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Sediment O_2 demand, density and biomass of the benthos and phytopigments along the northwestern Adriatic coast: the extent of Po enrichment

Adriatic
Sediment oxygen demand
Silicate and ammonium
Infauna
Phytopigments

Adriatique
Demande en oxygène du sédiment
Silicate et ammonium
Faune
Phytopigments

Tom M. TAHEY, Gerard C. A. DUINEVELD, Peter A. W. J. DE WILDE, Eilke M. BERGHUIS and Albert KOK

Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands.

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ABSTRACT

Sediment oxygen demand (SOD), silicate and ammonia fluxes, benthic macro- and meiofauna and phytopigments were measured during two cruises in March 1992 and August 1993 in the northwestern Adriatic Sea. Nine, mostly shallow (< 50 m) stations, on a transect stretching from the Po mouth southwards, were visited. Two major issues were addressed: (1) To what extent does the river Po affect the benthic communities along this transect ? and (2) Is there any indication of an eutrophic situation as described in earlier studies ?
The spatial patterns of SOD (range ± 100 to 1450 µmol $O_2 . m^{-2}. h^{-1}$) and benthic fauna do not provide evidence for a simple latitudinal decrease in organic enrichment from the Po to the south. However, northern stations generally had the highest SOD, faunal densities and biomass.
Water column characteristics (temperature, salinity, phytopigments) in August 1993 indicate a rough partition of the transect into two groups of stations, of which the northern cluster experiences the direct influence of Po water. This is in conformity with the vision of existing deviations of the general anticyclonic flow regime in the northern Adriatic in summer, whereby Po water is directed offshore instead of southwards. Compared to the southern North Sea, the present SOD and benthic fauna figures are moderate and do not indicate any alarming situation in terms of enrichment.

RÉSUMÉ

Demande en oxygène du sédiment, benthos et phytopigments dans le nord-ouest de l'Adriatique : zone d'enrichissement par le Pô.

La demande en oxygène du sédiment (DOS), les flux de silicate et d'ammonium, les macro- et méiofaune benthiques ainsi que les phytopigments ont été mesurés dans le nord-ouest de la mer Adriatique. Au cours de deux campagnes (mars 1992 et août 1993), neuf stations ont été effectuées, la plupart sur des fonds inférieurs à 50 m, le long d'une radiale partant de l'embouchure du Pô et orientée vers le sud. Deux questions principales ont été étudiées : 1) jusqu'où le Pô influence-t-il les communautés benthiques le long de la radiale ? 2) y a-t-il quelque indice d'une situation eutrophe comme décrite dans des travaux antérieurs ?
La répartition spatiale de la DOS (gamme ± 100 à 1450 µmol $O_2 . m^{-2} . h^{-1}$) et la faune benthique n'indiquent pas que l'enrichissement organique par le Pô diminue simplement avec la latitude, du nord au sud ; pourtant les stations du nord ont généralement les plus fortes valeurs de DOS, densité de faune et biomasse.

Les caractéristiques de la colonne d'eau (température, salinité, phytopigments) montrent en août 1993 que les stations de la radiale se répartissent en deux groupes, celui du nord étant sous l'influence directe du Pô. Cette observation confirme les écarts à la circulation générale anticyclonique du nord de l'Adriatique en été, et l'écoulement des eaux du Pô vers le large plutôt que vers le sud. En comparaison avec le sud de la mer du Nord, les chiffres de DOS et de faune benthique sont faibles et ne traduisent aucune situation inquiétante en termes d'enrichissement.

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INTRODUCTION

The Adriatic Sea is a semi-enclosed basin approximately 800 kilometres long and 100 to 200 kilometres wide, which at its southern end communicates with the Mediterranean Sea. The northern part of the Adriatic is shallow (< 100 m) with some deeper pits in the south. The sea-floor is smooth and slopes slightly towards the southeast. The river Po, the major discharge of fresh water in the northern Adriatic, is an important source of sediments, nutrients, and also pollutants (Frascari *et al.*, 1988). The discharge by the other rivers along the northern and western Adriatic coast is on a minor scale.

During recent decades, eutrophication of the northern Adriatic has become an increasing problem for the environment, tourism and fisheries (Justic, 1987; Vollenweider *et al.*, 1992). Eutrophication became manifest in the form of massive plankton blooms (diatoms and dinoflagellates) and hyper production of algal mucous excretions (*e.g.* in 1988, 1989), (Bucci *et al.*, 1992). Locally anoxic conditions developed in the bottom water, causing mass mortality of benthic macrofauna (Stachowitsch, 1991; Faganeli *et al.*, 1985). A direct correlation between the river discharges and the algal blooms in the coastal waters is assumed by several authors (Marchetti and Verna, 1992; Revelante and Gilmartin, 1976).

In response to these environmental problems in the northern Adriatic, and with the aim of obtaining a better insight into the functioning of the marine ecosystem, a joint Italian-Dutch research programme was established as part of the European Community - funded programme of Science and Technology for Environmental Protection (STEP). Central to this programme are questions concerning the extent to which the river Po affects the benthic habitat along the western Adriatic shore, and in particular the effects exerted by ambient conditions on the benthic standing stock and on aerobic sediment respiration. While the latter process is subject to seasonality because of its link with temperature, pulsed organic matter supply and the sediment content of labile organics, the standing stock of relatively long-living macrobenthos offers a time-integrated signal for the average benthic food resources.

Both parameters provide information about the status of the benthic community with respect to enrichment, as demonstrated by different studies. On a temporal scale, benthic biomass has increased in response to an increasing level of eutrophication in some northeastern Atlantic shelf habitats (Brey, 1986; Josefson, 1990). On a spatial scale, benthic biomass generally shows a clear decrease with increasing depth, which largely determines the food input to the bottom (Sanders and Hessler, 1969). Sediment O_2 demand is augmented in sediments with an elevated organic loading, as in the case of the shallow North Sea (Cramer, 1991). However, with increasing organic loading often in combination with lowered O_2 content of the bottom water, sediment mineralization may be transformed into a prevailing though less efficient anaerobic process with other electron acceptors than O_2 being used. The irrigation and bioturbation activities of benthic organisms play an important role in this respect since they supply O_2 and organic compounds to deeper sediment layers. This action increases the activity of deep-living bacteria and enlarges the capacity of the sediment community to deal with an enhanced supply of organic matter (Archer and Devol, 1992; van Duyl *et al.*, 1992).

Enrichment as revealed by benthic biota and processes finds its origin in the nutrient load of the water column. Addressing the eutrophication status of the water column requires frequent sampling, since the Adriatic is a very dynamic system. In spite of a general counter-clockwise current in the northern Adriatic which forces the water along the western Adriatic coast southwards, large differences in circulation can exist on small temporal and spatial scales (Franco *et al.*, 1982; Orlic *et al.*, 1992). Nor is the outflow of the Po constant in time. Although water column studies lay outside the scope of the present investigation, a number of characteristics of the water column at the sampling stations will be discussed (temperature, salinity, oxygen, nutrients, phytopigments). While part of these data are collected for calculating the benthic fluxes, they show at the same time whether the conditions at the time of sampling deviated from the general regime in the northern Adriatic.

MATERIALS AND METHODS

Site description

In March 1992 and August 1993 two cruises were undertaken, during each of which eight stations were visited. The stations were located along a north-south transect running more or less from the mouth of the Po down to Pescara (Fig. 1). The depth of the stations ranged from 25 to 45 m except for the most southern station (stn 10) which had a depth of 250 m. The geographic positions and depths of the stations are given in Table 1. The transect was assumed to cover the principal flow direction of particu-

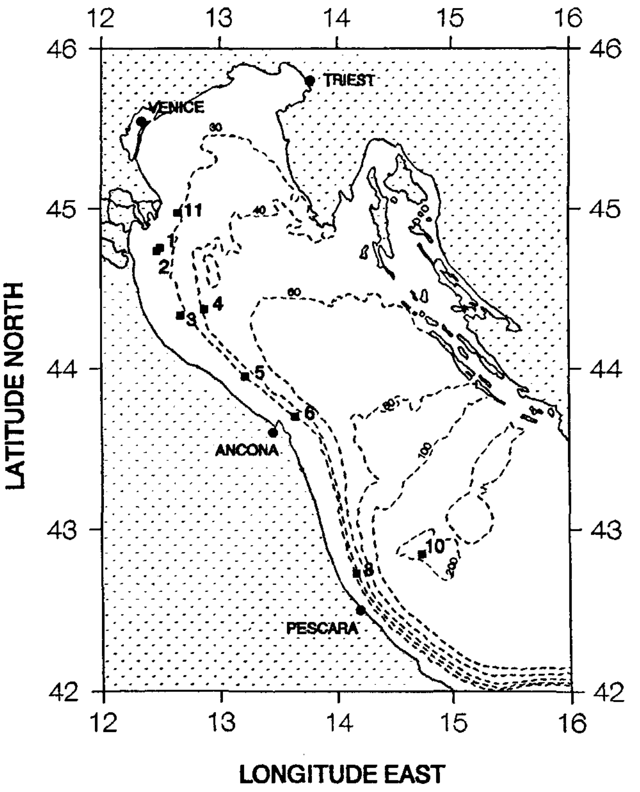

Figure 1

The study area in the Northern Adriatic Sea. Numbers refer to sampling stations. The station transect runs southwards from the river Po. Depth contours (m) are indicated.

lates and solutes derived from the Po (Buljan and Zore-Armanda, 1976). Faganeli *et al.* (1994) has shown by means of carbon isotopes that terrestrial carbon contributed by rivers is mainly deposited in a broad zone parallel to the coastline. Further evidence for deposition of river-borne material in this zone comes from the sediment grain-size distribution and carbon content in the area (Jorissen, 1987).

Sediment sampling

Sediment cores overlaid with the original bottom water were taken with a modified Reineck box corer (cylindrical corer of 31 cm ∅). The top of the core tube is open while the corer is lowered and is subsequently closed by a valve once the corer has penetrated the sea floor. Usually the cores revealed clear overlying water and undisturbed sediment surfaces. Disturbed cores with an oblique surface area, cracks, etc. were rejected. Comparison between the nutrient levels in bottom water collected with a rosette sampler and bottom water overlying the box-core samples was used to check the performance of the box corer.

Sediment oxygen demand and nutrient fluxes

SOD and nutrient fluxes were measured by enclosing an intact sediment core in an incubation chamber and monitoring the changes of solutes (O_2, nutrients) in the overlying water. In this way, the total flux, and hence both the exchange of a solute governed by molecular diffusion and the contribution by the benthic fauna (bioturbation, bioirrigation), is measured. This incubation technique was applied on deck with sediment cores kept at *in situ* temperature and entirely *in situ* with a bottom lander developed at the NIOZ. Both techniques are described in the following sections.

Shipboard incubation fluxes

Two core sizes were used for the shipboard incubations. In March 1992, four perspex cores of 10 cm ∅ were extracted from two box-core samples and closed on the underside with a rubber stopper. In August 1993, polyester cores of 31 cm ∅ were directly mounted in the box corer. Since in this case intact box-core samples were used for incubation purposes, the number of manipulations and therefore the degree of disturbance was reduced. All subsequent handling of the cores was similar in the 1992 and 1993 cruises. The cores were sealed with a lid containing an YSI 620 O_2 electrode and a magnetic stirrer before being placed in a thermostated incubator. The O_2 concentration in the overlying water was continuously recorded. Incubations lasted between 4 and 12 h. At the end of the incubation, two samples were taken from the overlying water for Winkler titration in order to calibrate the readings of the electrode. O_2 flux, expressed as μmol. m^{-2}. h^{-1}, was determined by means of a linear regression on the initial decrease of the O_2 concentration in the time series.

Since we used small cores, whereas the required sample volume for nutrient analysis would imply a significant disturbance during the O_2 uptake experiment, no nutrient flux measurements were performed during the March 1992 cruise. In August 1993, series of 25 ml samples (with 1 to 2 h interval) were taken from the headspace of the incubation cores with a syringe. The extracted volume was compensated by an equal volume of bottom water from a second syringe connected to the headspace. Prior to storage, the nutrient samples were filtered through 0.45 μm Acrodisc filters. Samples were stored and analysed for nutrients ($Si(OH)_4$, NH_4^+, NO_3^- + NO_2^- and PO_4^{3-}) according to Strickland and Parsons (1972) and Grasshoff *et al.*

Table 1

Sampling stations in the Northern Adriatic Sea, showing water depth, location and percentage silt (< 63 μm) of the sediment. Stations are ranked from north to south.

STATION	11	1	2	3	4	5	6	8	10
Depth in m	25	26	30	30	39	40	41	45	251
Latitude North	44 58′	44 44′	44 45′	44 20′	44 22′	43 57′	43 42′	42 44′	42 51′
Longitude East	12 39′	12 28′	12 30′	12 40′	12 52′	13 13′	13 39′	14 10′	14 45′
% Silt	95	95	98	96	19	92	98	97	99

(1983), with minor modifications. The fluxes were determined by linear regression of the time series.

Bottom lander

In situ measurements of sediment respiration were made with a free-falling bottom lander, BOLAS. This is a 3 m wide aluminium tripod, topped by a flotation rack holding 21 Benthos glass spheres and two independent acoustic releases. The basis of each leg contains a ballast weight (100 kg) in a special cavity designed to reduce bow-wave effects upon landing. The sinking speed of BOLAS is approximately $1 m.s^{-1}$. Special "shoes" at the base of the tripod, which direct the pressure wave caused by the sinking speed to the periphery, mitigate disturbance of the "fluff" layer on top of the sediment. In addition to the actual measurement device, the tripod accommodates the following components: two batteries; two cameras with flashlights; two Niskin bottles of 1.7 litre capacity which are triggered by a burnwire system; two Hydrobios single-cup sediment traps which are closed by a valve during the descent and the recovery; a tiltmeter; two hydraulically operated sediment grabs (100 cm^2 surface area); and finally, on top of the lander, various devices to facilitate the recovery of BOLAS when it has surfaced (intermittent flashlight, radio emitter and signal flag).

All actions by BOLAS are hydraulically driven and fully programmable. The heart of the system consists of two benthic chambers (32.5 cm ∅), made of inert Delrin (to avoid artifacts as described by Cramer, 1989), a magnetic stirrer and a probe for measuring electrical resistivity (Andrews and Bennet, 1981). After landing on the sea floor, a period of time is allowed to elapse before the chambers penetrate the sediment (± 0.5-1.0 h).Then, with the top valves of the chambers in open position, they are gently inserted into the sediment. When the resistivity probe reaches the sediment, a certain shift in electrical resistivity occurs, which arrests the descent of the chambers. Subsequently, the top valves move to their lower position and the chambers are closed. The enclosed volume of overlying water then amounts to about 5,900 ml.

On three occasions during the incubation, a syringe extracting 30 ml water from the interior of the chamber, is taken. At the same time, a similar sample is taken from the water just outside the incubation chamber. These samples are later analysed for nutrient concentrations and used to calculate sediment-water nutrient fluxes. In addition, each incubation chamber holds a semi-circular water sampler of 250 ml, containing two lids which are closed at the end of the incubation. The contents of the water sampler are used for determining the final O_2 concentration with the Winkler method. During the 1993 cruise, 2 Idronaut O_2 sensors (polarographic sensor with platinum-iridium cathode and silver anode) were mounted into each chamber which allowed continuous registration of the O_2 decrease. The electrodes are pressure compensated and have a typical output current of 15-60 nA in air at 20 °C and a zero output current which is less than 50 pA, with nitrogen.

O_2 fluxes were estimated differently during the two cruises. In March 1992, O_2 fluxes were calculated from the difference between the initial O_2 concentration of the bottom water (*i.e.* overlying box core samples) and the final O_2 concentration in the incubation chambers. During August 1993, fluxes were measured by means of the O_2 sensors. The sensor readings were calibrated with the initial and final O_2 concentrations (*see* above). Depending on location, bottom water temperature and expected flux magnitudes, *in situ* incubation times ranged between 4 and 18 hours.

The enclosed sediment sections are not retrieved after the incubations. However, in order to obtain visual information of the incubated surface area, a still camera is built into the top valve of the chambers.

Macro- and meiofauna

Macrofauna was collected from the shipboard-incubated cores by sieving the sediment gently over a perforated sieve. In March 1992, four sub-samples (± 20 cm length, 10 cm ∅) were sieved over a mesh size of 0.5 mm, while a 1-mm mesh size was used for the three cores (31 cm ∅) in August 1993. The residues on the sieve were preserved in buffered formalin. In the laboratory, organisms were sorted and counted under a stereo microscope and classified in various taxonomic groups. The ash-free dry weight of the groups was estimated from the blotted wet weight by means of the conversion factors in Rumohr *et al.* (1987).

Meiofauna samples were sub-sampled from a box core at every station, with a corer 10 cm in length and 2.1 cm ∅. Two such cores were pooled in one sample, which was preserved in buffered formalin. In the laboratory, the samples were sieved over 1-mm and 50-µm meshes to collect the meiofauna fraction (Uhlig *et al.*, 1973). To separate the meiofauna from the sediment fraction, the samples were centrifuged with Ludox HS 40 (specific gravity 1.18). The meiofauna was stained with rose bengal (Thiel, 1966) and subsequently counted. Organisms smaller than the meiofauna, *i.e.* protozoa and bacteria, were not considered.

Sediment silt and chlorophyll-*a* content

At each station, small sediment cores (2.9 cm ∅) of the upper 10 cm of the sediment were taken from the box cores. The core samples were immediately deep-frozen on board for later analysis in the laboratory. For grain-size analysis, the core samples were defrosted, diluted and sieved (63 µm). The < 63 µm fraction was caught on a pre-weighed filter. All sediment fractions were dried at 60 °C. The silt content (< 63 µm) was calculated as percentage of total sediment dry weight.

The relative amounts of chlorophyllous pigments and derivatives in the sediment were determined by means of reverse phase HPLC. The system consists of a Waters gradient pump, a Rosil C18 column and a Waters fluorescence detector plus photodiode array detector. The flow rate, solvent and gradient system are as described by Kraay *et al.* (1992). The preparation of sediment samples for HPLC analysis involved the following successive steps: slicing of the frozen cores, freeze drying of the slices, homogenization, addition of 5% methanol with 2% ammonium acetate buffer followed by sonication and finally centrifuging at

5000 RPM at 0 °C. All manipulations took place under dim light conditions. Pigments were identified by co-injection of known standards obtained from algal cultures and by their absorption spectra. In this paper only relative concentrations of pigments can be given because the calibration of the fluorescence signal of pigments other than chlorophyll-a is presently under way.

Water column

At all stations, a depth profile of temperature and salinity of the water column was made with a CTD probe mounted on a rosette sampler. At specific depths, water samples were taken with Niskin bottles for the analysis of nutrients and O_2 (Winkler method). Furthermore, surface and bottom water samples were filtered over Whatman GF/F filters for analysis of the chlorophyll content. Pigments were extracted and determined according to the protocol used for sediment samples (*see* above).

RESULTS

Water column

CTD-profiles

A detailed description of the hydrography, algal coenosis and nutrient concentrations in the water column of the stations is given by Innamorati *et al.* (1994). Following is a short summary of the most relevant hydrographic data. In March 1992, the northern stations had a surface layer of low-saline Po water, which progressively diluted in a southerly direction, as shown by the vertical salinity profiles. In spite of their similar latitude, this surficial layer was less distinct at stn 4 than at stn 3. The water column below this surface layer was mixed. Surface water temperatures ranged between approximately 9 and 12 °C. O_2 concentration generally decreased slightly with water depth. Stns 1 and 2 had lower O_2 saturation of the bottom water (± 60%) than the others (75-100%). Bottom water temperatures in March 1992 ranged from 8.4 to 11.2 °C and showed a steady increase towards the south, up to stn 8 (Tab. 2 A).

In August 1993, vertical temperature profiles showed that all stations had stratified water columns, but vertical structures were quite dissimilar along the transect. At the stns 11, 2, 3 and 4 the uppermost layer consisted of low-saline water, probably derived from the Po. This surficial layer was indistinct or weakly present at the southern stns 5, 6 and 8. Below the pycnocline delimiting this upper layer was a layer of uniform temperature and salinity. This intermediate layer was superimposed on a layer with slightly higher salinity and a downward-decreasing temperature. Fluorescence in this layer was generally highest or showed a secondary maximum. Notably at the northern stns 2, 3 and 4 distinct maxima in fluorescence and turbidity were recorded in the lowest part (few metres) of this bottom layer. Surface water temperatures along the transect ranged from 24.6 to 27.1 °C and bottom water temperatures at the shallow stations from 13 to 16.5 °C (Tab. 2 B). The bottom water temperature at stn 10 did not show any change between March and August. Especially remarkable is the relatively high bottom water temperature at stn 3 which is not in line with the adjacent stations. The O_2-saturation of the bottom water varied between 70% and 100% with lowest values at stns 2 and 3. Values at the northern stations were higher than in March 1992. Bottom water salinity was very similar among the stations (>38).

Nutrients

Table 3 A, B show the bottom water concentrations of nutrients for the two cruises. The values were derived from the water overlying box-core samples and from samples taken by the bottom lander. In March 1992, relatively low silicate and ammonium concentrations were found, with the exception of silicate at stn 10. Phosphate concentrations were very low (*ca.* < 0.1 μmol. l^{-1}). Nitrate concentrations were high at stns 1, 2 and 10 and somewhat lower at the remaining stations.

Table 2 A, B

Bottom water characteristics in March 1992 (A) and August 1993 (B). Shown are water depth, temperature, O_2 concentration and saturation and salinity. Stations are ranked from north to south.

A

STATIONS 1992	1	2	3	4	5	6	8	10
Depth in m	26	25	30	39	40	41	45	251
Temp °C	8.4	9.1	9.8	9.8	10.0	10.5	11.2	10.9
O_2 μmol. l^{-1}	182	163	238	282	277	275	255	201
O_2 sat (%)	63	58	86	102	100	101	95	74
S	37.5	37.7	38.1	38.1	38.2	38.3	38.3	38.4

B

STATIONS 1993	11	2	3	4	5	6	8	10
Depth in m	25	30	30	39	40	41	45	251
Temp °C	15.7	14.1	16.3	14.0	14.0	13.1	15.7	10.9
O_2 μmol. l^{-1}	215	178	175	203	251	244	216	218
O_2 sat (%)	88	70	72	80	99	94	88	81
S	38.2	38.1	38.1	38.2	38.2	38.3	38.1	38.3

Table 3 A, B

Nutrient concentrations (μmol. l^{-1}) of the near-bottom water in March 1992 (A) and August 1993 (B). Stations are ranked from north to south.

A

STATIONS 1992	$Si(OH)_4$	PO_4^{3-}	NO_x^-	NH_4^+
1	< 0.1	< 0.002	13.1	< 0.05
2	3.7	0.1	12.5	5
3	< 0.1	< 0.002	1.5	0.05
4	1.3	< 0.002	3.1	< 0.05
5	1.6	< 0.002	2.1	< 0.05
6	1.7	< 0.002	0.9	0.9
8	1.4	0.6	3.5	2.9
10	17.0	0.11	3	< 0.05

B

STATIONS 1993	$Si(OH)_4$	PO_4^{3-}	NO_x^-	NH_4^+
11	6.5	0.13	5.2	1.85
2	17.0	0.2	1.4	3.6
3	11	< 0.02	2.2	1.3
4	7.5	< 0.02	< 0.1	0.6
5	4.2	0.02	0.5	0.1
6	3.4	0.02	0.5	1
8	9.8	< 0.02	1.8	6
10	8.9	0.35	4.6	3.3

In August 1993, concentrations of silicate and ammonia were generally higher than in March 1992. Phosphate concentrations were still very low (generally < 0.2 μmol. l^{-1}) and nitrate concentrations were generally somewhat lower than in March 1992.

Chlorophyll bottom water

In March 1992, highest concentrations of chorophyll-*a* were found in the bottom water near the Po mouth (stn 1, 2), while stns 5 and 6 had slightly elevated concentrations compared to the adjacent stations (Tab. 4 A). The relatively high ratios of fucoxanthin and chlorophyll-$c_{1,2}$ to chlorophyll-*a* suggest an elevated proportion of diatoms at stns 1, 2, where as at the other stations (3 to 8) comparatively high proportions of Prymnesiophytes (*Emiliania huxleyi*) were found as shown by the relative amounts of chlorophyll-c_3 and 19'-hexanoyloxyfucoxanthin. The dominance of *Emiliania huxleyi* is in accordance with the results from cell counts by Innamorati *et al.* (1994). Detectable quantities of phaeopigments were only found at stns 1 to 3, with the highest proportions at stn 3. This suggests either resuspended sediment or heavy grazing of the phytoplankton biomass.

In August 1993, chlorophyll-*a* concentrations in the bottom water showed an increase from stns 11 to 4 with the highest level at stn 4 (Tab. 4 B). At the southern stns 5 to 8, much lower concentrations were found but with a similar increase from stn 5 to 8. All bottom water samples contained very little phaeophorbide. The ratios of other chlorophylls and phytopigments to chlorophyll-*a* suggest a great patchiness in the algal composition of the bottom layer along the transect. Among the northern stations, for instance, stns 1 to 3 have relatively high proportions of chlorophyll-*b* (green algae), whereas stn 4 has the highest proportion of fucoxanthin. In the southern part of the transect (stns 5 to 8), there is a dissimilarity between the bottom water samples from stn 5 and 6, on the one hand, and

Table 4 A

*Chlorophyll-*a *concentrations (μg. l^{-1}) and ratios of several other phytopigments (fucoxanthin, chlorophyll-c_1 + c_2, chlorophyll-c_3, β-hexanoyloxyfucoxanthin) to chlorophyll-*a *of the bottom water in March 1992. Ratios at station 10 were very low and are not shown. Chlorophyll-*a *flux (μg. m^{-2}. d^{-1}) to the bottom water, which was measured by the sediment traps on the bottom lander, is also shown. Stations are ranked from north to south.*

STATIONS 1992	chl-*a* (μg. l^{-1})	chl-*a* flux (μg. m^{-2}. d^{-1})	fucox/chl-*a*	chl-c_1+c_2/chl-*a*	chl-c_3/chl-*a*	hexa/chl-*a*
1	1.64	220	0.64	0.50	0.00	0.00
2	1.34	228	1.01	0.55	0.06	0.00
3	0.38	82	0.52	0.62	0.18	0.30
5	0.69	-	0.48	0.41	0.20	0.43
6	0.63	208	0.30	0.42	0.15	0.43
8	0.45	166	0.50	0.39	0.22	0.48
10	0.25	-	-	-	-	-

Table 4 B

*Chlorophyll-*a *concentrations (μg. l^{-1}) and ratios of several other phytopigments (chlorophyll-*b*, fucoxanthin, diadinoxanthin, chlorophyll-c_3, μ-hexanoyloxyfucoxanthin, zeaxanthin) to chlorophyll-*a *of the bottom water in August 1993. Ratios at station 10 were very low and are not shown. Chlorophyll-*a *flux (μg. m^{-2}. d^{-1}) to the bottom water, which was measured by the sediment traps on the bottom lander, is also shown. Stations are ranked from north to south.*

STATIONS 1993	chl-*a* (μg. l^{-1})	chl-*a* flux (μg. m^{-2}. d^{-1})	chl-*b*/chl-*a*	fuco/chl-*a*	diad/chl-*a*	chlc_3/chl-*a*	hexa/chl-*a*	zeax/chl-*a*
11	0.56	138	0.14	0.30	0.03	0.10	0.20	0.21
2	0.89	178	0.15	0.57	0.04	0.10	0.09	0.07
3	1.13	166	0.17	0.17	0.05	0.06	0.20	0.14
4	1.57	234	0.06	0.71	0.06	0.28	0.15	0.04
5	0.17	56	0.05	0.39	0.07	0.19	0.54	0.45
6	0.24	114	0.05	0.26	0.07	0.30	0.75	0.33
8	0.65	79	0.07	0.39	0.06	0.27	0.39	0.08
10	0.01	-	-	-	-	-	-	-

stn 8, on the other. This refers to the proportions of zeaxanthin (*a.o.* Cyanophycea, Prasinophycea) and of 19'-hexanoyloxyfucoxanthin (Prymnesiophytes). The presence of this latter pigment indicates, in contrast with the results obtained by Innamorati *et al.* (1994), that coccolithophorids are still present in summer.

Chlorophyll in sediment traps

The vertical fluxes of chlorophyll-*a* measured in the sediment traps that were attached to the benthic lander, are shown in Table 4 A, B. Both in March 1992 and August 1993 there was only partial correspondence between the vertical fluxes and the bottom water concentrations. The highest and lowest fluxes and bottom water concentrations appear to coincide, but the distribution of intermediate values of both quantities shows little relation. In March 1992, for instance, the vertical flux at the southern stn 5 was only slightly lower than close to the Po in spite of a much lower bottom water concentration. It should, however, be stressed that the differences in bottom water concentrations do not necessarily reflect the differences in the integrated chlorophyll content of the entire water column.

Sediment

Silt content

The silt content of the sediment is given in Table 1. All stations but one (stn 4) had high percentages of silt.

Chlorophyll-*a*

The distribution of chlorophyll-*a* in the top 1 and 5 cm of the sediment in both years is shown in Table 5. In March 1992, the highest content of chlorophyll-*a* in the top 5 cm of the sediment was found at stn 1 with the southernmost stn 8 second in rank. Stns 2 and 3 had intermediate levels which were still twice or more as high as those at stns 4, 5 and 6. In August 1993, maximum chlorophyll-*a* levels were found at the two northernmost stations (11 and 2), although in the meantime the concentrations in the upper 5 cm at the other stations had increased as well, compared to March 1992. Stn 8 is the only one where lower levels were found in August.

Although only three depth strata were analysed (0-1, 1-3, 3-5 cm), some temporal differences can be seen with regard to the vertical distribution of chlorophyll-*a*. While in March many of the stations show a sharp decrease in chlorophyll-*a* from the top 1 cm to 1-3 cm , this decrease is less steep in August 1993. This is probably due to a greater mixing activity of the infauna. Further support for a more intensive mixing of fresh phytodetritus in August comes from the vertical distribution of phaeopigments, in particular of phaeophorbides –which are the dominant phaeopigments– and moreover the products of chlorophyll digestion by metazoans (Bidigare *et al.*, 1986). Chlorophyll-*a*/phaeophorbide ratios in the 1-3 cm layer in August are similar to and sometimes even surpass those in the top 1 cm, indicating that the phytodetritus pool in the deeper layers is in the same state of degradation (age) as that in the top slice.

With respect to the chlorophyll-*a*/phaeophorbides ratios, stn 3 is distinguished by a strikingly low ratio over the complete upper 5 cm, both in March 1992 and, although somewhat less distinct, in August 1993. This could be due either to the deposition of more degraded material or to the action of macrofaunal organisms which intercept sedimenting fresh material, digest it and subsequently mix it throughout the upper sediment layers.

Sediment-water fluxes

Oxygen

The results from the shipboard incubation measurements and the *in situ* measurements (BOLAS lander) of sediment O_2 demand (SOD) are separately shown for both years in Fig. 2 *a, b*. In August 1993, SOD was on average higher than in March 1992, although there are major differences among the stations with respect to the temporal increase. Most stations show a temporal increase up to a factor 2, with a maximum factor of 3 at stn 4 (shipboard incubations). Highest SOD values (± 1000-1450 µmol. m^{-2}. h^{-1}) were measured at stns 11 and 3 in August 1993. Stn 10 in the 250 m deep Jabuka Pit had the lowest SOD during both years, with a small increase from March to August.

Although there is a substantial amount of variance in the individual measurements with the 10 cm cores in March 1992, the activity pattern along the transect seems to be the same in March 1992 as in August 1993. Highest rates were found at stations near the mouth of the Po (stns 1, 11) and at stn 3. In the 1993 cruise, stn 2 yielded more moderate rates which were comparable to those of the southern stns 5 to 8. Stn 4, which has a sediment texture different from the other stations, had the lowest SOD among the shallow stations in both seasons. The data from August 1993 show furthermore that shipboard and *in situ* incubation measurements agree reasonably well, although there are a few exceptions. Comparisons among the 1992 data are hampered by the small number of in situ measurements.

In order to obtain some indication of the carbon mineralization rates we converted our SOD figures. Canfield *et al.*

Table 5

*Chlorophyll-*a *concentrations (µg . cm^{-3} dry sediment) in the top-1 and the top-5 cm of the sediment in March 1992 and August 1993. Stations are ranked from north to south.*

STATION	11	1	2	3	4	5	6	8	10
March 1992 0-1 cm	-	2.20	0.53	0.43	0.31	0.31	0.48	1.18	-
March 1992 0-5 cm	-	4.75	2.35	1.50	0.75	0.85	0.75	3.30	-
August 1993 0-1 cm	1.95	-	0.82	0.53	0.55	0.77	0.80	0.72	0.02
August 1993 0-5 cm	3.55	-	3.90	2.70	1.90	2.90	2.80	2.40	0.10

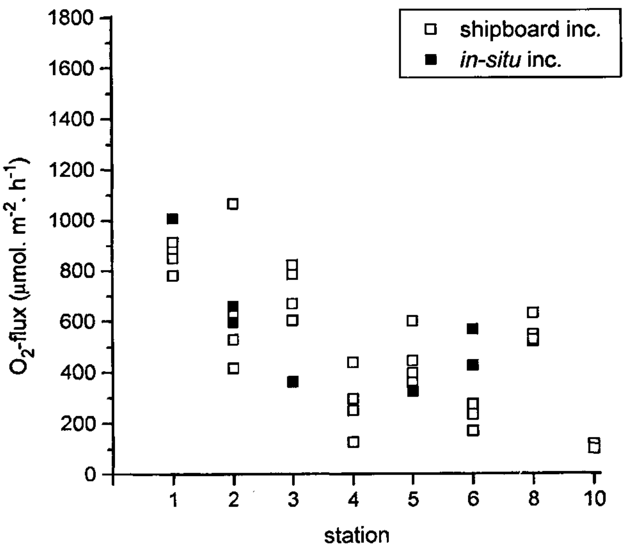

Figure 2 *a*

SOD (sediment O_2 demand in µmol. m^{-2}. h^{-1}) at the stations in March 1992. Estimates of individual shipboard (core diameter 10 cm) and in situ *incubation measurements are shown.*

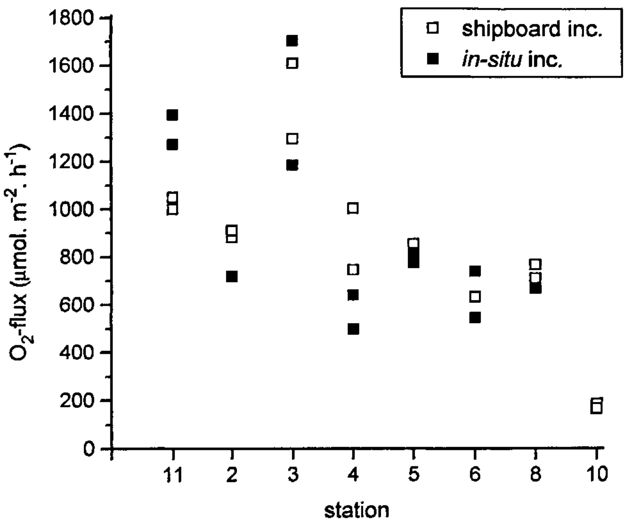

Figure 2 *b*

SOD (sediment O_2 demand in µmol. m^{-2}. h^{-1}) at the stations in August 1993. Estimates of individual shipboard (core diameter 31 cm) and in situ *incubation measurements are shown.*

(1993) showed that in the case of rapid biomixing by infaunal organisms, the total O_2 uptake includes the O_2 respiration as well as the oxidation of reduced compounds of the anaerobic mineralization (except denitrification). Using average SOD values for the stations, the resulting benthic carbon mineralization ranges roughly between 30 and 290 mg C m^{-2}. d^{-1} in March 1992 and between 50 and 420 mg C m^{-2}. d^{-1} in August 1993.

Nutrients

In March 1992, only *in situ* nutrient fluxes (BOLAS) were determined (Tab. 6 A). Silicate concentrations in the bottom water overlying box-core samples ranged from ± 3.4-17.3 µM. Silicate effluxes were highest (up to ± 170 µmol. m^{-2}. h^{-1}) at the stations near the Po, and decreased slightly towards stn 3. Much lower fluxes were recorded at the southern stns 5 and 6. Replicate chamber results were in fairly close agreement. Ammonium fluxes showed an erratic pattern along the transect with the highest value at stn 2 (± 30-60 µmol. m^{-2}. h^{-1}). Nitrate and phosphate fluxes did not yield consistent linear results in any of the *in situ* incubations, and are therefore not shown.

During the August 1993 cruise, nutrient fluxes were measured both *in situ* and in shipboard incubations. The estimates for silicate fluxes by the two methods agreed reasonably well (Tab. 6 B), showing relatively high flux rates at the northern stations (11, 2, 3, 4) and more depressed rates at the southern ones (5, 6, 8). Ammonium fluxes were highest at the three northern stations (11, 2, 3), with the highest value at stn 3, coinciding with a high SOD. Low fluxes of ammonium (< 10 µmol. m^{-2}. h^{-1}) in combination with technical errors prevented accurate assessment of rates at the remaining stations. Although the determination of rates for nitrate and phosphate was a delicate matter and in some cases not possible, the general pattern shows

Table 6 A, B

Sediment-water fluxes of silicate and ammonium (µmol. m^{-2}. h^{-1}) in March 1992 (A) and August 1993 (B). In March 1992 only in situ *fluxes were measured. Stations are ranked from north to south.*

A

STATIONS 1992	1	2	3	4	5	6	8	10
in situ Si flux	172	172/173	105/102	-	39/29	39	-	-
in situ NH_4 flux	20	58/30	0	-	22/11	11/5	-	-

B

STATIONS 1993	11	2	3	4	5	6	8	10
Shipboard Si flux	165	178	183	145	56	86	87	121
in situ Si flux	188	155	142	137	92	87	-	-
Shipboard NH_4 flux	29	30	101	< 10	< 10	< 10	< 10	< 10
in situ NH_4 flux	53	23	86	< 20	< 10	< 20	-	-

moderate rates at stns 1, 2 and 3 for nitrate (up to ± 20 µmol. m^{-2}. h^{-1}) and phosphate (± 5 µmol. m^{-2}. h^{-1}), and rates of ± 0 at the other stations.

Infauna

Macrofauna

Density (ind. m^{-2}) and biomass (g AFDW m^{-2}) of the macrofauna (fraction >1 mm) in August 1993 are given in Fig. 3 *a, b.* The macrofauna has been differentiated in gross taxonomic categories. Total macrofaunal density decreases along the transect in a southerly direction. Highest densities (± 2400-2800 ind. m^{-2}) are found at the stations near the river Po, the lowest density being found at the deepest station 10 (± 170 ind. m^{-2}). Polychaetes numerically dominated the macrofauna at all stations. Only at stns 11, 3 and 4 were significant numbers of filter-feeding bivalves (mainly *Corbula gibba*) found. Small crustaceans (mostly amphipodes) were quite numerous at stns 2 and 4. Burrowing Ophiuroids (*Amphiura filiformis* and *Amphipholis squarnata*) were found mainly at stns 11 and 3. When comparing the distribution of individuals at the individual stations over the main taxa, stn 2 clearly deviated from the other northern stations, the macrofauna there being dominated by small polychaetes and crustaceans. Unlike density, macrofaunal biomass does not show a steady decrease to the south along the transect. Stns 11 and 3 have the highest total biomass, resulting from high contributions of mud-anemones (*Cerianthus*), molluscs and echinoderms to the total biomass. The lowest total macrofaunal biomass is found at stns 2, 5 and 10. While this is not unexpected in the case of the deepest stn 10, the impoverished fauna at the shallow stn 2 is quite remarkable.

The density and biomass estimates for macrofauna obtained in March 1992 are not compatible with those from 1993, since a mesh size of 0.5 mm was used instead of 1 mm as in 1993. Moreover, the smaller core size in combination with the limited number of samples (total surface area of 320 cm^2 in 1992 *versus* 2100 cm^2 in 1993) led to large variations for the density estimates and even more so for the biomass estimates. Density and biomass in 1992 are given in Fig. 4 *a, b.* Despite the afore-mentioned drawbacks, some of the features are similar to those in August 1993. For instance, the somewhat deviating fauna of stn 2, with relatively low numbers of ophiuroids and high numbers of small crustaceans.

Fig. 5 *a, b* show the bottom topography from in situ incubated sediment sections of the highly divergent stns 3 and 6 on two pictures obtained by BOLAS (March 1992). These pictures visually demonstrate the numerous presence of the macrofauna, *i.e. Amphiura filiformis* and *Corbula gibba* (stn 3) and burrow entrances of *Squilla mantis* (stn 6).

Meiofaunal density

The density of meiofaunal taxa is shown in Fig. 6. No distinct gradient in total numbers along the transect was found in either year. Nematodes were always the dominant group, while copepodes also form a distinct group contributing significantly to total numbers. The generally low numbers of other taxa (crustaceans, turbilaria, foraminifera, gastropodes and kinorynchs) were pooled together in the group "others". At the sandy station 4, no greater relative abundance of copepodes is found, which could be expected because of the greater volume of interstitial space present in the sediment (Heip *et al.,* 1983). There are marked differences in total meiofaunal numbers between the two cruises. No explanation can be offered for this. Maximum densities are of the same order as reported by Herbert *et al.* (1995); however, these authors, stations had more shallow depths.

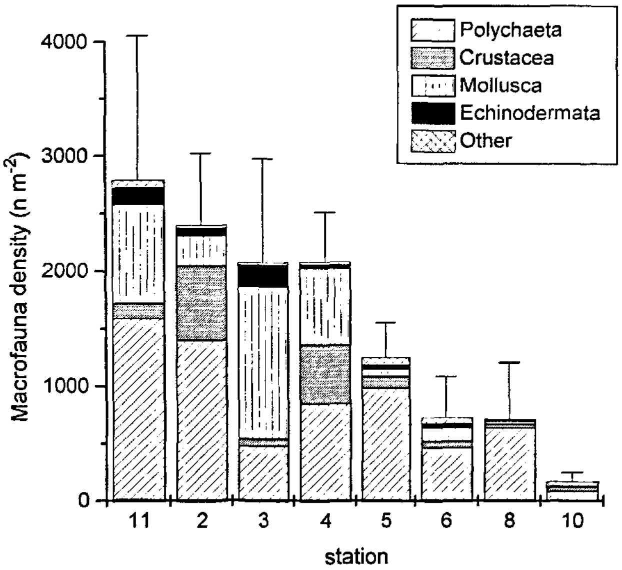

Figure 3 *a*

Macrofaunal density (ind. m^{-2}) at the stations in August 1993. The smallest macrofauna was retained on a sieve with a mesh size of 1 mm. Values are means of 2-3 box cores (diameter 31 cm) including the standard deviation for the total number of individuals.

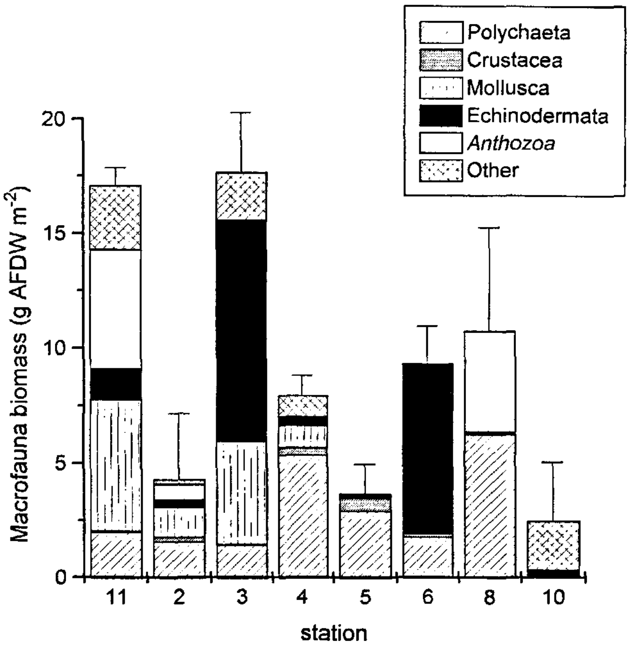

Figure 3 *b*

Macrofaunal biomass (g AFDW. m^{-2}) at the stations in August 1993. The smallest macrofauna was retained on a sieve with a mesh size of 1 mm. Values are means of 2-3 box cores (diameter 31 cm) including the standard deviation for the total biomass.

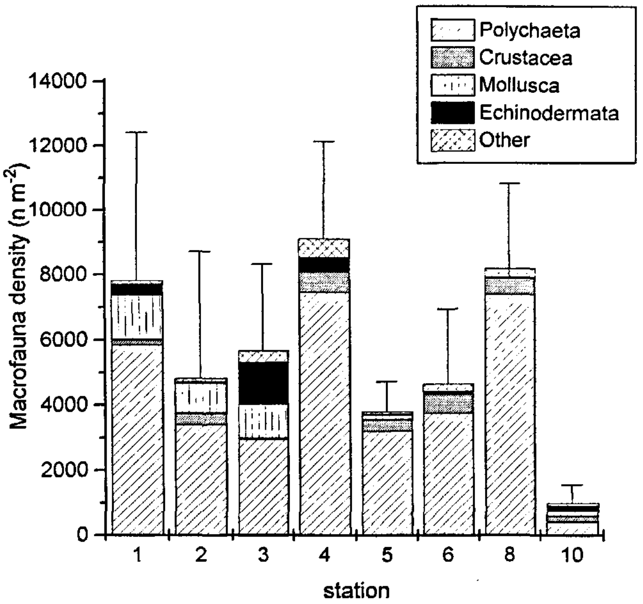

Figure 4 *a*

Macrofaunal density (ind. m^{-2}) at the stations in March 1992. The smallest macrofauna was retained on a sieve with a mesh size of 0.5 mm. Values are means of 4 incubation cores (diameter 10 cm) box cores including the standard deviation for the total number of individuals.

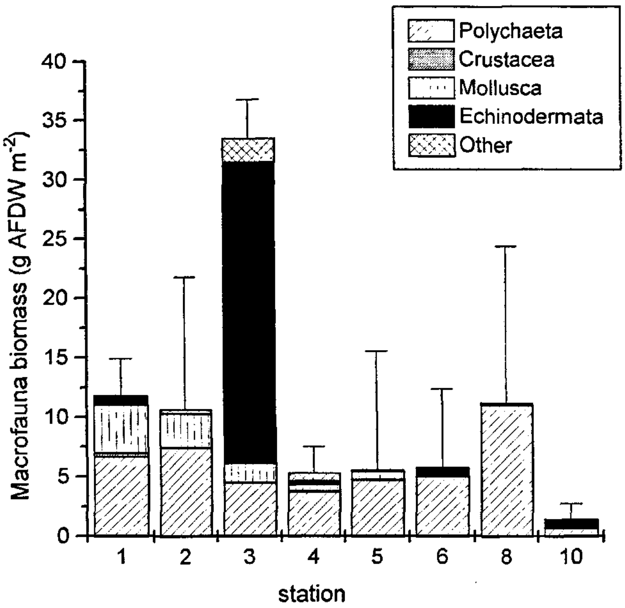

Figure 4 *b*

Macrofaunal biomass (g AFDW. m^{-2}) at the stations in March 1992. The smallest macrofauna was retained on a sieve with a mesh size of 0.5 mm. Values are means of 2-3 incubation cores (diameter 10 cm) box cores including the standard deviation for the total biomass.

DISCUSSION

The present study was designed to detect gradients in benthic fluxes and standing stock along the residual anticlockwise flow regime in the northwestern Adriatic. With the Po being the major source of organic and inorganic solutes (nutrients), we expected to find a gradient in enrichment with the strongest effects in the northern part of our transect and gradually diminishing effects in a southward direction. While this may seem an idealized concept, earlier study (Faganeli, 1994) has shown that terrestrially-derived carbon, of which the Po constitutes the principal supply, is mainly deposited in a zone running parallel to the Italian Adriatic coast. Moreover, peak values for annual primary production (120 g C. m^{-2}) and nutrient concentrations all refer to the area near the Po delta (Justic, 1987; Relevante and Gilmartin, 1976).

The benthic community as well as benthic mineralization rates in the Northern Adriatic are likely to be influenced by temporal and spatial variability due to climatic conditions and seasonal variations (*e.g.* river discharge). In order to cover the temporal variation, two cruises were conducted. Unfortunately, it turned out that both cruises were held in a period of low phytoplankton biomass (Innamorati *et al.*, 1994). The March 1992 cruise followed a massive bloom in February and preceded a diatom (*Chaetoceras*) bloom in April. Also during the August 1993 cruise, phytoplankton was scarce in comparison with the annual cycle. It seems, therefore, unlikely that our data set reflects the maximum contrast between the stations and the two seasons.

Nevertheless, because each of the parameters integrates variations in benthic food supply over a different time span, an important part of the temporal and spatial differences in food availability will still be preserved in the data that we collected. It is obvious that the water-column data and sediment trap results cover the shortest time span. SOD usually shows a rapid, but relatively short-lived response to a pulse of phytodetritus (Graf, 1992). In a mesocosm experiment it was found that the variations in chlorophyll-*a* covered about the same time scale as those of SOD, implying that the breakdown rate of chlorophyll-*a* is close to that of the most labile fraction of the organic material (Duineveld *et al.*, 1989).The fast response in SOD to a pulsed food input is for the major part due to bacteria, as was shown in an experimental mesocosm study (van Duyl *et al.*, 1992). Metazoans, on the other hand, integrate any short-term variations in food input over longer time scales, depending on their generation time. The biomass distribution of macrofauna hence forms a good starting point for the assessment of differences in the level of enrichment. Meiofauna will show a stronger correlation with rapid variations in food supply than the longer-living macrofauna.

Taking the biomass data from 1992 and 1993 together, it can be seen that highest biomass values are concentrated in the northern part of the transect, which is not surprising considering the geographical position near the Po. Although the two data sets are not completely comparable, stn 3 stands out with the highest values, which in both years can be ascribed to the burrowing Ophiuroid *Amphiura filiformis.* Other studies in silty boreal sediments suggested a strong link between the density of *Amphiura* and the input of organic matter (O'Connor *et al.*, 1986; Josefson, 1990; Cramer, 1991).

In contrast, the biomass of stn 2 in August 1993 appears to be strikingly low compared to the previous year and also to the biomass of the adjacent stns 11 and 3 in August 1993. We have no clear explanation for this. The low biomass

Figure 5 *a*

This picture obtained by BOLAS shows about 500 cm^2 of the incubated sediment at station 3 in March 1992. Visible is the muddy sediment surface with numerous protruding armtips of Amphiura filiformis *and the spectacle-like siphon openings of the bivalve* Corbula gibba. *On the right side, a single specimen of the mudanemone* Cerianthus *with an extended corona is visible.*

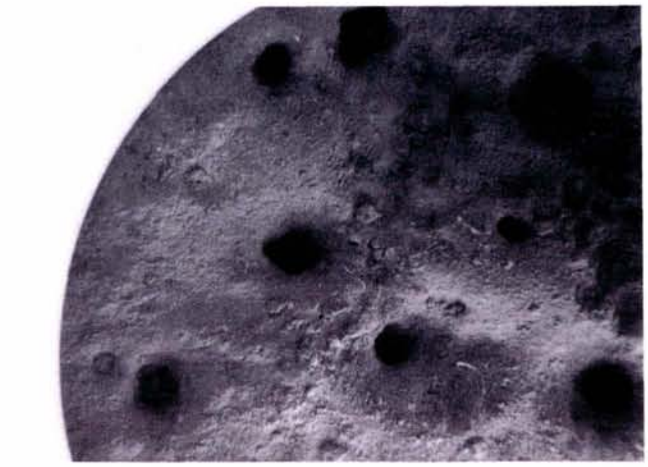

Figure 5 *b*

Similar picture taken at station 6 in March 1992. The conspicuous holes are attributed to the locust shrimp Squilla mantis *(not visible).*

could be due either to organic enrichment as postulated by Pearson and Rosenberg (1978) or to a catastrophic event such as coastal hypoxia/anoxia. The macrofauna at stn 2 in 1993 was dominated by small-sized animals, which is indicative of a community in an immature state, according to the empirical succession model for benthic communities (Pearson and Rosenberg, 1978).

The other stations near the Po mouth (1, 11) had a more diverse macrofauna and a much higher biomass. An important contributor to the total biomass and abundance is the filter-feeding bivalve *Corbula gibba*. According to Crema *et al.* (1991), *Corbula* can become abundant in areas which are polluted or enriched by organic material. The species, moreover, is quite tolerant to O_2 deficiency (Stachowitsch, 1991). Chlorophyll-*a* concentrations in the sediment indeed show that these stations are among the most enriched of the transect. The presence of a relatively high biomass under these conditions underscores the deviating macrofauna community at stn 2. While at the remaining stations lower biomass and abundance values were found, the values for stn 8 show a relative increase, which is caused not only by the incidental large organisms but also by a higher proportion of polychaetes. The deepest station clearly has the lowest biomass and density of bottom organisms.

The pattern in SOD reflects many features of the macrofaunal biomass distribution, such as: maximum values at the three northern stations; lower but constant rates along the shallow, southern part of the transect; and minimal rates at the deep southern station. In addition to this spatial pattern, a clear temporal trend is evident when the SOD values of 1992 and 1993 are compared (Fig. 2 *a, b*). The largest increase in SOD was observed at stn 3, *viz.* from 360-720 μmol. m^2. h^{-1} in March 1992 to at least twice this value in August 1993. Taking a Q_{10} of 2 (Schwinghamer *et al.*, 1986), this difference could be largely explained by the 6 °C temperature rise, at least when the amount of labile organic matter is not limiting. Because of the twofold increase of sediment chlorophyll-*a* and of the vertical chlorophyll-*a* flux in August 1993, it seems likely that this summer increase of SOD is caused by the combination of food supply and temperature rather than by temperature alone. The same arguments apply also to stns 4, 5 and 6, where SOD displays large temporal variation. In all these cases, doubling of SOD in August is accompanied by a sharp increase in the phytodetritus content of the sediment.

More moderate increases in SOD were observed at stations 1, 11, 2 and 8. While at stns 11 and 8, the sediment in August 1993 contained less chlorophyll-*a* than in March 1992, at stn 2 chlorophyll-*a* levels in the sediment showed a distinct increase within this time span. The August 1993 concentrations were even the highest on the transect. We have no clear explanation for the relatively small increase in SOD at stn 2 with respect to this clear increase in chlorophyll-*a* in the upper 5 cm of the sediment and the temperature rise of 5 °C. The O_2 saturation of the bottom water overlying stn 2, which can potentially affect the sediment-water flux of O_2 (Emerson, 1985), was not lower than that of stn 3. It could be that the low SOD increase is related to the apparent reduction in the macrofaunal biomass (*see* above), which affects both the irrigation flux and the O_2-demand of the organisms themselves. Banse (1982) gives empirical relationships between macrofaunal biomass and respiration rates, which illustrate that a low biomass results in lower respiration rates and thus a lower SOD. Usually, however, the metabolic contribution of subtidal macrofauna themselves to the SOD is regarded as being of minor importance, in contrast to their effect on sediment-water exchange (factor 2-3; Aller, 1980).

The temporal increase of SOD and phytodetritus at the stns 3 to 8 is, except for stn 3, not accompanied by a distinct increase of the NH_4-flux or any measurable change in the NO_3-flux. Moreover, all NH_4-fluxes in August seem to be rather low in comparison with values reported by Giordani *et al.* (1992, 1994) for the Adriatic. In contrast, the deposition of spring and summer production in the subtidal North

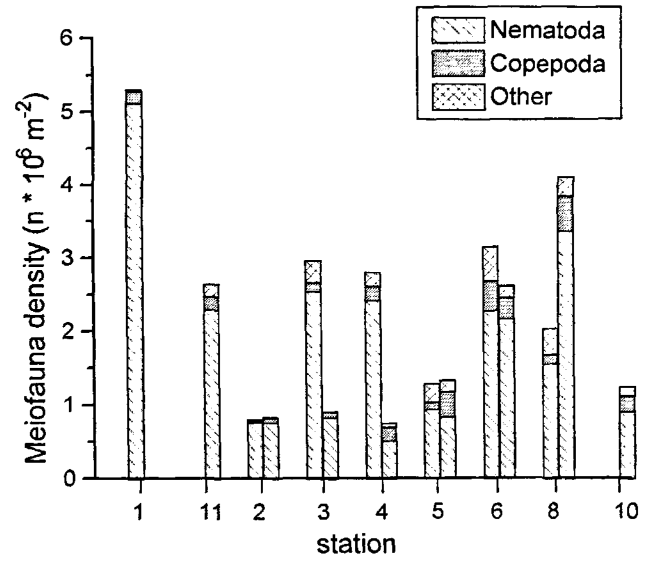

Figure 6

*Meiofaunal density (number of individuals * 10^6 m^{-2}) at the stations in March 1992 (first bar) and August 1993 (second bar).*

Sea, gives rise to a sharp increase of the NH_4-flux and to a reduction in the efflux of NO_3 in response to the lowered O_2 penetration (van Raaphorst *et al.*, 1992). Because the absolute SOD increases in the Adriatic (except stn 3) are modest in comparison with the North Sea, the potential changes in NH_4 and NO_3 may have fallen within the analytical error. There is little reason to assume a reduced irrigation activity of the benthic fauna to be responsible for the absence of a signal in NH_4 fluxes. The Si fluxes, for instance, did show an increase at many of the stations in August, despite enhanced concentrations in the near-bottom water.

Contrary to initial expectations, our data do not point to a linear decrease in biomass, SOD or nutrient fluxes towards the south. More realistically, we suggest a division of the transect into a northern and a southern area, with the former being the most enriched. This idea is supported by the observation that the low-saline surface water, which originates with the Po, was absent in the southern half of the transect in August 1993. Also, Innamorati *et al.* (1994) suggest that the summer discharge by the Po flows to a major extent offshore and less to the south. In spring, however, the fresh water from the Po moves predominantly southwards. This implies that during a major part of the year the southern stations are not affected by Po effluents and rely on local primary production. In the bottom water we also found a discontinuity between the northern and southern section of the transect, with regard not only to O_2 and chlorophyll-*a*, but also to nutrients and algal composition (Innamorati *et al.*, 1994). This discontinuity in algal composition is reflected in the composition of the phytodetritus in the sediments. The sediments at the northern stns 11, 2 and 3 contain relatively high proportions of chlorophyll-*b*, whereas the southern stns 4, 5, 6 and 8 have a relatively higher proportion of chlorophyll-*c* (mainly c_3 originating from *e.g. Emiliania huxleyi*). Some observations, *e.g.* the high biomass and phytodetritus content of stn 8, suggest that, also within the southern shallow section of the transect, the benthic food resources are not equally dispersed.

Insight into the degree of enrichment of the Adriatic stations in general can be gained from a comparison with maximum SOD, biomass values and nutrient fluxes recorded in the shallow southern North Sea. In a silty sand bottom near a highly productive frontal region, a maximum SOD of 2000 μmol. m^{-2}. h^{-1} and NH_4 efflux of 70 μmol. m^{-2}. h^{-1} was found in August 1989 (16 °C) by, respectively, Cramer (1991) and van Raaphorst *et al.* (1992). The biomass in this area is about 25 g AFDW. m^{-2} and mainly composed of the ophiuroid *Amphiura filiformis* (1000 ind. m^{-2}) and polychaetes. Estimates for the primary production for the three-month summer in this area amount to 200 g C. m^{-2}. These values are not matched by any of our Adriatic data, and show that benthic communities are potentially able to cope with much greater organic inputs than at present at the Adriatic stations. The records from the Adriatic, however, show that such an adaptation has a substantial chance of being curtailed by frequent hypoxic or anoxic periods leading to a reduction of the faunal biomass and, in all likelihood, of its metabolic activity as well.

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REFERENCES

Aller C. (1980). Quantifying solute distributions in the bioturbated zone of marine sediments by defining an average microenvironenment. *Geochim. Cosmochim. Acta* **44**, 1955-1966.

Andrews D., A. Bennet (1981). Measurements of diffusivity near the sediment-water interface with a fine-scaled resistivity probe. *Geochim. Cosmochim. Acta* **45**, 2169-2175.

Archer D., A. Devol (1992). Benthic oxygen fluxes on the Washington shelf and slope: a comparison of *in situ* microelectrode and chamber flux measurements. *Limnol. Oceanogr.* **37**, 3, 614-629.

Banse K. (1982). Mass-scaled rates of respiration and intrinsic growth in very small invertebrates. *Mar. Ecol. Prog. Ser.* **9**, 281-297.

Bidigare R.R., T.J. Frank, C. Zastrow, J.M. Brooks (1986). The distribution of algal chlorophylls and their degradation products in the Southern Ocean. *Deep-Sea Res.* **33**, 7, 923-937.

Brey T. (1986). Increase in macrozoobenthos above the halocline in Kiel Bay comparing the 1960s with the 1980s. *Mar. Ecol. Prog. Ser.* **28**, 299-302.

Buljan M., M. Zore-Armanda (1976). Oceanographical properties of the Adriatic Sea. Oceanograph. *Mar. Biol. Ann. Rev.* **14**, 11-98.

Bucci D., C. Mengarelli, C. Venanzini, C. Petrelli, L. Di Marino (1992). A year of monitoring of marine eutrophication on the coast of Ancona, in: *Science of the total environment,* edited by R.A. Vollenweider *et al.*, supplement Marine Coastal Eutrophication, Elsevier Science Publishers B.V., Amsterdam, 411-418.

Canfield D.E., B.B. Jørgensen, H. Fossing, R. Glud, J. Gundersen, N.B. Ramsing, B. Thamdrup, J.W. Hansen, L.P. Nielsen, P.O.J. Hall (1993). Pathways of organic carbon oxidation in three continental margin sediments. *Mar. Geol.* **113**, 27-40.

Cramer A. (1989). A common artifact in estimates of benthic community respiration caused by the use of stainless steel. *Neth. J. Sea Res.* **23**, 1, 1-6.

Cramer A. (1991). Activity of benthic macrofauna at a frontal system in the southern North Sea. Thesis, University of Amsterdam, The Netherlands, 53-62.

Crema R., A. Castelli, D. Prevedelli (1991). Long term eutrophication effects on macrofaunal communities in Northern Adriatic Sea. *Mar. Pollut. Bull.* **22**, 10, 503-508.

Duineveld G.C.A., P. Verburg, E.M. Berghuis, A. Kok, G.J. van Noort, P.A.W.J. de Wilde (1989). Metabolic responses of soft-bottom benthic mesocosms to enrichment and food deprivation, in: *The applicability of mesocosms in North Sea eutrophication studies*, edited by F.C. van Duyl. NIOZ-rapport 1991-**5**, 87-98.

van Duyl F.C., J.M. Kop, A. Kok, A.J.J. Sandee (1992). The impact of organic matter and macrozoobenthos on bacterial and oxygen variables in marine sediment boxcosms. *Neth. J. Sea Res.* **29**, 4, 343-355.

Emerson S. (1985). Organic carbon preservation in marine sediments, in: The carbon cycle and atmospheric CO$_2$: Natural variations Archean to present, edited by E. Sundquist and W. Broecker, *Am. Geophys. Union* 78-86.

Faganeli J., A. Avain, N. Fanuko, A. Malej, V. Turk, P. Tusnik, B. Vriser, A. Vukovic (1985). Bottom layer anoxia in the central part of the Gulf of Trieste in the late summer of 1983. *Mar. Pollut. Bull.* **16**, 2, 75-78.

Faganeli J., J. Pezdic, B. Ogorelec, M. Mišic, M. Nadjek (1994). The origin of sedimentary organic matter in the Adriatic. *Cont. Shelf Res.* **14**, 4, 365-384.

Franco P., L. Jeftic, P. Malanotte-Rizzoli, A. Michelato, M. Orlic (1982). Descriptive model of the Northern Adriatic Sea. *Oceanologica Acta* **5**, 3, 379-389.

Frascari F., M. Frignani, S. Guerzoni, M. Ravaioli (1988). Sediments and pollution in the northern Adriatic Sea, in: *Living in a chemical world: occupational and environmental significance of industrial carcinogens,* Annals New York Acad. Sci. **534**, 1000-1020.

Giordani P., D.E. Hammond, W.M. Berelson, G. Montanari, R. Poletti, A. Milandri, M. Frignani, L. Langone, M. Ravaioli, G. Rovatti, E. Rabbi (1992). Benthic fluxes and nutrient budgets for sediments in the Northern Adriatic Sea: burial and recycling efficiencies, in: *Science of the total environment,* edited by R.A. Vollenweider *et al.*, supplement Marine Coastal Eutrophication, Elsevier Science Publishers B.V., Amsterdam, 251-275.

Giordani P., S. Miserocchi, V. Baldoni, L. Moodley, M. Frignani, L. Langone (1994). Fluxes of particles and nutrients at the benthic boundary layer, in: *First workshop of the Mediterranean targeted project,* edited by M. Canals and E. Lipiatou, Barcelona, 157-163.

Grasshoff K., M. Erhardt, K. Kremling eds. (1983). Methods of seawater analyses. Verlag Chimie, Weinheim.

Graf G. (1992). Benthic-pelagic coupling: a benthic view. *Oceanogr. Mar. Biol. Annu. Rev.*, 30, 149-190.

Heip C., R. Herman, M. Vincx (1983). Subtidal meiofauna of the North Sea: a review. *Biol. Jb Dodonaea* **51**, 116-170.

Herbert R.A., A. Donnelly, C. Heip, L. Moodley, G. Honsell, P. Poniz, A. Malaguti (1995). Effect of physico-chemical gradients on biological processes in shallow coastal waters on the northern Adriatic, in: *First workshop of the Mediterranean targeted project,* edited by M. Canals and E. Lipiatou, Barcelona, 75-76.

Innamorati M., P. Massi, P. Nuccio, N. Biondi (1994). Spatial distribution and composition of phytoplankton biomass related to environmental factors during STEP '92 and '93 cruises. STEP-CT90-0067 (TSTS) final report, published at Netherlands Institute for Sea Research, Texel.

Jorissen F.J. (1987). The distribution of benthic Foraminifera in the Adriatic Sea. *Marine Micropaleontology* **12**, 21-48.

Josefson A.B. (1990). Increase of benthic biomass in the Skagerrak-Kattegat during the 1970s and 1980s-effects of organic enrichment ? *Mar. Ecol. Prog. Ser.* **66**, 117-130.

Justic D. (1987). Long-term eutrophication of the Northern Adriatic Sea. *Mar. Pollut. Bull.* **18**, 6, 281-284.

Kraay G.W., M. Zapata, M.J.W. Veldhuis (1992). Separation of chlorophylls c_1, c_2 and c_3 of marine phytoplankton by reverse-phased C18 high-performance liquid chromatography. *J. Phycol.* **28**, 708-712.

Marchetti R., N. Verna (1992). Quantification of the phosphorus and nitrogen loads in the minor rivers of the Emilia-Romagna coast (Italy). A methodological study on the use of theoretical coefficients in calculating the loads, in: *Science of the total environment*, edited by R.A. Vollenweider *et al.*, supplement Marine Coastal Eutrophication, Elsevier Science Publishers.

O'Connor B., T. Bowmer, T. McGrath, R. Raine (1986). Energy flow through an *Amphiura filiformis* (Ophiuroidae: Echinodermata) population in Galway Bay, west coast of Ireland: a preliminary investigation. *Ophelia* **26**, 351-357.

Orlic M., M. Gacic, P.E. La Violette (1992). The currents and circulation of the Adriatic Sea. *Oceanologica Acta* **15**, 2, 102-124.

Pearson T.H., R. Rosenberg (1978). Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceangr. Mar. Biol. Ann. Rev.* **16**, 229-311.

van Raaphorst W., H.T. Kloosterhuis, E.M. Berghuis, A.J.M. Gieles, J.F.P. Malschaert, G.J. van Noort (1992). Nitrogen cycling in two types of sediments of the southern North sea. (Frisian Front, Broad Fourteens): field data and mesocosm results. *Neth. J. Sea Res.* **28**, 4, 293-316.

Revelante K., M. Gilmartin (1976). The effect of Po river discharge on phytoplankton dynamics in the Northern Adriatic Sea. *Mar. Biol.* **34**, 259-271.

Rumohr H., T. Brey, S. Ankar (1987). A compilation of biometric conversion factors for benthic invertebrates of the baltic Sea. *Baltic mar. Biol. Publ.* **9**, 1-56.

Sanders H.L., R.R. Hessler (1969). Ecology of the deep-sea benthos. *Science* **163**, 1419-1424.

Schwinghamer, P., B. Hargrave, D. Peer, C. M. Hawkins (1986). Partitioning of production and respiration among size groups of organisms in an interdtidal benthic community. *Mar. Ecol. Prog. Ser.* **31**, 131-142.

Stachowitsch M. (1991). Anoxia in the Northern Adriatic Sea: rapid death, slow recovery, in: *Modern and ancient continental shelf anoxia,* edited by Tyson, R.V. and Pearson, T.H., Geological Society Special Publication **58**, 119-129.

Strickland J.D.H., T.R. Parsons (1972). A practical handbook of seawater analyses, 2nd edn. *J. Fish. Res. Bd Can.* **167**, 1-311.

Thiel H. (1966). Quantitative Untersuchungen über die Fauna des Tiefseebodens. *Veröff. Inst. Meeresforsch. Bremerh. (Sdbd)* **2**, 131-148.

Uhlig G., H. Thiel, J.S. Gray (1973). The quantitative separation of meiofauna. A comparison of methods. *Helgoländer wiss. Meeresunters.* **25**, 173-195.

Vollenweider R.A., R. Marchetti, R. Viviani (1992). Eutrophication, structure and dynamics of a marine coastal system: Results of ten-year monitoring along the Emilia-Romagna coast (Northwest Adriatic Sea), in: *Science of the total environment,* edited by R. A. Vollenweider *et al.,* supplement Marine Coastal Eutrophication, Elsevier Science Publishers B.V., Amsterdam, 63-106.