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Detritus–Bacteria–Meiofauna interactions in a seagrass bed (*Posidonia oceanica*) of the NW Mediterranean

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Abstract The biochemical composition of the sediment organic matter, and bacterial and meiofaunal dynamics, were monitored over an annual cycle in a *Posidonia oceanica* bed of the NW Mediterranean to test the response of the meiofauna assemblage to fluctuations in food availability. Primary production cycles of the seagrass and its epiphytes were responsible for relatively high (compared to other Mediterranean systems) standing stocks of organic carbon in sediments (from 1.98 to 6.16 mg C g^{-1} sediment dry weight). The biopolymeric fraction of the organic matter (measured as lipids, carbohydrates, and proteins) accounted for only a small fraction (18%) of the total sedimentary organic carbon. About 25% of the biopolymeric fraction was of microphytobenthic origin. Sedimentary organic carbon was mostly refractory (56 to 84%) and probably largely not utilizable for benthic consumers. The biopolymeric fraction of the organic matter was characterized by high carbohydrate concentrations (from 0.27 to 5.31 mg g^{-1} sediment dry weight in the top 2 cm) and a very low protein content (from 0.07 to 0.80 mg g^{-1} sediment dry weight), which may be a limiting factor for heterotrophic metabolism in seagrass sediments. RNA and DNA concentrations of the sediments varied significantly during the year. High RNA and DNA values occurred during the microphytobenthic bloom and in correspondence with peaks of bacterial abundance. Bacteria accounted for a small fraction of the total organic carbon (0.65%) and of the biopolymeric organic carbon (4.64%), whilst microphytobenthos accounted for 3.79% of total organic carbon and for 25.08% of the biopolymeric carbon. Bacterial abundance (from 0.8 to 5.8×10^8 g^{-1} sediment dry weight) responded significantly to seasonal changes of organic matter content and composition and was significantly correlated with carbohydrate concentrations. Bacteria might be, in the seagrass system, an important N storage for higher trophic levels as it accounted for 25% of the easily soluble protein pool and contributed significantly to the total DNA pool (on average 12%). Total meiofaunal density ranged from 236 to 1858 ind. 10 cm^{-2} and was significantly related, with a time lag, to changes in bacterial standing stocks indicating that microbes might represent an important resource. Bacterial abundance and biomass were also significantly related to nematode abundance. These results indicate that bacteria may play a key role in the benthic trophic chain of the Mediterranean seagrass system.

Introduction

One of the most important factors usually invoked for explaining distribution, seasonal cycles and metabolism of benthic communities is food availability (Montagna et al. 1983; Rudnick et al. 1985). However, the quantity of organic matter readily available to benthic consumers is not easy to assess. Generally, the nutritional importance of sediment detritus has been solely equated with its quantity (see Doyle and Garrels 1985). It is evident that the standing stocks of total organic carbon overestimate the labile fraction (i.e. readily utilizable) of the organic pool (Fabiano and Danovaro 1994). Detailed information on the biochemical composition of the sediment organic matter (measured as content of specific labile compounds such as carbohydrates, lipids, proteins and nucleic acids) may be of primary importance to estimate the amounts of readily available food (Fabiano et al. 1995).

Due to their life cycle and high turnover rates, meiofauna are thought to respond rapidly to changes in food availability. Temporal fluctuations of meiofaunal standing stock have been occasionally found to

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correlate to benthic diatoms or phytoplankton biomass (Tietjen 1969; Coull 1970; Montagna et al. 1983; Rudnick et al. 1985). Benthic bacteria have long been hypothesized as major food and carbon sources for meiofauna but, although trophic relationships have been investigated (Montagna 1984), no clear relationships were found (Montagna et al. 1983; Alongi 1988) and the factors which relate to the distribution and activity of meiofaunal communities have not been determined.

In the Mediterranean the most productive submerged aquatic macrophyte is the seagrass *Posidonia oceanica* (Ott 1980). Detrital material derived from the seagrass and exported to the adjacent sediments serves as the major source of organic matter supporting heterotrophic processes (Velimirov 1986, 1987; Velimirov and Walenta-Simon 1992, 1993). Energy flow studies on the seagrass system have shown that only a small portion of primary production is consumed directly by benthic organisms (Velimirov 1986) and that most of the plant material must be fractionated before entering the food chain. In particular, benthic bacteria contribute significantly to the organic carbon pool and, in certain periods of the year, may dominate the total organic carbon from living microbs in the Mediterranean seagrass system (Danovaro et al. 1994a; Danovaro and Fabiano 1995).

Meiofaunal density, community structure and dynamics are less well known in the seagrass *Posidonia oceanica* (Novak 1982) than in other seagrass systems (Bell et al. 1984; Hicks 1986; Walters and Bell 1986; Hall and Bell 1988, 1993). As a result no studies have simultaneously examined the biochemical composition of organic detritus together with bacterial and meiofaunal communities in *Posidonia oceanica* sediments.

In the present study, in order to gather additional information on the nature and quality of the organic matter, an attempt was made to quantify the organic fraction readily utilizable for consumers. Estimates of this were obtained using the major biochemical classes of organic compounds (as the sum of protein, lipid and carbohydrate carbon, sensu Fichez 1991; Danovaro et al. 1993, 1994a; Fabiano and Danovaro 1994). This portion of the sediment organic matter was referred to as the biopolymeric fraction (BPF, Mayer 1989). Changes in benthic bacteria, microphytobenthic biomass (measured as chlorophyll *a*) and the biopolymeric fraction of the organic matter, as well as DNA and RNA concentrations of the sediments, were monitored over an annual cycle. This study was designed to test for the response of bacterial and meiofaunal assemblages to seasonal fluctuations in food availability.

Materials and methods

Study site

This study was conducted from January 1991 to January 1992, at a depth of 4 m in a *Posidonia oceanica* bed in Prelo Bay, Golfo Marconi, Ligurian Sea (NW Mediterranean Sea, Fig. 1). Sediment samples were collected every 2 wk from March to June and on a monthly basis for the rest of the year by SCUBA divers. The study area is sheltered and characterized by the presence of a large *Posidonia oceanica* meadow that forms an almost continuous and dense belt (375 leaves m^{-2}) from a depth of about 0.4 to 9.0 m (Morri et al. 1986). During the study period, the dominant macrofauna in this station, mostly composed by deposit-feeders, included the polychaete *Spio decoratus* Bobretzky, the amphipod *Siphonocetes dellavallei* Stebbing, the bivalve *Dosinia lupinus* (Linnè) and the decapods *Diogenes pugilator* (Roux) and *Hippomedon massiliensis* (Bellan-Santini) (Albertelli et al. 1996).

Sampling

Meiofaunal samples were collected in replicate cores ($n = 2$ to 4, 3.7 cm, diam, 10.7 cm^2 surface area) down to a depth of 12 cm (which appeared to be adequate for quantitative analysis; Danovaro 1993). For bacterial analyses, replicate cores ($n = 3$ to 5) were collected from the same surface sediments (0 to 1 cm) of the meiofaunal cores, using sterile 10 ml syringes and processed within 2 h from collection. The sediment layer of three additional cores (3.7 cm diam) was sectioned into different sediment layers (0–2, 2–4, 4–6, 6–8 and 8–12 cm). Each sediment layer was mixed and frozen at −20°C for the analysis of organic carbon and nitrogen, lipids, proteins, carbohydrates, nucleic acids as well as photosynthetic pigments, water content and grain size.

Environmental parameters

Temperature, salinity and current speed were measured in situ using a current meter (Model SD 2000, Sensordata AS, Bergen) equipped with salinometer (Anderaa Instruments Inc.) and thermometer and placed 20 cm above the sediments for at least 3 h during sampling. Water content of the sediments ($n = 3$) was estimated as the difference between wet and dry (80 °C, 24 h) weight on each sediment

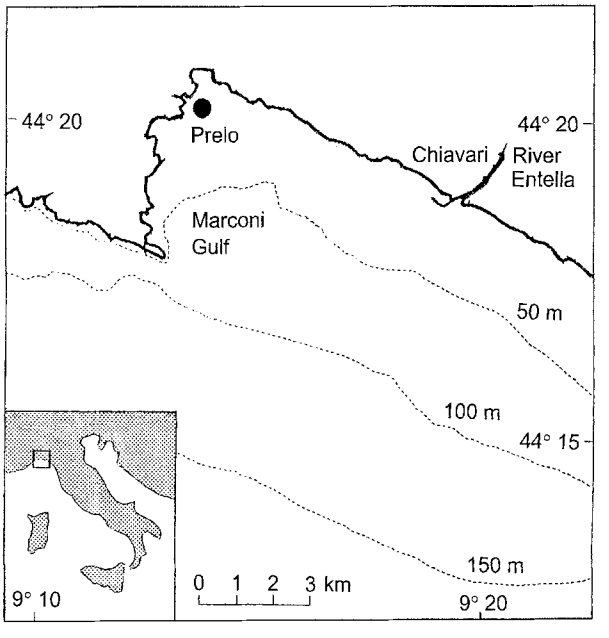

Fig. 1 The sampling station in the Golfo Marconi, Ligurian Sea (NW Mediterranean Sea)

layer. Grain size analysis was carried out using a dry sieve technique (Giere et al. 1988). Redox potential discontinuity (RPD) was visually estimated at the depth at which sediment color turns from brown to black.

Elemental and biochemical composition of sediment organic matter

Total sediment organic carbon (TOC) and nitrogen (TON) were measured, after acidification for 3 h with 0.1 *N* HCl in Ag tins (three drops were usually sufficient for completing the decalcification) for 3 h. The samples (about 200 mg) were then redried at 60 °C and weighed. Analyses were carried out in 2 to 4 replicates per sediment layer using a Carlo Erba CHN-Analyzer. Blanks were made using previously calcinated sediments (450 °C, 2 h). Cyclohexanone-2,4-dinitro-phenilhydrazone was used as standard (Hedges and Stern 1983).

Lipids were extracted from dried sediment samples by direct elution with chloroform and methanol. Analyses were carried out using the methods of Bligh and Dyer (1959) and Marsh and Weinstein (1966). The analysis was carried out on about 1 g of sediment that was sonicated for 30 min in distilled water and organic solvents. This treatment increased extraction efficiency by about 30%.

Protein analyses were performed after extractions with NaOH (0.5 *M*, 4 h) and evaluated according to Hartree (1972), with modification by Rice (1982) to compensate for phenol interference. Extraction efficiency of the first hydrolysis was 35 to 65% of total extractable proteins determined after a total of three hydrolytic steps. Proteins determined in this way were referred to as the easily soluble protein fraction. Concentrations are presented as albumin equivalents. For each analysis about 1 g of sediment was used.

Carbohydrates were analysed according to Gerchakov and Hatcher (1972) and expressed as glucose equivalents. The method is based on the same principles as the commonly used method of Dubois et al. (1956), but is specifically adapted for carbohydrate determination in sediments. Efficiency of the first extraction (on a total of three serial extractions) was about 40%. Absorbance was measured at 485 and 600 nm (for correction of the turbidity). For each analysis about 0.5 g of sediment was used.

Carbohydrate, protein and lipid concentrations were converted to carbon equivalent assuming a conversion factor of 0.40, 0.49 and 0.75, respectively. These factors were calculated from the standard used for the biochemical analyses (i.e. glucose, albumine and tripalmitine) using a CHN Analyzer. The sum of carbohydrate, protein and lipid carbon was referred to as the biopolymeric fraction (BPF) (Mayer 1989; Fichez 1991; Danovaro et al. 1993, 1994a; Fabiano and Danovaro 1994)

Nucleic acids (DNA and RNA) were analyzed according to Lukavsky et al. (1973), with modifications by Fontenvieille and Fevotte (1981) and Zachleder (1984). Briefly, 1 to 2 g of sediment were treated with 2.0 ml of 0.5 *N* perchloric acid, stirred and sonicated three times for 1 min. Hydrolysis and extraction of nucleic acids were carrried out at 70 °C for 15 min. The supernatant was measured at 260 nm for determination of total nucleic acid. DNA was quantified by a light-activated reaction of the diphenylamine reagent, which has proven to be particularly efficient for nucleic acid determination (Jones et al. 1995).

For each biochemical analysis, blanks were made using the same previously calcinated sediments (450 °C, 2 h). All analyses were carried out in four replicates per sediment layer.

Chlorophyll analysis

Chlorophyll *a* analysis ($n = 3$) was carried out according to Lorenzen and Jeffrey (1980). Pigments were extracted from about 1 to 2 g of sediment with 90% acetone. After centrifugation, the supernatant was used to determine the chlorophyll *a* concentration using a spectrophotometer (Model DMS90, Varian). Chlorophyll *a* concentration was converted to carbon content using the conversion factor 30 (Jonge 1980). Chlorophyll carbon was converted to DNA content using the conversion factor 50 (Jones et al. 1995).

Bacterial analysis

Bacterial analysis was carried out as described by Danovaro et al. (1994a). Briefly, each sediment replicate (about 1 cm^3) was added to 10 ml of 0.2 μm filtered seawater with prefiltered formaldehyde (2%). Samples were sonicated three times (Sonifier Tansonic Labor 2000, 50 W for 1 min). The efficiency of bacterial extraction in these sediments (about 75%) has been previously tested by Danovaro et al. (1994b). Subsamples were diluted 100 to 500 times. Portions of the subsamples were stained with Acridine Orange (final concentration 5 mg l^{-1} for 3 min) and filtered on black Nuclepore (polycarbonate, 0.2 μm filters, 25 mm diam). The frequency of dividing cells was estimated (Newell and Christian 1981; Fry 1990). The filters were analyzed using epifluorescence microscopy (Zeiss Universal Microscope) and normalized to dry weight as suggested by Montagna (1982). The contribution by different size classes of bacteria to the total biomass was evaluated by assigning bacteria to different size classes according to Palumbo et al. (1984). Bacterial biovolume was converted to carbon content assuming 310 fg C μm^{-3} (Fry 1990). Data was normalized to dry weight after desiccation (60° C, 24 h). DNA content of bacteria was calculated using the conversion factor 5×10^{-15} g DNA $cell^{-1}$ reported by Simon and Azam (1989). N content of bacteria was calculated from biomass assuming a bacterial C:N ratio of 4.

Meiofaunal analysis

Samples were fixed with a hot (60° C), 4% formaldehyde in 0.4 μm prefiltered seawater solution. Sediments were sieved through 1000 and 37 μm mesh nets. The fraction remaining on the 37 μm sieve was centrifuged three times with Ludox HS (density 1.18 g cm^{-3}) as described by Heip et al. (1985). All meiobenthic animals were counted and classified per taxon under a stereo microscope after staining with Rose Bengal (0.5 g l^{-1}).

Data analysis

Differences in sedimentological, microbial and meiofaunal parameters were tested using one-way analysis of variance (ANOVA). Microbial and meiofaunal data were log $(x + 1)$ transformed when homogeneity of variance was rejected by an F_{max} test. The integrated (0 to 12 cm) concentrations of carbohydrates, proteins, lipids and pigments were related to total meiofaunal density (0 to 12 cm). Only the surface layer was considered while testing for correlation of bacterial parameters (0 to 1 cm) and sediment chemistry (0 to 2 cm). A Spearman rank correlation analysis was used initially to examine relationships among organic chemistry, bacteria, meiofauna and other environmental factors (Sokal and Rohlf 1969).

A canonical correspondence analysis (CANOCO, Ter Braak 1988) was performed on the data set in order to investigate the relationships between environmental variables and meiofaunal parameters during any given sampling period. Redundant variables were excluded after a preliminary canonical correspondence analysis. Data were 4th-root transformed before analysis.

Results

Environmental parameters

Data on temperature, salinity, pore water content, grain size, current speed and RPD depth are reported in Table 1. Temperature varied with season and ranged between 12.3 and 24.3° C (February and September, respectively). Temperatures higher than 20°C only occurred in summer (June to September). Salinity ranged between 36.98 and 38.31‰ (June and January 1991, respectively) and varied little with season. Pore water content in the top 2 cm of the sediment ranged between 22.1 ± 1.40 and 55.7 ± 1.74% (February and early May, respectively). Pore water content integrated to a depth of 12 cm ranged between 21.3 ± 2.76 and 48.6 ± 3.36% (February and late April, respectively). Mean grain size generally varied between 0.384 and 0.842 mm (October and July, respectively) with the exception of early April (1.268 mm). Current velocity at 20 cm above the sediments was very low ranging between 0.4 ± 0.65 and 2.9 ± 0.43 cm s^{-1} (July and October, respectively). RPD depth varied strongly with season and ranged between 4.0 and 12.0 cm (January 1991 and early April, respectively). In general, RPD depth values were higher in spring and autumn and lower in summer and winter.

Elemental and biochemical composition of sediment organic matter

TOC and TON concentrations and C:N ratio fluctuated significantly during the year (Fig. 2). Highest TOC concentrations occurred in January 1991 and early April (6.16 ± 1.40 and 4.58 ± 0.51 mg C g^{-1} of sediment dry weight, respectively) and lowest in January 1992 (1.98 ± 0.10 mg C g^{-1} of sediment dry weight). TON concentrations presented two marked peaks: in January 1991 (0.46 ± 0.09 mg C g^{-1}) and in April (0.50 ± 0.03 mg C g^{-1}); and low concentrations during the rest of the year. C:N ratio ranged between 6.78 (late April) and 13.96 (late March). Carbohydrate, protein and lipid content of the sediments are illustrated in Fig. 3a, b and c, respectively. The three biochemical components showed common patterns characterized by high concentrations in January 1991 and April and low values during the rest of the year. Chlorophyll *a* concentrations were characterized by three main peaks: January and May 1991 and January 1992 (4.96 ± 0.49, 4.21 ± 0.67, 5.25 ± 1.06 μg g^{-1} sed. DW, respectively; Fig. 4). Integrated values (0 to 12 cm) of carbohydrate, protein and lipid content followed a pattern similar to that reported for the top 2 cm (Table 2).

The results of the correlation analysis applied to 0–12 cm integrated values is reported in Table 3. Chlorophyll *a* correlated significantly with all the organic compounds: carbohydrates ($p < 0.01$), proteins ($p < 0.01$), lipids ($p < 0.01$), organic carbon ($p < 0.01$) and organic nitrogen ($p < 0.01$).

Nucleic acid (DNA, RNA) content of the sediments and the RNA:DNA ratio are reported in Fig. 5a, b and c, respectively. Highest DNA concentrations occurred in spring (early May, 16.42 ± 1.41 μg g^{-1} sed. DW) in correspondence to the microphytobenthic bloom. RNA content reached a marked peak in late April (30.69 ± 3.61 μg g^{-1} sed. DW), and RNA:DNA ratio showed the highest value (1.69) in correspondence to one of the peaks of bacterial abundance.

Table 4 reports the carbon contribution of BPF, chlorophyll and bacterial biomass to the total organic

Table 1 Temperature, salinity, water content (in the uppermost 2 cm of the sediments and integrated to a depth of 12 cm, mean grain size, current speed and redox potential discontinuity depths (*RPD*) in Prelo Bay during 1991 to 1992 study period (*nd* not determined)

Sampling dates	Temperature (°C)	Salinity (‰)	Water content				Grain size (mm)	Current speed (cm s^{-1})		RPD (cm)
			0–2 cm (%)	[SE]	10–12 cm (%)	[SE]			[SE]	
17 Jan 91	13.5	38.31	52.8	[0.74]	41.7	[5.91]	0.777	nd	nd	4.0
20 Feb 91	12.3	38.13	22.1	[1.40]	21.3	[2.76]	0.585	nd	nd	4.5
21 Mar 91	14.5	38.04	27.3	[0.69]	30.9	[4.08]	0.658	2.5	[0.48]	8.0
08 Apr 91	14.6	38.22	50.5	[6.08]	42.3	[8.26]	1.268	2.4	[0.37]	12.0
02 Apr 91	14.8	38.13	44.7	[3.36]	48.0	[3.36]	0.573	nd	nd	10.0
08 May 91	17.3	37.64	55.7	[1.74]	40.7	[7.70]	0.430	nd	nd	8.0
29 May 91	18.3	37.64	31.2	[1.75]	35.1	[3.09]	0.487	1.6	[0.20]	6.0
28 Jun 91	20.5	36.98	28.6	[3.23]	32.7	[2.51]	0.741	2.1	[0.57]	8.0
18 Jul 91	21.3	37.91	26.9	[0.19]	26.0	[5.23]	0.842	0.4	[0.65]	9.0
01 Aug 91	23.6	37.55	41.7	[0.91]	39.1	[3.37]	0.451	0.6	[0.74]	9.0
05 Sep 91	24.3	38.13	40.5	[9.04]	31.2	[9.04]	0.764	2.3	[1.39]	11.5
31 Oct 91	18.5	38.04	39.2	[0.38]	38.7	[0.38]	0.384	2.9	[0.43]	11.0
30 Nov 91	15.2	37.07	38.9	[3.09]	31.2	[3.09]	0.641	0.6	[0.69]	11.5
23 Dec 91	14.5	38.22	35.7	[1.95]	37.3	[1.95]	0.797	2.7	[0.69]	9.5
07 Jan 92	13.5	37.99	40.8	[2.33]	37.1	[2.33]	0.685	1.4	[0.10]	6.0

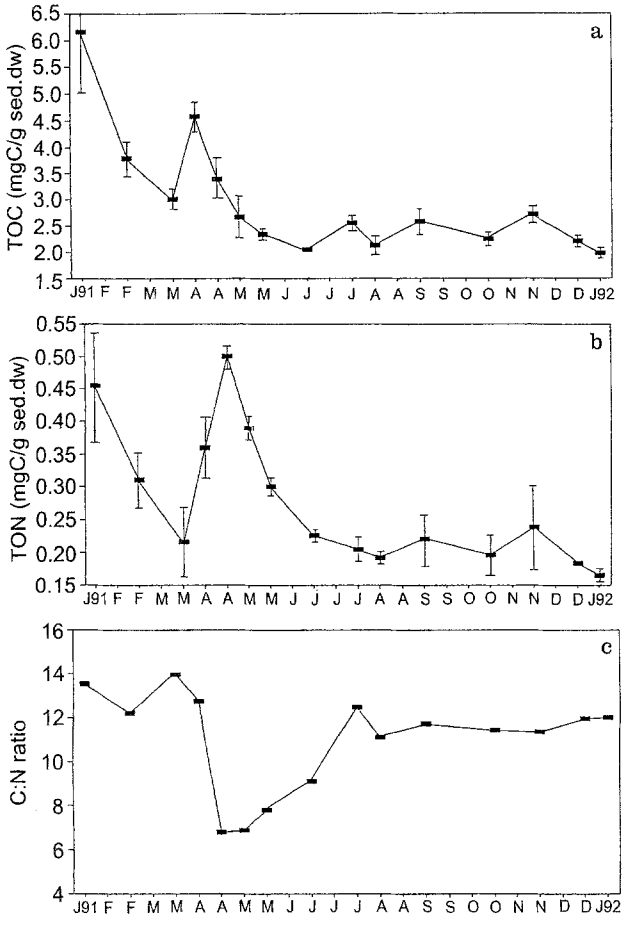

Fig. 2 Seasonal variations in the elemental composition of organic matter: (**a**) total organic carbon (*TOC*), (**b**) total organic nitrogen (*TON*), and (**c**) C:N ratio in the uppermost 2 cm sediment layer (mean values ± SD)

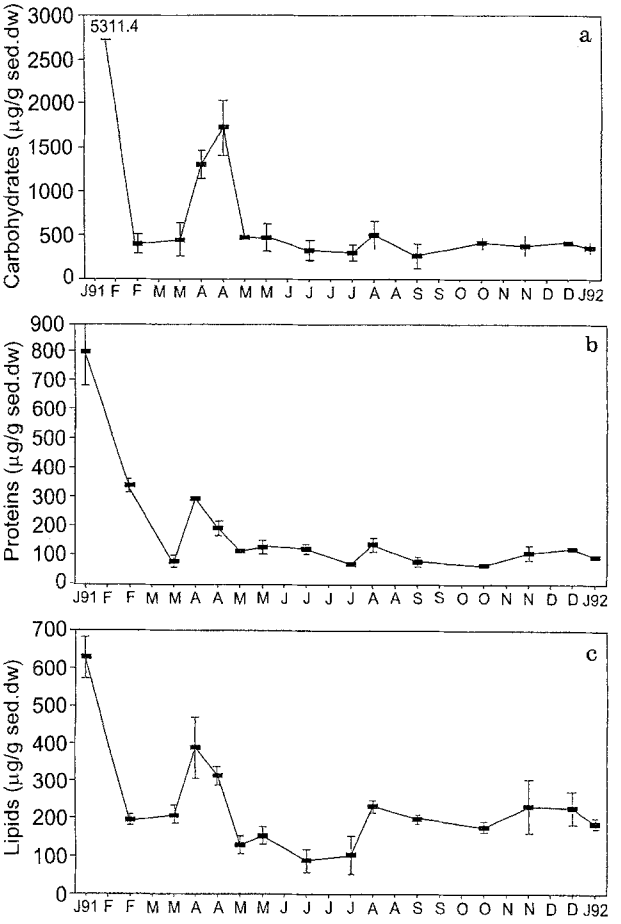

Fig. 3 Seasonal variations in the concentrations of (**a**) carbohydrates, (**b**) proteins and (**c**) lipids in the uppermost 2 cm sediment layer (mean values ± SD)

carbon pool. Carbon of the BPF accounted for a small fraction of the total organic carbon pool, ranging between 9.13 and 48.58% (July and January 1991, respectively, on average 18%). Microphytobenthic carbon accounted for a negligible fraction of the TOC (on average 3.79%), but for a more important fraction of the BPF-C (on average 25.08%). Microphytobenthic DNA contributed on average 18.9% to the total DNA pool (Table 5), ranging from 12.7 (February) to 32.0% (January 1992).

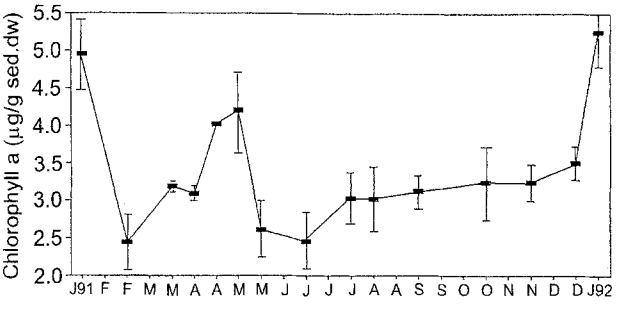

Fig. 4 Seasonal variations in photosynthetic pigments (as chlorophyll *a* concentrations, $\mu g\,g^{-1}$ sed. DW) in the uppermost 2 cm sediment layer (mean values ± SD)

Bacterial abundance and biomass

Bacterial abundance and biomass (Fig. 6a, b) fluctuated significantly over time with distinct seasonality. Bacterial abundance and biomass were significantly higher in summer (from June to September, *F*-ratio 3.48 and 4.70, $p < 0.05$ and $p < 0.01$, respectively) than in spring or autumn. Highest bacterial densities occurred in January 1991 and July (5.80 ± 1.05 and $5.58 \pm 0.21 \times 10^8$ cells g^{-1} sed. DW) and lowest in February ($0.83 \pm 0.19 \times 10^8$ cells g^{-1} sed. DW). Similarly, bacterial biomass ranged from 4.93 ± 0.76 µg C g^{-1} sed. DW in February to 44.35 ± 2.24 µg C g^{-1} sed. DW in July. Mean cell biomass (Fig. 6c) showed peaks in July and November (7.9 and 7.8×10^{-11} mg C $cell^{-1}$). Frequency of dividing cells ranged between 1.41 ± 0.20 and 2.89 ± 0.57% (March and December, respectively).

Table 2 Integrated values (0 to 12 cm) of chlorophyll *a*, carbohydrate, protein and lipid concentration. Chlorophyll *a*, five sediment layers, means of 3 replicates per layer with standard errors [SE]. Biochemical components: five sediment layers, means of 4 replicates per layer with standard errors [SE]

Sampling dates	Chlorophyll *a* ($\mu g g^{-1}$)	[SE]	Carbohydrates ($\mu g g^{-1}$)	[SE]	Proteins ($\mu g g^{-1}$)	[SE]	Lipids ($\mu g g^{-1}$)	[SE]
17 Jan 91	4.38	[0.64]	6506.27	[975.70]	1704.17	[529.89]	624.84	[72.98]
20 Feb 91	2.99	[0.37]	377.99	[40.48]	192.03	[25.72]	166.79	[30.31]
21 Mar 91	3.10	[0.16]	345.17	[48.70]	96.03	[14.28]	193.81	[22.04]
08 Apr 91	3.51	[0.64]	707.23	[319.04]	216.59	[51.00]	278.31	[88.36]
22 Apr 91	3.97	[0.38]	1303.97	[230.31]	183.73	[27.27]	264.79	[40.78]
08 May 91	3.57	[0.36]	681.59	[150.88]	120.22	[22.14]	225.81	[85.17]
29 May 91	3.06	[0.35]	417.83	[191.23]	390.08	[204.54]	220.60	[69.46]
28 Jun 91	2.74	[0.18]	348.55	[42.58]	140.75	[16.11]	82.77	[19.22]
18 Jul 91	3.24	[0.39]	306.51	[72.14]	66.16	[7.74]	77.21	[19.09]
01 Aug 91	3.11	[0.31]	428.30	[69.54]	99.72	[20.91]	191.95	[27.41]
05 Sep 91	3.03	[0.49]	494.62	[353.14]	100.86	[19.74]	191.63	[38.44]
31 Oct 91	3.03	[1.24]	425.95	[72.21]	71.99	[8.79]	176.77	[29.48]
30 Nov 91	2.94	[0.50]	362.01	[68.40]	101.30	[8.52]	205.60	[63.34]
23 Dec 91	3.15	[0.62]	454.76	[57.47]	110.44	[8.55]	224.54	[61.80]
07 Jan 92	3.26	[1.06]	292.30	[70.61]	105.75	[33.63]	157.29	[20.29]

Table 3 Correlation analysis between some environmental and sedimentary parameters collected in the Golfo Marconi: temperature (*T*), salinity (*S*), water content (*WC*) mean grain size (*MGS*), redox potental discontinuity depth (*RPD*), and concentration of chlorophyll *a* (*CHL*), carbohydrates (*CHO*), proteins (*PRT*), lipids (*LIP*), total organic carbon (*TOC*) and nitrogen (*TON*), and the carbon of the bipolymeric fraction (*BPF-C*). The biochemical parameters are relative to 0 to 12 cm

	T	S	WC	MGS	RPD	CHL	CHO	PRT	LIP	TOC	TON	BPF-C
T	1.000											
S	−0.352	1.000										
WC	−0.077	0.186	1.000									
MGS	−0.171	0.290	0.101	1.000								
RPD	0.375	−0.113	0.196	0.246	1.000							
CHL	−0.378	0.516	0.684	0.169	−0.247	1.000						
CHO	−0.284	0.340	0.474	0.134	−0.445	0.801	1.000					
PRT	−0.293	0.292	0.378	0.135	−0.546	0.714	0.975	1.000				
LIP	−0.395	0.426	0.612	0.153	−0.320	0.823	0.931	0.912	1.000			
TOC	−0.482	0.486	0.395	0.429	−0.293	0.749	0.814	0.798	0..837	1.000		
TON	−0.393	0.309	0.576	0.159	−0.072	0.808	0.584	0.466	0.605	0.730	1.000	
BPF-C	−0.374	0.403	0.505	0.244	−0.381	0.844	0.975	0.946	0.950	0.889	0.660	1.000

Bacterial abundance and biomass correlated significantly with carbohydrate content of the sediments ($r = 0.56$, $p < 0.05$). Bacterial biomass accounted for a small fraction of total organic carbon (from 0.13 to 1.74%, in February and July, respectively) but for a more significant fraction of the labile organic pool (from 0.61 to 19.04% in April and July, respectively, Table 4). Bacterial contribution to the total organic nitrogen pool, protein and DNA content of the sediments is reported in Table 5. Bacterial nitrogen accounted, on average, for 1.94% of total nitrogen and for 24.29% of protein nitrogen. Bacterial DNA accounted, on average, for 12% of the total sedimentary DNA pool and ranged between 3.62% in February and 35.97% in July. Bacteria and microphytobenthos accounted together for about 30% of the DNA pool.

Meiofauna

Meiofaunal density fluctuated significantly over time. Highest density occurred in October 1858 ± 246 and lowest density in early April 236 ± 62 ind $10\,cm^{-2}$ (Fig. 7a). Total meiofauna density correlated significantly with bacterial abundance and biomass ($r = 0.58$ and 0.57, respectively, $p < 0.05$). However, considering the data set from February 1991 (in January 1991 environmental and bacterial parameters were affected by a strong allochthonous input characterized by the presence of land material), a highly significant relationship was found with a time lag of 2 mo ($r = 0.782$, $p < 0.01$). Nematodes were dominant, accounting for 44% of total density (Fig. 7b), and correlated significantly, with the same time lag, only with bacterial parameters

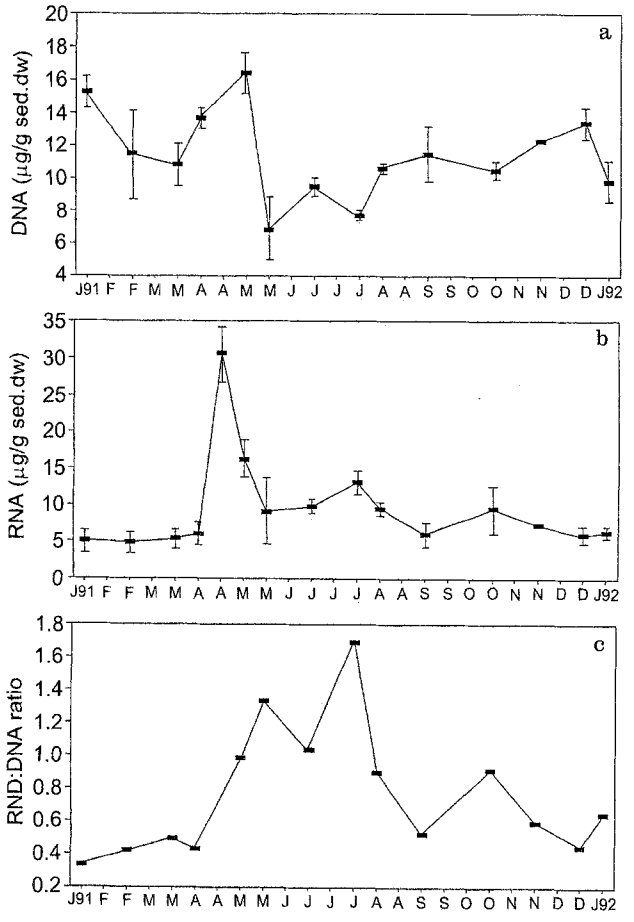

Fig. 5 Seasonal variations in (a) DNA and RNA concentrations and RNA:DNA ratio in the uppermost 2 cm sediment layer (mean values ± SD)

(abundance and biomass: $r = 0.81$ and $r = 0.80$, respectively, $p < 0.01$). Harpacticoids were the second most important taxon, representing 33% of total meiofauna density. A marked peak in harpacticoid copepod density occurred in October (1293 ± 189 ind. $10\,cm^{-2}$; Fig. 7c) and correlated significantly but negatively with chlorophyll *a* content ($r = -0.68$, $p < 0.01$). Polychaetes were the third most important taxon accounting for 8% of total meiofaunal density. They were followed by turbellarians, the density of which fluctuated irregularly during the year (average; 5% of total meiofaunal density). Oligochaetes, ostracods and bivalves accounted for less than 3% of total meiofaunal density and showed highest densities in November, October and April, respectively.

Multivariate analysis

The results of the CANOCO analysis allowed identification of some relationships between meiofauna, bacteria and other environmental variables (Fig. 8a, b, c). Both axes were significant. Superimposing the three outputs it is possible to identify which environmental and biological variables are related to the main meiofaunal taxa at each sampling time. Nematodes were clearly associated, in summer (July, August and September), with high bacterial densities and high concentrations of the biopolymeric fraction; in autumn (late October), copepods were associated with high RNA concentrations and high RNA:DNA ratios. Oligochaetes, nemertins and, to a lesser extent, polychaetes were associated with increasing TOC

Table 4 Amounts (µg C g^{-1} sed. DW) of different components of the organic matter in the total organic carbon pool (*TOC*, top 2 cm): microphytobenthic carbon (*CHL-C*, converted from chlorophyll *a* using a factor 30, Jonge 1980) and carbon of the biopolymeric fraction as sum of lipid, protein and carbohydrate carbon (*BPF-C*). Contribution (%) of microphytobenthos to biopolymeric organic carbon (*CHL-C/BPF-C*), bacterial carbon to total organic carbon (*B-C/TOC*) and bacterial carbon to biopolymeric carbon (*B-C/BPF – C*)

Sampling dates	TOC (µg C g^{-1})	CHL-C (µg C g^{-1})	BPF-C (µg C g^{-1})	BPF-C/TOC (%)	CHL-C/TOC (%)	CHL-C/BPF-C (%)	B-C/TOC (%)	B-C/BPF-C (%)
17 Jan 91	6157.11	148.69	2991.05	48.58	2.41	4.97	0.56	1.16
20 Feb 91	3789.70	73.19	472.39	12.47	1.93	15.49	0.13	1.04
21 Mar 91	3007.62	95.65	369.57	12.29	3.18	25.88	0.17	1.39
08 Apr 91	4580.17	92.64	959.03	20.94	2.02	9.66	0.17	0.79
22 Apr 91	3393.14	120.60	1020.90	30.09	3.55	11.81	0.18	0.61
08 May 91	2664.96	126.16	340.64	12.78	4.73	37.04	0.71	5.57
29 May 91	2339.65	78.33	363.21	15.52	3.35	21.57	0.74	4.78
28 Jun 91	2050.95	73.77	258.43	12.60	3.60	28.55	0.53	4.19
18 Jul 91	2550.46	90.95	232.94	9.13	3.57	39.04	1.74	19.04
01 Aug 91	2131.44	90.66	441.21	20.70	4.25	20.55	1.13	5.47
05 Sep 91	2586.62	94.06	293.89	11.36	3.64	32.01	0.67	5.91
31 Oct 91	2245.34	97.47	329.15	14.66	4.34	29.61	0.88	6.02
30 Nov 91	2712.94	97.47	378.52	13.95	3.59	25.75	0.95	6.83
23 Dec 91	2198.38	105.15	394.69	17.95	4.78	26.64	0.73	4.05
07 Jan 92	1980.30	157.64	330.51	16.69	7.96	47.69	0.47	2.79

Table 5 Amounts of total organic nitrogen (*TON*), proteins, protein nitrogen (*PRT-N*) and relative contribution to TON (*PRT-N/TON*); concentrations of bacterial carbon (*B-C*) and nitrogen (*B-N*) and relative contribution of B-N to PRT-N and TON; concentrations of total DNA (*DNA*), bacterial DNA (*B-DNA*) and bacterial contribution to total DNA pool in the sediments (*B-DNA/DNA*); concentration of microalgae DNA (*CHL-DNA*, calculated from C:DNA = 50, Jones et al. 1995) and contribution to total DNA pool (*CHL-DNA/DNA*). Data from top 2 cm of the sediment for chemical analyses and top 1 cm for bacterial parameters

Sampling dates	TON ($\mu g\,g^{-1}$)	Proteins ($\mu g\,g^{-1}$)	PRT-N ($\mu g\,g^{-1}$)	PRT-N/TON (%)	B-C ($\mu g\,C\,g^{-1}$)	B-N (μg^{-1})	B-N/PRT-N (%)	B-N/TON (%)	DNA ($\mu g\,g^{-1}$)	B-DNA ($\mu g\,g^{-1}$)	B-DNA/DNA (%)	CHL-DNA ($\mu g\,g^{-1}$)	CHL-DNA/DNA (%)
17 Jan 91	455.00	804.59	128.73	28.29	34.71	8.68	6.74	1.91	15.27	2.90	18.99	2.97	19.48
20 Feb 91	310.46	342.55	54.81	17.65	4.93	1.23	2.25	0.40	11.53	0.42	3.62	1.46	12.70
21 Mar 91	215.40	80.15	12.82	5.95	5.15	1.29	10.05	0.60	10.86	0.48	4.40	1.91	17.61
08 Apr 91	359.24	295.09	47.21	13.14	7.56	1.89	4.00	0.53	13.69	0.55	4.03	1.85	13.53
22 Apr 91	500.66	195.00	31.20	6.23	6.25	1.56	5.00	0.31	8.64	0.49	5.73	2.41	27.91
08 May 91	389.01	115.35	18.46	4.74	18.98	4.75	25.71	1.22	16.42	1.41	8.61	2.52	15.36
29 May 91	119.10	128.42	20.55	17.25	17.35	4.34	21.11	3.64	6.83	1.42	20.73	1.57	22.94
28 Jun 91	225.80	123.25	19.72	8.73	10.83	2.71	13.73	1.20	9.52	0.82	8.64	1.48	15.50
18 Jul 91	204.05	71.91	11.51	5.64	44.35	11.09	96.37	5.43	7.76	2.79	35.97	1.82	23.45
01 Aug 91	191.79	138.59	22.17	11.56	24.15	6.04	27.22	3.15	10.64	1.73	16.30	1.81	17.04
05 Sep 91	220.51	80.05	12.81	5.81	17.38	4.34	33.91	1.97	11.48	1.25	10.91	1.88	16.39
31 Oct 91	196.29	66.55	10.65	5.42	19.81	4.95	46.51	2.52	10.51	1.46	13.90	1.95	18.55
30 Nov 91	238.89	109.69	17.55	7.35	25.84	6.46	36.81	2.70	12.31	1.65	13.43	1.95	15.83
23 Dec 91	183.73	123.58	19.77	10.76	15.97	3.99	20.19	2.17	13.46	1.20	8.94	2.10	15.62
07 Jan 92	164.62	97.21	15.55	9.45	9.21	2.30	14.81	1.40	9.84	0.69	6.98	3.15	32.04

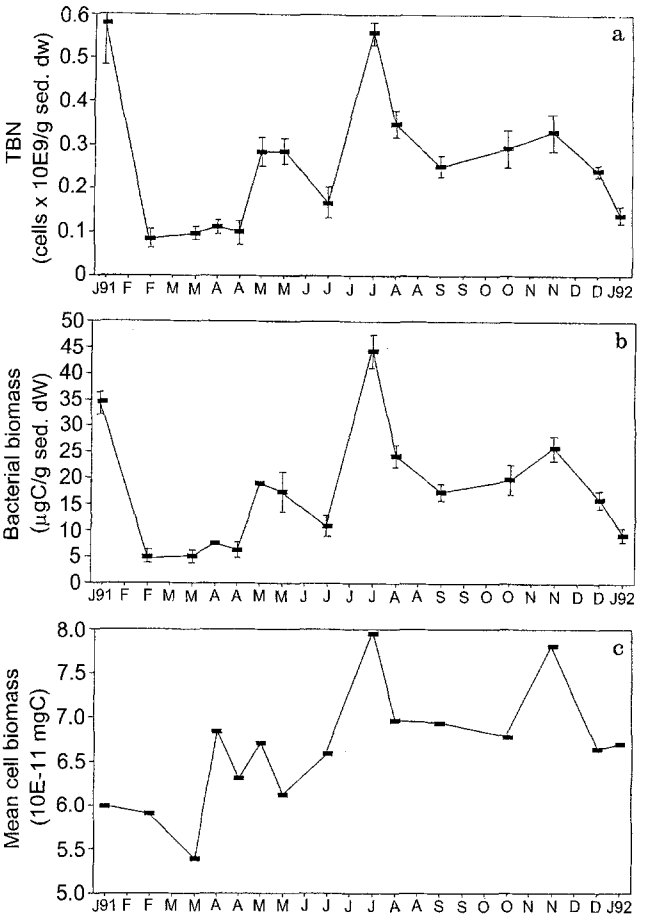

Fig. 6 Temporal changes in bacterial parameters (**a**) total bacterial number (*TBN*), (**b**) bacterial biomass (mean values ± SD), and (**c**) mean biomass $cell^{-1}$ in the uppermost 2 cm sediment layer

and protein concentrations (in March, May and November).

Discussion

Seasonal changes of food available for benthic metabolism

The results presented here suggest that total organic carbon pools in sediments are driven by primary production cycles of *Posidonia oceanica* and its epiphytes. In the study area, primary production values of this seagrass were high (about 311 g $DW\,m^{-2}\,yr^{-1}$, Boyer 1991), and since grazers are almost lacking (Ott 1981; Velimirov 1989), the seagrass leaves, as evident from field observations, are released to the sediment especially between late August and October. Organic carbon and nitrogen contents in the seagrass bed were about ten times higher than those observed at similar depths out of the seagrass bed in the same area (Fabiano et al. 1995) or in subtidal sediments of the

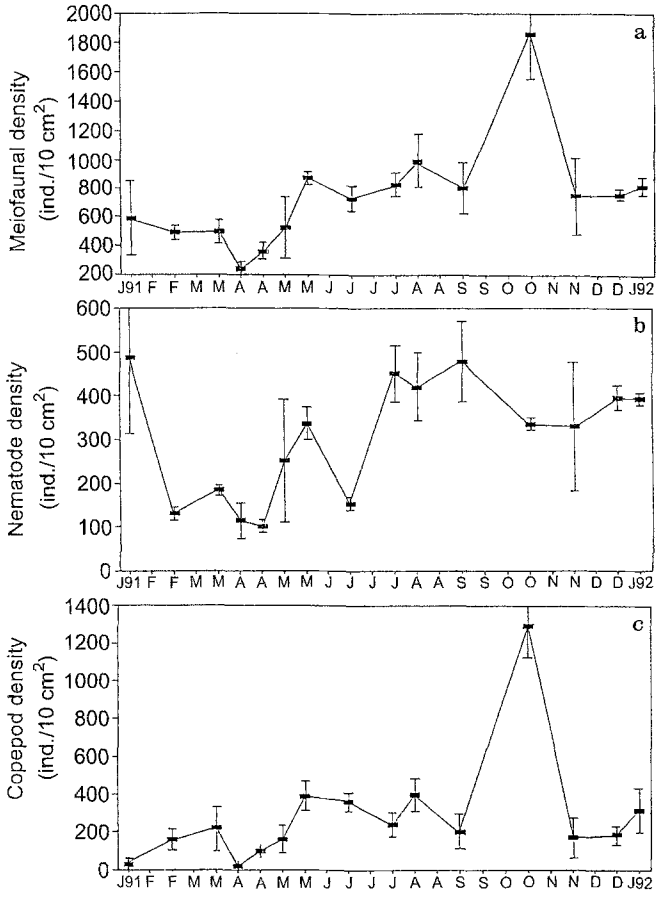

Fig. 7 Seasonal changes in meiofaunal assemblage. (**a**) Total meiofaunal density, (**b**) nematode density and (**c**) copepod density (mean values ± SD)

western Mediterranean Sea (Delille et al. 1990). Seasonal trends in the composition of organic matter between January 1991 and January 1992 were different from those reported in the previous sampling year (Danovaro et al. 1994a), when a much more massive release of vascular-plant detritus was observed in autumn. This input determined, in November 1990, high TOC, TON, lipid, protein and carbohydrate concentrations in the sediments. In contrast, all concentrations of the biochemical components of the organic matter were relatively low during the rest of the year.

Since the proximate composition of the *Posidonia oceanica* leaves and its epiphytes is highly refractory (Lawrence et al. 1989), the phyto-detritus accumulated in the sediments of Prelo Bay may not be directly utilizable by benthic consumers. In this regard, Kenworthy and Thayer (1984) demonstrated that, under in situ conditions and regardless of the concentration of organic matter in the sediments, 50 to 60% of the organic carbon of the seagrass leaves was lost within 170 d. Therefore, in seagrass sediments, despite a large input of organic matter from the seagrass leaves and their epiphytes, only a very small fraction is probably directly available to consumers (Kenworthy and Thayer 1984). In contrast, the microphytobenthic bloom in spring significantly added to the available organic carbon (BPF) in the system. As a result of the low contribution of BPF carbon to the total organic carbon pool, however, most of the sediment organic carbon (51 to 91%) was refractory (geopolymeric sensu Mayer 1989). Therefore, while the high TOC concentrations might be due to the accumulation of seagrass

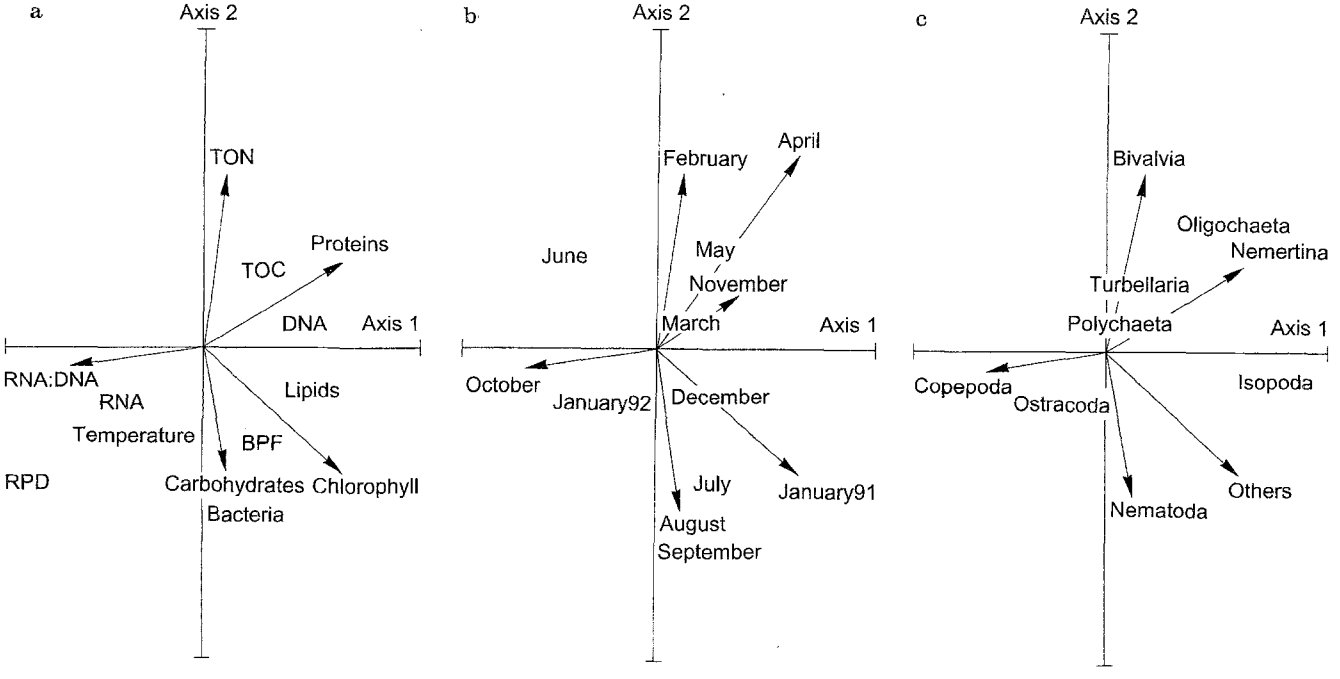

Fig. 8 Ordination of data defined by canonical correspondence analysis: (**a**) environmental parameters, organic matter composition and bacteria, (**b**) sampling periods, and (**c**) meiofaunal composition. Data were 4th-root transformed

leaves or to allochthonous inputs (such as in January 1991), the high concentrations of BPF-C were explained by the microphytobenthic bloom.

Analysis of the biochemical composition of the organic matter provided evidence that sediment organic matter was of low nutritional value due to the dominance of carbohydrates (which may include some structural carbohydrates of the seagrass debris) and a low protein content. Kenworthy and Thayer (1984) demonstrated that structural carbohydrates (as cell wall constituents) in *Zostera marina* leaves account for 31.8% of total carbohydrates. Proteins accounted for a very small fraction of the total nitrogen pool (on average about 10.5%; Table 5), indicating that most of the nitrogen was bound in a refractory complex and probably was not directly utilizable by consumers. As a result, despite the high standing stock of organic carbon, soluble proteins (here used as a measure of the readily digestible fraction) may be, in the seagrass bed, a limiting factor for heterotrophic metabolism.

Analysis of the seasonal changes in nucleic acid concentrations may provide additional information on the characteristics of the sediment organic matter (Danovaro et al. 1993). Analysis of the bacterial and microalgal contribution to the total DNA pool (Table 5) revealed that bacteria accounted, on average, for only 12% of total DNA, while microphytobenthos accounted for 18.9%. Therefore, most of the DNA pool is of unknown origin. However, in July the contribution of the two components rose to about 56%, suggesting that the RNA:DNA ratio, in certain periods of the year, may partially reflect variations in the activity of the microbial assemblages. Another interesting point is that the major DNA peak in spring followed the RNA peak. If we assume that, in general terms, DNA represents an index of biomass and the RNA content changes in relation to the processes of synthesis (Danovaro et al. 1995a), the patterns described above indicated an enhancement of the metabolic activity two weeks before the biomass peak.

Bacterial dynamics in relation to food quality and quantity

Mediterranean seagrass sediments are characterized by a large spatial heterogeneity as suggested by changes in mean grain size and water content. However, the low intercore variability of the bacterial densities and the lack of any correlation with the sedimentary parameters suggest that sedimentary structure had a limited influence on benthic bacterial dynamics. Previous investigations in a seagrass meadow demonstrated that changes in bacterial abundance were related to seasonal changes in temperature, food resources (labile organic matter and inorganic nutrients) and primary production (Danovaro et al. 1994a; Danovaro and Fabiano 1995). Data presented here suggest that bacterial abundance and biomass, in the seagrass sediments of Prelo Bay, were significantly enhanced by the organic matter inputs. Highest bacterial densities were observed in correspondence to the winter accumulation of vegetal debris (January 1991), after microphytobenthic bloom in May and at the end of the seasonal cycle in *Posidonia oceanica* (from July to November). All organic carbon inputs increased the average cell biomass of bacteria (Fig. 6c). Fluctuations of bacterial abundance and biomass were found to reflect, at least partially, changes in carbohydrate content. All the reported inputs of organic matter were, indeed, dominated by carbohydrates of both labile (due to microphytobenthos) and/or structural composition (due to seagrass leaves or, in January 1991, to terrigenous material).

Bacteria accounted for a large fraction of the protein-N pool (on average about 25%, Table 5). Therefore, it is likely that bacteria represent a suitable N source in potentially N limited environments (Newell and Field 1983). This was particularly evident in summer, when sedimentary organic matter was characterized by low N concentrations. The role of bacteria as a source of important precursors for heterotrophic metabolism was further confirmed by the significant contribution of bacterial DNA to the total DNA pool (about 12%).

Meiofaunal response to seasonal changes in food availability

Meiofaunal abundance was comparable to densities reported in other subtidal sandy sediments of the Mediterranean (see Soyer 1985 for a review) or seagrass environments (Novak 1982; Elmgren et al. 1984; Hall and Bell 1993). Although nematodes were dominant based on annual abundance, harpacticoid copepods represented an important fraction of seagrass meiofauna and were dominant in the October to November period. This community composition is typical of phytal assemblages and is consistent with previous investigations on seagrass blades (Lewis and Hollingworth 1982; Novak 1982; Coull et al. 1983; Hicks 1985). As suggested by Hall and Bell (1993), this may be explained by the trophic coupling between copepods and the seagrass epiphytes (particularly abundant in autumn, Boyer 1991). Interestingly, due to the higher harpacticoid density, seagrass meiofauna was characterized by a seasonality different from that observed at a similar depth, in the same year, in sandy sediments out of the seagrass bed (Danovaro et al. 1994c, 1995b).

The results of the present study indicate that meiofaunal dynamics in the seagrass bed of the Golfo Marconi were not significantly related to temperature or to any other physical factor, but were closely coupled to seasonal changes in food availability. As suggested by Tenore (1983), the relative importance of bacteria in the nutrition of benthic assemblages

depends on the quality of the organic carbon and nitrogen sources in the sediments. In the *Posidonia oceanica* system high quantity of organic material was offset by low availability to consumers (low BPF). A strong relationship between bacterial abundance and meiofaunal abundance was found when data were tested for time lags ($r = 0.782$, $p < 0.01$). Such a positive correlation suggests that microbes might be an important food resource in Prelo Bay. In particular, bacteria, as suggested by the significant positive correlation with carbohydrates, may represent the link between detrital particles and benthic consumers.

The significant relationship between bacteria and meiofauna is consistent with results reported by Findlay and Tenore (1982), which demonstrated that deposit-feeders incorporate more nitrogen from associated microbes than from the detritus itself. The relationships between meiofauna and nematodes with bacteria could indicate a preference for bacteria over microphytobenthos in the diet of this meiofaunal assemblage. This result is consistent with the experimental findings of Montagna and Bauer (1988) and other field investigations carried out in cold seeps (Montagna et al. 1987). Similarly, Tenore et al (1982) found a highly significant and positive correlation between bacterial parameters and nematode density. In this regard, Warwick (1987) reported that the structure of the nematode assemblage associated with detritus was dominated by selective deposit feeders and that bacteria may represent the most suitable food source for other nematodes as well. In contrast, Montagna (1984) found that diatom carbon was preferred, and Montagna et al. (1983) found diatoms positively correlated with meiofauna. On a spatial scale (transect with different depths), Meyer-Reil and Faubel (1980) reported an inverse relation between total meiofauna and bacterial biomass.

Further confirmation of the importance of bacteria for the community structure of the meiobenthos is provided by CANOCO analysis. In particular, as evident from Fig. 8a, bacterial biomass, carbohydrates and the BPF were closely associated and overlap with nematode density in the period between July and September. The results of this analysis suggest that the relationship between nematodes and bacteria, even though significant in the 13-mo investigation, was much more significant in certain periods of the year (such as in summer) when bacterial biomass and organic matter availability represented a suitable food source for consumers. Further confirmation of this conclusion is that seasonal changes in the trophic structure of the nematode assemblage are dependent upon the food sources (Danovaro 1993; Danovaro et al. in preparation). Selective and nonselective deposit-feeders (Type 1A and 1B, respectively, Wieser 1953; e.g. genera *Nemanema*, *Axonolaimus* and *Daptonema*) were found to dominate in periods of high bacterial biomass. These findings are consistent with the hypothesis that food availability (driven by microbial biomass) is the potential limiting factor for meiofaunal dynamics in the seagrass (*Posidonia oceanica*) sediments.

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