Spatial distribution in sediment characteristics and benthic activity on the northwestern Black Sea shelf

Jeroen W. M. Wijsman[1,*], Peter M. J. Herman[1], Marian-Traian Gomoiu[2]

[1]Netherlands Institute of Ecology, Centre for Estuarine and Coastal Ecology, PO Box 140, 4400 AC Yerseke, The Netherlands
[2]National Institute of Marine Geology and Geo-ecology, Constanta branch, Mamaia 304, RO-8700 Constanta, Romania

ABSTRACT: The influence of the River Danube as a major source of nutrients and suspended solids to the continental shelf of the Black Sea has been analyzed. In the framework of the EC project EROS-2000, sediment cores from 33 stations on the northwestern continental shelf were sampled in August 1995. Spatial patterns in structural sediment characteristics, macrobenthos composition and benthic mineralization rates were examined using ordination techniques. Three general areas could be distinguished according to the distribution of abiotic sediment characteristics and macrobenthos community: (1) The area just in front of the Danube Delta where large amounts of nutrients and suspended solids are discharged. High sedimentation rates of fine-grained sediments and high benthic mineralization rates characterized this area. The macrobenthos community was dominated by deposit feeders. (2) The northern part of the continental shelf where an anticyclonic gyre is located. The majority of the Danube discharges are transported to this region. This area was characterized by low sedimentation rates. However, the deposited material contained a larger fraction of fresh organic matter compared to the delta area, resulting in high benthic mineralization rates. Suspension feeders dominated the macrobenthos community. (3) The southern part of the continental shelf was characterized by low sedimentation rates and low rates of benthic mineralization. In this area suspension feeders dominated the macrobenthos community. Oxygen fluxes into the sediment ranged between 2 and 52 mmol O_2 m^{-2} d^{-1} (average 21 mmol O_2 m^{-2} d^{-1}) decreasing with water depth. Macrobenthos accounted for 20% of the total benthic oxygen consumption. In the northern part of the continental shelf and in the coastal stations, microorganisms, and micro- and meiobenthos dominated benthic community respiration, while macrobenthos became relatively more important in terms of oxygen consumption in the southern part of the continental shelf.

KEY WORDS: Black Sea · Danube · Macrobenthos · Benthic oxygen flux · Ordination · Benthic-pelagic coupling

INTRODUCTION

The Black Sea is the largest (537 000 km^3) permanently stratified marine basin of the world (Sorokin 1983). A strong pycnocline at 150 to 200 m depth forms a barrier for intermixing between anoxic, hydrogen sulfide containing deep water and oxic, productive surface water (Murray et al. 1989, Kempe et al. 1990, Lyons et al. 1993). The area shallower than 200 m, 27% of the total area, is mainly located in the northwest. The northwestern continental shelf, here defined as

the area shallower than 200 m, north of Varna and west of Sevastopol, covers an area of 70 000 km^2 (Fig. 1). Since the bottom water in the abyssal part of the Black Sea is anoxic, most benthic fauna is restricted to the continental shelf area. Also, many pelagic species depend on the continental shelf for foraging and spawning (Tolmazin 1985a, Niermann et al. 1994).

The ecosystem of the continental shelf is influenced by the major rivers, the Danube, the Dniester and the Dnieper, which together discharge more than 250 km^3 fresh water yr^{-1} in the 3000 km^3 continental shelf (Tolmazin 1985b, Sapozhnikov 1992, Fabry et al. 1993). The River Danube accounts for 75% of the total river input into the northwestern continental shelf of the
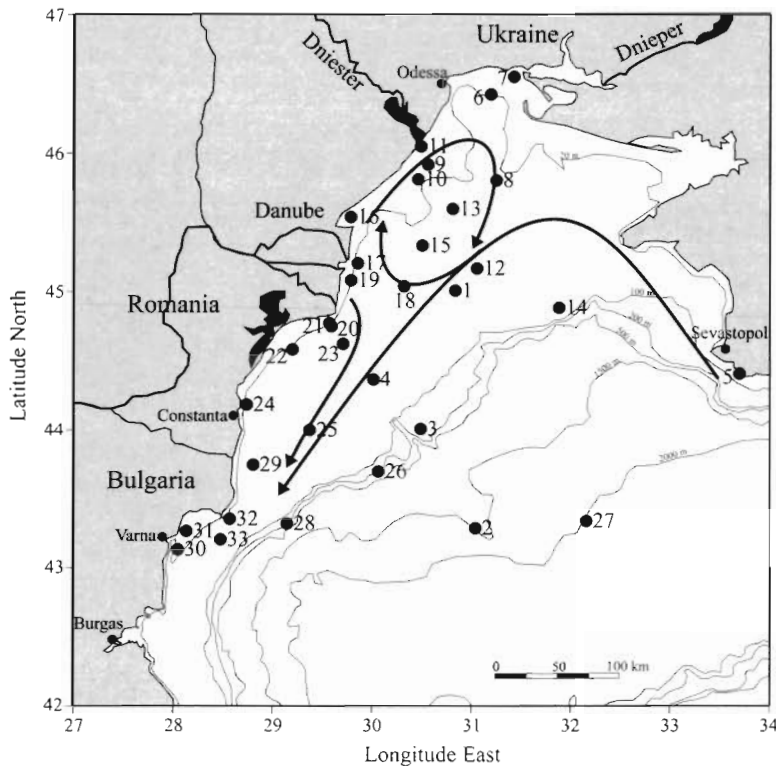
*E-mail: wijsman@cemo.nioo.knaw.nl

Fig. 1. Map of the study area in the northwestern part of the Black Sea with sampling stations. The arrows indicate the general circulation pattern based on the results of a high-resolution hydrodynamic model (M. L. Grégoire & J. M. Beckers pers. comm.)

Black Sea and is a major source of pollutants, nutrients and organic matter (Popa 1993). Each year, the Danube discharges 45 to 50×10^6 t of suspended solids into the Black Sea (Popa 1993). Due to intensification of agricultural and industrial activities in the catchment areas, the input of nutrients and waste products has increased since the 1960s (Konovalov 1995). Construction of dams in the River Danube has changed the nutrient composition of the Danube discharges (Humborg et al. 1997). As a result, the silicate to nitrogen ratio on the continental shelf has decreased, resulting in a shift in phytoplankton community from a diatom dominated phytoplankton community to a community dominated by non-siliceous species, such as coccolithophores and flagellates (Cociasu et al. 1996, Humborg et al. 1997, Mihnea 1997).

During the 1970s and 1980s, the ecosystem of the Black Sea changed significantly at various levels (Gomoiu 1992, Mee 1992, Zaitsev 1993, Bologa et al. 1995, Leppäkoski & Mihnea 1996). Many species disappeared or decreased in biomass, e.g. the macroalgae *Phyllophora* spp., the mussel *Mytilus galloprovincialis* (Zaitsev 1993) and fish species such as sturgeon and turbot (Gomoiu 1985a). Other species increased explo-

sively in biomass, e.g. *Mya arenaria* (bivalve) (Gomoiu 1985b), the flagellate *Noctiluca scintillans* (Porumb 1992) and the jellyfishes *Aurelia aurita* (Gomoiu 1980) and *Mnemiopsis leidyi* (Mutlu et al. 1994).

It is assumed that these modifications of the ecosystem were essentially caused by changes in nutrient discharges through major rivers, particularly the Danube (Gomoiu 1992, Mee 1992, Cociasu et al. 1996, Humborg et al. 1997). The majority of the Danube output is transported to the north, where it forms an anticyclonic gyre (Oguz & Malanotte-Rizzoli 1996, Grégoire et al. 1997, Grégoire et al. 1999). From there the water is transported southward over the continental shelf (M. L. Grégoire & J. M. Beckers pers. comm.). During the transportation, the composition of the watermass changes due to physical and biological processes. Sedimentation is a function of water column characteristics such as turbidity, current velocity and primary production. Sedimentation processes are reflected in the physico-chemical characteristics of the sediment such as grain-size distribution, organic carbon content, C/N ratio and iron concentration. Fluxes from the water column to the sediment also influence early diagenetic processes (Henrichs 1992) and biomass of the macrobenthos (Rowe et al. 1991). Changes in the benthic community during a process of eutrophication (Pearson & Rosenberg 1978, Weston 1990, Heip et al. 1995) show the sensitivity of the benthos to sedimentation, but since most interactions are complex and non-linear, the results are not always predictable. We hypothesize that if rivers can have such an impact on the ecosystem, the effect of the largest river, the Danube, must be visible in the spatial distribution of the biotic and abiotic sediment characteristics on the shelf.

In the framework of the EC project EROS-2000, the relationship between increased input of nutrients through the rivers and changes that occurred in the ecosystem of the Black Sea has been analyzed. The present paper focuses on the benthic part of the system. Structural sediment characteristics such as grain size and porosity that are indicative for the sedimentation regime and solid-phase constituents that are related to mineralization processes have been determined. The oxygen flux to the sediment has been measured as an estimation of the rate of benthic mineralization (Pamatmat 1971, Heip et al. 1995), and the contribution of macrobenthos in total sediment respira-

tion has been calculated. Spatial variations in biogeochemical characteristics were compared with the distribution of macrobenthos in order to identify common patterns. These distribution patterns have been related to the geographic location of the plume of the Danube.

MATERIAL AND METHODS

Sampling sites. From 5 to 27 August 1995, 33 stations were sampled on the northwest continental shelf on the 48th cruise of the RV 'Professor Vodyanitsky' (Table 1). The weather was calm and relatively constant during this period. From CTD profiles, a seasonal temperature stratification of the upper water layers could be detected at all stations. Sediment was sampled with a Reineck box corer ($60 \times 30 \times 30$ cm) at all stations, except Stns 21 and 27 where only water samples were taken.

Sediment parameters. Sediment cores from Stns 1–6, 11, 12, 14, 16–20, 22–26 and 28–31 were subsampled from the box corer with Plexiglas tubes (5.8 cm i.d., 50 cm length) and closed with silicon stoppers. The cores were sliced at several depth intervals: 0–0.5; 0.5–1; 1–1.5; 1.5–2; 2–3; 3–4; 4–5; 5–7; 7–9; 9–11; 14–16 and 19–21 cm. The sediment was stored frozen in 50 ml polycarbonate vials. Within 2 mo after sampling, the samples were dried by lyophylization. Water content was calculated from weight loss, and porosity was calculated from water content, assuming a sediment density of 2.55 g cm^{-3}. The shell fraction was separated from the sediment by sieving over a 0.6 mm sieve. The CaCO$_3$ content of the remaining sediment was determined through volumetric gas analysis after acidification of 0.4 g dry sediment with 10 ml hydrochloric acid (8 N) (Scheibler method). Total carbonate concentration was defined as the sum of the dispersed CaCO$_3$ content of the sediment and the shell remains of bivalves. It was assumed that the bivalve shell residues were mainly composed of carbonate. Total Fe and total Mn were determined with a Perkin Elmer atomic absorption spectrometer, and total P was determined by using spectrophotometry after microwave extraction with hydrochloric acid (12 N) and nitric acid (14 N) (Nieuwenhuize et al. 1991). Total iron content was expressed on a carbonate free basis {[g Fe/(g dry sediment – g CaCO$_3$ – g shells)] $\times$ 100%}. By correcting for carbonate content of the sediment, the iron content is made independent of dilution by CaCO$_3$. Organic carbon and total nitrogen were determined with a Carlo Erba NA 1500 elemental analyzer, after in situ hydrochloric acid (8 N) acidification to remove inorganic carbon (Nieuwenhuize et al. 1994). Grain-size distributions were determined using laser diffraction with a Malvern particle sizer (300 mm focal length) after removal of the organic matter and carbonates with peroxide (10 N) and hydrochloric acid (1 N).

Sediment community oxygen consumption (SCOC). SCOC was measured at Stns 1, 3–6, 11, 12, 14, 16–20, 22–26 and 28–30. Two Plexiglas core tubes (10.3 cm i.d., 30 cm length) were used to measure SCOC. Directly after retrieving the box corer, the cores were gently pushed 15 cm into the sediment and closed with a lid. In general, 10 to 20 cm of bottom water was still present on top of the sediment during sub-sampling. Only at Stns 6, 22 and 29 did the box corer not contain enough bottom water. At these stations, bottom water, sampled by the GO-FLO rosette bottles, was added gently on top of the sediment with a siphon. Within 30 min after retrieval, the cores were sealed with Plexiglas lids with O-rings, containing a YSI 5739 oxygen electrode and a Teflon coated magnetic stirrer. The cores were incubated in the dark at in situ temperature

Table 1. Location, sampling date and water depth of the sampling stations

Stn	Geographical position Latitude	Longitude	Sampling date (1995)	Water depth (m)
1	45° 00' 23"	30° 49' 55"	06 Aug	57
2	43° 17' 13"	31° 02' 19"	08 Aug	1536
3	44° 00' 23"	30° 29' 06"	09 Aug	134
4	44° 21' 55"	30° 00' 32"	10 Aug	69
5	44° 24' 24"	33° 41' 34"	12 Aug	58
6	46° 25' 28"	31° 11' 15"	13 Aug	20
7	46° 33' 02"	31° 25' 07"	13 Aug	12
8	45° 48' 08"	31° 14' 41"	13 Aug	31
9	45° 55' 04"	30° 33' 24"	14 Aug	17
10	45° 48' 35"	30° 27' 24"	14 Aug	25
11	46° 02' 58"	30° 29' 11"	14 Aug	12
12	45° 10' 01"	31° 02' 60"	15 Aug	53
13	45° 35' 47"	30° 48' 17"	15 Aug	38
14	44° 52' 58"	31° 52' 35"	16 Aug	63
15	45° 19' 57"	30° 29' 59"	17 Aug	37
16	45° 32' 18"	29° 46' 34"	17 Aug	16
17	45° 12' 14"	29° 50' 50"	18 Aug	26
18	45° 02' 19"	30° 18' 56"	18 Aug	45
19	45° 04' 53"	29° 46' 53"	19 Aug	21
20	44° 44' 57"	29° 34' 56"	19 Aug	25
21	44° 46' 17"	29° 33' 40"	20 Aug	8
22	44° 34' 56"	29° 11' 23"	20 Aug	27
23	44° 37' 20"	29° 42' 03"	20 Aug	49
24	44° 10' 59"	28° 43' 54"	21 Aug	27
25	43° 59' 57"	29° 21' 54"	22 Aug	56
26	43° 41' 50"	30° 03' 30"	22 Aug	141
27	43° 20' 21"	32° 09' 15"	23 Aug	1997
28	43° 19' 14"	29° 08' 21"	24 Aug	123
29	43° 44' 49"	28° 47' 51"	24 Aug	51
30	43° 07' 59"	28° 02' 39"	25 Aug	20
31	43° 15' 57"	28° 07' 47"	25 Aug	24
32	43° 21' 16"	28° 33' 58"	25 Aug	50
33	43° 12' 18"	28° 28' 24"	26 Aug	64

in a thermostated bath for 4 to 8 h. A magnetic stirrer mixed the bottom water continuously without visual disturbance of the sediment. Oxygen concentration and temperature of the overlying water were measured every 20 s and stored on a datalogger. The electrodes were calibrated with filtered seawater at various oxygen concentrations using Winkler titration (Parsons et al. 1984). Oxygen flux was determined using linear regression from the moment that *in situ* temperature was reached (after 1 to 1.5 h). Enclosed incubations change the solute concentrations in the overlying water (Devol & Christensen 1993, Duineveld et al. 1997a). Therefore, long time incubations change the concentration gradients and may, thus, influence the fluxes. To avoid this artifact only the initial, linear part of the curve was used to calculate the flux. A correction was applied for oxygen consumption by the probe and the bottom water through incubating non-filtered bottom water without sediment. On average this correction was 1.4 mmol O_2 m^{-2} d^{-1} (15 cm water column). All stations were sampled in duplicate from the same box corer, except Stns 1, 12, 16, 20 and 24 where only single cores could be incubated. After incubation, the cores from the incubators were sectioned into 2 cm slices and preserved in formaldehyde for macrobenthos analysis.

Macrobenthos. Macrobenthos was sampled at 30 stations on the continental shelf. At these stations, 8.6 cm i.d. cores were taken from the box corer down to 10–12 cm depth. On board, the samples were stained with Congo Red and preserved in buffered formaldehyde (4%). In the laboratory, the samples were washed through 1.0, 0.25 and 0.125 mm mesh sieves. Macrobenthic animals were identified and wet weight, including shells, was determined. Biomass was converted to g ash-free dry weight (AFDW) m^{-2} using conversion factors of Rumohr et al. (1987). For this study, only species larger than 1 mm were enumerated. Heterogeneity (Peet 1974) was calculated as Hill's diversity numbers (Hill 1973) of order 0, 1, 2 and ∞. $N_0 = S$; $N_1 = \exp[-\Sigma p_i \ln(p_i)]$; $N_2 = 1/\Sigma(p_i^2)$; $N_\infty = 1/p_1$, where p_i ($i = 1, 2, ..., S$) = relative abundance of the ith most dominant species (Heip et al. 1988, Soetaert et al. 1991).

Statistical analysis of data. The relationship between the sediment characteristics was investigated using Principal Components Analysis (PCA) (Jongman et al. 1987). The ordination was performed with the Systat-package on the correlation matrix of the variables using the varimax rotation. The data presented in Table 2, with addition of the sediment community oxygen consumption (SCOC), were used for the PCA. A complete set of data was available for 21 stations.

Correspondence Analysis (CA) was applied on the species abundance matrix using the software package CANOCO (Ter Braak 1988, 1990). Stn 28 was excluded from the analysis since only 2 species were found at this station: the cnidarian *Pachycerianthus imperator* and the polychaete *Heteromastus filiformis*. The hydrozoan *Obelia longissima* and the polychaete *Perinereis*

Table 2. Sediment characteristics averaged over the top 21 cm

Stn	Porosity (cm^3 cm^{-3})	Med. grain size (µm)	Silt < 63 µm (%)	$CaCO_3$ (%)[a]	Shells (%)[b]	Org. C (%)[a]	Total N (%)[a]	C/N ratio (mol mol^{-1})	Total Fe (%)[c]	Total Mn (‰)[a]	Total P (‰)[a]
1	0.79	15.67	99.38	42.97	44.73	2.71	0.31	10.25	3.45	0.71	0.80
2	0.89	18.59	99.97	59.70	0.00	4.69	0.36	15.36	4.02	0.38	0.65
3	0.75	10.23	93.40	34.64	11.47	1.38	0.13	12.25	3.42	0.38	0.57
4	0.79	9.35	99.81	40.89	40.14	2.64	0.28	11.00	4.60	0.91	0.87
5	0.64	9.50	95.28	15.88	1.81	1.01	0.11	10.77	3.79	0.37	0.71
6	0.87	19.81	99.88	10.75	1.67	3.36	0.41	9.59	3.39	0.60	0.74
11	0.67	19.84	86.21	9.78	1.93	0.89	0.09	11.29	1.93	0.47	0.54
12	0.71	21.37	96.04	50.32	68.65	3.03	0.33	10.69	2.80	0.84	0.74
14	0.79	9.50	99.98	24.49	37.58	2.84	0.32	10.31	4.13	0.90	0.72
16	0.81	11.32	99.98	11.91	0.19	2.00	0.23	9.94	3.70	0.58	0.78
17	0.82	9.67	99.93	9.46	0.70	2.01	0.24	9.73	3.80	0.57	0.85
18	0.70	6.64	94.11	27.19	47.71	1.82	0.24	8.79	2.94	0.40	0.53
19	0.74	12.22	99.04	9.88	0.00	1.88	0.19	11.25	3.94	0.77	1.20
20	0.74	11.78	98.88	11.08	0.00	1.40	0.17	9.88	3.61	0.70	0.94
22	0.76	11.22	99.87	9.29	1.24	1.58	0.18	10.45	3.94	0.63	0.75
23	0.63	7.80	79.79	17.30	25.40	0.94	0.12	9.25	2.25	0.25	0.37
24	0.54	34.89	62.14	10.96	33.42	0.51	0.05	11.35	2.01	0.31	0.42
25	0.63	58.09	51.54	13.26	38.61	1.26	0.14	10.51	1.34	0.21	0.27
26	0.62	70.89	45.97	28.97	29.05	0.82	0.09	10.86	1.38	0.22	0.52
28	0.77	9.95	99.99	41.87	44.44	3.21	0.33	11.37	3.82	1.75	0.59
29	0.67	10.62	92.01	31.28	22.93	0.87	0.11	9.39	2.96	0.34	0.37
30	0.54	57.99	54.44	10.20	0.94	0.33	0.04	8.80	1.89	0.32	0.61
31	0.83	10.01	99.86	9.95	0.01	2.51	0.31	9.45	4.08	0.69	0.91

[a]Shell-free dry weight basis, [b]dry weight basis, [c]carbonate-free dry weight basis

cultrifera were given zero weight since they were only found in high densities at Stns 13 and 15 and were absent at all other stations. All data were log-transformed and sample scores were scaled as weighed mean species scores. The axes of the CA were related to site-specific environmental variables as summarized through the first 3 axes of the PCA, water depth and O_2 flux into the sediment by means of indirect gradient analysis (Jongman et al. 1987). For Stns 7, 8, 9, 10, 13, 15, 32 and 33, no solid-phase data were available and at Stn 31, no oxygen flux was measured.

All contour plots were computer generated using kriging gridding algorithm. The contour maps were restricted between the 0 and 200 m isobaths, west of 32° longitude, south of Stn 6 and north of Stn 30. If data for Stns 2 and 5 were present, the value was visualized in a small rectangle.

RESULTS

Abiotic sediment characteristics

Table 2 summarizes the results of the sediment analysis. Since we were interested in spatial distribution rather than depth profiles, each variable was inte-

grated over the first 21 cm in the sediment, the zone in which most early diagenetic processes take place. The same analysis over the depth ranges 0–1 and 0–5 cm gave comparable results. Median grain sizes on the continental shelf varied between 6.6 μm at Stn 18 and 70.9 μm at Stn 26. The average grain size was 19.9 μm. Very fine-grained sediments, with a silt fraction (<64 μm) of more than 90%, were observed seaward of the Danube Delta and in the northern part of the continental shelf (Fig. 2A). The sediment became coarser grained south of the Danube Delta (Stns 24, 25 and 26) with median grain sizes of 35, 58 and 71 μm, respectively, probably as a result of higher current velocities in this area. Generally, the total carbonate content of the sediment increased with water depth (Fig. 2B), with lowest concentrations in front of the river mouths. Highest concentrations were found at the bivalve dominated, central part of the continental shelf, with carbonate concentrations up to 84% of the sediment dry weight. In general, the concentration of iron (Fig. 2C) was negatively related to the median grain size. Especially at the coarse-grained Stns 24, 25 and 26 the measured iron concentrations were low. Iron concentration in front of the Danube Delta was higher than in front of the rivers Dnieper and Dniester. The C/N ratio is low in the Danube prodelta and in the southern part
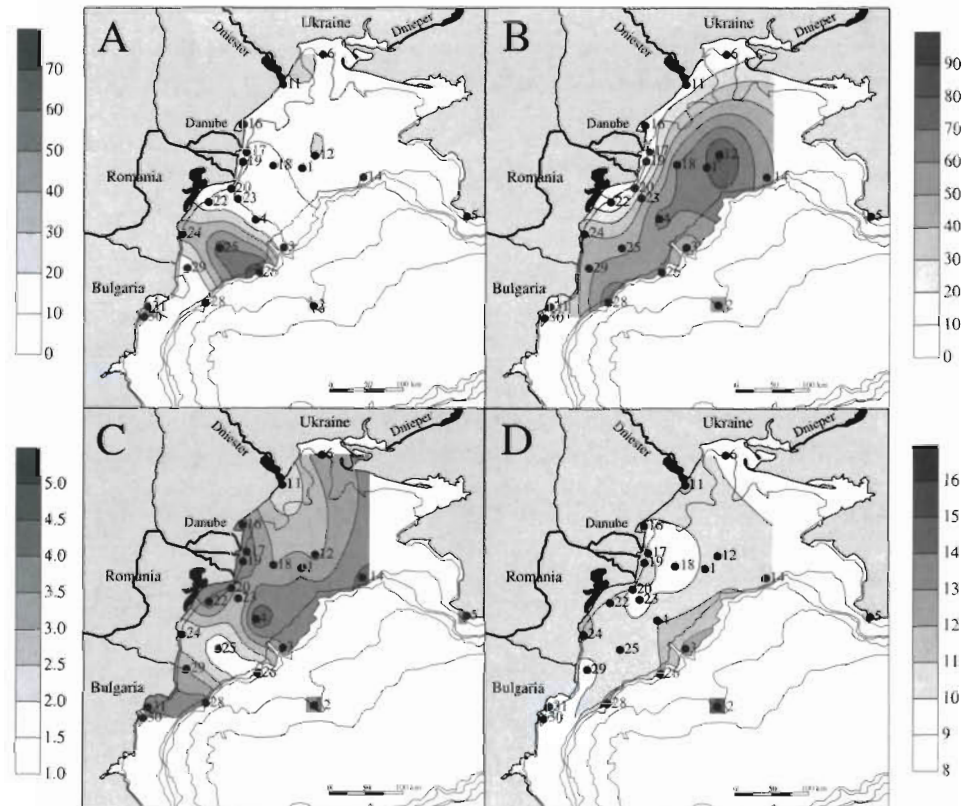

Fig. 2. Spatial distribution of (A) median grain size (μm), (B) total carbonate content (%), (C) iron content on a carbonate-free basis (%, see 'Material and methods') and (D) molar C/N ratio (–) on the continental shelf. Only the stations for which specific data were available are indicated
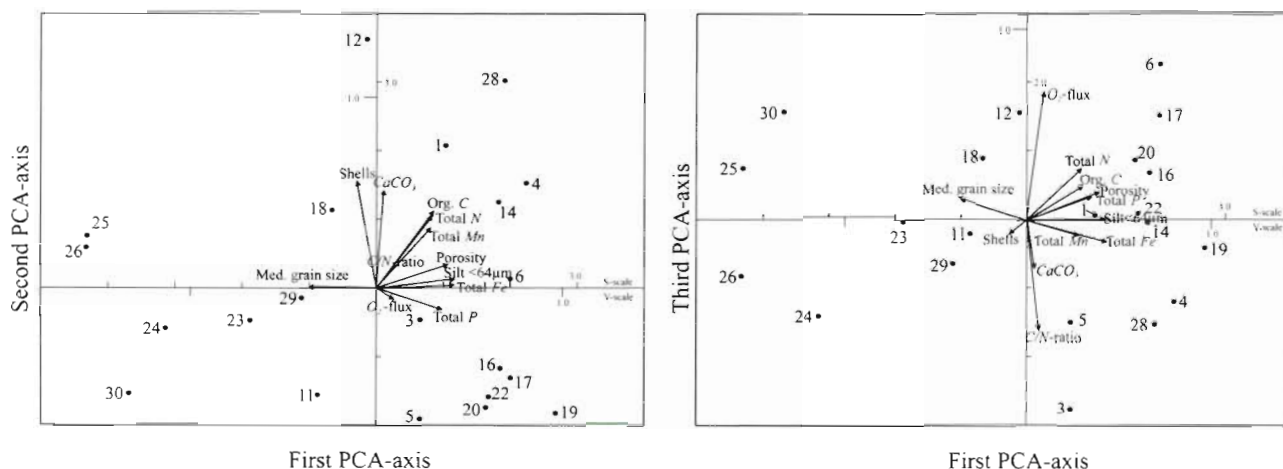
Fig. 3. Euclidean distance bi-plots of the sampling stations (•) and the abiotic sediment characteristics (——→) along the first 3 principal components. Note the different scale for sampling sites (S-scale) and variables (V-scale)

of the continental shelf (Stns 29, 30 and 31; Fig. 2D). The station in front of the River Dniester had a higher C/N ratio than the stations in front of the rivers Danube and Dnieper. In general, the C/N ratio increased with water depth, with the highest C/N ratio at Stn 2 located in the abyssal part of the Black Sea.

The first 3 principal components explained 43.5, 22.5 and 13.3 % respectively of the total variance in the data (Fig. 3). The first principal component ($\lambda_1 = 5.22$) was mainly related to sediment texture. Median grain size was, as expected, inversely related with porosity and silt fraction. Coarse-grained sediments were generally poor in total iron, manganese and phosphorus. This is probably related to the decreasing number of potential binding sites with increasing grain size. The second principal component ($\lambda_2 = 2.70$) was associated with carbonate parameters (shells and $CaCO_3$) and the third principal component ($\lambda_3 = 1.59$) was positively related to the oxygen flux to the sediment and negatively related to the C/N ratio. This confirms the notion that low C/N ratios indicate more labile organic matter and may therefore lead to higher rates of mineralization and higher oxygen fluxes.

The first principal component clearly separated the stations located on the southern part of the continental shelf (Stns 23, 24, 25, 26, 29 and 30) from the other stations. These coarse-grained sediments were relatively low in organic carbon and total nitrogen. Low carbonate contents were observed at the fine-grained sediments in front of the Danube Delta (Stns 16, 17, 19, 20 and 22). Highest carbonate contents were observed at bivalve-dominated stations on the central continental shelf (Stns 1, 4, 12, 14 and 18) and at Stn 28, located at the oxic-anoxic interface. The stations in front of the rivers Dniester and Dnieper (Stns 11 and 6, respectively) showed no clear similarity with the stations in

front of the Danube Delta. They were slightly coarser grained and Stn 6 had a higher organic carbon concentration (3.4 %) than the stations in front of the Danube Delta. Stn 11, in front of the Dniester River, had a low concentration of total iron compared to the stations in front of the Danube Delta. The 3 stations located near the oxic-anoxic interface (Stns 3, 26 and 28) showed no similarity in their biogeochemical characteristics.

Sediment community oxygen consumption

The average SCOC was 21.4 (SD 13.4) mmol O_2 m^{-2} d^{-1}. The difference between duplicate measurements averaged 24 % of the mean. The spatial distribution on the continental shelf is shown in Fig. 4. Highest rates were measured at the coastal stations and at Stn 12 on the continental shelf. Despite the absence of data in the relatively large area between Stns 6, 11 and 12, the algorithm interpolates between those stations. The average flux at the stations in the vicinity of the 3 major rivers (Stns 6, 11, 16, 17, 19, 20, and 22) was 32.1 (SD 5.6) mmol O_2 m^{-2} d^{-1}, which was significantly higher (t-test, p < 0.01) than the average flux at the other stations (16.1 [SD 13.0] mmol O_2 m^{-2} d^{-1}). The high flux at Stn 30 may have been caused by the influence of the harbor of Varna. The highest oxygen flux was recorded at Stn 12 (51.6 mmol O_2 m^{-2} d^{-1}). This station was dominated by the bivalves *Modiolus phaseolinus* and *Mytilus galloprovincialis* with a total biomass of 13 g AFDW m^{-2}. Lowest fluxes were measured at stations with low oxygen concentrations in the near bottom water, located at the oxic-anoxic interface (Stns 3, 26 and 28). Macrobenthos biomass was extremely low at these stations (0 to 0.01 g AFDW m^{-2}).
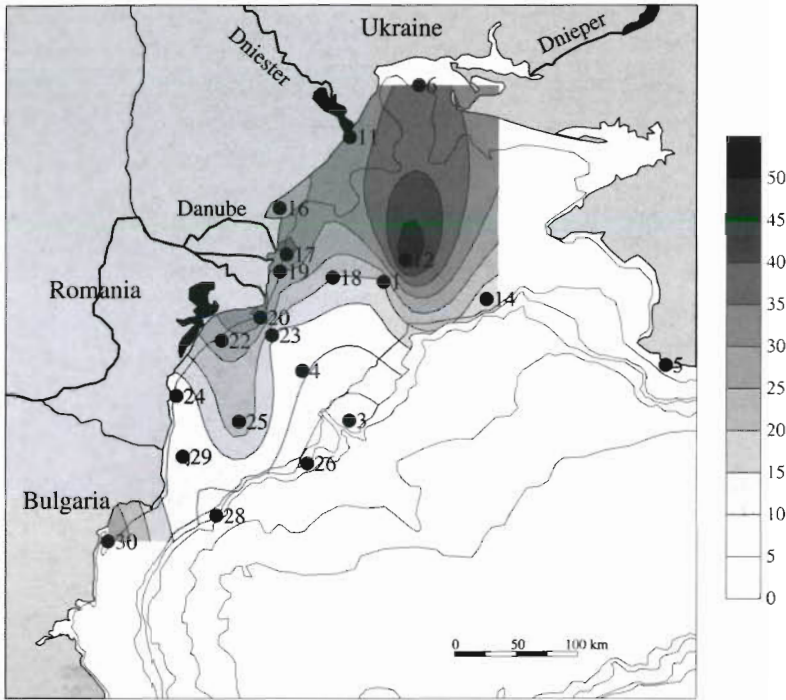
Fig. 4. Spatial distribution of sediment community oxygen consumption (SCOC) (mmol O_2 m^{-2} d^{-1}) on the continental shelf measured using deck incubation. (●) Stations where SCOC was measured
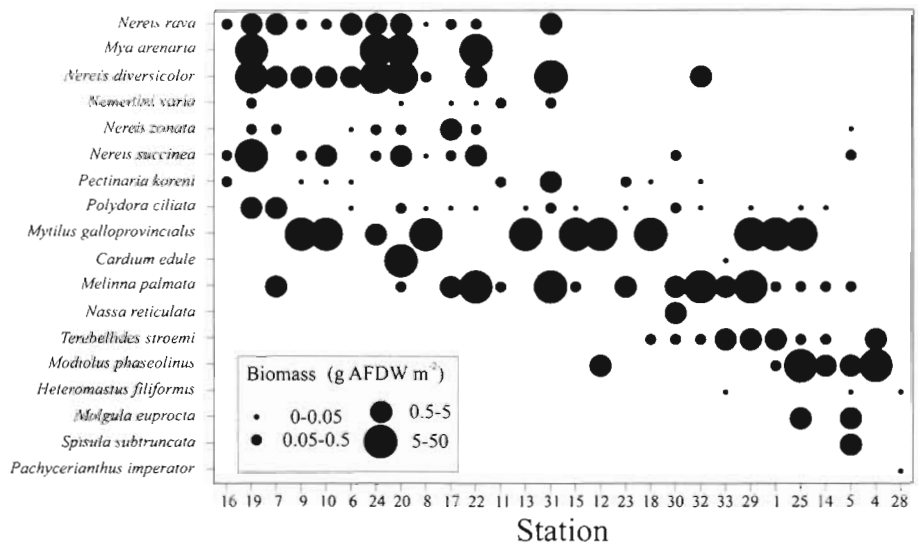
Macrobenthos

A total of 73 macrobenthos species (>1 mm) were identified. Dominant species were defined as species that account for more than 10% of the total AFDW at, at least, 1 station on the continental shelf. A total of 18 dominant species were distinguished (Fig. 5). The polychaetes *Polydora ciliata* and *Melinna palmata*

were most widely spread and found at 16 of the 30 stations on the continental shelf. The total macrobenthos biomass ranged from 0 g AFDW m^{-2} at Stns 3 and 26 to 31.9 g AFDW m^{-2} at Stn 29, which was dominated by the bivalve *Mytilus galloprovincialis*. On average, the macrobenthos biomass was 11.8 (SD 9.8) g AFDW m^{-2}. The average total density was 2520 (SD 3320) ind. m^{-2} Highest densities were found at Stn 19 in front of the Danube Delta with 18000 ind. m^{-2}. At the stations on the continental margin, the macrobenthos density was low (Stn 28) or zero (Stns 3 and 26). At Stn 28, only the polychaete *Heteromastus filiformis* (79 ind. m^{-2}) and the cnidarian *Pachycerianthus imperator* (158 ind. m^{-2}) were found. Species heterogeneity expressed as N_1 was highest at Stn 5 (N_1 = 16.6). Lowest diversity was recorded at Stns 8 and 28 (N_1 = 1.24 and 1.89 respectively). N_1 correlated strongly with N_2 (r = 0.97) but less with N_0 (r = 0.81) and N_∞ (r = 0.84).

The first 3 axes of the correspondence analysis explained 31.5% of the total variation in the species data (Fig. 6). The first axis (λ_1 = 0.60) was mainly related to water depth. The shallow coastal stations were dominated by the Nereidae species (*Nereis diversicolor, N. rava, N. succinea* and *N. zonata*) while the bivalve *Modiolus phaseolinus* and the polychaete *Terebellides stroemi* dominated the deeper stations. The second axis (λ_2 = 0.44) was indicative for Stn 30 (characterized by the gastropod *Nassa reticulata*) and Stn 5

Fig. 5. Distribution of the dominant macrobenthic species on the continental shelf. The biomass (g ash-free dry weight [AFDW] m^{-2}) is classified into 4 size groups as indicated by the size of the marker. Dominant species were defined as species that account for more than 10% of the total macrobenthos biomass (g AFDW m^{-2}) at, at least, 1 station. Both stations and species were ordered according to their location on the first CA-axis
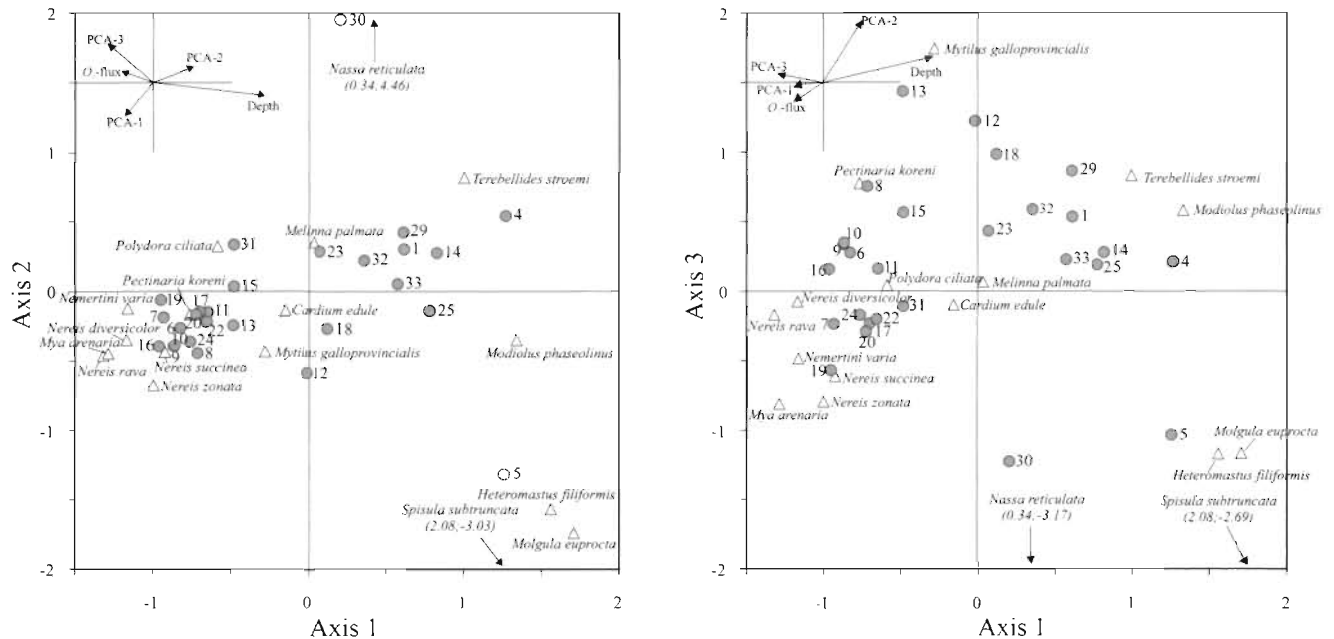
Fig. 6. Correspondence Analysis (CA) ordination diagrams of the macrobenthos data on the first 3 CA-axes. (●) Site scores, (Δ) species scores. Only the dominant macrobenthos species (>10% of the total biomass [g AFDW m^{-2}] at, at least, 1 station) on the continental shelf are plotted. The insets in the upper left corners show the vectors of some environmental variables. PCA-1, PCA-2 and PCA-3: first 3 axes of the PCA (Principal Components Analysis), Depth: water depth and O$_2$-flux: oxygen flux into the sediment. Stn 28 was excluded from the CA-ordination (see 'Material and methods')

(characterized by the bivalve *Spisula subtruncata*). The higher value of Stn 31 on the second axis compared to the other shallow water stations might be related to a different macrobenthos composition due to its southern geographical position. The third axis ($\lambda_3 = 0.39$) separated the stations on the northern part of the continental shelf (Stns 8, 9, 10, 13 and 15) from the stations in front of the river mouths. This division was mainly based on the absence of the bivalve *Mytilus galloprovincialis* at the stations in front of the major rivers that were characterized by fine-grained sediments (indicated by a high value of PCA-1). Although no abiotic data for the stations from cluster I (Stns 8, 9, 10, 13 and 15) were available, the relation with PCA-1 suggests that the sediments at these stations were relatively fine grained. The low carbonate content at the stations in front of the major rivers is reflected in the low value of the second principal component (PCA-2), which was mainly related to the third CA-axis.

DISCUSSION

Impact of the River Danube

Dissolved and particulate material input through large rivers has a substantial influence on both the qualitative and quantitative sedimentary regime in adjacent continental shelf systems. Rhoads et al. (1985) have developed a general model for sedimentary shelf processes related to discharges of effluents of larger rivers (Fig. 7). In general, they distinguished 3 areas: the delta area, the plume area and the shelf area outside the river influence. In the delta area the primary production is light limited due to high concentrations of suspended solids discharged through the river. Sediment deposition rates are generally high and, as a result, the labile algal material deposited on the seabed is diluted by large amounts of terrigenous material (Aller & Aller 1986). In the eutrophic plume area primary production increases due to increased visibility. Labile marine bioseston becomes a more important component of the organic matter flux to the benthos and can support a high standing stock of benthic populations. In the oligotrophic outer shelf region the primary production is nutrient limited. The carbon flux to the sediment is very low and therefore the benthic standing stock is reduced in this area (Rhoads et al. 1985, Rowe et al. 1991). The dimensions and locations of these different areas depend on both the river properties (amount of freshwater discharge, the concentration and composition of the nutrients and the amount and type of suspended solids) and the properties of the adjacent continental shelf (hydrodynamics, morphology).
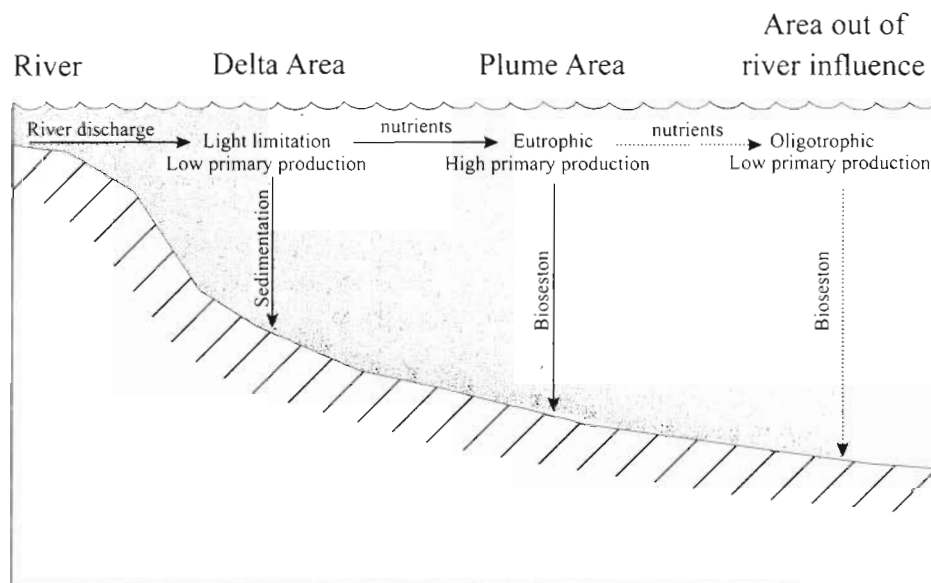
Fig. 7. Generalized model for influence of the discharge of a large river on the sedimentation processes on the shelf. Arrows indicate nutrient transport and sedimentation. Adapted from Rhoads et al. (1985)

In this paper we have attempted to identify the different sedimentological regions on the continental shelf in relation to the River Danube, which is by far the most important river on the continental shelf in terms of freshwater, suspended solids and nutrient discharge into the Black Sea (Popa 1993). Referring to the general current pattern on the continental shelf, we can indicate the 3 different areas. The stations located just in front of the River Danube (Stns 16, 17, 19, 20 and 22) are directly influenced by the Danube discharges and can be identified as the 'Delta' stations. The water is turbid in this area (Krustalev et al. 1990) with relatively high rates of sedimentation. From ^{137}Cs data at a station just in front of the Danube Delta (Curtis & Broadway 1992) the sedimentation has been estimated at 0.7 cm yr^{-1}. From here, the majority of the Danube water is transported north to the anticyclonic gyre (M. L. Grégoire & J. M. Beckers pers. comm., based on results of a high-resolution hydrodynamic model). Though the exact location of this gyre is dependent on wind patterns, it is very robust and generally located northwest of the mouth of the Danube (Stns 1, 8, 12, 13, 15 and 18). During the transportation, which takes about 2 wk, the concentration of suspended solids in the water column decreases (Krustalev et al. 1990), resulting in a higher light-penetration depth. It can be expected that this will lead to a higher primary production in this area, and, therefore, this area can be characterized as the 'eutrophic' area. From the gyre, the water is transported southward over the continental shelf along the Romanian shore towards Bulgaria. The decreased nutrient concentrations in the water column will reduce the primary production and, therefore, this area can be characterized as the 'oligotrophic' area.

The PCA showed that sediments in the Danube Delta area were very fine grained with median grain sizes ranging from 9.7 to 12.2 μm. Since high amounts of organic matter are generally transported by rivers (Ittekkot & Laane 1991), the carbon flux to the sediment is expected to be high in this area. This is also reflected in the relatively high SCOC recorded in this area. The source of the organic matter transported by the Danube can be either allochthonous (terrestrial) or the generally more labile autochthonous material such as river phytoplankton (Mook & Tan 1991). The C/N ratio of fresh terrestrial organic matter is typically higher than organic matter derived from phytoplankton (respectively >12 and 6 to 9) (Thornton & McManus 1994). During the process of aging, the C/N ratio of terrestrial-based detritus will decrease while the C/N ratio of algal-based detritus will increase (Rice & Tenore 1981, Jørgensen 1983). The C/N ratio can be used as a measure for the 'quality' of the organic matter to the benthos (Burdige 1991), but one should be aware of this source effect (Cowie & Hedges 1994). The relatively low C/N ratios in the Danube Delta area were an indication that the organic matter was mainly algal-based detritus. Probably the terrestrially derived material, transported by the river, was trapped in the inner-delta. The slight decrease in C/N ratio towards Stns 16, 17, 18 and 23 indicated that the deposited organic matter became more labile at these stations.

Going to the anticyclonic gyre in the northern part of the continental shelf (i.e. the 'eutrophic' area), the sedimentation rate decreases. However, the oxygen fluxes recorded in this area remained relatively high. At Stn 12, which was dominated by the filter-feeding bivalve Mytilus galloprovincialis, the highest SCOC was measured (52 mmol O$_2$ m^{-2} d^{-1}). This is an indication of a

high flux of labile organic carbon to the sediment in this area. All the stations in this area were high in carbonate content and dominated by *M. galloprovincialis*.

In the southern part of the continental shelf (i.e. the 'oligotrophic' area) the influence of the River Danube is reduced. The sediment became coarser grained and oxygen flux to the sediment decreased, indicating a low flux of labile detritus to the sediment.

The effect of the River Danube was also reflected in the macrobenthos distribution. The low carbonate concentrations recorded in the delta area already suggested that this region was less dominated by bivalves compared to the offshore area. The polychaetes *Nereis diversicolor*, *N. rava* and *N. succinea* and the bivalve *Mya arenaria*, characteristic for the delta area, are adapted to the high rates of sedimentation and corresponding factors such as sediment stability, food supply and larval supply (Snelgrove & Butman 1994). The macrobenthos community of the northern part of the continental shelf, where the anticyclonic gyre is located, was characterized by a high biomass of *Mytilus galloprovincialis*. This confirms the suggestion of a relatively high deposition rate of labile organic matter in this 'eutrophic' area.

Sedimentation and trophic structure

Abiotic environmental characteristics (hydrology and sediment composition) and population dynamics (competition, mortality/predation and reproduction) are the major factors determining the macrobenthos composition in the sediment (Gaston & Nasci 1988, Rosenberg 1995). In this study we were mainly interested in the effects of sedimentation on the macrobenthos community composition. Since feeding type of the macrobenthos community is an adaptation to the sedimentological environment, it can be expected that differences in sedimentation will be reflected in the distribution of the different trophic groups on the shelf.

Macrobenthos was classified into 6 different feeding groups according to Fauchald & Jumars (1979). The biomass of interface feeders and deep deposit feeders was, in general, less than 3% of the total macrobenthos population, except for Stn 7, where interface feeders accounted for 21% of the total biomass. Therefore, interface feeders and deep deposit feeders were grouped together with surface deposit feeders. In Fig. 8 the relative contribution of the different trophic groups to the total macrobenthos bio-
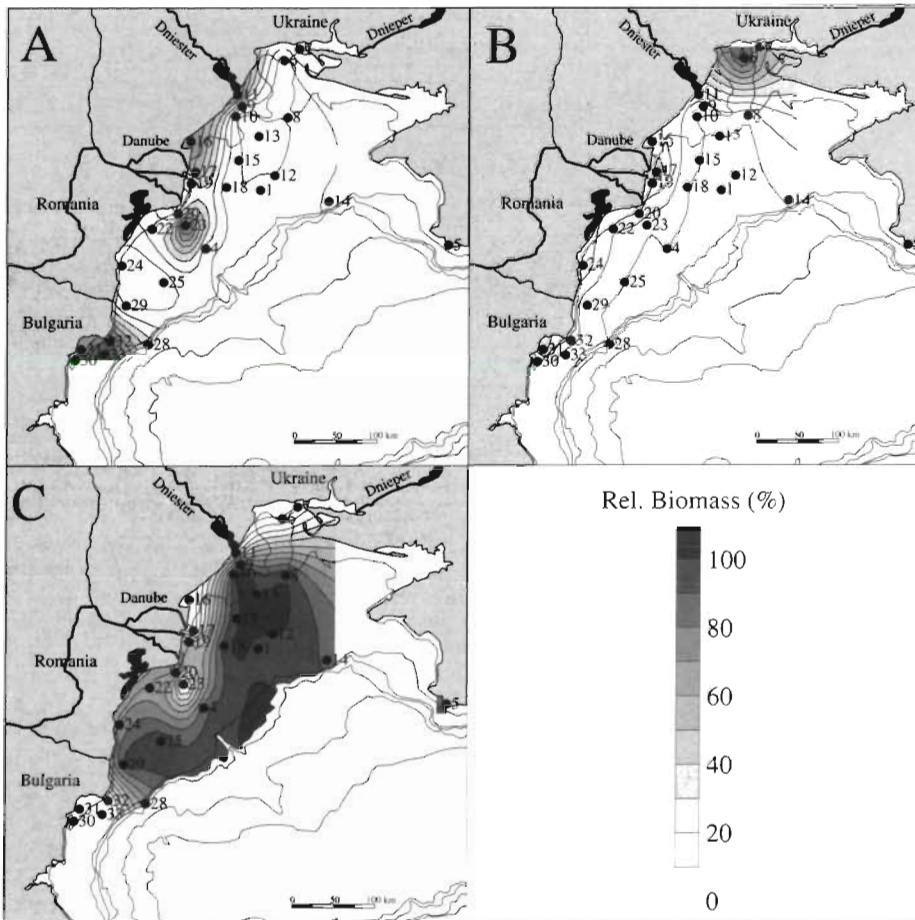

Fig. 8. Relative contribution (%) to the total macrobenthos biomass in the continental shelf of (A) the sum of interface, surface and deep deposit feeders, (B) omnivores/predators and (C) suspension feeders

mass is given. Stns 3, 26 and 28 were neglected in these figures.

Deposit feeders forage on organic matter in the sediment or deposited at the sediment-water interface. The standing stock of bacteria in the sediments is usually too low to supply the total carbon demand of the deposit feeders (Kemp 1987). Therefore, they need an additional (non-living) carbon source. Since deposit feeders subsist on a remarkably poor food source, they depend on high accumulation rates of organic carbon (Pearson & Rosenberg 1978, Lopez & Levinton 1987, Weston 1990). Deposit feeders dominated the macrobenthos biomass in the stations located in front of the river mouths (Stns 11, 16, 17 and 19) and in front of the Bulgarian coast (Stns 30 to 33), where the surface deposit feeder *Melinna palmata* was dominant. Stn 23, where the total biomass was low (2.3 g AFDW m^{-2}), was also dominated by *M. palmata*.

Omnivores and predators are more directed towards their food item, and will, in general, not consume the sediment as a whole as deposit feeders do. This is less energy consuming, but, since they are more selective, the proper food type is, in general, less abundant. Predators and omnivores were, like deposit feeders, abundant at the near-shore stations. This suggests that the carbon flux in this area is high enough to support a substantial density of higher trophic levels. Stns 6 and 7, located in front of the Dnieper river were dominated by *Nereis diversicolor*. This polychaete accounted for 83 and 47%, respectively, of the total macrobenthos biomass at these stations.

Suspension feeders retrieve their food directly from the water column. When the food source in the near bottom water is continuously renewed, suspension feeders can locally increase the flux of organic matter to the sediment (Heip et al. 1995). Suspension feeders are often negatively related to the percentage of mud in the sediment (Eleftheriou & Basford 1989, Aller & Stupakoff 1996). Depending on morphology, the filtering apparatus may be vulnerable to clogging at high concentrations of suspended solids in the near bottom water. The lack of suspension feeders in front of the river mouths may be caused by high concentrations of suspended solids in this area. Both in the northern part (Stns 1, 8, 9, 10, 13, 14, 15 and 18) and in the southern part of the continental shelf (Stns 4, 22, 24, 25 and 29), suspension feeders replace the deposit feeders. At low carbon fluxes it is expected that suspension feeders dominate since they have first access to the sedimenting organic matter (Pearson & Rosenberg 1978, Weston 1990). This might be the case in the southern part of the continental shelf and at the oxic-anoxic interface, but the high SCOC recorded at Stns 1, 12, 18 and 25, however, do not support this idea for the northern part of the continental shelf. The sediments in this sediment

starvation zone consisted of 39 to 69% of shell remains. Apparently deposit feeders in this area have no access to the organic matter between the shell remains.

Macrobenthos oxygen consumption

Only part of the oxygen flux into the sediment is consumed through respiration of macrobenthos. The rest is used by micro- and meiobenthos, microorganisms and chemical re-oxidation of reduced substances. In estuaries the macrobenthos can account for up to 90% of the total SCOC (Heip et al. 1995). Typical values for the part of the SCOC consumed by the macrobenthos reported by various authors are 23% in the northwestern Barents Sea (Piepenburg et al. 1995), 38% in the northwestern Adriatic Sea (Moodley et al. 1998) and 16 to 50% in the Goban Spur area with the lowest values in the lower slope and the abyss (Heip et al. in press).

We used data on individual body mass to assess the oxygen demand of the macrobenthos. Species-dependent allometric relations ($R = aW^b$) are often used to calculate individual respiration rate (R) from the body mass (W) (Banse 1982, Bayne & Newell 1983). It is impossible to retrieve from literature these relations for all Black Sea species. Even if we were able to find these relations for all species, application of the relations in calculating the total respiration rate of the macrobenthos would not be straightforward. For a well-known species, such as the blue mussel (*Mytilus edulis*) for example, the reported estimations of the parameters a and b range from 0.164 to 0.698 and 0.595 to 0.930 respectively, depending on factors such as temperature, feeding, activity, oxygen tension and salinity (Bayne et al. 1976). In this study we used the relation of Mahaut et al. (1995) based on a compilation of shallow water organisms, ranging from bacteria and nematodes to fish.

$$R = 0.0174 \cdot W^{-0.156}$$

where R = weight-specific respiration rate (d^{-1}) and W = individual weight (mg C). Carbon biomass was estimated assuming that 50% of the AFDW was organic carbon. Respiration rates were converted to oxygen consumption (mmol O$_2$ m^{-2} d^{-1}) assuming a respiratory coefficient of 0.85 (Hargrave 1973) and corrected for temperature assuming a Q_{10} value of 2 (Wells 1980, Piepenburg et al. 1995).

It is obvious that a number of uncertainties are involved in the calculation of macrobenthos respiration. Beside errors in sampling and determination of the macrobenthos, there are many assumptions made for the calculation of the respiration rates of the macrobenthos. Conversion factors to AFDW are based on species from the Baltic Sea (Rumohr et al. 1987). The
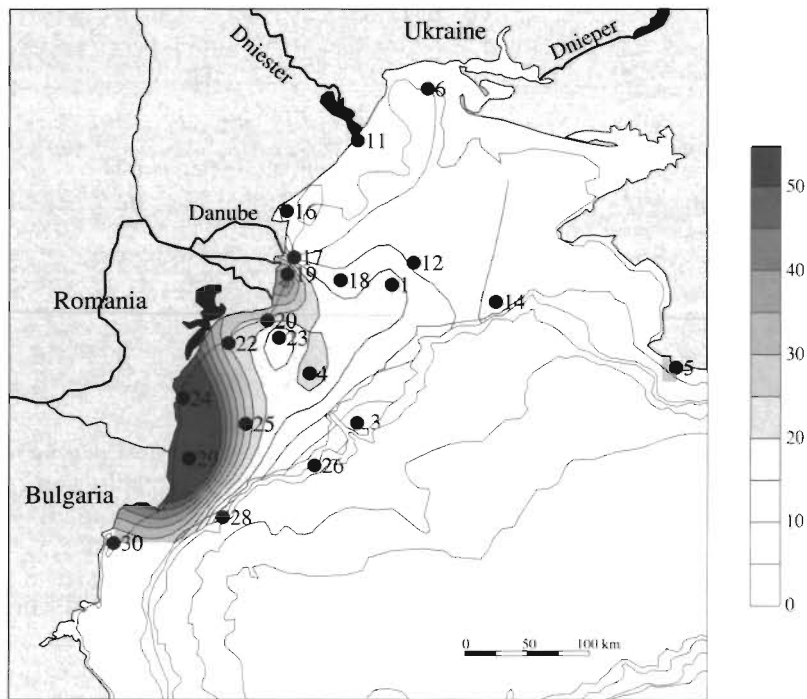
Fig. 9. Spatial distribution of the fraction of the total SCOC (%) consumed by the macrobenthos on the continental shelf

relation of Mahaut et al. (1995) is a compilation of data from a wide range of different species in different marine shallow water environments.

On average, 21% of the total oxygen flux to the sediment at the continental shelf of the Black Sea was consumed by macrobenthos (Fig. 9). From the SCOC, it was concluded that the carbon supply to the sediment in front of the major rivers and in the northern part of the continental shelf was high. High mineralization rates result in anoxic conditions in the sediments, which is unfavorable for many macrobenthos species. Therefore, macrobenthos was not important in terms of oxygen consumption in the northern part of the shelf (Stns 6, 11, 12, 16 and 17) and microorganisms, micro- and meiobenthos became more important. At Stns 19, 20 and 22, where high mineralization rates were also recorded, the contribution of macrobenthos to the total SCOC was higher. This was mainly due to the high biomass of *Mya arenaria*, a bivalve buried deep in the anoxic sediment, that can transport oxygenated water from the water column with its siphons. The lack of burrow-building organisms at the shell-rich stations in the northern part of the continental shelf prevented oxygen to be transported into the deeper sediment layers. The contribution of macrobenthos to the total SCOC was low in these bivalve-dominated sediments. Since micro- and meiobenthos is also dependent on oxygenated sediments, it can be

expected that a large part of the oxygen consumption was due to the (microorganism mediated) re-oxidation of reduced substances in the sediments (Wijsman et al. in press).

South of the Danube Delta the contribution of macrobenthos to the total oxygen consumption increased. At Stns 24 and 29 most of the SCOC was used by the macrobenthos (75 and 89%, respectively). Stn 24 was characterized by a high biomass (14 g AFDW m^{-2}) of large individuals of *Nereis diversicolor*, which accounted for 53% of the total oxygen consumption of the macrobenthos. Stn 29 had a high biomass (26 g AFDW m^{-2}) of *Mytilus galloprovincialis*, accounting for 73% of the oxygen consumption of the macrobenthos.

The importance of the macrobenthos in the total oxygen consumption decreased towards the oxic-anoxic interface. The stations at the oxic-anoxic interface (Stns 26 and 28) had little or no macrobenthos. Frequently occurring upwellings of anoxic water from the deep sea makes this area a harsh environment for macrobenthos (Kempe et al. 1990). Microorganisms, and micro- and meiobenthos probably consume most of the oxygen in this area.

For the Goban Spur area (200 to 4500 m), Soetaert et al. (1997) and Heip et al. (in press) found that the relative importance of smaller organisms, such as bacteria and protozoa, on the total oxygen consumption increased with decreasing carbon flux. This is probably caused by the low turnover rate of these organisms in the sediment. The relative importance of the macrobenthos in the total carbon respiration also decreased with water depth in this area. The absolute amount of organic carbon supply to the sediment in the deep-sea area may not be sufficient for the larger macrobenthos species to occur. In the Goban Spur area, (SCOC = 0.3 to 5.4 mmol O_2 m^{-2} d^{-1}) (Duineveld et al. 1997b), the carbon flux is limiting the benthic community. In the shallow continental shelf of the Black Sea, where the SCOC ranged from 2 to 52 mmol O_2 m^{-2} d^{-1}, the benthic community is likely to be more inhibited by the oxygen conditions in the sediment resulting from the high carbon input.

CONCLUSIONS

The influence of the Danube could be traced back in the biotic and abiotic sediment composition of the con-

tinental shelf of the Black Sea. Fine-grained, carbonate-poor sediments and a high SCOC characterized the delta area. Only a minor part of the oxygen consumption could be attributed to the macrobenthos community, which was dominated by deposit feeders, and predators such as *Nereis* spp. In the northern part of the continental shelf, where the anticyclonic gyre was located, the rate of sedimentation was lower. However, high oxygen fluxes into the sediment were recorded, indicating a high flux of labile organic matter to the sediment. The macrobenthos community in this area, dominated by suspension feeders such as *Mytilus galloprovincialis*, was responsible for only a small fraction of the total SCOC. The southern part of the continental shelf can be characterized as the 'oligotrophic' area. Low oxygen fluxes into the sediment were recorded in these coarse-grained sediments. The scarce organic matter arriving at the sediments in this area is efficiently used by the mostly suspension feeding macrobenthos, accounting for a major part of the SCOC.

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