

Relation between sediment-water fluxes of oxygen and silicate and faunal abundance at continental shelf, slope and deep-water stations in the northwest Mediterranean

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ABSTRACT: Measurements of sediment oxygen demand (SOD), silicate fluxes, benthic macro- and meiofauna and phytopigments were made on continental shelf, slope and deep-water sediments in the northwest Mediterranean in November–December 1991. The mean SOD (\pm SD), measured by onboard incubations of sediment cores with overlying water, was $301 \pm 83 \mu\text{mol m}^{-2} \text{h}^{-1}$ for the shelf stations, $146 \pm 53 \mu\text{mol m}^{-2} \text{h}^{-1}$ for the slope stations, and $44 \pm 10 \mu\text{mol m}^{-2} \text{h}^{-1}$ for the deep-water stations. The SOD values for the slope and deep-water stations are comparable to earlier reported data from open oceanic sites. Considering the limited data set that we present, substantial downslope transport of organic matter at these stations cannot be concluded. Mean silicate effluxes from the sediment, measured in the same incubation experiments, amounted to 52 ± 14 , 48 ± 20 and $16 \mu\text{mol m}^{-2} \text{h}^{-1}$ for shelf, slope and deep-water stations, respectively. Diffusive oxygen and silicate fluxes were calculated from pore-water profiles with Fick's first law of diffusion. The irrigation flux was defined as the difference between incubation and diffusive flux. The oxygen irrigation flux contributed on average $39 \pm 10\%$, $17 \pm 15\%$ and $5 \pm 5\%$ to the oxygen incubation flux for the shelf, slope and deep-water stations, respectively, and showed a strong positive relation with macrofaunal density, illustrating the importance of macrofaunal activities on sediment-water solute exchanges. In contrast to the oxygen irrigation fluxes, the silicate irrigation fluxes showed less distinction between shelf and slope stations and contributed on average $60 \pm 6\%$, $61 \pm 9\%$ and 19% to the silicate incubation fluxes for the shelf, slope and deep-water stations, respectively. The relation between silicate irrigation flux and macrofaunal density was not significant. Another indication for the lack of organic matter transport across the slope was the monotonic decrease of faunal density, biomass and phytopigments with increasing depth. Only at the upper slope station were traces of a past deposition event found. Below this depth phytopigments were below detection level. The absence of phaeopigments in the near-bottom water and their high concentration in the shelf sediments indicated little resuspension of sediment.

KEY WORDS: Mediterranean · Sediment oxygen demand · Silicate fluxes · Infauna · Phytopigments

INTRODUCTION

The bottom of the Gulf of Lions in the NW Mediterranean is characterized by a relatively narrow and shallow continental shelf, connected to the abyssal depths by a steep slope. The slope is intersected by numerous submarine canyons (Got et al. 1985). Despite a widely open south side, the Gulf is rather isolated due to the prevailing hydrographic conditions. The continuous SW surface flow over the slope (Liguro-

Provincial current) entrains the less saline coastal water, admixed with Rhône input, on the shelf (Millot 1987). The water masses in the deep offshore area and in coastal areas are separated by a frontal zone, with a wedge of saline water next to it consisting of upwelled Levantine Intermediate Water (Minas & Minas 1989). According to Cruzado & Velasquez (1989), import of open sea water is mainly confined to the eastern half of the Gulf, whereas a mixture of open sea water and fresh water is exported at the southwest end of the

Gulf. An alternative way for particulate matter from the shelf to reach the offshore area is by means of water cascading down the slope, as has been observed in cold winters (Minas & Minas 1989). Aloisi et al. (1982) and Monaco et al. (1987) reported that particulate organic matter can be transported from the shelf to the slope and the deep sea via a nepheloid bottom layer which is directed offshore by submarine canyons.

During a cruise in November–December 1991 in the Gulf of Lions as part of the EROS 2000 (European River Output System) project, sediment oxygen demand (SOD) was measured at 8 sampling sites in the shelf, upper slope and deep-water areas by means of ship-board incubation of intact sediment cores. In combination with these measurements, the abundance and standing stock of macro- and meiofauna in the incubation cores were analysed, as well as the phytopigment content of the sediment and of the surface and bottom water. All these parameters give information on the availability and, therefore, also on the possible redistribution of organic particles which have sunk from the euphotic production zone.

Since oxygen respiration is the principal mineralization process in the sediments of the Gulf of Lions (Helder 1989b), SOD measurements yield a minimum estimate for carbon flux to the sediment. Oxygen uptake by the microbial community is governed by diffusion of O_2 . This process can be adequately described by modelling pore-water profiles of O_2 (Revsbech et al. 1980, Rasmussen & Jørgensen 1992). Larger fauna, on the other hand, usually have some means to actively ventilate burrows and tubes, giving rise to an irrigation flux. This activity may also enhance the respiration of the microbial community (Aller 1980, Emerson et al. 1985, Aller & Aller 1992, van Duyl et al. 1992). Irrigation fluxes along the transect were calculated by subtracting diffusive fluxes of O_2 and silicate from their (total) incubation fluxes (Kannevorf & Christensen 1986, Archer & Devol 1992, Rasmussen & Jørgensen 1992). Combining these measurements with data on the standing stock of meio- and macrofauna provides insight into the specific activity of the community. Furthermore, because of their relatively long life-span, macro- and meiofauna standing stock can be considered an integrated measure for benthic food input (Schaff et al. 1992). In addition, earlier flux measurements for oxygen in the area of interest in combination with the present ones could shed some light on the seasonal variation of benthic respiration and could provide an estimate for the annual carbon input to the sediment.

Finally, phytopigments in the sediment can, because of their differential stability (Abele-Oeschger 1991), provide insight into recent as well as past deposition events, whereas phytopigment fingerprints of the bottom water can reveal different sources of phytodetritus input.

MATERIALS AND METHODS

Site description. Fig. 1 shows the location of the 8 stations visited during the cruise with the RV 'Tyro' in the Gulf of Lions in November–December 1991. Four of them are situated on the shallow shelf (Stns 12 & 23) and the adjacent upper slope (Stns 14 & 20) of the Gulf of Lions. Two stations (Stns 3 & 19) are located in the deep-water region, and another two on the shallow shelf near the mouth of the Ebro (Stns 29 & 30). Locations, dates of sampling and water depth at the stations are summarized in Table 1.

Box coring. Box cores were taken with a modified Reineck box corer (cylindrical corer of 50 cm diameter), which was equipped with a hydraulically dampened closing lid containing a valve to compensate for pressure effects during retrieval. Visual inspection of the core usually revealed clear overlying water and the presence of microstructures at the sediment surface. Any disturbed cores were rejected. In order to check whether leakage of the overlying water of the box core had occurred during retrieval, silicate concentrations in the overlying water of the box core were compared with those of the deepest CTD bottle (5 m above the sea floor) at each station (see 'Water column' section). Because silicate concentrations in the water column were always increasing with water depth (Helder et al. unpubl.), and silicate concentrations in the overlying box core water were always higher than those of the deepest CTD bottle, displacement or mixing of the original overlying box core water with water of more shallow origin could be excluded.

Sediment grain size, carbon, nitrogen. At every station, small sediment cores (2.5 cm diameter) 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, the upper 5 cm slices of these samples were defrosted, diluted and sieved (63 μm). The fraction <63 μm 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 dry weight. The residual fractions (>63 μm) were too small in volume to subdivide into more categories. The percentages of organic carbon and organic nitrogen in the sediment were determined with a Carlo Erba NA 1500 CN analyser, after sample acidification according to Verardo et al. (1990).

Water column. At all stations, a depth profile of temperature and salinity of the water column was made with a CTD mounted on a rosette sampler. Simultaneously, water samples were taken at specific depths with Niskin bottles for the analysis of nutrients, oxygen (Winkler method) and phytopigments. Water samples for pigment analysis (ca 20 l) were filtered (Whatman GF/F filters, 0.7 μm) and subsequently deep-frozen.

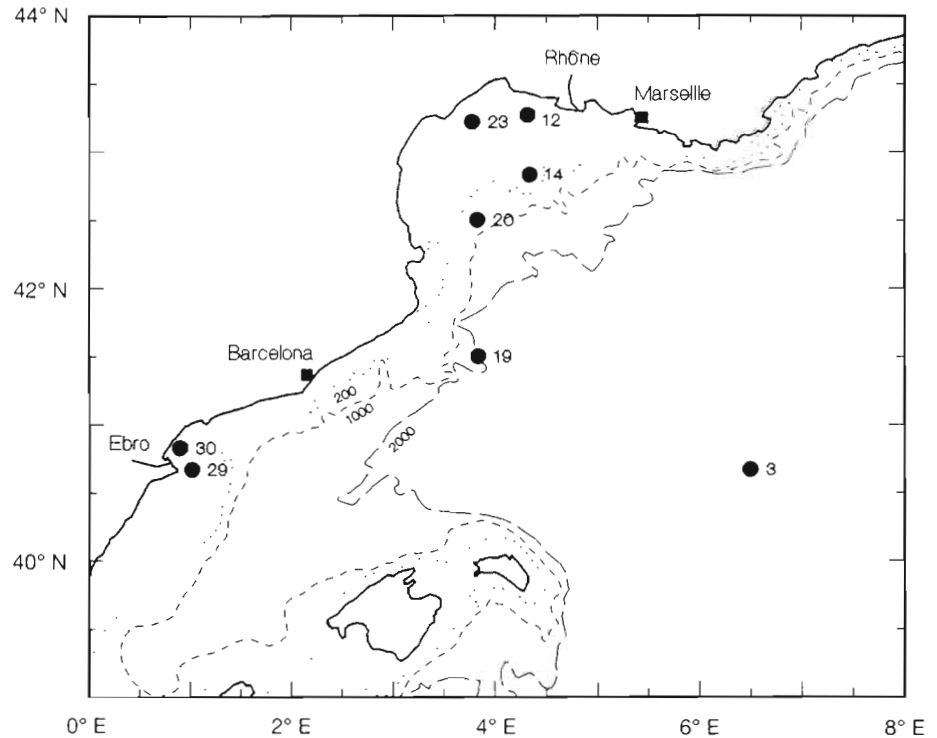


Fig. 1 The study area in the northwest Mediterranean. Numbers refer to sampling stations. Depth contours (m) are indicated

Pore-water profiles. Oxygen profiles were made in subcores on deck at *in situ* temperature with an oxygen microelectrode (Diamond electrode type 737, with an electrode-tip diameter of 50 μm), attached to a micro-manipulator, at every 0.5 mm depth interval. Pore-water profiles of dissolved silicate were made with a depth resolution of 0.5 cm in surface sediments (0 to 2 cm) and at 1 to 2 cm intervals deeper down in the cores. Procedures for oxygen and silicate profiles were according to Helder (1989a). Detailed results of pore-water profiling will be reported elsewhere (Helder et al. unpubl.).

Diffusive fluxes. Pore-water profiles of O_2 and silicate were used to calculate diffusive fluxes, assuming molecular diffusion (Bernier 1980) and applying Fick's first law:

$$J = -\Phi \cdot D_s \cdot (dC/dx)_{x=0}$$

where Φ = porosity; D_s = the whole-sediment molecular diffusion coefficient; and $(dC/dx)_{x=0}$ = the concentration gradient across the sediment-water interface, with x positive downward. In the case of O_2 , dC/dx was determined as the largest difference in O_2 concentration at the point where the microelectrode penetrated the sediment. In the case of silicate the pore-water concentrations in the upper 2 cm ($n = 5$) were fitted by a second order polynomial, and dC/dx was derived from the formula. Silicate was chosen as a tracer because it is not significantly involved in redox reactions and, because of the magnitude of the concentration

gradient across the sediment-water interface, usually shows significant fluxes (Helder & Andersen 1987). A porosity of 0.85 at the sediment-water interface was used, on the basis of earlier studies (Helder 1989b). The molecular diffusion coefficient, D_o , was adjusted to the *in situ* temperature using the Stokes-Einstein relation (Li & Gregory 1974). D_o values for silicate and oxygen were derived from Wollast & Garrels (1971) and Broecker & Peng (1974), respectively. The whole-sediment molecular diffusion coefficient (D_s) was then calculated according to Ullman & Aller (1982):

$$D_s = D_o \cdot \Phi^2$$

Incubation fluxes. On deck, a perspex chamber (31 cm diameter) was gently inserted into the box core, which still had the *in situ* bottom water on top. The chamber was sealed with a lid containing a YSI 620 electrode and stirrer and subsequently placed in a thermostatically controlled incubator at *in situ* temperature.

O_2 flux was derived by continuously recording the O_2 concentration in the overlying water during the time of incubation, which was, depending on location, between 3 and 24 h. At the end of the incubation period, 3 samples were taken from the overlying water for Winkler titration in order to calibrate the readings of the electrode. O_2 flux, expressed as $\mu\text{mol m}^{-2} \text{h}^{-1}$, was determined by means of a linear regression on the initial decrease in O_2 concentration in the chamber time series (Hall et al. 1989).

Silicate concentrations in the incubation cores were measured by taking 10 ml water samples with a syringe from overlying water at regular time intervals (1 to 2 h) during the incubation. The fluxes were determined by linear regression on the concentration-time series. The removal of the sample volume was compensated by adding a similar volume of bottom water to the incubation core by a second syringe. The samples were sieved through 0.45 μm Nuclepore filters and silicate was analysed on a Technicon-TRAACS 800 auto-analyser, following with minor modifications the methods described in Strickland & Parsons (1972).

Fauna. The sediments of the incubation chamber were washed over a 0.5 mm sieve at the end of the incubation for analysis of macrofauna. The residue on the sieve was preserved in a buffered solution of formalin (4% in seawater). Organisms were identified to higher taxonomic levels (Family, Order). Biomass was estimated from the shell-free wet weight (blotted), and converted into ash-free dry weight (AFDW) with the appropriate conversion factors given by Rumohr et al. (1987). The faunal similarity of the stations was determined by means of cluster analysis with the Bray-Curtis index as a measure of dissimilarity (Bloom 1981).

Meiofauna was collected from the sediment section outside the incubation chamber with a corer of 1.5 cm diameter and 10 cm length. Five such cores were pooled into one sample. In the laboratory the samples were coloured with rose bengal/phenol (Thiel 1966). The meiofauna in these samples was retrieved by means of elutriation and sieving over a 50 μm screen (Uhlir et al. 1973) and subsequently counted. Fauna smaller than the meiofauna, i.e. protozoa and bacteria, were not quantified.

Pigment analysis. Pigments in surface and bottom waters as well as in the top sediment layer (0 to 1 cm) were analysed by means of reverse phase HPLC, using a Waters Associate liquid chromatograph equipped with a RoSil C18 column and a Model 991 Waters photodiode array spectrophotometer. Prior to extrac-

tion, sediment (ca 3 g dry wt) and filters were freeze-dried and homogenized. Pigments were extracted in 5 ml methanol with 2% ammonium acetate. The solvent and gradient system was similar to that described by Kraay et al. (1992). The flow rate was set at 0.80 ml min⁻¹. Pigments were identified by comparing their absorbance spectra with those of reference standards obtained from algal cultures. Calibration curves were made after isolating a pigment and diluting it in a specific solvent to a series of different concentrations. The appropriate solvents and the corresponding extinction coefficients were derived from the literature (Bidigare 1991). The dilution series were injected in the system and the resulting peak areas were recorded. Concentrations were quantified from the maximum absorption with the Lambert-Beer law.

RESULTS

Sediment and water column characteristics

All stations had uniformly high percentages of silt (Table 1). The percentages of organic carbon and organic nitrogen are shown in Fig. 2a and b respectively. It appears that there is a decrease in percentage organic carbon with depth in the sediment. Little variation in organic carbon content between the stations was detected. The nitrogen content of the sediment displayed no obvious relation with depth in the sediment. C/N ratios (Fig. 2c) varied little with depth in the sediment as well as between stations (range 4 to 9), except for the top layer of Stn 3 (C/N ratio of 17), which was due to the high percentage organic carbon in this layer. The low C/N ratios, with mean values of ca 8, are an indication of relatively fresh organic detritus (Jørgensen 1983).

The vertical temperature differences in the water column were small at all stations, i.e. temperatures ranged between 13 and 17 °C. At the deep-water

Table 1. Sampling stations in the Gulf of Lions, NW Mediterranean, showing location, sampling date, water depth and percentage silt (<63 μm). The last 4 columns show characteristics of the bottom water, viz. temperature, salinity, oxygen concentration and oxygen saturation. Stations are ranked according to depth

Stn	Location		Date (1991)	Depth (m)	Silt (%)	Temp. (°C)	Sal. (‰)	O ₂ conc. (μM)	O ₂ sat. (%)
	°N	°E							
12	43.16	4.19	25 Nov	60	98.3	13.7	38.216	214	84
23	43.13	3.47	01 Dec	80	97.7	14.0	38.172	207	81
29	40.40	1.01	04 Dec	60	98.2	15.0	38.151	243	98
30	40.50	0.54	04 Dec	60	96.9	15.3	37.932	249	100
14	42.50	4.20	26 Nov	480	90.9	13.4	38.540	195	76
20	42.30	3.50	29 Nov	680	95.8	13.3	38.520	193	75
19	41.30	3.50	29 Nov	2300	93.7	13.1	38.447	209	81
3	40.40	6.30	21 Nov	2725	92.5	13.2	38.446	211	82

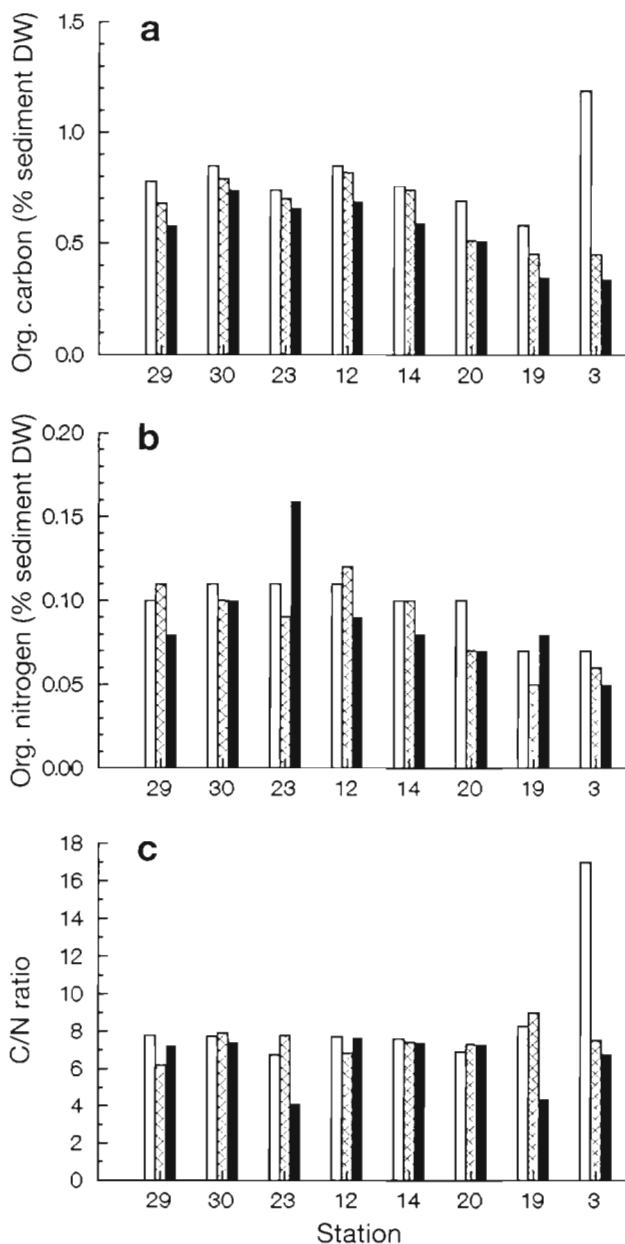


Fig. 2. (a) Organic carbon content, and (b) organic nitrogen content, of the sediment (% sediment dry wt) for 3 sediment depth layers at the 8 stations. (c) C/N ratio for the 3 sediment depth layers. Depths in the sediment are: 0 to 5 mm (Stn 23: 0 to 10 mm), 40 to 60 mm, and 100 to 140 mm (Stn 23: 140 to 180 mm; Stn 30: 80 to 100 mm). Stations are ranked according to water depth

Stns 3 & 19 and the slope Stns 14 & 20, the thermocline was situated at a depth of 50 to 70 m. Stns 29 & 30 near the Ebro had a homogeneous, well-mixed water column. Table 1 gives the temperature, salinity, oxygen concentration and oxygen saturation of the bottom water. The temperature of the bottom water ranged between 13.1 and 15.3°C at the stations, whereas the

oxygen concentration of the bottom water varied between 193 and 249 $\mu\text{mol l}^{-1}$. A distinction can be noticed in Table 1 between the bottom water over the slope (Stns 14 & 20) and the deep water (Stns 3 & 19) with respect to all parameters measured (O_2 , salinity, temperature).

Flux measurements

Oxygen

The similarity of *in situ* conditions in overlying bottom water (temperature, O_2 concentration; Table 1) among stations facilitated direct comparison of oxygen fluxes (for effects of variation in overlying water O_2 concentration on fluxes see Rasmussen & Jørgensen 1992). Fluxes in the incubation chambers ranged from 190 to 412 $\mu\text{mol m}^{-2} \text{h}^{-1}$ (mean \pm SD: 301 \pm 83) at the shelf stations (<100 m), from 85 to 182 $\mu\text{mol m}^{-2} \text{h}^{-1}$ (146 \pm 53) at the slope stations (100 to 1000 m), and from 37 to 55 $\mu\text{mol m}^{-2} \text{h}^{-1}$ (44 \pm 10) at the 2 deep stations (Table 2). Estimates from duplicate incubations were very close, with the largest discrepancy at Stn 12. The range of incubation fluxes at the shallow stations was rather large, due mainly to the relatively low rates at Stn 23.

Examples of contrasting pore-water oxygen profiles, representative for relatively high (Stn 12) and low (Stn 3) organic carbon input to the sediment, are given in Fig. 3. The range of diffusive oxygen fluxes was 190 to 248 $\mu\text{mol m}^{-2} \text{h}^{-1}$ (mean \pm SD: 192 \pm 62) at the shelf stations, 89 to 130 $\mu\text{mol m}^{-2} \text{h}^{-1}$ (110 \pm 29) at the slope stations, and 35 to 95 $\mu\text{mol m}^{-2} \text{h}^{-1}$ (65 \pm 42) at the deep stations (Table 2).

Fig. 4 shows the decrease in SOD with water depth. In contrast to the slope and deep stations, the diffusive fluxes at the shallow stations appear to be significantly

Table 2. Oxygen fluxes ($\mu\text{mol m}^{-2} \text{h}^{-1}$) measured in incubations and calculated from pore-water profiles, and the resulting irrigation fluxes. Irrigation fluxes marked with an asterisk are given as zero, because the negative difference between incubation and diffusive flux is theoretically meaningless (see text). Values separated by a slash are the results of duplicate box cores. Stations are ranked according to depth

Stn	Depth (m)	Incubation	Diffusive	Irrigation
12	60	412/318	248	164/70
23	80	190/215	105	85/110
29	60	338	194	144
30	60	334	219	115
14	480	170/182	130	40/52
20	680	85	89	0*
19	2300	55	95	0*
3	2725	37/39	35	2/4

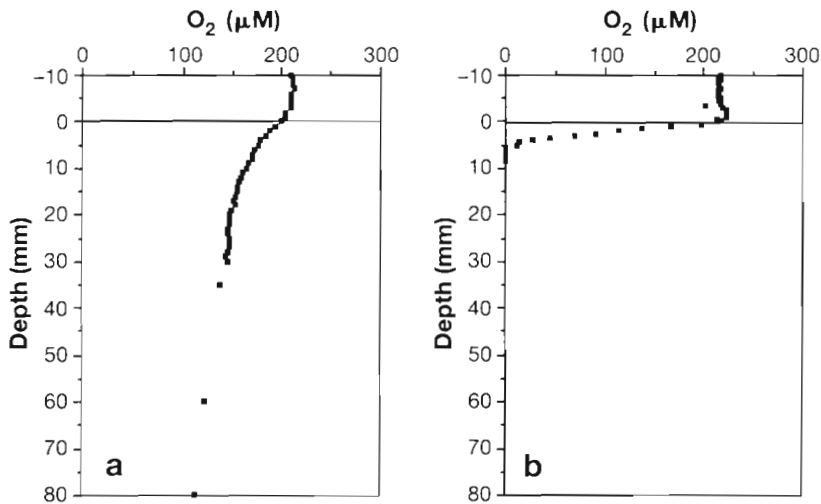


Fig. 3. Examples of contrasting pore-water O_2 profiles. (a) O_2 is present ($>100 \mu\text{M}$) over the entire depth range of the profile (Stn 3). (b) O_2 concentration reaches zero at 5 mm depth in the sediment (Stn 12)

lower than the incubation fluxes. It can furthermore be noticed that the 2 deep stations have slightly different values for incubation as well as for diffusive O_2 fluxes.

The irrigation flux (incubation minus diffusive flux) ranged from 70 to $164 \mu\text{mol m}^{-2} \text{h}^{-1}$ at the shelf stations, from 0 to $52 \mu\text{mol m}^{-2} \text{h}^{-1}$ at the slope stations, and from 0 to $4 \mu\text{mol m}^{-2} \text{h}^{-1}$ at the deep stations (Table 2). In cases where the calculated irrigation flux was negative, which is theoretically impossible and attributable to variability and measurement error, it was considered to be 0 . Fig. 5 shows the positive relation between macrofauna density and the oxygen irrigation flux ($r = 0.95$, $n = 12$, $p < 0.01$).

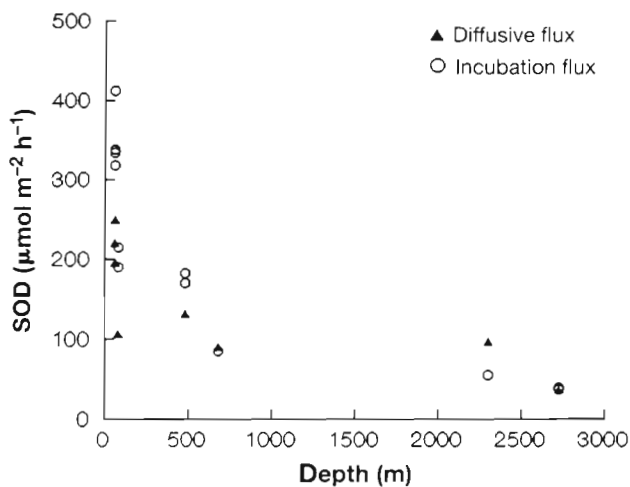


Fig. 4. SOD (sediment oxygen demand) at various water depths measured on board in November–December 1991 (Table 2). Incubation and diffusive fluxes are given. The O_2 fluxes are directed into the sediment

Oxygen incubation fluxes can be used to calculate carbon demand for the sediment, using a respiratory coefficient of 0.85 (Hargrave 1973). The resulting benthic carbon demand varies between 47 and $101 \text{ mg C m}^{-2} \text{d}^{-1}$ for the shelf stations, 21 to $45 \text{ mg C m}^{-2} \text{d}^{-1}$ for the upper slope stations, and 9 to $14 \text{ mg C m}^{-2} \text{d}^{-1}$ for the deep stations.

Silicate

The diffusive as well as incubation fluxes of silicate showed a less distinct difference between shelf, slope and abyssal stations. Incubation flux ranged from 31 to $66 \mu\text{mol m}^{-2} \text{h}^{-1}$ (mean \pm SD: 52 ± 14) at the shallow stations, from 29 to $66 \mu\text{mol m}^{-2} \text{h}^{-1}$ (48 ± 20) at the slope stations, and was $16 \mu\text{mol m}^{-2} \text{h}^{-1}$

at the deep Stn 19 (no measurement made at Stn 3; Table 3). Diffusive silicate fluxes ranged from 11 to $26 \mu\text{mol m}^{-2} \text{h}^{-1}$ (mean \pm SD: 18 ± 8 ; no measurement at Stn 30) at the shelf stations, from 13 to $20 \mu\text{mol m}^{-2} \text{h}^{-1}$ (17 ± 5) at the slope stations, and from 2 to $13 \mu\text{mol m}^{-2} \text{h}^{-1}$ (8 ± 8) at the deep stations. The diffusive flux at shelf Stn 23 was close to the low diffusive flux of the deep Stn 19. Slope Stn 14 exhibited a slightly elevated diffusive silicate flux, comparable to the shelf stations (except Stn 23). In Fig. 6 both the incubation and the diffusive silicate fluxes are plotted against water depth. Diffusive fluxes were always lower than the corresponding incubation fluxes. However, in contrast

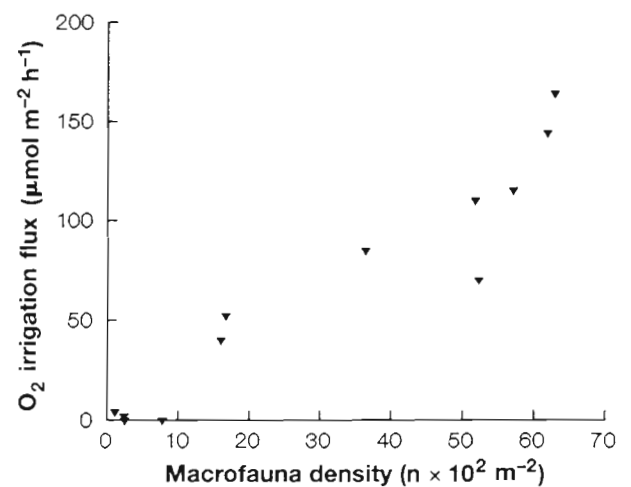


Fig. 5. O_2 irrigation fluxes at the stations, with the corresponding macrofaunal densities (Tables 2 & 4). The correlation between both variables has a coefficient of $r = 0.95$ ($n = 12$, $p < 0.01$)

Table 3. Silicate effluxes from the sediment ($\mu\text{mol m}^{-2} \text{h}^{-1}$) measured in incubations and calculated from pore-water profiles, and the resulting irrigation fluxes. Values separated by a slash are the results of duplicate box cores. Stations are ranked according to depth

Stn	Depth (m)	Incubation	Diffusive	Irrigation
12	60	53/66	26	27/40
23	80	31	11	20
29	60	49	18	31
30	60	62	-	-
14	480	48/68	20	28/48
20	680	28	13	15
19	2300	16	13	3
3	2725	-	2	-

to the oxygen fluxes (Fig. 4), the differences between incubation and diffusive silicate fluxes at the slope stations were rather large.

Irrigation flux of silicate ranged from 20 to 40 $\mu\text{mol m}^{-2} \text{h}^{-1}$ at the shallow stations and from 15 to 48 $\mu\text{mol m}^{-2} \text{h}^{-1}$ at the slope stations, and was 3 $\mu\text{mol m}^{-2} \text{h}^{-1}$ at the deep Stn 19. In Fig. 7 the silicate irrigation flux is plotted against macrofauna density. The relation with macrofauna density is less obvious than in the case of the O_2 irrigation fluxes ($r = 0.42, n = 8, p > 0.05$).

Benthic fauna

Table 4 shows the biomass and density of total macrofauna and the density of the meiofauna. Densities of both groups decreased with increasing water depth. Stn 23 had a significantly lower meiofaunal density than

the other slope stations. In contrast to the macrofauna, meiofaunal density differed clearly between the 2 deep-water Stns 3 and 19 (Table 4). Despite the low meiofaunal density at Stn 23, the relation between macro- and meiofaunal density is clear ($r = 0.85, n = 12, p < 0.01$). Although both macro- and meiofauna are capable of enhancing solute transport, macrofauna is generally the most important group in this respect (Aller & Aller 1992). For this reason we used only macrofaunal density in comparisons with the irrigation fluxes of silicate and oxygen. Macrofaunal biomass was more variable than the density because of the incidental occurrence of large specimens. At the shallow stations biomass ranged from 940 to 3350 mg AFDW m^{-2} , at the shallowest station on the slope (Stn 14) biomass was still 1750 mg on average, but deeper on the slope (Stn 20) and in the abyssal plain (Stns 19 & 3) macrofaunal biomass decreased by 1 and 2 orders of magnitude, respectively. Both macrofaunal biomass and densities of our 2 deep stations compare well to those of a study at NE Atlantic deep-sea sites (4000 to 5000 m) by Rutgers van der Loeff & Lavaleye (1986).

The taxonomic composition of the macrofauna at the shallow stations showed a high degree of similarity, especially at Stn 12 in the Gulf of Lions and at the 2 stations near the Ebro (Stns 29 & 30; Table 5). Dominant taxa at these stations were small polychaetes (spionids, cirratulids and paraonids), the bivalve genus *Thyasira* and small crustaceans (amphipods, cumaceans). The other shallow station in the Gulf of Lions (Stn 23) had lower numbers of polychaetes and bivalves but a higher density of isopods. The macrofauna on the continental slope (Stns 14 & 20) still comprised a fair number of taxa, but densities

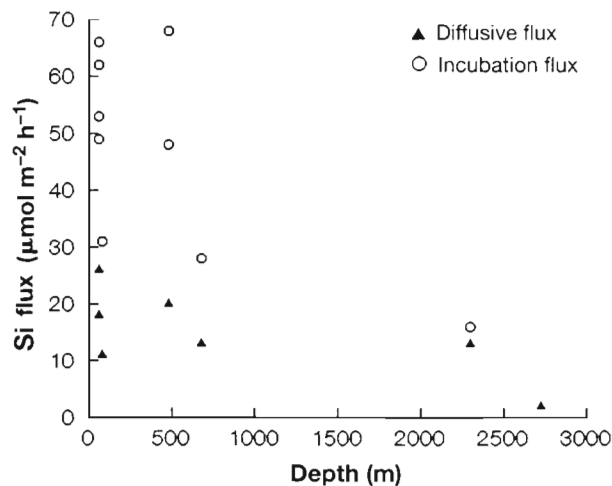


Fig. 6. Incubation and diffusive silicate fluxes at various water depths measured on board in November–December 1991 (Table 3). The Si fluxes are directed out of the sediment

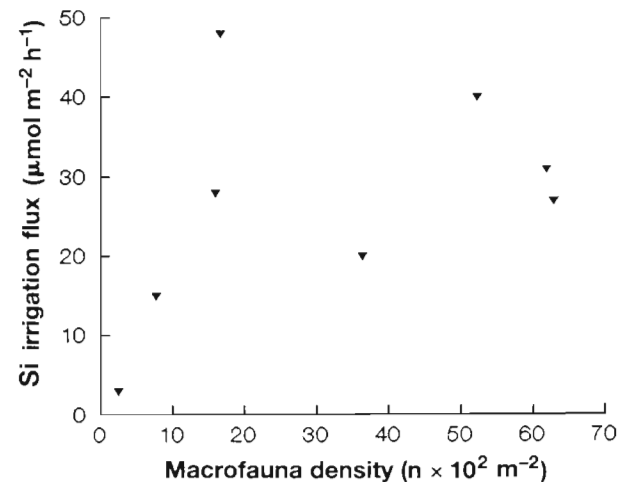


Fig. 7. Si irrigation fluxes at the stations, with the corresponding macrofaunal densities (Tables 3 & 4). The correlation between both variables has a coefficient of $r = 0.42$ ($n = 8, p > 0.05$)

Table 4. Macrofaunal biomass (mg AFDW m⁻²) and density (ind. × 10² m⁻²) and meiofaunal density (ind. × 10⁶ m⁻²) at the stations. Values separated by a slash are the results of duplicate box cores. Stations are ranked according to depth

Stn	Depth (m)	Macrofauna		Meiofauna density
		Biomass	Density	
12	60	2010/2140	62.9/52.3	1.83
23	80	940/1290	36.4/51.8	0.38
29	60	1060	61.9	1.64
30	60	3350	57.1	1.92
14	480	1510/1990	16.0/16.7	0.55
20	680	270	7.8	0.42
19	2300	29	2.5	0.34
3	2725	14/10	2.4/1.1	0.07

were considerably lower, notably those of the dominant shelf polychaetes. Only 1 taxon, viz. sipunculids, occurred on the slope but not on the shelf, albeit in very low densities. The macrofauna at the deep stations was quite impoverished in terms of both number of taxa and density.

Table 5. Density (ind. m⁻²) of selected dominant taxa at the stations. Stations are ranked according to their faunal similarity by means of cluster analysis with the Bray-Curtis index as a measure for dissimilarity

Stn:	29	30	12	23	14	20	19	3
Depth (m):	60	60	60	80	480	680	2300	2725
No. of taxa:	28	27	27	37	27	21	12	5
POLYCHAETA								
Sternaspidae	312	28	99	14				
Nephtyidae		14	57	71				
Pilargidae	14		21	85	7			
Ampharetidae	99	57	21	43	43	28		
Lumbrineridae	170	57	92	71	36	14		
Magelonidae	185	128	149	28	7	28		
Nemertini	469	327	192	107	36	14		
Paraonidae	738	682	596	383	121	71	14	
Cirratulidae	1250	1605	767	561	28	28	43	14
Spionidae	1732	2144	1988	653	170	85	14	92
Capitellidae	14		85	85	78	28	28	
Maldanidae				7	28	185	14	7
Sipunculida					28	14		
CRUSTACEA								
Cumacea	185	57	731	320	121			
Amphipoda	454	440	447	682	270	57		
Isopoda	28	99	36	746	114	28	43	21
MOLLUSCA								
<i>Thyasira</i>	710	71	206	14	57		14	
<i>Abra</i>	14	85	312	57	270			
<i>Hyala</i>	14	99	28	36				
<i>Odostomia</i>	14	14	28	43				
<i>Chaetoderma</i>				78	99	28		
<i>Yoldiella</i>						99		
ECHINODERMATA								
<i>Amphiura</i>		28	14	21	14			

Phytopigments

Table 6 summarizes the concentrations of the principal pigments found in the bottom water and sediments with HPLC analysis. Samples of the upper sediment layer from the deep stations did not yield any detectable amounts of phytopigments. The same was true for the deepest slope Stn 20. Samples from the more shallow slope Stn 14, however, contained a relatively modest amount of a chl *a* derivative, phaeophorbides and fucoxanthin (+ fucoxanthin-like) pigments. A similarly modest amount of chl *a* was found at the shelf Stn 12, but with a higher fucoxanthin-like component. The sediment at the remaining 3 shelf stations contained much higher levels of chl *a* and accessory pigments and also displayed a greater number of unidentified peaks. When considering only the fresh pigments (marked with asterisks in Table 6), sediments from the Ebro stations yielded the highest concentrations, although the relative amounts of the different pigments differed greatly at both stations. The chl *a* content at Stn 30 was almost twice that found at the adjacent Stn 29, whereas the sediment at the latter station contained twice as much fucoxanthin.

The bottom water over the slope and deep stations was fairly similar in phytopigment composition (Table 6), with minimal amounts of fresh chl *a* and fucoxanthin. The bottom water over the shelf had, in general, much higher concentrations of chl *a* and accessory pigments, especially fucoxanthin (+ fucoxanthin-like) compounds. None of the bottom water samples contained quantifiable traces of phaeopigments (phaeophorbides, phaeophytin). The bottom water over the Ebro Stns 29 & 30 was different from that over the Gulf of Lions in that it contained chl *c*, which was not found elsewhere. With respect to the labile pigment chl *a*, there was reasonable agreement between concentrations in the bottom water and in the corresponding sediment. The most striking difference between bottom water and sediment pigment concentrations was found at the slope Stn 14. At this station moderate amounts of fucoxanthin (+ fucoxanthin-like) and chlorophyll derivatives were found in the sediment and only very low concentrations of fresh chl *a* and fucoxanthin in the bottom water.

Table 6. Principal phytopigment concentrations at the stations, in (a) ng l⁻¹ for bottom water, (b) ng g⁻¹ dry sediment for the 0 to 1 cm sediment layer. 'Fresh' phytopigments are marked with an asterisk. -: concentrations below detection level

Pigment	Deep stations		Slope stations			Shelf stations		
	3	19	20	14	12	23	29	30
(a) Bottom water								
Chlorophyll c ₃ *	-	-	-	-	-	-	7	9
Chlorophyll c ₁ *	-	-	-	-	-	-	-	2
Chlorophyll c ₂ *	-	-	-	-	-	-	2	15
Fucoxanthin-like	-	-	-	-	-	4	12	17
Fucoxanthin*	-	-	<1	1	10	13	29	11
β-Hexanoyloxyfucoxanthin*	-	-	-	-	1	7	15	37
Alloxanthin*	-	-	-	-	-	-	2	5
Zeaxanthin*	-	-	-	-	2	3	5	14
Chlorophyll b*	-	-	-	-	-	12	17	41
Chlorophyll a*	<1	2	<1	2	33	50	110	183
β-Carotene*	-	-	-	-	-	3	3	5
(b) 0-1 cm sediment								
Fucoxanthin*	-	-	-	17	75	30	188	127
Fucoxanthin-like	-	-	-	14	10	18	17	13
Σ Phaeophorbides	-	-	-	48	5	35	99	231
Alloxanthin*	-	-	-	-	14	24	44	70
Zeaxanthin*	-	-	-	-	15	4	31	153
Chlorophyll b*	-	-	-	-	-	19	-	44
Chlorophyll a*	-	-	-	8	29	55	107	230
Chl a derivative	-	-	-	31	-	-	-	-
β-Carotene*	-	-	-	-	7	26	14	234

Analysis of samples from the surface water (not shown in Table 6) showed the highest concentrations of chl *a* to be present over the slope Stns 14 & 20, and over the inner shelf Stn 23. Relatively low concentrations were found over the Ebro stations. Comparing bottom and surface water pigment compositions confirms the CTD results indicating that the water mass was stratified in the Gulf of Lions and completely mixed near the Ebro.

DISCUSSION

In order to quantify the export of organic matter from the shelf to deeper regions of the Gulf of Lions, information concerning a range of processes, including annual primary production, vertical particle fluxes from the water column, sedimentation rates and total metabolism of the benthic biota, is required. An example of such an extensive study is the SEEP project, carried out in the Mid-Atlantic Bight (Walsh 1988). Some of these processes have been the subject of earlier studies in the NW Mediterranean. Zuo et al. (1992) found a concomitant decrease in sediment accumulation and mixing rates going from the mouth of the Rhône across the shelf and slope to the deep basin. According to Zuo et al. (1992), 50% of the material supplied by the Rhône is deposited near the river mouth and 10% or less is exported from the shelf to the upper slope.

If shelf export is restricted to and directed by canyons (Aloisi et al. 1982, Monaco et al. 1987), then the activity of the biota on the slope and in the deep basin outside the influence of these canyons should merely reflect vertical particle fluxes. One such vertical flux event has been measured by Peinert et al. (1991) in the deep basin south of Toulon. They recorded a maximum particle flux during the spring phytoplankton bloom of ca 20 mg C m⁻² d⁻¹ in a moored sediment trap at 2000 m depth in combination with a sinking velocity of >140 m d⁻¹. Two months later (August) this flux had decreased to <5 mg C m⁻² d⁻¹. The values from Peinert's study agree reasonably well with our present estimates for the benthic carbon demand at this depth (9 to 14 mg C m⁻² d⁻¹), suggesting that the vertical carbon flux might be sufficient to sustain the SOD rates for the deep stations.

During the present November cruise, the shelf stations yielded the highest incubation and diffusive fluxes of oxygen, as well as the highest irrigation fluxes, indicating a relatively high sediment content of metabolizable carbon in combination with intensified infaunal irrigation. The higher respiration rate at the nearshore Stn 19 compared to the offshore Stn 3, in combination with the lack of an irrigation flux at both stations (Table 2), suggests a relatively elevated detrital pool near the foot of the slope. Our data on C/N ratios and sediment pigment, however, failed to show a clear difference between the 2 deep stations.

Although both incubation and diffusive silicate fluxes decreased with increasing water depth, the differences between them were not the same as for oxygen (Tables 2 & 3, Figs. 4 & 6). For silicate, for instance, the differences between incubation and diffusive fluxes at the shelf stations and Stn 14 seem to be greater than for oxygen fluxes at these stations. This might be primarily the result of underestimation of the diffusive Si fluxes, due to lack of vertical resolution in the pore-water Si profiles (0.5 cm) compared to that in the oxygen profiles (0.5 mm). Secondly, the different kinetic behaviour of oxygen and silicate in the sediment (zero-order consumption for oxygen vs first-order dissolution of biogenic silicate) could be responsible for different effects of bioirrigation on the fluxes of these compounds (Aller 1980, Berner 1980, Rutgers van der Loeff et al. 1984, Helder & Andersen 1987).

Earlier flux measurements in this area have been carried out by Blackburn & Lomstein (1989), Helder (1989b) and Blackburn (1991). Both incubation and diffusive fluxes of oxygen and silicate were determined in these studies. Generally, their flux rates were of the same order as those in the present study, with some exceptions, such as the higher oxygen incubation fluxes of December 1988 reported by Blackburn & Lomstein (1989). Diffusive silicate fluxes measured in December 1988 by Helder (1989b) were considerably lower than the present ones. With respect to the seasonal variation of SOD in the area, it seems that the rates of November–December are maintained throughout the second half of the year, without large summer/winter differences. This pattern probably also holds for the early spring, as can be deduced from the data reported by Blackburn (1991) from April–May 1991. Because of the good correlation between SOD and macrofaunal density (Tables 2 & 4), it is reasonable to assume that the observed pattern also reflects the annual pattern in benthic food input and activity. There are, however, no respiration data to support this supposition for the period of the spring phytoplankton bloom, which is an important source of benthic carbon (Peinert et al. 1991).

Our present SOD values for the 3 depth zones fit in the global ranges given in 2 compilations of various SOD studies by Jørgensen (1983) and Canfield (1989). The SOD data for deep-sea sediments given in these compilations are based either on *in situ* incubations or on pore-water profiles. According to Smith (1978), shipboard incubations of deep-sea sediment result in overestimates due to pressure effects on the biota. Also in the case of shipboard-measured pore-water profiles, a flux calculation can be overestimated due to the decompression of deep-sea sediment cores, leading to upward displacement of pore waters and artificially

steepened interfacial gradients (Jahnke et al. 1989, Helder unpubl. results). Although we realize that, especially for the deeper stations, this makes a comparison between our shipboard-measured fluxes and the earlier reported *in situ* SOD values disputable, the fact that these values are of the same order, even if our data are really overestimated, suggests there is little evidence for substantial downslope transport of organic matter at our stations.

Supplementary evidence for the lack of a substantial export can be derived from a comparison between primary production and SOD assuming loss rates given by Suess (1980), i.e. 1% of the primary production for the deep sea and less than 10% for the slope. In the oligotrophic surface waters overlying the slope, primary production varies between 50 and 100 g C m⁻² yr⁻¹ (150 g C m⁻² yr⁻¹ at the adjacent front). Primary production over the deep area is estimated to range between 80 and 150 g C m⁻² yr⁻¹ (M. Minas & H. J. Minas pers. comm.). These values would correspond to an input of 5 to 10 g C m⁻² yr⁻¹ for the slope and 2 g C m⁻² yr⁻¹ or less for the deep area. When we convert our present SOD estimates into carbon, assuming no seasonal variation, the resulting carbon demands for the 2 areas are quite close to the predicted carbon inputs, i.e. 3 to 5 g C m⁻² yr⁻¹ for the deep stations and 8 to 16 g C m⁻² yr⁻¹ for the slope stations, given the imprecision of the calculations.

The benthic activity pattern we found in November corresponded to some extent with the distribution of phytodetritus in the sediment, viz. relatively high amounts of fresh material on the shelf sediments and lower, more degraded material at the shallowest slope Stn 14. We were unable to detect phytopigments in surface sediments of deeper stations, probably because of the small amounts of sediment that we used for the analysis. But even with larger amounts the difference between Stn 14 and the deeper stations would have remained and would still contrast with the uniformity of the bottom water over the slope and deep stations. We therefore assume that Stn 14 received a pulse of phytodetritus prior to our visit, probably from a source other than the present layer of bottom water, as can be inferred from the high proportion of fucoxanthin-like pigments. Shelf bottom water or resuspended shelf sediments, which both could have been the source for this phytodetritus, were obviously not present at the time of the expedition. The bottom water over the slope and shelf differed clearly in pigment content and composition, indicating no exchange between shelf and slope. Moreover, the absence of phaeophorbides in any of the bottom water samples, although abundantly present in the shelf deposits, indicates that little or no resuspended phytodetritus was present on the shelf.

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