

Diatoms as a tool for reconstructing sedimentary environments in coastal wetlands; methodological aspects

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Abstract

This paper presents a method for reconstructing sedimentary environments on the basis of diatoms in clastic deposits of coastal wetlands. The method includes improvements and updates of previously described approaches of coding ecological data on diatom species for computer utilization and of combining diatom species into ecological groups, which are related to specific environments.

The assessment of autochthonous and allochthonous diatoms is the major problem in the palaeoenvironmental diatom research in tide-influenced coastal areas, because the allochthonous influx by tidal currents (mainly marine planktonic and tycho planktonic diatoms) is significant. In tidal deposits, the allochthonous diatoms often outnumber the autochthonous assemblage. Criteria for the assessment regarding which diatoms are 'in or out of place' are discussed.

Introduction

The study of diatoms is a valuable tool in reconstructing palaeoecological changes in coastal areas (e.g. Stabell, 1982, 1985; Palmer & Clague, 1991; Pienitz *et al.*, 1991). The siliceous cell walls of diatoms generally fossilize well and the species composition depends on many biochemical and physical factors. In coastal sediments, diatoms are used to record palaeoenvironmental changes in salinity (e.g. Hustedt, 1953; Simonsen, 1962; Juggins, 1992) and tidal exposure (e.g. Simonsen, 1962; Denys, 1991). In freshwater sediments, they provide (palaeo-)information about characteristics like trophic state and pH (e.g. Chlcnoky, 1968).

The Geological Survey of The Netherlands has focussed its palaeoecological diatom research on

the reconstruction of the sedimentary environments of the Dutch Holocene coastal deposits (e.g. tidal channels, sand flats, mud flats, salt-marshes, lagoons). The information acquired in this research is used in palaeogeographic reconstructions and studies about palaeotide levels.

In order to facilitate the use of computerized methods in palaeoenvironmental reconstructions, an ecological code system was developed (De Wolf, 1982). Seven factors were selected: diatom life form, salinity, pH, nutrients, temperature, tides and current velocity (Fig. 1). Each of these factors was subdivided into different categories, which were assigned a number (code). A code list containing the most common diatoms in the Holocene coastal deposits of the Netherlands was presented by De Wolf (1982). Vos & De Wolf (1988) classified these diatoms into 'ecological

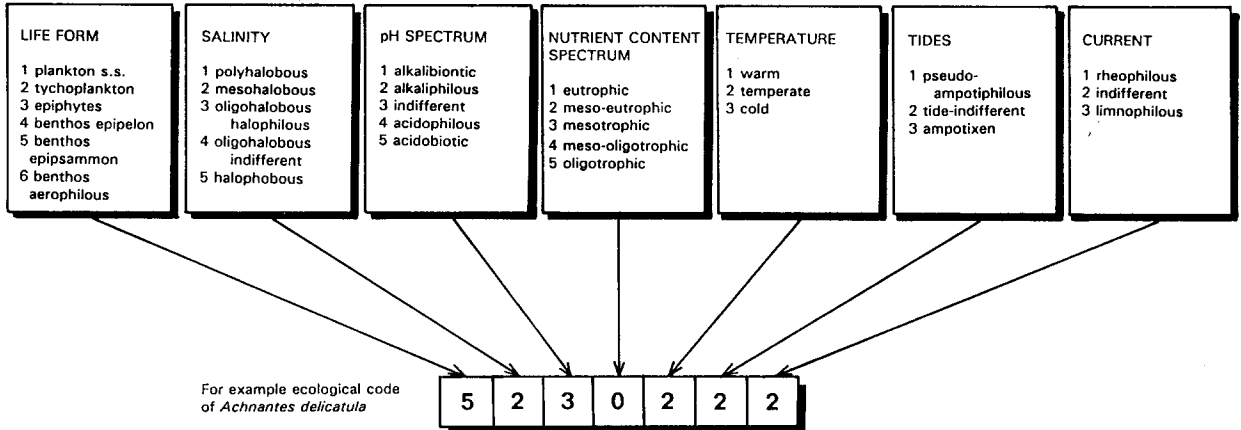


Fig. 1. Summary of the environmental codes, code 0 means no information available, modified after De Wolf (1982).

groups' for palaeogeographic applications and related these groups to the different near-shore (tidal or non-tidal) (palaeo-)sedimentary environments.

Since the publications of De Wolf (1982) and Vos & De Wolf (1988), both the ecological codes and the terminology of ecological groups have been altered. These alterations are presented in this paper. The application of the method is demonstrated in a case study by Vos & De Wolf (1993).

Ecological codes

The ecological coding of the taxa which are frequently observed in the Holocene coastal sequence of the Netherlands is mainly based on a literature survey. For the 7 environmental factors (Fig. 1), many publications have been consulted, including Hustedt, 1958 (life form); Brockmann, 1950; Simonsen, 1962; Hustedt, 1957; Miller, 1964 (salinity); Haworth, 1976; Florin, 1977 (pH); Hustedt, 1957 (nutrients); Hustedt, 1955; Baudrimont, 1974 (temperature); Edsbagge, 1968; Simonsen, 1962 (tides); Haworth, 1976; Schoeman, 1973 (current velocity). Besides literature information, also our own ecological data on recent diatoms have been used (especially those from the Oosterschelde tidal basin: on epipellic and epipsammic diatoms living in the intertidal zone; Vos, 1986; Vos *et al.*, 1988). Al-

though the ecological coding has been based primarily on a literature survey, it should be emphasized that because of different opinions in the literature the ecological codes are often subjective.

In general, lack of reliable data is one of the main problems in the ecological coding of diatoms. Most publications on marine and brackish diatoms deal with taxonomy and in these studies the environmental information is often restricted to only salinity gradient and life form. Moreover, it is not clear if these authors studied living (autochthonous) diatoms or just the empty frustules (which might be allochthonous), so it is not always certain that the ecological data are reliable.

Another problem which might cause ambiguity about the ecology of marine and brackish species in tidal environments is that the occurrence of diatoms is determined by a complex of ecological factors (Van den Hoek *et al.*, 1979; Admiraal, 1984). In field studies, it is not always easy to separate out the role of each of the individual factors. Laboratory studies show that for some factors the tolerance ranges may be different than those found in field observations: for instance for the salinity gradient this has been demonstrated by Admiraal (1977) and Admiraal & Pelletier (1980).

Since the publication of De Wolf (1982), the ecological code-system for the diatom species

Table 1. List of the most common diatom species in the Holocene coastal deposits and their environmental codes, modified after De Wolf, 1982. Code 0 means no information available. The salinity tolerance spectrum is according to Hustedt (1953), pH spectrum from Hustedt (1939), nutrient content spectrum from Naumann (1932), tidal tolerance from Simonsen (1962).

Marine plankton

1100230	<i>Actinocyclus ehrenbergii</i> Ralfs
1100230	<i>Actinoptychus splendens</i> (Shadbolt) Ralfs
1100230	<i>Actinoptychus undulatus</i> (Bailey) Ralfs
1100230	<i>Aulacodiscus argus</i> (Ehrenb.) A. Schmidt
1100230	<i>Coscinodiscus kutzingii</i> A. Schmidt
1100220	<i>Odontella rhombus</i> (Ehrenb.) Kütz.
1100220	<i>Paralia sulcata</i> (Ehrenb.) Cleve
1100220	<i>Podosira stelliger</i> (Bailey) Mann
1100230	<i>Skeletonema costatum</i> (Greville) Cleve
1100230	<i>Thalassionema nitzschioides</i> Grun.
1100230	<i>Thalassiosira decipiens</i> (Grun.) Jörgensen
1100230	<i>Thalassiosira eccentrica</i> (Ehrenb.) Cleve
1100230	<i>Triceratium favus</i> Ehrenb.

Brackish plankton

1200200	<i>Actinocyclus normanii</i> (Gregory) Hustedt
1220200	<i>Coscinodiscus lacustris</i> Grun.
1100230	<i>Coscinodiscus rothii</i> (Ehrenb.) Kütz.
1230200	<i>Cyclotella striata</i> (Kütz.) Grun.

Brackish/freshwater plankton

1321202	<i>Cyclotella meneghiniana</i> Kütz.
1331200	<i>Diatoma elongatum</i> (Lyngbye) Ag.
1200200	<i>Thalassiosira baltica</i> (Grun.) Ostensfeld

Freshwater plankton

1421202	<i>Aulacoseira granulata</i> (Ehrenb.) Ralfs
1533200	<i>Aulacoseira italica</i> (Ehrenb.) Kütz.
1421203	<i>Cyclotella comta</i> (Ehrenb.) Kütz.
1421200	<i>Melosira varians</i> Ag.
1423201	<i>Meridion circulare</i> (Grev.) Ag.
1411202	<i>Stephanodiscus astrea</i> (Ehrenb.) Grun.
1433202	<i>Synedra berolinensis</i> Lemmermann

Marine tychoplankton

2100230	<i>Campylosira cymbelliformis</i> (A. Schmidt) Grun.
2100220	<i>Cymatosira belgica</i> Grun.
2100210	<i>Delphineis surirella</i> (Ehrenb.) Andrews
2100200	<i>Melosira westii</i> W. Smith
2100220	<i>Odontella aurita</i> (Lyngbye) Ag.
2100200	<i>Plagiogramma vanheurckii</i> Grun.
2100210	<i>Rhaphoneis amphiceros</i> Ehrenb.
2100200	<i>Rhaphoneis minutissima</i> Hustedt

Table 1. (Continued)

Brackish/freshwater tychoplankton

2424202	<i>Fragilaria brevistriata</i> Grun.
2422202	<i>Fragilaria construens</i> (Ehrenb.) Grun.
2300200	<i>Fragilaria construens</i> var. <i>subsalina</i> Hustedt
2422202	<i>Fragilaria construens</i> var. <i>venter</i> (Ehrenb.) Grun.
2300200	<i>Fragilaria inflata</i> (Heiden) Hustedt
2421303	<i>Fragilaria pinnata</i> Ehrenb.
2422202	<i>Fragilaria virescens</i> Ralfs

Marine epiphytes

3100030	<i>Grammatophora oceanica</i> Grun.
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Marine/brackish epiphytes

3201220	<i>Achnanthes brevipes</i> Ag.
3100220	<i>Cocconeis scutellum</i> Ehrenb.
3100220	<i>Grammatophora oceanica</i> var. <i>macilenta</i> (W. Smith) Grun.
3200220	<i>Hyalodiscus scoticus</i> (Kütz.) Grun.
3201200	<i>Melosira jurgensii</i> Ag.
3110200	<i>Melosira moniliformis</i> (O.F. Müller) Ag.
3200200	<i>Navicula gracilis</i> var. <i>schizonemoides</i> Van Heurck
3330220	<i>Rhopalodia acuminata</i> (Ehrenb.) O. Müller
3230220	<i>Rhopalodia constricta</i> (W. Smith) Krammer
3200220	<i>Rhopalodia gibberula</i> var. <i>vanheurckii</i> O. Müller
3221220	<i>Synedra pulchella</i> (Ralfs) Kütz.
3231220	<i>Synedra tabulata</i> (Ag.) Kütz.

Brackish/freshwater epiphytes

3420200	<i>Cocconeis disculus</i> (Schumann) Cleve
3321201	<i>Cocconeis pediculus</i> Ehrenb.
3421202	<i>Cocconeis placentula</i> Ehrenb.
3421221	<i>Rhoicosphenia curvata</i> (Kütz.) Grun.
3411222	<i>Rhopalodia gibba</i> (Kütz.) O. Müller

Freshwater epiphytes

3422201	<i>Achnanthes lanceolata</i> (Bréb.) Grun.
3511202	<i>Cocconeis diminuta</i> Pantocsek
3400200	<i>Cocconeis disculoides</i> Hustedt
3421200	<i>Cymbella cymbiformis</i> (Kütz.) Hustedt
3410201	<i>Diatoma vulgare</i> Bory
3414203	<i>Epithemia sorex</i> Kütz.
3412202	<i>Epithemia turgida</i> (Ehrenb.) Kütz.
3414202	<i>Epithemia zebra</i> (Ehrenb.) Kütz.
3544303	<i>Eunotia exigua</i> (Bréb.) Grun.
3545300	<i>Eunotia veneris</i> (Kütz.) O. Müller
3422203	<i>Gomphonema angustatum</i> (Kütz.) Rabenh.
3432201	<i>Gomphonema parvulum</i> (Kütz.) Grun.
3421202	<i>Nitzschia amphibia</i> Grun.
3431202	<i>Nitzschia palea</i> (Kütz.) W. Smith
3432202	<i>Synedra ulna</i> (Nitzsch) Ehrenb.

Table 1. (Continued)

Marine epipelon

- 4100100 *Diploneis weissflogii* (A.Schmidt) Cleve
 4100200 *Navicula distans* (W. Sm.) Van Heurck
 4100220 *Nitzschia panduriformis* Gregory
 4100220 *Trachineis aspera* (Ehrenb.) Cleve

Marine/brackish epipelon

- 4200220 *Amphora exigua* Gregory
 4200220 *Amphora proteus* Gregory
 4200200 *Caloneis formosa* (Gregory) Cleve
 4200200 *Campylodiscus echeenei* Ehrenb.
 4100220 *Diploneis bombus* Ehrenb.
 4201220 *Diploneis didyma* Ehrenb.
 4100220 *Diploneis smithii* (Bréb.) Cleve
 4411201 *Gyrosigma acuminatum* (Kütz.) Rabenh.
 4411203 *Gyrosigma attenuatum* (Kütz.) Cleve
 4220220 *Gyrosigma spenceri* (W. Smith) Cleve
 4100220 *Navicula abrupta* Gregory
 4100220 *Navicula cancellata* Donkin
 4321221 *Navicula cincta* (Ehrenb.) Kütz.
 4100200 *Navicula crucifera* Grun.
 4323222 *Navicula cryptocephala* Kütz.
 4200220 *Navicula digitoradiata* (Gregory) A.Schmidt
 4100200 *Navicula dissipata* Hustedt
 4201200 *Navicula elegans* W. Smith
 4100220 *Navicula finmarchica* Cleve & Grun.
 4100200 *Navicula flantica* Grun.
 4100220 *Navicula forcipata* Grev.
 4422220 *Navicula gracilis* Ehrenb.
 4423202 *Navicula hungarica* Grun
 4100220 *Navicula palpebralis* Bréb.
 4200220 *Navicula peregrina* (Ehrenb.) Kütz.
 4100200 *Navicula phyllepta* Kütz.
 4211220 *Navicula pygmaea* Kütz.
 4423202 *Navicula rhynchocephala* Kütz.
 4220200 *Navicula rostellata* Kütz.
 4230220 *Navicula salinarum* Grun.
 4220202 *Nitzschia apiculata* (Gregory) Grun.
 4200200 *Nitzschia bilobata* W. Smith
 4100230 *Nitzschia constricta* (Gregory) Grun.
 4420200 *Nitzschia debilis* (Arnott) Grun.
 4100200 *Nitzschia granulata* Grun.
 4320202 *Nitzschia hungarica* Grun.
 4200200 *Nitzschia navicularis* (Bréb.) Grun.
 4200220 *Nitzschia punctata* (W. Smith) Grun.
 4231200 *Nitzschia scalaris* W. Smith
 4230220 *Nitzschia sigma* W. Smith
 4300200 *Nitzschia triblionella* Hantzsch
 4100210 *Pleurosigma angulatum* (Quekett) W. Smith
 4200210 *Scoliopleura tumida* (Bréb.) Rabenh.
 4200200 *Stauroneis gregori* Ralfs
 4200220 *Surirella gemma* Ehrenb.

Table 1. (Continued)

- 4231200 *Surirella ovalis* Bréb.
 4421201 *Surirella ovata* Kütz.

Freshwater epipelon

- 4421202 *Amphora ovalis* Kütz.
 4421202 *Amphora ovalis* var. *lybica* (Ehrenb.) Cleve
 4422200 *Cymatopleura elliptica* (Bréb.) W. Smith
 4422200 *Cymatopleura solea* (Bréb.) W. Smith
 4423203 *Diploneis elliptica* (Kütz.) Cleve
 4423202 *Navicula bacillum* Ehrenb.
 4421200 *Navicula oblonga* Kütz.
 4433202 *Navicula pupula* Kütz.
 4433202 *Navicula radiosa* Kütz.
 4421202 *Navicula viridula* Kütz.
 4432203 *Pinnularia maior* (Kütz.) Cleve

Marine/brackish epipsammon

- 5230222 *Achnanthes delicatula* (Kütz.) Grun.
 5425202 *Achnanthes exigua* Grun.
 5230202 *Achnanthes lemmermannii* Hustedt
 5421202 *Amphora ovalis* var. *pediculus* (Kütz.) Van Heurck
 5200200 *Catenula adhaerens* Mereschkowsky
 5100220 *Cocconeis peltoides* Hustedt
 5100220 *Dimerogramma minor* (Gregory) Ralfs
 5100220 *Opephora pacifica* (Grun.) Petit
 5100232 *Opephora parva* (Van Heurck) Krasske
 5200220 *Opephora schulzii* (Brockmann) Simonsen
 5100220 *Plagiogramma staurophorum* (Gregory) Heribaud

Marine/brackish aerophilous

- 6201200 *Diploneis interrupta* (Kütz.) Cleve
 6420202 *Diploneis ovalis* (Hilse) Cleve
 6201200 *Nitzschia vitrea* Norman

Brackish/freshwater aerophilous

- 6431202 *Hantzschia amphioxys* (Ehrenb.) Grun.
 6525200 *Navicula contenta* Grun.
 6422200 *Navicula minima* Grun.
 6331222 *Navicula mutica* Kütz.
 6430200 *Navicula pusilla* W. Smith
 6433302 *Pinnularia borealis* Ehrenb.
 6433202 *Pinnularia viridis* var. *minor* Cleve

(Fig. 1) has not been changed significantly. In the nomenclature (Table 1) only widely accepted changes have been introduced. The checklist of Denys (1991), which accepted changes as proposed by Hartley (1986), Williams *et al.* (1988) and Krammer & Lange-Bertalot (1986, 1988), serves as the main guide in this respect.

The classification of life form has been changed. The new categories can be related to tidal exposure and desiccation gradient so that they can be used to reconstruct palaeosedimentary environments (subtidal, intertidal, supratidal and non-tidal). Therefore, the benthic (in and on sediment living) diatoms are subdivided (cf. Round, 1971; Van den Hoek *et al.*, 1979) into epipellic taxa (mobile diatoms, which migrate actively through the sediment) and epipsammic taxa (immobile diatoms, which are firmly attached to sand grains). Those benthic diatoms which are adapted to being irregularly flooded have been classified in a special category; benthos aerophilous. De Wolf (1982) combined all taxa which normally live firmly attached to any kind of substratum (rocks, sand grains, macrophytes, ice, etc.) into one group. Now two categories are distinguished: benthos/epipsammon and epiphytes. Here, the epiphytic group only includes taxa which live attached to macrophytes. The plankton group is now subdivided in plankton *sensu stricto* (s.s.) and tychoplankton. Planktonic diatoms s.s. are species which only live in the plankton habitat (metabolize and reproduce in the water column), whereas the tychoplanktonic diatoms are species

which occur frequently in the water column but are also related to another (benthic/epiphytic) habitat.

Ecological groups

For the reconstruction of sedimentary environments in the Holocene coastal deposits of the Netherlands, a new approach of diatom research was introduced by Vos & De Wolf (1988). Based on the factors 'life form' and 'salinity', the diatoms were classified into ecological groups (Fig. 2) and the occurrence of the different ecological groups was related to specific sedimentary environments in the coastal wetlands (Table 2). Vos & De Wolf (1988) named the ecological groups after a characteristic member of the group. However, this terminology can lead to misunderstandings. It suggests that the species after which the group has been named is the most representative species of the group, but this was not the case in many of the investigated sediments. Therefore, in this publication, the ecological groups have been renamed with more neutral terms, which are derived from the basal factors

		Salinity												
		Poly-halobous			Meso-halobous				Oligo-halobous					
		S (%)												
		30			20		10		5		1	0.5	0.2	0.1
		17000			10000		5000		1000		500	100	0	
Life form	Plankton	Plankton s.s.	Marine plankton		Brackish plankton				Brackish/freshwater plankton		Freshwater plankton			
		Tycho-plankton	Marine tychoplankton		-----				Brackish/freshwater tychoplankton					
	Epiphytes	Epiphytes	Marine epiphytes		Marine/brackish epiphytes				Brackish/freshwater epiphytes		Freshwater epiphytes			
		Epipelon	Marine epipelon		Marine/brackish epipelon						Freshwater epipelon			
	Benthos	Epi-psammon			Marine/brackish epi-psammon				-----					
		Aero-philous			Marine/brackish aerophilous				Brackish/freshwater aerophilous					

Fig. 2. Classification of ecological diatom groups, based on life form and salinity tolerance of the individual species, modified after Vos & De Wolf (1988).

Table 2. Relation between the relative abundance (%) of the ecological groups and sedimentary environments, modified after Vos & De Wolf (1988).

Ecological groups	Macro- and mesotidal environments					Microtidal and non-tidal environments			
	Subtidal area	Intertidal area	Supratidal area		Marine/brackish tidal lagoons, small tidal range	Marine/brackish lagoons, no tides	non-marine (fresh) rivers, ditches and lakes		
	open marine tidal channels	estuarine tidal channels	sand-flats	mud-flats				salt-marshes, around MHW	salt-marshes, above MHW
Marine plankton	10-80	10-60	10-80	10-70	10-70	10-50	10-60	0-10	0-5
Marine tychoplankton	20-90	15-60	10-70	10-70	10-70	10-50	10-60	0-10	0-5
Brackish plankton	1-10	20-70	1-10	1-30	1-30	1-15	1-15	0-10	0-5
Marine/brackish epipsammon	1-40	1-45	50-95	1-45	0-15	0-15	0-25	0-5	0-1
Marine/brackish epipelon	0-5	0-5	1-30	15-50	1-40	0-5	5-50	5-60	0-1
Marine/brackish aerophilous	0-1	0-1	0-1	0-1	10-40	10-40	0-1	0-1	0-1
Brackish/freshwater aerophilous	0-1	0-1	0-1	0-1	10-40	10-40	0-1	0-1	0-10
Marine/brackish epiphytes	0-1	0-1	0-5	0-5	0-5	10-60	10-75	10-90	0-5
Brackish/freshwater plankton	0-1	0-25	0-1	0-1	0-1	0-1	0-20	0-25	0-5
Brackish/freshwater tychoplankton	0-1	0-1	0-5	0-5	0-5	5-50	5-50	5-80	0-10
Brackish/freshwater epiphytes	0-1	0-1	0-5	0-5	0-5	1-50	1-50	1-80	0-10
Freshwater epiphytes	0-1	0-1	0-1	0-1	0-5	0-10	0-10	0-10	1-75
Freshwater epipelon	0-1	0-1	0-1	0-1	0-1	0-10	0-5	0-10	1-75
Freshwater plankton	0-1	0-1	0-1	0-1	0-1	0-5	0-15	0-20	10-95

'salinity' and 'life form', e.g. marine tychoplankton. Also the scheme has been slightly adapted, for instance the group of sessile diatoms on seston (formerly, the *Rhaphoneis minutissima* Hustedt group) is now integrated in the marine tychoplankton group.

Only those diatoms which are frequently observed in the Holocene coastal deposits of the Netherlands have been taken up in the classification.

The salinity classes of the ecological groups are largely based on the system of Hustedt (1957). Our classification is different with respect to the subdivision of the mesohalobous class: a brackish group and a brackish/freshwater group are distinguished. For the boundary between these groups the 4‰ salinity mark has been taken, because it has been found that the biological limit for many estuarine taxa is in the 2–5‰ salinity range (Moore & McIntire, 1977; Admiraal, 1984; Juggins, 1992).

Although the salinity classes have broad ranges, the ranges of some euryhaline or indifferent species do not fit within these boundaries. Diatoms with the salinity code 4 (oligohalobous-indifferent) can live in both fresh and brackish waters. In the species list (Table 1) these diatoms have been classified in the freshwater or brackish/freshwater groups; however, the ultimate classification of these diatoms depends on the association with which they occur. For instance, when encountered in drillcore samples the (salinity indifferent) epiphytic species *Cocconeis placentula* Ehrenb. is found together with brackish epiphytes like *Cocconeis scutellum* Ehrenb. and *Rhopalodia musculus* (Kütz.) O. Müll; in this case the diatom *Cocconeis placentula* will be classified in the marine/brackish epiphytes group.

The results of the diatom analysis have to be synthesized in the form of percentage diagrams for both the individual species and the ecological groups. The palaeoenvironmental interpretations are based on the major trends of relative abundances of the ecological groups. Therefore, the amount of diatom frustules counted per sample can be restricted to 200 valves.

Relation between ecological groups and sedimentary environments

The autochthonous/allochthonous problem

A problem in palaeoecological diatom research is the distinction between allochthonous and autochthonous species. Autochthonous diatoms are species which have lived at the place of deposition and give information about the local environment, whereas allochthonous diatoms are species which have been transported (e.g. by tidal currents or rivers) from elsewhere and only supply information about wider surroundings. Generally, in low-energy environments the influx of allochthonous diatoms is low. Therefore, in palaeoecological studies of lakes, the question of the autochthonous or allochthonous origin is less relevant. However, in tidal environments the issue is of major importance (Brockmann, 1940). In coastal areas, the allochthonous influx of diatoms may even outnumber the autochthonous population (Simonsen, 1969).

Several authors have proposed methods to distinguish between autochthonous and allochthonous diatoms. Fragmentation of diatom frustules has often been used as a criterion for long-distance transport (Voorrips & Jansma, 1974; Heyworth *et al.*, 1985). This approach is not satisfactory, since also other processes such as natural chemical leaching, diagenesis and compaction (Andrews, 1972; Beyens & Denys, 1982), sample treatment (Beyens & Denys, 1982) and predation (Romeyn & Bouwman, 1983) may damage the diatom valves.

Simonsen (1969) proposed that only benthic taxa should be used in palaeoecological reconstruction since plankton forms are by definition allochthonous. Beyens & Denys (1982) attempted to quantitatively distinguish between allochthonous and autochthonous components in coastal deposits by considering salinity dependence and benthic life form. For this purpose, they used the salinity classification of Van der Werff & Huls (1957–1974). The salinity group with the largest percentage of benthic forms is called the 'optimal group' and the taxa in the adjacent salinity groups

are classified as the 'neighbour groups'. Together, the optimal and the neighbour groups form the autochthonous component. However, since the salinity classification is based on preference groups this method potentially ignores any euryhaline taxa which are classified outside the 'central' autochthonous group (Juggins, 1992). Also, the epiphytic diatoms are excluded and these taxa together with the benthic taxa supply valuable information about the palaeosedimentary environments (Vos & De Wolf, 1988).

In the absence of any detailed empirical data on the allochthonous diatom component of coastal sediments, Vos & De Wolf (1988) used several diatom and non-diatom related criteria for the assessment regarding which diatoms are 'in or out of place'.

Criteria related to the diatoms proper:

- Composition of the different ecological groups. If the habitats of two ecological groups do not overlap (e.g. freshwater or marine groups) at least one of the two groups must be allochthonous.
- Positive trends of the different ecological groups within the sedimentary sequence, especially of the benthic and epiphytic groups.
- Occurrence of relatively rare taxa, only in those zones where diatoms of the same ecological group show a positive trend.
- Amount of broken diatom valves of fragile elongated or weakly silicified species. When most of them are unbroken, this indicates that these taxa have not been transported. However, the reverse is not the case. If a high percentage of these diatoms are fragmented, they may also be autochthonous.

Non-diatom criteria:

- Palaeogeographic location. For instance, if it is known that the sediments are formed in the hinterland of the coastal area, all marine diatoms from the offshore zone are allochthonous.
- Lithology and sedimentary structures. For example, epipsammic diatoms are allochthonous in heavy clays, because a muddy environment is not the habitat of the sand species.

- Other palaeoecological indicators, such as molluscs and ostracodes may be useful in the assessment of the autochthonous diatom groups.

In the assessment of the autochthonous groups in the Holocene coastal deposits of the Netherlands, the palaeogeographic criteria are of major importance. The Holocene coastal deposits have been formed inland from the open sea, so that all the species of the marine plankton group, which live in the offshore zone and in the tidal inlets, are qualified as allochthonous. The benthic and/or epiphytic groups are considered as the autochthonous component, but as stated above, the salinity ranges of these groups must show overlap. If the salinity ranges of these groups do not overlap, the one with the lowest relative abundance will be taken for allochthonous.

In the Dutch coastal deposits, we also consider the marine tycho plankton group as allochthonous, because these species, like the species of the marine plankton group, live in the offshore zone of the North Sea (including the tidal inlets). They are transported by the tidal currents into the hinterland of the coastal area. Species of this tycho plankton group often reach high relative abundances in the Holocene coastal deposits of the Netherlands. The most prominent representatives of this group are *Cymatosira belgica* Grun. and *Rhaphoneis minutissima* Hustedt (Vos & De Wolf, 1993).

Characterization of sedimentary environments

The relations between sedimentary environments and ecological diatom groups are presented in Table 2.

As stated in the previous section, the allochthonous marine planktonic and tycho planktonic diatoms are problematic groups for the characterization of sedimentary environments. If marine plankton and tycho plankton account for more than 80% of the relative abundance, the reconstruction of the sedimentary environment is difficult. A dominance of tide transported plank-

tonic and tycho planktonic diatoms is often found in sediments of tidal channels and tidal inlets (Table 3). In these environments, the conditions (high current velocities and subsequent low irradiance at the bottom of the channel) are permanently unfavourable for the development of a (autochthonous) benthic or epiphytic diatom population. However, the dominance of marine plankton and tycho plankton species is not exclusively specific for deposits in tidal inlets and channels but may also occur in any other tide-influenced sedimentary environment where the allochthonous diatom input is very high compared with the *in situ* die off in the sediment of the autochthonous (benthic and epiphytic) species.

On intertidal sand flats, the autochthonous benthic community is generally well represented in the fossil records. The major part of the benthic community consists of small epipsammic diatoms (Vos *et al.*, 1988; Sabbe & Vyverman, 1991). Actually, these sand species are not exclusively typical for tidal sand flats. Epipsammic diatoms are found in the near-shore environments of the Öresund and of the Baltic Sea (Sundbäck, 1983, 1987; Thulin, 1987). In contrast to the tidal sand flats of the Netherlands (Vos, 1986), in the near-shore (non-tidal) environments of the Baltic the sand species occur together with epiphytic species (such as *Cocconeis scutellum*, *C. placentula* and *Achnanthes lemmermannii* Hustedt; Sundbäck, 1983). The allochthonous component is small on intertidal sand flats, because of the high energetic conditions in these environments. Due to the high current velocities and reworking of the sediment, particles from the water phase (among others clay aggregates and diatoms) can hardly settle.

Marine brackish epipellic diatoms also live on the sand flats, but the largest numbers of this group are found on the tidal mud flats (Van den Hoek *et al.*, 1979; Admiraal, 1984). However, in the sediments of a mud flat, also the allochthonous component is generally very large. A large part of the fine-grained sediment on the mud flats, including the marine tycho plankton and plankton species, is derived from the water phase. Often, the allochthonous plankton and tycho plankton diatoms are in the majority in the thanatocoenose

of the mud flat deposits. In mud flat deposits, the relative abundances of the autochthonous marine brackish epipellic groups generally fluctuate between 15–40% and the relative abundances of the epiphytic groups are normally low (<5%). Epiphytic diatoms rarely live on mud flats because the substratum of these diatoms, macrophytes, is mostly absent in this environment. Also, the allochthonous import of these epiphytic diatoms into the intertidal environments is small, because the source areas of these species are limited in the tidal areas.

A special category of the epipellic diatoms consists of the aerophilous diatoms, which live on muddy soils and are adapted to being irregularly flooded. These aerophilous diatoms are indicators for supratidal environments (salt marshes). Also in the salt marshes, the allochthonous component of marine tycho plankton and plankton groups might reach high relative abundances (up to 75%). The abundances of the aerophilous species generally vary between 15 and 80%.

Epiphytic diatoms which live on macrophytes (macro-algae and water plants) are characteristic of low-dynamic environments that are permanently submerged, e.g. ditches, ponds, lakes and lagoons (Vos & De Wolf, 1988). Besides epiphytic diatoms, epipellic diatoms are also frequently observed in these environments. Epipellic diatoms can live on both tide and non-tide exposed water-soils. The allochthonous components of marine tycho plankton and plankton species are also prominent in the sediments of tide-influenced lagoons and ponds.

A mixture of ecological groups is found in shallow ponds, located within the supratidal area, which are periodically desiccated. In this specific environment, epiphytic, epipellic and aerophilous groups form the autochthonous component.

Evaluation of the method

The method of palaeoenvironmental diatom research, developed by the Geological Survey, has been set up, for palaeogeographic reasons, to help in the reconstruction of sedimentary environ-

ments. The concept is rather pragmatic, since the method utilises only those factors (salinity and life form) of which sufficient ecological data are available. Also, the method is time saving because the environmental reconstruction is based on the major trends of the ecological groups (a complete species list is not necessary), so that the diatom counts can be restricted to 200 valves per sample.

Comparative diatom research in coastal deposits from other parts of the world is rather limited, and most of these studies took place in sediments of non-tidal basins or seas (e.g. Stabell, 1982; Pienitz *et al.*, 1991) or small lowland catchment areas (Brown & Barber, 1985). In those palaeoenvironments, the allochthonous/autochthonous question is less relevant because the allochthonous influx of diatoms by tidal currents is negligible. Investigations analogous to the studies in the Dutch tide-influenced coastal areas have been carried out in the adjacent Belgian coastal plain (Beyens & Denys, 1982; Denys & Verbruggen, 1989) and in the coastal area south of Vancouver, Canada (Palmer & Clague, 1991). Our method (using ecological diatom groups) differs from these studies with regard to the question which diatoms are 'in or out of place'. Beyens & Denys (1982) use the benthic life form in relation to 'salinity groups' for the assessment of allochthonous and autochthonous diatoms (see section: 'the autochthonous/allochthonous problem'), while Palmer & Clague (1991) do not go further into the matter.

Our method does not provide information about other ecological parameters such as energy gradients (current and wave action) and tolerance gradients of phosphate, ammonia and sulphide. These factors do influence the composition of the diatom assemblages in tidal ecosystems (e.g. Colijn & Dijkema, 1981; Admiraal, 1984). However, ecological studies on these subjects are limited in number and therefore the relations are not yet fully understood. Insight into these relations is relevant to the understanding of the differences between the fossil and modern assemblages. It has been shown that the (autochthonous) fossil assemblages of the Poortvliet boring (Vos & De Wolf, 1993) differ in some respects from the

present-day assemblages. However, some of the differences between the modern and fossil assemblages can be explained by post-depositional processes such as differential dissolution (Flower, 1993) of diatom valves. For a better understanding of the ecological significance of the fossil assemblages, more comparative diatom studies have to be carried out. Up to now only a few comparative diatom analyses have been applied to the tidal environments, most of them on salinity (e.g. Flower, 1982; Juggins, 1992).

Knowledge of the environmental conditions of the past is especially relevant to the understanding of man-induced changes in the coastal areas. The palaeoecological data, derived from the fossil diatom assemblages, can be used as natural reference levels for the assessment of recent changes (Anderson & Vos, 1992).

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