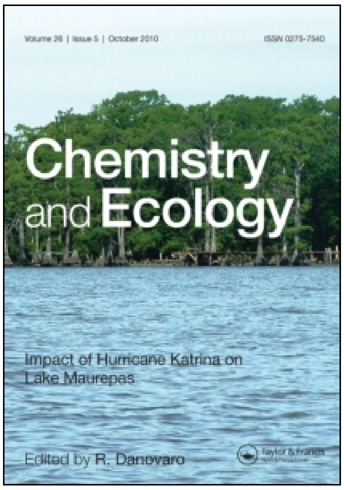

Chemistry and Ecology
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713455114

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To cite this Article Albertellli, G. , Chiantore, M. , Harriague, A. Covazzi , Danovaro, R. and Della Croce, N.(1999) 'Community Experiments Using Benthic Chambers: 2. Meio- and Macrofaunal Community Structure and Metabolism', Chemistry and Ecology, 16: 1, 51 — 66

To link to this Article: DOI: 10.1080/02757549908037637

URL: http://dx.doi.org/10.1080/02757549908037637

Chemistry and Ecology, 1999, Vol. 16, pp. 51-66
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COMMUNITY EXPERIMENTS USING BENTHIC CHAMBERS: 2. MEIO- AND MACROFAUNAL COMMUNITY STRUCTURE AND METABOLISM

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(Received 7 September 1998; In final form 8 September 1998)

In the framework of a benthic flows study in suboxic environments, the relationships between macro- and meiobenthic community structure were investigated. Experiments were performed using benthic chambers in the Rapallo Harbour (Eastern Ligurian Sea) in autumn 1996. A relatively rich and diversified macrobenthic community (45 species) was found. Macrobenthos (> 1 mm) was characterized by high densities of highly tolerant species, typical of fluctuating and organically enriched environments, such as the bivalve, *Corbula gibba*, and capitellid polychaetes. By contrast, bivalve juveniles (*Lucinella divaricata*) dominated the 0.5-1 mm macrofauna. Metazoan meiofauna was mostly composed of nematodes (71% of the total density) but also characterized by relatively high density of temporary meiofauna. In contrast with most benthic studies on more oligotrophic environments, benthic metabolism in sediments characterized by high organic contents was clearly dominated by the microbial component that accounted alone for about 98.7% of the total oxygen consumption.

Keywords: Macrobenthos; meiofauna; benthic oxygen consumption

1. INTRODUCTION

In the last decades, several investigations have been focused on benthic community structure and energetics, and particularly on the benthic

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*Corresponding author.

response to enhanced food quantity, quality and availability, supplied by water column sedimentation processes (Graf *et al.*, 1982; Graf *et al.*, 1983; Kanneworff and Christensen, 1986; Grant and Hargrave, 1987; Graf, 1992; Van Duyl *et al.*, 1992; Danovaro *et al.*, this volume). Due to the generally highly refractory composition of the sedimentary organic matter, a primary role in marine sediment energetics is played by bacteria by consumption of detrital organic matter and the transfer of this secondary production to higher trophic levels (protozoa, meio- and macrofauna) (Danovaro *et al.*, this volume).

In organically enriched environments, such as harbours and closed embayments, benthic oxygen demand increases (Jensen *et al.*, 1990; Hansen and Blackburn, 1991), leading to complete oxygen-depletion in eutrophic and/or dystrophic conditions (Hansen and Blackburn, 1992).

Although there is a variety of approaches to the study of benthic metabolism, the measurement of oxygen consumption remains one of the most practical methods, when metabolism is aerobic (Pamatmat, 1977). Such studies have been performed through laboratory measurements on intact cores (Pamatmat, 1971), by means of experimental sand columns (Munro *et al.*, 1978; Wormald and Stirling, 1979) and by the use of *in situ* bell-jars (Odum, 1957; Hargrave, 1969; Smith *et al.*, 1972; Smith *et al.*, 1973; Kanneworff and Christensen, 1986) or benthic chambers (Reimers *et al.*, 1992).

In the present study, carried out in a suboxic and unstable environment characterized by organically enriched sediments (Rapallo Harbour, Western Mediterranean Sea), oxygen consumption by meio- and macrofauna compartments were investigated and their community structure related to the microbial component.

2. MATERIALS AND METHODS

2.1. Study Area and Sampling

This study was carried out between September 30th and October 4th, 1996 at a depth of 5 m, in the Rapallo Harbour, Golfo Marconi, Eastern Ligurian Sea (Fig. 1). Benthic chamber (~ 120 l, 0.4 m^2, Ciceri *et al.*, 1992) deployment was carried out for a period of 71 h in order to

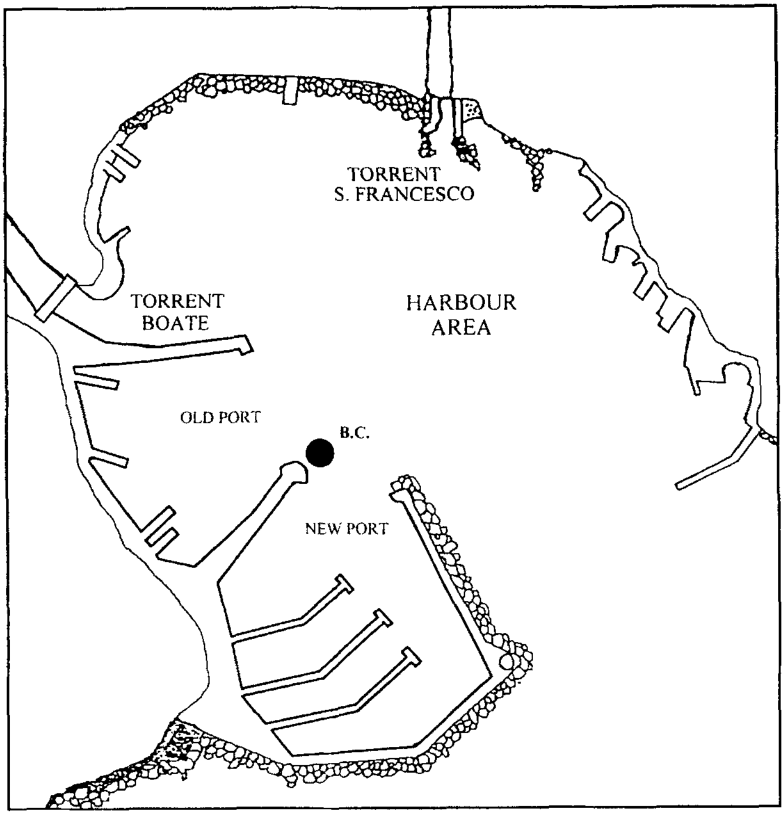

FIGURE 1 Study site (B.C. = location of the benthic chamber).

determine oxygen consumption rates, nutrient flows (Ceradini *et al.*, 1997) and changes in bacteria, protozoa and organic matter content into the sediment (Della Croce *et al.*, 1997). Macrobenthic samples were collected using a suction device system ($0.1\,m^2$) at the sampling station, before chamber deployment, and in the sediments under the chamber itself after its removal, sieving the sediments through 1.0 and 0.5 mm mesh nets, preserving the fraction retained in 10% formalin. Similarly, meiofaunal samples were collected in replicate cores ($n = 4$, diam. 3.8 cm, $11.3\,cm^2$ surface area) down to a depth of 10 cm. Sediment cores were vertically sectioned into different layers (0–4, 4–8 and 8–10 cm), fixed in 4% buffered formalin in 0.4 μm pre-filtered solution and stained with Rose Bengal ($0.5\,g\,l^{-1}$).

2.2. Macrofaunal Analyses

Macrofaunal samples were sorted in laboratory under a stereomicroscope and specimens of all taxa were identified at species level. Biomass values were expressed as organic carbon after conversion of ash-free dry weight (AFDW) (550°C, 4 hours in a muffle furnace after being oven-dried at 60°C for 24 hours), using the factor 0.4 (Feller and Warwick, 1988).

2.3. Meiofaunal Analyses

Sediments were sieved through 1000 μm and 37 μm mesh nets. The fraction retained by the 37 μm mesh net was centrifuged three times with Ludox HS (density arranged to 1.18 $\mathrm{g\,ml^{-1}}$). All meiobenthic animals were counted and classified per taxon under a stereomicroscope. Meiofaunal biomass was determined using the values of individual body weight reported for the same area (Danovaro, 1993).

3. RESULTS AND DISCUSSION

3.1. Macrofaunal Community Structure in Organic Enriched Environments

In the macrobenthic fraction > 1 mm 45 species were identified (Tab. I) constituting a total abundance value of 1440 and 188 $\mathrm{ind.\,m^{-2}}$ at the beginning and at the end of the study. Macrobenthos was dominated by polychaetes (25 species): *Heteromastus filiformis* and *Chaetozone setosa* (460 and 100 $\mathrm{ind.\,m^{-2}}$) displayed the highest densities followed by *Tharyx heterochaetus* (120 $\mathrm{ind.\,m^{-2}}$ and 12.5 $\mathrm{ind.\,m^{-2}}$, at the beginning and at the end). A relatively rich mollusc fauna was found, represented by 14 species. The bivalve, *Corbula gibba*, was the dominant species (230 and 70 $\mathrm{ind.\,m^{-2}}$, at the beginning and at the end).

Crustaceans and echinoderms were found only at the beginning of the experiment and were scarcely represented, both in terms of species richness and number of individuals.

Macrobenthos of the 0.5 to 1 mm fraction displayed a community structure (Tab. II) quite different from the larger one, and character-

TABLE I Macrofaunal species (> 1 mm sieve) found at the beginning and at the end of the benthic chamber experiment in the Rapallo Harbour

			> 1 *mm* 30/09/96 1 m^2	> 1 *mm* 04/10/96 1 m^2
Polychaetes	*Amaea trilobata*	(Sars)		2.5
	Aonides oxycephala	(Sars)	50	15
	Aricidea assimilis	Tebble	20	
	Aricidea pseudoannae	Katzmann & Laubier	10	
	Aricidea quadrilobata	Webster & Benedict		2.5
	Capitomastus minimus	(Langherans)		10
	Chaetozone setosa	Malmgren	100	
	Eunice vittata	(Delle Chiaje)		2.5
	Glycera convoluta	Keferstein	20	
	Glycera celtica	O'Connor		5
	Heteromastus filiformis	Claparède	460	
	Leiocapitella dollfusi	(Fauvel)	10	
	Lumbrineris gracilis	(Ehlers)	50	
	Lumbrineris neonatoi	Ramos		5
	Mediomastus fragilis	Rasmussenn		30
	Neopseudocapitella brasiliensis	Rullier & Amoroux		2.5
	Nephthys hombergi	(Savigni)	10	
	Ophiodromus flexuosus	Delle Chiaje		2.5
	Paradoneis armata	Glemarec	10	
	Paradoneis ilvana	Castelli	10	
	Peresiella clymenoides	Harmelin	10	
	Piromis eruca	(Claparède)	10	
	Prionospio caspersi	Laubier	20	
	Scoloplos armiger	(O. F. Muller)	10	
	Tharyx heterochaetus	Laubier	120	12.5
Bivalves	*Abra cfr. nitida*	(O. F. Muller)	30	5
	Corbula gibba	(Olivi)	230	70
	Gouldia minima	(Montagu)	40	
	Loripes lacteus	(L.)	10	
	Myrtea spinifera	(Montagu)		2.5
	Nucula nucleus	(L.)		2.5
	Parvicardium exiguum	(Gmelin)	30	2.5
	Parvicardium scabrum	(Philippi)	20	
	Sphaerocardium paucicostatum	(Sav.)	10	
	Spisula subtruncata	(Da Costa)	60	
	Tellina donacina	L.	10	
Gastropods	*Nassarius cfr. pygmaeus*	(Lamarck)		2.5
Scaphopods	*Dentalium inaequicostatum*	Dautzenberg		7.5
	Fustiaria rubescens	(Deshayes)		2.5
Echinoderms	*Ophiura albida*	Forbes	10	
Crustaceans	*Iphinoe sp.*		10	
	Upogebia typica	(Nardo)	10	
Others	Nemertines		20	
	Oligochaetes		20	2.5
	Fishes		10	
Total N° of species			31	20
Total N° of individuals			1440	187.5

TABLE II Macrofaunal species (0.5 to 1 mm) found at the beginning and at the end of the benthic chamber experiment in the Rapallo Harbour

			0.5–1 *mm* 30/09/96 1 m^2	0.5–1*mm* 04/10/96 1 m^2
Polychaetes	*Aricidea quadrilobata*	Webster & Benedict	10	2.5
	Capitomastus minimus	(Langerhans)		7.5
	Cirrophorus furcatus	(Hartmann)		2.5
	Cossura soyeri	Laubier	10	7.5
	Heteromastus filiformis	Claparède		12.5
	Mediomastus fragilis	Rasmussen		12.5
	Nephthys cirrosa	(Ehlers)	10	
	Paradoneis ilvana	Castelli	20	2.5
	Peresiella clymenoides	Harmelin	30	
	Prionospio malmgreni	Claparède		2.5
	Tharyx heterochaetus	Laubier	10	12.5
Bivalves	*Lucinella divaricata*	(L.)	30	165
	Gouldia minima	(Montagu).	10	
	Tellimia ferruginosa	(Montagu)		2.5
Crustaceans	*Jaxea nocturna*	Nardo	10	
	Perioculodes aequimanus	Kossmann		2.5
Others	Oligochaetes		10	17.5
Total N° of species			10	13
Total N° of individuals			150	250

ized by a lower number of species and individuals. Eleven polychaete, 4 molluscs and 2 crustaceans species were found, reaching a total density of 150 and 250 ind. m^{-2}, at the beginning and at the end of the experiment. *Lucinella divaricata* was mainly responsible for the increased abundance observed at the end of the chamber deployment, increasing its density by 5 times at the end of the experiment (30 *vs.* 165 ind. m^{-2}).

Despite such high bivalve densities, the macrofauna >0.5 mm density reported in this study was about half of the densities reported by Covazzi-Harriague (1996) in the adjacent sandy area of the Tigullio Gulf.

Macrofaunal biomass (in terms of AFDW and carbon content) is reported in Table III. Macrofaunal biomass ranged from 27.1 to 46.0 mg AFDW m^{-2} in the >1 mm fraction and from 1.0 to 1.9 mg AFDW m^{-2} in the smaller size fraction. These values were about twenty-fold lower than those reported for the adjacent areas (Zoagli–

TABLE III Macrofaunal biomass expressed as ash free dry weight (mg AFDW m^{-2}) and as carbon content (mg C m^{-2})

	Date	*mg AFDW m*$^{-2}$		*mg C m*$^{-2}$	
		1 *mm*	0.5 *mm*	1 *mm*	0.5 *mm*
Crustaceans	30/9	1.2	0.2	0.5	0.1
Polychaetes	30/9	17.9	0.6	7.2	0.2
Molluscs	30/9	7.0	0.2	2.8	0.1
Echinoderms	30/9	1.0	–	0.4	–
Total		27.1	1.0	10.9	0.4
Crustaceans	4/10	–	0.2	–	0.1
Polychaetes	4/10	11.6	1.3	4.6	0.5
Molluscs	4/10	34.4	0.4	13.8	0.1
Total		46.0	1.9	18.4	0.7

Western Ligurian Sea, Covazzi-Harriague, 1996). These results evidence a generally poor macrofaunal community and suggest a reduction of the average body size, typical of the macrofaunal organisms living in highly enriched environments.

The contribution of the different taxa to the total biomass is illustrated in Figures 2a–2b. In the > 1 mm fraction, at the beginning of the experiment, polychaetes represented the dominant taxon (66%), followed by molluscs (25.9%), crustaceans (4.5%) and echinoderms (3.7%). By contrast, at the end of the experiment, molluscs were the dominant taxon (74.8%) whereas polychaetes accounted only for 25.2% of the total biomass. In the macrofauna of the 0.5 to 1 mm fraction, polychaetes dominated both at the beginning and at the end of the experiment (58.5 and 71.4%), followed by molluscs (25.5 and 20.0%) and crustaceans (16.0 and 8.6%).

Surprisingly, macrofaunal biomass of both fractions increased from the beginning to the end of the experiment. This result is difficult to explain and could be related to the patchy distribution of the benthic organisms, but appears consistent with the increase of the organic matter quality observed at the end of the sampling period (Danovaro *et al.*, this volume).

3.2. Meiofaunal Community Structure in Organic Enriched Environments

Meiofaunal densities displayed relatively low densities, when compared to other subtidal systems during autumn (see Soyer, 1985;

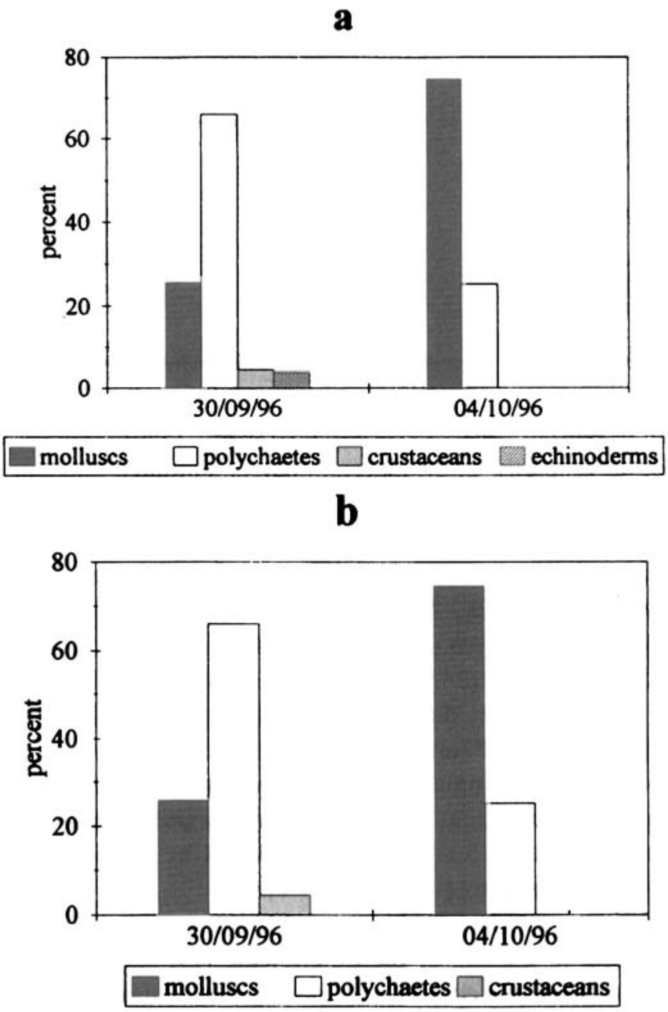

FIGURE 2 Contribution of the different taxa to total biomass: (a) macrofauna > 1 mm sieve; (b) macrofauna 0.5 – 1 mm.

Danovaro *et al.*, 1995), therefore it is likely that the presence of large organic matter amounts in constant suboxic conditions did not favour meiofaunal development (Fig. 3). Meiofaunal density, indeed, ranged from 576.6 ± 215.0 to 363.4 ± 218.2 ind. $10\,cm^{-2}$, at the beginning and at the end of the sampling period. Biomass values in the upper 4 cm of

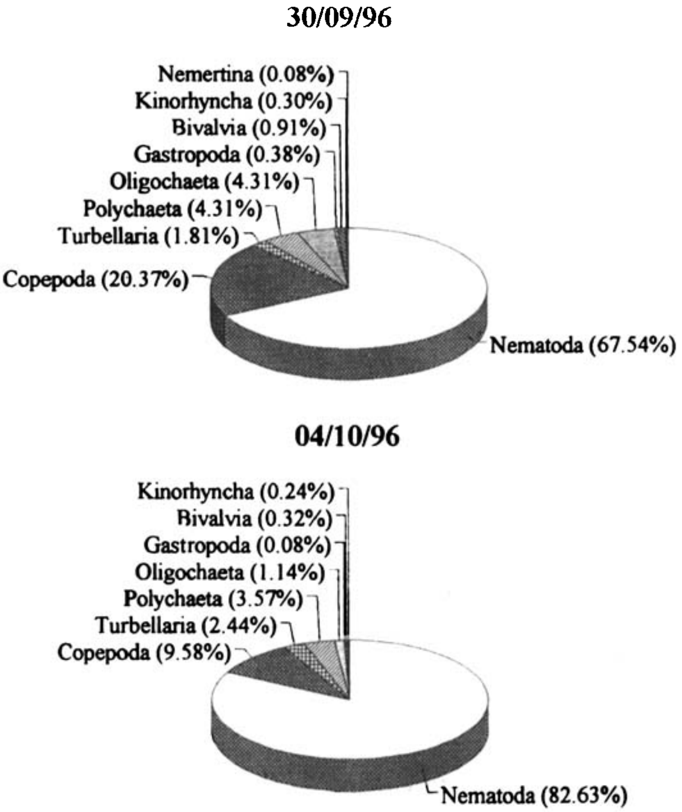

FIGURE 3 Meiofaunal community structure, in terms of dominance, at the beginning and at the end of the experiment.

sediments ranged from 305.8 μgC 10 cm^{-2} (30/09) to 167.9 (04/10), while values integrated in the upper 10 cm ranged from 389.7 to 260.7 μgC 10 cm^{-2}, respectively (Tab. IV). A general density decrease, particularly evident for copepods, was observed between sampling events.

Meiofaunal community was characterized by a clear vertical pattern (Fig. 4). The large majority of meiofauna was concentrated in the top 4 cm of the sediment (77 and 89% at the beginning and at the end of the sampling period). Such high values clearly suggest a strong confinement of the meiofaunal component in the most oxygenated sediments. The observed and evident short-term changes in meiofaunal

TABLE IV Depth density distribution of meiofauna in the Rapallo Harbour at the beginning and at the end of the benthic chamber experiment

Taxonomic group	*Sediment layer*	30/09/96	04/10/96	*unit*
Nematodes	0–4 cm	285.8 ± 103.8	283.3 ± 199.2	ind. 10 cm^{-2}
	4–8 cm	120.5 ± 68.4	32.5 ± 14.5	
	8–10 cm	40.5 ± 25.0	6.0 ± 1	
Total	0–10 cm	446.8 ± 87.5	309.0 ± 221.9	ind. 10 cm^{-2}
Copepods	0–4 cm	126.8 ± 81.9	37.0 ± 12.8	ind. 10 cm^{-2}
	4–8 cm	7.3 ± 4.0	1.0 ± 1.0	
	8–10 cm	0.8 ± 0.4	0.5 ± 0.5	
Total	0–10 cm	134.8 ± 90.4	38.0 ± 14.7	ind. 10 cm^{-2}
Polychaetes	0–4 cm	22.0 ± 10.6	11.3 ± 5.7	ind. 10 cm^{-2}
	4–8 cm	5.8 ± 2.4	2.0 ± 1.0	
	8–10 cm	1.5 ± 0.5	0	
Total	0–10 cm	28.5 ± 13.9	12.7 ± 5.5	ind. 10 cm^{-2}
Bivalves	0–4 cm	6.7 ± 4.6	2.0 ± 1.0	ind. 10 cm^{-2}
	4–8 cm	2.0 ± 0	0	
	8–10 cm	0	0	
Total	0–10 cm	6.0 ± 6.4	1.3 ± 1.5	ind. 10 cm^{-2}
Others	0–4 cm	39.0 ± 30.5	7.0 ± 3.6	ind. 10 cm^{-2}
	4–8 cm	5.5 ± 2.2	1.0 ± 0	
	8–10 cm	1.0 ± 0	0	
Total	0–10 cm	45.5 ± 35.7	7.7 ± 3.8	ind. 10 cm^{-2}
Total meiofauna density	0–10 cm	661.5 ± 170.1	368.7 ± 246.3	ind. 10 cm^{-2}
Total meiofauna biomass	0–4 cm	305.8	167.9	μg C 10 cm^{-2}
	0–10 cm	389.7	260.7	

density might be related to changes in the quantity of biopolymeric carbon and microphytobenthic biomass, or even attributed to other manipulation effects due to the introduction of the chamber into the system.

The extremely low number of taxa provides further insight to the conditions of the meiofaunal assemblages. In this study, only nine taxa were encountered (in order of dominance): nematodes, copepods, polychaetes, oligochaetes, turbellarians, bivalves, kinorhynchs, gastropods and nemertines. The number of taxa encountered in this study was very low when compared to the 14–18 taxa generally encountered in similar subtidal sediments (Zoagli–Ligurian Sea, Danovaro, 1993), suggesting stressed environmental conditions.

Meiofaunal community structure (Fig. 3) was characterized by the dominance of nematodes that accounted, on average, for 77% (range: 69–84%) of the total meiofaunal density, followed by copepods (average 15%, range 19.3–9.8%), polychaetes (4%, range 4.5–3.5%) and oligochaetes (2.8%; range 4.5–1.1%).

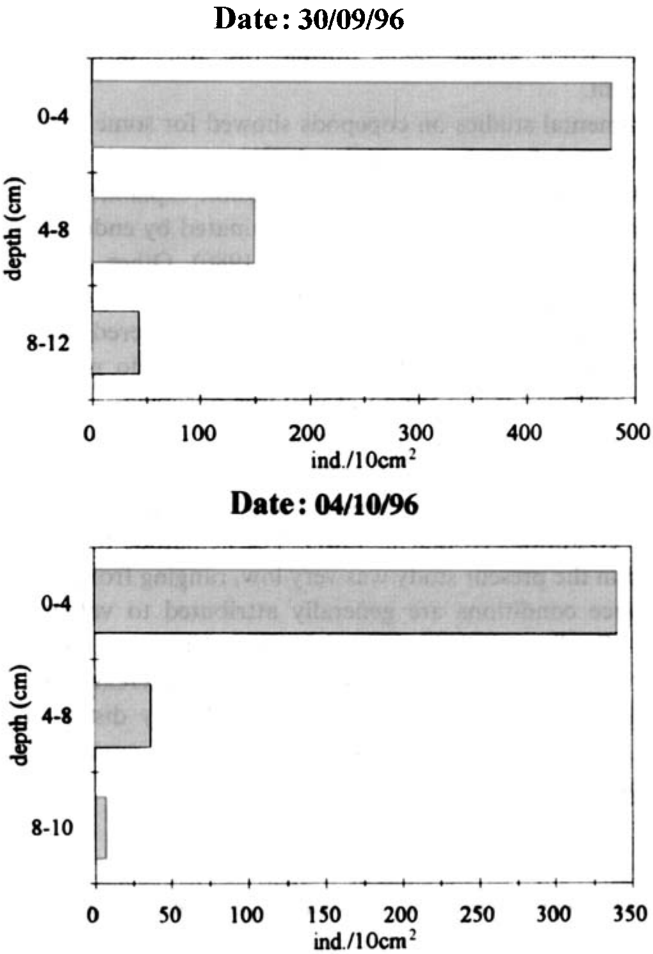
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FIGURE 4 Vertical distribution of meiofauna in the sediments of the Rapallo Harbour.

Nematodes, the numerically dominant taxon, appeared to be the most insensitive taxon to experimental conditions. By contrast, copepods have been reported to be severely affected by organic contamination (Sandulli, 1986) and to recover more slowly than nematodes when disturbed (Wormald, 1976; Giere, 1979). Copepod mortality (about 60%) observed between sampling times was the most evident feature affecting the meiofauna community structure. This had important consequence in terms of total meiofaunal biomass that decreases from about 50% during the four days of chamber deployment.

Experimental studies on copepods showed for some species a great sensitivity and, for others, a high tolerance to organic contamination (Dalla Venezia and Fossato, 1977). A possible explanation of the large copepod mortality is that they were dominated by endobenthic forms or non-opportunistic species (Sandulli, 1986). Other groups showed clear density decrease during the experiment (*e.g.*, polychaetes and oligochaetes). However, the low density encountered and the large degree of aggregation (high standard deviation) do not allow us to infer on reasons for the temporal patterns observed.

Due to the apparent high sensitivity of copepods and to the nematode tolerance to organic carbon load, it might be expected that the ratio of nematodes to copepods might represent an easy indicator of stress conditions (Raffaelli, 1981). The nematode to copepod ratio reported in the present study was very low, ranging from 2.1 to 7.5. As disturbance conditions are generally attributed to values exceeding 50–100 (Coull *et al.*, 1981; Warwick, 1981; Vincx and Heip, 1991), it clearly emerges that, despite the significant decrease in copepods density, this ratio cannot be applied to identify disturbance effect induced by organic contamination, at least when permanent enriched conditions are considered.

3.3. Community Partitioning in Benthic Oxygen Consumption

Simultaneous *in situ* measurements of sediment oxygen consumption (SOC) revealed high values of SOC (1320 mg $O_2\,m^{-2}\,d^{-1}$, Ceradini *et al.*, 1997). These values, consistent with those obtained in other highly productive environments (such as the Venice Lagoon, Ciceri pers. com.), when converted into carbon demand ($RQ = 0.85$), are equivalent to about 50 mg C $m^{-2}\,d^{-1}$.

Total macrofaunal oxygen consumption was estimated according to Flach and Heip (1996), calculating the mean individual oxygen consumption, following the equation: $R = 0.0074 \times W^{-0.24}$, where: R = individual respiration rate (day^{-1}), and W = mean individual weight (mg organic C), and then calculating the total community oxygen consumption (TCOC) as follows: TCOC = $B \times R$(mg organic $\mathrm{C\,m^{-2}\,d^{-1}}$), where B = biomass (mg organic $\mathrm{C\,m^{-2}}$). Macrofaunal oxygen consumption was, on average, $0.22\,\mathrm{ml\,O_2\,m^{-2}\,d^{-1}}$ and was lower than values previously reported for different environments (Dye, 1981; Kanneworff and Christensen, 1986; Flach and Heip, 1991). The smaller macrofaunal fraction contributed only for 9.1% of the total macrofaunal oxygen consumption. Meiofaunal oxygen consumption, estimated using conversion factors reported in the literature (Dye, 1981) in the top 1 cm of the sediment, was significantly higher, reaching $11.8\,\mathrm{ml\,O_2\,m^{-2}\,d^{-1}}$.

Using conversion factors reported in the literature for oxygen consumption of the different benthic components (*i.e.*, protozoa according to Dye, 1981, and bacteria by difference), it is possible to estimate that the microbial component (*i.e.*, bacteria and protozoa) accounted for about 98.7% of the total oxygen demand of the benthic assemblages, meiofauna accounted for 1.3% and macrofauna oxygen consumption was almost negligible, accounting only for 0.03% of the total oxygen consumption. Comparing our results with those reported by Dye (1981) and obtained applying the same conversion factors, it clearly emerges that, in oxic sandy environments, meiofaunal oxygen consumption accounted for 45–97% of the total SOC. These data indicate that the relevance of the microbial component in the overall benthic metabolism is significantly enhanced in organic enriched environments.

4. CONCLUSIONS

Data reported in this study indicate that the use of benthic chambers may have induced changes in benthic community structure. The community structure of temporary meiofauna, 0.5 to 1 mm and > 1 mm macrofauna were clearly different, indicating the presence of a selective post-recruitment mortality on different macrofaunal species. Macrobenthos was characterized by high densities of highly tolerant species typical of organically enriched environments, such as the bivalve, *Corbula gibba*, and capitellid polychaetes. Meiofaunal community structure appeared characterized by a low number of taxa and by low densities. Meiofaunal density decreased during the four days of the experiment. Benthic metabolism in sediments characterized by high organic contents is clearly dominated by the microbial component that accounted alone for about 98.7% of the total oxygen consumption.

Acknowledgements

The authors are indebted with Dr. Fabio Fiori (University of Parma) and Dr. Antonio Pusceddu (University of Ancona) for collaboration during sampling and Mr. Drago (University of Genoa) for providing identification of macrofaunal species. This work was partially supported by MURST 60% funding (Prof. Della Croce, Institute of Marine Environment Sciences, University of Genoa).

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