Influence of spring phytodetritus sedimentation on intertidal macrozoobenthos in the eastern English Channel

Nicolas Desroy*, Lionel Denis

Station Marine de Wimereux, Université de Lille 1, CNRS UMR 8013 ELICO, 28 Avenue Foch, 62930 Wimereux, France

ABSTRACT: The North Sea shallow waters of the eastern English Channel are recurrently affected by the high algal spring bloom of the Prymnesiophyte *Phaeocystis* spp. When the bloom has run its course, foam accumulations resulting from the release of mucilaginous polysaccharides can be observed both on the sea surface and on beaches. Four beach sites, 2 that were affected and 2 that were not, were sampled from April to December 2001 and from April to August 2001 respectively. The physical and chemical conditions of the sediment, as well as the macrofauna associated with it, were assessed in the Canche Bay before, during and after the phytodetritus sedimentation period. *Phaeocystis* spp.-derived material significantly changed the grain-size distribution in accumulation areas as shown by the resulting fine-particle input (>60%) observed. Due to the rapid decomposition of decaying colonies, organic content increased in the sediments towards the end of the bloom, marked by a single peak on sands or strong, persistent enrichment on muds. As a result of this increase in organic matter, oxygen flux increased over time. In the low-energy silty environment, severe anoxic conditions rapidly occurred whereas on areas subject to tidal or wind-induced turbulence, superficial residual crusts resulting from drying foam prevented oxygen diffusion into sandy sediment. At the impacted sites, all macrobenthic taxa were affected, and both the number of species and their densities were simultaneously reduced. Sandy assemblages showed a better recovery, starting in July, due to more suitable environmental conditions, while on muddy assemblages full recovery had still not occurred by the end of the year. Spring recruit mortality was partly responsible for the lack of faunal recovery, which was mainly dependant on the migration of adults from the surrounding area.

KEY WORDS: *Phaeocystis* spp. bloom · Organic matter input · Macrobenthos · Recovery

INTRODUCTION

In the eastern English Channel and the Southern Bight of the North Sea, high biomass algal blooms (over 20 µg chl *a* ml^{-1}) are recurrent spring events. Blooms are composed primarily of strains of the Prymnesiophycae *Phaeocystis* spp., but diatoms are also present (Adams 1987, Reid et al. 1990, Tett & Mills 1991, Boon et al. 1998). The information currently available would seem to indicate that the *Phaeocystis* spp. complex in the eastern English Channel–North Sea coastal waters includes both the dominant non-toxic alga *Phaeocystis globosa* (Baumann et al. 1994)

and the toxic alga *P. pouchetti* (Lancelot et al. 1987). However, differences between the 2 species are still ill defined, and the existence of 2 species remains uncertain (Baumann et al. 1994). One of the characteristic features of *Phaeocystis* spp. blooms is the production of large amounts of mucoid colonial material, representing up to 90% of total algal biomass (Rousseau et al. 1990). Historical and contemporary records indicate that *Phaeocystis* spp. colony blooms are closely related to changes in land use and/or hydraulic and waste management systems that, over the last century, have increased the presence of nitrates in the coastal area (Lancelot 1995). Harmful events have been linked to

the gelatinous nature of the *Phaeocystis* spp. colony matrix, which releases mucilaginous polysaccharides after disrupting senescent colonies. At the end of the spring bloom, massive sedimentation takes place, with sedimentation rates >800 mg C m^{-2} d^{-1} being reported in the Barents Sea (Wassmann et al. 1990). In intertidal areas, a spectacular consequence of the post-bloom sedimentation is the formation of large amounts of foam on the beaches (Lancelot et al. 1987, Lancelot 1995). Two to 3 wk after the *Phaeocystis* spp. bloom, massive phytodetritus deposits and associated organic material inputs result in large numbers of dead benthic or other moribund organisms in intertidal depositional areas (N. Desroy pers. obs.). Although the ecological effects of *Phaeocystis* spp. on the pelagic food web have been relatively well studied, the impact of this increase in organic matter on the intertidal fauna and on the benthic food web has received only incidental interest (Weisse et al. 1994). Sedimentation can cause changes in (1) the physical environment at the sediment-water interface by modifying the sediment characteristics (Wassmann 1994), (2) the microbiology and chemistry of the underlying sediments by inducing benthic anoxia problems through the remineralization of sedimented phytodetritus-derived organic matter (Graf et al. 1983, Wassman et al. 1996, Boon et al. 1998, 1999), and (3) benthic fauna (Boon et al. 1998).

The aim of this paper is to describe the impact of phytodetritus post-bloom sedimentation (comprised mainly of the decaying remains of *Phaeocystis* spp. colonies) on the intertidal benthic habitat and macrofauna in the Canche Bay, situated on the French coast of the eastern English Channel. As the greatest proportion of organic matter is likely to sediment out in accumulating areas, sediment characteristics are important variables in an evaluation of the possible impact of sedimentation. For this reason, standard physical parameters (granulometry, pigment concentration and sedimentary organic matter content) were measured, as were certain biological parameters (macrofauna). Given that the extent of areas exhibiting oxic and anoxic degradation provides indications of biogeochemical changes (Smetacek et al. 1991, Justic et al. 1994), oxygen profiles were also measured to emphasize the mineralization processes in superficial sediments.

MATERIALS AND METHODS

Study site and sampling strategy. The Canche Bay, whose intertidal surface covers ca. 630 ha, is situated in the eastern part of the English Channel (Fig. 1). The average tidal range is ca. 7 m for a spring tide and 3 m for a neap tide. River discharge varies seasonally, from a maximum of 100 m^3 s^{-1} in winter to a minimum of 60 m^3 s^{-1} in summer. Previous observations have shown that foam deposits resulting from sedimentation at the end of *Phaeocystis* spp. blooms are highly variable, both spatially and temporally. However, the north side of the bay is more frequently affected by foam sedimentation than the south side (L. Denis pers. obs.). The resulting sampling strategy integrated 4 intertidal sites that were daily immersed and emerged, 2 situated on either side of the upstream bay. To the north, north sand (NS) was characterized by medium to fine sands and north mud (NM) was characterized by mud; while to the south, south sand (SS) was characterized by muddy fine sands and south mud (SM) by mud (Fig. 1). The NM and SM sites emerged at high tide (HT) + 2 h, and the NS and SS sites at HT + 3 h. Benthic assemblages at these sites were the *Macoma balthica* community (Petersen 1913) at Sites NM, SM and SS, and an impoverished form of the *Abra alba–Corbula gibba* community (Cabioch & Glaçon 1975), characterized by *Donax vittatus* and *Macoma balthica*, at Site NS.

Sampling was performed with the dual purpose of gathering quantitative data concerning the physical and chemical parameters of the sediment as well as the different macrobenthic populations; the sampling periods depended on the parameters under study (Table 1). Because recovery was faster at southern than northern sites, different sampling timelines were
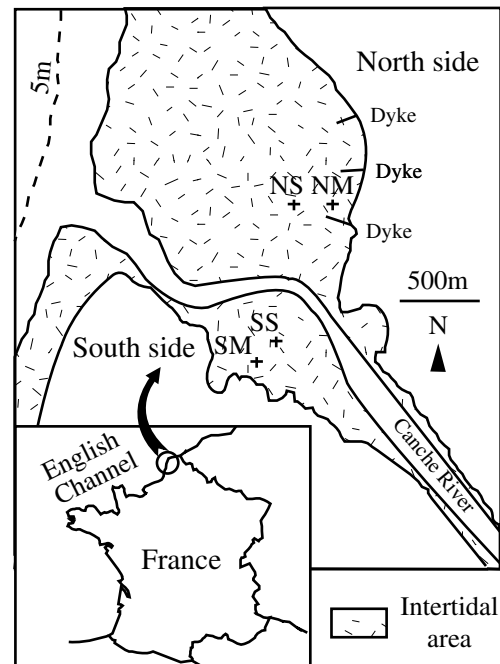

Fig. 1. Location of the Canche Bay and the benthic sampling sites (NM: north mud, NS: north sand, SM: south mud and SS: south sand)

Table 1. Sampling dates of the physical, chemical and biological parameters studied at each site (Year 2001). Foam accumulation (visual obs.) evident on 3/05, 14/05, 23/05, 4/06 and 13/06. NS: north sand; NM: north mud; SS: south sand; SM: south mud

	05/04	13/04	25/04	03/05	14/05	23/05	04/06	13/06	05/07	24/08	01/10	19/10	12/12
Sites NM and NS													
Granulometry	x					x					x		
Organic matter	x	x	x	x	x	x	x		x	x	x		
Oxygen flux	x	x	x	x	x	x	x	x	x				
Benthic pigments	x	x	x	x		x	x	x	x	x			
Macrofauna	x	x	x	x	x	x	x	x	x	x	x	x	x
Sites SM and SS													
Granulometry	x					x					x		
Organic matter	x	x	x	x	x	x	x		x	x			
Oxygen flux	x	x	x	x	x	x	x	x	x				
Benthic pigments	x	x	x	x		x	x	x	x	x			
Macrofauna	x	x	x	x	x	x	x	x	x	x			

required; the north was observed from April to December 2001 and the south from April to August 2001. A total of 13 surveys were conducted in the northern sites while 10 were done in the southern sites. An approximately 10 d sampling frequency was maintained during the main period of foam accumulation (from April to June), slowing to a monthly sample after July.

Phytoplanktonic bloom monitoring. The monitoring networks SOMLIT (Réseau National des Stations Marines–CNRS INSU) and REPHY (Ifremer) provided data concerning the chl *a* concentration and the numeration of *Phaeocystis* spp. cells in coastal waters (50° 46.190 N, 00° 13.605 E) near the Canche Bay.

Sediment samples. *Granulometry and organic matter:* Two replicate cores of sediment were taken at low tide with a hand corer (7 cm diameter) and were subsequently analyzed at the laboratory. Particle size distribution was assessed (wet sieving) before the foam began accumulating (4 April), during foam accumulation (23 May) and after it stopped (1 October, Table 1). Organic matter content was calculated from measurements of weight loss after 6h at 600°C (Luczak et al. 1997).

Oxygen content: Dissolved oxygen concentrations were measured in 2 sediment samples to take spatial heterogeneity in foam accumulation into account and to limit the time required to realize (manually) microprofiles before oxygen concentration evolved in surficial sediments. Samples were taken using a cylindrical core (2.6 cm diameter) that enclosed a 20 cm long sediment column. A sealing top valve prevented disturbance of the sampled sediment-air interface. Oxygen microprofiles were measured immediately on returning to the laboratory, under minimal light conditions. Dissolved O_2 concentrations were measured with an oxygen microelectrode that had a built-in reference and an internal guard cathode (Revsbech 1989). The O_2 microsensor had an outer tip diameter of 100 µm and a 95 % response time of 5 s. The vertical resolution

of the measurements was 50 µm. The position of the sediment-air interface was determined from O_2 microprofiles, using a modified version of the technique developed by Sweerts et al. (1989), which consists of assigning the interface position to a break in the oxygen concentration gradient. Because our method for measuring dissolved oxygen concentrations is nondestructive, study samples were also used to determine sediment porosity.

The flux was estimated from the oxygen microprofiles using the following formula:

$$J = \varphi \times D_s \times \left(\frac{dC}{dz}\right)_{z=0} \qquad (1)$$

where J is the diffusion flux (µmol m^{-2} h^{-1}), φ is the porosity, D_s is the diffusion coefficient (cm^2 s^{-1}), dC is the estimated concentration gradient just below the sediment-water interface, and z is the depth in the sediment scale positively downward. D_s is calculated using the following formula: $D_s = D_m/\theta^2$, where D_m is the molecular diffusion rate at *in situ* temperature and θ is the sediment tortuosity. D_m was calculated according to the formula:

$$D_m = D_0 + at \qquad (2)$$

where D_0 is the molecular diffusion rate at 0°C, a is a coefficient relative to the oxygen (Soetaert et al. 1996) and t is the ambient temperature. θ can be calculated from the porosity according to the formula:

$$\theta = \varphi^{(1-m)} \qquad (3)$$

where m is an adjustment value depending on sediment granulometry ($m = 2$ for muddy sands and mud with $\varphi < 0.7$; Ullman & Aller 1982).

Benthic pigments: Following the bloom and the resulting phytodetritus sedimentation, pigments characterizing *Phaeocystis*, e.g. 19'-hexanoyloxyfucoxanthin (Liaan-Jensen 1985, Adams 1987, Reid et al. 1990, Tett

& Mills 1991, Boon et al. 1998, Goffart et al. 2000) are generally too degraded to be detected in the sediment (Boon et al. 1998). Consequently, quantitative estimations of the contribution of *Phaeocystis* spp.-derived material to the organic matter input in the sediment are not easily provided. The single observable indication is the depth of foam accumulations and the presence of cells or colony fragments in the sediment. Although chl *a* and phaeopigments do not characterize *Phaeocystis* spp.-derived material and do not provide evidence of a change in the composition of material reaching the benthos over the sampling season, the concentrations of these pigments were measured at all sites in order to assess the extent of phytodetritic sedimentation. Benthic chl *a* and phaeopigment concentrations were determined for each sampling date, using 2 sample cores (2.6 cm diameter × 20 cm deep) taken at each site. The top 3 centimeters were sliced and frozen (–25°C) for later analyses. Samples were thawed, and pigments were extracted, using 15 ml of 90% acetone for 4 h in the dark at 8°C. Pigment concentrations were determined before and after acidification, using standard spectrophotometric techniques (Lorenzen 1967).

Biological samples: At each site, 4 replicates for benthos analysis were collected using a 0.027 m^2 hand corer (20 cm depth), which provides a total surface of 1/9 m^2, 0.1 m^2 constituting the minimal sampling area in the bay (N. Desroy pers. obs.). The collected organisms were sieved through 1 mm mesh, fixed with 10% formalin containing Rose Bengal stain, sorted, identified and counted at the laboratory.

Data analysis. Macroinvertebrate community structure was described at each site and for each sampling date by determining the number of species and their abundance as well as the Shannon-Wiener diversity. The significance of the changes in the sedimentary variables (e.g. granulometry, organic matter content, oxygen flux and pigment content) and in the biological index over the course of the sampling period was tested using a 1-way ANOVA. Prior to completing the ANOVAs, a preliminary test for variance homogeneity (Cochran's test) was conducted in each case, and when necessary, heterogeneity was removed by performing a log (*x* + 1) transformation.

Significance tests concerning the differences in macrobenthic community descriptors for the different sites and times were performed, using a 2-way ANOVA. Seasonal changes in community composition were visualized through non-metric multidimensional scaling (MDS) plots, based on triangular matrices of the Bray-Curtis similarities, by performing a square-root transformation of the species abundance data. The faunal groups contributing to the dissimilarity between samples, observed via MDS ordination, were investigated using the similarity percentages procedure, SIMPER (Clarke & Warwick 1994), and these results were used to help interpret the faunal changes responsible for the patterns observed in the MDS ordination. The contribution of each species to the average similarity within each group was also analyzed. Finally, the relationships between the sedimentary and biological variables were analyzed separately, using the BIO-ENV procedure developed by Clarke & Warwick (1994) to define the environmental variables (organic matter content, oxygen flux, chl *a* and phaeopigment contents) that explain assemblage structures. The BIO-ENV procedure (using Spearman's rank correlation method) was used on the untransformed environmental variables and the square root transformations of abundance data for each site. Correlations were calculated only on the data collected from 4 April to 5 July, because the oxygen flux measurements were not measured beyond this date.

RESULTS

Initiated in March, the phytoplanktonic bloom peak was observed in April/May, with values of chl *a* up to 20 µg ml^{-1} (Fig. 2). In the water column, the numeration of *Phaeocystis* spp. cells was documented from a
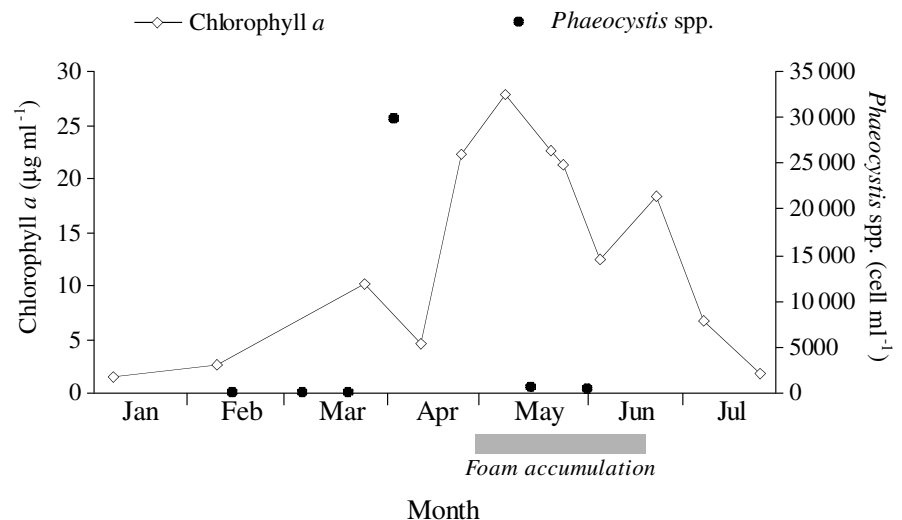

Fig. 2. Chl *a* rates (µg ml^{-1}, data provided by the SOMLIT monitoring framework) and *Phaeocystis* spp. cells ml^{-1} (data provided by the Reseau phytoplancton [REPHY] monitoring framework — Ifremer) in the nearshore coastal waters near Canche Bay from January to July 2001. The period of foam accumulation on the north side of the bay is indicated (grey bar)

Table 2. Variations in sediment granulometry (±SD) at the sampling sites in April (B: before the bloom), May (D: during the deposition) and October (A: after the deposition). Significance levels from a 1-way ANOVA are indicated: *$p < 0.05$; no asterisk = $p > 0.05$ (not significant). NS: north sand; NM: north mud; SS: south sand; SM: south mud

Site	% Silt-clay (<63 µm)			% Sand/gravel (≥500 µm)			Median particle size		
	B	D	A	B	D	A	B	D	A
NM	27.3 ± 11.5	74.8 ± 4.7*	70.0 ± 4.8*	0.5 ± 0.8	0.5 ± 0.1	0.7 ± 0.0	0.10 ± 0.0	0.03 ± 0.0	0.04 ± 0.0
NS	3.1 ± 0.6	7.58 ± 5.1	0.4 ± 0.0	1.4 ± 0.0	1.7 ± 1.3	1.6 ± 0.3	0.14 ± 0.0	0.14 ± 0.0	0.14 ± 0.0
SM	23.9 ± 2.0	27.1 ± 26.5	14.4 ± 0.3	2.5 ± 0.2	4.0 ± 5.0	1.7 ± 0.2	0.11 ± 0.0	0.09 ± 0.0	0.11 ± 0.0
SS	4.5 ± 2.1	0.3 ± 0.3	0.2 ± 0.0	0.5 ± 0.0	1.3 ± 0.6	0.2 ± 0.2	0.14 ± 0.0	0.14 ± 0.0	0.15 ± 0.0

minimal monitoring, providing 6 values from February to June. Despite their limited range, data emphasized that reaching a concentration of 30 000 cells ml^{-1} at the beginning of April, *Phaeocystis* spp. contributed heavily to this high primary production. When the *Phaeocystis* spp. bloom ended, large amounts of foam containing fine particles settled on the north side of the bay from the end of April to the middle of June. The presence of numerous decaying colony fragments in the superficial sediments underlined the significant quantities of *Phaeocystis* spp.-derived material in the phytodetritus accumulations at Sites NM and NS. The difference in bentho-pelagic coupling on the 2 sides of the bay was assessed by the absence of foam accumulation in the southern sites.
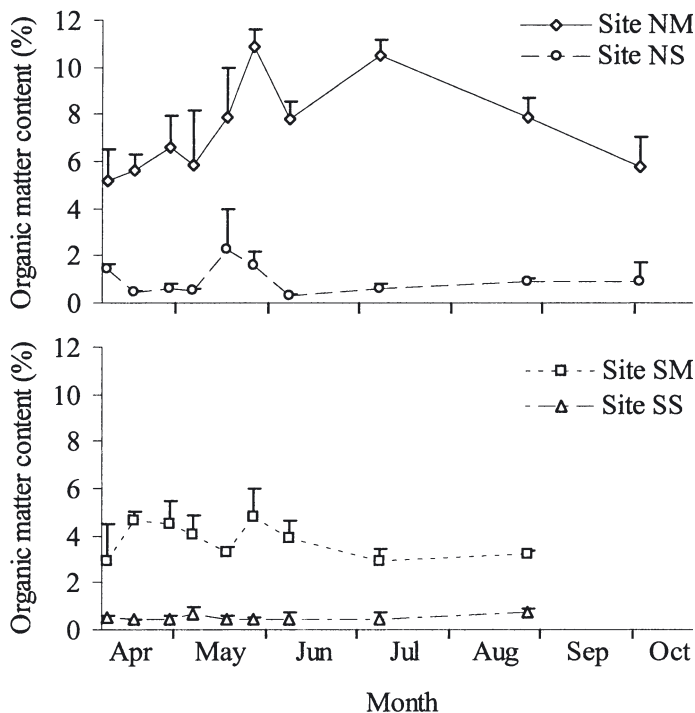

Fig. 3. Organic matter content (% dry weight) variations at north mud (NM), north sand (NS), south mud (SM) and south sand (SS) sites from March to October 2001. Error bars denote +SD

Granulometry

The north side of the bay, particularly the mudflat (Site NM), was most affected by foam accumulations. As a result, the granulometric change was obvious at Site NM, where silt-clay fractions increased significantly, e.g. up to 60% ($p < 0.05$) in the sediment sample of 23 May (Table 2). At the other sites, changes in granulometric composition were insignificant ($p > 0.05$).

Organic matter content

As suggested by Fig. 3, the significantly highest organic matter percentages were consistently measured at Sites NM and SM (month pooled; $p < 0.001$). One-way ANOVAs indicate significant changes in organic matter over time at Sites NM ($p < 0.001$) and NS ($p < 0.01$). An increase in the organic matter content following the accumulation period was observed on 23 May and 5 July at Site NM and on 14 May at Site NS. Values reverted more rapidly to initial levels at Site NS (from 4 June) than at Site NM (from 1 October). A significant change over time was also observed at Site SM (1-way ANOVA, $p < 0.01$), despite the apparent stability of organic matter content, though no significant changes were apparent at Site SS ($p = 0.22$).

Oxygen flux

An overall significant difference between the oxygen flux in the muddy and the sandy sediments was observed from April to July (months pooled; $p < 0.001$), with mean values of 1690 ± 925 (Site NM) and 1527 ± 504 (Site SM) µmol m^{-2} h^{-1} and mean values of 356 ± 524 (Site NS) and 495 ± 286 (Site SS) µmol m^{-2} h^{-1}, respectively. Although some temporal trends were obvious, ANOVA yielded insignificant differences at each site ($p = 0.098$, Site NM; $p = 0.101$, Site NS) due to the heterogeneous replicate values of the measured flux (Fig. 4).

On the north side of the bay most affected by the foam, the patterns of the changes in oxygen flux varied
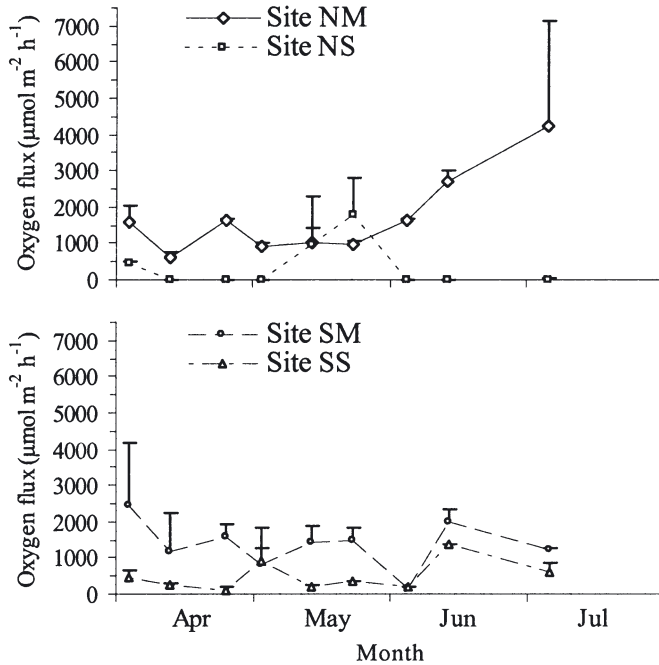
Fig. 4. Mean oxygen fluxes at north mud (NM), north sand (NS), south mud (SM) and south sand (SS) sites. Vertical bars represent +SD
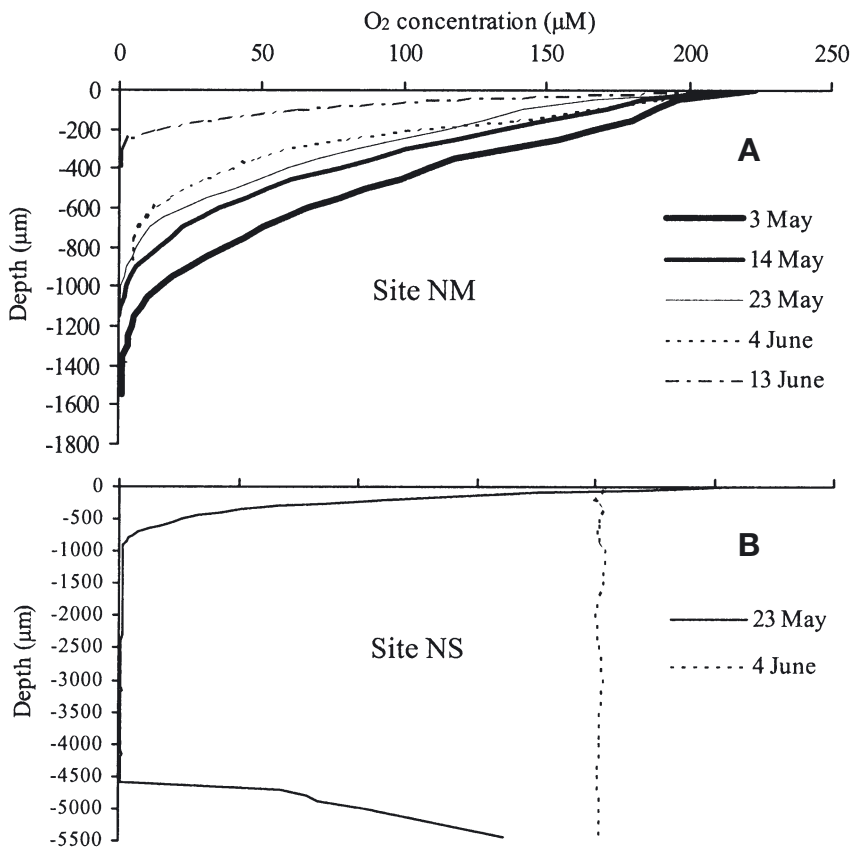

Fig. 5. Average oxygen profiles measured at (A) Site NM (north mud) from 3 May to 13 June, and at (B) Site NS (north sand) on 23 May and 4 June 2001

according to the nature of the sediment. At Site NM, oxygen flux increased consistently from 23 May (~950 µmol m^{-2} h^{-1}) to 5 July (>4000 µmol m^{-2} h^{-1}), whereas at Site NS, values were highest on 14 and 23 May, as compared to earlier and later dates where no significant oxygen gradients were detected. At Sites SM and SS, insignificant differences (p = 0.582 and 0.094 respectively) were obtained because too few replicates were taken to detect apparent differences shown in Fig. 4.

Fig. 5A shows the changes in average oxygen concentrations (calculated on 2 profiles) in the superficial layers of Site NM from 3 May to 13 June. During this period, the oxygen penetration depth decreased, resulting in enhanced diffusive oxygen flux. At Site NS, superficial residual crusts resulting from drying foam prevented oxygen diffusion in the sandy sediment. Although the top few centimeters were saturated by oxygen as in normal conditions, the sediment showed an oxygen deficit in the top 4 to 5 mm where dried foam existed (Fig. 5B).

Benthic pigments

Fig. 6A,B shows the temporal changes in chl a and phaeopigment a m^{-2} in the top 3 centimeters of the sediment at each site. Overall, significantly higher concentrations of both pigments were found at Sites NM and SM as compared to Sites NS and SS (month pooled; p < 0.001). With the exception of the high value recorded on 25 April at Site SM (1211 ± 585 mg m^{-2}), sediment chl a concentrations ranged between 100 and 600 mg m^{-2} during the study period at each site. Changes were significant at Sites NM (p < 0.05) and NS (p < 0.05), where the highest concentrations were found following foam accumulation in May and June, but were insignificant at Sites SM (p = 0.074) and SS (p = 0.122).

Similarly, phaeopigment concentrations changed significantly at Sites NM and NS. Values increased from April to May at Site NS (p < 0.05), and from May to July at Site NM (p < 0.001). Phaeopigment values were variable throughout the sampling period at Site NM, with maximal and minimal values of 3568 ± 96 mg m^{-2} and 651 ± 312 mg m^{-2}, respectively. Concentrations at Site SM remained stable, and decreased gradually at Site SS during the study, with respective values of p = 0.461 and p = 0.728.
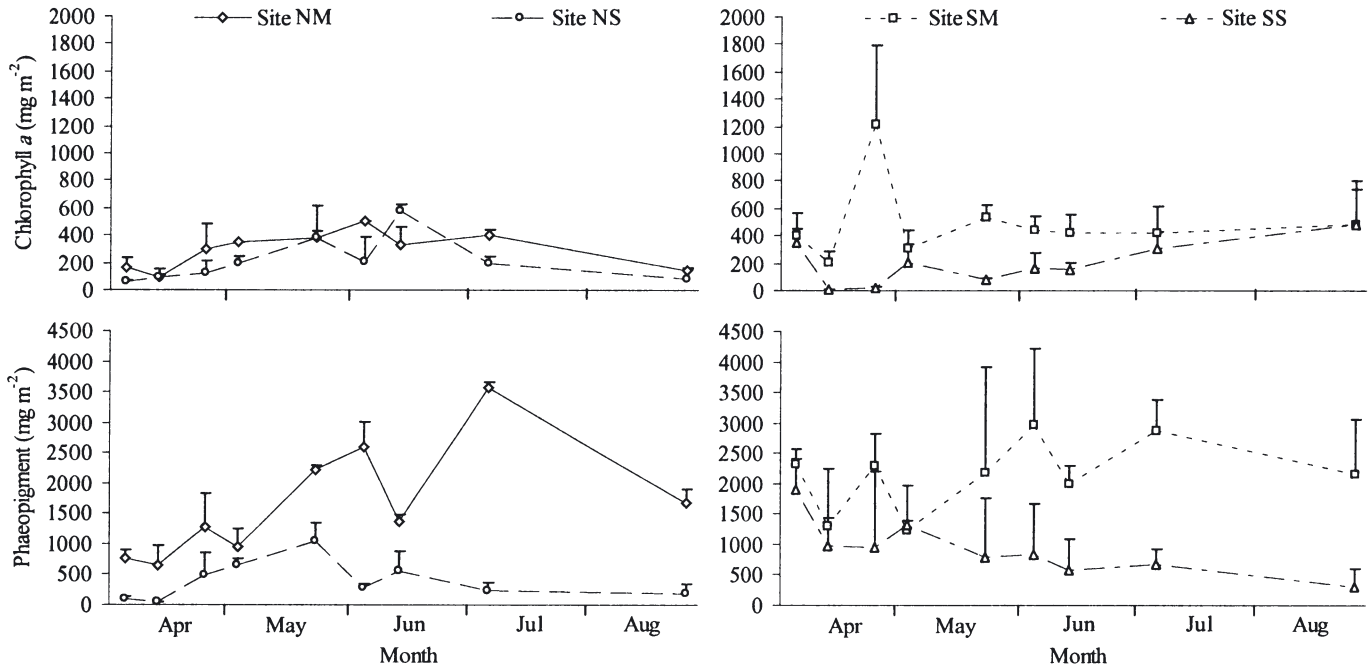
Fig. 6. (Top panels) Chl *a* (mg m^{-2}) and (bottom panels) phaeopigment (mg m^{-2}) concentrations in surficial sediments (3 cm depth integrated) at the 4 sites. NM: north mud; NS: north sand; SM: south mud; SS: south sand. Vertical bars represent +SD

Macrofauna

A total of 35 species was identified from the core samples. The fauna was composed almost exclusively of polychaetes, mollusks and crustaceans, in various proportions depending on the site (Table 3). Most of the numerically dominant taxa during the study period were estuarine species, such as *Hydrobia ulvae*, *Macoma balthica* and *Pygospio elegans* at Sites NM and SM, *Bathyporeia pilosa* and *Cerastoderma edule* at Site NS and *Hediste diversicolor*, *Heteromastus filiformis* and *Macoma balthica* at Site SS.

Two-way ANOVA conducted on data recorded from 4 April to 24 August (a common data set for each site) showed that values of community descriptors (number of species and total abundance of all species per sample) varied greatly with time (p < 0.001), with no significant differences among the sites (Table 4). The Shannon diversity results, however, were significantly influenced by both time and site (p < 0.001, Time; p < 0.01, Site).

Both sites located on the north and the south sides of the bay showed variations in number of species and the abundance of all species pooled, but these variations were different depending on whether the site was on the north side or the south (Fig. 7). At Sites NM and NS, the number of species changed significantly (p < 0.001). This trend was characterized at both sites by a strong reduction in species numbers: on 14 May, 2

and 0.25 species on average (on 1/9 m^2) were recorded at Sites NM and NS respectively, versus 7 and 8.25 on 5 April. After a peak observed on 4 June at both sites, the number of species remained low (<4 species) at Site NM and increased at Site NS, where the initial number of species was partially restored by the end of the sampling period. The significant change in total abundance at both sites (p < 0.001) appears consistent with variation patterns described for specific richness: after a rapid spring decrease, densities remained low throughout the season. The high densities recorded at Site NS on 4 April were mainly due to the presence of 2 species, *Cerastoderma edule* and *Pygospio elegans*, which rapidly disappeared. Changes in Shannon diversity were highly significant (p < 0.001) and consistent at both sites (Fig. 8).

On the south side of the bay, at Sites SM and SS, stability in the number of species was the overall trend (Fig. 7). No significant difference was detectable over the course of the sampling season at Site SM. Density, however, varied significantly (p < 0.001), increasing by a factor of 4 from 25 April to 13 June. At Site SS, despite a high variability from one month to the other, density varied consistently with species number. The overall stability recorded over the course of the sampling season was punctuated by one significant decrease on 4 June (p < 0.05). Shannon diversity changed significantly (p < 0.01) at both sites over the course of the sampling period (Fig. 8).

Table 3. Number of taxa (per group and total) and mean (±SD) abundances (ind. m^{-2}) of infauna at each site (4 April to 12 December for Sites NM and NS; 4 April to 24 August for Sites SM and SS). Groups are classified according to the decreasing number of species. NS: north sand; NM: north mud; SS: south sand; SM: south mud

Species	NM	SM	NS	SS
Crustacea: 12 spp.	5 spp.	6 spp.	9 spp.	8 spp.
Bathyporeia pilosa	0.7 (5)	–	239.5 (490.4)	24.9 (77.9)
Bathyporeia sarsi	–	0.9 (5.7)	–	0.9 (5.8)
Carcinus maenas	9.7 (22.7)	215.1 (309.2)	2.8 (20.0)	1.8 (8.0)
Corophium arenarium	–	–	2.8 (15.7)	–
Corophium volutator	0.7 (5.0)	1.8 (11.3)	–	–
Crangon crangon	6.2 (22.2)	45 (75.5)	2.1 (8.5)	34.2 (60.1)
Eurydice pulchra	2.1 (8.5)	13.5 (85.4)	51.9 (97.07)	0.9 (5.8)
Gammarus sp.	–	–	1.4 (7.0)	0.9 (5.8)
Haustorius arenarius	–	–	0.7 (5.0)	–
Neomysis integer	–	2.7 (17.1)	1.4 (10.0)	6.5 (21.6)
Pinnotheres pisum	–	–	0.7 (5.0)	–
Sphaeroma rugicauda	–	–	–	0.9 (5.8)
Annelida: 10 spp.	8 spp.	9 spp.	6 spp.	7 spp.
Arenicola marina	2.1 (11.1)	15.3 (29.3)	–	9.2 (22.9)
Capitella capitata	12.5 (27.5)	883.8 (1076.3)	6.2 (23.3)	129.2 (230.61)
Eteone longa	99.0 (244.8)	436.5 (767.3)	39.5 (157.7)	14.8 (24.4)
Hediste diversicolor	33.2 (87.8)	720 (535.0)	6.9 (28.6)	426.5 (217.2)
Heteromastus filiformis	29.8 (115.6)	31.5 (78.3)	42.9 (190.6)	427.4 (401.1)
Lanice conchilega	2.1 (15.0)	23.4 (131.1)	–	–
Polydora antennata	–	11.7 (62.8)	–	–
Pygospio elegans	1299.5 (2812.5)	4834.8 (4131.6)	720.0 (2716.7)	105.2 (399.1)
Scolelepis squamata	–	–	92.8 (429.7)	1.8 (8.0)
Spio martinensis	1.4 (7.0)	1.8 (7.9)	–	–
Mollusca: 7 spp.	6 spp.	6 spp.	3 spp.	7 spp.
Abra tenuis	3.5 (16.3)	29.7 (52.8)	–	2.8 (17.3)
Cerastoderma edule	330.9 (603.0)	171.9 (418.1)	337.1 (1145.1)	76.6 (243.2)
Hydrobia ulvae	1383.9 (2334.7)	10471.5 (11637.7)	68.5 (370.2)	48.0 (74.5)
Macoma balthica	222.9 (76.01)	18151.2 (20826.2)	4.8 (21.4)	520.6 (790.2)
Mya arenaria	2.8 (9.7)	8.1 (17.3)	–	1.8 (8.0)
Scobicularia plana	2.1 (15.0)	8.1 (20.8)	–	1.8 (8.0)
Tellina tenuis	–	–	–	0.9 (5.8)
Insecta: 2 spp.	2 spp.	1 sp.	2 spp.	
Chironomidae sp.	1.4 (7.0)	–	2.1 (11.1)	–
Diptera sp.	2.8 (9.7)	2.7 (9.6)	54 (90.3)	–
Pisces: 2 spp.	1 spp.	1 sp.		2 spp.
Gobidae sp.	–	–	–	0.9 (5.8)
Solea solea	1.4 (7.0)	1.8 (7.9)	–	1.8 (8.0)
Nemertean: 1 sp.	1 sp.		1 sp.	1 sp.
Nemertean sp.	1.4 (7.0)	–	0.7 (5.0)	1.8 (8.0)
Oligochaeta: 1 sp.	1 sp.	1 sp.	1 sp.	1 sp.
Oligochaeta sp.	31.2 (70.2)	649.8 (804.0)	33.2 (80.9)	12.0 (38.14)
Total	24 spp.	24 spp.	22 spp.	26 spp.

Table 4. Results of a 2-way ANOVA used to test for site and time effects on the number of taxa, the number of individuals and the diversity among sites and times (macrofaunal cores were individually considered). ns: not significant, $p \geq 0.05$; *$p < 0.01$; **$p < 0.001$

Source of variation	df	Number of taxa		Abundance		Shannon diversity	
		F	p	F	p	F	p
Time	3	11.34	<0.001**	15.71	<0.001**	8.82	<0.001**
Site	9	1.43	0.223ns	0.61	0.781 ns	3.59	0.005*
Residual	27						

The SIMPER analyses indicated that 11 taxa contribute most to the dissimilarities between sites (cut-off 90%; Table 5). Since most of these taxa were generally present at all sites (Table 3), differences between sites would appear to be the result of the variations in their relative abundance.

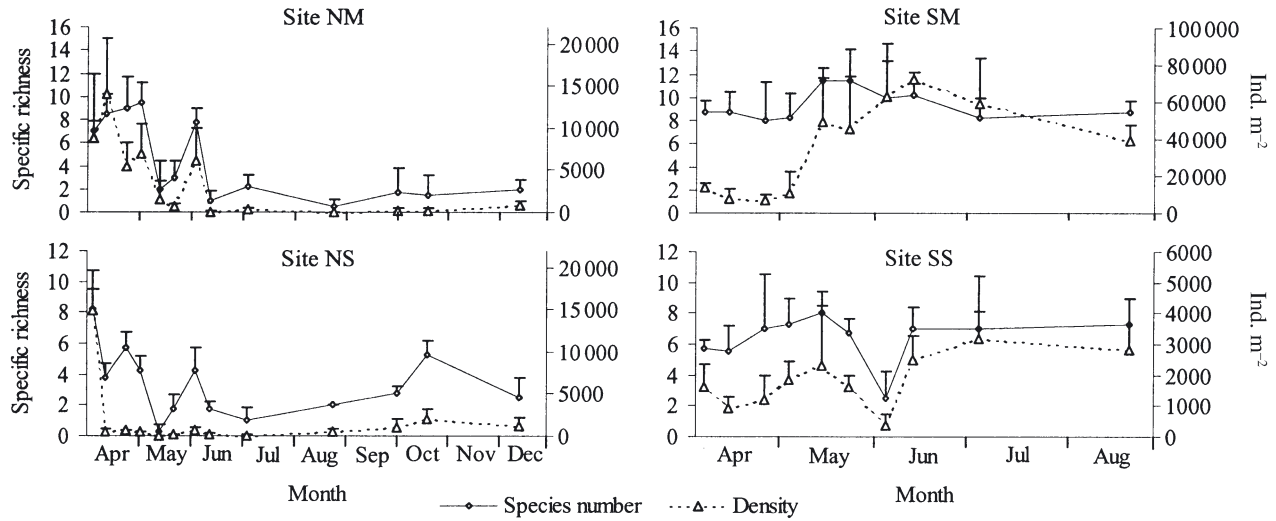As shown by the clusters on the plot projections, assemblage structures were comparable and stable at SM and

Fig. 7. Number of species (+SD) per core and number of individuals of all species per sample (m²) (+SD) at north mud (NM), north sand (NS), south mud (SM) and south sand (SS) sites
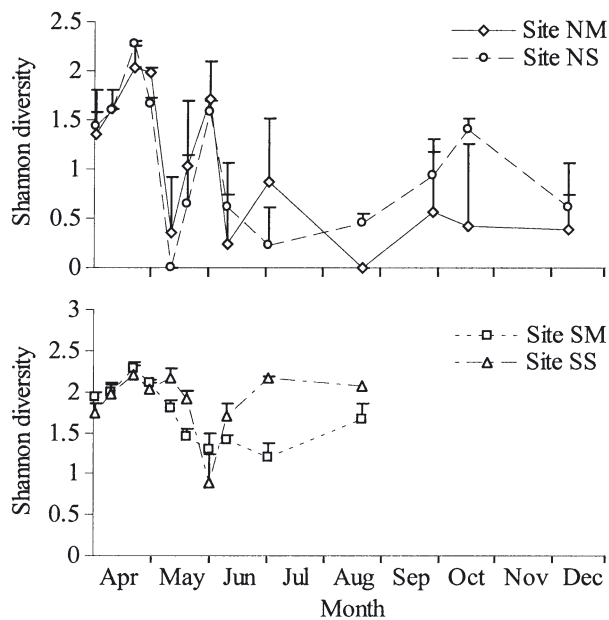

Fig. 8. Mean values +SD of Shannon-Wiener diversity at the 4 sites: north mud (NM), north sand (NS), south mud (SM) and south sand (SS)

Hediste diversicolor was recorded with an abundance of 0.25 ind. m⁻². A similar pattern was observed for Sites NS and SS. While Site SS samples during the study period show the tight plot clustering that indicates high assemblage stability, Site NS samples are much more diffusely distributed. The most disturbed stage was observed on 14 May (sample NS5) when only *Cerastoderma edule* was present (0.5 ind. m⁻²).

At Site NM, the highest correlation (r = 0.718, BIO-ENV procedure) was obtained for the combination of organic matter and oxygen flux, while at Site NS, this correlation was based only on oxygen flux measurements (r = 0.227). At Sites SM and SS, the highest values were associated with the chl *a* content (r = 0.239) and the combination of organic matter, chl *a* and phaeopigment contents (r = 0.198).

DISCUSSION

The pronounced foam accumulation in the spring, followed by the subsequent decomposition that provokes hypoxia and increased sulphate-reduction activity, is a recurrent and dominant event on the eastern English Channel–North Sea coasts. The low grazing pressure exerted by copepods on *Phaeocystis* spp. (Gasparini et al. 2000) is likely to favour the sedimentation of algal cells or colonies ungrazed to the sea floor. Although deposits of algal matter in varying states of decay are presumed to represent the majority of the particulate organic material available to the benthos (Boon & Duineveld 1996), these deposits may adversely affect benthic ecosystems. Our study is the first to investigate the effects of foam accumulation on

NM sites in the early spring (Fig. 9). These structures began to change and were heavily differentiated as of mid-May, when large foam deposits began to form on the north side of the bay. Samples from Site NM became much more widely spaced in the ordination plane than those in the SM group, revealing that changes in the overall community structure and composition had occurred. The most impoverished stage was recorded on 24 August (sample NM10), when only

Table 5. SIMPER analyses results: average Bray-Curtis % dissimilarities among sites (**bold**) and the 5 taxa contributing most to dissimilarity (%).NS: north sand; NM: north mud; SS: south sand; SM: south mud. See Table 3 legend for genus names

NM vs SM	NM vs NS	NM vs SS	SM vs NS	SM vs SS	NS vs SS
67.2	**84.6**	**73.0**	**88.4**	**69.9**	**84.3**
16.7: *M. balthica*	20.3: *H. ulvae*	12.1: *H. ulvae*	19.5: *M. balthica*	16.2: *M. balthica*	13.6: *H. diversicolor*
12.0: *H. ulvae*	14.5: *P. elegans*	9.7: *P. elegans*	18.7: *H. ulvae*	16.0: *H. ulvae*	13.0: *H. filiformis*
10.2: *P. elegans*	10.1: *C. edule*	9.3: *H. diversicolor*	14.4: *P. elegans*	12.3: *P. elegans*	12.8: *M. balthica*
5.4: *C. capitata*	7.3: *M. balthica*	8.8: *H. filiformis*	6.7: *C. capitata*	4.0: Oligochaeta	6.6: *P. elegans*
4.8: *H. diversicolor*	6.9: *B. pilosa*	8.4: *M. balthica*	6.0: *H. diversicolor*	4.0: *C. capitata*	6.4: *C. capitata*

the benthic habitat and its associated macrofauna.

The evidence regarding the effects of *Phaeocystis* spp.-derived material deposits observed at affected sites (NM and NS) are summarized in Table 6. Although chl *a* and phaeopigments do not characterize *Phaeocystis* spp.-derived material, both pigment concentrations changed significantly over the course of the sampling period at Sites NM and NS, consistent with field observations of large accumulations of decaying remains of *Phaeocystis* spp. colonies (Fig. 6). Unlike the toxic algal bloom of other Prymnesiophytes, such as *Chrysochromulina polylepis* or *Karenia brevisulcata*, which Olsgard (1993) and Wear & Gardner (2001) have respectively shown do not change the predominant sediment type pre- to post-bloom, *Phaeocystis* spp.-derived material may profoundly change post-bloom grain size distribution. The resulting fine particle input (>60%) observed at Site NM in May was significantly higher as compared to other sites, and was persistent over time. At Site NS, a major part of the sedimented phytodetritic material was resuspended by the turbulence generated by wind-waves and subsequently transported by tidal currents. Residual deposits, exposed to sunshine at low tide, developed impervious, heterogeneous distributed crusts. As a result of the rapid decomposition of decaying colonies, the organic content of the sediments at Sites NM and NS increased consistently, the presence of
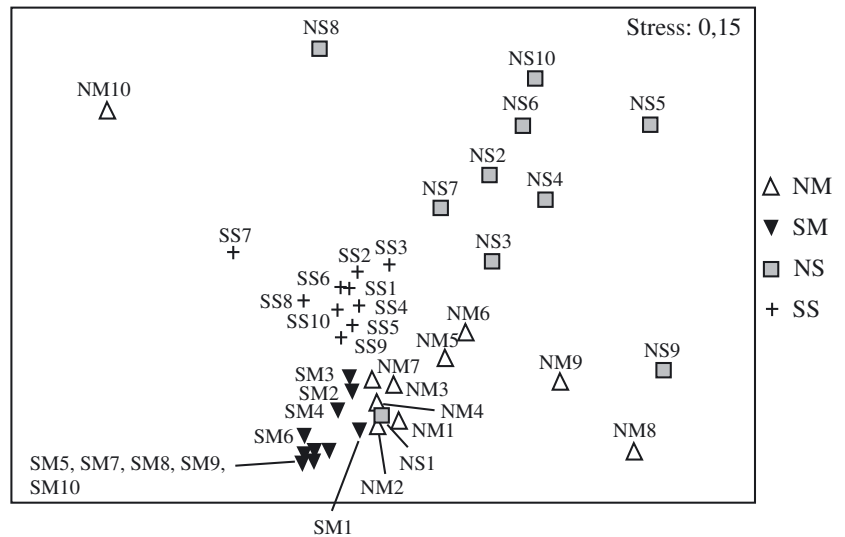

Fig. 9. Two-dimensional configuration for non-metric multidimensional scaling (MDS) ordinations of macrofaunal assemblages from north mud (NM), north sand (NS), south mud (SM) and south sand (SS) from April to August 2001 (1 = 4 April, 2 = 13 April, 3 = 25 April, 4 = 3 May, 5 = 14 May, 6 = 23 May, 7 = 4 June, 8 = 13 June, 9 = 5 July and 10 = 24 August)

Table 6. Main effects of foam accumulation on the muddy and sandy sediments of the Bay of Canche. NS: north sand; NM: north mud

| Presence of foam | Sediment characteristics | | | Biological parameters |
	Granulometry	Organic matter content	Oxygen fluxes	Number of species, abundance and diversity
Low turbulence (Mudflats—NM)				
High accumulation	Significant and lasting increase in silt-clay content	Significant enrichment (strong and persistent)	Overall insignificant increases Development of anoxic conditions	Rapid significant reduction Slow recovery Few opportunistic species
High turbulence (Sandflats—NS)				
Low accumulation	No effect	Significant enrichment (low and sporadic)	Insignificant increases Formation of crusts preventing oxygen diffusion	Rapid significant reduction Rapid recovery Few opportunistic species

organics indicated by a single peak on sand and the strong, persistent enrichment of the mud. Subsequently, oxygen flux increased at Sites NM and NS. Although insignificant, these changes were the consequence of the enhanced aerobic and anaerobic mineralization rates that resulted from the presence of increased organic matter (Soetaerts et al. 1996, Denis 1999). This condition occurred despite the advanced degradation of particulate organic matter in the foam and its associated resistance to microbial degradation (Thingstad & Billen 1994). The decomposition rate of the organic matter was high at Site NM, depleting oxygen resources during the degradation process (Bucci et al. 1992, Millet & Guelorget 1994). This depletion rapidly led to severe anoxic conditions, accompanied by a release of H_2S from the bottom.

The decrease rates of oxygen penetration in the sediment at Site NM from 3 May to 13 June were partly due to increased mineralization activity and the reduced solubility of oxygen as water temperatures increased (Rasmussen & Jorgensen 1992). On the other hand, the sediment's recolonization by macrofauna and the bioturbation activity may facilitate oxygen penetration into sediment (Nilsson & Rosenberg 2000). The average diffusion flux values calculated for muddy sediment (1690 ± 925 µmol m^{-2} h^{-1}, Site NM; 1368 ± 532 µmol m^{-2} h^{-1}, Site SM) accord with those recorded by Böttcher et al. (2000) on intertidal Weser mudflats at similar temperatures. In the Weser flats, oxygen flux ranged from 1245 to 2195 µmol m^{-2} h^{-1}, with a mean of 1630 µmol m^{-2} h^{-1}. During our survey, the oxygen flux variability observed at Site NM increased (2947 to 6294 µmol m^{-2} h^{-1} on 5 July) as a result of 'organic hotspots' produced by the small-scale spatial heterogeneity of foam distribution. At Site NS, the high concentrations of oxygen recorded downcore are due to the high permeability of the sediments and to the discontinuous character of the surficial crusts. Although lower, our average diffusive oxygen flux values (356 ± 524 µmol m^{-2} h^{-1}, Site NS; 495 ± 286 µmol m^{-2} h^{-1}, Site SS) are of the same order of magnitude as the overall oxygen flux values measured for intertidal sands in the bay of Somme (eastern English Channel, 500 to 1360 µmol m^{-2} h^{-1}) with benthic chambers in the emerging sediments (Spilmont pers. comm.).

The macrobenthic assemblages were characterized by a small total number of species, with an overall low diversity and the strong dominance of a few of the existing taxa. The MDS analyses provided evidence that foam sedimentation influenced the macrobenthic assemblages on the north side of the bay. The development of anoxic conditions affected all taxa, and both the number of species and their abundance were simultaneously reduced. The most affected taxa at Site NM were *Cerastoderma edule*, *Eteone longa* and

Pygospio elegans, and at Site NS were *Bathyporeia pilosa*, *Eurydice pulchra* and *P. elegans*. Reductions of abundance were either due to migration as presumed for amphipods and isopods, mortality as shown for *C. edule* that rapidly die when buried below 10 cm sediment depth (Jackson & James 1979), or predation by waders. As reported by Everett (1994) during macroalgal blooms, we observed in foam accumulation areas that infaunal species such as bivalves (*C. edule*, *Macoma balthica*) and polychaetes (*Arenicola marina*, *E. longa*) were forced to the sediment surface in response to the development of anoxic conditions, increasing their chance of being eaten by waders (N. Desroy unpubl. data). Due to the increased accessibility of infauna by upward vertical migration, the combined presence of foam and predation can intensify the effects of each factor on benthic invertebrate densities. At Site NM, only the gastropod *Hydrobia ulvae* remained abundant during foam sedimentation. Since this species feeds on diatoms (Austen et al. 1999), snails were able to migrate towards sites characterized by high biomass of benthic diatoms. The abundance of opportunistic species did not increase in the northern sites, whereas they were abundant on the south side of the bay (Site SM and SS), which is unusual in coastal systems after a succession of organic enrichments. A common community response to stress, after a short period of stimulation, is a reduction in the number of species, an increase in total abundance due to an increase in the opportunistic species, and a corresponding reduction in diversity (Pearson & Rosenberg 1978). Similar situations with a reduction in both the number of species and their abundance, and the absence of opportunistic species, has already been described in studies of benthic faunal response to both heavy metal pollution (Rygg 1986) and toxic algal bloom (Olsgard 1993).

Our results show that faunal recovery essentially depended on the spatial and temporal scales of the disturbance and the hydrodynamics of the area. An increasing current decreased the negative effect of organic enrichment, most likely by increasing oxygen concentrations in the sediment (Ford et al. 2001). Sandy assemblages showed a quicker recovery as of July due to more suitable environmental conditions. The recovery at Site NS after the foam was resuspended by wind-induced waves was mainly due to *Pygospio elegans*, *Bathyporeia pilosa* and *Eurydice pulchra*. Many amphipods or isopods are highly mobile and can increase opportunistically in response to increased food supplies (Colan 1994). At Site NM, the polychaetes *Hediste diversicolor* and *P. elegans* were the first settlers, but the high organic matter content recorded at the end of the summer suggested that, at that time, the habitat was not yet fully restored. Full

recovery had still not occurred by the end of the year, as witnessed by the low numbers of species and individuals. Disturbed areas may take months or years to recover (Beukema et al. 1999) but there is still the possibility of initial and rapid colonization by opportunistic species that were previously not present or not abundant in a site. In the present study, there was no sign of an initial increase in diversity following disturbance. The lengths of organisms in samples indicated that recolonization was mainly due to the migration of adults from surrounding areas. Spring recruit mortality was partly responsible for this lack of faunal recovery following sedimentation. Although macroalgal detritus are assumed to induce larval settlement or to result in enhanced survival of newly settled infauna (Renaud et al. 1999), the recruits observed on 4 June at Sites NM (*Cerastoderma edule*, *Hydrobia ulvae*, *Macoma balthica* and *P. elegans*) and NS (*C. edule*, *E. pulchra* and *P. elegans*) failed rapidly, maybe in response to hypoxic conditions. Observations directly relating the benthic faunal changes and nontoxic phytodetritus accumulations are lacking and no other comparable data sets are available. The closest similar event to foam accumulations is the proliferation of green macroalgae on intertidal flats, the effects of which can be either direct, due to physical interference with macroinvertebrate feeding behaviour (Raffaelli et al. 1991), or indirect, due to changes in physico-chemical characteristics of the sediment (Hull 1987).

Large amount of foam recurrently occurred at spring in the north side of the bay mainly in response to the dominant SW winds. Their persistence on depositional areas was variable from one year to another, mainly depending on winter storm intensity and on the colonization level by the polychaete *Pygospio elegans*. After a severe winter storm, part of the non-cohesive sediment layer deposed in spring and non colonized can easily be eroded, uncovering the original sediment and disturbing the recovery process. When densely colonized by *P. elegans*, sediment characterized by a higher level of physical stability was preserved from erosion. Macrofaunal assemblages that had been affected for several years had similar composition to preserved ones, but abundance of organisms remained low. The absence of long-term baseline data prevent us from quantifying environmental consequences of phytodetritus accumulation on a large time-scale. However, the recurrent disturbance involved a high level of variability in habitats and may preserve benthic assemblages in a juvenile stage.

In conclusion, the spring algal bloom dominated by *Phaeocystis* spp. had a widespread and profound impact upon the biological communities. Although the low-energy silty environment was impacted more severely than areas subjected to tidal or wind-induced turbulence, the effects documented here show that the effect of foam accumulation must be taken into account even when deposits are temporary or are limited in size, as is the case in the sandy sediments that predominate in the Canche Bay. In comparison, mudflats and depositional areas represented only 10% of the surface (i.e. 60 ha), and the sedimentation of *Phaeocystis* spp.-derived material leading to impoverished assemblages observed at Site NM primarily affects these depositional areas. Visual estimation showed that more than 50% of the sandy sediments were covered by foam, with the attendant disturbance of the benthic communities. These results will support the quantification of effects upon the community structure and dynamics on the scale of the eastern English Channel–North Sea intertidal area.

LITERATURE CITED

Adams JA, (1987) The primary ecological subdivisions of the North Sea: some aspects of their plankton communities. In: Bailey RS, Parrish BB (eds) Development in fisheries research in Scotland. Fishing News Books, Fulham, p 165–181

Austen I, Andersen TJ, Edelvang K (1999) The influence of benthic diatoms and invertebrates on the erodibility of an intertidal mudflat, the Danish Wadden sea. Estuar Coast Shelf Sci 49:99–111

Baumann MEM, Lancelot C, Brandini FP, Sakshaug E, John DM (1994) The taxonomic identity of the cosmopolitan prymnesiophyte *Phaeocystis*: a morphological and eco-physiological approach. J Mar Syst 5:5–22

Beukema JJ, Flach EC, Dekker R, Staring M (1999) A long-term study of the recovery of the macrozoobenthos on large defaunated plots on a tidal plot in the Wadden Sea. J Sea Res 42:235–254

Boon AR, Duineveld GCA, (1996) Phytopigment and fatty acids as molecular markers for the quality of near-bottom particulate organic matter in the North Sea. J Sea Res 35: 279–291

Boon AR, Duineveld GCA Berghuis EM, Van Der Weele JA (1998) Relationships between benthic activity and the annual phytopigment cycle in near-bottom water and sediment in the Southern north Sea. Estuar Coast Shelf Sci 46: 1–13

Boon AR, Duineveld GCA, 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

Böttcher ME, Hespenheide B, Llobet-brossa E, Beardsley C and 6 others (2000) The biogeochemistry, stable isotope geochemistry, and microbial community structure of a temperate intertidal mudflat: an integrated study. Cont Shelf Res 20:1749–1769

Bucci M, Ghiara E, Gorelli V, Gragnani R, Izzo G, Morgana L, Naviglio L, Ucelli R (1992) Ecological conditions in the Ortebello lagoon and suggested actions for its restoration. Sci Total Environ 2:1179–1188

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

Clarke KR, Warwick RM (1994) Changes in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth

Colan KE (1994) Amphipod crustaceans and environmental disturbance—a review. J Nat Hist 28:519–554

Denis L (1999) Dynamique des flux d'oxygène et de sels nutritifs à l'interface eau-sédiment sur la marge continentale du Golfe du Lion (Méditerranée Nord-Occidentale). PhD thesis, University of Marseille

Everett RA (1994) Macroalgae in marine soft-sediment communities: effects on benthic faunal assemblages. J Exp Mar Biol Ecol 150:223–247

Ford RB, Thrush SF, Probert PK (2001) The interacting effect of hydrodynamics and organic matter on colonization: a soft-sediment example. Estuar Coast Shelf Sci 52:705–714

Gasparini S, Daro MH, Antajan E, Tackx M, Rousseau V, Parent JY, Lancelot C (2000) Mesozooplankton grazing during the Phaeocystis globosa bloom in the southern bight of the North Sea. J Sea Res 43:345–356

Goffart A, Catalano G, Hecq JH (2000) Factors controlling the distribution of diatoms and Phaeocystis in the Ross Sea. J Mar Syst 27:161–175

Graf G, Schultz R, Peinert R, Meyer-Reuil LA (1983) Benthic response to sedimentation events during autumn to spring at a shallow-water station in the Western Kiel Bight. Mar Biol 77:235–246

Hull SC (1987) Macroalgal mats and species abundance: a field experiment. Estuar Coast Shelf Sci 25:519–532

Jackson MJ, James R (1979) The influence of bait digging on a cockle Cerastoderma edule population in North Norfolk. J Appl Ecol 16:671–679

Justic D, Rabalais NN, Turner RE (1994) Riverbone nutrient, hypoxia and coastal ecosystem evolution: biological responses to long-term changes in nutrient loads carried by the Po and the Mississippi rivers. In: Dyers KR, Orth RJ (eds) Changes in fluxes and estuaries. Olsen & Olsen, Denmark, p 161–167

Lancelot C (1995) The mucilage phenomenon in the continental coastal waters of the North Sea. Sci Total Environ 165:83–102

Lancelot C, Billen G, Sournia A, Weisse T, Coljin F, Veldhuis MJW, Davies A, Wassmann P (1987) Phaeocystis blooms and nutrient enrichment in the coastal zones of the North Sea. Ambio 16:4–38

Liaan-Jensen S (1985) Carotenoids of lower plants-recent progress. Pure Appl Chem 57:649–658

Lorenzen CJ (1967) Determination of chlorophyll and phaeopigments: spectrophotometric equations. Limnol Oceanogr 12:343–346

Luczak C, Janquin MA, Kupka A (1997) Simple standard procedure for the routine determination of organic matter in marine sediment. Hydrobiol 345:87–94

Millet B, Guelorget O (1994) Spatial and seasonal variability in the relationships between benthic communities and physical environment in a lagoon ecosystem. Mar Ecol Prog Ser 108:161–174

Nilsson HC, Rosenberg R (2000) Succession in marine benthic habitats and fauna in response to oxygen deficiency analysed by sediment profile-imaging and by grab sam-

ples. Mar Ecol Prog Ser 197:139–149

Olsgard F (1993) Do toxic algal blooms affect subtidal soft-bottom communities? Mar Ecol Prog Ser 102:269–286

Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr Mar Biol Annu Rev 16:229–311

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

Raffaelli D, Limia J, Hull S, Pont S (1991) Interactions between the amphipod Corophium volutator and macroalgal mats on estuarine mudflats. J Mar Biol Assoc UK 71:899–908

Rasmussen H, Jorgensen BB (1992) Microelectrode studies of seasonal oxygen uptake in a coastal sediment: role of molecular diffusion. Mar Ecol Prog Ser 81:289–303

Reid PC, Lancelot C, Gieskes WWC, Hagmeier E, Weichart G (1990) Phytoplankton in the North Sea: a review. Neth J Sea Res 26:295–331

Renaud P, Syster DA, Ambrose WG (1999) Recruitment patterns of continental shelf benthos off North Carolina, USA: effects of sediment enrichment and impact on community structure. J Exp Mar Biol Ecol 237:89–106

Revsbech NP (1989) An oxygen microsensor with a guard cathode. Limnol Oceanogr 34:472–476

Rousseau V, Mathot S, Lancelot C (1990) Conversion factors for the determination of Phaeocystis sp. carbon biomass in the Southern Bight of the North Sea on the basis of microscopic observations. Mar Biol 107:305–314

Rygg B (1986) Heavy-metal pollution and log-normal distribution of individuals among species in benthic communities. Mar Poll Bull 17:31–36

Smetacek V, Bathmann U, Nöthig EM, Scharek R (1991) Coastal eutrophication: causes and consequences. In: Mantoura RFC, Martin JM, Wollast R (eds) Ocean margin processes in global change. Wiley, Chichester, p 251–279

Soetaert K, Herman PMJ, Middelburg JJ (1996) A model of early diagenetic processes from the shelf to abyssal depths. Geochim Cosmochim Acta 60:1019–1040

Sweerts JPRA, St Louis V, Cappenberg TE (1989) Oxygen concentration profiles and exchange in sediment cores with circulated overlying water. Freshw Biol 21:401–409

Tett PB, Mills DK (1991) The plankton of the North Sea-pelagic ecosystems under stress? Ocean Shoreline Manage 16, 233–257

Thingstad F, Billen G (1994) Microbial degradation of Phaeocystis material in the water column. In: Lancelot C, Wassmann P (eds) Ecology of Phaeocystis dominated ecosystems. J Mar Syst 5:55–65

Ullman WJ, Aller RC (1982) Diffusion coefficients in nearshore marine sediments. Limnol Oceanogr 27:552–556

Wassmann P (1994) Significance of sedimentation for the termination of Phaeocystis blooms. J Mar Sci 5:81–100

Wassmann P, Vernet M, Mitchell BG (1990) Mass sedimentation of Phaeocystis pouchetti in the Barents Sea. Mar Ecol Prog Ser 66:183–195

Wassmann P, Andreassen I, Reigstad M, Slastad D (1996) Pelagic-benthic coupling in the nordic sea: the role of episodic events. Mar Biol 17:447–471

Wear RG, Gardner JPA (2001) Biological effects of the toxic algal bloom of February and March 1998 on the benthos of Wellington Harbour, New Zealand. Mar Ecol Prog Ser 218:63–76

Weisse T, Tande KS, Verity P, Hansen F, Gieskes W (1994) The trophic significance of Phaeocystis blooms. In: Lancelot C, Wassmann P (eds) Ecology of Phaeocystis-dominated ecosystems. J Mar Syst 5:67–79