

Organic enrichment and structure of the macrozoobenthic community in the northern Adriatic Sea in an area facing Adige and Po mouths

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The structure of the macrozoobenthic community and the vertical distribution of organisms in the sediment were studied in order to assess the effects of river outflows and organic enrichment on the benthic community of the North Adriatic Sea. Sampling was carried out at one offshore sandy station (S3) and at two coastal muddy stations (S1 and S2), near to river Po and Adige deltas. Samples were collected in four surveys covering one year from April 1995 to January 1996. In all surveys, the offshore sandy station showed a complex trophic structure, high species richness and diversity, with the occurrence of tubicolous or burrowing polychaetes like *Nothria conchylega*, *Aponuphis bilineata*, *Maldane sarsi*, *Nematonereis unicornis* and *Eunice vittata*, which also colonized the deeper sediment layers. On the other hand, the coastal muddy stations both exhibited similar species composition and a great abundance of dominant, opportunistic species such as the bivalve *Corbula gibba*, typical of unstable sea bottoms with a high rate of sedimentation, and some polychaetes typical of sublittoral muddy bottoms such as *Levinsenia gracilis*, *Aricidea claudiae*, *Prionospio malmgreni*, *Sternaspis scutata* and *P. cirrifera*. The high density of a few opportunistic species (mainly surface-deposit feeders) and the scant penetration of organisms within sediments that characterized the stations S1 and S2 support other evidence of the eutrophication of the coastal areas of the north-western Adriatic Sea. However, the high biomass values, the species richness and diversity observed in S1 and S2 suggest the occurrence of less extreme conditions than at other highly-eutrophicated coastal areas. River outflows, eutrophication and, especially, the increasing frequency of acute dystrophic events may be recognized as the driving forces determining the structure and composition of the macrozoobenthic community at coastal areas of north-western Adriatic Sea.

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Introduction

Factors affecting animal distributions in nature still represent a critical issue in ecological research. In the marine environment, both biotic interaction and abiotic factors play an important role in determining benthic activity and community structure (Rhoads and Young, 1970; Dauer and Conner, 1980; Wildish and Peer, 1983; Weinberg, 1984; Hyland *et al.*, 1991; Levin *et al.*, 1991; Aller and Stupakoff, 1996; Moodely *et al.*, 1998; Mancinelli *et al.*, 1998; Prevedelli *et al.*, 2001; Mancinelli and Rossi,

2002). Among abiotic factors, sedimentation rates and the quality and quantity of organic matter in the sediment can determine not only trophic structure, abundance and biomass but also the pattern of colonization in the sediment layer (Pearson and Rosenberg, 1978; Gray and Mirza, 1979; Warwick, 1986; Weston, 1990; Marsh and Tenore, 1990; Dauer and Alden, 1995; Dauwe *et al.*, 1998). An increase in the amount of organic matter can lead not only to an increase in the biomass and in the density of the benthic organisms but also to dystrophic events, such as episodes of hypoxia or anoxia, which can cause massive

reductions in, or elimination of, the benthic fauna. Such phenomena are frequent and well documented in the northern Adriatic Sea (e.g. Justic 1987; Ambrogi *et al.*, 1990; Crema *et al.*, 1991; Moodely *et al.*, 1998). In recent decades the northern Adriatic Sea has been subjected to a strong anthropogenic impact that has resulted in an artificially high input of nutrients and organic matter and raised the organic content of the sediment in relation to natural levels. In particular, the Po and Adige rivers make the greatest contributions to total freshwater, nutrients and pollutants and exert a major influence on the production and distribution of organic matter and sediments in the northern Adriatic Sea (Crema *et al.*, 1991; Bucci *et al.*, 1992; Marchetti and Verna, 1992; Vollenweider *et al.*, 1992; Justic *et al.*, 1995). In the framework of the PRISMA1 project, the biogeochemical characteristics of the northern Adriatic Sea in an area facing Adige and Po mouths were investigated at two coastal muddy stations, near to river deltas and characterized by high eutrophication and bottom organic enrichment, and at one offshore sandy station, located in an area for which few data were available. In this study we examine the structure of the macrozoobenthic community and the distribution of organisms in the vertical profile of sediment at the three stations, and we compare the communities of inshore stations with other published findings for muddy habitats, in order to assess the effects of eutrophication on the benthic community of the North Adriatic Sea.

Material and methods

Study area

Samples were taken at three stations in the North Adriatic Sea (Figure 1). Stations S1 (Po prodelta) and S2 (Adige-Brenta prodelta) lie in the coastal zone (4–5 km offshore) with bottom depths of 20 and 21 m, respectively, near to the Po (S1) and Adige-Brenta river deltas (S2). The third station (S3) is located about 37 km offshore with a bottom depth of 29 m, far from river outflows. Samples from the three stations were collected in four surveys covering one year (April, July, October 1995 and January 1996). Hydrology, downward fluxes of particulate carbon, nitrogen and phosphorus and sediment characteristics were reported by Mancinelli *et al.* (1998), Giani *et al.* (2001) and Mancinelli and Rossi (2001). Vertical mixing of the water column at S1 was very low so bottom waters were frequently confined. In contrast, station S2 shows high hydrodynamism: water column mixing was pronounced and SE currents prevailed during the measurement periods. At coastal stations, bottom waters were well oxygenated during winter and spring but become increasingly oxygen depleted in summer through to autumn (Giani *et al.*, 2001). The sediment at station S1 is made up of silty clay, with <1% sand. Sediment at S2 is made up of clayed silt, with 1–4% sand. The sediments of the offshore station (S3) are

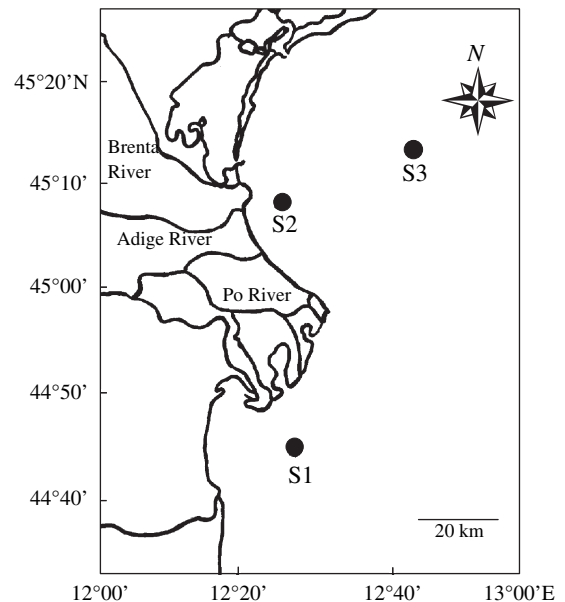


Figure 1. Sampling stations in the northern Adriatic Sea.

mainly relict sands of the last holocene transgression with a 20% pelitic fraction (Giani *et al.*, 2001). Net annual vertical fluxes (due to primary flux and advection) of organic carbon, total nitrogen and phosphorus in the coastal stations were: $71\text{--}97\text{ g C m}^{-2}\text{ year}^{-1}$, $8\text{--}14\text{ g N m}^{-2}\text{ year}^{-1}$, $2.1\text{--}2.3\text{ g P m}^{-2}\text{ year}^{-1}$, with the highest values recorded at S1. The offshore station was characterized by net annual fluxes of particulates, C, N and P approximately one order of magnitude lower than the above. Total organic matter content was lower at offshore station S3 ($2.67 \pm 0.29\%$) than in the coastal stations ($8.10 \pm 1.00\%$ in S1 and $8.98 \pm 2.54\%$ in S2) (Mancinelli *et al.*, 1998, Giani *et al.*, 2001).

Sampling methods and data analysis

Each sample consisted of six replicates collected using a box-corer with a surface of $10 \times 20\text{ cm}$. Each replicate was then subdivided into four layers (0–2, 2–5, 5–10 and 10–20 cm of depth): these sample subdivisions permitted an accurate analysis of the distribution of organism down the sediment profile (Clavier, 1984; Hayashi, 1991; Bonvicini Pagliai *et al.*, 1996; Dauwe *et al.*, 1998; Prevedelli *et al.*, 2001). Sediments were processed through a sieve (mesh size 0.5 mm) and the retained material was preserved in 4% neutral formalin in seawater. The animals were extracted from the residual sediment and separated into the principal taxonomic groups. A preliminary investigation revealed that the macrofauna was largely dominated by polychaetes and molluscs that represented more than 90% of the whole community in terms both of abundance and of biomass, so only the polychaete–mollusc fraction

was identified to species level and counted. The biomass was determined as wet-weight with the exclusion of the mollusc shells. The trophic status of each species was assigned by classification into feeding groups using information from the literature (Fauchald and Jumars, 1979; Gambi and Giangrande, 1985; Gambi, 1989; Dauwe *et al.*, 1998). Four trophic categories were determined: suspension feeders (s.f.), carnivorous–omnivorous (c.o.), surface-deposit feeders (s.d.f.) and sub-surface deposit feeders (s.s.f.). The data relating to 5–10 cm and 10–20 cm layers were combined because of the scant number of individuals and the great variability observed in the deeper layers, so only three layers (0–2 cm, 2–5 cm, 5–20 cm) were considered.

Multivariate and univariate analyses of macrobenthic community structure were performed on matrices of species abundance and biomass obtained (a) for each station replicate (on the whole sample) at each sampling time and (b) for each depth layer at each station (mean values among replicates) at each sampling time. Multivariate analysis was performed after square-root transformation of abundance and biomass data. Outputs from cluster analysis and non-metric multidimensional scaling (MDS) ordination model of the Bray–Curtis similarity matrices were obtained. Differences among sampling stations and times, and depth layers and sampling stations were tested using a two-way crossed ANOSIM randomization/permutation test. Significant differences among sampling stations at different times and sediment depths were further analysed using a *posteriori* one-way ANOSIM. Species making the greatest contribution to dissimilarity among sampling stations at different times and sediment depths were investigated using the similarity percentage breakdown procedure SIMPER. Univariate and multivariate analyses were conducted using PRIMER V5 software (Clarke and Warwick, 2001).

Univariate indices included number of individuals (abundance, N), number of species (S), Shannon–Wiener diversity (H' , natural logarithm) and total biomass. Density and biomass with respect to sediment depth were standardized as individuals dm^{-3} and g dm^{-3} according to Dauwe *et al.* (1998). The significance of univariate index differences among sampling stations and times, and depth layers and sampling stations, was tested using a two-way crossed ANOVA. Before analyses, data normality and homogeneity of variances were examined and, if necessary, data were transformed [$\ln(x + 1)$]. Significant differences in univariate indices evidenced by ANOVA were further analysed using a *posteriori* Student–Newman–Keuls (SNK) tests. Statistical analysis was performed using SPSS software.

Results

Throughout the course of the investigation 115 taxa were found, mainly polychaetes (89 species) and bivalves (20 species). Gastropod and scaphopod molluscs were

Table 1. Results of global and pairwise test (global r and p) from two-crossed ANOSIM for differences among sampling stations and dates.

	Global test		Pairwise test		
	r	p	Group	r	p
Between stations	0.918	<0.01	S1–S2	0.778	<0.01
			S1–S3	0.999	<0.01
			S2–S3	0.956	<0.01
Between dates	0.795	<0.01	Apr–Jul	0.746	<0.01
			Apr–Oct	0.828	<0.01
			Apr–Jan	0.731	<0.01
			Jul–Oct	0.909	<0.01
			Jul–Jan	0.760	<0.01
			Oct–Jan	0.812	<0.01

represented only by five and one species, respectively. The coastal stations differed mainly in individual abundance: 1298 individuals belonging to 57 species and 452 individuals belonging to 55 species were collected during the four surveys at S1 and S2, respectively. The offshore station, S3, exhibited higher species diversity (92 taxa collected during the four surveys).

Comparison between sampling sites and times

Two-way crossed ANOSIM between the four sampling dates and the three stations showed significant differences for these two factors (Table 1). Pairwise comparison carried out both on the sum of the data and separately for each season showed significant differences between the three stations. Differences between sites were greater than those observed between sampling dates (Table 2).

Table 2. Results of global and pairwise test (global r and p) from one-way ANOSIM for differences among sampling stations in each sampling date.

Sampling date	Global test		Pairwise test		
	r	p	Group	r	p
April	0.918	<0.01	S1–S2	0.819	<0.01
			S1–S3	1.000	<0.01
			S2–S3	0.913	<0.01
July	0.889	<0.01	S1–S2	0.781	<0.01
			S1–S3	0.994	<0.01
			S2–S3	0.972	<0.01
October	0.996	<0.01	S1–S2	1.000	<0.01
			S1–S3	1.000	<0.01
			S2–S3	1.000	<0.01
January	0.865	<0.01	S1–S2	0.550	<0.01
			S1–S3	1.000	<0.01
			S2–S3	0.937	<0.01

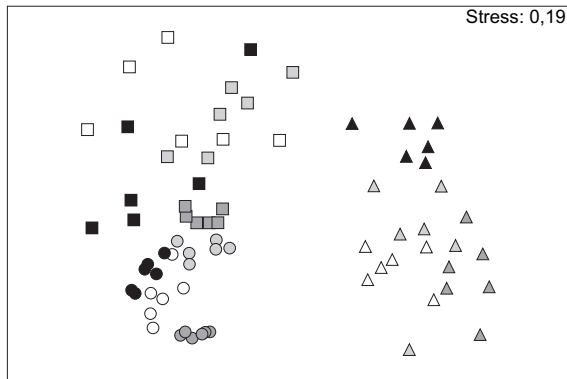


Figure 2. MDS ordination of square root transformed abundance data of stations at sampling date. Symbols: circle = S1; square = S2; triangle = S3. Colours: white = April; light grey = July; dark grey = October; black = January.

MDS ordination performed on data relating to single replicates at each site and season separated, along the horizontal axis, the offshore sandy station S3 from the two coastal muddy stations S1 and S2, which resembled each other more closely. The points relating to S1 and S2, however, were differentiated on the vertical axis, which very probably indicates a gradient of abundance (Figure 2).

The species making the greatest contribution to dissimilarity among the three stations within each sampling date (SIMPER, cut-off 50%) are reported in Table 3. Coastal muddy stations S1 and S2 were characterized by high density and biomass of the bivalve mollusc *Corbula gibba* and by polychaetes typical of sublittoral muddy bottoms such as *Levinsonia gracilis*, *Aricidea claudiae*, *Prionospio malmgreni*, *Sternaspis scutata* and *Prionospio cirrifera*, which are mainly surface-deposit feeders; all these species were more abundant at S1 than at S2 at all sampling dates. In the offshore sandy station S3 the polychaetes *Nothria conchylega* (CO), *Aponuphis bilineata* (CO), *Owenia fusiformis* (SDF), *Maldane sarsi* (SSDF), *Nematonereis unicornis* (CO) and *Eunice vittata* (CO), some of them strongly typical of heterometric bottoms, were abundant, together with some species of small surface-deposit feeders.

The number of species, number of individuals, Shannon–Wiener diversity and total biomass for each station and sampling date are reported in Figure 3. All univariate indices varied according to the sampling stations and dates, but differences between stations appeared more important than those observed between dates (Table 4). The number of species and the Shannon diversity index were higher at the offshore station (S3) than at the Adige prodelta station (S2) and Po prodelta station (S1). S1, on the other hand, displayed the highest values of abundance and biomass. The lowest values of abundance and biomass were observed in the July survey.

The relative importance of the different trophic groups in terms of abundance and biomass varied at the three stations

(Figure 4). The offshore sandy community (S3) displayed a complex and balanced trophic structure: surface-deposit feeders (s.d.f.) were the most important trophic group (about 60% of abundance and biomass) but the numerous species of carnivorous–omnivorous (c.o.) organisms accounted for almost 40% of the individuals and of the total biomass. In contrast, coastal muddy station communities were largely dominated by surface-deposit feeder species. In particular, surface-deposit feeders accounted for more than 90% and 85% of total abundance and biomass at S1 and at S2, respectively: only a small percentage of total abundance and biomass at the inshore station was made up of carnivorous–omnivorous and suspension-feeder species. Sub-surface deposit feeders (s.s.f.) and suspension-feeders (s.f.) were rare at all stations.

Vertical distribution of macrozoobenthos

Two-way crossed ANOSIM between the three sampling areas and the three strata showed significant differences. The lowest *R* values were observed comparing the inshore muddy stations S1 and S2 and between the 0–2 cm and 2–5 cm layers, suggesting that there is greater similarity in the composition and distribution of the macrofauna between the coastal stations and the more superficial layers (Table 5). ANOSIM was also carried out for each layer separately, and here again the inshore muddy stations S1 and S2 resembled each other most closely (Table 6).

MDS ordination performed on the data relating to each layer and station separated, along the vertical axis, the offshore sandy station from the coastal stations, which resemble each other more closely. The points relating to inshore muddy stations S1 and S2, on the other hand, differentiate along the horizontal axis which very probably represents a gradient associated with the depth of sediment (Figure 5).

SIMPER analysis of differences in average abundance of species between stations at each depth considered (cut-off 50%) is reported in Table 7. At all stations differences among sediment depth layers were due both to the reduction of species densities and to the species substitution along the profile of the sediment. Surface layers are characterized by large populations of suspension-feeder species such as the polychaetes *Ampharete acutifrons*, *Levinsonia gracilis*, *Prionospio cirrifera*, *P. malmgreni* and the molluscs *Corbula gibba* and *Nucula nucleus*, while the deeper layers were colonized by carnivorous–omnivorous or sub-surface deposit feeders species such as *Glycera rousii*, *Marphysa bellii*, *Nephtys incisa*, *Paralacydonia paradoxa* and *Pilargis verrucosa*. The community of the offshore sandy station differs from the others on account of its different species and trophic composition: in fact in S3 the first layer is populated by surface-deposit feeders together with numerous carnivorous–omnivorous and some suspension-feeders species. At the two inshore muddy stations the first layer is populated almost exclusively by surface-deposit

Table 3. Differences in average abundance of species which contributes to dissimilarity (cut-off 50%) between Bray–Curtis clusters among stations at each sampling date (SIMPER). Class (C.): P = polychaetes; B = bivalves. Trophic category (t.c.): S.F. = suspension feeders; C.O. = carnivores–omnivores; S.D.F. = surface deposit feeders; S.S.D.F. = sub-surface deposit feeders.

C.	t.c.		April			July			October			January		
			S1	S2	S3	S1	S2	S3	S1	S2	S3	S1	S2	S3
P	s.d.f.	<i>Ampharete acutifrons</i>	—	—	—	66.7	8.3	33.3	166.7	41.7	8.3	—	—	—
P	s.d.f.	<i>Amphitrite gracilis</i>	—	—	—	—	—	—	—	—	—	0.0	0.0	83.3
P	c.o.	<i>Aponuphis bilineata</i>	0.0	0.0	191.7	0.0	0.0	66.7	0.0	0.0	166.7	—	—	—
P	s.d.f.	<i>Aricidea assimilis</i>	16.7	58.3	—	—	33.3	50.0	—	125.0	0.0	25.0	66.7	125.0
P	s.d.f.	<i>Aricidea catherinae</i>	16.7	41.7	175.0	—	—	—	—	—	—	—	—	—
P	s.d.f.	<i>Aricidea claudiae</i>	108.3	41.7	—	100.0	25.0	8.3	375.0	233.0	0.0	—	—	—
P	s.d.f.	<i>Cossura soyeri</i>	—	—	—	—	—	—	175.0	8.3	0.0	—	—	—
P	s.d.f.	<i>Euchone rosea</i>	0.0	0.0	83.3	—	—	—	—	—	—	—	—	—
P	c.o.	<i>Eunice vittata</i>	—	—	—	0.0	0.0	66.7	—	—	—	—	0.0	50.0
P	s.d.f.	<i>Levinsonia gracilis</i>	—	—	—	150.0	33.3	0.0	833.3	33.3	16.7	108.3	25.0	0.0
P	c.o.	<i>Lumbrineris latreilli</i>	16.7	66.7	125.0	141.7	—	58.3	—	—	—	—	—	—
P	c.o.	<i>Lumbrineris tetraura</i>	50.0	0.0	—	—	—	—	—	—	—	—	—	—
P	s.s.d.f.	<i>Maldane sarsi</i>	83.3	0.0	116.7	75.0	16.7	25.0	75.0	0.0	83.3	50.0	16.7	—
P	c.o.	<i>Marphysa bellii</i>	0.0	0.0	108.3	—	—	—	—	0.0	58.3	—	—	—
P	s.d.f.	<i>Melinna palmata</i>	—	—	—	—	—	—	—	—	—	41.7	0.0	—
P	s.d.f.	<i>Micronephrys sphaerocirrata</i>	—	—	—	—	66.7	16.7	—	—	—	—	—	—
P	s.d.f.	<i>Myriochele oculata</i>	0.0	8.3	66.7	—	0.0	33.3	—	—	—	—	—	—
P	c.o.	<i>Nematoneis unicornis</i>	0.0	0.0	91.7	0.0	0.0	41.7	0.0	0.0	100.0	0.0	0.0	66.7
P	c.o.	<i>Nothria conchilega</i>	0.0	0.0	175.0	0.0	0.0	83.3	—	0.0	75.0	0.0	0.0	291.7
P	s.d.s.	<i>Owenia fusiformis</i>	0.0	16.7	158.8	—	8.3	41.7	0.0	83.3	—	0.0	8.3	100.0
P	s.d.f.	<i>Paralacydonia paradoxa</i>	—	—	—	—	0.0	33.3	—	—	—	—	—	—
P	s.d.f.	<i>Prionospio cirrifera</i>	58.3	16.7	91.7	—	—	—	308.3	200.0	0.0	—	—	—
P	s.d.f.	<i>Prionospio malmgreni</i>	133.3	33.3	133.3	—	—	—	1458.3	108.3	58.3	0.0	41.7	—
P	s.d.f.	<i>Sigambra tentaculata</i>	41.7	0.0	83.3	—	—	—	—	—	—	—	—	—
P	s.d.f.	<i>Spiochaetopterus costarum</i>	0.0	50.0	—	—	—	—	—	—	—	—	—	—
P	s.d.f.	<i>Spiophanes bombyx</i>	—	—	—	—	—	—	—	0.0	66.7	41.7	0.0	75.0
P	s.d.f.	<i>Sternaspis scutata</i>	50.0	8.3	0.0	58.3	16.7	0.0	—	—	—	50.0	25.0	—
B	s.d.s./s.f.	<i>Corbula gibba</i>	950.0	100.0	8.3	875.0	50.0	8.3	1375.0	458.3	0.0	916.7	208.3	8.3
B	s.d.f.	<i>Loripes lacteus</i>	—	—	—	—	—	—	—	—	—	—	0.0	66.7
B	s.d.f.	<i>Mysella bidentata</i>	—	—	—	41.7	8.3	0.0	—	—	—	—	—	—
B	s.d.f.	<i>Nucula nucleus</i>	0.0	8.3	66.7	25.0	100.0	0.0	—	—	—	8.3	8.3	91.7
B	s.f.	<i>Paphia aurea</i>	—	—	—	—	—	—	—	—	—	0.0	41.7	0.0
B	s.d.f.	<i>Tellina distorta</i>	0.0	17.0	75.0	—	—	—	—	—	—	8.3	16.7	66.7

feeders: the communities living in the 0–2 cm layer of depth differed mainly in the abundance of the dominant species *C. gibba*, *L. gracilis*, *P. cirrifera* and *P. malmgreni*, but the dissimilarity between the S1 and S2 tended to reduce with increasing sediment depth with smaller differences in abundance.

Vertical profiles of numbers of species, numbers of individuals and biomass at the three stations are represented in Figure 6. Results of ANOVA and SNK tests for differences in univariate indices between sampling stations and sediment depth are reported in Table 8. The number of species decreased slightly in the upper 5 cm then declined dramatically. At the offshore sandy station S3 the number of species at all the levels under consideration was always greater than in the other two. At the stations close to the river deltas few species had succeeded in colonizing to

depths greater than 5 cm. As regards abundances and biomass, however, the greatest differences were found at S1, which was characterized by a particularly dense surface population. At all stations the vertical distribution of macrofaunal biomass and abundance showed a steeply decreasing gradient, most of the animals being restricted to the upper 5 cm of sediment.

Discussion

The macrozoobenthic community of the investigated stations showed significant variation in composition and abundance during the four surveys, due to hydrographic-climatic variation during the year (Arntz and Rumhor, 1982; Ambrogi *et al.*, 1990). Unsurprisingly, most of the

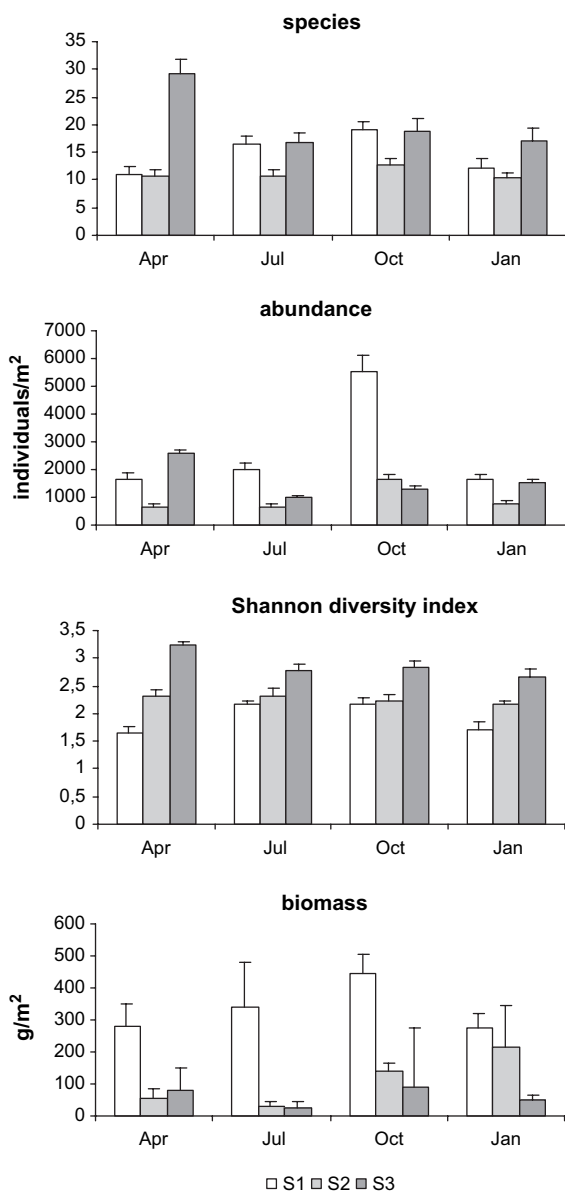


Figure 3. Number of species, number of individuals, Shannon–Wiener diversity and total biomass (mean \pm s.d.) at the three stations at each sampling date.

differences between the sampling stations emerged when comparing the communities of the two coastal stations with the offshore one. The offshore station S3 not directly affected by river outflows, in which sediments are mainly relict sands with relatively low organic matter content showed a composition different from the others, with the presence of several carnivorous–omnivorous or burrowing polychaetes which also colonized the deeper sediment layers. The differences in the species composition and trophic structure of the offshore community are probably linked not only to the substratum type but also to the reduced

availability of organic matter in the sediment and to its seasonal variations. In autumn and winter the anti-clockwise circulation of the Adriatic confines terrigenous sedimentation to the coastal strip. Only in summer, when the currents are weak, do the plumes of the Po and of the other rivers reach the areas at the center of the basin. These supplies are sufficient to promote a primary production which, together with the inorganic particulates, eventually contributes to forming temporary summer deposits at the seabed that are swept away by the autumn storms (Giani *et al.*, 2001).

In all surveys, the macrozoobenthic communities found at coastal stations S1 and S2, characterized by silty-clay sediment with high organic content and located near the Po and Adige deltas, exhibited similar species composition and a great abundance of dominant, opportunistic species that attained high densities, such as the paraonids *Levinsonia gracilis* and *Aricidea claudiae*, and the spionids *Prionospio malmgreni* and *P. cirrifera*. At these stations the trophic structure of the community was dominated by surface-deposit feeders with the limited but constant presence of organisms belonging to other trophic-ecological categories. A similar ecologic-trophic structure with the occurrence of large populations of small-size paraonids and spionids was also reported by Crema *et al.* (1991) and Prevedelli *et al.* (2001) for the northern Adriatic Sea, south of Po river.

Also, at stations S1 and S2 there was a high abundance of *Corbula gibba*, a bivalve widely distributed in estuaries in northern Europe and in the Mediterranean and typical of unstable sea bottoms with a high rate of sedimentation. *C. gibba* is one of the most resistant species to severe hypoxia, and is often abundant in eutrophic areas (Christensen, 1970; Pearson and Rosenberg, 1978; Diaz and Rosenberg, 1995). Jensen (1990) reported a mean abundance of around 9500 ind. m² in the Limfjord, Denmark, and Rosenberg (1977) recorded about 4500 ind. m² in an eutrophic Swedish fjord. In our study *C. gibba* was the most important species in terms of biomass and abundance: its densities varied between 900 and 1400 ind. m² at station S1 and between 50 and 450 ind. m² at station S2, accounting from 60 to 80% of total biomass in both stations. The dominance of *C. gibba* in the north-western Adriatic Sea has been observed also in earlier research (Picard, 1965; Salen-Picard, 1981; Hrs-Brenko, 1980; Ambrogi *et al.*, 1990; Tahey *et al.*, 1996). Previous studies reported that the densities of *C. gibba* varied between 900 and 1800 ind. m² (Crema *et al.*, 1991; Moodely *et al.*, 1998; Prevedelli *et al.*, 2001) accounting from 50 to 90% of the total biomass.

Most of the dissimilarity between the two coastal stations, characterized by a very similar species composition, was due to the lower abundance observed at S2 with respect to S1. Station S1, which exhibited the highest carbon flux and organic contents in the sediment, also supported the largest macrofaunal biomass. The high hydrodynamism and sediment instability observed at S2 throughout the surveys could have affected the benthic

Table 4. Results of two-way ANOVA and SNK test on means for differences in univariate indices among sampling stations and date.

	Source	d.f.	F	p	SNK
Species	Stations	2	190.38	<0.001	S2 < S1 < S3
	Dates	3	21.79	<0.001	Jan < Jul < Oct = Aug
Abundance	Stations×Dates	6	44.53	<0.001	
	Stations	2	494.66	<0.001	S2 < S3 < S1
	Dates	3	156.53	<0.001	Jul < Jan < Aug < Oct
	Stations×Dates	6	99.00	<0.001	
Shannon	Stations	2	418.42	<0.001	S1 < S2 < S3
	Dates	3	17.33	<0.001	Jan < Aug = Oct = Jul
	Stations×Dates	6	25.25	<0.001	
	Stations	2	74.08	<0.001	S3 < S2 < S1
Biomass	Dates	3	6.28	<0.001	Jul < Aug = Oct = Jan
	Stations×Dates	6	4.83	<0.001	
	Stations	2	74.08	<0.001	S3 < S2 < S1
	Dates	3	6.28	<0.001	Jul < Aug = Oct = Jan

communities, reducing the infaunal population (Rhoads *et al.*, 1985; Aller and Aller, 1986; Moodely *et al.*, 1998).

At S1 and S2 stations the colonization of the sediment profile essentially involved the first 5 cm. Only a few species had managed to colonize the deep layers beyond 10 cm, even though, in all seasons, colonization extended to a depth of at least 20 cm. A similar sharp decline in densities and biomass of macrofauna with depth into the sediment was also observed in a previous investigation on

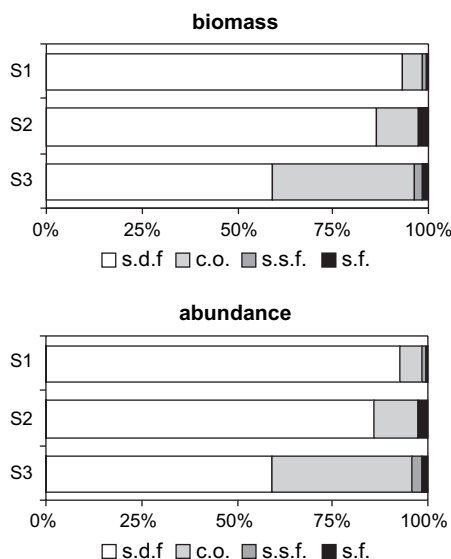


Figure 4. Relative contribution of each trophic group to total biomass at the three stations. S.F. = suspension feeders; C.O. = carnivores–omnivores; S.D.F. = surface deposit feeders; S.S.D.F. = sub-surface deposit feeders.

Table 5. Results of global and pairwise test (global r and p) from two-crossed ANOSIM for differences among sampling stations and depth layers of sediment.

	Global test		Pairwise test		
	r	p	Group	r	p
Between stations	0.660	<0.01	S1–S2	0.434	<0.01
			S1–S3	0.802	<0.01
			S2–S3	0.823	<0.01
Between layers	0.611	<0.01	0–2 to 2–5	0.424	<0.01
			0–2 to 5–20	0.882	<0.01
			2–5 to 5–20	0.726	<0.01

sublittoral muddy bottoms of northern Adriatic Sea (Moodely *et al.*, 1998). The distribution of the organisms in the three stations followed a well-defined pattern, in which the filter- and surface-deposit feeders were found in the surface layers, the burrowers in the deep layers and the carnivores–omnivores throughout the sediment profile. A similar vertical distribution of the macrobenthic fauna down the sediment profile was also observed by Dauwe *et al.* (1998) at German Bight (North Sea), a station characterized by high amount–high quality TOC sediment, where most of the organisms were found at shallow sediment depth (<2 cm), mainly feeding on deposited or (re-) suspended material. At the three stations, in all seasons, surface colonization, above all by surface-deposit feeder species, was abundant, so much so that in the two coastal stations about 90% of the population consisted of this trophic group. At coastal stations the communities were relatively diverse in terms of species but not in terms of trophic structure. The high organic enrichment and sedimentation rate could have sustained an increase in surface- and sub-surface deposit feeders with a corresponding decrease in the other trophic groups, particularly the

Table 6. Results of global and pairwise test (global r and p) from one-way ANOSIM for differences among sampling stations in each layer considered.

Layer	Global test		Pairwise test		
	r	p	Group	r	p
0–2 cm	0.727	<0.01	S1–S2	0.573	<0.05
			S1–S3	0.906	<0.05
			S2–S3	0.781	<0.05
2–5 cm	0.762	<0.01	S1–S2	0.479	>0.05 (n.s.)
			S1–S3	1.000	<0.05
			S2–S3	0.990	<0.05
5–20 cm	0.493	<0.01	S1–S2	0.250	>0.11 (n.s.)
			S1–S3	0.500	<0.05
			S2–S3	0.698	<0.05

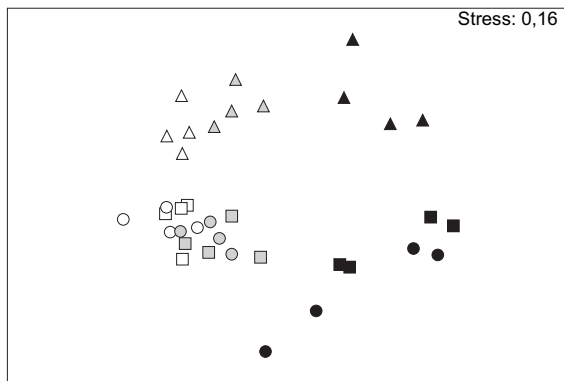


Figure 5. MDS ordination of square root transformed abundance data of depth layers at the three stations. Symbols: circle = S1; square = S2; triangle = S3. Colours: white = 0–2 cm; grey = 2–5 cm; black = 5–20 cm.

suspension feeders. According to Young and Rhoads (1971), who developed the concept of “amensalism” of trophic groups, surface-deposit and suspension feeders are incompatible, since the high level of instability of surface sediments induced by the surface-deposit feeders prevents colonization by the suspension feeders.

Several models have been proposed to explain the relationship between organic matter content in the sediment and macrozoobenthic community structure (Pearson and Rosenberg, 1978; Rhoads and Boyer, 1982; Weston, 1990; Gray, 1992; Dauwe *et al.*, 1998). The most widely accepted model was proposed by Pearson and Rosenberg (1978), who suggested that, as the organic matter content increases, the species diversity decreases, the number of individuals increases and the individual biomass for each species decreases. Also, as the organic matter content increases, the depth of the colonized layer is reduced and the

Table 7. Differences in average abundance of species which contributes to dissimilarity (cut-off 50%) between Bray–Curtis clusters among stations at depth layers considered (0–2 cm; 2–5 cm; 5–20 cm) (SIMPER). Class (C.): P = polychaetes; B = bivalves. Trophic category (t.c.): SF = suspension feeders; CO = carnivores–omnivores; SDF = surface deposit feeders; SSDF = sub-surface deposit feeders.

C.	t.g.		0–2 cm			2–5 cm			5–20 cm		
			S1	S2	S3	S1	S2	S3	S1	S2	S3
P	s.d.f.	<i>Ampharete acutifrons</i>	2.40	0.63	—	0.76	0.21	—	—	—	—
P	c.o.	<i>Aponuphis bilineata</i>	0.00	0.00	3.23	0.00	0.00	1.25	0.00	0.00	0.06
P	s.d.f.	<i>Aricidea assimilis</i>	—	—	—	0.97	1.18	1.32	0.01	0.10	0.03
P	s.d.f.	<i>Aricidea catherinae</i>	—	0.21	2.08	—	—	—	—	—	—
P	s.d.f.	<i>Aricidea claudiae</i>	5.10	1.15	0.63	2.15	2.01	0.21	0.01	0.04	—
P	s.d.f.	<i>Euchone rosea</i>	—	0.10	0.94	—	—	—	—	—	—
P	c.o.	<i>Eunice vittata</i>	0.00	0.10	1.67	0.00	0.00	0.42	—	—	—
P	c.o.	<i>Glycera rouxii</i>	—	—	—	—	0.00	0.28	0.01	0.00	0.08
P	s.d.f.	<i>Levinsonia gracilis</i>	11.88	—	0.10	1.32	0.42	0.14	0.00	0.04	0.04
P	c.o.	<i>Lumbrineris latreilli</i>	3.44	2.19	3.33	0.76	1.18	0.35	—	0.06	0.03
P	s.s.d.f.	<i>Maldane sarsi</i>	—	0.00	0.73	0.28	0.00	0.56	0.26	0.00	0.18
P	c.o.	<i>Marphysa bellii</i>	—	—	—	0.00	0.00	0.56	0.00	0.00	0.11
P	s.d.f.	<i>Melinna palmata</i>	—	—	—	0.35	0.07	0.35	—	—	—
P	s.d.f.	<i>Micronephthys sphaerocirrata</i>	—	1.04	0.52	—	—	—	—	—	—
P	s.d.f.	<i>Myriochele oculata</i>	—	0.10	0.73	—	—	—	—	—	—
P	c.o.	<i>Nematonereis unicornis</i>	—	0.00	0.63	0.00	0.00	1.39	0.00	0.00	0.14
P	c.o.	<i>Nephtys incisa</i>	—	—	—	—	—	—	0.07	0.00	0.00
P	c.o.	<i>Nothria conchilega</i>	0.00	0.00	5.63	0.00	0.00	0.49	0.00	0.00	0.19
P	s.d.s.	<i>Owenia fusiformis</i>	0.21	0.94	3.96	0.07	0.14	0.63	—	—	—
P	s.s.d.f.	<i>Paralacydonia paradoxa</i>	—	—	—	—	—	—	0.00	0.00	0.06
P	c.o.	<i>Pilargis verrucosa</i>	—	—	—	—	—	—	0.04	0.03	0.00
P	s.d.f.	<i>Prionospio cirrifera</i>	3.54	1.25	0.63	0.97	1.39	0.42	—	—	—
P	s.d.f.	<i>Prionospio malmgreni</i>	19.79	2.71	3.54	0.56	0.14	0.00	—	—	—
P	s.d.f.	<i>Sigambra tentaculata</i>	1.04	0.00	0.73	0.49	0.00	0.83	—	—	—
P	s.d.f.	<i>Spioclaetopterus costarum</i>	—	—	—	0.00	0.42	0.00	—	—	—
P	s.d.f.	<i>Spiophanes bombyx</i>	—	—	—	0.07	0.00	0.56	0.00	0.00	0.06
P	s.d.f.	<i>Spiophanes kroyeri reysii</i>	—	—	—	—	—	—	0.04	0.00	0.00
P	s.d.f.	<i>Sternaspis scutata</i>	—	—	—	0.69	0.21	0.00	0.14	0.01	0.01
B	s.d.s./s.f.	<i>Corbula gibba</i>	36.69	9.27	0.21	6.81	0.49	0.07	0.21	0.03	0.00
B	s.d.f.	<i>Nucula nucleus</i>	0.73	1.35	1.67	—	—	—	—	—	—
B	s.d.f.	<i>Tellina distorta</i>	0.00	0.31	1.15	—	0.28	0.49	—	—	—

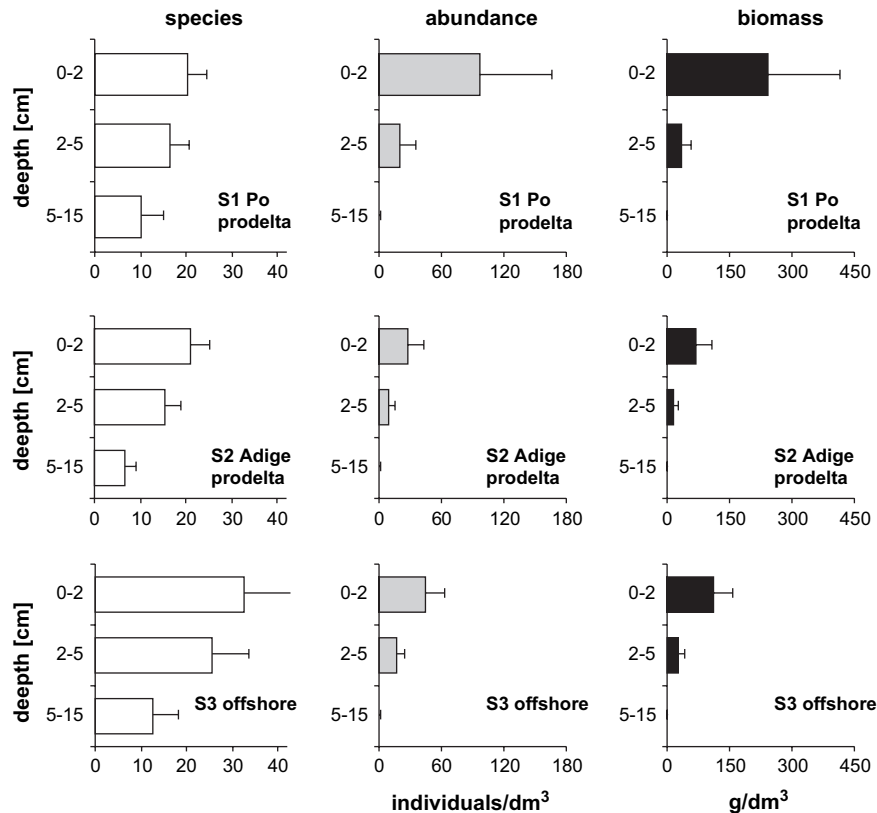


Figure 6. Number of species, abundance and biomass (annual mean \pm s.d.) in the sediment layers of the three stations.

community ends up consisting mainly of surface-deposit feeders. Species composition and distribution at the coastal stations considered in this study appeared to be in agreement with this model. The high density of a few opportunistic species (mainly surface-deposit feeders) and the scant penetration of organisms within the sediment that characterized the macrozoobenthic communities found at

stations S1 and S2 support other evidence for eutrophication of the coastal areas of the north-western Adriatic sea (Crema *et al.*, 1991; Vollenweider *et al.*, 1992; Moodely *et al.*, 1998; Prevedelli *et al.*, 2001). However, the relatively high species richness and diversity, the high biomass values and the dominance of suspension feeders observed in S1 and S2 suggest the occurrence of more

Table 8. Results of two-way ANOVA and SNK test on annual means for differences in univariate indices among sampling stations and sediment depth.

	Source	d.f.	f	p	SNK
Species	Station	2	28.10	<0.001	S2 = S1 < S3
	Depth	2	7.84	<0.01	5-20 < 2-5 = 0-2
	Station \times Depth	4	0.44	>0.40 (n.s.)	
Shannon	Station	2	8.40	<0.001	S1 = S2 < S3
	Depth	2	15.27	<0.001	5-20 < 2-5 = 0-2
	Station \times Depth	4	2.00	>0.10 (n.s.)	
Abundance	Station	2	151.95	<0.001	S2 < S3 = S1
	Depth	2	7.27	<0.001	5-20 < 2-5 < 0-2
	Station \times Depth	4	0.99	>0.43 (n.s.)	
Biomass	Station	2	310.90	<0.001	S2 < S3 = S1
	Depth	2	6.36	<0.01	5-20 < 2-5 < 0-2
	Station \times Depth	4	1.41	>0.25 (n.s.)	

stable and less extreme conditions in the north-western Adriatic Sea than at the coastal areas of other eutrophicated seas such as the Baltic Sea, the Gulf of Mexico and the Black Sea (Moodely *et al.*, 1998; Rabalais *et al.*, 2002).

Even biotic interactions may play an important role (Moodely *et al.*, 1998); river outflows, eutrophication and periodic dystrophic events (in particular summer hypoxic/anoxic events) may be recognized as the driving forces determining the structure and composition of the macrozoobenthic community for many estuarine and coastal ecosystems (Seliger *et al.*, 1985; Rabalais *et al.*, 2002). The structure and compositions of the macrozoobenthic community in the north-western Adriatic Sea can be explained in terms of an intermittent recovery from periodic disturbances that maintain for long periods of time, and probably indefinitely, immature, transitory successional stages, caused by the increasing frequency of acute dystrophic events and the consequent shortening of the time between successive disturbance (Crema *et al.*, 1991).

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