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MEIOFAUNA AND BENTHIC MICROBIAL BIOMASS IN A SEMI-ENCLOSED MEDITERRANEAN MARINE SYSTEM (STAGNONE OF MARSALA, ITALY)

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Microbial and meiofaunal dynamics and their relationships with the biochemical composition of the sedimentary organic matter were investigated in a semi-enclosed marine system (Marsala lagoon, Western Sicily, Mediterranean Sea).

Sediment samples were collected on a monthly basis from March 1996 to February 1997 in four stations located along a N–S transect characterized by different hydrodynamic regimes. Total sedimentary organic matter concentration ranged from 5.68 ± 1.11 to 156.28 ± 12.63 mg g^{1}, while the biopolymeric fraction of organic carbon (BPC, measured as sum of the lipids, carbohydrates and proteins) accounted for only a small fraction (~24%) of total organic matter. Total meiofaunal density was extremely low, accounting for, on annual average, 112 ± 29 ind.=10 cm^{-2} and largely dominated by nematodes (on annual average from 40% to 91% of total meiofaunal density). Benthic microbial density ranged from 0.22 ± 0.02 x 10^{9} to 106.83 ± 16.77 x 10^{9} g^{-1} sediment dry weight (DW). Microbial biomass ranged from 0.01 ± 0.003 to 7.04 ± 0.14 mg C g^{1} sediment DW and accounted for a significant fraction of BPC at all stations (~10%). Low chlorophyll-a concentration in the sediments of the Marsala lagoon (on annual average from 2 to 16 mg g^{1} sediment DW) suggests that organic detrital and heterotrophic bacteria largely dominate the sedimentary organic matter and do not promote the transfer of carbon towards the higher trophic state.

Keywords: Sedimentary organic matter; Benthic microbial community; Meiofauna; Mediterranean lagoon

1 INTRODUCTION

In lagoon environments, the large amounts of primary production (i.e. from macrophytes and salt marsh plant) generally exceed consumption by herbivores (Newell, 1982), and might be utilized by consumers only after fragmentation or decomposition processes operated by bac- teria (Hansen and Blackburn, 1992). As a consequence, the semi-enclosed system, particu- larly if affected by low tidal range, behaves as a 'detrital trap' (Pusceddu et al., 1999). The quantity and the quality of this large amount of detritus accumulated in the sediment are the most important factors structuring benthic communities (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 measure of standing stocks of total organic carbon

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overestimates the labile fraction (readily utilisable) of the organic pool (Fabiano and Danovaro, 1994). Detailed information on the biochemical composition of the sedimentary organic matter (measured as content of specific labile compounds such as carbohydrates, lipids and proteins) may be of primary importance to estimate the amounts of readily available food (Fabiano et al., 1995; Pusceddu et al., 1996). Benthic bacteria play a fundamental role in converting organic matter into living biomass and, being largely consumed by protozoa (Danovaro et al., 1999) and meiofauna (Danovaro, 1996), allow the transfer of material and energy to higher trophic levels (Kemp, 1988; Bak and Nieuwland, 1989; Hondeveld et al., 1994). Nevertheless, quantitative information on trophic interaction between protozoa, bacteria, meiofauna and organic matter within the benthic ecosystem is extremely scarce (Kemp, 1988; Bak and Nieuwland, 1989; Deming and Barross, 1993; Hondeveld et al., 1994; Danovaro, 1996).

In the present study, the seasonal changes of meiofauna and benthic microbial assemblages were investigated in relation to seasonal variation of sedimentary organic matter in four different stations in the Stagnone of Marsala, a semi-enclosed marine system (Western Sicily, Mediterranean Sea). An attempt was made to quantify the organic fraction readily utilisable for consumers. Estimates of these were obtained using the major biochemical classes of organic compounds (as the sum of protein, lipid and carbohydrate carbon equiva- lent, sensu Fichez, 1991; Danovaro et al., 1994; Fabiano and Danovaro, 1994). This portion of the sedimentary organic matter was referred as the biopolymeric fraction of organic carbon (BPC, Mayer, 1989). The aims of the present study were to investigate the dynamics of benthic microbes and meiofaunal community, in relation to the biochemical composition of the sedimentary organic matter.

2 MATERIALS AND METHODS

2.1 Study Site and Sampling

The Marsala lagoon (Fig. 1) is a semi-enclosed marine system characterized by two main com- munication channels with the open sea. A platform separates the rest of the basin from the open sea. The northern channel is 450 m wide and is characterized by turbulent inputs of seawaters. The southern mouth, 1450 m wide, is open to continuous seawater inflow. The basin is very shallow, with a depth ranging from 2 m along the eastern shore of the platform to 0.5 m in the western area. Depth gradually increases to about 2.5 m in the southernmost area. The hydrography of the central area is greatly influenced by two small islands, which act as mechanical obstacles to water circulation and generate turbulent currents. In this area a Posidonia oceanica reef deeply influences water circulation.

The area is characterized by microtidal regime, evident seasonal changes in temperature (from 11.4 °C in January to 28.5 °C in August) and salinity (from 32.9‰ in March to 46.9‰ in July). Temperature and salinity did not vary significantly between stations. Sediment samples were manually collected on a monthly basis by SCUBA divers from March 1996 to February 1997 in four stations located along a N–S transect and characterized by different hydrodynamic regimes.

Meiofaunal samples were collected in replicate plexiglas cores (n = 3, diam. 3.7 cm, 10.7 cm^2 surface area) down to a depth of 10 cm. This depth appeared to be adequate for quan- titative analysis as the evaluation of the top 15 cm of the sediment core revealed that <1% of the total meiofaunal density was present in the 10–15 cm sediment horizon. For bacterial analyses, replicate cores (n = 3) were collected from the same surface sediments using sterile

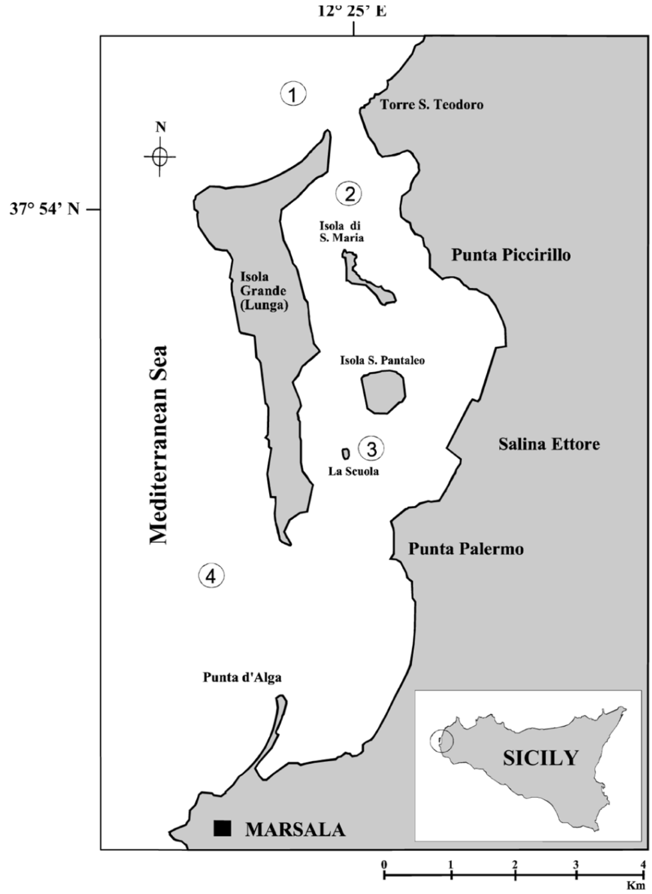

FIGURE 1 Location of sampling stations in the Stagnone of Marsala (Italy).

10 ml plastic tubes. The sediment of two additional cores (diam. 3.7 cm) was mixed and frozen at 20 $^\circ$C for the analysis of photosynthetic pigments and organic matter variables.

2.2 Environmental Parameters

Sediment was treated with 10% HCl to remove carbonates (Buchanan and Kain, 1971). Total organic matter (TOM) was determined as the difference between the DW (80 $^\circ$C, 24 h) of the sediment and the residue left after combustion at 450 $^\circ$C for 4 h (Parker, 1983).

Lipids were extracted from sediment samples by direct elution with chloroform and methanol according to Bligh and Dyer (1959) and determined after Marsh and Weinstein (1966). Protein analyses were carried out according to Hartree (1972). Concentrations are presented as albumin equivalents. Carbohydrates were analysed according to Gerchacov and Hatcher (1972), specifi- cally adapted for carbohydrate determination in sediments. 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 0.40, 0.49 and 0.75, respectively (Fichez, 1991). The sum of protein, lipid and carbohydrate carbon equivalent was referred as BPC (Fabiano and Danovaro, 1994). For each biochemical analysis, blanks were made using the same previously calcinated sediments (450 $^\circ$C, 4 h). All analyses were carried out in three replicates.

Analyses of sedimentary chlorophyll-a (Chl-a) and phaeopigments (Phaeo) were carried out according to Lorenzen and Jeffrey (1980). Pigments were extracted with 90% acetone (24 h in the dark at 4 $^{\circ}$C). After centrifugation, the supernatant was used to determine the functional Chl-a and acidified with 0.1 N HCl to estimate the amounts of Phaeo (Plante-Cuny, 1974). Data were normalized to dry weight (60 $^{\circ}$C, 24 h) and expressed as mg g ^{1}.

2.3 Microbial Analyses

Bacterial analyses were carried out only on surface sediments (0–1 cm) according to Epstein and Rossel (1995). Each sediment replicate (n = 3, about 1 cm^{3}) was immediately fixed with buffered formaldehyde (2% final concentration) and stored at 4 $^{\circ}$C. Sediment samples were sonicated three times (Sonifier Transonic Labor 2000, 50 W for 1 min) and diluted with ster- ile water. Samples were then stained with acridine orange. Bacterial cells were counted using epifluorescence microscopy on at least 10 fields randomly selected for a total count of more than 400 cells. The frequency of dividing cells (FDC) was estimated as the percentage of cells showing a clearly visible invagination (Newell and Christian, 1981; Fry, 1990). Data were normalized to DW (after desiccation, 60 $^{\circ}$C, 24 h). Data on microbial biomass from the top 1 cm of the sediment were expressed as mg C g ^{1}.

2.4 Meiofaunal Analyses

Samples were fixed with 4% buffered formaldehyde in 0.4 mm prefiltered seawater. Sediments were sieved through 1000 and 37 mm mesh nets. The fraction remaining on the 37 mm 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 for taxon under a stereo microscope after staining with Rose Bengal (0.5 g l ^{1}).

Meiofaunal biomass was calculated as the sum of the product between individual body weight (expressed as mg C) and total density of each taxon, and expressed as mg C 10 cm ^{2}. For all taxa, an average individual body weight of 1 mg was assumed constant throughout the period of investigation (Danovaro, 1993).

3 RESULTS

3.1 Phytopigments and Organic Matter in the Sediment

Chlorophyll-a concentrations ranged, on annual average, from 1.81 ± 0.33 (station 1) to 11.70 ± 6.84 mg g ^{1} (station 3). Similar spatial pattern was displayed by chloroplastic pigment

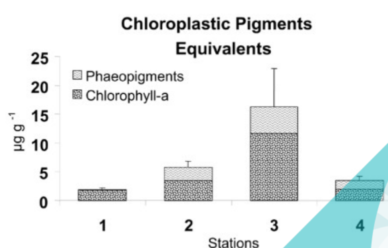

FIGURE 2 Chloroplastic pigment equivalents (CPE) concentrations in the sediment of the Stagnone of Marsala. The contribution of Chl-a and phaeopigments (Phaeo) is reported.

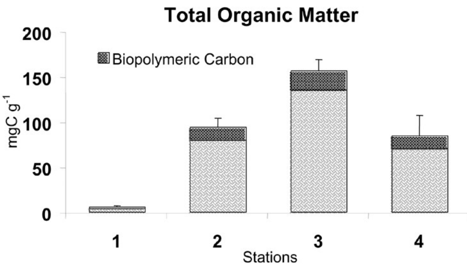

FIGURE 3 Biochemical composition of sedimentary organic matter: carbohydrates (CHO), proteins (PRT) and lipids (LIP).

equivalent concentrations (CPE) ranging from 1.86 ± 0.31 (station 1) to 16.32 ± 6.63 mg g ^{1} (station 3) (Fig. 2).

Total organic matter content fluctuated remarkably during the year and between the four stations. Station 1 showed, on annual average, the lowest concentration of TOM (5.68 ±1.11 mg g ^{1}), while highest contents were measured at station 3 (156.28 ± 12.63 mg g ^{1}).

Carbohydrate, protein and lipid contribution to organic matter (converted to carbon content, by dividing by a factor 2), in the top 1 cm of the sediments are illustrated in Fig. 4. Among the three biochemical classes of organic compounds, carbohydrates were the dominant component, ranging, on annual average, from 9.3% (station 1) to 33.2% of organic matter (station 2), followed by proteins ranging from 16.3% (station 1) to 26.6% of TOM (station 3) and lipids ranging from 9.5% (station 2) to 74.3% (station 1) of TOM. The biopolymeric carbon at station 1, showed lowest values (2.06 ± 0.88 mg C g ^{1}, on annual average), while high values were recorded in the station 3 (20.80 ± 5.64 mg C g ^{1}, on annual average) (Fig. 3).

3.2 Bacterial Abundance and Biomass

Data concerning bacterial parameters are reported in Table I. Total bacterial numbers (TBN) ranged from 0.22 ± 0.02 (June, station 1) to 106.8 ± 16.77 ± 10^9 cells g ^{1} sediment DW (November, station 3). On annual average, highest values were reported in station 2 (30.18 ± 8.74 x 10^9 cells g ^{1} sediment DW) and station 3 (32.69 ± 5.50 x 10^9 cells g ^{1} sedi- ment DW). Station 1, during the entire study period, showed lower bacterial density and TBN accounted for 1.33 ± 0.39 x 10^9 cells g ^{1} sediment DW, on annual average. In station 4, bacterial density ranged from 1.96 ± 0.04 to 76.54 ± 0.93 x 10^9 cells g ^{1} sediment DW (in January and March, respectively).

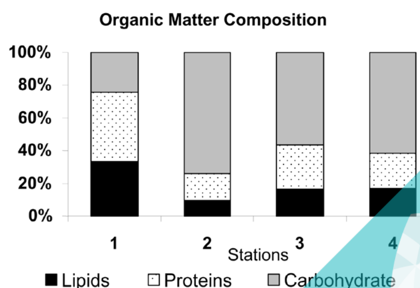

FIGURE 4 Total organic matter and contribution of biopolymeric fraction (BPC) in the sediment of the Stagnone of Marsala.

TABLE I Temporal changes in total bacterial number (TBN), bacterial biomass (BBM), frequency of dividing cells (FDC), meiofaunal density and BBM to total meiofaunal biomass (TMB) ratio in the sediments of the Stagnone of Marsala.

	TBN		BBM		FDC		Meiofaunal density		
	n x 10^9 cell g^{1}	±s.d.	mg C g^{1}	±s.d.	%	±s.d.	ind. 10 cm^{2}	±s.d.	BBM=TMB
Station 1									
Mar	0.53	0.01	0.02	0.00	5.11	0.05	20	15	0.87
Apr	3.54	0.21	0.16	0.01	10.26	1.53	51	54	3.19
May	0.40	0.02	0.01	0.00	3.31	0.55	49	13	0.26
Jun	0.22	0.02	0.01	0.00	5.95	1.76	44	8	0.29
Jul	0.35	0.01	0.02	0.00	7.18	0.85	87	28	0.19
Aug	0.36	0.04	0.02	0.00	7.41	1.51	136	60	0.11
Sep	2.98	0.26	0.19	0.04	5.25	0.80	70	55	2.66
Oct	0.24	0.02	0.01	0.00	7.21	0.51	38	8	0.26
Nov	2.33	0.28	0.12	0.04	5.67	0.60	50	6	2.44
Dec	3.58	0.28	0.16	0.00	7.25	1.12	263	101	0.61
Jun	1.04	0.05	0.04	0.00	8.31	1.24	130	13	0.29
Feb	0.43	0.06	0.02	0.00	6.33	1.25	397	30	0.04
Average ± S.E.*	1.33	0.39	0.06	0.02	6.60	0.51	111	32	0.94
Station 2									
Mar	4.00	0.17	0.24	0.01	5.88	0.20	92	0	2.56
Apr	41.35	0.29	1.91	0.08	6.87	1.20	303	47	6.31
May	22.99	2.79	1.15	0.10	7.33	0.73	151	78	7.61
Jun	15.37	1.95	0.43	0.08	2.59	0.82	142	116	3.06
Jul	29.83	0.16	1.47	0.02	4.64	1.12	11	10	133.93
Aug	5.65	0.16	0.29	0.04	6.24	0.70	78	38	3.71
Sep	7.20	0.95	0.51	0.08	3.78	0.09	16	9	31.62
Oct	15.51	0.35	0.91	0.06	2.98	0.42	20	7	45.67
Nov	106.83	16.77	7.04	0.14	5.47	0.63	106	15	66.40
Dec	17.15	0.31	1.00	0.04	13.10	0.79	67	5	14.85
Jun	70.18	3.55	3.14	0.32	9.13	1.92	84	24	37.40
Feb	26.15	3.55	1.18	0.22	4.26	0.48	92	11	12.78
Average ± S.E.*	30.18	8.74	1.61	0.55	6.02	0.84	97	23	30.49
Station 3									
Mar	39.23	2.55	2.49	0.27	4.90	0.84	78	78	31.88
Apr	31.41	1.40	2.16	0.06	6.42	0.25	311	168	6.95
May	1.77	0.47	0.09	0.01	6.30	1.42	171	50	0.50
Jun	0.39	0.09	0.02	0.00	3.71	0.94	18	16	1.07
Jul	30.48	2.50	1.00	0.03	4.78	1.12	87	75	11.44
Aug	31.39	1.01	2.02	0.02	7.74	0.40	110	10	18.36
Sep	33.17	3.46	1.83	0.29	4.30	0.43	177	33	10.35
Oct	31.03	2.44	1.59	0.07	3.80	0.33	147	49	10.82
Nov	70.52	7.05	3.90	0.36	8.36	1.78	184	168	21.17
Dec	35.56	0.88	2.12	0.00	8.02	0.12	72	11	29.44
Jun	32.24	0.23	1.33	0.04	3.55	0.21	105	29	12.68
Feb	55.15	0.95	2.98	0.25	3.79	0.36	133	53	22.40
Average ± S.E.*	32.69	5.50	1.79	0.32	5.47	3.46	133	22	14.76
Station 4									
Mar	76.54	0.93	4.03	0.24	6.98	0.46	77	26	52.39
Apr	3.10	0.18	0.17	0.00	5.55	0.16	196	18	0.86
May	29.71	0.76	1.16	0.07	5.89	0.05	230	103	5.05
Jun	26.94	0.90	1.42	0.03	7.13	0.95	53	23	26.70
Jul	10.97	0.30	0.64	0.05	2.88	0.78	70	30	9.11
Aug	25.05	0.87	1.61	0.02	7.18	0.96	184	165	8.75
Sep	14.56	2.14	0.82	0.10	4.69	0.25	134	30	6.11
Oct	5.53	1.11	0.31	0.05	4.83	0.20	63	20	4.93
Nov	42.45	1.04	3.07	0.06	6.96	0.10	28	24	109.53
Dec	22.70	3.06	1.48	0.09	12.10	0.80	102	14	14.54
Jun	1.96	0.04	0.07	0.01	5.83	0.22	104	15	0.63
Feb	30.43	1.69	1.25	0.21	5.12	0.55	44	31	28.33
Average ± S.E.*	24.16	5.97	1.34	0.34	6.26	0.64	107	19	22.25

*Standard error.

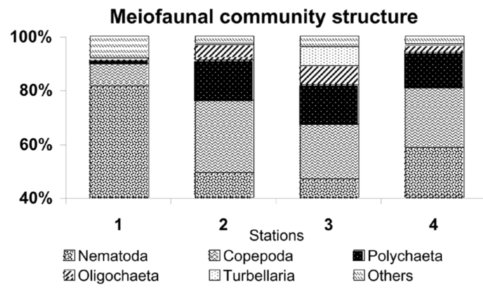

FIGURE 5 Meiofaunal community structure in the sediment of the Stagnone of Marsala.

Bacterial biomass ranged from 0.01 ± 0.00 (in June at station 1) to 7.04 ± 0.14 mg C g^{1} sediment DW (in November at station 2). Station 3 showed, on annual average, the highest bacterial biomass (1.79 ± 0.32 mg C g^{1} sediment DW), while the lowest value was at station 1 (0.06 ± 0.02 mg C g^{1} sediment DW). The FDC showed similar values in all sampled stations, ranging, on annual average, from 5.47 ± 3.46% to 6.60 ±0.51% (at sta- tions 3 and 1, respectively).

3.3 Meiofauna

Data on meiofaunal abundance, integrated to 10 cm depth, are reported in Table I. Meiofaunal density was extremely low, ranging from 11 ± 10 to 397 ± 30 ind. (July, station 2) 10 cm^{2} (February, station 1). The highest mean meiofaunal abundance was observed at station 3 (133 ± 21 ind. 10 cm^{2}) and the lowest at station 2 (97 ± 23 ind. 10 cm^{2}). Nematodes repre- sented the dominant taxon accounting, on annual average, for 81.4% at station 1, 49.1% at station 2, 46.7% at station 3 and 58.6% at station 4, of total meiofaunal density (Fig. 5). The second most abundant taxon was the harpacticoid copepods, representing from 18% to 27% of total meiofauna (at station 1 and 2, respectively) (Fig. 5). Polychaetes, the third most important taxon, generally accounted for only a small fraction in all stations, (2% station 1, 15% stations 2 and 3, 13% station 4) of the total density. All the other meiobenthic taxa accounted for a small percentage of the total meiofaunal density (Fig. 5).

4 DISCUSSION

Chlorophyll-a and CPE concentrations registered in the sediments of the Stagnone of Marsala were very low compared to other enclosed basins or Mediterranean coastal lagoons, suggesting a relatively low input of fresh primary organic matter from micro-algae. These values are comparable to those reported in oligotrophic environments (Plante et al., 1986; Fabiano et al., 1995; Albertelli et al., 1999). Higher concentrations were recorded at the end of summer and in autumn, in relation to the seasonal cycle of the marine phanerogams present in the area (P. oceanica and Cymodocea nodosa). In this period, in fact, takes place a massive release of vascular-plant detritus in the sediments due to the detachment of the sea- grass leaves (Danovaro, 1996; Scilipoti, 1998). Since the composition of marine phanero- gams and epiphytes is highly refractory (Lawrence et al., 1989), the phyto-detritus accumulated in the sediments of Stagnone of Marsala may not be directly utilisable by benthic consumers (Pusceddu et al., 1997). Therefore, despite a large input of organic matter, (TOM concentration, except at station 1, is higher than values found in other coastal lagoons; Le Guellec and Bodin, 1992), only a very small fraction is directly available to consumers (Kenworthy and Thayer, 1984). The available fraction of organic carbon, represented, on average and at all stations, only the 24% of total sedimentary organic matter. Besides, ana- lyses of the biochemical composition of sedimentary organic matter provided evidence of low nutritional value (Pusceddu et al., 1996), due to the dominance of carbohydrates (from 24% to 74%, on annual average) and a low protein fraction (from 17% to 42%, on annual average) at all sampled stations. As a result, despite the high standing stock of organic carbon, soluble protein (used as a measure of the readily digestible fraction) may be a limit- ing factor for microbial metabolism (Danovaro, 1996).

Bacterial density and biomass recorded in the sediments of Stagnone of Marsala were con- siderably higher than those found in other coastal areas (Albertelli et al., 1999; La Rosa et al., 2001). The distribution of benthic bacteria, especially in oligotrophic areas, varies in response to the food quality (Deming and Yager, 1992).

Benthic bacterial biomass accounted for a significant fraction (10%, on average) of the sedimentary biopolymeric carbon, suggesting that a strong microbial loop dominates the sedimentary compartment in the Stagnone of Marsala.

Meiofaunal density was very low when compared to values reported for coastal and lagoon areas characterized by high organic loads (Dinet et al., 1990; Le Guellec and Bodin, 1992; Guelorget et al., 1994). This apparently would suggest that the large amount of organic matter accumulated in the Stagnone of Marsala sediment is not able to support high meiofaunal densities, due to its origin, biochemical composition and low nutritional value. In this study, the presence of marine phanerogams in the south basin, reducing the hydrodynamical regime, induces a massive accumulation of organic matter in the sediments, producing anoxic or suboxic conditions, unfavourable for a major part of meiofaunal taxa (Frid and Mercer, 1989; Weston, 1990; Mazzola et al., 1999; Mirto et al., 1999; 2002), except for thiobios biota (Powell et al., 1983; Meyers et al., 1988). Moreover, anoxic conditions are more evident in depth sediments, so that meiobenthic organisms colonize only the superficial layer of the sediment, where they are subject to disturbance effects (i.e. predation or sediment resuspension; Giere, 1973; Reise, 1987). The dominance of nematodes, especially at station 1 (90% of the total meiofaunal den- sity), could be related to their capacity to colonize deeper (suboxic) sediment layers, where resuspension effects are less evident. The relevance of copepods at stations 2 and 3 is related to elevated microphytobenthos (as Chl-a biomass), probably utilised as primary food source.

Previous studies demonstrated that the accumulation of large amounts of organic matter in the sediment induces long-term changes in the structure of the benthic assemblages, increas- ing the relative importance of the smaller components (i.e. bacteria) of the benthic food web (Danovaro et al., 1999; La Rosa et al., 2001).

An approach for identifying the effect of organic accumulation on the benthic communities structure and functioning is based on the analysis of changes in the relative importance of the microbial versus metazoan components (Danovaro et al., 1999; Danovaro, 2000). The eco- logical background of such an approach is that in highly enriched environments, microbial components tend to increase their dominance, whereas metazoans (such as the highly sensi- tive meiofauna) are reduced (Koop and Griffiths, 1982), so that the ratio of the bacteria to meiofaunal biomass (as an example) is much higher in sediments displaying organic matter enrichment. Ratio of benthic microbial biomass (BBM) to total meiofaunal biomass (TMB) can provide information on the energy transfer pathways in the benthic food webs. The high values of BBM=TMB ratio clearly indicate that the benthic community is strongly dominated by microbial components and a large part of bacterial biomass is not converted into meio- benthic biomass. The high values of BBM=TBM ratio are determined, also, by the ability of bacteria to exploit refractory compounds (Hansen and Blackburn, 1992). So, bacteria in the sediments of the Stagnone of Marsala play a primary role as a trophic reservoir converting refractory compound into available food (i.e. bacterial biomass). However, a large part of organic carbon, even though converted into microbial biomass, is not channelled towards higher trophic levels, due to the lack of consumers (i.e. meiofaunal taxa) determined by restrictive conditions of lagoon sediments.

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