at station 1 was associated with the high level of suspended matter falling down to the bottom. The filter feeder *Callista chione* was the main contributor and its dominance decreased gradually to lesser exposed sites of the bay. Trophic group diversity increased at station 2, with biomass distributed among several species, a typical structure of undisturbed habitats. Habitat complexity is associated with the trophic groups' growth (Gambi and Giangrande, 1985a, b) and with the important role of carnivore and filter feeder species (Bianchi

and Morri, 1985). At station 3, trophic complexity decreased and surface deposit feeders and mixed groups became the dominant groups as sedimentation rates increased the accumulation of detritus at the bottom. The surface deposit feeder *Owenia fusiformis* develops an alternative feeding mechanism related to environmental conditions. When high plankton input is produced and flow conditions change, *O. fusiformis* can behave as a filter feeder (Gambi, 1989).

In summary, seasonal dynamics of the soft-bottom macrobenthic component of Blanes Bay is related to several species of polychaetes, bivalves and echinoderms. These species are characterised by a high recruitment from March to June, followed by a high mortality of recruiters. The variation of benthic macroinfauna does not seem to respond to the pulses of freshwater inputs based on the measured organic matter accumulation in the sediment. We

Table V. Regression coefficients between the three measured variables at sampling stations. (*): $p < 0.05$, (**): $p < 0.01$ and (***): $p < 0.001$, (n. s.): differences not significant, (n): number of observations and (r): Pearson correlation index.

STATION	VARIABLES	REGRESSION		
		n	r	
General	abundance-biomass	66	0.74	***
	abundance-biomass	21	0.47	*
	abundance-o. matter	21	-0.05	n. s.
1	biomass-o. matter	19	0.01	n. s.
	abundance-biomass	21	0.64	*
	abundance-o. matter	21	-0.50	*
2	biomass-o. matter	21	-0.19	ns
	abundance-biomass	24	0.84	***
	abundance-o. matter	24	0.78	***
3	biomass-o. matter	24	0.58	*

believe that seasonal dynamics of soft-bottom communities is coupled with the pelagic ecosystem, and is directed by other factors rather than terrestrial inputs.

ACKNOWLEDGEMENTS

This research was supported by project CICYT MAR-91-0503, by a predoctoral fellowship from the Education and Science Office (S. Pinedo) and by a postdoctoral fellowship from the CSIC (D. Martín). We thank Gustavo Carreras for his help during the sampling.

REFERENCES

- Ben-Tuvia, A. 1983. The Mediterranean Sea. B. Biological aspects. In: *Ecosystems of the World 26, Estuaries and Enclosed Seas*. B. H. Ketchum (ed.): 239-248. Elsevier Scientific Publishing Company. Amsterdam, Oxford and New York.
- Bhaud, M. 1987. Description and identification of polychaete larvae; their implications in current biological problems. *Oceanis* 13 (6): 158 pp.
- Bianchi, C. N. and C. Morri. 1985. Policheti come descrittori della struttura trofica degli ecosistemi marini. *Oebalia* 11: 203-214.
- Dauvin, J. C. 1984. *Dynamique d'écosystèmes macrobenthiques des fonds sédimentaires de la baie de Morlaix et leur perturbation par les hydrocarbures de l'Amoco Cadiz*. Université P. et M. Curie. Paris: 468 pp.
- Dauvin, J. C. and F. Ibanez. 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.
- Dörjes, J., H. Michaelis and B. Rhode. 1986. Long-term studies of macrozoobenthos in intertidal and shallow subtidal habitats near the island of Norderney (East Frisian coast, Germany). *Hydrobiologia* 142: 217-232.
- Fauchald, K. and P. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Annu. Rev.* 17: 193-284.
- Gambi, M. C. 1989. Osservazioni su morfologia funzionale e comportamento trofico di *Owenia fusiformis* Delle Chiaje (Polychaeta, Oweniidae) in rapporto ai fattori ambientali. *Oebalia* 15: 145-155.
- Gambi, M. C. and A. Giangrande. 1985a. Analisi della struttura trofica del popolamento dei Policheti nei fondi mobili di due aree del Mar Tirreno. *Oebalia* 11: 215-222.
- Gambi, M. C. and A. Giangrande. 1985b. Caratterizzazione e distribuzione delle categorie trofiche dei policheti nei fondi mobili del Golfo di Salerno. *Oebalia* 11: 223-240.
- Guelorget, O. and P. Michel. 1979a. Les peuplements benthiques d'un étang littoral languedocien, l'étang du Prévost (Hérault). 1. Etude quantitative de la macrofaune des vases. *Thetys* 9: 49-64.
- Guelorget, O. and P. Michel. 1979b. Les peuplements benthiques d'un étang littoral languedocien, l'étang du Prévost (Hérault). 2. Etude quantitative de la macrofaune des sables. *Thetys* 9: 65-77.
- Ibanez, F. and J. C. Dauvin. 1988. Long-term changes (1977 to 1987) in a muddy fine sand *Abra alba-Melinna palmata* community from the Western English Channel: multivariate time-series analysis. *Mar. Ecol. Prog. Ser.* 49: 65-81.
- Ketchum, B. H. 1983. Estuarine characteristics. In: *Ecosystems of the World, 26. Estuaries and Enclosed Seas*. B. H. Ketchum (ed.): 1-13. Elsevier Scientific Publishing Company. Amsterdam, Oxford and New York.
- Künitzer, A. 1992. Does settlement influence population dynamics of macrobenthos? A case study in the central North Sea. In: *Marine Eutrophication and Population Dynamics. Proceedings of the 25th EMBS* (Ferrara, 1992). G. Colombo et al. (eds.): 285-291. Olsen and Olsen. Fredensborg.
- Levinton, J. S. 1982. *Marine Ecology*. Prentice-Hall Inc., Englewood Cliffs. New Jersey: 526 pp.
- López-Jamar, E., G. González and J. Mejuto. 1986. Temporal changes of community structure and biomass in two subtidal macroinfaunal assemblages in La Coruña bay, NW Spain. *Hydrobiologia* 142: 137-150.
- Martín, D. 1991. *Macroinfauna de una bahía mediterránea. Estudio de los niveles de organización de las poblaciones de anélidos poliquetos*. Ph.D. thesis. Universitat de Barcelona: 456 pp.
- Millet, B. and O. Guelorget. 1994. Spatial and seasonal variability in the relationships between communities and physical environment in a lagoon ecosystem. *Mar. Ecol. Prog. Ser.* 108: 161-174.
- Muus, B. J. 1967. The fauna of Danish estuaries and lagoons. Distribution and ecology of dominating species in the shallow reaches of the mesohaline zone. *Medd. Dan. Fisk. Havunders.* 5: 1-316.
- Pearson, T. H. 1971. The benthic ecology of Loch Linnhe and Loch Eil, a sea-loch system on the west coast of Scotland. III. The effect of the benthic fauna of the introduction of pulp mill effluent. *J. Exp. Mar. Biol. Ecol.* 6: 211-223.
- Pérès, J. M. 1967. Méditerranéan Benthos. *Oceanogr. Mar. Biol. Annu. Rev.* 5: 449-533.
- Pérès, J. M. 1982. Major benthic assemblages. In: *Marine Ecology*. O. Kinne (ed.) 5: 373-521.
- Pérès, J. M. and J. Picard. 1964. Nouveau manuel de bionomie benthique de la mer Méditerranée. *Recl. Trav. Stn. Mar. Endoume. Fac. Sci. Mars.* 31: 1-138.
- Sanders, H. L. 1960. Benthic studies in Buzzards Bay. III. The structure of soft-bottom communities. *Limnol. & Oceanogr.* 5: 138-153.
- Sardá, R., D. Martín, S. Pinedo, A. Dueso and M. J. Cardell. 1995. Seasonal dynamics of shallow soft-bottom communities in Western Mediterranean. In: *The Biology and Ecology of Shallow Coastal Waters. Proceedings of the 28th EMBS* (Creta, 1993). Eletheriou (ed.): 191-198. Olsen and Olsen, Fredensborg.
- Starr, M., J. H. Himmelman and J. C. Therriault. 1990. Direct coupling of marine invertebrate spawning with phytoplankton blooms. *Science* 247: 1071-1074.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates. *Meddelelser fra Danmarks Fiskeri-og Havundersøgelser, ser. Plankton* 4: 1-523.

Wentworth, W. 1972. A scale of grade and class terms for clastic sediments. *J. Geology*. 30: 377-392.

Wolff, W. J. 1973. The estuary as a habitat. An analysis of data on the soft bottom macrofauna of the estuarine area of the rivers Rhine, Meuse, and Scheldt. *Zool. Verh.* 126: 1-242.