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Spatio-temporal variability in benthic mineralization processes in the eastern English Channel

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Abstract The effect of phytodetritus derived from *Phaeocystis* sp. bloom on benthic mineralization processes has been determined at four intertidal stations along the French coast of the eastern English Channel. Sites were chosen to offer a diversity of sediment types, from permeable sandy beach to estuarine mudflats. Sediment Oxygen Demand (SOD) as well as total fluxes of Dissolved Inorganic Nitrogen (DIN) at the sediment–water interface were determined by using whole core incubation technique and diffusive fluxes were predicted from interstitial water concentrations. In the absence of phytodetritus deposits, a marked gradient of granulometric characteristics and organic matter contents were observed, and resulted in more intensive mineralization processes in muddy sediments. Highly significant correlations ($P < 0.05$) were evidenced between SOD and porosity, bacterial biomass, Organic Carbon and Organic Nitrogen, evidencing the direct link between sediment texture, organic matter accumulation and microbial activity. The spring bloom led to a massive input of organic matter in surficial sediments and mineralization rates significantly increased while higher DIN release towards the water column was observed. A modification of the mineralization pathways was evidenced but clearly depended on the sediment type. With a global view, benthic mineralization processes in the intertidal zone provided significant a part of DIN inputs in the coastal zone while water column was depleted in nutrients.

Keywords Intertidal · Organic matter mineralization · *Phaeocystis* sp. · Sediment–water fluxes

Introduction

During recent decades, intensive studies of coastal ecosystems have shown the major role of sediments in nutrient recycling and organic matter decomposition. When organic matter settles into the sediment, it can be permanently buried or may provoke a sequence of degradation reactions that remove carbon from the sediment system by oxidizing it to CO_2. A well-defined sequence of oxidants was described by Froelich et al. (1979), oxygen being consumed first, followed by nitrate and nitrite, manganese oxide, iron oxides, sulphate, and finally oxygen bound to organic matter. Microbial processes play a key role in those mineralization processes (Blackburn 1988), but it has also been acknowledged that the role of macrofauna in sediment–water exchange processes cannot be neglected (Gilbert et al. 1995; Aller et al. 1998).

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Bioturbation mainly increases the surface area available for exchange and modifies the redox and adsorption–desorption characteristics of the sediments (Rosenberg et al. 2001).

Benthic–pelagic coupling usually plays a major role in coastal systems especially in shallow areas submitted to intense hydrodynamic forcing (Vidal and Mogui 2000). Like most coastal systems, the intertidal area consists of a complex mosaic of sedimentary types, from muddy cohesive sediments to permeable sandy beaches. In the past, most investigations focused on muddy sediments because many traditional methods were not adapted to permeable sediments (Viollier et al. 2003). Sandy sediments, despite their prevalence on continental shelves, have remained largely unstudied up to very recent years (Boudreau et al. 2001; Jahnke et al. 2005).

The eastern English Channel is characterized by very strong hydrodynamic features in a macrotidal regime (tidal range up to 9 m). During late spring, the coastal zone of the English Channel is recurrently affected by a massive phytoplankton proliferation dominated by the Prymnesiophyceae algae *Phaeocystis* sp. (Lancelot 1995; Gentilhomme and Lizon 1998). While the bloom is ending, sediments receive the disrupting senescent colonies that agglomerate biotic and abiotic material and accumulate in impressive layers of brownish and stinking foams along the intertidal zone of French coasts, covering beaches (Lancelot et al. 1987) and estuaries (Desroy and Denis 2004). As a consequence, the sediment–water interface is subjected to a succession of organic matter deposition/resuspension events resulting from the combination of hydrodynamic forcing and organic matter settling (Cadée 1996).

Two main hypotheses were tested to explain the variability on benthic fluxes. First of all, it is well known that there is a strong link between sediment nature and biogeochemical functioning, sediment type reflecting the hydrodynamic conditions. Consequently the impact of such forcing on biogeochemistry was tested by selecting a diversity of sediment types, from a permeable sandy beach to estuarine mudflats. The second main forcing tested here was the organic matter supply to the sediments. With this goal, our investigations were performed during two sampling cruises in March and May 2003, before and during the massive foam deposition consecutive to *Phaeocystis* sp. dominated spring bloom.

The quantification of exchanges at the sediment–water interface was performed by using whole-core incubation technique, a common method to study the biogeochemistry of surficial sediments (Grenz et al. 2000; Denis et al. 2001). A complementary approach of biogeochemical reactions was achieved by describing nutrient concentrations in pore water. In parallel with fluxes measurements, a study of sediment characteristics (fine particles %, porosity, Total Organic Carbon and Total Nitrogen content) as well as benthic bacteria and macrofauna biomass was also performed.

Materials and methods

Site description

This study was conducted on the intertidal zone along the French coast of the eastern English Channel. In order to take into account a part of the spatial variability of this area, four stations were chosen and were visited during two campaigns in March and in May 2003 (Fig. 1). The first station was located on Sainte-Cécile beach (Station SC) about 2 km north of the Canche estuary. Two other stations were located inside the estuary, in an area generally exposed to large phytodetritus deposits (Desroy and Denis 2004). One of them was largely sheltered behind a dyke and had muddy sediments (Station Estuary Mud, EM) while the other station was located on the other side of this dyke, hence more exposed to tidal currents (Station Estuary Sand, ES). The last station located on the beach of Wimereux (Station W) was chosen as representative of the sandy exposed environment (Spilmont et al. 2005). In this site, the sampling station was located in the higher part of the beach between mean high water of neap tides and mean tidal level.

Sampling and incubation device

All samplings were performed at the end of the immersion period, with approximately 50 cm of overlying water. Sediment samples were collected by hand in Perspex tubes (i.d.: 15 cm, length: 35 cm), sampling around 15 cm of sediments and 20 cm of overlying water. Four cores were placed in dark refrigerated cabinets at in situ temperature ±1°C. A fifth core was used for oxygen microprofiling and granulometric analysis. At each station, bottom water (ca. 15 l) was

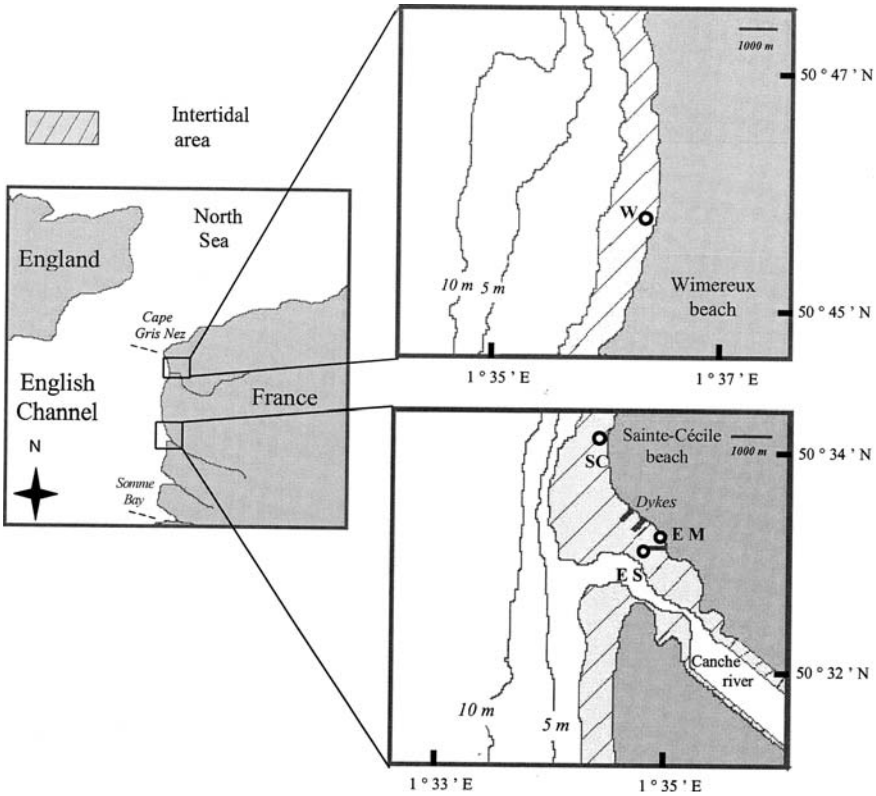


Fig. 1 Location of the stations (*open circles*) sampled along the intertidal area during March and May 2003 campaigns (W: Wimereux; SC: Sainte-Cécile; ES: Estuary Sand; EM: Estuary Mud)

sampled using an inflatable reserve tank and stored under the same conditions as the incubated cores. For the incubation, each core was connected to this reserve tank, and any volume of the overlying water removed from a core was replaced by an equivalent volume of water from the reserve tank. No statistical difference between oxygen or nutrient concentrations at initial sampling for the incubated cores and the reserve tank was observed (*t*-test, $P < 0.05$). Rotating magnets fixed on the upper cap of each sealed core prevent any gradient formation. Further detailed description of the incubation device can be found in Denis et al. (2001). During an incubation period of 24 h, the overlying water of each core and the reserve tank was sampled every 3 h by means of a 60 ml plastic syringe. The difference between concentration changes in the overlying water of each core and bottom water allowed the calculation of sediment–water fluxes. A correction for water replacement was systematically applied and non-significant regressions (Pearson correlation, $P > 0.05$) were interpreted as zero fluxes. At the end of the incubation period, each core was sub-sampled with 2.7 cm i.d. cores for pore water extraction, porosity profile measurements and elemental analysis.

Analytical procedure for oxygen and nutrient determination

The flasks were rinsed once before sample collection and oxygen was immediately analysed in triplicate using Winkler micro titration (Aminot and Chaussepied 1983). The remaining sample was filtered through GF/C Whatman glass fibre filters. Ammonium analyses were carried out according to Koroleff (1969). Samples for the analysis of nitrate and nitrite were frozen for later analysis using an Alliance autoanalyzer following the protocol of Tréguer and Le Corre (1975).

Pore water profiles and predicted flux calculation

Oxygen concentration in pore water was measured in a non-incubated core by using a miniaturized Clarck-type O_2 microsensor (100 µm tip diameter) equipped with an internal reference and a guard cathode. Six oxygen microprofiles were determined for each station. The position of the sediment–water interface was considered as a break in the dissolved oxygen gradient (Glud et al. 1995). Oxygen Diffusive Uptake

(DOU) was calculated according to Berg et al. (1998) by using the PROFILE software, which uses a curve fitting approach by adjusting the calculated oxygen profile to the observed one.

Nutrient profiles were determined on subcores after rapid slicing with a vertical resolution of 1 cm down to 10 cm depth. Interstitial waters were extracted by simultaneous centrifugation (3000 rpm, 20 min) and filtration (Whatman GF/F, 0.7 µm) of sediment slices. Samples were analysed following the same procedure as described for overlying water and Fick's first law of diffusion was used to calculate the diffusive nutrient fluxes (Berner 1980):

$$F_{Diff} = -\phi \cdot Ds \cdot (dC/dZ)_{z=0} \quad (1)$$

where ϕ is the porosity, D_s is the effective diffusion coefficient of the solute in the sediment, $(dC/dz)_{z\,=\,0}$ is the estimated concentration gradient just below the sediment–water interface, and z is the depth in the sediment scaled positively downward. The effective diffusion coefficient (D_S) of a solute in the sediment was calculated as detailed in Denis et al. (2001). To estimate the gradient close to the sediment–water interface $(dC/dz)_{z\,=\,0}$, different calculations were applied. For ammonium, a linear gradient was taking into account. For nitrate and nitrite, a peak was observed in the upper centimetre followed by an exponential decrease at depth. Those profiles were fitted to the following empirical formulation (Christensen et al. 1989):

$$C_z = C_{max} + (C_{surf} - C_{max}) \cdot \exp^{(-Ccoef \cdot z)} - (L_{coef} \cdot z) \quad (2)$$

where C_{max} is the maximum nutrient concentration in pore water and C_{surf} the nutrient concentration at the sediment–water interface. The coefficient of exponential decrease of nutrient concentration at depth is C_{coef} and the coefficient of linear change with depth is L_{coef}. In the calculation of diffusive fluxes, irrigation was neglected and the diffusion coefficient only includes molecular diffusion around sediment particles. So the calculated diffusive fluxes must therefore be considered as minimal diffusive fluxes.

Sediment characteristics

Duplicate subcores were sliced every centimetre for the determination of porosity profiles by drying in an oven (80°C) for 72 h. Afterwards, the dry sediment was used for the analysis of organic matter content. The total organic carbon (TOC) and total nitrogen (TN) contents were determined after acidification with 2N HCl using a Thermoquest NA200 Protein elemental analyser. Moreover grain size distribution of the 10 upper centimetres of sediment was determined for each cruise (dry sieving).

Bacteria and macrofauna biomass

For each cruise, additional sediment samples were collected for bacteria biomass estimation. Triplicate samples were taken by coring the sediment to a depth of 1 cm. Samples were immediately preserved in sterile 40 ml bottles with borate-buffered formalin in filtered seawater. Subsamples of 5 ml were treated with 150 µl of Tween 80 and were sonicated for 5 min in a ultrasound bath (Chevaldonné and Godfroy 1997). After centrifugation (3000 rpm, 10 min) and staining following the protocol of Porter and Feig (1980), subsamples were filtered onto 0.2 µm pore-size Isopore black-coloured filters. Ten randomly chosen counting grids of three parallel filters per sample were counted under an epifluorescence microscope (Artigas 1998). Abundances were expressed in number of cells per sediment volume unit (10^7 cells ml^{-1}) and biomass conversion was made by using a constant factor of 20 fg C $bacteria^{-1}$ (Christaki 1995). The incubated cores were used for macrofauna determination. The sediment remaining after subsampling for pore water analysis was sieved through a 1-mm circular mesh sieve. Macrofauna was identified to the lowest possible taxon and the biomass of each taxon was determined as g of AFDW m^{-2} (loss of weight of dry organisms after 6 h at 520°C).

Statistics

Changes in sediment characteristics between March and May were tested using the paired *t*-test (*t*-test, $P < 0.05$; Scherrer 1984). For flux measurements, because of the small number of replicates and the variability of highest values, all data were considered non-normalized and non-parametric tests were applied. Comparisons between cruises were performed with the Wilcoxon–Mann–Whitney test (WMW, $P < 0.05$), whereas differences between stations were demonstrated using the Kruskal–Wallis test (KW, $P < 0.05$) and followed by a multiple comparisons test (S.N.K.; $P < 0.05$; Scherrer 1984).

Results

Hydrological variables

Due to the short time between core sampling and the beginning of incubation procedure, the first sampling performed in the overlying water of incubated cores was considered as representative of oxygen and nutrient concentrations in the water column (Table 1). Both spatial and temporal variations of temperature in the water column were limited, in the range 10.0–11.7°C, with higher temperature values measured at estuarine stations. Average temperature increased from March to May but this warming up did not exceed 1°C. Oppositely to temperature, dissolved inorganic nutrient concentrations strongly fluctuated during the study. Ammonium concentrations exhibited marked spatial variations with higher values in the water column of estuarine stations and averaged concentrations decreased from March to May for all the stations, undoubtedly due to the phytoplankton consumption. In March, nitrate concentrations were higher in Wimereux than in muddy stations but the inverse trend was observed in May. No particular evolution was observed in Sainte Cécile which was characterized by the lowest nitrate concentrations.

Sedimentary characteristics

Stations W, SC and ES showed a typical fine sands aspect (Table 2) with unimodal distribution centred on the class (0.160–0.200 mm). On the contrary, the sediments of station EM showed a bimodal structure with a major fine sands fraction (0.125–0.160 mm) and a minor clay fraction (<0.063 mm) that could be qualified of sandy mud according to the classification of Chamley (1987). Porosity profiles of the stations W and SC were vertically homogenous with little variations from March to May. Estuarine stations were characterized by an exponential decrease with higher porosity values in the first 3 cm whereas at depth, porosity was close to that of the other stations, around 0.3–0.4. Moreover, those two stations showed a significant difference of surface porosity with higher values in May (*t*-test, $P < 0.05$). The vertical variations of TOC and TN contents of the surficial sediments generally showed an accumulation of organic matter in the surface centimetres. For further calculations, the average value of the first three centimetres was considered. TN varied from 0.0017 to 0.22% dry weight with lowest values at stations W and SC while higher contents were found at estuarine stations. TOC varied from 0.067 to 2.81% and followed a spatial distribution similar to nitrogen. The C:N atomic ratios of surficial sediments were in the range 6.33–37.91, but most of the values were between 6.33 and 9.19. A high C:N ratio was observed only in March at W and SC stations (respectively 37.91 and 25.28) and uncertainties of TN determination (values close to zero) may explain such abnormally high values.

Table 1 Temperature, ammonium and nitrate concentrations in the water column for the different samplings

Station	Water temperature (°C)		NH_4^+ (μmol l^{-1})		NO_3^- (μmol l^{-1})	
	March	May	March	May	March	May
Wimereux	10.0	11.0	2.05	1.54	1.04	0.84
Sainte-Cécile	10.0	11.0	5.23	4.17	0.34	0.30
Estuary sand	11.1	11.7	9.31	7.23	0.74	1.23
Estuary mud	11.1	11.7	14.99	12.34	0.47	1.80

Sediment–water fluxes

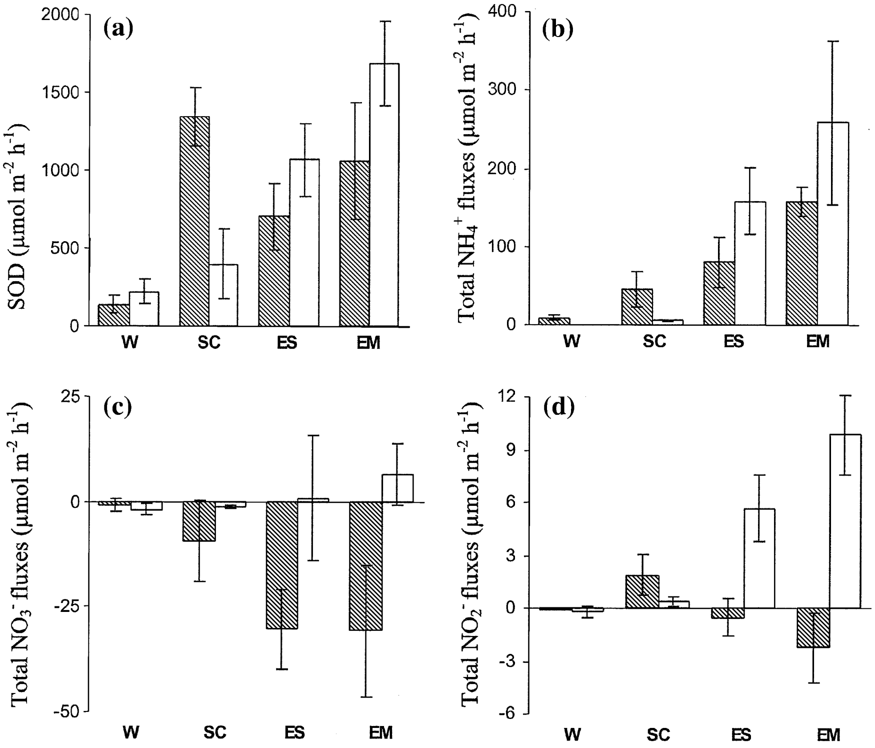
All incubations showed a significant oxygen flux directed towards the sediment. However we used the common term of Sediment Oxygen Demand (SOD) and oxygen exchanges were therefore regarded as positive. Average SOD values ranged from 139 to 1683 μmol m^{-2} h^{-1} (Fig. 2a). For each campaign, a gradient of SOD was evidenced with lowest values measured at station W and highest values at station EM. SOD significantly increased from March to May (WMW, $P < 0.01$) for all stations except station SC which had not follow this general trend with an extremely high SOD in March (1547 μmol m^{-2} h^{-1}). Total ammonium fluxes (Fig. 2b) were generally significant and directed towards the water column, in the range 6.3–157.8 μmol m^{-2} h^{-1} in March and 2.6–240.0 μmol m^{-2} h^{-1} in May. As for oxygen fluxes, an increase in ammonium exchanges from W to EM was systematically observed. Significant differences between stations were observed for both campaigns (KW, $P < 0.05$) with higher ammonium fluxes recorded in May for the estuarine stations whereas they significantly decreased at stations W and SC,

Table 2 General characteristics of surficial sediments at the different locations

Station	March					May				
	% clay	Porosity (0–1 cm/ 9–10 cm)	% T (0–3 cm)	% TOC (0–3 cm)	C:N ratio	% clay	Porosity (0–1 cm/ 9–10 cm)	% TN (0–3cm)	% TOC (0–3 cm)	C:N ratio
Wimereux	0.02	0.368/0.351	0.0017	0.06	37.91	0.07	0.385/0.373	0.0082	0.07	9.90
Sainte-Cécile	0.57	0.393/0.370	0.0039	0.17	25.28	1.10	0.371/0.362	0.0212	0.27	7.05
Estuary Sand	1.01	0.646/0.373	0.0329	0.45	7.63	2.23	0.655/0.364	0.0913	0.79	8.30
Estuary Mud	10.31	0.780/0.417	0.2115	1.92	6.33	18.55	0.882/0.517	0.2253	2.81	7.12

Average porosity, Total Nitrogen (TN), Total Organic Carbon content (TOC) and C:N atomic ratio are also mentioned

Fig. 2 Average (±S.D.) Sediment Oxygen Demand (SOD) (**a**), total ammonium (**b**), nitrate (**c**) and nitrite (**d**) fluxes measured during the March (*in grey*) and May (*in white*) samplings at the different locations (W: Wimereux; SC: Sainte-Cécile; ES: Estuary Sand; EM: Estuary Mud)



down to very low values. In contrast with ammonium and oxygen fluxes, more than 20% of the incubations resulted in nitrate fluxes that were not significantly different from zero. Nitrate fluxes across the sediment–water interface were largely dominated by nitrate uptakes (Fig. 2c). The intensity of these nitrate exchanges were maximal at station EM (−30.83 µmol m^{-2} h^{-1}) and minimal at the station W (−0.81 µmol m^{-2} h^{-1}). Significant differences between stations were observed in March with an increase of nitrate consumption from W to EM but this gradient disappeared in May, resulting in non-significant differences between the stations (KW, $P < 0.05$) and fluxes generally close to zero. However, a clear inversion in the sign of nitrate fluxes was observed for estuarine stations, from a large nitrate uptake in March to a low release in May. When fluxes were significant, a nitrite release was generally observed (Fig. 2d). The average exchange of nitrite reached maximal intensities for estuarine station from a significant uptake in March to a release in May. On the contrary, nitrite fluxes remained low at station W, with values ranging from −0.05 to −0.22 µmol m^{-2} h^{-1}. A significant difference between stations was noticed for each cruise (KW, $P < 0.05$). For both nitrate and nitrite fluxes, the standard deviations obtained for each station were high and indicated a strong spatial heterogeneity of nitrogen recycling processes in surficial sediment.

Pore water profiles and diffusive fluxes

All oxygen profiles showed a similar pattern, with concentrations close to oxygen saturation in the water column and a sharp decrease at depth (Fig. 3). Oxygen penetration depth was relatively similar during both campaigns, shallow for stations ES, EM and SC (respectively averaging 1.8; 2.0 and 3.4 mm) but higher values were recorded at station W (from 8 mm in March up to 10 mm in May). Based on the entire concentration profile concentration gradients, diffusive oxygen uptake varied from 80.05 to 2207 μmol m^{-2} h^{-1} with a clear gradient from station W to EM for both campaigns (Fig. 4a). The vertical distribution of dissolved ammonium followed the expected pattern of concentration increase with depth in the upper layer of the sediment (Fig. 5). In March, all stations showed very similar profiles but marked differences appeared in May, with highest concentrations in depth for estuarine stations. Average diffusive fluxes ranged from 2.49 (Station W) to 54.93 μmol m^{-2} h^{-1} (Station EM). A significant increase in ammonium release from March to May was observed, especially for the estuarine stations (Fig. 4b). Interstitial nitrate concentrations varied between low values at depth and maximum concentrations near the sediment water interface (Fig. 6). The sub-surface peak was generally located between the first and the third centimetres of sediment. Resulting diffusive fluxes ranged between 0.76 (Station SC in May) and 24.66 μmol m^{-2} h^{-1} (Station EM in May). Nitrate diffusive fluxes were significantly lower in May than in March at stations W and SC, whereas these fluxes significantly increased at the estuarine stations during the same period (WMW, $P < 0.05$). Measured pore water nitrite concentrations were always lower than 12 μmol l^{-1} and showed the same pattern as nitrate (Fig. 7). Consequent positive diffusive fluxes of nitrite (Fig. 4d) ranged from 1.03 (Station SC) to 29.93 μmol m^{-2} h^{-1} (Station EM) and significant differences between stations were observed in March with a gradient from station W to EM (KW, $P < 0.05$). This gradient disappears in May and no difference between stations was evidenced.

Biological characteristics

The estimated bacterial biomass in the first centimetre of sediment ranged from 1.27 to 4.36 mg C m^{-2} in March and from 1.78 to 6.51 mg C m^{-2} in May

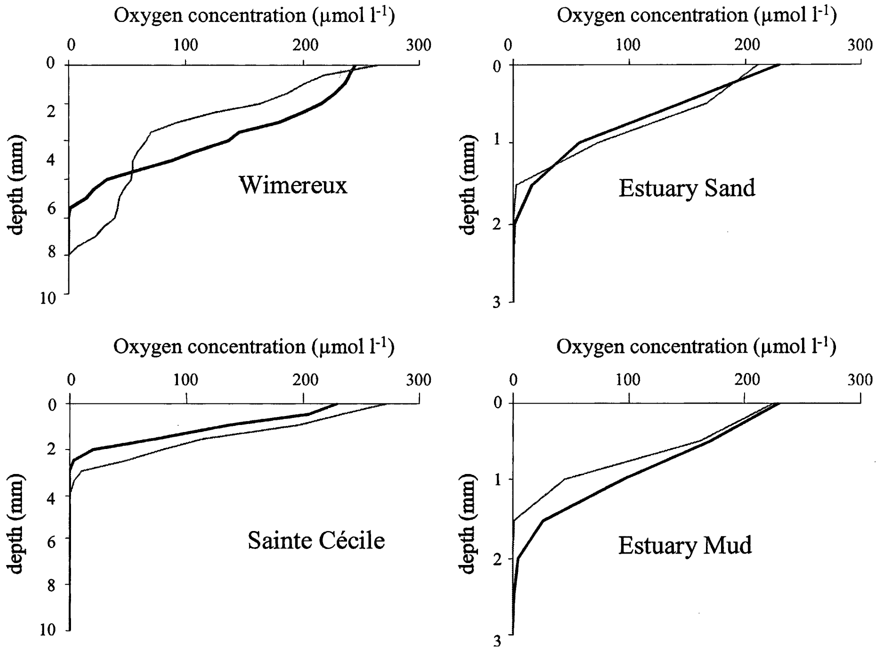


Fig. 3 Average oxygen concentration (μmol l^{-1}) profiles with depth (mm) measured in March (*thin line*) and May (*bold line*) at the different locations. Note the different ordinate scale

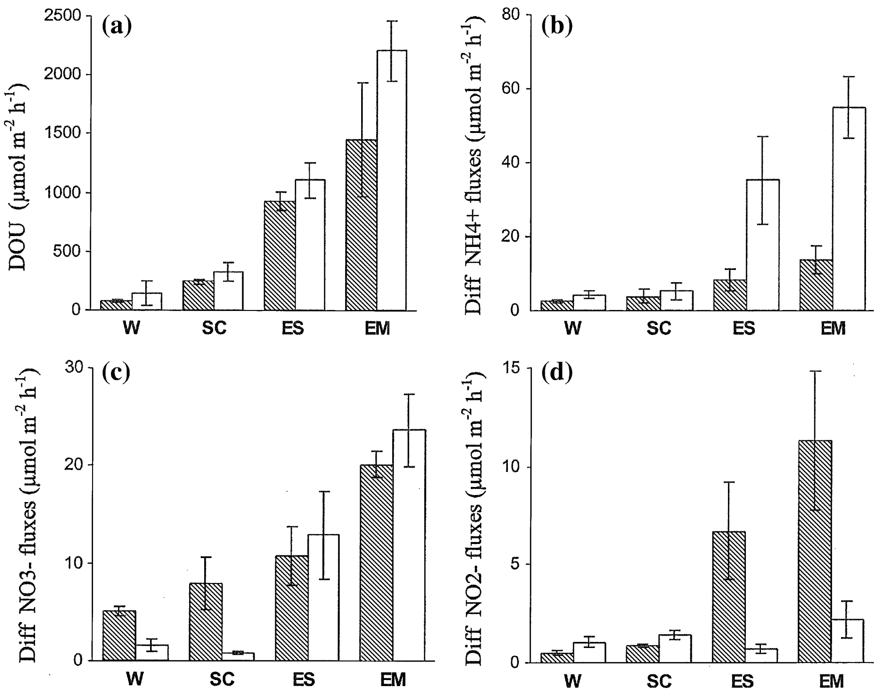


Fig. 4 Diffusive fluxes calculated from interstitial pore water profiles of oxygen (**a**), ammonium (**b**), nitrates (**c**) and nitrites (**d**) during March (*in grey*) and May (*in white*) samplings at the different locations (W: Wimereux; SC: Sainte-Cécile; ES: Estuary Sand; EM: Estuary Mud). Average predicted fluxes (±S.D.) of four replicates are given

(Table 3). For each sampling campaign, a significant difference between stations was evidenced with minimal values at station W and maximal values at station EM (KW, $P < 0.05$). Moreover, for all stations, bacterial biomass was significantly higher in May than in March (WMW, $P < 0.05$).

A total of 16 macrofaunal species were identified. The macrobenthic community observed at Wimereux was paucispecific, dominated by the amphipods *Bathyporeia sarsi* and *Bathyporeia pilosa*. Macrofaunal communities identified at stations ES and EM were composed almost exclusively of polychaetes *Hediste diversicolor* and *Heteromastus filiformis*, and contrasted with station SC. The values of average macrofaunal biomasses ranged from 4 to 493 mg AFDW m^{-2} (Table 3), except for station SC during the first cruise (more than 1860 mg AFDW m^{-2}). In this particular case, a large number of bivalves *Cerastoderma edule* were found and explained the high biomass observed. These macrofauna biomasses strongly decrease from March to May for the whole of the stations.

Relationship between variables

In order to describe the relationships between variables, Pearson's correlation coefficients were calculated by considering the whole data set (Table 4). With a global view, edaphic parameters (TOC and fine particles %) were strongly correlated with bacterial biomass estimations. Inversely macrofauna biomass was not correlated to any parameters. Biogeochemical descriptors were also linked to environmental variables. Total fluxes of oxygen, ammonium and nitrite exhibited a significant relationship with sedimentary characteristics Calculated diffusive fluxes derived from pore water profile were generally strongly correlated with edaphic parameters but might be partly explained by use of the porosity in the calculation of diffusive fluxes.

Discussion

Total versus diffusive fluxes

From a general point of view, diffusive fluxes calculated from pore water gradients did not fully agree with total fluxes measured by whole core incubation. Except for oxygen, diffusive fluxes were always lower than total fluxes, phenomenon often observed (Hammond et al. 1985; Lerat et al. 1990). Moreover, nutrient diffusive exchanges were always positive while the direction of total fluxes varied (especially for nitrate

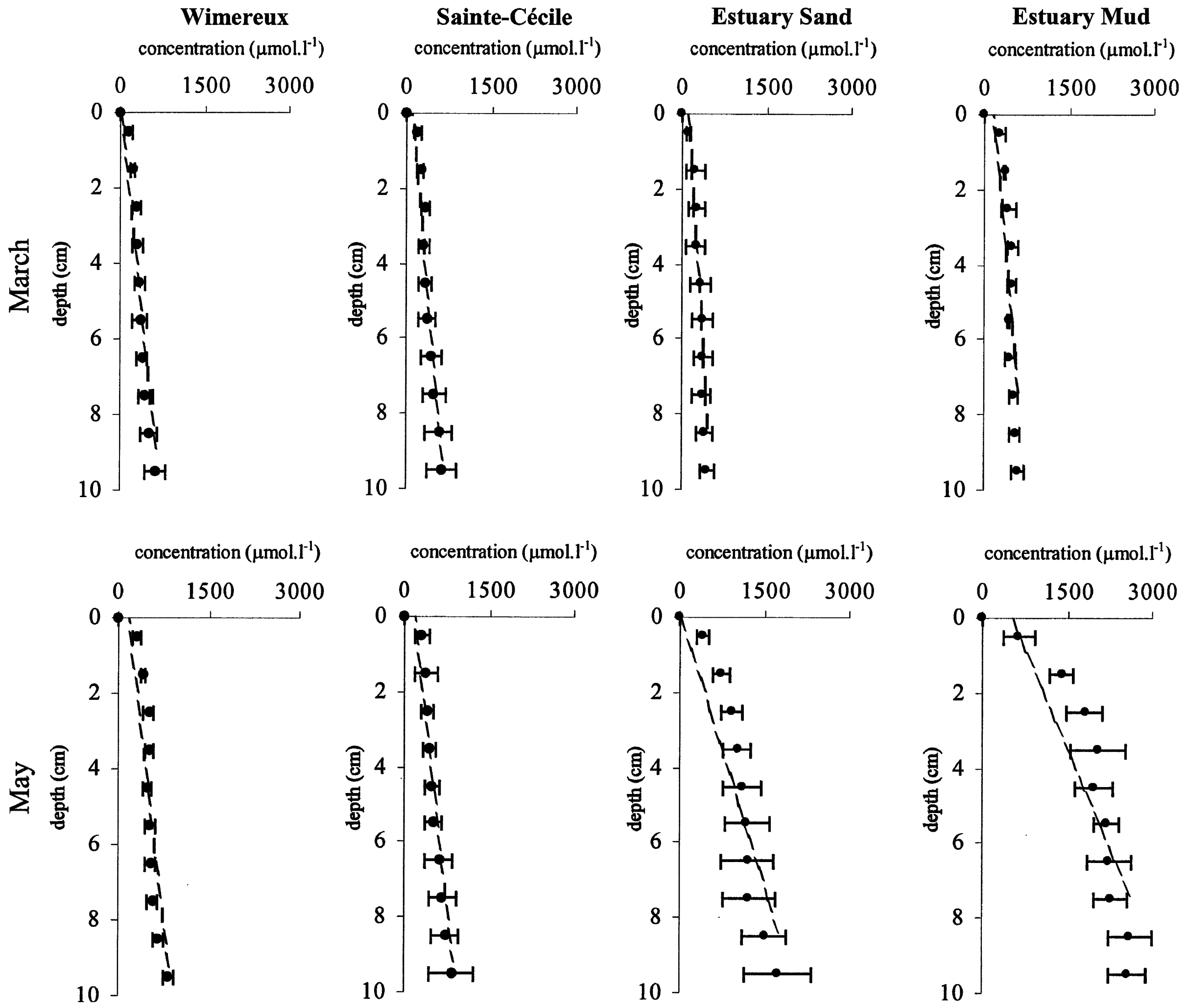


Fig. 5 Variation with depth (0–10 cm) in the sediment of ammonium concentration (µmol l^{-1}) in interstitial water at the different locations. Average values of four incubated cores (±S.D.) are given and lines correspond to the best linear fit

and nitrite). More than a possible regulation of exchanges by benthic fauna, the discrepancy between measured and calculated fluxes might result from fine scale heterogeneity. Our diffusive flux estimations of nutrients are based on coarse profiles (centimetric scale) and should be considered as minimum estimates as steep gradients exist near the sediment water interface, which might only be captured at microscale. Meyer et al. (2005) by using a microscale biosensor show that $NO3^{-}$ concentration peak occurs at a millimetric scale. During this study, nitrate peak was often located below the oxic zone. Nevertheless it was difficult to know if the depth of the peak was correct or if it was only consecutive to the migration of interstitial nitrate during slicing.

Spatial variability and sedimentary gradient

A granulometric gradient was clearly evidenced from station W to station EM (with respectively 0.04% and 14.43% of fine particles). The estuarine stations were partly sheltered and limited hydrodynamic forcing conducted to the accumulation of fine sedimentary material. By contrast, the strong hydrodynamic forcing on the exposed beach of Wimereux prevented the accumulation of fine particles. SC station, located near a trough, corresponded to a medium hydrodynamism and resulted in an intermediate percentage of fine particles. Numerous other parameters were tightly linked to this granulometric gradient. Thus, a low and uniform porosity was recorded at stations W

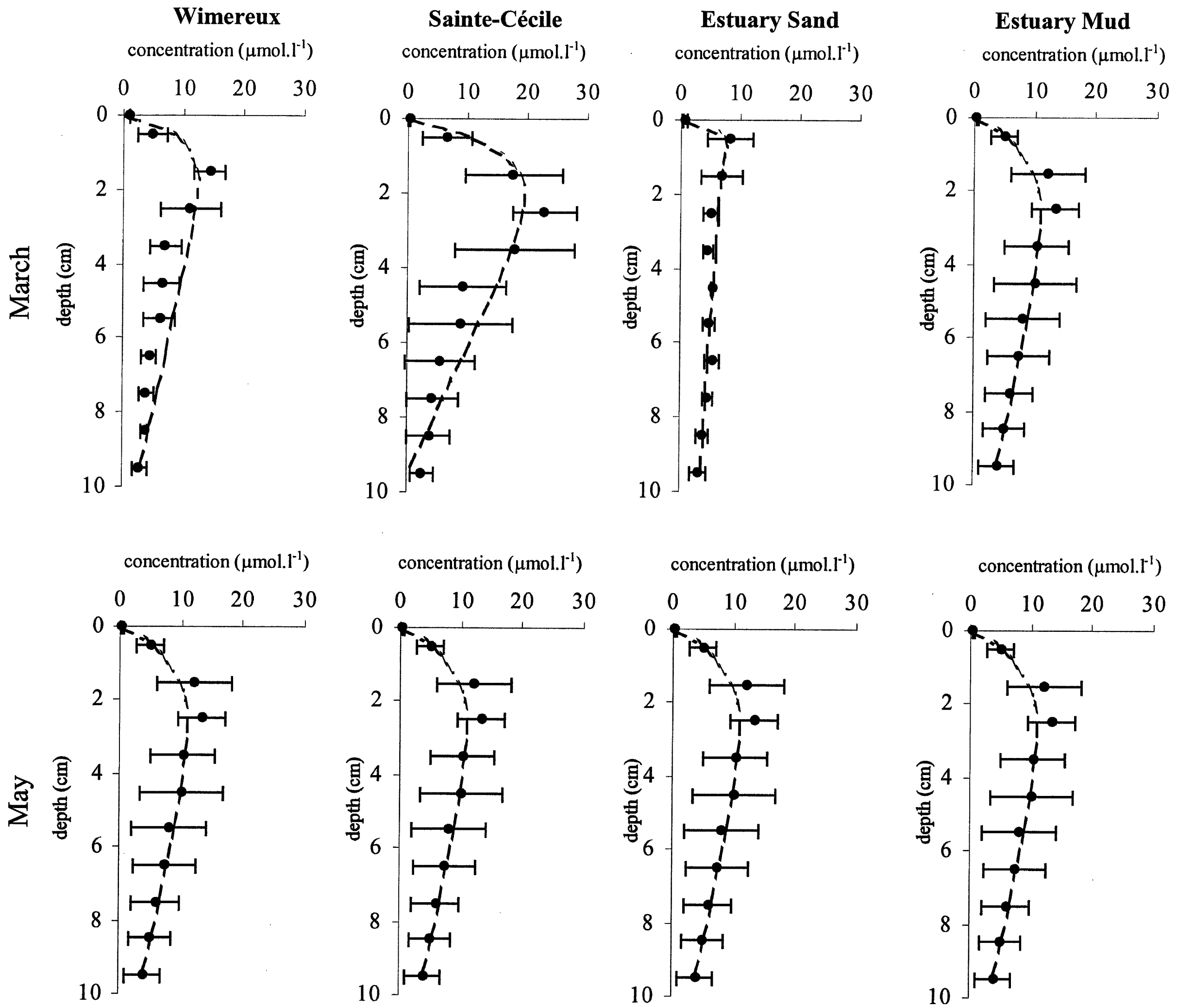


Fig. 6 Variation with depth (0–10 cm) in the sediment of nitrate concentration (µmol l^{-1}) in interstitial water at the different locations. Average values of four incubated cores (±S.D.) are given and lines correspond to the best fit to an empirical formulation (*see details in text*)

and SC (approximately 0.3), characterizing permeable sediments (Huettel and Rusch 2000), whereas an exponential vertical gradient resulting from compaction was observed at estuarine stations, up to a surface porosity around 0.9. Benthic bacteria presented a stronger biomass in estuarine sediments than at stations W and SC, in accordance with Meyer-Reil et al. (1977) who reported a negative correlation between bacterial abundance and the average size of particles. As the intensity of benthic mineralization depends on the abundance and activity of mineralizing organisms as well as the quantity of organic matter (Arnosti and Holmer 2003), spatial variations already described were logically found for biogeochemical parameters. Consequently, strongly significant correlations appeared between total and diffusive fluxes of oxygen and ammonium and the sedimentary characteristics such as fine particles percentage or TOC (Table 4).

Our data were compared with the limited literature dealing with sediment biogeochemistry in intertidal ecosystems. Authors generally reported that SOD in muddy environments (Boon et al. (1999): 406–1704 µmol m^{-2} h^{-1}; This study: 707–1683 µmol m^{-2} h^{-1}) was higher than in permeable sands (Dauwe et al. (2001): 95–175 µmol m^{-2} h^{-1}; This study:

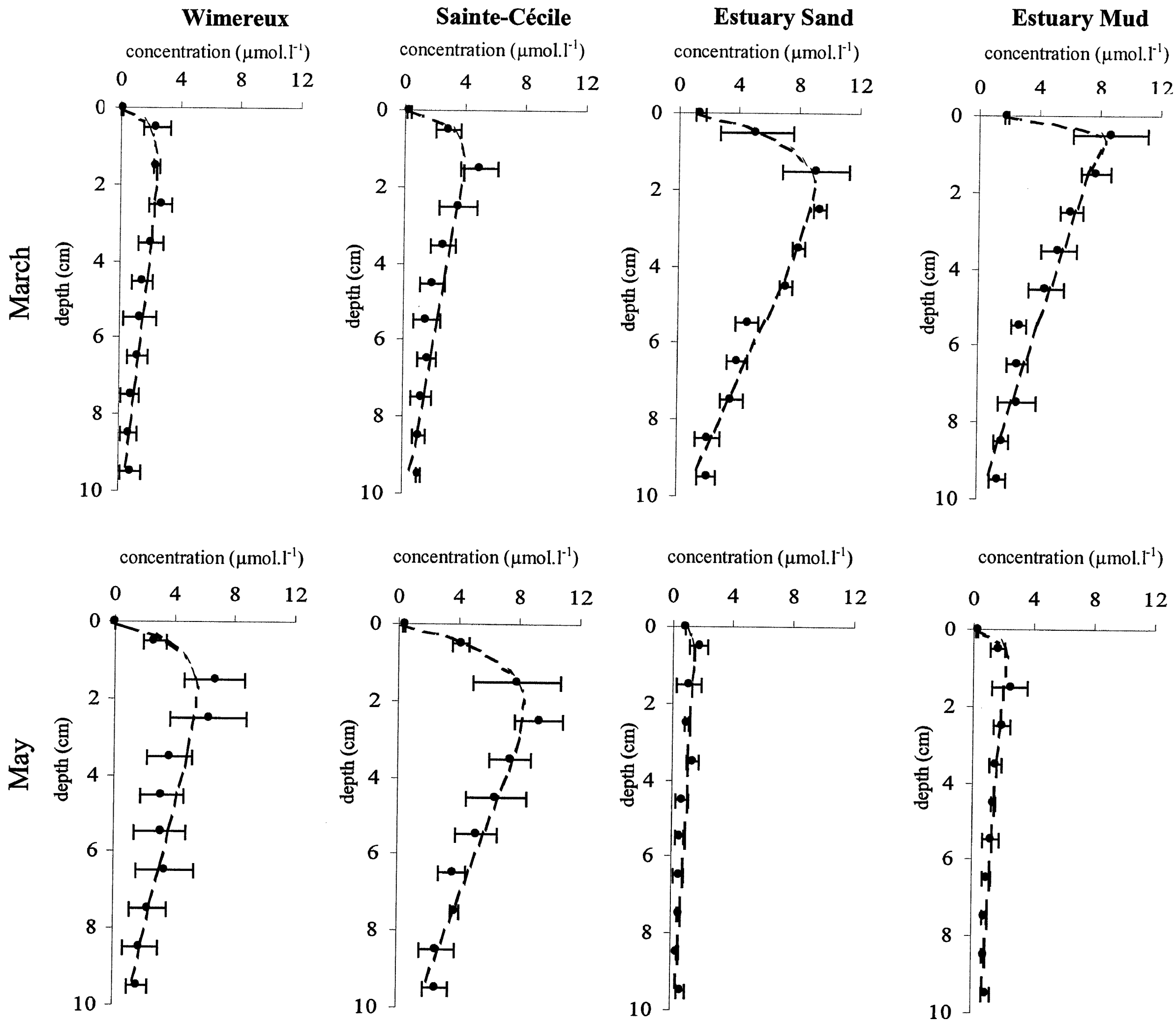


Fig. 7 Variation with depth (0–10 cm) in the sediment of nitrite concentration (µmol l^{-1}) in interstitial water at the different locations. Average values of four incubated cores (±S.D.) are given and lines correspond to the fit to an empirical formulation (*see details in text*)

Table 3 Biological characteristics of the stations studied during the two sampling cruises

Station	Bacterial abundance (10^7Cell ml^{-1})		Bacterial biomass (mg C m^{-2})		Macrofauna biomass (mg m^{-2})		Macrofauna density (ind m^{-2})	
	March	May	March	May	March	May	March	May
Wimereux	0.64	0.89	1.27	1.78	68.7	11.3	31.8	81.3
Sainte-Cécile	0.73	1.31	1.44	2.6	1894.6	176.2	346.7	45.9
Estuary sand	1.78	2.91	3.54	5.77	167.3	9.1	166.2	24.8
Estuary mud	2.19	3.27	4.36	6.51	492.8	4.3	434.9	10.6

139–400 µmol m^{-2} h^{-1}). Measurements of intertidal ammonium fluxes demonstrated a great participation of estuarine stations to NH4+ release (Hammond et al. (1985): 40–208 µmol m^{-2} h^{-1}; This study: 79–240 µmol m^{-2} h^{-1}) with regard to sand (Hammond et al. (1985): 4–67 µmol m^{-2} h^{-1}; This study: 0.5–

Table 4 Pearson correlation coefficients ($n = 32$) calculated between total fluxes measured by whole core incubation (*Tot xx*), diffusive fluxes calculated from pore water gradients (*Diff xx*), macrofauna biomass (*MacF*), bacterial biomass (*Bact*), and differents parameters measured in the sediment (clay %, Total Organic Carbon: TOC)

	Tot O_2	Tot NH_4^+	Tot NO_3^-	Tot NO_2^-	Diff O_2	Diff NH_4^+	Diff NO_3^-	Diff NO_2^-	MacF	Bact	clay %	TOC
TOC	**0.647**	**0.801**	−0.023	0.541	**0.917**	**0.808**	**0.864**	0.437	−0.249	**0.905**	**0.950**	1.000
clay %	**0.634**	**0.775**	0.039	**0.616**	**0.944**	**0.839**	**0.883**	0.324	−0.214	**0.849**	1.000	
Bact	**0.641**	**0.874**	0.274	**0.661**	**0.962**	**0.885**	**0.786**	0.251	−0.361	1.000		
MacF	0.444	−0.117	−0.163	−0.123	−0.321	−0.266	−0.024	−0.046	1.000			
Diff NO_2^-	0.249	0.262	−0.446	−0.388	0.448	−0.050	0.469	1.000				
Diff NO_3^-	**0.708**	**0.762**	−0.162	0.437	**0.903**	**0.712**	1.000					
Diff NH_4^+	0.551	**0.670**	0.240	**0.819**	**0.897**	1.000						
Diff O_2	**0.682**	**0.798**	0.124	**0.609**	1.000							
Tot NO_2^-	0.520	0.494	0.434	1.000								
Tot NO_3^-	−0.148	0.003	1.000									
Tot NH_4^+	**0.714**	1.000										
Tot O_2	1.000											

Coefficients significant at $P < 0.05$ are in bold

49 µmol m^{-2} h^{-1}). Such comparisons were more difficult for nitrate due to the high variability in fluxes direction, as reported in Grenz et al. (2000).

Macrofaunal influence

Macrobenthic assemblages at estuarine stations corresponded to the *Abra alba—Macoma balthica—Donax vittatus* facies of the *Abra alba* settlement (Desroy et al. 2002) generally identified as the oligospecific *Macoma balthica* community (Petersen 1913). In contrast, faunistic composition observed on the beach of Wimereux corresponded to the intertidal clean fine sands settlements (Dewarumez et al. 1988) generally considered as a part of the impoverished *Abra alba—Corbula gibba* community described by Cabioch and Glaçon (1975). For many authors, faunistic diversity is directly related to the sediment nature. Macrofaunal assemblages in the estuarine stations were dominated by polychaetes and bivalves, as commonly reported for estuarine mudflats (Mortimer et al. 1999; Desroy and Denis 2004) while the fine sands of Wimereux were characterized by a dominance of crustaceans already described for intertidal sandy beaches (Lastra et al. 2006). SC station showed strong macrofaunal biomass in March (related to the very high densities of the bivalve *Cerastoderma edule*) that largely explained the very high values of oxygen consumptions and ammonium releases. This event was remarkable, because if all stations and dates were considered, no parameter was correlated with macrofauna biomass (Table 4). However, there was a significant correlation between macrofaunal biomass and total fluxes of oxygen, ammonium and nitrate for station SC in March. The ordinates at the origin of each linear regression (Fig. 8) gives the theoretical

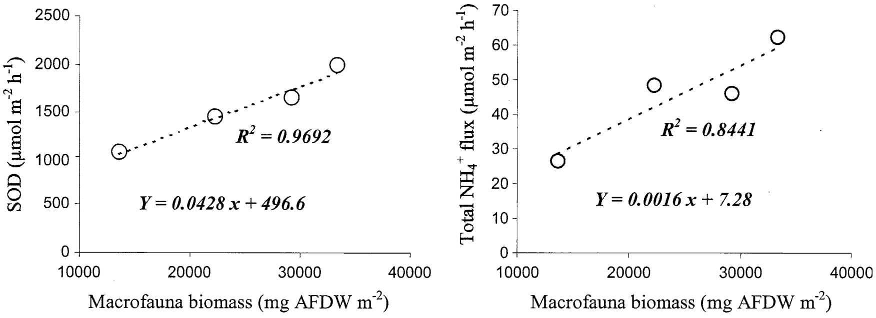


Fig. 8 Sediment Oxygen Demand (SOD) and total ammonium fluxes as a function of macrofauna biomass (in mg Ash Free Dry Weight m^{-2}) at Station SC in March. Equations of best linear fit are given

fluxes in the absence of macrofauna, values that were close to the values measured at Sainte-Cécile beach in May (Theoretical values obtained: 496.6 and 7.28 µmol m^{-2} h^{-1} respectively for the SOD and ammonium fluxes in March, against 400 and 5.43 µmol m^{-2} h^{-1} in May). Although bacteria are generally the key actors in organic matter degradation processes, macrofauna activity might directly influence dissolved exchanges at the sediment–water interface during such periods of exceptionally high macrofaunal biomasses (Kristensen et al. 1992; Pelegri et al. 1994, Mortimer et al. 1999).

Temporal variability and mineralization processes

Factors such as nutrient concentrations in the water column and temperature were often suggested being regulators of sediment–water exchange rates (Dollars et al 1991; Grenz et al 2000). In our study, temperature variations were very limited, in the range of 10.0–11.7 and could not explain the variability of benthic processes (Table 1). The same constatation could be made for hydrological variables. Even if a decrease of ammonium in the water column was evidenced for all stations, this evolution was too limited to explain changes in diffusive fluxes. For nitrate, the change was too erratic to be linked to the temporal evolution of nutrient fluxes. So the spring bloom was probably the main explicative factor of temporal variability. The massive sedimentation of organic matter on the intertidal zone was the major consequence of *Phaeocystis* sp. spring bloom on the benthic system (Cadée 1996) and was confirmed in our study by a significant increase of TOC in all stations (WMW, $P < 0.05$) but muddy substrates were more enriched in organic carbon (+0.34% dry weight) than sandy substrate (+0.03% dry weight). As previously stated by Desroy and Denis (2004) hydrodynamic forcing was probably the essential parameter controlling this mechanism, with perennial deposits in sheltered estuarine area whereas sandy environments were submitted to a fast dispersion of the organic matter. The difference in the impact of foam deposition between stations could be evidenced by means of a 2-way ANOVA. Although the raw data did not allow the use of a parametric test, a logarithmic transformation of these data was performed to fit the assumption of homoscedasticity (Bartlett test, $P < 0.05$). The 2-way ANOVA (Table 5) confirmed the result of the non parametric test about the effect of date (due to organic matter supply) and the difference among stations (due to hydronamism) but for most of the biogeochemical descriptors (oxygen, ammonium and nitrites fluxes), we could also evidence a significant interaction between dates and sites. Such interactive effect indicated that the influence of foam deposits was not similar in the four stations. With a global view, two groups of stations were characterized, that strongly differed by their sedimentary characteristics but also in their temporal evolution.

The beaches of Wimereux and Sainte Cécile (to a lower extend) showed lower nutrients fluxes during both campaigns, in accordance with previous works that generally consider sandy shores as low reactive environments. The coarse granulometry resulted in enhanced advective transport of dissolved compounds but also of organic matter. Moreover, limited accumulation occurred, as a consequence of the short residence time of the interstitial water at a given depth, that limiting dissolved species transformation by the bacterial metabolic pathways. The biogeochemical mechanisms were characterized by an ammonium release associated with a moderate consumption of nitrates and foam deposition did not change this pattern. Nevertheless, a significant increase in the

Table 5 Results of a 2 way ANOVA used to test date and station effects on the total fluxes of oxygen, ammonium, nitrate and nitrite (log transformed data, *see details in text*)

Source of variation	df	O_2 flux		NH_4^+ flux		NO_3^- flux		NO_2^- flux	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Date	1	10.71	<0.001***	2.22	0.149 ns	6.16	0.020*	40.02	<0.001***
Station	3	24.27	<0.001***	82.82	<0.001***	1.81	0.174 ns	3.92	0.021*
Date × station	3	6.85	0.002**	10.01	<0.001***	2.62	0.074 ns	23.42	<0.001***

ns: not significant,* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 6 Summary of primary production and respiration in the intertidal area of the eastern English Channel

		$t\ C\ d^{-1}$	Source	Study site
Benthic respiration				
Flooded	Sand	0.68	This study	Wimereux beach
	Mud	0.56	This study	Bay of Canche
	Total	1.24		
Exposed	Sand	0.32	Spilmont et al. 2005	Wimereux beach
	Mud	0.75	Migné et al. 2004	Bay of Somme
	Total	1.07		
Total benthic respiration		2.31		
Primary production				
Flooded (water column)		2.61	Lizon et al. unpublished data	Wimereux beach
Exposed (microphytobenthos)	Sand	0.64	Spilmont et al. 2005	Wimereux beach
	Mud	0.70	Migné et al. 2004	Bay of Somme
	Total	1.34		
Total primary production		3.95		

exchanges of dissolved compounds is evidence of a stimulation of mineralization processes and indicated a fast response time of the bacterial communities to organic matter inputs. Sandy beaches, usually neglected in the biogeochemical studies and often regarded as largely inactive due to their low organic content (Boudreau et al. 2001; Viollier et al. 2003), can show moderate but measurable responses to organic matter supply. However the use of whole-core incubation technique is not well adapted for the sandy zones exposed to the waves. Fluxes were certainly underestimated because pore water renewal (i.e., pumping effect; Rusch et al. 2000) was not taken into account. Recent studies suggest that large volumes of water generally flush through permeable sands. For example, Precht and Huettel (2003) estimated filtering rate of sandy beaches around 42 $l\ m^{-2}\ h^{-1}$ whereas at 50 m depth on the continental shelf near the Eel River this rate was only 4.3 $l\ m^{-2}\ h^{-1}$.

The most intensive fluxes appeared on the level on the muddy stations where high organic matter supply maintained an intense nutrient recycling. Contrary to sandy beaches, foam deposits were accompanied by some profound changes of biogeochemical reactions, particularly for nitrogen cycling. An inversion of nitrate fluxes was noticed, from consumption in March to a low release from the sediments in May. This nitrate production could result from an intensification of nitrification (dues to organic matter supply) and simultaneous nitrites releases confirm such assumption. The nitrates profiles do not show any change but many authors confirm that nitrification processes were generally coupled to denitrification in estuarine sediment (Lohse et al. 1996; Caffrey et al. 2003). The efficiency of this coupling in coastal sediment may be extremely variable and the part of nitrate lost by denitrification ranged from 9% in Odawa Bay (Nishio et al. 1983) to 99% in Chesapeake Bay (Jenkins and Kemp 1984). Then, the nitrate release measured in May could result from an incomplete nitrification/denitrification coupling. The reduction of this coupling has already been experimentally evidenced for muddy sediment after adding $NH4^{+}$ (Jensen et al. 1993). These authors explained these uncoupling by the spatial plasticity in the microdistribution of nitrification activity in response to $NH4^{+}$ sources, with a shift in the relative diffusion distance from the site of $NO3^{-}$ production to the overlying water and to denitrification layers.

Ecological implications of mineralization processes

We constructed a budget of mineralization processes. Oxic respiration being the main carbon mineralization process, a conversion of SOD (in $\mu mol\ O_2 m^{-2}\ h^{-1}$) into organic carbon mineralization (in $mg\ C\ m^{-2}\ h^{-1}$) was performed with a respiratory quotient of 0.85 (Denis and Grenz 2003). Based on both campaigns, SOD averaged 253.3 μmol O_2 m^{-2} h^{-1} in sandy stations (W and SC) and 1130 μmol O_2 m^{-2} h^{-1} in estuarine stations (ES and EM) resulting in mineralization rates of 2.58 and 11.53 mg C m^{-2} h^{-1} respectively. Cohesive sediments show higher apparent mineralization rates, as previously pointed out by numerous authors (Boon et al. 1999; Trimmer et al. 1999). For accurate budget calculation, one needs to consider the area covered by the different substrates. For the area located between the Somme Bay and Cape Griz Nez (Fig. 1) intertidal substrates consist in approximately 4.2km^2 of rocky coast (6.1% of the intertidal area), 56 km^2 of sandy beaches (79.4%) and 9.8 km^2 of intertidal mudflats (14.5%). Taking into account the quantitative importance of each sediment type, benthic mineralization by permeable sediments then represents up to 0.68 t C d^{-1} against 0.56 t C d^{-1} for cohesive sediments. In spite of reaction rates 5 times lower than muds (and certainly underestimated because of methodological limitations), the consideration of areas covered by permeable sediments (70% of continental shelves to the world scale (Emery 1968)) could change the common perception of sandy beach as geochemical deserts. This first approach only considered benthic respiration during the immersion period, which represent approximately half of the time. A more realistic carbon budget considering water column primary production, benthic respiration and microphytobenthic production during the emersion period was presented in Table 6. These results suggest that sediments account for approximately 59% of carbon recycling in this intertidal area, with a large participation of permeable sand (40%). It could be objected here that the total primary production is underestimated due to the absence on data about the microphytobenthic production during immersion, but according to Migné et al. (2004), this production is very low and can be neglected due to high turbidity of bottom water (Particulate Suspended Material averaging 60 mg l^{-1} for English Channel coastal water, Smaoui et al. 2007). Moreover, pelagic mineralization was not taken into account, but few measurements in the coastal zone close to Wimereux gave very low values of pelagic respiration, inferior to 0.035 t d^{-1} (Lizon et al. unpublished data). Rather surprisingly while considering their low TOC content, the influence of permeable sediments was already pointed out by Jahnke et al. (2005) who found that 50% of the primary production could be respired in South Atlantic Bight continental shelf permeable sediments.

The nutrient releases from the sediments are rapidly exported because of tidal movements. To quantify the influence of benthic nutrient recycling in a realistic context, we compared the relative importance DIN releases from the intertidal sediments with other inputs of DIN. In the area of interest, a coastal water mass which drifts along the shore is individualized near the French coast. This water mass, named *''Coastal Flow''*, separated from the open sea by a tidally-maintained frontal area has an

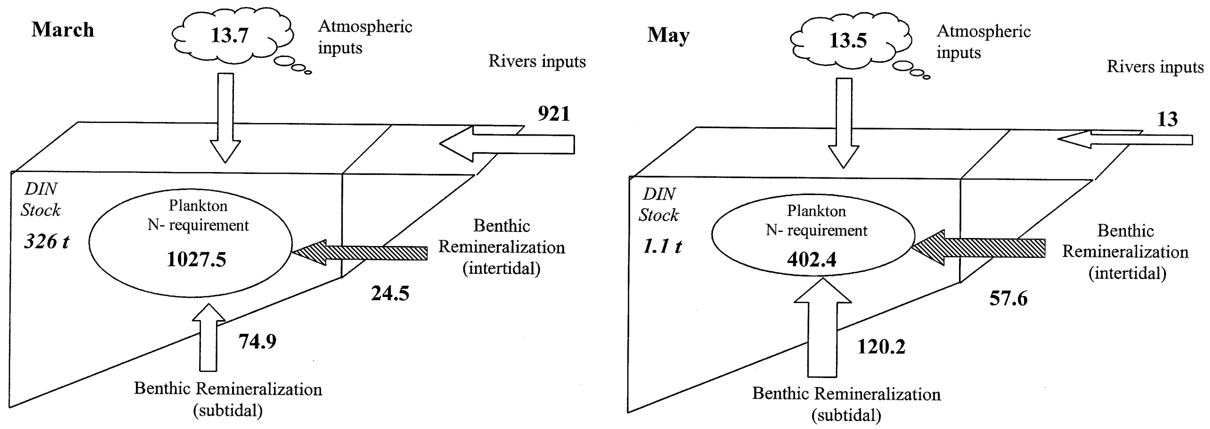


Fig. 9 Evolution of DIN budget from March 2003 to May 2003 (t month^{-1}). DIN stock, atmospheric and rivers inputs are given in Boulart et al. (2006). Water column DIN requirements are estimated assuming Redfield stoechiometry and the primary production measured by Lamy et al. (2006)

approximate total area of 111 km^2 and the volume of the water body was about 3 km^3 (Boulart et al. 2006). Figure 9 shows the contribution of each source in the supply of DIN to the water column. Atmospheric and fluvial inputs as well as water column DIN stock are given in Boulart et al. (2006) whereas benthic DIN release of subtidal area were derived from permeable sediments mineralization rates (rocky shores and cohesive sediments were almost absent in the subtidal area (Anthony 2002)). The contribution of these nitrogen releases was compared to the DIN requirements of phytoplankton calculated assuming Redfield stoechiometry and the primary production measured in the same area in March and May 2003 by Lamy et al. (2006). When the pelagic bloom occurs (March), the strong DIN requirement of phytoplankton (due to the intense primary production) could easily be supported water column DIN stock and fluvial inputs. During the post-bloom phase (May) water column was nutrient-depleted while riverine inputs strongly decreased, hence potentially limiting primary production. In the same time, DIN release by intertidal sediments was stimulated by the phytodetritus deposits and the contribution of benthic mineralization, negligible in March, could support up to 14% of the total primary production. Thus benthic recycling may supply a substantial fraction of the nutrient requirement for primary production in coastal areas, as observed in other coastal systems (Dollars et al. 1991; Denis et al. 2001).

Conclusions

The French coast of eastern English Channel is marked by a strong spatial variability of the biogeochemical environments dues to the sedimentary texture (mainly under the control of hydrodynamic forcing). The strong correlation between bacterial biomass and the biogeochemical descriptors confirm the importance of micro organism for the organic matter recycling. The spring efflorescence of *Phaeocystis* sp. resulted in a high organic matter input, leading to an increase of SOD and nutrients fluxes at the sediment–water interface. This strong release of dissolved substances results from various processes according to the sedimentary type. The muddy environment undergoes some profound changes of biogeochemical processes, particularly of the nitrogen cycling with a clear inversion of nitrate fluxes, passing from consumption in March to a low release from the sediments in May. On the contrary, the balance of biogeochemical reactions remains similar in sandy sediments even if the mineralization of organic matter is stimulated. Finally, this work highlights that benthic regeneration processes were significant in intertidal sediments of eastern English Channel as a source of nutrient for primary production. Since the quantity of organic matter inputs is highly variable on an annual scale, a seasonal study is necessary to quantify the importance of benthic regeneration in ecosystem functioning. Future work will have to give a detailed attention to the permeable sediments which have largely been neglected up to date.

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References

Aller RC, Hall PO, Rude PD, Aller JY (1998) Biogeochemical heterogeneity and suboxic diagenesis in hemipelagic sediments of the Panama Basin. Deep Sea Res Part I 45:133–165

Aminot A, Chaussepied M (1983) Manuel des analyses chimiques en milieu marin, Centre National pour l'Exploitation des Océans (CNEXO)

Anthony E (2002) Long term marine bedload segregation and sandy versus gravelly Holocene shorelines in the eastern English Channel. Mar Geol 187:221–234

Arnosti C, Holmer M (2003) Carbon and continental margin sediment: contrasts between organic matter characteristics and remineralization rates and pathways. Estuar Coast Shelf Sci 58:197–208

Artigas F (1998) Seasonal variability in microplanktonic biomasses in the Gironde dilution plume (Bay of Biscay): relative importance of bacteria. Oceanol Acta 21:563–580

Berg P, Risgaard-Petersen N, Rysgaard S (1998) Interpretation of measured concentration profiles in sediment pore water. Limn Oceanogr 43:1500–1510

Berner RA (1980) Early diagenesis: a theoretical approach. Princeton Univ. Press, Princeton

Blackburn TH (1988) Benthic mineralization and bacterial production. In: Blackburn TH, Sørensen J (eds) Nitrogen cycling in coastal marine environments. Wiley, New York

Boon AR, Duineveld A, Kok A (1999) Benthic organic matter supply and metabolism at depositional and non-depositional areas in the North Sea. Estuar Coast Shelf Sci 49:747–761

Boudreau BP, Huettel M, Forster S, Jahnke R, McLachlan A, Middelburg J, Nielsen P, Sansone F, Taghon G, Van Raaphorst W, Webster I, Marcin Weslawski J, Wiberg P, Sundby B (2001) Permeable marine sediment: overturning an old paradigm. Est Coast Shelf Sci 82:133–136

Boulart C, Flament P, Gentilhomme V, Deboudt K, Migon C, Lizon F, Schapira M, Lefebvre A (2006) Atmospherically-promoted photosynthetic activity in a well-mixed ecosystem: significance of wet deposition events of nitrogen compounds. Est Coast Shelf Sci 69:449–458

Cabioch L, Glaçon R (1975) Distribution des peuplements benthiques en Manche Orientale, de la Baie de Somme au Pas-de-Calais. CR Acad Sci Paris 280:491–494

Cadée G (1996) Accumulation and sedimentation of *Phaeocystis globosa* in the dutch Wadden Sea. J Sea Res 36:321–327

Caffrey J, Harrington N, Solem I, Ward B (2003) Biogeochemical processes in a small California estuary. 2. Nitrification activity, community structure and role in nitrogen budgets. Mar Ecol Prog Ser 248:27–40

Chamley H (1987) Sédimentologie. Dunod, Paris

Chevaldonné P, Godfroy A (1997) Enumeration of microorganisms from deep sea hydrothermal chimney samples. FEMS Microbiol Lett 146:211–216

Christaki U (1995) Régulations trophiques et interactions microbiennes en milieu pélagique, relation avec les métazoires. phD Thesis, Université d'Aix-Marseille II

Christensen JP, Nielsen LP, Revsbech NP, Sorensen J (1989) Microzonation of denitrification activity in stream sediments as studied with a combined oxygen and nitrous oxide microsensor. Appl Environ Microbiol 55:1234–1241

Dauwe B, Middelburg J, Herman P (2001) Effect of oxygen on the degradability of organic matter in subtidal and intertidal sediments of the North Sea area. Mar Ecol Prog Ser 215:13–22

Denis L, Grenz C (2003) Spatial variability in oxygen and nutrient fluxes at the sediment-interface on the continental shelf in the Gulf of Lions (NW Mediterranean). Oceanol Acta 26:373–389

Denis L, Grenz C, Alliot E, Rodier M (2001) Temporal variability in dissolved inorganic nitrogen fluxes at the sediment–water interface and related annual budget on a continental shelf (NW Mediterranean). Oceanol Acta 24:85–97

Desroy N, Denis L (2004) Influence of spring phytodetritus sedimentation on intertidal macrozoobenthos in the eastern English Channel. Mar Ecol Prog Ser 270:41–53

Desroy N, Warembourg C, Dewarumez J-M, Dauvin J-C (2002) Macrobenthic resources of the shallow soft-bottom sediments in the eastern English Channel and southern North Sea. ICES J Mar Sci 60:120–131

Dewarumez J-M, Davoult D, Prygiel J, Glaçon R, Richard A (1988) Macrozoobenthic communities assemblages in the southern part of the North Sea (French coast). Coast Newsl 1988:103–106

Dollars SJ, Smith SV, Vink SM, Obrbski S, Hollibaugh JT (1991) Annual cycle of benthic nutrient fluxes in Tomates Bay, California, and contribution of the benthos to total ecosystem metabolism. Mar Ecol Prog Ser 79:115–125

Emery K (1968) Relict sediments on continental shelves of the world. Am Ass Petrol Geol Bull 52:445–464

Froelich PN, Klinkhammer GP, Bender ML, Luedtke NA, Heath GR, Cullen D, Dauphin P (1979) Early oxidation of organic matter in pelagic sediments of the eastern equatorial Atlantic: suboxic diagenesis. Geochim Cosmochim Acta 43:1075–1090

Gentilhomme V, Lizon F (1998) Seasonal cycle of nitrogen and phytoplancton biomass in a well-mixed coastal system (Eastern English Channel). Hydrobiologia 361:191–199

Gilbert F, Bonin P, Stora G (1995) Effect of bioturbation on denitrification in a marine sediment from the West Mediterranean littoral. Hydrobiologia 304:49–58

Glud R, Gundersern J, Revsbech N, Jorgensen B, Huettel M (1995) Calibration and performance of the stirred flux chamber from the benthic lander Elinor. Deep Sea Res 42:1029–1042

Grenz C, Cloern J, Hager SW, Cole BE (2000) Dynamics of nutrient cycling and related benthic nutrient and oxygen fluxes during a spring phytoplankton bloom in south San Francisco Bay (USA). Mar Ecol Prog Ser 197:67–80

Hammond D, Fuller C, Harmon D, Hartman B, Korosec M (1985) Benthic fluxes in San Francisco Bay. Hydrobiol 129:69–90

Huettel M, Rusch A (2000) Transport and degradation of phytoplancton in permeable sediments. Limnol Oceanogr 43:534–549

Jahnke R, Richards M, Nelson J, Robertson J, Rao A, Jahnke D (2005) Organic matter remineralization and pore water exchange rates in permeable South Atlantic Bight continental shelf sediments. Cont Shelf Res 25:1433–1452

Jenkins M, Kemp M (1984) The coupling of nitrification and denitrification in two estuarine sediment. Limnol Oceanogr 29:609–619

Jensen K, Revsch NP, Nielsen LP (1993) Microscale distribution of nitrification activity in sediment determined with a shielded microsensor for nitrate. Appl Env Microbiol 59:3287–3296

Koroleff F (1969) Direct determination of ammonia in natural waters as indophenol blue. ICES CM 9:1–6

Kristensen E, Andersen F, Blackburn TH (1992) Effects of benthic macrofauna and temperature on degradation of macroalgal detritus: fate of organic carbon. Limnol Oceanogr 37:1404–1419

Lamy D, Artigas L-F, Jauzein C, Lizon F, Cornille V (2006) Coastal bacterial viability and production in the eastern English Channel: a case study during a *Phaeocystis globosa* bloom. J Sea Res 56:227–238

Lancelot C (1995) The mucilage phenomenon in the coastal waters of the north sea. Sci Tot Env 165:83–102

Lancelot C, Billen G, Sournia T, Weisse T, Colijn F, Davis A, Wassman P (1987) *Phaeocystis* bloom and nutrient enrichment in the continental coastal zones of the North Sea. Ambio 16:38–46

Lastra R, de La Huz A, Sánchez-Mata IF, Rodil K, Aerts S, Beloso S, López J (2006) Ecology of exposed sandy beaches in northern Spain: environmental factors controlling macrofauna communities. J Sea Res 55:128–140

Lerat Y, Lasserre P, le Corre P (1990) Seasonal changes in pore water concentrations of nutrients and their diffusive fluxes at the sediment–water interface. J Exp Mar Biol Ecol 135:135–160

Lohse L, Kloosterhuis R, Van Raaphorst W, Helder W (1996) Denitrification rates in continental shelf sediments of the North Sea: acetylene block technique vs. isotope pairing. Mar Ecol Prog Ser 132:169–179

Meyer RL, Risgaard-Petersen N, Allen DE (2005) Correlation between anammox activity and microscale distribution of nitrite in a subtropical mangrove sediment. Appl Environ Microbiol 71:6142–6149

Meyer-Reil LA, Dawson R, Liebezeit G, Tiedge H (1977) Fluctuations and Interactions of bacterial activity in sandy beach sediments and overlying waters. Mar Biol 48:161–173

Migné A, Spilmont N, Davoult D (2004) In situ measurements of benthic primary production during emersion: seasonal variations and annual potential production in the bay of Somme (eastern English Channel, France). Cont Shelf Res 24:1437–1449

Mortimer R, Davey J, Krom M, Wartson P, Frickers P, Clifton R (1999) The effect of macrofauna on pore water profiles and nutrient fluxes in the intertidal zone of the Humber estuary. Estuar Coast Shelf Sci 48:683–699

Nishio T, Koike I, Hattori A (1983) Estimates of denitrification and nitrification in coastal and estuarine sediments. Appl Environ Microbiol 45:444–450

Pelegri S, Nielsen LP, Blackburn TH (1994) Denitrification in estuarine sediment stimulated by the irrigation of the amphipod *Corophium volutator*. Mar Ecol Prog Ser 105:285–290

Petersen CG (1913) Valuation of the sea. The animal communities of the sea-bottom and their importance for marine zoogeography. Rep Dan Biol Stat 21:1–42

Porter KG, Feig YS (1980) The use of DAPI for identifying and counting aquatic microflora. Limnol Oceanogr 25:943–948

Precht E, Huettel M (2003) Advective pore water exchange driven by surface gravity waves and its ecological implications. Limnol Oceanogr 48:1674–1684

Rosenberg R, Nilsson HC, Diaz RJ (2001) Response of benthic fauna and changing sediment redox condition over a hypoxic gradient. Estuar Coast Shelf Sci 53:343–350

Rusch A, Huettel M, Forster S (2000) Particulate organic matter in permeable marine sands—dynamics in time and depth. Estuar Coast Shelf Sci 51:399–414

Scherrer B (1984) Biostatistique. G. Morin, Boucherville

Smaoui H, Boughanim F, Chapalain G (2007) 1D vertical model for suspended sediment transport in turbulent tidal flow: application to the English Channel. Comp & Geos 33:1111–1129

Spilmont N, Migné A, Lefebvre A, Artigas LF, Rauch M, Davoult D (2005) Temporal variability of intertidal benthic metabolism under emersed conditions in an exposed sandy beach (Wimereux, eastern English Channel, France). J Sea Res 53:161–167

Tréguer P, Le Corre P (1975) Manuel d'analyse des sels nutritifs dans l'eau de mer (utilisation de l'autoanalyseur Technicon II). Université de Bretagne Occidentale, Brest

Trimmer M, Gowen RJ, Stewart BM, Nedwell DB (1999) The spring bloom and its impact on benthic mineralization rates in western Irish Sea sediments. Mar Ecol Prog Ser 185:37–46

Vidal M, Morgui J-A (2000) Close and delayed benthic–pelagic coupling in coastal ecosystems: the role of physical constraints. Hydrobiol 429:105–113

Viollier E, Rabouille C, Apitz SE, Breuer E, Chaillou G, Dedieu K, Furukawa Y, Grenz C, Hall P, Janssen F, Morford JL, Poggiale J-C, Roberts S, Shimmield T, Taillefert M, Tengberg A, Wenzhofer F, Witte U (2003) Benthic biogeochemistry: state of the art technologies and guidelines for the future of in situ survey. J Exp Mar Biol Ecol 286:5–31