

## Short communication

## Observations of resuspended diatoms in the turbid tidal edge

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**Abstract**

Observations of resuspended diatoms in the shallow waters (<60 cm) of the turbid tidal edge are described for single sites on two tidal flats—the Molenplaat in the Westerschelde estuary, and the Hond in the Ems-Dollard estuary, The Netherlands. High concentrations of chlorophyll-a (chl-a) were observed in the trailing edge of the ebbing tide in water depths of <20 cm, after which concentrations decreased markedly. Peak mean values were  $19 \mu\text{g chl-a l}^{-1}$  in 10 cm of water at the Molenplaat, and  $45 \mu\text{g chl-a l}^{-1}$  in 5 cm of water at the Hond. Similar trends were observed on the flooding tide, although peak values were far less pronounced (6 and  $30 \mu\text{g chl-a l}^{-1}$  respectively). Microscopic examination of the diatom community within the turbid tidal edge at the Molenplaat revealed that peaks in biomass were caused by suspended benthic diatoms, as well as the large centric diatom *Coscinodiscus* sp., particularly on the ebb tide. Planktonic diatoms other than *Coscinodiscus* sp. were more randomly distributed and did not appear to follow any particular trend. It would seem that as the tide recedes, resuspended benthic diatoms and large *Coscinodiscus* sp. cells become concentrated in the shallow water. However, the virtual absence of *Coscinodiscus* sp. from the leading edge of the flooding tide suggests that most of the resuspended cells do not settle to the seabed, but are washed away into the channels. The small peak of benthic diatoms at the leading edge of the flood tide is most likely resuspended locally from the sediment, along with large numbers of diatom frustules.

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**1. Introduction**

Understanding the cycle of erosion, transport and deposition of sediments and associated biological particles in estuarine tidal flats is of fundamental importance for measurements of sediment stability, water quality (suspended particulate load, nutrients

and sediment-bound contaminants), fluxes of particles between tidal flats and the main estuary, and food quality and quantity available to benthic and pelagic food webs. Resuspension occurs as a result of tidal currents and wave action. Although waves in shallow water may not be very large, they can cause considerable resuspension in general (De Jonge, 1995), and in just a few centimetres of water due to their turbulent action (Dyer, 1989). High concentrations of suspended sediment are often found at the leading edge of tidal waters due to a combined

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action of local current speed and wave action, or advection of accumulated suspended material onto the tidal flat. These may potentially deposit large quantities of material across the tidal flat. Nevertheless, as Christie and Dyer (1998) pointed out, interactions between the seabed and combined wave and current action in shallow water (<1 m depth) are not well understood, and very few measurements are available.

It is well known that resuspended benthic diatoms temporarily enhance phytoplankton populations, and in shallow estuaries much of the spatial variability in chlorophyll-a (chl-a) concentration occurs as a result of resuspended benthic cells (Shaffer and Sullivan, 1988) being redistributed to and from the tidal flats. For example, De Jonge and Van Beusekom (1992) estimated that benthic diatoms contributed up to 60% to total water column chl-a in the Ems estuary. The principal mechanisms of benthic diatom resuspension are tidal currents (Baillie and Welsh, 1980; Lucas et al., 2000) and wind-generated waves which increase turbulent action at the seabed (Demers et al., 1987; De Jonge and Van Beusekom, 1995), especially in shallow (<1 m) waters. What is not generally considered is that resuspension of microbial populations may occur as the incoming tide advances across a tidal flat (but see Gallagher, 1975). These mechanisms are likely to be influenced by the cohesive properties and depositional history of the sediment, as well as the presence of bioturbators (Blanchard et al., 1997).

Although epipelagic diatoms are characterised by endogenous tidal and diurnal migratory rhythms (Paterson, 1986) resulting in downward migration into the sediment as the incoming tide approaches, some diatoms may still be resuspended. During the ECOFLAT Project, small sections of diatom biofilm, as well as detritus and sand grains were observed in the leading edge of the tide as it advanced over the tidal flat, apparently picked up in the surface tension of the water. Christie and Dyer (1998) also commented on such observations at the Skeffling mudflats in the Humber estuary. This paper describes semi-quantitative measurements and observations made of this phenomenon at two locations: the Molenplaat tidal flat in the Westerschelde estuary, and the Hond tidal flat (near the Hond-Paap) in the Ems-Dollard estuary of the Dutch Wadden Sea.

## 2. Materials and methods

### 2.1. Study sites

The Molenplaat tidal flat is located in the mid-region of the Westerschelde estuary, SW Netherlands (Fig. 1). The majority of the tidal flat is situated between  $-1$  and  $+1$  m mean tide level, and the tidal range is  $\sim 5$  m. The sediment consists mainly of fine to very fine sand, although silt ( $<63 \mu\text{m}$ ) accumulation occurs in the central region during the summer months (NIOO Progress Report, 1996; Herman et al., 2001). Benthic diatoms dominate the microphytobenthos community, although summer populations of cyanobacteria and *Euglena* occur in the sandier regions (Barranguet et al., 1997). Sediment chlorophyll-a (chl-a) reflects the spatial and temporal variation in grain size across the Molenplaat, with mean values in 1997 ranging from  $6.8$ – $58.9 \mu\text{g gDW}^{-1}$  in June and  $1.9$ – $6.8 \mu\text{g gDW}^{-1}$  in September. Particular reference is given to ECOFLAT Site 1 (hereafter called 'MOLEN') located in the middle of the southern edge of the flat, where turbid tidal edge samples were collected. Table 1 summarises the sediment granulometry, water, organic, and chl-a contents (Lucas et al., 2003), and erosion thresholds (Widdows et al., 2000) of site MOLEN.

The Hond tidal flat, located near the Hond-Paap tidal flat in the Ems-Dollard estuary (Fig. 1) has a similar range of sedimentological and biological characteristics to that of the Molenplaat. Tidal range is  $\sim 3$  m, and the Hond tidal flat is located between  $-0.2$  and  $0.0$  m mean tide level (De Jonge, pers. comm., 2003). In June 1998, chl-a content of the tidal flat ranged between  $3.2$  and  $48.7 \mu\text{g gDW}^{-1}$  in the upper 2 mm of the sediment. Particular reference is given to ECOFLAT Site B (hereafter called 'HOND'), which was chosen as a sampling site for turbid tidal edge observations. Although median grain size data are unavailable, silt (8.1%), ash free dry weight (1.3%), water (32.8%) and chl-a ( $11.4 \mu\text{g gDW}^{-1}$ ) contents are similar to those of site MOLEN for the same time of year. The greatest difference, however, lies in macrofauna community structure, with the cockle *Cerastoderma edule* and gastropod *Hydrobia ulvae* present in high densities at site HOND (Table 1).

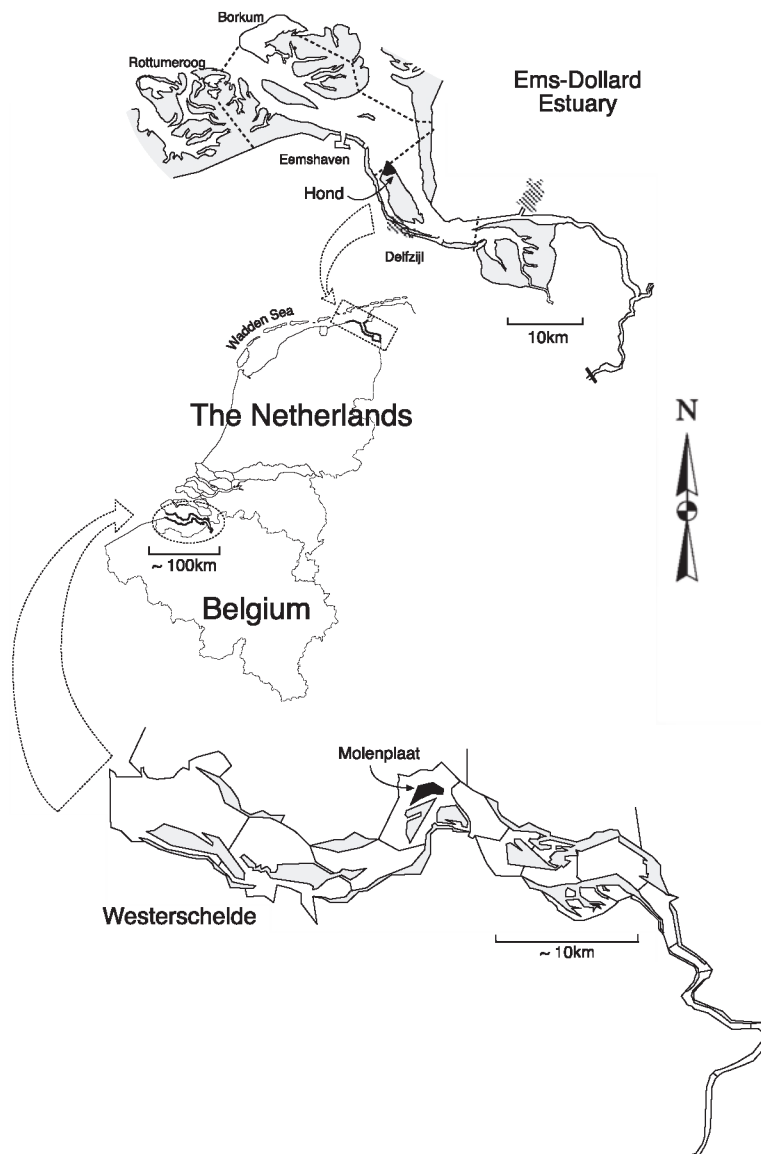


Fig. 1. Map of the Netherlands showing the location of the Hond tidal flat in the Ems-Dollard estuary and the Molenplaat tidal flat in the Westerschelde estuary.

## 2.2. Water sampling

Sampling of the tidal edge was carried out in September 1997 (MOLEN) and June 1998 (HOND). As the tidal front approached (flooded) or receded (ebbed) from each site, single water samples were collected at 5-cm depth intervals between 5 and 60 cm water depth. A total of 24 samples were collected on

each flood-ebb cycle for each site. A wide-necked plastic bottle was plunged near to the seabed and ~250 ml of water collected. Chl-a analysis was carried out in duplicate. Between 25 and 100 ml of the sample was filtered through a Whatman GF/C filter (pore size ca. 1.2  $\mu\text{m}$ ), depending on the turbidity of the water. (Up to 20–25 cm depth, the water was extremely turbid.) Two to three drops of  $\text{MgCO}_3$

Table 1

Summary of the main physical, chemical and biological characteristics of the turbid tidal edge sampling sites at the Molenplaat (1997) and Hond (1998) tidal flats

Parameter (mean)	Month	MOLEN	HOND
Median grain size ( $\mu\text{m}$ )	June	156.8	–
	September	164.0	–
% Silt ( $< 63 \mu\text{m}$ )	June	14.2	8.1
	September	14.6	–
% Water	June	31.9	32.8
	September	32.3	–
% AFDW (of DW)	June	1.8	1.3
	September	2.0	–
Chlorophyll-a ( $\mu\text{g gDW}^{-1}$ ) (0–2 mm)	June	12.6	11.4
	September	5.4	–
EPS ( $\mu\text{g gluc.equ. gDW}^{-1}$ ) (0–2 mm)	June	38.22	171.7
	September	35.39	–
$U_{\text{crit}}$ ( $\text{cm s}^{-1}$ )	June	20.4	16.7
	September	18.6	–
<i>Macoma balthica</i> (g AFDW $\text{m}^{-2}$ )	June	9.1	0.39
	September	4.6	–
<i>Cerastoderma edule</i> (g AFDW $\text{m}^{-2}$ )	June	0.04	170.8
	September	0.02	–
<i>Hydrobia ulvae</i> (no. $\text{m}^{-2}$ )	June	0	233 000
	September	0	–

MOLEN = Ecoflat site 1; HOND = Ecoflat site B; – = no data.

were added to prevent acidification of the filter, after which they were folded and frozen at  $-70^\circ\text{C}$  until analysis. Water samples for diatom identification and enumeration were transferred into 50 ml brown bottles and preserved with 2–3 drops of Lugol's solution.

### 2.3. Laboratory analyses

Filtered samples for chl-a analysis were extracted in 90% acetone, ultra-sonicated for 30 s, and centrifuged at 3000 rpm ( $2000 \times g$ ) for 15 min. Chl-a and phaeopigment concentrations, expressed as  $\mu\text{g l}^{-1}$ , were measured fluorometrically using a Turner 10-AU fluorometer. Samples from the Molenplaat were also analysed by ion-pairing reverse-phase HPLC using a 5  $\mu\text{m}$  C-18 column (Barlow et al., 1993), to determine community composition based on algal pigment fingerprints. Pigment analysis was unavailable for the Hond samples. Details of these procedures are given in Lucas et al. (2000).

Microscopic examination of the Lugol-preserved water samples was carried out in duplicate to determine the composition of resuspended microalgal material. Each sample was thoroughly mixed before a known volume was transferred into a settling

chamber and prepared for examination using Utermöhl settling chambers. The chambers were scanned at both  $100 \times$  and  $200 \times$  magnification using an inverted light microscope (Leica DMIRB) fitted with phase contrast and brightfield illumination. In order to determine the type and quality of resuspended material (Lucas et al., 2001) both 'live' cells (i.e., containing chloroplasts) and diatom frustules were identified. Between 100 and 500 live cells counted per sample. Initial tests revealed that this protocol produced reproducible results. Abundance was expressed in no. cells  $\times 10^3 \text{ l}^{-1}$ .

### 3. Results and discussion

Direct comparisons between the Molenplaat and Hond tidal flats are difficult because, although extremely poor weather conditions were experienced in the Ems-Dollard in June 1998 making September 1997 and June 1998 conditions similar, sampling was carried out at different times of the year. The amount of surface chlorophyll-a (chl-a) available for resuspension, macrofauna community composition and grazing/bioturbation activities, sediment critical

erosion velocity ( $U_{crit}$ ), and wind (wave) climate are all likely to differ (De Jonge and Van Beusekom, 1995; Widdows et al., 2000). Additionally, the light regime and growth status of the diatom community subsequently affect EPS production (Staats et al., 2000) and resistance to erosion. Sites HOND and MOLEN did have similar values of chl *a* ( $11.4 \mu\text{g l}^{-1}$  and  $5.4 \mu\text{g l}^{-1}$ ),  $U_{crit}$  ( $16.7 \text{ cm s}^{-1}$  and  $18.6 \text{ cm s}^{-1}$ ), water content (32.3% and 32.8%) and other sedimentological properties (see Table 1), but macrofauna composition was significantly different, as dense populations of *Cerastoderma edule* and *Hydrobia ulvae* were found at site HOND in June 1998. The surface deposit feeder *H. ulvae* grazes on benthic microalgae, disturbing the sediment surface as they feed and move, while the suspension feeder *C. edule* filters pelagic algae from the overlying water column (Herman et al., 2000).

Chl-*a* concentrations in the shallow waters (<60 cm) of the turbid tidal edge of flood and ebb tides at the Molenplaat and Hond tidal flats are illustrated in Fig. 2. Sites MOLEN and HOND displayed similar trends, with significant peaks of chl-*a* biomass in very shallow water (<20 cm), particularly in the trailing edge of the ebb as the tide receded offshore. During the ebb tide, peak mean ( $\pm$  sd) chl-*a* values of  $18.6 \pm 2.5 \mu\text{g l}^{-1}$  (MOLEN) and  $45.0 \pm 4.1 \mu\text{g l}^{-1}$  (HOND) were measured in water depths of 10 cm and 5 cm, respectively. At these shallow depths, the water was extremely turbid, consisting of fine sedimentary and detrital material being washed off the tidal flats. Christie and Dyer (1998) suggest that high concentrations on the ebb tide are due to mixing of highly concentrated near-bed suspensions formed by settling over slack water periods. The leading edges of the flood tides were less turbid, with mainly coarser sand particles and some biofilm being lifted off the sediment surface. Peak flood chl-*a* values did occur in water depths <20 cm, but these were less pronounced ( $5.4 \pm 1.0$  and  $30.5 \pm 2.4 \mu\text{g l}^{-1}$  respectively), particularly at site MOLEN. Chl-*a* values were relatively constant between 20 and 60 cm depth on both the flood and ebb tides.

HPLC analysis of the MOLEN water samples revealed that diatoms dominated the microalgal community. Fucoxanthin is a marker pigment for diatoms (see Jeffrey et al., 1997), and trends in its distribution were very similar to those of chl-*a* (Fig. 2). Micro-

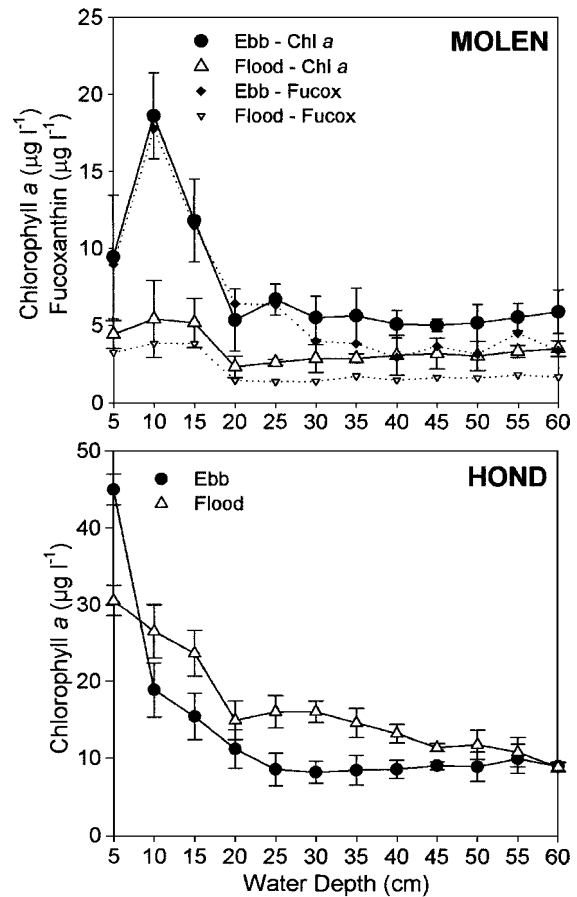


Fig. 2. Mean ( $\pm$  sd) chlorophyll *a* and fucoxanthin concentrations in the ebbing and flooding turbid tidal edge at the Molenplaat (site MOLEN) and Hond (site HOND) tidal flats. Water depth (cm) serves as a proxy for horizontal distance between the sampling sites and main channel.

scopic examination of the Lugol-preserved samples confirmed this.

In the very shallow waters (<20 cm) of the trailing edge of the ebb tide, the diatom community was numerically dominated by benthic diatoms, >60% of total abundance, consisting of members of the genera *Navicula* (25–40% of total diatom abundance) and *Nitzschia* (7–21%), as well as the epipsammic form *Rhaphoneis* (9–22%) (Fig. 3). Trends in the abundance of the large centric diatom *Coscinodiscus* sp. were similar to those of the benthic diatoms in the trailing edge of the ebb tide. Their contribution to total abundance was 1.6–7.7%. Although not as numerically abundant as the benthic species (max.  $190 \times 10^3$



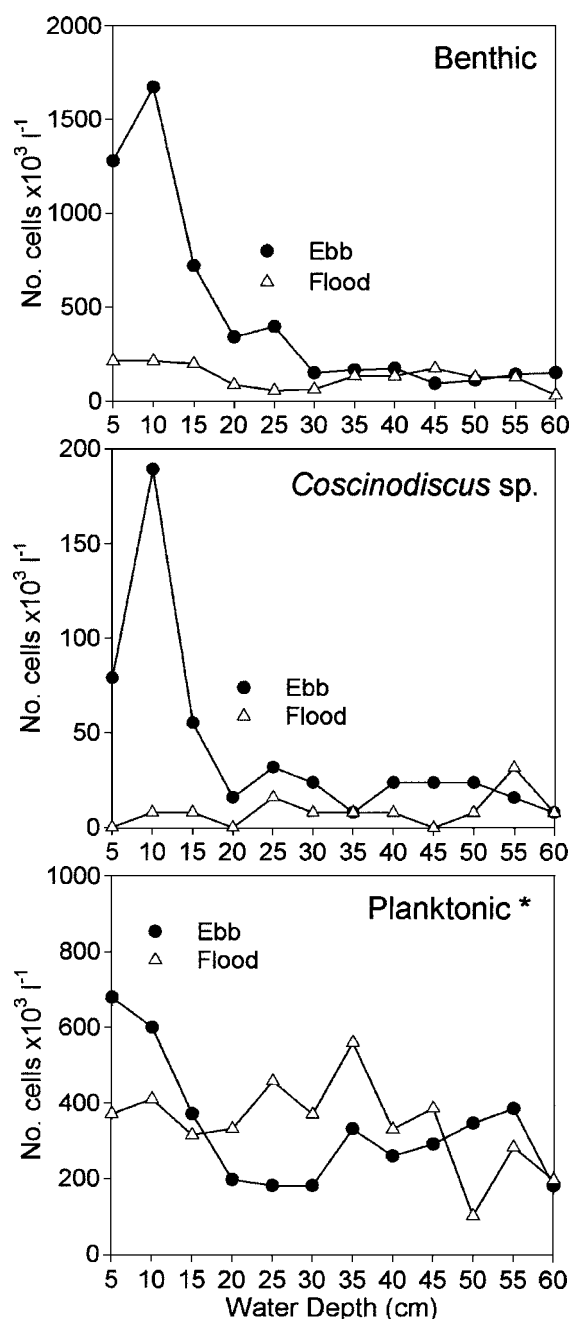


Fig. 3. Abundance (no.  $\times 10^3 \text{ l}^{-1}$ ) of live benthic diatoms, *Coscinodiscus* sp. and planktonic diatoms (\* excluding *Coscinodiscus* sp.) in the tidal edge at site 1 of the Molenplaat.

$\text{l}^{-1}$  compared with  $\sim 1700 \times 10^3 \text{ l}^{-1}$ ), its considerably larger volume leads one to consider that its contribution to diatom biomass can be substantial (see Lucas et al., 2001). The significant contribution of *Coscinodiscus* sp. to short-term biomass changes near the seabed during maximum tidal currents has previously been described by Lucas et al. (2001), with up to 78% of diatom biomass in the water above site MOLEN (ECOFLAT Site 1) resulting from the presence of *Coscinodiscus* sp. Planktonic diatoms did not display any obvious trends with depth, with densities ranging between 181 and  $678 \times 10^3 \text{ l}^{-1}$  on the ebb tide, and between 102 and  $560 \times 10^3 \text{ l}^{-1}$  on the flood tide. Nevertheless, at depths exceeding 20 cm, planktonic diatoms typically outnumbered resuspended benthic diatoms by a factor of 2, as benthic diatom numbers decreased.

As well as observations of the composition of the diatom community in the turbid tidal edge, the 'quality' (i.e., proportion of live and dead microalgae) of resuspended material was determined through phaeopigment measurements and diatom frustule counts (Fig. 4). On the ebb tide, it was clear that resuspended detrital material was being washed away as the water left the tidal flat, since frustules outnumbered live diatoms by nearly 4:1 in the shallow ebbing tide. Although the incoming water contained considerably less dead material, a large proportion of frustules were also observed at the very leading edge of the flood tide ( $<10\text{--}15$  cm depth). Visual observations revealed that these were lifted off with accompanying sand grains in a surface biofilm, after which they were rapidly broken up by wave action, and deposited higher up the flat.

In summary, it appears that as the tide receded from the Molenplaat tidal flat, resuspended benthic diatoms and large *Coscinodiscus* sp. settled out of suspension, becoming concentrated in the shallow water, accounting for up to 68% and 7.7% of total abundance, respectively. The virtual absence of *Coscinodiscus* sp. from the leading edge of the flooding tide ( $<1.5\%$  of total abundance) suggests that these cells did not settle to the seabed, but continued offshore, although this would depend on wind conditions prior to sampling (De Jonge, pers. comm., 2003). It is supposed that the small peak (38% of total abundance) of benthic diatoms at the leading edge of the flood tide was supplied locally through resuspension

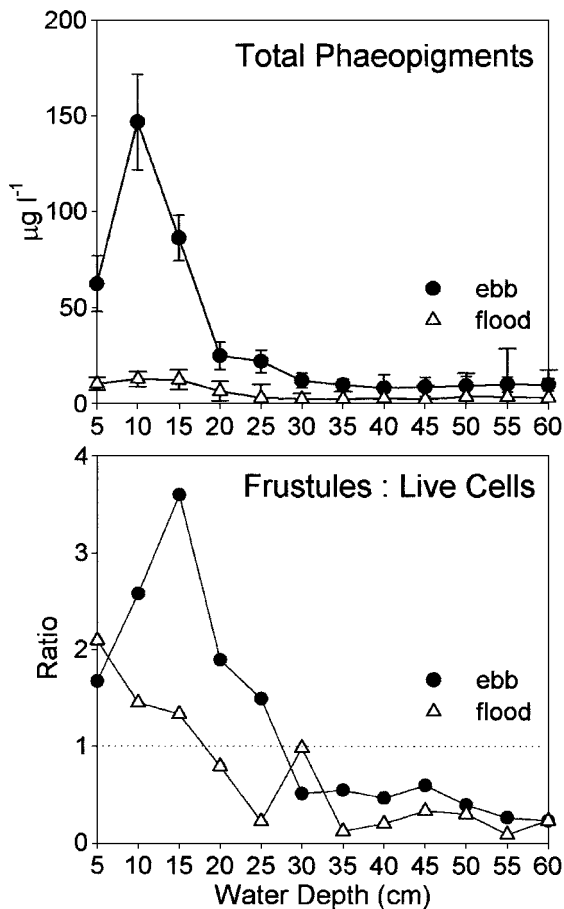


Fig. 4. 'Quality' of diatom biomass in the tidal edge at site 1 of the Molenplaat, indicated by mean ( $\pm$  sd) total phaeopigments ( $\mu\text{g l}^{-1}$ ) and the ratio between diatom frustules and live cells.

of the sediment as a result of turbulent action (Christie and Dyer, 1998). At site HOND, where *Hydrobia ulvae* were present in densities of ca.  $233\,000\text{ m}^{-2}$ , chl-*a* resuspension at the leading edge of the flood tide was also considerable, probably due to their bioturbating and grazing activities. Although vertical migration of diatoms down into the sediment during inundation (Paterson, 1986; Happey-Wood and Jones, 1988) minimises significant loss through resuspension, the increased interactions between the seabed and combinations of waves and currents in shallow water would cause resuspension events. De Jonge and Van Beusekom (1995) found that in the Ems estuary, resuspension of microphytobenthos from the top 5-mm layer of sediment could be described as a linear function of

wind speed. It should be noted that in the days leading up to sampling at site HOND, weather conditions were windy—near to gale force.

The data presented in this paper show that large numbers of diatoms can become concentrated in the very shallow waters of the leading and trailing edge of the tidal front as it moves across a tidal flat. Factors such as emersion period, affecting the dehydration and stabilisation of the diatom biofilm (Paterson et al., 1990) as well as depositional history of suspended material, weather conditions (including storms), seabed morphology and tidal currents can all influence events occurring at the turbid tidal edge. This poorly studied transport mechanism has implications for the redistribution of organic matter within and between estuarine tidal flat systems.

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### References

- Baillie, P.W., Welsh, B.L., 1980. The effect of tidal resuspension on the distribution of intertidal epipelagic algae in an estuary. *Est. Coast. Shelf Sci.* 10, 165–180.
- Barlow, R.G., Mantoura, R.F.C., Gough, M.A., Fileman, T.W., 1993. Pigment signatures of the phytoplankton composition in the northeastern Atlantic during the 1990 spring bloom. *Deep-Sea Res.* II 40, 459–477.
- Barranguet, C., Herman, P.M.J., Sinke, J.J., 1997. Microphytobenthos biomass and community composition studied by pigment biomarkers: importance and fate in the carbon cycle of a tidal flat. *J. Sea. Res.* 38, 59–70.
- Blanchard, G.F., Sauriau, P.-G., Cariou-Le Gall, V., Goulet, D., Garet, M.-J., Olivier, F., 1997. Kinetics of tidal resuspension of microbiota: testing the effects of sediment cohesiveness and bioturbation using flume experiments. *Mar. Ecol. Prog. Ser.* 151, 17–25.

- Christie, M.C., Dyer, K.R., 1998. Measurements of the turbid tidal edge over the Skeffling mudflats. In: Black, K.S., Paterson, D.M., Cramp, A. (Eds.), *Sedimentary Processes in the Intertidal Zone*. Geol. Soc., London, Spec. Publ., vol. 139, pp. 45–55.
- De Jonge, V.N., 1995. Wind driven tidal gross transports of mud and microphytobenthos in the Ems estuary, and its importance for the ecosystem. In: Dyer, K.R., D'Elia, C.F. (Eds.), *Changes in fluxes in estuaries*, pp. 29–40.
- De Jonge, V.N., Van Beusekom, J.E.E., 1992. Contribution of resuspended microphytobenthos to total phytoplankton in the Ems estuary and its possible role for grazers. *Neth. J. Sea Res.* 30, 91–105.
- De Jonge, V.N., Van Beusekom, J.E.E., 1995. Wind- and tide-induced resuspension of sediment and microphytobenthos in the Ems estuary. *Limnol. Oceanogr.* 40, 766–778.
- Demers, S., Theriault, J.C., Bourget, E., Bah, A., 1987. Resuspension in the shallow sublittoral zone of a macrotidal estuarine environment: wind influence. *Limnol. Oceanogr.* 32, 327–339.
- Dyer, K.R., 1989. Sediment processes in estuaries: future research requirements. *J. Geophys. Res.* 94, 14327–14339.
- Gallagher, J.L., 1975. The significance of the surface film in salt marsh plankton metabolism. *Limnol. Oceanogr.* 29, 120–123.
- Happey-Wood, C.M., Jones, P., 1988. Rhythms of vertical migration and motility in intertidal benthic diatoms with particular reference to *Pleurosigma angulatum*. *Diatom Res.* 3, 83–93.
- Herman, P.M.J., Middelburg, J.J., Widdows, J., Lucas, C.H., Heip, C.H.R., 2000. Stable isotopes and trophic tracers: combining field sampling and manipulative labeling of food resources for macrobenthos. *Mar. Ecol. Prog. Ser.* 204, 79–92.
- Herman, P.M.J., Middelburg, J.J., Heip, C.H.R., 2001. Benthic community structure and sediment processes on an intertidal flat: results from the ECOFLAT project. *Cont. Shelf Res.* 21, 2055–2071.
- Jeffrey, S.W., Mantoura, R.F.C., Wright, S.W., 1997. *Phytoplankton pigments in oceanography: guidelines to modern methods*. UNESCO Publishing, Paris. 661 pp.
- Lucas, C.H., Widdows, J., Brinsley, M.D., Salkeld, P.N., Herman, P.M.J., 2000. Benthic-pelagic exchange of microalgae at a tidal flat. 1. Pigment analysis. *Mar. Ecol. Prog. Ser.* 196, 59–73.
- Lucas, C.H., Banham, C., Holligan, P.M., 2001. Benthic-pelagic exchange of microalgae at a tidal flat. 2. Taxonomic analysis. *Mar. Ecol. Prog. Ser.* 212, 39–52.
- Lucas, C.H., Widdows, J., Wall, L., 2003. Relating temporal and spatial variability in sediment chlorophyll *a* and carbohydrate distribution with erodibility of a tidal flat. *Estuaries* (in press).
- NIOO Progress Report, 1996. In: Middelburg, J.J., Mooij, W., van der Putten, W. (Eds.), 1996. Netherlands Institute of Ecology Progress Report. Ponsen & Looijen bv, Wageningen. 192 pp.
- Paterson, D.M., 1986. The migratory behaviour of diatom assemblages in a laboratory tidal micro-ecosystem examined by low temperature scanning electron microscopy. *Diat. Res.* 1, 227–239.
- Paterson, D.M., Crawford, R.M., Little, C., 1990. Subaerial exposure and changes in stability of intertidal sediments. *Est. Coast. Shelf Sci.* 30, 541–556.
- Shaffer, G.P., Sullivan, M.J., 1988. Water column productivity attributable to displaced benthic diatoms in well-mixed shallow estuaries. *J. Phycol.* 24, 132–140.
- Staats, N., Stal, L.J., Mur, L.R., 2000. Exopolysaccharide production by the epipellic diatom *Cylindrotheca closterium*: effects of nutrient conditions. *J. Exp. Mar. Biol. Ecol.* 249, 13–27.
- Widdows, J., Brinsley, M.D., Salkeld, P.N., Lucas, C.H., 2000. Influence of biota on spatial and temporal variation in sediment erodibility and material flux on a tidal flat (Westerschelde estuary). *Mar. Ecol. Prog. Ser.* 194, 23–37.