Belg. Journ. Bot. **135** (1-2) : 15-26 (2002)

MICROPHYTOBENTHOS COMMUNITIES IN THE FRESHWATER TIDAL TO BRACKISH REACHES OF THE SCHELDE ESTUARY (BELGIUM)

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ABSTRACT. — In late summer 1995, intertidal flats situated in the freshwater tidal and brackish reaches of the Schelde estuary were sampled to study the microphytobenthos in the upper estuarine reaches. Diatoms dominated the microphytobenthos community at all sites while coccoid green algae, flagellates or cyanobacteria never contributed significantly to total cell abundance. Epipelic and epipsammic diatoms were the dominant organisms at the brackish sites and disappeared in the oligohaline and freshwater sites, where planktonic diatoms dominated the microphytobenthos community. In oligohaline to freshwater tidal reaches, a turbidity maximum is present which is maintained by repeated resuspension and sedimentation of suspended matter from and to the intertidal areas. Probably, this intense reworking of the sediment surface prevents epipelic and epipsammic diatoms from colonising intertidal mudflats in this part of the estuary.

KEY WORDS. — Schelde estuary, microphytobenthos, epipelon, epipsammon, diatoms, maximum turbidity zone.

INTRODUCTION

Intertidal mudflats in estuaries often sustain very dense populations of micro-algae. Diatoms are usually a very important component of these estuarine microphytobenthos communities and can form dense biofilms on the sediment surface (MACINTYRE *et al.* 1996). Locally and/or seasonally, cyanobacteria or euglenophytes can also be of importance (BARRANGUET *et al.* 1997). Areal biomass of microphytobenthos on estuarine mudflats often exceeds 100 mg chl a m^{-2} and primary productivity can exceed primary productivity in the water column (UNDERWOOD & KROMKAMP 1999). Moreover, resuspension of microphytobenthos by wind- or tide-induced turbulence can give rise to a significant contribution of benthic algae to planktonic biomass (DE JONGE & VAN BEUSEKOM 1992). As a result, in estuaries with extensive intertidal areas, benthic micro-algae often contribute significantly to total ecosystem primary production (e.g. SCHREIBER & PENNOCK 1995). Through production of extracellular polysaccharides, microphytobenthos also plays an important role in stabilising intertidal sediments (DE WINDER *et al.* 1999).

In the past decades, several techniques have been developed to study the microphytobenthos. Chlorophyll a analysis using fluorometry or spectrophotometry yields reproducible results and allows a large number of samples to be processed in a relatively short time but provides no information on community composition (e.g. GUARINI *et al.* 1998). Using high performance liquid chromatography one can identify the major taxonomical groups (e.g. BARRANGUET *et al.* 1997) but the distinction between some important functional groups like planktonic, epipelic and benthic diatoms remains difficult. While being relatively time-consuming and providing no direct information on total biomass, methods involving microscopical cell counts can provide detailed information on microphytobenthic community composition (e.g. SABBE 1993, LAURIA *et al.* 1999).

Benthic micro-algae, however, are notoriously difficult to extract from the sediment. The lens-tissue technique (e.g. COLIJN & DIJKEMA 1981) makes use of the phototactic behaviour of micro-algae to extract them from the sediment but excludes non-motile organisms and introduces a bias towards the most motile taxa. Density gradient centrifugation (e.g. DE JONGE 1979) allows for the separation of micro-algae from detritus and sediment particles but whether epipsammic diatoms are quantitatively separated from the sand grains to which they are attached remains to be tested. Treatment with strong acids separates epipsammon from sediment particles but does not allow to distinguish between living and dead cells (e.g. SABBE 1993). In this study we used a combination of different techniques in an attempt to quantify the different groups of microphytobenthos (diatoms and other algae, epipsammon and epipelon) by means of microscopical analysis and to distinguish between living and dead cells.

Most studies dealing with microscopical analysis of estuarine microphytobenthos include only the brackish and marine reaches of the estuary while the freshwater tidal estuary is seldom investigated (e.g. ASMUS & BAUERFEIND 1994). Several of the studies that deal with the entire estuarine gradient focus only on diatoms (e.g. WILDERMAN 1987, AMSPOKER & MCINTIRE 1986, JUGGINS 1992). JOHN *et al.* (1990) and CLAPS (1996) included all algal groups in their study but focused only on the transition between the river and the estuary. In this paper we studied the microphytobenthos at a series of mudflats situated in upper reaches of the Schelde estuary in order to deduce information on the factors regulating microphytobenthos community composition and abundance in the freshwater tidal and brackish estuarine reaches of a macrotidal estuary. Our results suggest that processes associated with the maximum turbidity zone in the freshwater tidal reaches are important in regulating the microphytobenthos in the upper estuary.

METHODS

STUDY AREA

The Schelde estuary is a coastal plain estuary situated between Belgium and The Netherlands (Fig. 1). Discharge of the estuary is relatively low compared to its total volume, which results in gradual salinity gradient that is stable in time and space. The estuary is heavily anthropogenically influenced and inputs of nutrients and organic matter are very high (HEIP 1988). In contrast to many other European estuaries, the Schelde estuary is characterised by the presence of an extensive freshwater tidal area (MEIRE *et al.* 1995).

This study focuses on mudflats situated in the mesohaline to freshwater tidal reaches of the Schelde estuary. In this part of the estuary, intertidal areas comprise approximately 28 % of the total estuarine surface ; of these intertidal areas, 56 % of the surface is occupied by intertidal mudflats, the remaining part being vegetated by dense *Phragmites* and *Salix* stands (MEIRE *et al.* 1995). Sediments on the intertidal flats are generally muddy and rich in organic matter. Inorganic matter and mud content tend to increase in upstream direction and are usually lower near the mean low water line where tidal currents are stronger (YSEBAERT *et al.* 1993). Tidal range increases from 4.6 m near the Dutch-Belgian border to a maximum of 5.3 m near Dendermonde after which it decreases again to 2 m near Gent, where the tidal wave is arrested by locks. In the plankton of the freshwater tidal reaches, dense phytoplankton blooms dominated by centric diatoms (mainly *Cyclotella* spp. and *Actinocyclus normannii*) and coccoid green algae (*Scenedesmus* spp.) occur in spring and summer. While diatoms are dominant in terms of biomass, numerical abundances of diatoms and coccoid green algae are in the same order of magnitude (MUYLAERT *et al.* 1997, 2000).

In the freshwater tidal reaches, silt particles resuspended by the tides coagulate with organic matter of terrestrial and riverine origin to form macro-aggregates called estuarine flocs (EISMA 1993). Due to their high sedimentation rates (10-100 m day^{-1}, LARGIER 1993) and the specific hydrodynamics of estuaries,

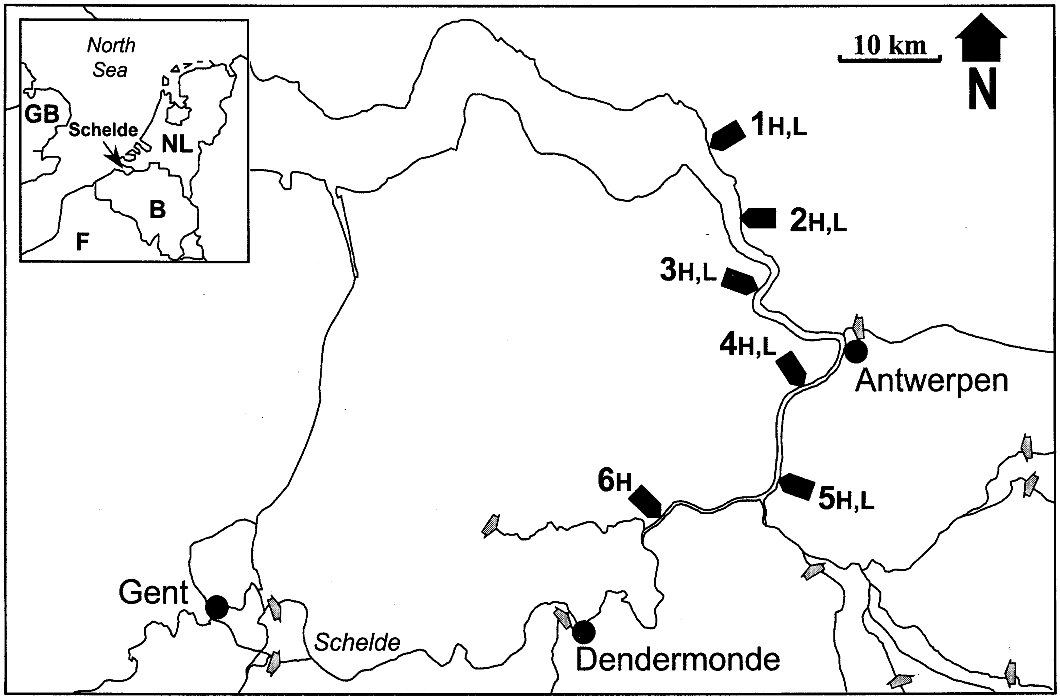

FIG. 1. — Map of the Schelde estuary showing the location of the sampling sites. At each site (except for site 6) a station near the mean high water line (H) and a station near the mean low water line (L) was sampled. The upper limit of tidal influence in the estuary and its side-basins is indicated with grey arrows.

these flocs accumulate in a maximum turbidity zone situated in the freshwater to mesohaline reaches of most estuaries. Two processes are important in the formation of turbidity maxima in the Schelde estuary and these give rise to two separate peaks in turbidity along the estuarine gradient (Fig. 2). The first process involves the entrapment of fast-sinking aggregates in the baroclinic circulation associated with the salt wedge (LARGIER 1993). This 'hydrodynamic trapping' is responsible for the turbidity peak situated in the mesohaline stations of the Schelde estuary, where a slight salinity stratification is usually present (BAEYENS *et al.* 1997). The second process is referred to as 'tidal pumping' and is caused by an asymmetry of the tidal cycle (WOLANSKI 1995) : in the freshwater tidal reaches of many estuaries, including the Schelde estuary, flood currents are stronger than ebb currents (CLAESSENS 1988) and more sediment is resuspended during flood than during ebb tide. This results in a net upstream transport of large particulates and the formation of a second, more pronounced turbidity peak in the freshwater tidal zone.

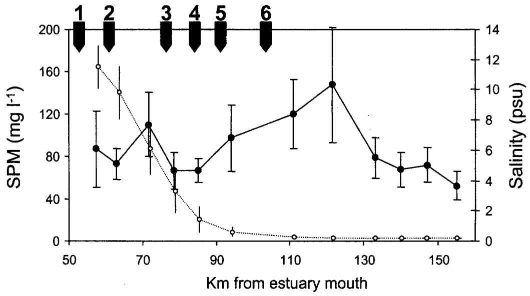

FIG. 2. — Annually averaged spatial variation in suspended particulate matter (SPM, solid line) concentrations and salinity (dotted line) in the upper reaches of the Schelde estuary in 1996 (data from BILLIONES 1998). Error bars indicate ± 0.5 standard deviation. The locations of the six intertidal flats sampled for this study are indicated.

SAMPLING

Six intertidal mudflats situated along a gradient from the mesohaline to the freshwater reaches of the Schelde estuary were sampled at the end of August

1995 (Fig. 1). At each site (except for site 6) two stations were sampled : one near the mean high water line (H) and one near the mean low water line (L). The upper 10 mm of the sediment were collected using a Perspex corer (22 mm diameter). To average out small-scale patchiness, 5 replicate cores collected within 1 m^2 were pooled into one composite sample. Samples were fixed with 40 ml of 33 % formalin (final concentration 4 %). Non-quantitative samples of the upper 10 mm of the sediment were collected and were analysed for sediment grain size distribution and sediment water content.

ABIOTIC MEASUREMENTS

Salinity of interstitial water was measured *in situ* using a refractometer. Sediment grain size distribution was determined automatically using a Coulter Counter LS100. Sediment water content was estimated by determining the difference in weight before and after drying of the sediment at 60°C for 24 hours.

MICROSCOPICAL ANALYSES

To quantify the microphytobenthos, we used the technique described by SUNDBÄCK & SNOEIJS (1991) that aims at separating the epipelon from the epipsammon by means of resuspension and decantation. In this paper, we define the epipsammon as those organisms living in close association with individual sand grains. According to this definition the epipsammon contains only small, motile and non-motile, attached diatoms. The epipelon is defined as organisms moving freely in and on the sediments and contains diatoms as well as all other algal groups with a truly benthic or planktonic lifestyle (ROUND *et al.* 1990).

For enumeration of the microphytobenthos, the fixed samples were gently homogenised after which the largest sediment particles were allowed to settle for 30 seconds and the supernatant was decanted. The supernatant was assumed to contain the epipelon only and will be referred to as the 'resuspended fraction'. Subsamples of the resuspended fraction were transferred to a Bürker counting chamber. The microphytobenthos cells were identified up to genus level and 300 cells were enumerated using a Leitz Diaplan microscope equipped with Nomarski interference contrast optics. Bengal rose B was added to the samples to aid in distinguishing between cells and detrital particles. Only cells containing intact chloroplasts (which were assumed to be living cells) were included in the counts. The sediment remaining after decantation of the supernatant was assumed to contain only epipsammic diatoms (SUNDBÄCK & SNOEIJS 1991) and will be referred to as the sediment fraction. For enumerating diatoms in this fraction, a subsample of the sediment was oxidised with equal parts sulphuric acid and nitric acid to separate diatoms from the sediment and to clean diatom frustules (KRAMMER & LANGE-BERTALOT 1986). Samples were heated for two hours after which sediment and frustules were rinsed twice with water and twice with ethanol by means of centrifugation. After the final rinse, the pellet containing diatom valves was resuspended in a known volume of ethanol. 50 µl of this suspension was transferred to a coverslip and air-dried. Coverslips were mounted in Naphrax and inspected using Nomarski interference contrast microscopy. At least 200 diatom frustules were identified and enumerated within a known surface area. This surface area was extrapolated to the total surface of the dried drop in order to estimate the number of frustules per volume of sediment. Afterwards, subsamples from the sediment fraction were resuspended in 4 % formalin and stained with Bengal rose B. In this suspension, the fraction of living cells was determined in order to correct the counts of the Naphrax slides for dead diatoms. The total number of living microphytobenthos cells per volume of sediment was then calculated from the sum of the counts in the resuspended and sediment fractions.

All taxa were assigned to one of the following functional groups : epipelic, epipsammic and planktonic diatoms, coccoid green algae, flagellates and cyanobacteria. For diatoms, the assignment to a specific group was based on personal observations on fixed material (for distinguishing epipelic from epipsammic forms) as well as information published by RICARD (1987), DENYS (1991) and SABBE (1997) on the autoecology of diatoms.

MATHEMATICAL ANALYSIS OF THE DATA

Redundancy analysis (RDA) was used to determine the influence of environmental variables on the distribution of the dominant functional groups in the microphytobenthos. Abundance data were log(x+1) transformed prior to analysis to obtain normal distribution. The environmental variables included were salinity, sediment median grain size, clay and silt fraction in the sediment, sediment water content and position near high or low water line. For the position near high or low water line, dummy variables were used, while all other environmental variables were quantitative. For all multivariate analyses, the CANOCO software package, version 3.1 was used. First the significance of each environmental variable in explaining variation in the abundance data was tested by means of a Monte Carlo permutation test (999 unrestricted permutations) and only environmental variables significantly explaining variation in the data were included. Of all environmental variables, only salinity and median grain size significantly explained variation in microphytobenthos abundance data. By determining the variation explained by salinity and median grain size separately and of each variable with the other variable as a covariable, we were able to partition the variation in the data among salinity and median grain size (cfr. BORCARD *et al.* 1992).

RESULTS

ABIOTIC MEASUREMENTS

The results of the abiotic measurements are summarised in Fig. 3. Salinity of interstitial water decreased from 18.5 psu at site 1 to less than 0.5 psu at sites 5 and 6 and was generally comparable for the stations near the high and low water line. Only site 6 can be considered freshwater (salinity < 0.5 psu). Having a salinity between 0.5 and 5, site 5 can be considered oligohaline. The other sites have mesohaline interstitial water, with a salinity between 5 and 18. Median grain size of the sediment varied between 16 and 196 µm. Clay (< 4 µm) and silt (4-63 µm) content varied respectively between 0.8 and 20 % and 2.6 and 89 %. Sediments at sites 2 and 6 were characterised by the lowest median grain size and highest clay and silt content. With the exception of site 2, the stations near mean low water were always characterised by a higher median grain size and a lower clay and silt content. Water content of the sediment varied between 23 and 71 % and decreased with increasing median grain size.

SPECIES COMPOSITION AND CELL ABUNDANCE

A list with all the taxa which contributed to more than 5 % of total cell abundance of a particular functional group in at least one sample is given in Table 1. The dominant epipsammic diatoms in our samples were *Planothidium delicatulum*, *Opephora guenter-grassii*, *Fragilaria schulzii*, *Catenula adhaerens* and a small unidentified *Navicula* species. The dominant epipelic diatoms were *Cocconeis placentula*, *Navicula phyllepta*, *Parlibellus* sp., *Nitzschia dissipata*,

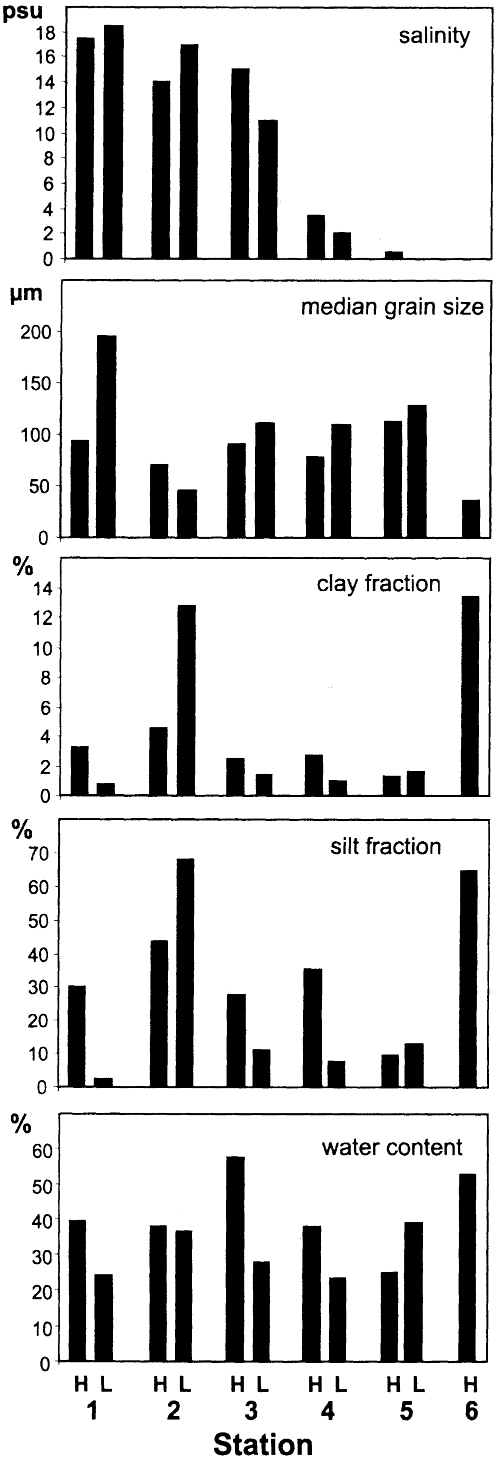

FIG. 3. — Salinity, median grain size and clay, silt and organic matter content of the sediment at all sampled stations.

TABLE 1

List of the taxa contributing to more than 5% of the total cell numbers of a functional group in at least one sample

Epipsammic diatoms

Planothidium delicatulum (Kützing) Round & Bukthiyarova
Amphora spp.
Biremis lucens (Hustedt) Sabbe, Witkowski & Vyverman
Catenula adhaerens Mereschkowsky
Cymatosira belgica Grunow
Delphineis minutissima (Hustedt) Simonsen
Fragilaria schulzii Brockmann
Navicula sp. 1
Navicula sp. 4
Navicula perminuta Grunow
Opephora guenter-grassii (Witkowski & Lange-Bertalot) Sabbe & Vyverman
Opephora mutabilis (Grunow) Sabbe & Vyverman
Pseudostaurosira perminuta (Grunow) Sabbe & Vyverman
Rhaphoneis amphiceros (Ehrenberg) Ehrenberg

Epipelic diatoms

Biddulphia alternans (Bailey) van Heurck
Cocconeis placentula Ehrenberg
Diploneis spp.
Frustulia sp.
Gomphonema parvulum (Kützing) Kützing
Luticola cohnii (Hilse) Mann
Luticola mutica var. *ventricosa* (Kützing) Mann
Placoneis clementis (Grunow) Cox
Navicula flanatica Grunow
Nitzschia fonticola Grunow
Navicula gregaria Donkin
Navicula phyllepta Kützing
Navicula recens (Lange-Bertalot) Lange-Bertalot
Navicula sp. 2
Navicula sp. 3
Navicula trivialis Lange-Bertalot
Nitzschia debilis
Nitzschia dissipata (Kützing) Grunow
Nitzschia palea (Kützing) Smith
Nitzschia perspicua Cholnoky
Nitzschia sigma (Kützing) Smith
Parlibellus sp.
Psammodictyon constrictum (Gregory) Mann
Staurophora salina Smith
Surirella brébissonii Krammer & Lange-Bertalot

Planktonic diatoms

Actinocyclus normanii (Gregory) Hustedt
Asterionella formosa Hassall
Cyclotella atomus Hustedt
Cyclotella meneghiniana Kützing
Cyclotella scaldensis Muylaert & Sabbe
Thalassionema nitzschioides Grunow
Thalassiosira angulata (Gregory) Hasle
Thalassiosira decipiens (Grunow) Jörgensen
Thalassiosira proschkinae Makarova

Coccoid green algae

Scenedesmus spp.
Tetrastrum spp.
Pediastrum spp.
Staurastrum sp.
Crucigenia spp.
Chlorococcus-like cells

Cyanobacteria

Oscillatoria spp.
Pseudanabaena spp.
Merismopedia spp.

Flagellates

Euglena spp.
Phacus spp.

Nitzschia sigma, *Navicula flanatica* and *Staurophora salina*. Planktonic diatoms were mainly represented by centric taxa like *Thalassiosira proschkinae* and *Cyclotella* species. Coccoid green algae were dominated by *Scenedesmus* and *Crucigenia* species. The most important flagellates were *Euglena* and *Phacus* species while cyanobacteria were dominated by *Oscillatoria* and *Merismopedia* species.

Abundance of the different functional groups in all samples is presented in Fig. 4. Epipsammic diatoms were the most abundant organisms in our samples, attaining on average 4.4 10^6 cells cm^{-3} sediment. The second most abundant group were planktonic diatoms (on average 1.1 10^6 cells cm^{-3} sediment) followed by epipelic diatoms (on average 0.4 10^6 cells cm^{-3} sediment). Autotrophic flagellates, coccoid green

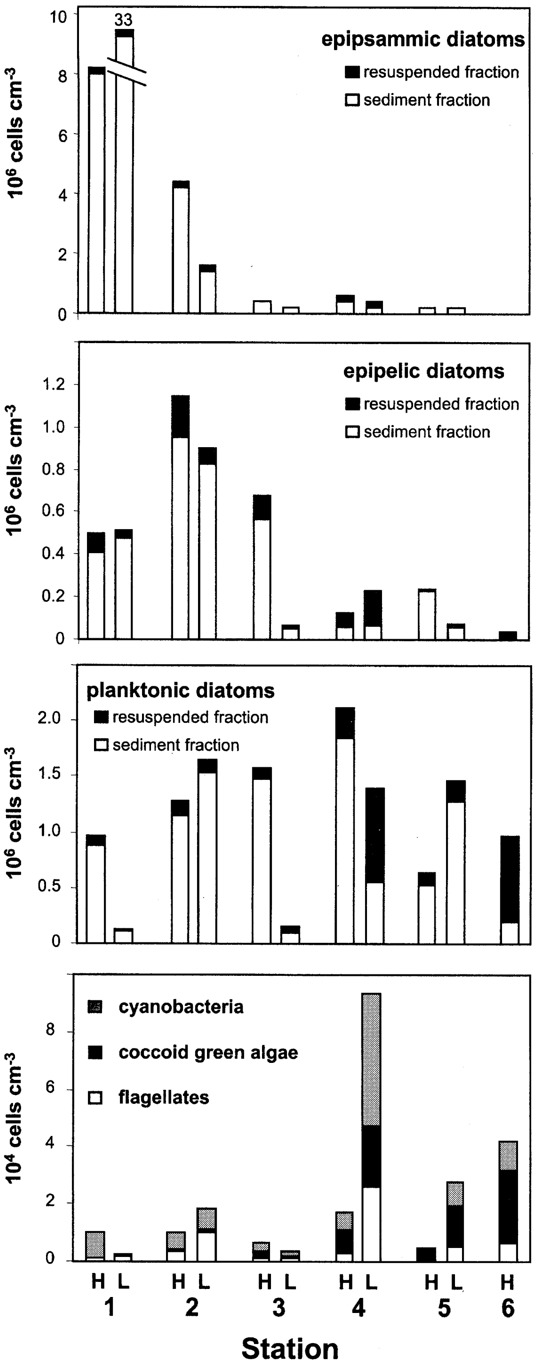

FIG. 4. — Cell abundance of the dominant functional groups at all sampled stations. For the diatoms, which were enumerated in the resuspended as well as the sediment fraction, the contribution of total cell abundance to both fractions is indicated.

algae and cyanobacteria attained comparable cell numbers and abundance of these groups was on average about 1 to 2 orders of magnitude lower than those of diatoms.

Epipsammic and (to a lesser extent) epipelic diatoms decreased strongly in abundance in the most upstream sites sampled. Abundance of planktonic diatoms was comparable at all stations except for the sandy stations situated near the mean low water line at sites 1 and 3. Coccoid green algae were found mainly in the oligohaline to freshwater part of the estuary (sites 4, 5 and 6). Cyanobacterial and flagellate abundance did not vary systematically among the stations but was especially high at the station near the low water line at site 4.

Diatoms were enumerated in the resuspended as well as in the sediment fraction of the samples. On average 88.1 % of the epipsammic diatoms were found in the sediment fraction ; this percentage decreased from more than 99 % at site 1 to 42 % in the freshwater part of the estuary at site 6, where epipsammic diatom abundance was much lower. Of the epipelic and planktonic diatoms, on average only 19.6 % and 23.1 % respectively were found in the resuspended fraction ; especially for the planktonic diatoms, this percentage increased towards the most upstream sites.

MULTIVARIATE ANALYSIS

Salinity and median grain size explained 53.4 % ($p < 0.01$) and 21.2 % ($p < 0.05$), respectively, of the variation in the abundance data. Together, salinity and median grain size explained 66.2 % of the variation in the data set. When the effect of salinity was removed (by introducing salinity as a covariable in the analysis), median grain size still explained 12.8 % of the variation ($p < 0.05$). When the effect of median grain size was removed, salinity still explained 44.9 % of the variation in the abundance data ($p < 0.01$). There was an 8.4 % overlap in variation explained by salinity and median grain size (Fig. 5B).

In the RDA ordination diagram (Fig. 5A) epipsammic and epipelic diatoms clustered on the right side of the diagram separate from the other

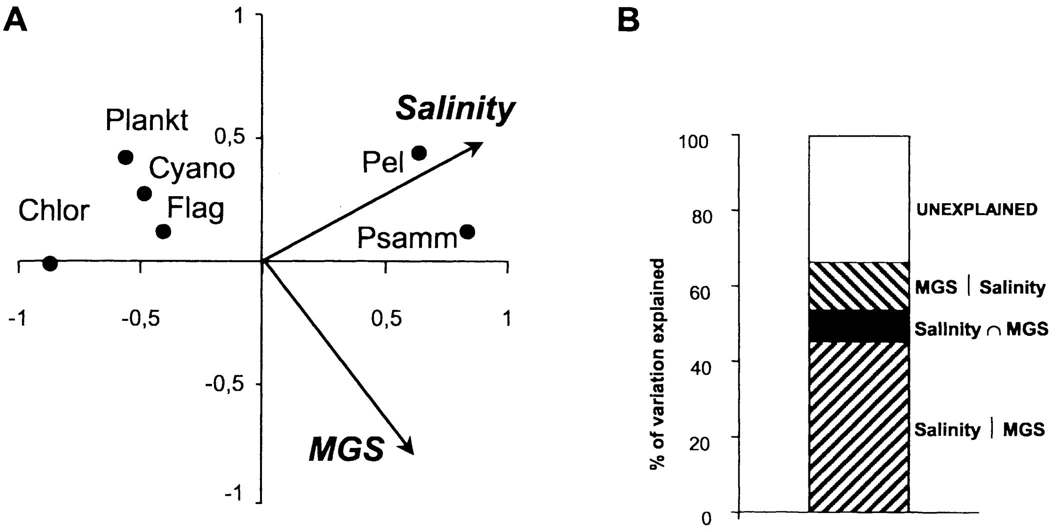

FIG. 5. — Results of the multivariate analysis.

(a) Biplot based on the redundancy analysis of the functional groups in the microphytobenthos [coccoid green algae (Chlor), flagellates (Flag), cyanobacteria (Cyano), planktonic (Plankt), epipelic (Pel) and epipsammic (Psamm) diatoms] and the abiotic variables salinity and median grain size (MGS)

(b) Partitioning of the variation in the abundance of the functional groups among median grain size and salinity :
MGS I Salinity : variation explained by MGS but not by salinity ;
Salinity I MGS : variation explained by salinity but not by MGS ;
Salinity ∩ MGS : variation explained by salinity as well as by MGS ;
UNEXPLAINED : unexplained variation in the data.

functional groups. Both groups were strongly positively related to salinity. Coccoid green algae showed a strong negative relation to salinity. Planktonic diatoms, cyanobacteria and flagellates take a position near the origin and these functional groups were only weakly negatively related to median grain size.

DISCUSSION

In this study, the microphytobenthos was quantified using a technique described by Sundback & Snoeijs (1991) in which the epipelon is separated from the epipsammon by means of resuspension and decantation. A similar technique was used by Asmus & Bauerfeind (1994). In our samples, this method proved to be unsuccessful in separating epipsammic from epipelic organisms. While in most samples, the majority of the epipsammic diatoms were found in the sediment fraction, the bulk of the epipelic and planktonic diatoms were found in the sediment instead of the resuspended fraction. This may be explained by the fact that in sediments these algae sometimes occur in association with large and fast-sinking aggregates of detritus and silt particles (Admiraal & Peletier 1980). Sedimentation rates of these aggregates are likely to be similar to those of large sand grains and, therefore, these aggregates and the associated epipelon would probably become included in the sediment fraction.

Diatoms numerically dominated the microphytobenthos community at all stations. However, it should be noted that coccoid green algae, flagellates and cyanobacteria were only enumerated in the resuspended fraction and cell numbers of these algal groups may therefore be seriously underestimated. As these algae belong to the epipelon one could assume that the extraction efficiency of these algae is comparable to that of epipelic and planktonic diatoms. Consequently, the abundance of these groups should probably be increased about five-fold. Even then, they only contributed to at most 2 % of total cell numbers. The observed patterns in cell abundance data can not be directly translated into biomass but even assuming that the dominant phytoflagellates and cyanobacteria are one order of magnitude larger in size than the dominant diatoms, diatoms would still dominate microphytobenthos biomass at all stations. Cyanobacteria and flagellates tend to be more abundant under calm conditions (MacIntyre *et al.* 1996). In the part of the estuary studied, the intertidal flats are relatively narrow and tidal currents are very strong which probably prevents cyanobacteria and flagellates from dominating microphytobenthic biomass. Cyanobacteria and flagellate abundance displayed little variability among the sites. In the ordination, these groups were positioned near the centre of the biplot and showed only a weak negative correlation with median grain size (Fig. 5), probably because growth conditions for these organisms were unfavourable over the entire range of environmental conditions sampled.

Epipelic and epipsammic diatoms abundance was much lower in the oligohaline and freshwater sites when compared to the more downstream situated locations and, in the ordination diagram, epipsammic and epipelic diatoms were separated from the other algal groups mainly based on their positive correlation with salinity (Fig. 5). The decrease in abundance of these organisms in the more upstream-situated sites cannot only be ascribed to the absence of suitable substrates in this part of the estuary as sediments with high median grain size occurred along the entire gradient sampled (Fig. 3). This does not necessarily imply that salinity is directly responsible for the observed decline in epipelic and epipsammic diatom abundance. Salinity stress is often found to have a negative influence on estuarine biota, giving rise to a minimum in biomass and diversity at around 5 psu (Remane & Schlieper 1958). However, although many microphytobenthos studies report a change in community composition of epipelic and epipsammic diatoms near the 5 psu isohaline, this change is in many cases not accompanied by a decrease in biomass or total cell abundance (Wilderman 1987, Snoeijs 1994). In our study, we found only typical brackish water to marine epipsammic diatoms while freshwater taxa commonly found in other freshwater tidal estuaries (Juggins 1992), rivers (Van Dam *et al.* 1994) or even tributaries to the Schelde estuary (Van de Vijver 1996) were either absent or only present in very low numbers (e.g. *Frustulia* spp., *Navicula trivialis*, *Nitzschia palea* and *N. fonticola*). Several diatom taxa that we observed only in the mesohaline stations occurred at much lower salinities in the Thames estuary (e.g. *Navicula phyllepta* and *N. gregaria*, Juggins 1992). This illustrates that low salinity alone cannot explain the absence of epipsammic and epipelic diatoms on mudflats in the oligohaline and freshwater tidal reaches of the Schelde estuary.

Most estuaries are characterised by the presence of a maximum turbidity zone. While in most estuaries the maximum turbidity zone is restricted to the region of salt-wedge stratification (e.g. the Elbe, Herman & Heip 1999), in the Schelde estuary, a second turbidity maximum is present in the oligohaline and freshwater tidal reaches (Fig. 2). In this part of the estuary, the asymmetry of the tidal cycle is maximal and the turbidity maximum is maintained by the process of tidal pumping. In this type of turbidity maxima, high current velocities are combined with high sedimentation rates. As a result, on the intertidal flats, suspended sediments constantly settle and are resuspended again (Wolanski 1995). This constant reworking of the sediments probably prevents epipelic and epipsammic diatoms from colonising mudflats in the oligohaline and freshwater tidal reaches of the estuary. High sedimentation rates were also considered to be responsible for the lower numbers of microphytobenthos in the freshwater tidal reaches of the Thames estuary when compared to the non-tidal Thames River (John *et al.* 1990). In an experimental study, Wulff *et al.* (1997) also found a strong effect of fine sediment deposition on the microphytobenthos dynamics. Cahoon *et al.* (1999) observed a negative relationship between total microphytobenthic biomass and the fraction of fine particles (< 125 µm) and suggested that high sedimentation of fine particles may negatively influence microphytobenthos in intertidal areas. The turbidity maximum found in the mesohaline reaches is situated in a region of salt wedge stratification and is mainly maintained by hydrodynamic trapping, a process that takes place within the water column and does not involve a cycle of sedimentation and resuspension. Therefore, its influence on the microphytobenthos is probably less important and does not inhibit growth of epipelic and epipsammic diatoms.

Coccoid green algae were found predominantly in the oligohaline and freshwater sites and were in the ordination related to low salinities (Fig. 5). Planktonic diatoms displayed a relatively weak negative relation with median grain size. In the Schelde estuary, species of the genera *Cyclotella* and *Scenedesmus* dominate the phytoplankton community in the freshwater tidal estuary while the genus *Thalassiosira* is the dominant phytoplankton genus in the oligo- to mesohaline reaches (MUYLAERT *et al.* 1997, 2000). The same species are also the most important contributors to the functional groups of planktonic diatoms and coccoid green algae in the microphytobenthos of the same estuarine reaches. The presence of planktonic diatoms and coccoid green algae in the benthos can therefore probably mainly be ascribed to influx from the plankton. This is confirmed by the negative relation of planktonic diatoms with sediment grain size, as low median grain sizes are indicative of higher sedimentation rates. AMSPOKER & MCINTIRE (1986) and CLAPS (1996) also found a large contribution of planktonic algae in the microphytobenthos of other estuaries.

While abundance of coccoid green algae and diatoms in the plankton of the freshwater tidal reaches is comparable (MUYLAERT *et al.* 1997, 2000), planktonic diatoms are relatively much more abundant in the benthos of the freshwater tidal estuary than coccoid green algae. This suggests a larger flux from the plankton to the benthos for diatoms when compared to green algae. This may be explained by the presence of a siliceous exoskeleton in diatoms, which results in their high sedimentation rates. Moreover, in estuaries, many planktonic diatoms are known to occur in association with sediment and detritus particles (ERNISSEE & ABBOT 1975, MUYLAERT & SABBE 1996). It has been suggested by some authors that diatoms may exploit sedimentation onto intertidal flats to prevent them from being washed out of the estuary (SMETACEK 1986, SCHUCHARDT & SCHIRMER 1991, MUYLAERT & SABBE 1996). Thanks to their high sedimentation rates, diatoms may behave like estuarine flocs and as such accumulate in estuarine turbidity maxima by hydrodynamic trapping and/or tidal pumping (CLOERN *et al.* 1983). Recent observations confirm this hypothesis by demonstrating sedimentation and resuspension cycles of planktonic diatoms in estuaries (VERITY *et al.* 1998, LAURIA *et al.* 1999). Periodic sedimentation onto intertidal mudflats may also provide diatoms with periods of high light availability, allowing them to photosynthesize and grow at maximal capacity whereas primary production is strongly light-limited in the water column.

Our data as well as previous studies on microphytobenthic species composition in the Schelde estuary (SABBE & VYVERMAN 1991, SABBE 1993) showed that in the meso- to polyhaline reaches of the Schelde estuary, diatoms with a truly benthic lifestyle like epipsammic and epipelic species tend to dominate microphytobenthos communities. In the oligohaline to freshwater tidal reaches, however, planktonic diatoms are the major contributors to the microphytobenthos and microphytobenthic biomass is probably mainly controlled by influx from the plankton. Whether the benthos in this part of the estuary is a sink for planktonic diatoms or whether they use the benthos to increase their residence time in the estuary and/or increase their growth rates remains to be evaluated.

ACKNOWLEDGEMENTS

The research presented in this paper was carried out in the framework of the Flemish OMES project ('Onderzoek naar de Milieu-Effekten van het Sigmaplan'). The research also contributed to the project 'Biotic interactions in turbid estuarine systems' (Fund for Scientific Research) and the BOF-project GOA 12050398 (University Gent). Koenraad Muylaert and Koen Sabbe are post-doctoral fellows of the Fund for Scientific Research (Flanders).

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Revised manuscript received 31 January 2002.