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Methodological aspects of paleo-ecological diatom research in coastal areas of the Netherlands

P.C. Vos[1] & H. de Wolf[2]
[1] *Comparative Sedimentology Division, Institute of Earth Sciences, Budapestlaan 4, 3581 TA Utrecht, The Netherlands;* [2] *Geological Survey of the Netherlands, Spaarne 17, 2000 AD Haarlem, The Netherlands*

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Abstract

A major problem in paleo-ecological research of diatoms in tidal environments is the distinction of autochthonous and allochthonous diatom valves. A new approach applying several diatom- and non-diatom-related criteria is introduced in order to solve the autochthonous/allochthonous problem. A classification of coastal diatoms in ecological groups, and the relation between these ecological groups and the sedimentary environments are discussed.

Introduction

The three main factors controlling the Holocene coastal development in the western Netherlands are (a) the relative rise of the sea level; (b) the geometry of the coastal area (Pleistocene morphology); and (c) the fluvial input (rivers Rhine, Meuse and Scheldt). Those factors strongly influenced the coastal processes through longshore currents and onshore-offshore currents in the foreshore and through tidal currents, fluctuations in tidal amplitude and of tidal prisms in the coastal basins and estuaries. Water movements and sediment transport either built up (a.o. coastal barriers, tidal flats) or broke down the coast (e.g. by deepening the sea bottom).

Paleo-ecological diatom research plays an important role in reconstructing these Holocene coastal processes, since diatoms are known to be very sensitive to changes in environmental variables such as salinity, tidal currents, flooding frequency, trophic conditions and pH.

The study of diatoms has proved to be a valuable tool in reconstructing sea level changes and related trans- and regressive coastal developments (Haynes et al., 1977; Stabell, 1982; Miller, 1982; Sato et al., 1983; Denys, 1984).

Since 1930, stratigraphical and paleo-ecological diatom research has been carried out by the Geological Survey of the Netherlands. At the moment the Diatom Department of the Geological Survey is involved in a project on coastal development, initiated by the Ministry of Transport and Public Works in 1985. Within this framework – based on a new methodological approach presented in this paper – an inventory has been drawn up and reinterpretation carried out of all diatom studies of Holocene coastal deposits of the Netherlands.

The most important question regarding the interpretation of diatom thanatocoenose in fossil/subrecent tidal environments (Brockmann, 1940) is: have the diatoms lived at the place of deposition (autochthonous) or were they transported from elsewhere by water or wind (allochthonous). Autochthonous diatoms provide information about the local paleo-environment, while allochthonous diatoms supply information concerning the environment of the surroundings (e.g. river influence, König (1983)).

In this paper we introduce a new approach to determine autochthonous and allochthonous diatoms in Holocene coastal deposits of the Netherlands. For this purpose, the classification of diatoms in ecological groups is very important. Furthermore, the relation between the ecological groups and the related sedimentary environments in the coastal areas is discussed.

Autochthonous and allochthonous diatoms

Autochthonous diatoms are defined as the diatom frustules (or valves) which have lived at the place of deposition. Therefore autochthonous diatoms sensu stricto are benthic species. In low-energy environments (e.g. lakes and lagoons) also the diatoms that live just above the bottom (epiphytic and planktonic diatoms) reflect the local conditions because they are not transported by currents (autochthonous sensu lato). Generally, in low-energy environments the influx of allochthonous diatoms is small. Therefore, in most paleo-ecological studies of fresh-water lakes and non-tidal bays, the question of the autochthonous or allochthonous origin of the species is not relevant. In contrast, in tidal environments the autochthonous/allochthonous issue is of major importance (Brockmann, 1940). In certain case the allochthonous thanatocoenosis may outnumber the autochthonous thanatocoenosis (Simonsen, 1969).

Several authors have proposed methods to distinguish between the autochthonous and allochthonous diatoms. Fragmentation of diatom frustules has often been used as a criterion for long-distance transport. However, also other processes such as natural chemical leaching, diagenesis and compaction (Andrews, 1972, Beyens & Denys, 1982), heating and strong temperature fluctuations, sample pretreatment (Beyens & Denys, 1982) and predation (Romeyn & Bouwman, 1983) may damage the diatom valve. An additional problem in using fragmentation as a criterion is that elongated and weakly silicified valves break more easily than roundish and strongly silicified diatoms.

Simonsen (1969) proposed to use the benthic diatoms as indicators for the autochthonous population. In particular, benthic species, which are typical for a well-defined environment, are autochthonous when they occur in high density in a given deposit (Brockmann, 1940).

Beyens & Denys (1982) attempted to quantitatively distinguish between allochthonous and autochthonous components in coastal deposits by considering salinity dependence and benthonic life form. For this purpose, they used the salinity classification of Van der Werff and Huls (1957–1974). The salinity group with the largest percentage of benthic forms is called the 'optimal group' and the diatoms in the adjacent salinity groups are classified as the 'neighbour groups'. Together, the optimal and the neighbour groups form the autochthonous component. However, a problem with this approach is that the epiphytic and planktonic diatoms (here defined as autochthonous sensu lato) are excluded although they may supply valuable information about the paleo-environment.

In paleo-ecological diatom studies of Holocene coastal deposits by the Diatom Department of the Geological Survey of the Netherlands, the allochthonous and autochthonous diatoms are distinguished on the basis of a number of diatom- and non-diatom-related criteria.

Criteria related to the diatoms proper:
- composition of the different ecological groups;
- trends (succession) of the different ecological groups within the sedimentary sequence;
- occurrence of relatively rare taxa within the ecological groups;
- percentage of broken diatom valves of fragile (elongated and weakly silicified) species.

Non-diatom criteria:
- paleo-geographic location;
- lithology and sedimentary structures;
- other paleo-ecological indicators.

Regarding the diatom criteria, the classification of the diatoms in ecological groups is elementary for the distinction between autochthonous and allochthonous diatoms. If the habitats of two ecological groups do not overlap (if they occur together) at least one of the two groups must be allochthonous. Thus marine plankton cannot possibly have lived in the same environment as aerophile benthos (Fig. 1).

In determining which of the ecological groups are autochthonous, the trend in the relative importance of the ecological groups within a sedimentary sequence plays a prominent role. The simultaneous occurrence of ecological groups which can live in the same environment in a certain zone of the vertical sequence suggests that these groups are autochthonous. This interpretation is strengthened if the vertical succession of the ecological groups reflects a natural sequence (e.g. a regressive sequence).

The sole occurrence of a relatively rare species (e.g. Navicula pusilla of the Hantzschia amphioxys group) in a zone dominated by the ecological group to which it belongs, strongly indicates that this group is autochthonous. Besides, the percentages of unbroken frustules of elongated (e.g. *Synedra tabulata*, Fig. 2) and weakly silicified (e.g. *Asterionella formosa*) diatoms can also be an important criterion. When most of the diatoms are unbroken, this indicates that these diatoms have not been transported. As said before, the reverse is not the case; if a high percentage of the weakly silicified and elongated diatoms are broken, they can be autochthonous.

The non-diatom criteria are also important for distinguishing between autochthonous and allochthonous diatoms. The paleo-geographic location can be very important in separating the marine littoral groups from those living in the hinterland. If the relevant deposits have been formed inland of e.g. a coastal barrier system, this implies that all the marine littoral groups found (Melosira sulcata Skeletonema costatum Rhaphoneis amphiceros and Cymatosira belgica groups) must be allochthonous. The marine littoral groups then are called 'coast allochthonous'.

Another non-diatom criterion is the sediment composition. An example is the presence of epipsammic diatoms in heavy clays. In these clays the substrate (sand) needed by epipsammic diatoms (Fig. 3) is missing and therefore these diatoms must be allochthonous if present. Furthermore, it is obvious that also sedimentary structures and other paleo-ecological indicators (a.o. molluscs and ostracodes) can be important in the recognition of the autochthonous character of certain groups.

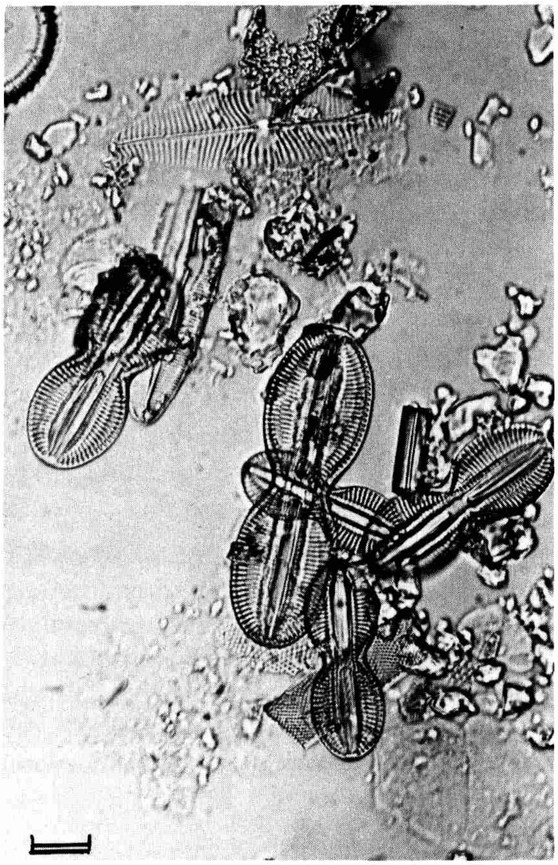

Fig. 1.

Classification of ecological groups

The diatoms in Holocene coastal deposits of the Netherlands can be classified in large ecological groups. As yet we have distinguished 21 ecological groups (Table 1). The ecological groups have been named after a characteristic member of the group. The main subdividion is based on two ecological characteristics: life form (plankton, benthos, epiphytes) and salinity (polyhalobe, mesohalobe, oligohalobe; Hustedt (1957). A more refined subdivision (Table 1) is based on a more detailed specification of life form (epiphytic on seston, Fig. 4,

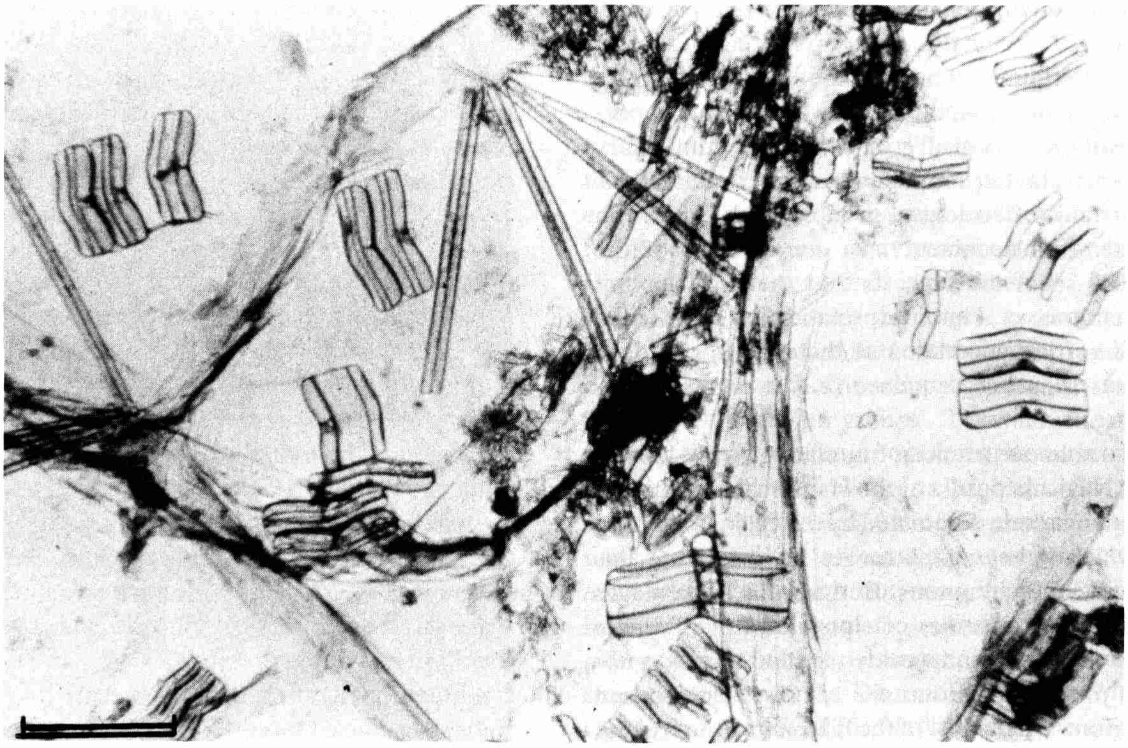

Fig. 2.

Fig. 3.

semi-plankton, epipsammon and epipelon), the degree of silicification of the valves (marine plankton) and the composition of the sediment (benthos).

Those diatom species which live in chains just above the bottom are classified as 'semi-plankton'. During certain periods these chains may be attached to the bottom or to waterplants. When the water is turbulent, these diatoms may also occur suspended in the water column and behave as plankton sensu stricto.

The ecological data used for the classification of ecological groups are mainly derived from the review by De Wolf (1982, Table 2; environment codes 1 and 2). For practical reasons we did not update his nomenclature. In addition, ecological data from a diatom study of the sandy intertidal shoals in the Oosterschelde (Vos, 1986) were used (Achnanthes delicatula and Amphora proteus groups).

Some species are assigned to more than one group because these species inhabit more biota, or because they have a wide salinity range. An example is *Auliscus sculptus* (Fig. 3) which can live both as plankton and as epipsammon on sand grains (Vos et al., 1987). An example of a species showing a broad salinity tolerance (fresh and brackish water) is *Cocconeis placentula.*

Ecological groups in Holocene coastal deposits of the Netherlands

Marine planktonic and semi-planktonic groups (marine littoral groups)

Melosira sulcata group
Habitat: Marine plankton, salinity range: 15000–17000 mg Cl/L.
Sedimentary environment: Marine littoral (North-sea), tidal inlets and large tidal channels.
Species: Actinocyclus ehrenbergii Ralfs, *Actinoptychus undulatus* (Bail.) Ralfs, *Actinoptychus splendens* (Shadb.) Ralfs, *Aulacodiscus argus* (Ehr.) A. Schmidt, *Auliscus sculptus* (W. Sm.) Ralfs, *Biddulphia aurita* (Lyngb.) Berb. et Godey, *Cerataulus smithii* Ralfs, *Coscinodiscus kützingii* A. Schmidt, *Melosira sulcata* (Ehr.) Kutz., *Melosira westii* W. Sm., *Thalassiosira decipiens* (Grun.) Joerg., *Thalassiosira eccentrica* (Ehr.) Cl., *Triceratium alternans* Bail., *Triceratium favus* Ehr.

Sceletonema costatum group
Habitat: Marine plankton, weakly silicified valves, salinity range: 15000–17000 mg Cl/L.
sedimentary environment: Marine littoral (North-sea), tidal inlets and large tidal channels.
Species: Chaetoceros spec., Rhizosolenia spec., Sceletonema costatum (Grev.) Per.

Rhaphoneis amphiceros group (Fig. 4)
Habitat: Marine plankton, often attached to big planktonic diatoms or to seston, salinity range: 15000–17000 mg Cl/L.
Sedimentary environment: Marine littoral (North-sea), tidal inlets and large tidal channels.
Species: Rhaphoneis amphiceros Ehr., *Rhaphoneis*

Table 1. Relation between ecological diatom groups, salinity and life form.

Salinity: polyhalobions | mesohalobions | oligohalobions
S (‰): 30, 20, 10, 5, 1, 0.5, 0.2, 0.1
Cl (mg/L): 17000, 10000, 5000, 1000, 500, 100, 0

Life form					
Plankton	strongly silicified	Melo sulc group	Cycl stri group	Step astr group	
	weakly silicified	Scel cost group		Asterionella group	
	epiphytic on seston	Rhap amph group			
	semi-plankton	Cyma belg group	Melo moni group	Frag cons group	Melo vari group
Benthos	Epipsammon		Achn deli group		
	epipelon sand		Amph prot group		
	epipelon silt/clay	Navi dist group	Navi digi var. min. group	Nitz debi group	Pinn majo group
	epipelon aerophile		Dipl inte group	Hant amph group	
Epiphyte			Syne tabu group	Rhoi curv group	Epit zebr group

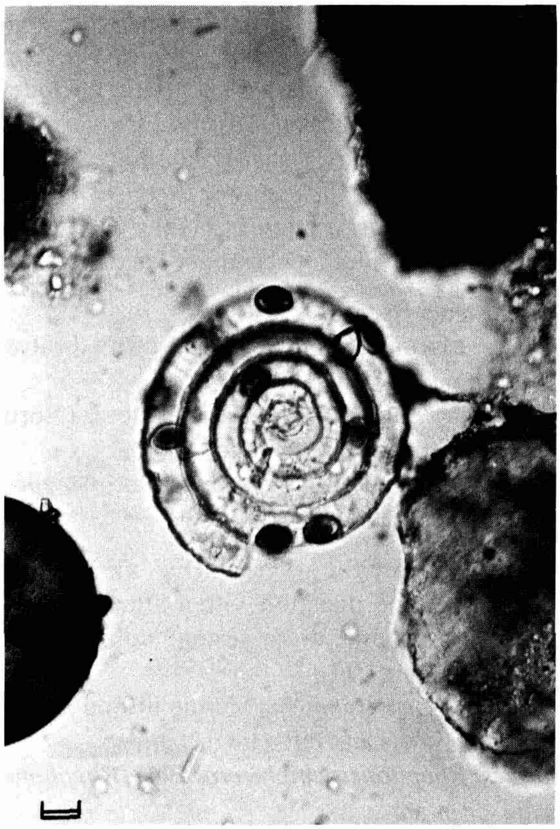

Fig. 4.

minutissima Hust., *Rhaphoneis surirella* (Ehr.) Grun.

Cymatosira belgica group
Habitat: Marine semi-plankton, salinity range: 15000–17000 mg Cl/L.
Sedimentary environment: Marine littoral (North-sea), tidal inlets and large tidal channels. Presumably the littoral zone off the coast with a water depth of 3–10 metre is the optimum environment for this group.
Species: Biddulphia aurita (Lyngb.) Breb. et Godey, *Campylosira cymbelliformis* (A. Schmidt) Grun., *Cymatosira belgica* Grun., *Plagiogramma vanheurckii* Grun., *Plagiogramma brockmannii* Hust.

Brackish and fresh-water planktonic and semi-planktonic groups

Cyclotella striata group
Habitat: Estuarine plankton, salinity range: 1000–17000 mg Cl/L.
Sedimentary environment: Tidal channels in estuaries.
Species: Actinocyclus normannii (Greg.) Hust., *Coscinodiscus lacustris Grun., Cyclotella meneghiniana* Kutz., *Cyclotella striata* (Kutz.) Grun.

Melosira moniliformis group
Habitat: Semi-plankton, salinity range; 1000–17000 mg Cl/L.
Sedimentary environment: Brackish lagoons and bays.
Species: Biddulphia subaequa (Kutz.) Ralfs, *Hyalodiscus scoticus* (Kutz.) Grun., *Melosira moniliformis* (O.F. Muller) Ag.

Fragilaria construens group
Habitat: Semi-plankton, salinity range: 100–1000 mg Cl/L.
Sedimentary environment: Fresh-water lagoons, lakes, pools, ditches.
Species: Fragilaria brevistriata Grun., *Fragilaria construens* (Ehr.) Grun., *Fragilaria construens v. venter* (Ehr.) Grun., *Fragilaria construens v. subsalina* Hust., *Fragilaria pinnata* Ehr.

Melosira varians group
Habitat: Semi-plankton, salinity range: 0–100 mg Cl/L.
Sedimentary environment: Lakes, pools, ditches.
Species: Melosira varians Ag.

Stephanodiscus astrea group
Habitat: Plankton, not too shallow fresh water (>1 metre), salinity range: 0–500 mg Cl/L.
Sedimentary environment: Fresh-water lagoons, lakes, pools, rivers.
Species: Melosira ambigua (Grun.) O. Muller, *Melosira granulata* (Ehr.) Ralfs, *Melosira italica* (Ehr.) Kutz., *Stephanodiscus astrea* (Ehr.) Grun.

Asterionella formosa group
Habitat: Weakly silicified plankton, salinity range: 0–500 mg Cl/L.

Table 2. Relation between ecological groups and sedimentary environments.

Macro-, meso-, and microtidal environments:		
Sedimentary environments:		Autochthonous ecological groups:
Subtidal area	– tidal inlets tidal channels	Current velocities too high and irradiance values too low for the development of benthic and epiphytic groups. These environments are dominated by (allochthonous/autochthonous s.l.) marine littoral groups (Melosira sulcata, Sceletonema costatum, Rhaphoneis amphiceros, and Cymatosira belgica groups).
Intertidal area	– sandy shoals sand flats	Sand species of the Achnananthes delicatula and Amphora proteus groups, which can also live in the shallow part of the subtidal area when the irradiance is sufficient for photosynthesis.
	– mud flats	Navicula digitoradiata var. min. and Nitzschia debilis groups; NB: absence or very low relative importance of epiphytic and semi-planktonic groups.
Supratidal area	– tidal levees back levee marshes	Aerophile species of the Diploneis interrupta and Hantzschia amphioxys groups. Near the mean high-water level species of the Navicula digitoradiata v. min. group and the Diploneis interrupta group can occur together.
	– pools in the back levee marshes	In pools (which are periodically dry) within the back levee marshes, both aerophile groups (Diploneis interrupta and Hantzschia amphioxys group) and epiphytic groups (Synedra tabulata and Rhoicospenia curvata groups) can live in the same environment.
Microtidal and non-tidal environments:		
Sedimentary environments:		Autochthonous ecological groups:
Subtidal area	– tidal lagoons (small tidal range)	Brackish water; a lot of ecological groups can live together here. On the bottom of the lagoon, some species of the Navicula digitoradiata v. min. group can live if the irradiance is sufficient. Epiphytic groups (Synedra tabulata and Rhoicosphenia curvata groups) may occur on the waterplants and macro algae, and also the Melosira moniliformis group (semi-plankton). When the lagoon becomes temporarily fresh, the Stephanodiscus astrea and Epithemia zebra groups may appear.
	– lagoons (no tides)	The same ecological groups occur as in the tidal lagoons; the difference between the tidal and non-tidal lagoon is that in the non-tidal lagoon the numbers and percentages of the (allochthonous) marine littoral groups are very low.
Fluvial and lake environments		These environments are characterized by eutrophic fresh-water diatoms of the Stephanodiscus astrea, Pinnularia maior and Epithemia zebra groups.

Sedimentary environment: Lakes, pools, rivers.
Species: Asterionella formosa Hassall, *Asterionella ralfsi* W.Sm.

Benthonic groups

Navicula distans group
Habitat: Epipelic diatoms, living in the subtidal zone, salinity range: 17000 mg Cl/L.
Sedimentary environment: Subtidal marine basins.
Species: Dimerogramma fulvum (Greg.) Ralfs, *Navicula distans* (W. Sm.) HvH., *Scoliotropis latestriata* (Breb.) Cl.

Achnanthes delicatula group (Fig. 3)
Habitat: Epipsammic diatoms (living on sandgrains) in the intertidal or (shallow) subtidal zone where irradiance is sufficient for photosynthesis (clear water), salinity range: 5000–17000 mg Cl/L.
Sedimentary environment: Intertidal sandy shoals, sand flats and beaches, and subtidal (shallow) marine basins.
Species: Achnanthes delicatula (Kutz.) Grun., *Achnanthes lemmermannii* Hust., Auliscus sculptus (W.Sm.) Ralfs, *Catenula adherens* Mereschk., *Cocconeis peltoides* Hust., *Dimerogramma minor* (Greg.) Ralfs, *Eunotogramma dubium* Hust., *Navicula biskanteri* Hust., *Navicula cryptolyra* Brockm., *Navicula diserta* Hust., *Nitzschia frustulum var. perminuta* Grun., *Opephora pacifica* (Grun.) Petit, *Opephora parva* (HvH.) Kras., *Plagiogramma staurophorum* (Greg.) Herib., *Trachysphenia australis* Petit.

Amphora proteus group
Habitat: Epipelic diatoms, living in sandy sediments in the intertidal zone or (shallow) subtidal zone where irradiance is sufficient for photosynthesis (clear water), salinity range: 5000–17000 mg Cl/L.
Sedimentary environment: Intertidal sandy shoals, sand flats and beaches, and subtidal (shallow) marine basins.
Species: Amphora proteus Greg., *Diploneis fusca* (Greg.) Cl., *Gyrosigma rectum* (Donk.) Cl. *Hantzschia virgata* (Rop.) Grun., *Navicula abrupta* Greg., *Navicula atlantica* A. Schmidt, *Navicula cancellata* Donk., *Navicula flanatica* Grun., *Navicula finmarchica* Cl. et Grun., *Navicula forcipata* Grev., *Navicula humerosa* Breb., *Navicula palpebralis* Breb., *Navicula peregrina* (Ehr.) Kutz., *Navicula rostellata* Kutz., *Nitzschia apiculata* (Greg.) Grun., *Nitzschia spathulata* De Breb., *Pinnularia ambigua* Cl., *Pinnularia cruciformis* (Donk.) Cl., *Tropidoneis lepidoptera* (Greg.) Cl.

Navicula digitoradiata var. minima group
Habitat: Epipelic diatoms, living in clayey sediments in the intertidal zone or (shallow) subtidal zone where irradiance is sufficient for photosynthesis (clear water), salinity range: 5000–17000 mg Cl/L.
Sedimentary environment: Intertidal to lower supratidal mudflats and creeks, subtidal marine basins and lagoons.
Species: Caloneis formosa (Greg.) Cl., *Diploneis didyma* Ehr., *Diploneis ovalis* (Hilse) Cl., *Gyrosigma scalproides* (Rabn.) Cl., *Gyrosigma spenceri* (W. Sm.) Cl., *Navicula cryptocephala* Kutz., *Navicula digitoradiata* (Ehr.) W. Sm., *Navicula digitoradiata var. minima* (Greg.) A. Schmidt, *Navicula peregrina* (Ehr.) Kutz., *Navicula phyllepta* Kutz., *Navicula pygmaea* Kutz., *Navicula salinarum* Grun., *Nitzschia navicularis* (Breb.) Grun., *Nitzschia sigma* W. Sm., *Scoliopleura brunkseiensis* Hend., *Scoliopleura tumida* (Breb.) Cl., *Surirella gemma* Ehr.

Nitzschia debilis group
Habitat: Epipelic diatoms, living in clayey sediments in the intertidal zone or (shallow) subtidal zone where irradiance is sufficient for photosynthesis (clear water), salinity range: 100–1000 mg Cl/L.
Sedimentary environment: Intertidal to lower supratidal mudflats and creeks, and lagoons.
Species: Gyrosigma acuminatum (Kutz.) Rabh., *Gyrosigma attenuatum* (Kutz.) Cl., *Navicula gracilis* Ehr., Navicula rhynchocephala Kutz., *Nitzschia debilis* (Arn.) Grun., *Nitzschia hungarica* Grun., *Nitzschia tryblionella* Hantz.

Pinnularia maior group
Habitat: Epipelic diatoms, living in eutrophic fresh-water environments, salinity range: 0–100 mg Cl/L.
Sedimentary environment: Intertidal to lower su-

pratidal mudflats and creeks, and lagoons.
Species: Cymbella aspera (Ehr.) Herib., *Cymbella ehrenbergii* Kutz., *Cymbella lanceolata* (Ehr.) HvH., *Caloneis bacillum* (Grun.) Cl., *Navicula cuspidata* Kutz., *Navicula oblonga* Kutz., *Neidium affine* (Ehr.) Cl., *Pinnularia gibba* Ehr., *Pinnularia maior* (Kutz.) Cl., *Pinnularia nobilis* Ehr.

Diploneis interrupta group (Fig. 1)
Habitat: Epipelic diatoms, aerophile, living in the supratidal zone, with a large salinity range: 500–18000 mg Cl/L.
Sedimentary environment: Salt marshes.
Species: Diploneis interrupta (Kutz.) Cl., *Diploneis ovalis* (Hilse) Cl., *Navicula cincta* (Ehr.) Kutz., *Nitzschia vitrea* Norman.

Hantzschia amphioxys group
Habitat: Epipelic diatoms, aerophile, and a salinity range: 0–1000 mg Cl/L.
Sedimentary environment: Wet soils, salt marshes, flood basins, downpour and trenches.
Species: Hantzschia amphioxys (Ehr.) Grun., *Navicula pusilla* W. Sm., *Navicula mutica* Kutz., *Pinnularia borealis* Ehr.

Epiphytic groups

Synedra tabulata group (Fig. 2)
Habitat: Epiphytes on waterplants in shallow water, salinity range: 1000–10000 mg Cl/L.
Sedimentary environment: Brackish lagoons and ditches.
Species: Achnanthes brevipes Ag., *Cocconeis placentula* Ehr., *Cocconeis scutellum* Ehr., *Rhopalodia gibberula* (Ehr.) O. Mull., *Rhopalodia musculus* (Kutz.) O. Mull., *Synedra tabulata* (Ag.) Kutz.

Rhoicosphenia curvata group
Habitat: Epiphytes on waterplants in shallow water, salinity range: 500–2000 mg Cl/L.
Sedimentary environment: Fresh/brackish lagoons, pools and ditches
Species: Cocconeis placentula Ehr., *Diatoma elongatum* Bory, *Fragilaria inflata* (Heiden) Hust., *Rhoicosphenia curvata* (Kutz.) Grun., *Rhopalodia gibba* (Kutz.) O. Mull.

Epithemia zebra group
Habitat: Epiphytes in shallow water living on waterplants, salinity range: 100–500 mg Cl/L.
Sedimentary environment: Fresh-water lagoons, lakes, abandoned rivermeanders, fresh-water ditches.
Species: Cocconeis pediculus Ehr., *Cocconeis placentula* Ehr., *Diatoma vulgare* Bory, *Epithemia sorex* Kutz., *Epithemia turgida* (Ehr.) Kutz., *Epithemia zebra* (Ehr.) Kutz., *Gomphonema angustatum* (Kutz.) Rabh., *Opephora martyi* Herib., *Tabellaria flocculosa* (Roth.) Kutz., *Tabellaria fenestrata* (Lyngb.) Kutz.

Relation between ecological groups and sedimentary environments

In coastal areas, the tide is the most important factor for the classification of different sedimentary environments: sub-, inter-, and supratidal environments in macro-, meso-, and microtidal systems and (tidal) lagoons in microtidal and non-tidal systems. Although the classification of the ecological groups is not based on the tidal range, an indirect relation between the different ecological groups and the various sedimentary environments exists since the distribution of the life forms depends a.o. on tidal energy and frequency of flooding.

The following examples reflect this indirect relation:

- Brackish-water epiphytes (Synedra tabulata and Rhoicospenia curvata groups), which live on macroalgae and waterplants, are characteristic for low-energy environments that are permanently under water and they therefore indicate lagoonal conditions;
- Sand populations (Achnanthes delicatula and Amphora proteus groups) indicate a high-energy environment below the mean high-water level. Because in these high-energy environments – due to strong turbulence – the irradiance below the mean low-water level strongly decreases, these species only occur in the shallow parts of the subtidal and intertidal zones. In the Oosterschelde the sandy shoal appeared to be the optimum environment for these species, and (before the completion of the storm surge barrier)

they hardly occurred alive more than 1 metre below the mean low-water level;
- Aerophile species (Diploneis interrupta and Hantzschia amphioxys groups) are characteristic for a supratidal area.

The relation between environment and ecological groups is elaborated in Table 2.

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