



## Benthic activity in sediments of the northwestern Adriatic Sea: sediment oxygen consumption, macro- and meiofauna dynamics

Leon Moodley\*, Carlo H.R. Heip, Jack J. Middelburg

*Netherlands Institute of Ecology (NIOO), Centre for Estuarine and Coastal Ecology (CEMO), P.O. Box 140,  
4400 AC Yerseke, Netherlands*

Received 14 August 1997; accepted 20 February 1998

### Abstract

Benthic activity was examined at three stations (18 m water depth) in the northwestern Adriatic Sea. Carbon mineralisation rates, as based on sediment oxygen consumption rates, ranged from 54 to 89 g C m<sup>-2</sup> y<sup>-1</sup>. The relatively high carbon mineralisation rates, large macrofaunal biomass (9 to 16 g C m<sup>-2</sup>) and macrofaunal production (11 to 19 g C m<sup>-2</sup> y<sup>-1</sup>) provide evidence of high organic-matter input and intense benthic–pelagic coupling. This is further supported by the high dominance of the suspension-feeding bivalve *Corbula gibba*, which accounts for 52 to 63% of the total annual macrofaunal biomass production. Although the infaunal distribution of total macrofauna showed a sharp decline in densities and biomass with depth into the sediment, different patterns within the dominant taxa were observed. Whilst the bivalve *Corbula gibba* and the amphipod *Ampelisca* sp. were restricted to the surface layer, other species such as the dominant bivalve *Mysella* sp. and the gastropod *Hyala* sp. were not confined to a specific depth level and the majority of the populations occurred deeper than 5 cm into the sediment. Bioturbation, based on the occurrence of macrofauna, extended to at least 20 cm. Nematodes and foraminifera together formed 80 to 90% of the meiofaunal community in the upper 5 cm of the sediment. Annual mean densities ranged from 3.40 to 6.07 × 10<sup>6</sup> ind. m<sup>-2</sup>. Maximum abundance of meiofauna was not encountered at the station where maximum macrofaunal activity was recorded, and this could reflect the negative effect of biological interaction on meiofaunal densities in areas that have a high food supply. © 1998 Elsevier Science B.V. All rights reserved.

**Keywords:** northwestern Adriatic Sea; eutrophication; sediment oxygen consumption; carbon flux; benthic–pelagic coupling; bioturbation; macrofauna; meiofauna; biotic interactions

### 1. Introduction

Eutrophication of the marine environment is usually defined as a complex set of phenomena ultimately triggered by the increase of limiting nutrients, especially nitrogen and phosphorus from terrestrial

sources. In short, increase in limiting nutrients leads to increased primary production and subsequently increased amounts of organic material can be deposited to the sediments. This may eventually lead to increases in benthic biomass and densities but also to hypoxic/anoxic conditions in the sediment that can result in massive reduction or die-off of benthic animals (e.g. Kemp and Boynton, 1992; Heip, 1995). Increasing eutrophication has also been documented

\* Corresponding author. Fax: +31 (113) 573616; E-mail: moodley@cemo.nioo.knaw.nl

in the northern Adriatic Sea, especially in the north-western area, which receives the inflow of the Po River (e.g. Bucci et al., 1992; Marchetti and Verna, 1992; Vollenweider et al., 1992; Justic et al., 1995) and seasonal hypoxic bottom-water conditions have been related to increased fluxes of organic matter and strong stability due to density and thermal stratification of the shallow water column (Justic, 1987; Justic et al., 1987, 1993; Degobbis, 1989; Franco and Michelato, 1992).

There are several river mouths distributed along the northwestern Adriatic coast, the most important of these rivers being the Po. Fluvial inflow has shaped the bottom morphology of the northern Adriatic on a geological time scale (Nelson, 1970), a prominent consequence of which is the well-defined clay belt along the Italian coast (Colantoni et al., 1979). Currently, at shorter time scales, the freshwater input influences the density structure, dynamics and biogeochemical processes of the waters inside the basin (Franco and Michelato, 1992).

The water circulation in the northern Adriatic Sea is characterised by seasonal dynamics that are strongly conditioned by thermohaline factors and, to a lesser extent, by winds (Franco et al., 1982; Orlic et al., 1992). In winter, the water column is vertically mixed and the water circulation consists of a cyclonic system. In summer, the cyclonic water circulation is very slow and the system is stratified by riverine input of warm, fresh water. Frontal systems often develop and confine high-nutrient waters and algal blooms to the western coastal region; as a result, bottom-water oxygen concentrations may be greatly reduced in late summer (Franco and Michelato, 1992).

The Po River is evidently an important source of sediments, nutrients and pollutants and exerts a major influence on the production and, through its principal flow regime, distribution of organic matter in the northern Adriatic. Prevailing hydrographic dynamics and subsequent seasonal variation in the benthic environment (e.g. carbon flux and bottom-water oxygenation) will also inevitably play an important role in benthic activity and benthic community structure.

In this study we examine several aspects of benthic activity in order to assess the effects of eutrophication on the benthic habitat along the western

Adriatic shore and to improve knowledge of key benthic biological elements. Two following proxies were used to assess benthic activity.

(1) Benthic respiration: sediment oxygen consumption (SOC) closely reflects rates of organic matter degradation. Several factors affect the decomposition of organic matter within sediments. For example, organic-matter decomposition is strongly temperature-dependent (Nixon et al., 1976), while benthic macrofauna can influence both the magnitude and timing of decomposition (e.g. Kanneworff and Christensen, 1986; Rudnick and Oviatt, 1986). Ultimately, however, rates of organic-matter decomposition in sediments are controlled by organic-matter supply to the sediments, which is in turn a function of water depth, rates of primary production or allochthonous input (Hargrave, 1973; Suess, 1980; Graf et al., 1982; Banta et al., 1995) and heavily dependent on the bulk sediment accumulation rates (Graf, 1992; Heip et al., 1995; Rosenberg, 1995).

(2) Zoobenthos (macro- and meiofauna): the standing stock of the relatively long-living macro- and meiobenthos offers a time-integrated signal that reflects the average benthic food resources or carbon flux (Schaff et al., 1992; Tahey et al., 1996).

Both approaches provide information about the status of the benthic community with respect to organic enrichment. Three stations were chosen along the residual anti-clockwise flow regime in the northwestern Adriatic.

## 2. Material and methods

### 2.1. Sampling sites

Benthic activity and benthic community structure were studied at three coastal stations (18 m water depth, Fig. 1). Sediment oxygen consumption measurements were conducted in February and September 1994 and April 1995. The macrofauna was studied in February and June 1994; the meiofauna was studied in February, June and September 1994.

### 2.2. Sediment parameters

Sediment cores (using perspex pipes with 3.6 cm i.d.) were collected either by SCUBA divers or

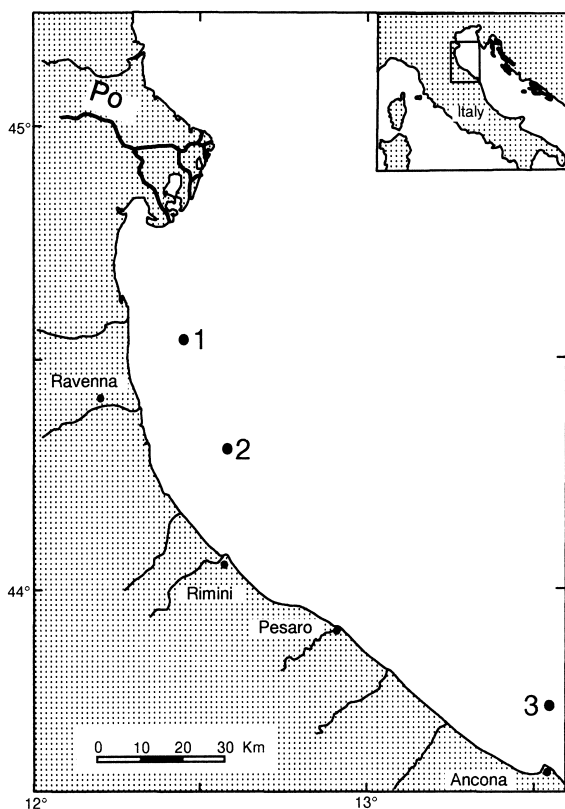


Fig. 1. Location of sampling stations.

taken from undisturbed boxcore samples. Cores were sliced on board within 2 h.

#### 2.2.1. Grain-size analysis

Samples were stored cool until analysed with a Malvern Particle Analyser. Only sediment collected in February 1994 was used for this analysis.

#### 2.2.2. Porosity

Porosity was calculated from the water content of the sediment, assuming a density of 2.55 for sediment and  $1.003 \text{ g cm}^{-3}$  for seawater.

#### 2.2.3. Organic carbon and nitrogen content

Freeze-dried samples were homogenised, acidified, and analysed with a Carlo Erba NA 1500 CN Analyser. %C and %N were converted to content per volume or area unit using the porosity and assuming a dry density of  $2.55 \text{ g cm}^{-3}$  for sediment.

#### 2.2.4. Chlorophyll-*a* content

Samples were frozen until analysed by means of reverse-phase HPLC. Concentrations were converted to content per volume or area unit using the porosity and assuming a dry density of  $2.55 \text{ g cm}^{-3}$  for sediment.

#### 2.2.5. Oxygen penetration depth

Oxygen penetration depth was determined with glass microelectrodes with a built-in reference electrode connected to a Keithley picoammeter. Profiling was done using a micro-manipulator.

#### 2.2.6. Porewater sulphide content

Sediment was profiled for sulphide, using a metal microelectrode (lower limit of detection is approx.  $10 \mu\text{mol S}^{2-}$  per  $\text{dm}^3$ ) and a calomel reference electrode, connected to a Radiometer pH/millivolt meter. For calculations of sulphide concentrations, pH profiles were also made using a pH milli-electrode.

### 2.3. Benthic activity

#### 2.3.1. Sediment oxygen consumption

A system was designed for in-situ measurements that can be handled by SCUBA divers; it consists of a perspex chamber (i.d. 19 cm) with a detachable lid containing a YSI 5739 oxygen electrode and a Teflon-coated magnetic stirrer. After careful insertion to a predetermined depth to ensure a fixed volume of water, lids were mounted that were connected to an underwater data logger preset aboard for continuous measurements of oxygen concentration at intervals of 60–90 s. Incubations lasted between 4 and 8 h. The electrodes were calibrated between the oxygen concentrations of ambient seawater as determined either by Winkler titration or with a YSI 58  $\text{O}_2$  meter. SOC, expressed as  $\mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ , was calculated by means of linear regression of the initial decrease in oxygen concentration in time (i.e. the first 3 h excluding the first 30 min allowed for stabilization of the system). All measurements were done in the absence of light; for the in-situ measurements this was achieved by covering the chambers with black plastic. This system was also used for deck incubations in temperature-controlled water baths. In February 1994, deck incubations were done and in September 1994 the SOC was measured in situ. In

April 1995, deck incubation was done using cores with a smaller inner diameter (10.4 cm).

### 2.3.2. Macrofauna

Boxcores were subsampled with perspex cores (i.d. 19 cm). Duplicate sediment samples were cut into 5-cm slices down to 20 cm and then washed over a 0.5-mm sieve. The fraction >0.5 mm was preserved in borax-buffered 4% formalin with rose Bengal. In the laboratory, organisms were sorted and counted under a stereo microscope and categorised in taxonomic groups. Biomass determinations were made by weighing formalin-preserved samples (including shells of molluscs but excluding tubes of polychaetes, phoronids and amphipods), after blotting on absorbent paper. Biomass values were converted to organic C content per major taxon or lower taxonomic levels using the conversion factors given by Rowe (1983). For non-specified groups the carbon content was estimated as 4.3% WW (Rowe, 1983). Macrofauna production ( $P$ ) was calculated for each phylum separately using formulas given by Brey (1990) which include estimates of mean annual biomass ( $B$ ) and mean individual weight ( $W$ ) according to:

$$\log_{10}(P) = a + c_1 \log_{10}(B) + c_2 \log_{10}(W).$$

The coefficients  $a$ ,  $c_1$ , and  $c_2$  for the different phyla were taken from Brey (1990). The biomass in AFDW was estimated as  $2 \times g C = g AFDW$  (Lalli and Parsons, 1993). The production of dominant species was calculated separately and then added to the rest to obtain total production.

### 2.3.3. Meiofauna

Duplicate samples (perspex pipes with i.d. of 3.6 cm) were taken from boxcores in February 1994 and collected by SCUBA divers in June and September 1994. The upper 5 cm was sampled for meiofauna and stored in borax-buffered 4% formalin with rose Bengal. In the laboratory, the fraction >38  $\mu\text{m}$  was analysed. Meiofauna was first separated from the sediment by centrifuging with Ludox HS 40. Stained specimens of permanent meiofauna and foraminifera were identified and counted. The residue was also examined for fauna as most hard-shelled foraminifera, in contrast to nematodes and soft-shelled foraminifera, remained in the sediment.

All counts were ln-transformed before statistical analysis by two-way analysis of variance (ANOVA) followed by pairwise comparisons (Tukey HSD test) using the MGLH module of SYSTAT (Systat Inc.).

## 3. Results

### 3.1. Environmental parameters

Examination of the meiofaunal samples (0–5 cm sediment layer) showed that station 1, closest to the Po, was rich in plant debris, wood chips and pieces of charcoal; station 2 (~30 km south of station 1) had less plant remains and more shell debris; and station 3 (~100 km south of station 2) was generally free of plant remains or wood chips and was rich in shell debris (both fragmented and complete shells). Porous fine-grained sediment (muddy silt) was characteristic of all stations (Fig. 2a). Stations 1 and 2 had comparable characteristics but station 3 had a larger median grain size (26.9  $\mu\text{m}$ ) and a lower silt content (Fig. 2a).

Bottom-water temperature and oxygen content showed clear seasonal variation (Fig. 2b,c). Temperature ranged from 9 to 20°C. Bottom-water oxygen content ranged from 165 to 274  $\mu\text{M O}_2$  (Fig. 2c). The organic-carbon content showed little or no consistent spatial or temporal trend (Fig. 2d). The same holds for the nitrogen content and C/N ratios (Fig. 2e,f).

The chlorophyll-a content in the upper 5 cm of the sediment ranged from 14 to 190 mg Chl.-a  $\text{m}^{-2}$  and exhibited strong spatial and temporal variations (Fig. 2g) without any distinct spatial gradient. Chlorophyll a was encountered to the maximum depth analysed in sediment cores (10 cm) with the common occurrence of subsurface peaks (Fig. 3).

Oxygen penetrated only a few millimetres into the sediment; in winter (February 1994) the penetration depths were 4, 7 and 8 mm at stations 1, 2 and 3, respectively; in April 1995 they were <2 mm for all stations. No measurements were made in summer, but penetration depths are expected to be shallower than in winter. The sediment was profiled for sulphide down to 15 cm but no free sulphide was detected at any of the stations or during any of the seasons.

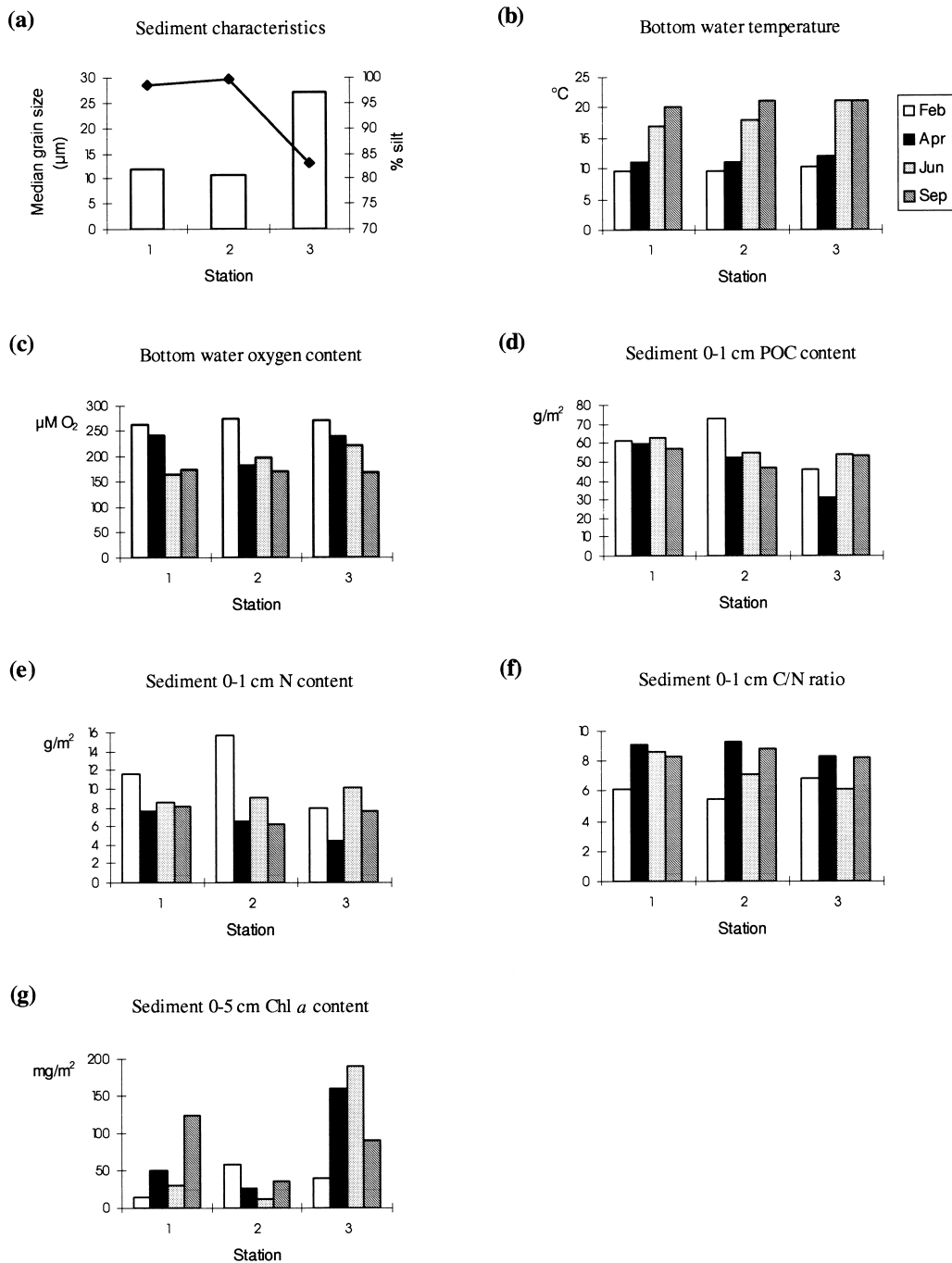


Fig. 2. Bottom-water and sediment parameters observed on four sampling occasions at the three sampling stations (Fig. 1). (a) Median grain size (bars) and silt content ( $<63 \mu\text{m}$ , line) of surface sediments (0–1 cm). (b) Bottom-water temperature. (c) Bottom-water oxygen content. (d) POC content in the upper cm of the sediment column. (e) N content in the upper cm of the sediment column. (f) Molar C/N ratio in the upper cm. (g) Sediment chlorophyll-a content.

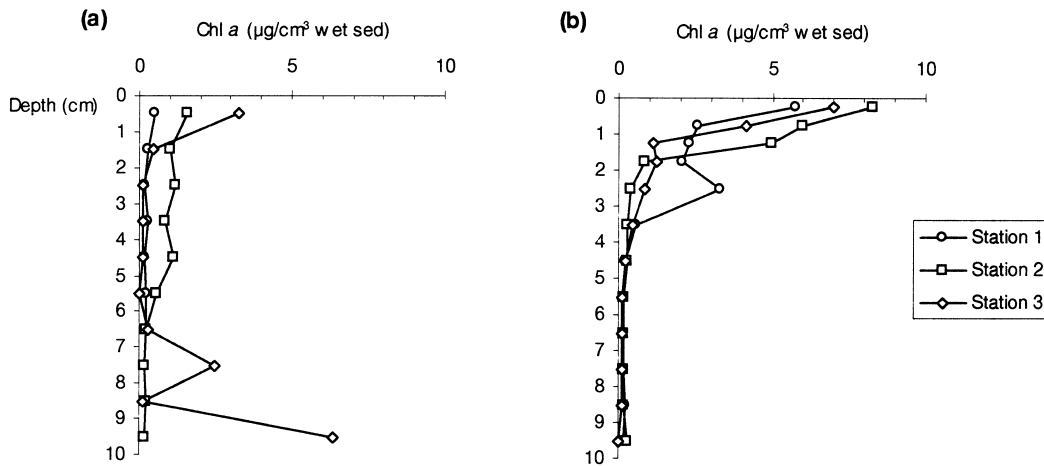


Fig. 3. Chlorophyll-a profiles in sediment collected at the three stations in (a) February 1994 and (b) February 1995.

### 3.2. Benthic activity

#### 3.2.1. Sediment oxygen consumption

Sediment oxygen uptake was measured during three seasons and ranged from  $118 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$  at station 1 in February to  $1981 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$  at station 1 in September (Fig. 4). Minimum SOC was found in February ( $p < 0.001$ , Fig. 4). Highest consumption rates were obtained in September for all three stations ranging from 945 to  $1981 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ . SOC values were comparable between stations in the spring (April).

#### 3.2.2. Macrofauna

The macrofauna ( $>0.5 \text{ mm}$ ) was studied in February and June 1994. Densities in the upper 20 cm were

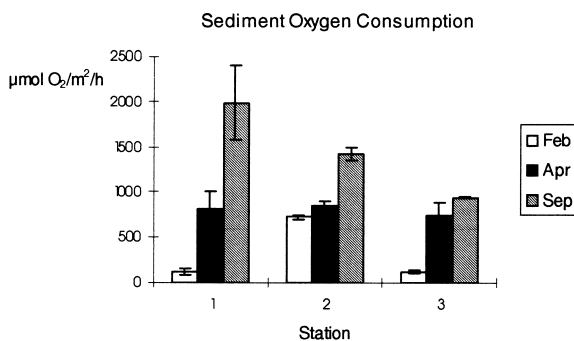


Fig. 4. Sediment oxygen consumption (SOC) as measured in benthic chambers in February and September 1994 and April 1995 (mean  $\pm$  SD).

significantly higher in June ( $p = 0.004$ , Fig. 5a) and the highest densities were encountered at station 2 ( $p = 0.002$ ). Average densities ranged from 4400 to 10200 and from 8400 to 21400 individuals per  $\text{m}^2$  in February and June, respectively. In February, Polychaeta and Mollusca were the dominant groups (Fig. 5c). Dominant species among the molluscs included the suspension-feeding bivalve *Corbula gibba*, the gastropod *Hyala* sp. and the bivalve *Mysella* sp. At station 2, crustaceans outnumbered the polychaetes and the filter-feeding amphipod *Ampelisca* sp. in particular was abundant. The rest group included phoronids, nemertean and sipunculids. In June the importance of crustaceans increased (Fig. 5d), mainly due to *Ampelisca* which reached extremely high numbers (e.g. 10,000 ind.  $\text{m}^{-2}$  at station 2). The densities of the most abundant mollusc *C. gibba* varied between 900 and 1800 ind.  $\text{m}^{-2}$ . Other common molluscs, although not particularly dominant, included the bivalves *Nucula* sp., *Abra* sp. and *Tellina* sp. and the gastropod *Cylichna* sp.; *Amphiura* sp. (Echinodermata) were only encountered at station 1 (214 and 339 ind.  $\text{m}^{-2}$  in February and June, respectively).

Unlike densities, biomass values were not significantly different between stations or seasons ( $p > 0.05$ , Fig. 5b). Biomass ranged from 5.8 to 17.3 and from 11.7 to 14.3  $\text{g C m}^{-2}$  in February and June, respectively. This was equivalent to 69 to 128 and 123 to 129  $\text{g m}^{-2}$  blotted WW (excluding shells), respectively. The contribution of the differ-

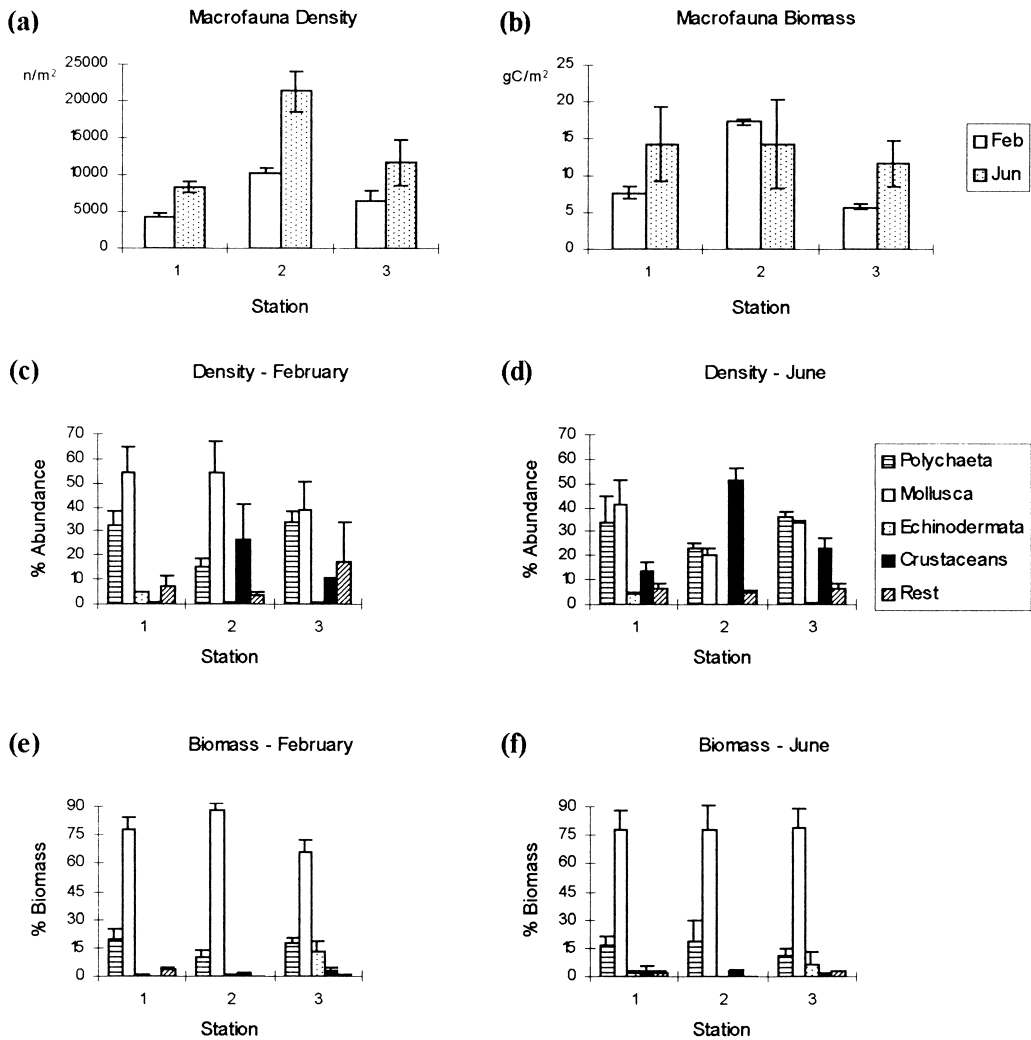


Fig. 5. Macrobenthos characteristics. (a) Macrofauna ( $>0.5$  mm) abundance ( $n m^{-2}$ ) in the upper 20 cm of the sediment. (b) Macrofauna biomass ( $g C m^{-2}$ ) in the upper 20 cm of the sediment. (c, d) Percentage contribution of the different taxa to the total abundance in the upper 20 cm at the two sampling dates. (e, f) Percentage contribution of the different taxa to the total biomass in the upper 20 cm at the two sampling dates. Values are means of two cores  $\pm$  SD.

ent taxa to the total biomass is shown in Fig. 5e,f. Mollusca and Polychaeta were the most important groups and among the molluscs the suspension-feeding bivalve *C. gibba* was the most dominant species, accounting for 48 to 88% of total biomass. Among the polychaetes, the bamboo worms Maldanidae (tube-dwelling subsurface feeders) formed 2 to 21% of the total biomass. Echinodermata (sea cucumbers) formed an important part of the biomass in subsurface layers at station 3. The large increase

in *Ampelisca* densities in June could not be observed in the biomass trend due to its low individual weight.

Macrofauna production was estimated at 12.8, 19.0 and 10.9  $g C m^{-2} y^{-1}$  at stations 1, 2 and 3, respectively (Table 1, Fig. 6). Mollusca accounted for an average of 65.8% of the total annual production and *C. gibba* alone accounted for 52 to 63%. Maldanidae accounted for 19% of total annual production at station 1, but only  $\sim$ 8% at stations 2 and 3.

Table 1  
Annual carbon input and benthic activity data

	Station 1	Station 2	Station 3
Carbon input ( $\text{g C m}^{-2} \text{ y}^{-1}$ )	115.3	132.9	59.7
Carbon mineralisation ( $\text{g C m}^{-2} \text{ y}^{-1}$ )	86.9	89.3	53.9
Macrofauna annual mean densities ( $\text{n m}^{-2}$ )	6339	15783	9087
Meiofauna annual mean densities ( $\text{ind.} \times 10^6 \text{ m}^{-2}$ )	5.0	3.4	6.1
Macrofauna annual mean biomass ( $\text{g C m}^{-2}$ )	11.0	15.8	8.7
Macrofauna production ( $\text{g C m}^{-2} \text{ y}^{-1}$ )	12.8	19.0	10.9

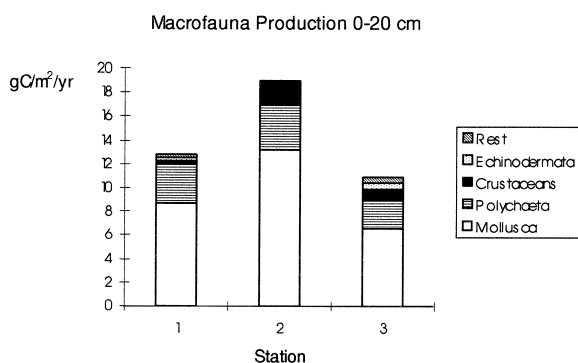


Fig. 6. Macrobenthos production: contribution of the different taxa to annual production in the upper 20 cm at all three stations.

The sediment column was colonised to the maximum depth sampled albeit with a strong decline both in densities and biomass with depth (Fig. 7). On average, 59% of the individuals were concentrated in the upper 5 cm in February and this fraction increased to 77% in June, mainly due to the numeric increase in the suspension feeders *Ampelisca* and *C. gibba*. However, although some species such as the suspension feeders (*C. gibba* and *Ampelisca*) were confined to surface layers (Fig. 8), others were not; polychaetes were found at all depths; large sea cucumbers were found only in deeper layers and a large fraction of the populations of the dominant gastropod *Hyala* and the bivalve *Mysella* was encountered deeper than 5 cm (Fig. 8). Infaunal activity, based on the occurrence of macrofauna, extended to at least 20 cm.

### 3.2.3. Meiofauna

The permanent meiofauna and foraminifera in the upper 5 cm were studied on three occasions (Fig. 9a). Mean densities ranged from  $2.04 \times 10^6 \text{ ind. m}^{-2}$  at

station 2 in June to  $9.80 \times 10^6 \text{ ind. m}^{-2}$  at station 3 in September (Fig. 9a). Annual mean densities were estimated at 4.97, 3.40 and  $6.07 \times 10^6 \text{ ind. m}^{-2}$  at stations 1, 2 and 3, respectively. Meiofauna densities at station 3 were significantly higher than those at station 2 ( $p = 0.015$ , Fig. 9a). Maximum densities were encountered in September ( $p < 0.001$ ) and a clear seasonal trend was seen only at station 3 (Fig. 9a). Nematodes and foraminifera contributed 44 to 80% and 13 to 52%, respectively, to the meiofaunal community; copepods accounted for 1 to 8% (Fig. 9b–d).

## 4. Discussion

### 4.1. Methodological considerations

A major limitation in this study is the relatively small size of macrofaunal samples and the absence of summer samples so that possible recruitment could have been missed. This could lead to an underestimation of macrofaunal densities and biomass. We also observed that large echinurids (coelomate worms, 20–25 cm long and 3–4 cm in diameter) were sometimes present near the bottom of boxcore samples (25–30 cm deep); these were not encountered in our macrofauna samples. This illustrates that large specimens may be under-represented in small samples. These large echinurids, belonging to the megafauna, require a totally different sampling strategy. Additionally, June and August density and biomass values reported for the northwestern Adriatic Sea in studies sampling a larger area are within the range or even lower than that found during our study (Crema et al., 1991; Tahey et al., 1996). However, small macrofauna samples remain a drawback and large

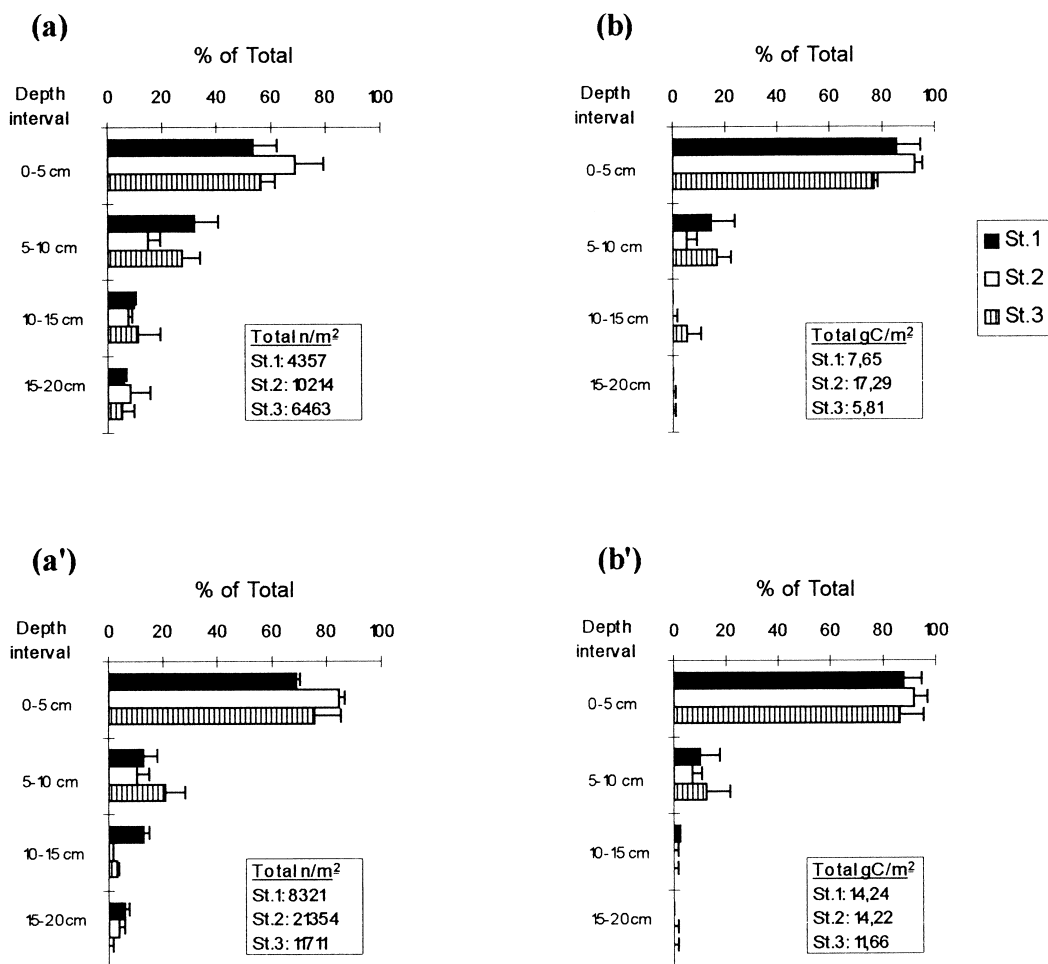


Fig. 7. Vertical distribution of macrofauna (>0.5 mm) in the sediment. Left-hand graphs (a and a') represent the vertical distribution of numerical densities in February and June, respectively. Right-hand graphs (b and b') represent the vertical distribution of biomass in February and June, respectively.

variation in the June biomass values (Fig. 5b) was primarily due to large organisms (sipunculids, sea cucumbers and echiurids) found in deeper layers of the sediment column.

#### 4.2. Environmental parameters

The decrease in the amount of terrestrial components in surficial sediments towards the south suggests that direct influence from the Po (in terms of detrital input) is limited south of stations 1 and 2. Physical energy above the seafloor is an important factor for the spatial distribution of different sediment types. Prevailing hydrographic conditions

evidently allow fine sediments to settle out at these coastal stations but coarser sediments at station 3 suggest stronger bottom currents at this station, as was also experienced by the SCUBA divers.

The organic-carbon content in surficial sediments showed little or no consistent spatial or temporal trends (Fig. 2d), neither did the nitrogen content and C/N ratios (Fig. 2e,f). Organic-carbon content is probably, especially in an area with large terrestrial input (Faganeli et al., 1994), an unsuitable measure of labile organic matter as it mainly reflects the preservation of bulk refractory carbon (Banta et al., 1995; Soetaert et al., 1997). Chlorophyll a is generally a better indicator of labile organic-matter

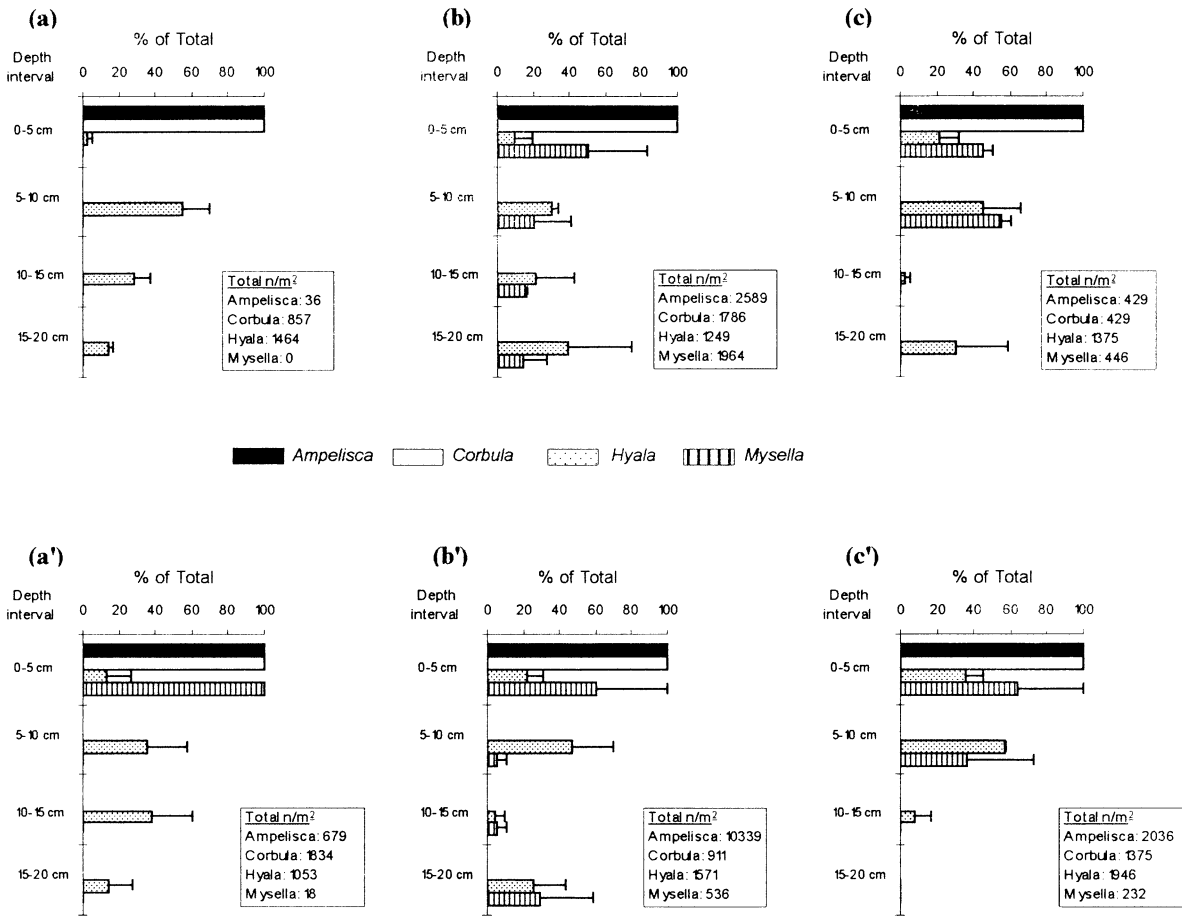


Fig. 8. Vertical distribution of selected genera in the sediment. The upper graphs (a, b, and c) represent stations 1, 2, and 3, respectively, in February; the lower graphs (a', b' and c') represent the same stations in June.

input to sediments (e.g. Christensen and Kanneworff, 1985; Van Duyl and Kop, 1994; Banta et al., 1995; Josefson and Conley, 1997) and strong spatial and temporal variation of this parameter was recorded, but without a distinct gradient (Fig. 3a). As observed in another river-impacted coastal ecosystem, the northern Gulf of Mexico, the site of maximum primary production and the site of maximum vertical export of POC from the photic zone can vary strongly with season (Redalje et al., 1994). Additionally, as shown in previous studies in the northeastern and northwestern Adriatic Sea, sufficient light penetrates to the bottom to support microphytobenthic primary production (Herndl et al., 1987, 1989; Epping and Helder, 1997). During a pilot study of benthic primary production (in April 1995, author's

unpublished data) using the oxygen microelectrode method (Revsbech and Jørgensen, 1983), indications of benthic primary production were found only at station 3. Additionally, many benthic diatoms were found in meiofauna sediment samples of station 3, especially in September. However, in June, some benthic diatoms were found also at station 1. Microphytobenthos production may also exhibit seasonal spatial variation in relation to, for example, variation in turbidity. This complicates the use of the Chl.-a content of the sediment as an indicator of vertical organic matter input to the benthos. However, as a whole, the values of organic carbon, nitrogen and Chl. a reflect the general organic enrichment expected in this river-impacted coastal ecosystem. This is supported by the rapid consumption of oxygen

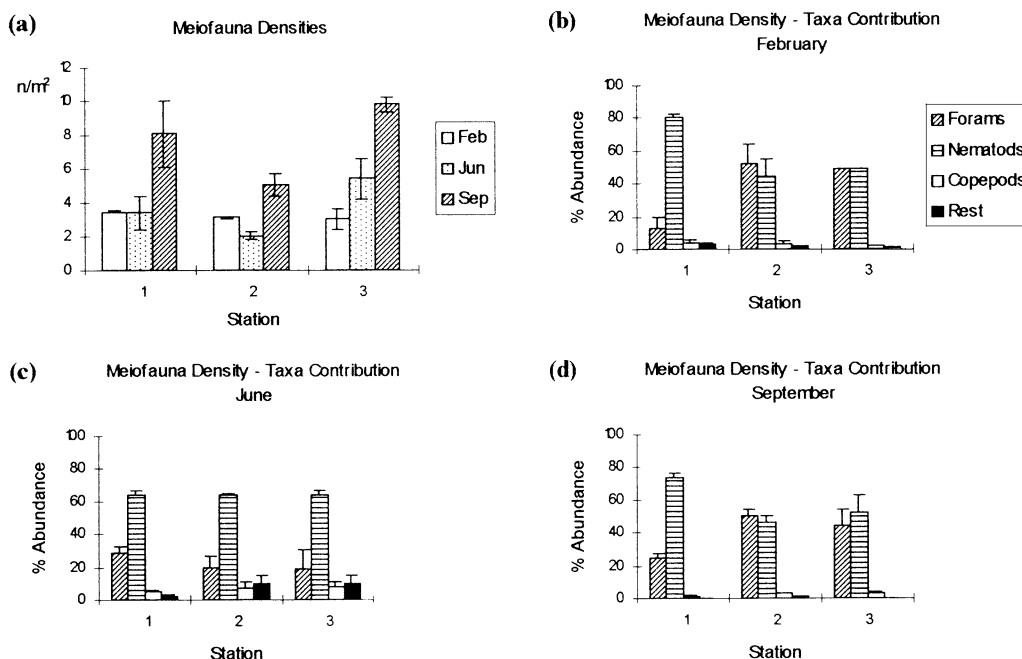


Fig. 9. Meiobenthos characteristics. (a) Permanent meiobenthos numerical abundance ( $>38 \mu\text{m}$ ), including foraminifera, in the upper 5 cm at the different sampling dates (numbers  $\times 10^6 \text{ m}^{-2}$ , mean  $\pm$  SD). (b, c, d). Percentage contribution of the different taxa to total density (mean % abundance  $\pm$  SD) on the three sampling occasions.

in surface sediments as reflected by shallow penetration of oxygen (a maximum of 4 to 8 mm in winter), which is in accordance with earlier observations (Epping and Helder, 1997) and typical of shallow coastal sediments rich in organic matter (e.g. Revsbech et al., 1980; Rasmussen and Jørgensen, 1992). Also in accordance with earlier observations, no free sulphide was detected either by the electrode or by smell and this has been related to the high reactive-Fe content of the sediment (Barbanti et al., 1995).

#### 4.3. Benthic activity and benthic community structure

Except for the values measured in September at station 1 ( $47 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ), the sediment oxygen consumption rates reported in this study (3 to  $34 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ) are within the range of rates reported previously ( $5$  to  $43 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ) for the northern Adriatic Sea (Herndl et al., 1987, 1989; Giordani et al., 1992; Tahey et al., 1996; Epping and Helder, 1997). In September, a flash flood occurred

in the Po valley that led to strong bottom-water currents and strong resuspension of surficial sediments at station 1 (SCUBA diver observations) which may have accounted for the high oxygen consumption rates measured at this station. However, in agreement with Herndl et al. (1989), maximum rates were measured in September.

We integrated the seasonal benthic respiration rates, and utilising an RQ of 0.85 (Wassmann, 1984) we estimated that 87, 89, and  $54 \text{ g C m}^{-2}$  were respired annually at stations 1, 2, and 3, respectively. Highest benthic respiration rates were found in the northern stations and these rates are evidence of a relatively high organic-matter input. The total carbon flux can be estimated as the sum of the burial and respiration rates, as based on sediment oxygen uptake (Middelburg et al., 1993). The burial rate was estimated by multiplying the bulk sediment accumulation rates (Frignani et al., 1996) by the background POC content. The sediment accumulation rate was the highest at station 2 ( $6 \text{ mm y}^{-1}$ , Frignani et al., 1996). Resulting annual carbon fluxes were 115, 133, and  $60 \text{ g C m}^{-2} \text{ y}^{-1}$  at stations 1, 2, and 3, respec-

tively, with the lowest flux at the southern station. These values reflect the general eutrophic conditions in the northwestern Adriatic Sea.

The relatively large macrofaunal biomass and annual production (Table 1) provide further evidence of relatively high organic-matter input. Macrofaunal annual respiration can be calculated assuming 33% production efficiency (Banse, 1979; Rudnick et al., 1985) and it is estimated that, on average, the total macrofauna community was responsible for ~38% of the annual carbon respiration or sediment oxygen uptake of which ~61% is attributed to the dominant suspension feeders (*C. gibba* and *Ampelisca*). Given these production and respiration rates, it is estimated that these suspension-feeders directly assimilated (production + respiration) an average of ~27% of the estimated C-flux which is direct evidence of intense benthic–pelagic coupling. Therefore, these filter feeders are expected to substantially increase the flux of organic matter to the benthic habitat (Heip et al., 1995). This supports the assumption that a major fraction of the productivity in surface waters reaches the seafloor (Giordani et al., 1992).

One of the striking features of macrobenthic dynamics is the strong numeric increase of ampeliscid amphipods in June (Fig. 8). *Ampelisca* resides in ‘capsules’ or tubes that extend into the water column and they can form dense carpets on the seafloor. Several studies have reported the quantitative importance of *Ampelisca* at different times of the year (e.g. Harper et al., 1981; Nichols and Thompson, 1985; Rhoads and Germano, 1986; Kemp and Boynton, 1992). They are not just passive recipients of particulate organic-matter deposition but have been observed to actively filter the water (SCUBA diver observations) and this could probably explain the relatively low Chl.-a values measured in surficial sediments at station 2 where the maximum abundance of *Ampelisca* was found (Fig. 2g). This phenomenon is probably enhanced by the other dominant suspension feeder, the bivalve *C. gibba*, which is by far the most important species in terms of biomass. The possibility that a substantial portion of the fresh detritus is captured before reaching the sediment surface complicates the use of Chl. a as a proxy for food supply to explain macrofaunal trends. Additionally, biological interactions may also be involved; the

dense stands of *Ampelisca* will certainly influence the structure and density of the community deeper down. Evidence of this is seen in the relationship between *Ampelisca* and *C. gibba*: at stations 1 and 3 there was an increase in abundance of both *Ampelisca* and *C. gibba* in June, but at station 2 the number of *C. gibba* decreased in June when *Ampelisca* had the maximum increase (Fig. 8). This suggests that *C. gibba* abundance could also be controlled locally by the presence of large populations of *Ampelisca*. Analogous species interactions have been found elsewhere (the amphipod *Pontoporeia* and the bivalve *Macoma*, Segerstråle, 1973; *Ampelisca* and *Macoma*, Nichols and Thompson, 1985). In our study area, the highest mean abundance of *C. gibba* was around 1800 ind. m<sup>-2</sup>, similar to the range reported by Crema et al. (1991) for the northwestern Adriatic Sea. In areas where ampeliscid amphipods do not form a dominant part of the benthos, higher numbers of *C. gibba* have been reported: Jensen (1990) reported a highest mean abundance of around 9500 ind. m<sup>-2</sup> in the Limfjord, Denmark, and Rosenberg (1977) recorded about 4500 ind. m<sup>-2</sup> in a eutrophic Swedish fjord.

On broad time and space scales, however, it is expected that secondary production of macrofauna will be proportional to deposition rates of particulate organic matter from the overlying waters to the sediment (e.g. Josefson, 1987; Grebmeier et al., 1988; Kemp and Boynton, 1992), i.e. the flux of organic matter, with hydrographic conditions strongly determining the sites of sediment or organic-matter accumulation (Rosenberg, 1995). Therefore, a more appropriate indication of food availability may be derived from estimates of total carbon flux at each site (Schaff et al., 1992; Soetaert et al., 1997). The station with the highest carbon flux supports the largest macrofaunal production (station 2), but station 3 with a relatively low C-flux supports a relatively high macrobenthos production as well (Table 1, Fig. 6). As already discussed, benthic primary production could be an important extra source of organic matter, especially at station 3.

The dominance of *C. gibba* in the shallow northwestern Adriatic Sea has been observed in earlier studies (Hrs-Brenco, 1981; Ambrogi et al., 1990; Crema et al., 1991; Tahey et al., 1996) and in our study it was the most important species in terms

of biomass and production, which was 8.1, 10.2, and 5.7 g C m<sup>-2</sup> y<sup>-1</sup> at stations 1, 2, and 3, respectively, accounting for 52 to 63% of the total production at those stations. *C. gibba* is a widely distributed bivalve in estuaries in northern Europe and the Mediterranean and is often abundant in eutrophicated areas where it is believed to benefit from organic enrichment (Rosenberg, 1977; Pearson and Rosenberg, 1978; Jensen, 1990). Jensen (1990) reported a wide range (0.7 to 72 gAFDW m<sup>-2</sup> y<sup>-1</sup>) and an average production of 26.8 gAFDW m<sup>-2</sup> y<sup>-1</sup> (~13.4 g C m<sup>-2</sup> y<sup>-1</sup>) for *C. gibba* in the westernmost part of the Limfjord and suggested that the high organic load in the eutrophic fjord and the high oxygen concentrations created optimal conditions for a high production. In our study area the average production of this bivalve was 8 g C m<sup>-2</sup> y<sup>-1</sup>, but production of this single species can evidently be much higher (Jensen, 1990).

Bottoms with excess food availability can harbour rich benthic communities which suggests that the benthic fauna in many areas may be considered food-limited (Rosenberg, 1995; Beukema and Cadée, 1997). An important factor that could counteract a high food supply is the occurrence of long-term severe hypoxic or anoxic conditions (e.g. Rosenberg, 1977; Kemp and Boynton, 1992; Diaz and Rosenberg, 1995). However, *C. gibba* is one of the most resistant species to severe hypoxia (see review in Diaz and Rosenberg, 1995) and laboratory experiments have shown that this bivalve is able to survive long periods of anoxia (Christensen, 1970). Therefore, this bivalve is not expected to be strongly inhibited by seasonal depletions in bottom-water oxygenation which are relatively short-lived (Crema et al., 1991; Regione Emilia–Romagna, 1993).

Long-term changes in the macrobenthic communities of the northwestern Adriatic Sea have been attributed to eutrophication. In contrast to the pre-eutrophication biocenosis, the recent biocenosis is largely dominated by a polychaete–mollusc fraction, with a large numeric abundance and biomass of the bivalve *C. gibba* (Crema et al., 1991). This indicates that *C. gibba* may not be strongly inhibited by the prevailing conditions (organic enrichment and seasonal depletion in bottom-water oxygenation). Severe oxygen depletion was not recorded during our study (Fig. 2) but may have been missed as it was

expected in late summer (Justic et al., 1993; Regione Emilia–Romagna, 1993). Although it remains speculative, and the effects of repeated, seasonal hypoxic conditions cannot be excluded, it seems that *C. gibba* in the northwestern Adriatic Sea may also be food- and/or space-limited in direct competition with *Ampelisca*. The apparent inhibition by the amphipods may also be due to direct consumption of settling larvae or to alteration of the benthic boundary layer flow regime by the dense stand of amphipod tubes, resulting in reduced particle settlement (Nichols and Thompson, 1985).

The infaunal distribution of the macrobenthos indicates that the sediment column was colonized by macrobenthos to the maximum depth sampled of 20 cm (Fig. 7) and as expected from their feeding-mode, the suspension-feeders *Ampelisca* sp. and *C. gibba* were not encountered in deeper layers of the sediment (Fig. 8). Other common molluscs, *Nucula* sp., *Abra* sp., *Tellina* sp. and *Cylichna* sp. were also confined to the upper layer of the sediment (data not shown). Some species, however, were not confined to a specific layer, viz. *Mysella* sp. and *Hyala* sp. (Fig. 8). *Mysella* is known to live in association with amphiuroids or sipunculids (Hayward, 1990) and their numbers are correlated in some areas (Ockelmann and Muus, 1978), but not in others (Rosenberg, 1995). *Amphiura* sp. was not dominant at our study sites and was found only at station 1, where *Mysella* was virtually absent (Fig. 8). *Amphiura* has, however, been reported to form a dominant part of the macrofauna in slightly deeper waters (25 to 30 m) in the northwestern Adriatic (Tahey et al., 1996). The presence of a large fraction of the *Mysella* population in deeper sediment layers suggests that this bivalve is not restricted to filter feeding but can also feed on deposited particles (Rosenberg, 1995).

The majority of the *Hyala* population was found deeper than 5 cm (Fig. 8) and this species is probably a predator. No direct associations of these two species with burrowing organisms were observed in this study, but large sipunculids (~71 ind. m<sup>-2</sup> at station 3 and ~36 ind. m<sup>-2</sup> at station 1, none at station 2) were present and large subsurface-dwelling sea cucumbers were encountered at station 3 (~60 ind. m<sup>-2</sup>).

As in other shallow, productive systems, oxygen penetration depth was shallow (maximum 8

mm), but macrobenthic animals were found living deeper than 20 cm in the sediment. In general, the absence of oxygen and the presence of sulphide may impose severe physiological constraints (Heip et al., 1995). The deep colonization in our sediments is probably due to the absence of free sulphide. Although many species can cope with short-term hypoxia/anoxia (Rosenberg et al., 1991; Diaz and Rosenberg, 1995), the combination with sulphide appears to be highly critical (Jørgensen, 1980; Diaz and Rosenberg, 1995). Large burrowing organisms probably provide oxygen for species like *Hyala* that apparently do not have direct contact with the overlying water. The apparent absence of a direct association with burrowing organisms suggests that subsurface-dwelling organisms, lacking their own supply of oxygenated water, are probably resistant to short-term hypoxia/anoxia, as was recently established for some common macrofauna species that were previously thought to require much higher levels of oxygenation (Rosenberg et al., 1991).

Bioturbation, as based on the occurrence of macrofauna, extends deeper than 20 cm. Because chlorophyll a is highly degradable, deep penetration of chlorophyll a cannot be a consequence of mere sedimentation. The Chl.-a profiles (Fig. 3) suggest mixing and active drawing of Chl.-a into the sediment by organisms. This is in accordance with the faunal distribution (Fig. 7). Although bioturbation extends deeper than 20 cm, the mixed layer (as estimated from  $^{210}\text{Pb}$  profiles) was only 7 to 10 cm deep (Frignani et al., 1996) and apparently represented the layer of maximum activity in which the major part of the macrobenthos was found: on average, excluding the dominant filter feeders (*C. gibba* and *Ampelisca* sp.), 40 to 69% of the individuals were found in the upper 5 cm and 73 to 95% of the individuals were found in the upper 10 cm of the sediment column. However, large organisms (sipunculids, sea cucumbers and echiurids) found in deeper layers may have a substantial impact on the biogeochemical properties of the sediment, as bioturbation is related to the square of body length (Wheatcroft et al., 1990) and deposit feeders can process several times their own body weight in sediment each day (Lopez and Levinton, 1987).

Meiofauna densities ( $2.04$  to  $9.80 \times 10^6$  ind.  $\text{m}^{-2}$ , Fig. 9a) found during this investigation were sim-

ilar or slightly higher than those found in other marine areas (Rudnick et al., 1985; De Bovée et al., 1996). However, values were much higher than recent estimates of meiofauna densities in the north-western Adriatic Sea (Tahey et al., 1996). Estimates of meiofauna densities are strongly dependent on the methodology (e.g. sieve size and whether or not foraminifera are included, Rudnick et al., 1985). Foraminifera were not included in the study by Tahey et al. (1996). However, in accordance with their observations, we also found that nematodes formed the dominant group among the metazoan meiofauna with annual mean densities ranging from  $1.90$  to  $3.82 \times 10^6$  ind.  $\text{m}^{-2}$ . One of the striking features is that the maximum abundance of meiofauna was not found at station 2, where maximum macrofaunal activity was recorded (Table 1). A positive correlation between abundance or biomass of benthic meiofauna and food availability has been demonstrated in areas with low productivity (e.g. Elmgren, 1978; Thiel, 1983; Widbom, 1988; Tietjen et al., 1989; Soetaert et al., 1997), indicating the importance of food availability as one factor controlling the meiofauna populations. However, in more productive areas and within a narrower depth range, this relationship may not be straightforward (e.g. Widbom, 1988; Soetaert and Heip, 1995). In the Skagerrak (northeastern North Sea), meiofauna density peaked at intermediate carbon fluxes, while both at lower and higher organic fluxes densities were reduced (De Bovée et al., 1996; see Soetaert et al., 1997). The positive effect of an increased food supply in more productive areas may be counteracted by negative biological interactions both with the macrofauna and with ciliates and other protozoans, except in hypoxic regions, where the meiofauna has a high relative importance (Elmgren, 1978; Widbom, 1988; Widbom and Elmgren, 1988; Moodley et al., 1993, and references therein). This could explain the reduced meiofaunal densities at station 2, where maximum macrofaunal activity was encountered (Table 1). Negative interactions include both indirect competition for food and more direct interactions, such as predation (e.g. Bell and Coull, 1978) and other forms of disturbance (e.g. Thorson, 1966; Coull and Bell, 1979; Creed and Coull, 1984).

#### 4.4. Comparison with other river-impacted coastal systems

Our estimates of organic-carbon fluxes in the northern part of our study area are similar to those estimated for the northern Gulf of Mexico (130 to 155 g C m<sup>-2</sup> y<sup>-1</sup>; Justic et al., 1993; Turner and Rabalais, 1994), another river-impacted coastal ecosystem often compared to the northwest Adriatic Sea (Justic et al., 1993, 1995). However, sediment oxygen consumption rates on the Louisiana shelf are low in comparison with other estuaries (Dortch et al., 1994) and macrofauna biomass is generally lower than in the northern Adriatic: benthic biomass estimates for the northern and western Gulf of Mexico were around 3 to 4.7 g C m<sup>-2</sup>, including macrofauna, meiofauna and bacteria, and in most cases biomass was dominated by bacteria (60 to 90%) rather than invertebrates (Miller-Way et al., 1994; Liz Cruz-Kaegi, pers. commun., 1997). These differences are probably related to the large differences in the water and sediment discharge rates, which for the Mississippi river system are, respectively, about 12 and 15 times higher than for the Po river system (Nelson, 1970; Wright and Nittrouer, 1995). Additionally, the Mississippi delta is a dispersal system with a low oceanographic energy regime and this favours relatively high sediment accumulation rates (Wright and Nittrouer, 1995). Coleman (1981) estimated an average sediment accumulation rate of 20 cm y<sup>-1</sup> for the prodelta area and within 50 km of the river delta sedimentation rates range from 0.5 to 2 cm y<sup>-1</sup> (Turner and Rabalais, 1994). High accumulation rates (>2 cm y<sup>-1</sup>) have been noted to inhibit habitation by benthic organisms in the Changjiang dispersal system (Rhoads et al., 1985). However, in the Skagerrak a rich fauna of deposit feeders was observed at sites with relatively high accumulation rates (Rosenberg, 1995), indicating the importance of other factors such as sediment instability in river-dominated coastal areas (e.g. Rhoads et al., 1985; Aller and Aller, 1986). On shelves immediately off the mouths of rivers like the Amazon (northeastern Brazil continental shelf) and Changjiang (east China Sea), the high degree of physical disturbance and unstable seabeds (fluid muds) significantly reduce infaunal populations (e.g. Rhoads et al., 1985; Aller and Aller, 1986), and promote the dominance

of bacteria, relative to large benthos (e.g. Aller and Stupakoff, 1996; Aller and Todorov, 1997). The relatively rich benthic community and the dominance of suspension feeders in our study area suggest more stable and less extreme conditions in the northwestern Adriatic Sea than in the Gulf of Mexico.

In conclusion, both our estimates of carbon mineralisation rates and total carbon fluxes confirm the general eutrophic setting in the northwestern Adriatic Sea but, in accordance with recent studies (Tahey et al., 1996; Epping and Helder, 1997), these values do not suggest extreme eutrophication, at least not during the period of investigation.

Furthermore, trends in the faunal data indicate that, in addition to the strong dependence of the benthos on organic-matter supply, biotic interactions may be an important factor governing the structure and abundance of the benthic community (Elmgren, 1978; Widbom, 1988; Widbom and Elmgren, 1988; Widbom and Frithsen, 1995).

#### Acknowledgements

Peter Herman is acknowledged for valuable discussions during the various phases of this study as are Karlina Soetaert and Els Flach for critically reading the manuscript. Helpful comments from W. Helder and two anonymous reviewers improved the manuscript. Yvonne Maas, Joop Nieuwenhuize and Jan Sinke were responsible for the numerous chemical analyses. Eric Slim, Jan Belgers and Adri Sandee assisted during the field trips. Pieter de Koyer sorted out the macrofauna samples and processed the meiofauna samples. We are grateful to the captains and crews of the *Urania* and *Daphne* for their assistance in the collection of the samples and supervision of the diving work. Paola Giordani and Stefano Miserocchi are thanked for the pleasant co-operation and co-ordination of the various field trips. This work has been undertaken in the framework of the Mediterranean Targeted Project (MTP)–Euromarge-AS project. We acknowledge the support from the European Commission's Marine Science and Technology (MAST) Programme under contract MAS2-CT93-0052. This is publication No. 2413 of the NIOO-CEMO.

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