UNIVERSITEIT GENT
FACULTEIT DER WETENSCHAPPEN
Academiejaar 1996-1997

Systematics and ecology of intertidal benthic diatoms of the Westerschelde estuary (The Netherlands)

Systematiek en ecologie van intertidale benthische diatomeeën van het Westerschelde-estuarium (Nederland)

By

Koen Sabbe

Part 1. Text, tables and figures

Proefschrift ingediend tot het behalen van de graad van
Doctor in de Wetenschappen, Groep Biologie

Promotor: Prof. Dr. W. Vyverman
Co-promotor: Prof. Dr. E. Coppejans

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Voor Ziggy en Max

'He said that the wolf is a being of great order and that it knows what men do not: that there is no order in the world save that which death puts there. [...]. He said that men wish to be serious but they do not understand how to be so. Between their acts and their ceremonies lies the world and in this world the storms blow and the trees twist in the wind and all the animals that God has made go to and fro yet this world men do not see. They see the acts of their own hands or they see that which they name and call out to one another but the world between is invisible to them.'

Cormac McCarthy, 'The crossing' (1994)

'There is also the question of what ornithologists believe avian taxonomy is for. Is it primarily a tool rather than an end in itself? Should taxonomists be mainly seen as serving 'customers' in the wider scientific and amateur ornitological community? [...] Seeing taxonomy and the definition of species as tools was a powerful theme of the meeting, with most of the customers present being happy with the biological species concept, and in no mood to purchase the new-and-improved tool of a phylogenetic species concept if it is to be based upon 'invisible' mitochondrial DNA.'

Martin, G., 'Birds in double trouble', Nature 380: 666-667 (1996)

'And last but not least: in challenging scientists to do science (and not to do mythology) I do not wish to imply that biodiversity does not require our efforts to be conserved. Certainly, we must do our best to defend all forms of life, including the genetic diversity of populations and species, as well as the diversity of communities and landscapes. I suppose that justifications from the spheres of ethics and aesthetics must be used much more broadly.'

Ghilarov, A., 'What does 'biodiversity' mean - scientific problem or convenient myth?', Trends Ecol. Evol. 11: 304-306 (1996)

'[...], Pauly made a convincing case that one third of all marine net primary production has been highjacked to support human fisheries. Say it again: one third. As Pauly put it, one in every three diatoms in the sea ends up in a fish caught by humans.'

John Lawton's View from the Park 12, Oikos 71: 353-354 (1994)

'[...] which fills his mind with wonder in the contemplation of forms at once so minute and perfect, so humble in their individual capacity, and yet by their numbers and wide diffusion occupying an important position in the organic world, and fulfilling the purposes of Power, Wisdom and Benignity.'

W. Smith, 'Synopsis of the British Diatomaceae' (1854)

Dankwoord - Acknowledgements

Het proefschrift dat u nu in uw handen houdt zou er nooit gekomen zijn zonder de hulp en de mentale steun van een groot aantal mensen.

Hartelijk dank aan het NFWO en FKFO voor de financiële steun tijdens de eerste 4 jaren van deze studie.

Bedankt en nog eens bedankt Wim V. Niettegenstaande het feit je pas in extremis officieel promotor van dit proefschrift geworden bent, is vooral aan jou te danken dat dit proefschrift er nu ook is. Zonder de vele faxen, e-mails, pep-talk, verlichte (en ook donkere) discussies en werklunchen was het er waarschijnlijk nooit van gekomen.

Mijn co-promotor, Prof. Dr. Eric Coppejans, dank ik voor het vertrouwen en alle mogelijke financiële en logistieke steun. Bedankt ook Prof. Dr. Paul Goetghebeur, 'the human ICBN', voor alle hulp bij taxonomische en nomenclaturale problemen. Bedankt Prof. Dr. Maurice Hoffmann, voor alle mogelijke hulp tijdens multivariate nachtmerries.

Hartelijk bedankt Prof. Dr. Magda Vincx, voor alle wijze raad en steun, moreel en logistiek, Dirk, Daniëlle en Andy, voor de analyses, de hyperbenthische Jan Mees, Jan Schrijvers, Nancy, Tom, Maaike, Guy en all marine creatures great and small: voor van alles en nog wat. Bedankt Rita voor alle SEM en andere praat. All hail Kris, lord of the network.

Mijn oprechte dank ook aan Dr. Dick de Jong, voor de gelegenheid om deel te nemen aan de staalnamecampagnes van het Directoraat-Generaal Rijkswaterstaat, Rijksinstituut voor Zee (Middelburg) en het ter beschikking stellen van diverse gegevens. De bemanning van de Schenge, Wim, Ko, Cees, Maarten en Bert, voor de onvergetelijk dagen op de Westerschelde, voor alle hulp, voor de interesse, en natuurlijk voor de koffie. Bedankt Prof. Dr. C. Heip, Dr. P. herman, Dr. J. Kromkamp en Dr. N. Goosen voor de open deur bij het NIOO-CEMO.

Merci Dr. Pierre Compère, pour toute assistance en cas d'urgence taxonomique. Special thanks to all those diatom people, Kristina, Hannelore, Claes, Angela, Luc and all the rest - for interest and support.

Het thuisfront: de supersonische Koenraad (en Truus natuurlijk, dat spreekt voor zich): voor alle kritische opmerkingen, de hulp, de afleiding, het medeleven, Rosette en Marcel, die de grenzen van het menselijke doorzettingsvermogen verlegden tijdens het afdrukken van onzichtbare diatomeeën, Adelin, voor wie niets nooit teveel is, Cathy (koffie! potjes!), Christelle en Pascale (post! fax! etc.!), Olivier, Mieke, Conrad, Kathleen, Marc, Christine, Arnout, Dirk en alle studenten: bedankt.

Oprechte dank aan het verplegend personeel: Wim W., vriend, partner-in-crime, en oprechte vriend der natuur, Ann D., beste vriendin, Peter en Sophie, Henk, Kristof, Luk, Yves, Ilse, voor de kaarsen, Ides, Ruth en alle anderen die ik hier natuurlijk vergeten ben.

Zeven anjers en zeven rozen voor Kathleen, Johan en Liesbeth, zonder wie het huishouden Sabbe-Van Cauwelaert onherroepelijk naar de verdoemenis was gegaan. B-e-d-a-n-k-t.

De reddingsploeg: Tammy en Cindy - bedankt voor de auto.

David and Lu, Paul and Von: for your infinite kindness, for your Australian paradise.

Lulu and Paul, for your remarkable daughter, for Ireland, for making me believe that love of one's neighbour really exists, John-Paul, larger than life, Alicia and Filip (no thanks, I'm fine), for all your help when it really mattered, Ella and Frans, thank you for all and congratulations!

Ma en pa: er zijn geen woorden voor alles wat jullie voor mij, Mia, Ziggy en Max gedaan hebben. Bedankt voor jullie onvoorwaardelijke steun en vertrouwen in moeilijke dagen, maanden, jaren. Ik hou van jullie.

Ziggy en Max: heerlijk dat jullie er zijn, heerlijk om van jullie te houden.

Finally, Mia. I don't know what keeps you believing in me, but it keeps me believing in myself. I don't even want to think about what you have been through - an ever-absent, stressed and worried husband on your hands. Two kids. You must be mad. Thank you so very much, and love you.

All praise to the Great Unknown.

Gent, 10 maart 1997

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Samenvatting

Het Westerschelde-estuarium is een macro-tidaal estuarium in Zuidwest-Nederland; het omvat de meso-, poly- en euhaliene zones van het Schelde-estuarium. De Westerschelde is uniek in Europees opzicht door de lange residentietijd van het water (wat resulteert in een erg stabiele saliniteitsgradiënt) en de erg hoge graad van organische (en andere) vervuiling. Het estuarium wordt ook gekenmerkt door de aanwezigheid van uitgestrekte intergetijdegebieden (zandplaten en slikken), die samen ongeveer 45 % van de totale oppervlakte van het estuarium uitmaken. In de bovenste sedimentlagen van deze gebieden komen dichte populaties benthische diatomeeën voor, die een belangrijke rol spelen in de produktie- en mineralisatieprocessen in de sedimenten en in het hele estuariene ecosysteem.

In deze intertidale benthische diatomeeëngemeenschappen zijn een groot aantal verschillende levensvormen aanwezig, die ruwweg in 2 belangrijke categorieën ingedeeld kunnen worden: het epipelon, dat de vrijlevende fractie omvat, en het epipsammon, dat voornamelijk bestaat uit taxa die in nauwe associatie met individuele sedimentpartikels leven. Onderzoek naar deze laatste fractie wordt nog steeds bemoeilijkt door methodologische problemen in verband met de kwantitatieve scheiding van de epipsammische cellen van het sediment en determinatieproblemen; het meeste systematische, ecologische maar vooral experimentele en fysiologische onderzoek heeft zich om die redenen vooral toegespitst op het epipelon.

Bij de aanvang van deze studie was vrijwel niets gekend over de samenstelling en de ecologie van de intertidale benthische diatomeeëngemeenschappen van het Westerschelde-estuarium. Daarom werd in 1991 een uitgebreid onderzoek gestart naar de taxonomische en ecologische structurele aspecten van deze gemeenschappen. Hierbij stonden de volgende onderzoeksvragen centraal:

1. Welke taxa zijn aanwezig in de intertidale benthische diatomeeëngemeenschappen van het Westerschelde-estuarium?
2. Welke gemeenschappen kunnen onderscheiden worden, en wat zijn hun ruimtelijke en temporele verspreidingspatronen?
3. Wat zijn de relaties tussen de gemeten abiotische omgevingsfactoren en de waargenomen patronen, en in welke mate hebben deze relaties betrekking op de hele benthische diatomeeëngemeenschap?
4. Welke hypothesen met betrekking tot de ecologie en populatiedynamica van benthische diatomeeëngemeenschappen kunnen ontwikkeld worden op basis van een gedetailleerde multivariate analyse van de ruimtelijke en temporele verspreidingspatronen van deze gemeenschappen?

Tijdens deze studie werd speciale aandacht besteed aan de systematiek en ecologie van de weinig gekende epipsammische gemeenschappen.

In de periode oktober 1991-oktober 1992 werd maandelijks de bovenste 10 mm van het sediment in 32 staalnamestations, gelegen langs 11 intertidale transecten, bemonsterd; de staalnamestations werden zodanig geselecteerd dat het volledige saliniteitsbereik en de verschillende sedimenttypes vertegenwoordigd waren. De monsters werden vervolgens gebruikt voor zowel de diatomeeënanalyse (determinatie en kwantitatieve tellingen) als de fysische en chemische analyses van het sediment en het interstitiële water.

Een groot deel van deze studie is gewijd aan een nauwgezette systematische beschrijving van de aanwezige diatomeeënflora (hoofdstuk 4). De meeste taxa werden bestudeerd aan de hand van geavanceerde licht- en rasterelektronenmicroscopische technieken. Van een aantal geselecteerde taxa werd een gedetailleerde morfometrische studie gemaakt. Typemateriaal en materiaal van andere plaatsen (met inbegrip van niet-Europese) werden bestudeerd om de identiteit van een aantal taxa op te helderen. Levend en gefixeerd (maar niet geoxideerd) materiaal werden geregeld bekeken om de structuur van de chloroplasten te bestuderen of om precieze informatie over de microhabitat te verkrijgen. Autecologische informatie verkregen uit de ecologische analyses werd verwerkt in het systematische gedeelte; deze informatie omvat gegevens over de seizoenaliteit en de verspreiding van de waargenomen taxa in relatie tot de saliniteitsgradiënt en de sedimentsamenstelling.

In totaal werden 316 taxa (soorten en infraspecifieke taxa) waargenomen (Tabel 18). De meeste hiervan zijn geïllustreerd in het tweede deel van deze studie (Platen). Hierbij werd getracht om de morfologische variabiliteit van probleemtaxa zo goed mogelijk weer te geven.

Terwijl 223 taxa tot op soorts- (of infraspeciek) niveau gedetermineerd konden worden, bleek het onmogelijk om de identiteit van 93 andere taxa (d.i. ongeveer 29 % van alle taxa) te achterhalen. Vijfentwintig taxa hiervan werden voorlopig ondergebracht bij een gekende soort; ze zijn aangeduid met het tussenvoegsel 'cf.' tussen de genusnaam en het soortsepitheton. Deze groep omvat vooral taxa die goed lijken op een soort waarvan de taxonomische of autecologische identiteit onvoldoende gekend is. Daarnaast konden 63 taxa niet met zekerheid gedetermineerd worden; ze kregen een volgnummer binnen het genus waartoe ze waarschijnlijk behoren. Hieronder bevinden zich soorten en waarschijnlijk ook genera die nieuw zijn voor de wetenschap (bv. *Fallacia* sp. 3 and 4, *Lunella* sp. 1, Incertae sedis sp. 1), maar ook een groot aantal algemeen voorkomende taxa waarvan we vermoeden dat ze steeds verkeerd gedetermineerd zijn in floristische studies (bv. *Achnanthidium* sp. 2, een taxon dat in brakwatermilieus bijna zonder uitzondering als *Achnanthes lemmermannii*, een zoetwatersoort, gedetermineerd wordt).

Acht nieuwe nomenclaturale combinaties werden voorgesteld; vier hiervan werden reeds gepubliceerd, nl. *Biremis lucens* (Sabbe *et al.* 1995), *Opephora guenter-grassii*, *O. mutabilis* and *Pseudostaurosira perminuta* (Sabbe & Vyverman 1995). Vier andere (*Plagiogrammopsis minimum*, *P. sigmoideum*, *Tryblionella levidensis* var. *salinarum*, *T. parvula*) werden hier voorlopig geïntroduceerd en moeten nog formeel gepubliceerd worden.

In de huidige diatomeeënsystematiek zijn determinatieproblemen vooral te wijten aan de volgende 3 factoren:

1. Problemen in verband met de interpretatie van morfologische variatiepatronen, meer bepaald met betrekking tot het voorkomen van cryptische diversiteit bij diatomeeën;
2. Problemen veroorzaakt door het gebrek aan gespecializeerde brakwaterflora's en het algemeen gebruik van Europese flora's in andere continenten, wat in beide gevallen leidt tot 'force-fitting' van taxa;
3. Nomenclaturale en taxonomische problemen veroorzaakt door recente ontwikkelingen in de diatomeeënsystematiek.

De morfologie van de diatomeeënfrustule kan veranderingen ondergaan onder invloed van het milieu. Diatomeeën die brakwatermilieus koloniseren vertonen vaak een hoge graad van morfologische plasticiteit langsheen de saliniteitsgradiënt. Daarnaast hebben recente morfometrische studies aangetoond dat (vaak subtiele) morfologische discontinuïteiten in vorm, afmetingen en ultrastructurele kenmerken kunnen bestaan binnen gevestigde diatomeeënsoorten. Deze cryptische diversiteit is vaak gecorreleerd met ecologische verschillen; in een aantal gevallen werd aangetoond dat dit fenomeen een genetische basis heeft. De consistente erkenning van dit fenomeen is belangrijk, niet enkel voor het systematisch en fylogenetisch onderzoek naar diatomeeën, maar ook voor de talrijke toepassingen van diatomeeëntaxonomie, zoals waterkwaliteitsonderzoek, biogeografie, paleo-ecologie en geologie.

Determinatieproblemen met estuariene diatomeeën worden ook veroorzaakt door het quasi ontbreken van gespecializeerde brakwaterflora's. Een gevolg hiervan is dat nogal wat brakwatersoorten, niettegenstaande bepaalde verschillen, ondergebracht worden bij de zoetwater- of mariene soort waar ze het meest op lijken ('force-fitting'). Het gebruik van Europese flora's buiten Europa verdoezelt ook heel wat verborgen diversiteit.

Gezien deze problemen is de correcte beschrijving en interpretatie van de waargenomen morfologische variatiepatronen van groot belang voor toekomstige herkenning en referentie. Daarom werd tijdens deze studie een inspanning geleverd om originele, ondubbelzinnige beschrijvingen van de meeste taxa te maken. Hierbij werd speciale aandacht besteed aan algemene en/of problematische taxa, zoals vertegenwoordigers van de genera *Anorthoneis*, *Opephora*, *Amphora*, *Fragilaria* s.l. en *Navicula* s.l., en moeilijke soortscomplexen zoals de *Amphora coffeaeformis*/*A. acutiuscula*, *Navicula perminuta* en de *Navicula apiculata* clusters.

De invoering van een grondig herziene diatomeeënclassificatie door Round *et al.* (1990) heeft belangrijke nomenclaturale implicaties. Daarbij is de gerechtvaardigde maar niet altijd universeel aanvaarde opsplitsing van verschillende 'oude' genera verantwoordelijk voor de huidige dubbele identiteit van een aantal grote genera (bv. *Fragilaria*, *Navicula*). In beide gevallen zijn grondige (en dus tijdrovende) literatuurstudies vereist om alle relevante informatie op te sporen.

Alhoewel gedurende de staalnameperiode in totaal 316 taxa werden waargenomen in het Westerschelde-estuarium, was slechts een beperkt aantal taxa dominant in de verschillende diatomeeëngemeenschappen van de 32 stations. Deze taxa zijn opgenomen in Tabel 41. De meeste hiervan zijn algemeen in een groot aantal stations, bv. de epipelische taxa *Cymatosira belgica*, *Delphineis minutissima*, *N. arenaria* var. *rostellata*, *N. flanatica*, *N. gregaria*, *Navicula* cf. *perminuta*, *N. phyllepta*, *Paralia sulcata*, *Rhaphoneis amphiceros*, *Thalassiosira decipiens* en *T. proschkinae*, en de epipsammische taxa *Achnanthidium delicatulum*, *A.* sp. 2, *Amphora* cf. *pediculus*, *A.* cf. *subacutiuscula*, *Biremis lucens*, *Catenula adhaerens*, *Cocconeis peltoides*, *Fragilaria* cf. *atomus*, *Navicula diserta*, *N.* sp. 1, *Nitzschia* cf. *frustulum*, *Opephora mutabilis*, *O. guenter-grassii* en *Pseudostaurosira perminuta*. Andere taxa zoals *Achnanthes amoena*, *Amphora* sp. 5, *A.* sp. 6 en *Navicula* sp. 7 waren alleen plaatselijk algemeen en eerder zeldzaam in de meeste stations. *Anorthoneis* spp. en *Fallacia cryptolyra* waren alleen codominant in stations die bestaan uit medium zand.

De bovenvermelde taxa blijken eveneens dominant te zijn in intertidale en subtidale benthische diatomeeëngemeenschappen in brakwatergebieden in Noordwest-Europa. Het is echter heel wat moeilijker om hun voorkomen en verspreiding buiten Europa in te schatten. Een groot aantal is ook aangetroffen in bv. Amerikaans, Afrikaans en Australaziatisch materiaal en schijnt dus kosmopoliet te zijn. Er moet echter rekening gehouden worden met het feit dat in de meeste gevallen een brede soortsopvatting (s.l.) gehanteerd werd; m.a.w. de meeste (of alle) infraspecifieke morfologische variatie werd genegeerd. Zoals reeds vermeld hebben recente studies aangetoond dat deze variatie aanzienlijk is en vaak ook discontinu; in een groot aantal gevallen is ze bijzonder subtiel. Een goed voorbeeld hiervan is *Biremis lucens*. Onze studie van deze soort heeft aangetoond dat binnen deze soort minstens 2 duidelijke morfologische vormen (morfotypes) aanwezig zijn; ze worden onderscheiden aan de hand van kleine maar consistente verschillen in de dichtheid van de striae en de afmetingen. Gedetailleerde ecologische analyses tonen bovendien aan dat er ook autecologische verschillen bestaan. Het interessante aan deze 2 morfotypes in biogeografisch opzicht is het feit dat ze allebei consistent onderscheiden kunnen worden in Europees materiaal (Nederland, Engeland en Polen) maar dat ze niet met zekerheid aanwezig zijn in niet-Europees materiaal uit Tanzanië, Papoea Nieuw-Guinea en Australië. Het lijkt ons daarom niet onwaarschijnlijk dat *Biremis lucens* geen kosmopoliete soort is die gekenmerkt wordt door een variabele morfologie, maar veeleer bestaat uit verschillende morfotypes die ofwel sympatrisch zijn en in ecologisch opzicht van elkaar verschillen (cf. de Europese morfotypes) ofwel allopatrisch (het Europese versus het niet-Europese materiaal). Verschillende andere gelijkaardige gevallen werden waargenomen tijdens deze studie (zowel in literatuurgegevens als in onze eigen data). Verder onderzoek is nodig om deze voorlopige bevindingen te bevestigen.

Het ecologisch gedeelte van deze studie handelt voornamelijk over de ruimtelijke en temporele dynamiek in de structuur van diatomeeëngemeenschappen. Multivariate technieken [Principal Components Analysis (PCA) and Redundancy Analysis (RDA)] werden gebruikt om (1) de ruimtelijke en temporele verspreidingspatronen van de intertidale benthische diatomeeëngemeenschappen van het Westerschelde-estuarium te kwantificeren ('variation partitioning') en te beschrijven (aan de hand van ordinatiediagrammen), en (2) ze te relateren aan de gemeten abiotische omgevingsfactoren. Daarnaast werden zuiver ruimtelijke structuren expliciet geïntroduceerd in de dataset (met behulp van de 'variation partitioning' benadering) om de ruimtelijk verschillen in gemeenschapsstructuur die niet in verband gebracht konden worden met de gemeten milieuvariabelen in rekening te brengen. Analoog hieraan werden ook zuiver temporele variabelen ingevoerd.

Verkennend onderzoek had duidelijk aangetoond dat er verschillende variatiepatronen bestonden in het epipelon en het epipsammon. Deze bevinding bevestigde ook vroegere waarnemingen in het kader van een studie naar de korte-termijn fluctuaties in coëxistente epipelische en epipsammische diatomeeënpopulaties (Sabbe 1993), waarbij werd aangetoond dat de schommelingen in de epipelische en epipsammische populaties onafhankelijk van elkaar optraden. We besloten daarom om beide categorieën gescheiden te analyseren. Daarnaast werd ook speciale aandacht besteed aan de relatie tussen de verschillende levensvormen binnen het epipsammon en epipelon [nl. adnate, gesteelde, kleine (< 10 µm) beweeglijke, beweeglijke tussen 10-20 µm, grote (> 20 µm) beweeglijke, tychoplanktonische en interstitiële vormen) en de gemeten milieuvariabelen.

Niettegenstaande het feit dat het belang van fysiognomische aspecten van benthische diatomeeëngemeenschappen algemeen erkend wordt, is nog slechts weinig gekend over de relatie tussen de verschillende levensvormen en het milieu, en over de implicaties van de specifieke fysiognomie van een gemeenschap en haar temporele en ruimtelijke dynamiek.

De RDA-analyse toonde aan dat gedurende de staalnameperiode de structuur van de intertidale benthische diatomeeëngemeenschappen van het Westerschelde-estuarium sterk gerelateerd was aan ruimtelijke gradiënten in sedimentsamenstelling (korrelgrootte en watergehalte), zoutgehalte en, in mindere mate, hoogteligging. Temporele patronen waren minder sterk uitgesproken dan ruimtelijke. De fysische verstoring van het sediment door getijde- en windwerking en bioturbatie blijkt dus de belangrijkste structurerende factor in intertidale benthische diatomeeëngemeenschappen te zijn. De wisselwerking tussen deze factoren aan plaatselijk verschillende intensiteiten en frequenties creëert een mozaïek van sedimenttypes, gaande van geëxposeerde grofkorrelige zandplaten tot erg slibrijke slikken.

Er bestaat een nauwe relatie tussen zowel epipelische celaantallen en gemeenschapsstructuur en de hoeveelheid slib in het sediment. Dichte epipelische gemeenschappen kunnen enkel voorkomen op relatief beschutte plaatsen, die gekenmerkt worden door een meer fijnkorrelige sedimentsamenstelling en slibaccumulatie; het slibgehalte kan dus gebruikt worden als een goede indicator voor de aanwezigheid van epipelische populaties. Deze relatie met het slibgehalte is het meest uitgesproken voor tychoplanktonische taxa zoals *Cymatosira belgica*, *Delphineis minutissima*, *Paralia sulcata*, *Thalassiosira decipiens* en *Navicula* cf. *perminuta*, wat suggereert dat deze diatomeeën zich eigenlijk als slibpartikels gedragen en dus onderhevig zijn aan dezelfde resuspensie- en afzettingsprocessen. De temporele dynamiek van de tychoplanktonische fractie is merkwaardig genoeg nogal onduidelijk (in vergelijking met die van de beweeglijke epipelische fractie, zie verder): sterke schommelingen in relatieve soortensamenstelling werden niet waargenomen, en toenames van celaantallen waren niet zo uitgesproken als bij beweeglijke epipelische diatomeeën.

Gemeenschappen van beweeglijke epipelische diatomeeën worden gekenmerkt door een typische voorjaarsbloei: celaantallen nemen toe aan het einde van de winter/begin van de lente (februari-maart) en bereiken maximale waarden aan het einde van de lente/begin van de zomer (mei-juni). In de zomer nemen de aantallen sterk af, gevolgd door een beperkte toename in de herfst. Gedurende de voorjaarsbloei treedt een duidelijke successie van soorten op. Het begin van de voorjaarsbloei valt samen met een stijging in temperatuur en straling. Beweeglijke epipelische diatomeeën kunnen actief migreren doorheen de bovenste mm's van het sediment. Bij eb, wanneer de lichtomstandigheden het meest gunstig zijn, vormen ze dichte matten aan het sedimentoppervlak. Bij vloed trekken ze zich in het sediment terug waardoor ze minder gemakkelijk in resuspensie gaan (zie echter verder). Deze levensstrategie heeft een aantal belangrijke ecologische implicaties, die voor een groot deel de ruimtelijk en temporele dynamiek van deze gemeenschappen bepaalt. Afgezien van de voor de hand liggende voordelen van deze actieve migratie, die deze diatomeeën in staat stelt om optimaal gebruik te maken van bv. betere lichtomstandigheden, heeft de vorming van dichte matten ook negatieve implicaties. Ten eerste kan tijdens perioden van hoge primaire productie plaatselijk een tekort aan nutriënten (vooral anorganische koolstof) optreden. Ten tweede verhoogt de dichte opeenstapeling van cellen de kans op interspecifieke competitie, wat verantwoordelijk zou kunnen zijn voor de duidelijke successie binnen deze gemeenschappen. Ten derde verhoogt de hoge concentratie van cellen in dunne verticale lagen de kans op efficiënte begrazing, vooral door 'deposit feeders', waarvan er een aantal (bv. *Corophium volutator*) bijzonder algemeen zijn in de sedimenten van de Westerschelde. Tenslotte maakt de concentratie van cellen in de bovenste mm's van het sediment de populaties gevoeliger voor resuspensie in sterk dynamische omstandigheden. Aangezien deze niet voorkwamen in de zomer van 1992 lijkt begrazing door macrofauna de meest plausible verklaring voor de sterke afname van de beweeglijke epipelische populaties gedurende de zomer.

?
cf. Li ?

De taxonomische structuur van de epipelische gemeenschappen wordt ook bepaald door het zoutgehalte. De verspreiding van een aanzienlijk aantal epipelische taxa is grotendeels beperkt tot de brakke (mesohaliene) zones van het estuarium (bv. *Navicula gregaria*, *N. phyllepta*, *N. flanatica*, *Parlibellus* sp. 2, etc.) terwijl andere soorten vooral in de poly- en euhaliene zones voorkomen (bv. *Brockmaniella brockmannii* en *Plagiogrammopsis vanheurckii*).

De hoogteligging in het intergetijdegebied heeft geen belangrijk structurerend effect op de epipelische diatomeeëngemeenschappen, of toch tenminste niet binnen het hoogtebereik waarin onze stations gelegen waren. Er blijkt echter wel een negatief verband te bestaan met de celaantallen. In de lagere delen van het intertidaal zou licht een limiterende factor kunnen zijn.

hoe diep?

Epipsammische diatomeeën zijn talrijker dan epipelische in een groot aantal stations in het Westerschelde-estuarium: de maximale celaantallen liggen in dezelfde grootte-orde als die van het epipelon. Een opvallend resultaat van deze studie is dat terwijl de epipsammische celaantallen duidelijk gecorreleerd zijn met de hoeveelheid erg fijn en vooral fijn zand in de sedimenten, er geen verband blijkt te zijn met het slibgehalte: epipsammische diatomeeën kunnen even talrijk zijn in een slibrijk als in een zandig sediment. Ze zullen echter alleen groeien in de aanwezigheid van slib als er een geschikt substraat aanwezig is, nl. voldoende grote zandkorrels. In dit opzicht wordt de relatie tussen het epipsammon en de fysische verstoring van het sediment niet in de eerste plaats bepaald door de stabiliteit van het sediment (zoals voor het epipelon) maar wel door de aanwezigheid van een geschikt substraat. De dichtheden, de taxonomische structuur en de fysiognomie van een epipsammische gemeenschap is echter wel sterk gerelateerd aan de expositiegraad van het sediment.

De structuur van epipsammische gemeenschappen is sterk gerelateerd aan de korrelgrootte van de sedimenten waarin ze voorkomen, wat op zich dan weer een indicatie is van de expositiegraad van het sediment. Niet alleen verandert de taxonomische samenstelling met de korrelgrootte, maar ook de fysiognomie van de gemeenschap blijkt opvallend nauw verbonden te zijn met deze factor. Zoals verwacht zijn gesteelde levensvormen (zoals *Fragilaria* cf. *atomus*, *Opephora guenter-grassii* en *O. mutabilis*) talrijker in fijn zandige en erg fijn zandige sedimenten, die minder geëxposeerd zijn en dus minder dynamisch dan medium zandige sedimenten. In deze laatste verhindert het tegen elkaar schuren van de zandkorrels de kolonisatie door gesteelde vormen. Adnate vormen, die met hun platte zijde stevig vastgehecht zijn aan het oppervlak van de zandkorrels en bovendien ook vooral beschutte microhabitats zoals spleten en valleien koloniseren, raken minder gemakkelijk los. Kleine (< 10 µm) beweeglijke vormen (zoals *Navicula* sp. 2, *N*. sp. 4 and most *Fallacia* spp.) zijn het talrijkst in medium zandige sedimenten; hun beweeglijkheid stelt hen in staat om beschutting te zoeken wanneer hun milieu te dynamisch wordt (bv. bij vloed), terwijl ze in kalmere omstandigheden (bij eb, maar ook op langere termijn tijdens periodes van gunstige weersomstandigheden) over het oppervlak van de zandkorrel kunnen migreren op zoek naar betere lichtomstandigheden of om overbevolking in de spleten tegen te gaan.

Met behulp van de multivariate analyses konden geen significante temporele patronen in de epipsammische dataset gedetecteerd worden. Een mogelijke verklaring voor dit fenomeen werd voorgesteld door Van den Hoek *et al.* (1979) die argumenteerden dat de continue omwoeling van zandige sedimenten biomassaschommelingen in epipsammische gemeenschappen maskeert. Er zou echter ook nog een tweede factor kunnen zijn die de trage toename van de celaantallen in epipsammische gemeenschappen verklaart, nl. competitie voor ruimte. Fijn zandige en erg fijn zandige sedimenten worden vaak gekenmerkt door het voorkomen van bijzonder dichte epipsammische gemeenschappen. Het is dan ook niet ondenkbaar dat gedurende langere periodes van gunstige weersomstandigheden de zandkorrels in de bovenste sedimentlagen overbevolkt raken en de groei van de populaties gelimiteerd wordt. De afwezigheid van sterke afnames in celaantallen kan aan verschillende factoren te wijten zijn. Ten eerste hebben verschillende studies aangetoond dat epipsammische diatomeeën gedurende lange tijd kunnen overleven in ongunstige omstandigheden (bv. wanneer ze begraven zijn in de donkere, en vaak ook anoxische, diepere lagen van het sediment). Ten tweede kan de afwezigheid van hevige stormen tijdens de staalnameperiode verantwoordelijk zijn voor het voortbestaan van dichte epipsammische populaties in de erg fijn zandige en fijn zandige sedimenten. Tenslotte is het mogelijk dat begrazing een minder belangrijke factor is in epipsammische dan in epipelische gemeenschappen.

Dezelfde aanpassingen die de epipsammische diatomeeën in staat stellen om langere periodes van begraving te overleven laten waarschijnlijk ook de coëxistentie met dichte epipelische populaties toe.

Alhoewel een belangrijk deel van de waargenomen variatie in de epipelische en epipsammische gemeenschappen (42.5 % en 30.5 % respectievelijk) gerelateerd kan worden aan schommelingen in de bovenvermelde milieuvariabelen (nl. sedimentsamenstelling, saliniteit en klimaatsfactoren), blijkt uit de resultaten van de ‘variance partitioning’ dat vooral in het epipsammon een aanzienlijk deel van de variatie (8.4 %) ruimtelijk gestructureerd is maar niet gerelateerd kan worden aan de gemeten sedimentkarakteristieken, saliniteit of hoogteligging. Deze zuiver ruimtelijke variatie zou verklaard kunnen worden door niet gemeten of onmeetbare milieufactoren, maar ook door andere factoren zoals 'contagious' biologische processen (bv. klonale populatie-aangroei) of infecties door bv. Chytridiomyceten, die plaatselijke volledige populaties kunnen uitroeien.

De hoge diversiteit in benthische diatomeeëngemeenschappen zou ook verklaard kunnen worden door de voortdurende fysische verstoring van de sedimenten, wat de diversiteitstoename veroorzaakt door het aantal organismen van iedere soort beperkt te houden en zodoende de intensiteit en het belang van interspecifieke competitie verlaagt. De belangrijkste verstoring in benthische diatomeeëngemeenschappen wordt veroorzaakt door wind- en getijdewerking. Gemeenschappen gedomineerd door epipsammische diatomeeën hebben doorgaans een hogere diversiteit en een lagere graad van dominantie dan die gedomineerd door epipelisch diatomeeën. Dit zou te wijten kunnen zijn aan het feit dat in dichte epipelische matten interspecifieke competitie, wat de diversiteit doet afnemen, een belangrijker fenomeen is. Sedimenten gedomineerd door epipsammische gemeenschappen zijn doorgaans ook gekenmerkt door een hogere graad van fysische verstoring, wat het optreden van sterke structurerende processen belemmert.

Afgezien van verstoringshypothese is er mogelijk ook een andere factor die de coëxistentie van een groot aantal epipsammische soorten bevordert, nl. de grote verscheidenheid aan microhabitats binnen een zandkorrel. Het voorkomen van duidelijke microspatiële verspreidingspatronen op een zandkorrel toont aan dat microhabitat heterogeniteit een belangrijke structurerende factor is in epipsammische gemeenschappen: de diversiteit aan microhabitats voor gespecializeerde taxa is hoger dan algemeen aangenomen.

Er is nog weinig gekend over de exacte levensstrategieën van benthische diatomeeën in estuariene en kustsedimenten. Zoals de resultaten van deze studie echter aantonen, heeft de specifieke samenstelling aan levensvormen van een benthische diatomeeëngemeenschap belangrijke ecologische implicaties: niet alleen beïnvloedt de levensvorm in belangrijke mate de reactie van een diatomee op veranderingen in het abiotische milieu, maar houdt hun specifieke levensstrategie ook een verschillend gedrag in tegenover allo- en autogene biologische processen.

Summary

The Westerschelde estuary, which comprises the meso-, poly- and euhaline reaches of the Schelde estuary, is a macro-tidal coastal plain estuary situated in the Southwest Netherlands; it takes a unique position amongst European estuaries because of the very long water residence time (resulting in a very stable salinity gradient) and the extremely high organic (and other) pollution. It is also characterized by the presence of extensive intertidal sand- and mudflats which in total comprise about 45 % of the total surface area of the estuary. The superficial sediments of these flats support dense benthic diatom populations, which play an important role in the production and mineralization processes in the sediments and in the estuarine ecosystem as a whole.

Intertidal benthic diatom communities are characterized by the presence of a multitude of life-forms, which can roughly be grouped into 2 main categories: the epipelon, which comprises the free-living fraction, and the epipsammon, which consists of taxa which live within the sphere of individual sand grains. Research on the epipsammon is still seriously hampered by methodological problems with the quantitative separation of the cells from the sediment and identification problems; therefore, systematic, ecological, but above all experimental and physiological studies have mainly focused on the epipelic fraction.

At the outset of the present study, virtually nothing was known about the composition and ecology of the intertidal benthic diatom communities of the Westerschelde estuary. In 1991, we therefore started an extensive study on the structural aspects, both taxonomic and ecological, of these communities. Throughout the study, special attention was paid to the systematics and ecology of the little-known epipsammic communities. The main aims of this study were to provide an answer to the following questions:

1. **Which taxa are present in the intertidal benthic diatom communities of the Westerschelde estuary?**
2. **Which communities can be distinguished, and what are their distributional patterns, both in space and time?**
3. **What are the relationships between the measured abiotic factors and the observed patterns and to what extent can these be generalized to the whole benthic diatom community?**
4. **Which hypotheses can be generated from a detailed multivariate analysis of the spatial and temporal distribution patterns of the communities in relation to estuarine benthic diatom ecology and population dynamics?**

During the period October 1991-October 1992, sediment samples (upper 10 mm) were taken at monthly intervals in 32 sampling stations along 11 intertidal transects, covering the entire range in salinity and sediment type in the Westerschelde estuary. These samples were used for diatom analysis (identification and quantitative cell counts) and physical and chemical analyses of the sediment and interstitial water.

A large part of this study has been devoted to a detailed **systematic account** of the observed diatom flora (chapter 4). Most taxa were studied using light microscopy and scanning electron microscopy. Detailed morphometric analyses were performed on selected taxa. When necessary, type material and material from other (including non-European) localities were studied in order to check the identity of some taxa. On numerous occasions, live and fixed (non-oxidized) material was studied in order to document plastid structure and to obtain detailed information on micro-habitat occupation. Autecological information on most taxa was drawn from the ecological analyses (see below) and

incorporated into the systematic account. This information includes data on their seasonal dynamics and their occurrence along gradients of salinity and sediment grain size.

In total, 316 diatom taxa (species and infraspecific taxa) were observed (Table 18). Most of these are illustrated in the Part 2 (Plates) of this study. Special care was taken to fully represent the morphological variability of problematic taxa.

While 223 taxa could be identified to species (or infraspecific) level, we were not able to determine the identity of 93 taxa (about 29 % of all taxa). Twenty-five taxa from the latter group have been provisionally assigned to a known species; they are indicated by the abbreviation 'cf.' in the binomial. This group mainly comprises taxa that closely resemble species whose taxonomic or autecological identity is as yet uncertain or unknown. In addition, 63 taxa could not be unambiguously identified; these have been given a serial number in the genus we believe they belong to. This group includes species and probably also genera which are most likely to be new to science (e.g. *Fallacia* sp. 3 and 4, *Lunella* sp. 1, Incertae sedis sp. 1) but also many taxa which are common and widespread but which we suspect have consistently been given the wrong name in floristic studies (e.g. *Achnanthidium* sp. 2 which in brackish areas is almost without exception identified as *Achnanthes lemmermannii*, a freshwater species).

Eight new nomenclatural combinations are proposed, four of which have already been published, viz. *Biremis lucens* (Sabbe *et al.* 1995), *Opephora guenter-grassii*, *O. mutabilis* and *Pseudostaurosira perminuta* (Sabbe & Vyverman 1995). Four others (*Plagiogrammopsis minimum*, *P. sigmoideum*, *Tryblionella levidensis* var. *salinarum*, *T. parvula*) have been provisionally introduced and await formal publication.

Identification problems in contemporary systematics of brackish-water diatoms mainly relate to the following three factors:

1. problems related to the interpretation of morphological variation patterns, and more specifically in relation to the occurrence of cryptodiversity in diatoms;
2. problems related to the lack of specialized brackish-water floras and the widespread use of European identification works in other continents, which both lead to force-fitting of taxa;
3. nomenclatural and taxonomic problems related to recent developments in diatom systematics.

Diatom frustule morphology can change under differing environmental conditions. For example, diatoms invading brackish-water environments often exhibit a high morphological plasticity along the salinity gradient. In addition, however, recent detailed morphometric studies have shown that (often subtle) morphological discontinuities in shape, size and ultrastructural features exist within several diatom species. This cryptic diversity often appears to be correlated with ecological differences; in a number of cases, it has been shown to have a genetic basis. The consistent recognition of this phenomenon is important, not only for systematic and phylogenetic research on diatoms, but also for the the numerous applications of diatom taxonomy, such as water quality assessment, biogeography, palaeo-ecology and geology.

Identification problems in estuarine diatoms are also caused by the lack of specialized brackish-water floras. As a consequence many brackish-water diatoms have been force-fitted into marine or freshwater taxa. In addition, the widespread use of European floras in other continents obscures much hidden diversity.

Given these problems, the correct description and interpretation of the observed morphological variation patterns is of paramount importance for future reference. In this study, we have therefore provided original, unambiguous descriptions of most taxa observed, with special attention for common and/or difficult taxa (such as representatives of the genera *Anorthoneis*, *Opephora*, *Amphora, Fragilaria* s.l. and *Navicula* s.l.) and species complexes (e.g. the *Amphora coffeaeformis/A. acutiuscula*, the *Navicula perminuta* and the *Navicula apiculata* clusters).

The introduction of a profoundly revised diatom classification system by Round *et al.* (1990) has important nomenclatural implications. In addition, the justified but not always universally accepted split of numerous 'old' genera is responsible the present double identity of some, mainly large, genera (e.g. *Fragilaria, Navicula*). Both necessitate thorough (and hence time-consuming) literature searches in order to retrieve all relevant information.

Although the total number of diatom taxa observed in the Westerschelde estuary during the sampling period amounts to 316, only a limited number of taxa dominated the various diatom communities at the 32 sampling stations. These taxa are listed in Table 41. Most of these are common in many stations, such as the epipelic taxa *Cymatosira belgica, Delphineis minutissima, N. arenaria* var. *rostellata, N. flanatica, N. gregaria, Navicula* cf. *perminuta, N. phyllepta, Paralia sulcata, Rhaphoneis amphiceros, Thalassiosira decipiens* and *T. proschkinae*, and the epipsammic taxa *Achnanthidium delicatulum, A.* sp. 2, *Amphora* cf. *pediculus, A.* cf. *subacutiuscula, Biremis lucens, Catenula adhaerens, Cocconeis peltoides, Fragilaria* cf. *atomus, Navicula diserta, N.* sp. 1, *Nitzschia* cf. *frustulum, Opephora mutabilis, O. guenter-grassii* and *Pseudostaurosira perminuta*. Others (such as *Achnanthes amoena, Amphora* sp. 5, *A.* sp. 6 and *Navicula* sp. 7) were only locally abundant and were rare in the majority of stations. *Anorthoneis* spp. and *Fallacia cryptolyra* were codominant in medium sandy stations only.

The above-mentioned taxa are also often reported as dominant constituents of intertidal and also subtidal brackish-water benthic diatom communities in areas throughout North-West Europe. However, it is more difficult to assess their occurrence and distribution outside Europe. Many are also present in e.g. American, African and Australasian material and thus appear to be cosmopolitan. However, in most cases the species have been interpreted in their broadest sense (s.l.), i.e. ignoring most if not all morphological variation within the taxon. As already mentioned, recent studies have shown that this variation can be considerable and is often discontinuous; in many cases it is very subtle. A good example in this respect is *Biremis lucens*. Our studies have shown that within this species at least two distinct morphological forms can be distinguished; they are characterized by small but distinct differences in stria density and size. Detailed ecological analyses revealed additional differences in their autecological requirements. However, the interesting fact from a biogeographical point of view is that the two morphotypes which were consistently present in the European material (from The Netherlands, England and Poland), could not be found with certainty in non-European material from Tanzania, Papua New Guinea and Australia. In our opinion, it is therefore not unconceivable that *Biremis lucens* is not a cosmopolitan species with variable morphology, but instead consists of different morphotypes which are sympatric and have different ecological requirements (cf. the European morphotypes) or are allopatric (the European versus the non-European material). During this study, we encountered (both in our own material and in data drawn from the literature) other similar cases. However, further study is necessary to confirm our preliminary findings.

The **ecological part** of this study mainly focuses on the spatial and seasonal structural dynamics of the diatom communities. We used multivariate tecniques (Principal Components Analysis and Redundancy Analysis) to (1) quantify (variation partitioning) and describe (ordination diagrams) the spatial and seasonal distribution patterns of the benthic diatom communities of the Westerschelde estuary, and (2) relate them to the measured abiotic environment. In addition, we explicitly introduced purely spatial structures into our data set (using the variation partitioning approach) to account for all the spatial differences in community structure between the stations that could not be accounted for by the measured variables. By analogy, purely temporal variables were introduced as well.

Preliminary analyses clearly indicated that different variations patterns existed in the epipelon and epipsammon. This finding also confirmed earlier observations made in the framework of a study on the short-term temporal fluctuations in co-existing populations of epipelic and epipsammic diatoms (Sabbe 1993), where it was found that the fluctuations in epipsammic and epipelic populations occurred independently from one another. We therefore decided to run separate analyses on the two main life-form groupings, viz. the epipelic and the epipsammic species groups. In addition, special attention was paid to the relationship between between the various life-forms *within* the epipsammon and the epipelon (viz. adnate, stalked, motile < 10 µm, motile 10-20 µm, motile > 20 µm, tychoplanktonic and interstitial) and the measured environmental parameters. Although the importance of physiognomic aspects of benthic diatom communities is widely recognized, only little is known about the relationship between the various life-forms with the environment, and the implications of community physiognomy for the spatial and temporal dynamics of these communities.

Redundancy analysis indicated that during the sampling period the structure of the benthic diatom communities of the Westerschelde estuary was strongly related to **spatial gradients** in ***sediment composition*** (grain size composition and water content), ***salinity*** and, to a lesser degree, ***elevation*****.** **Temporal patterns** were clearly subordinate to spatial ones. The primary structuring factor in intertidal benthic diatom communities thus appears to be the **physical disturbance of the sediment** caused by tidal currents, wind-induced waves and bioturbation. The interplay of these factors at locally varying frequencies and intensities creates a mosaic of sediment types, ranging from exposed, coarse to medium sandy flats to extremely silty mudflats.

An intricate relationship exists between both epipelic cell numbers and community structure and the amount of **silt** in the sediment. Dense epipelic communities can only develop in relatively sheltered places, which are characterized by finer average grain size and silt accumulation; silt content therefore is a good indicator of the degree of exposure of a sediment and can be used as a predictor for the presence of epipelic populations. The relationship with silt is strongest for tychoplanktonic taxa such as *Cymatosira belgica*, *Delphineis minutissima*, *Paralia sulcata*, *Thalassiosira decipiens* and *Navicula* cf. *perminuta*, which suggests that they might actually behave as silt particles and are subject to the same processes of resuspension and deposition. Remarkably, their temporal dynamics are rather obscure (in comparison with those of the motile epipelic fraction, cf. below): no strong changes in relative species composition occur, and increases in cell numbers are not as pronounced as in the motile epipelic fraction.

Motile epipelic communities in the Schelde estuary are characterized by a typical spring bloom: cell numbers increase in late winter-early spring (February-March) and reach maximum values in late spring-early summer (May-June). In summer, the populations collapse, followed by a slight increase in autumn. A distinct succession of different species occurs during the spring bloom. The onset of the spring bloom coincides with both increasing **temperature and irradiance**. Motile epipelic forms are capable of active migration through the upper mm's of the sediment. At low tide, when light conditions are most favourable, they aggregate near the sediment surface and form dense mats. At high tide, they retreat into the sediment and are thus better protected against resuspension. This life strategy has some important ecological implications, which largely determine the temporal but also the spatial dynamics of these diatoms. Apart from the obvious advantages of active motility, which enables these species to take maximal advantage of increases in e.g. irradiance, the formation of dense mats also has negative implications. First, periods of high primary production can cause nutrients (mainly inorganic C) to become locally limiting. Second, the dense accumulation of cells increases the occurrence of competitive interactions, which could cause the distinct seasonal succession events in these communities. Third, the concentration of cells in narrow vertical layers makes them more susceptible for grazing, especially by deposit feeders, some of which (e.g. *Corophium volutator*) are very abundant in the intertidal Westerschelde sediments. Finally, the concentration of cells in the upper mm's of the sediments makes them more sensitive to strong resuspension events. As the latter did not occur during summer 1992, grazing by macrofauna seems to be the most plausible cause for the summer decline of motile epipelic populations.

The taxonomic structure of the epipelic diatom communities also shows an unequivocal relationship with **salinity**. The distribution of a considerable number of epipelic taxa is largely restricted to the brackish (mesohaline) reaches of the estuary (e.g. *Navicula gregaria*, *N. phyllepta*, *N. flanatica*, *Parlibellus* sp. 2, etc.) while others are predominantly found in the poly- and euhaline reaches (e.g. *Brockmaniella brockmannii*, *Plagiogrammopsis vanheurckii* and others).

Elevation does not have an important structuring influence on the epipelic diatom communities, at least not within the intertidal elevation range sampled during this study. However, there does appear to be a negative relationship with cell abundance. In the lower intertidal zone, light might be limiting diatom growth.

Epipsammic diatoms are numerically dominant in many stations in the Westerschelde estuary: maximal cell numbers are in the same order of magnitude as those of the epipelon. A striking result of this study is that while epipsammic cell abundance is correlated to the amount of very fine sand and especially fine sand in the sediments, it is not correlated to silt content: epipsammic cell numbers can be as high in silty as in sandy sediments. However, epipsammic diatom communities will only develop in the presence of silt when a suitable substrate for growth is present, i.e. sufficiently large sand grains. In this respect the relationship between the *occurrence* of epipsammic communities and physical sediment disturbance does not primarily concern the stability of the sediment (as for the epipelon) but the availability of a substrate. However, the *density, taxonomic structure and physiognomy* of an epipsammic community is closely related to the degree of exposure of a sediment.

The structure of epipsammic communities is predominantly related to the specific grain size composition of the sediments in which they occur, which itself is an indicator of the **degree of exposure** of the sediments. Not only does the taxonomic composition change with grain size, but there also appears to be a striking relationship with the physiognomy of the communities. As expected, stalked forms (e.g. *Fragilaria* cf. *atomus*, *Opephora guenter-grassii* and *O. mutabilis*) are more abundant in fine sandy and very fine sandy sediments, which are less exposed and hence less dynamic than medium sandy sediments. In the latter sediments, intensive abrasion prevents stalked forms from colonizing the sand grains. Adnate forms, which tightly adhere to the sand grain surface and also preferentially colonize sheltered microhabitats such as crevices and valleys, are less easily abraded. Small (< 10 µm) motile forms (such as e.g. *Navicula* sp. 2, *N.* sp. 4 and most *Fallacia* spp.) are most abundant in medium sandy sediments; their motility might enable them to go for shelter (in crevices) when circumstances are most dynamic (e.g. at high tide), while in calmer periods (low tide, or on the longer term: prolonged periods of better weather conditions), they can migrate across the sand grain surface in search of optimal light conditions or to avoid crowding in the crevices.

The multivariate analyses were unable to detect any significant **temporal patterns** in the epipsammic data set. A possible explanation for this phenomenon was put forward by Van den Hoek *et al.* (1979) who argued that the constant reworking of sandy sediments would mask biomass fluctuations in epipsammic communities. However, there could also be a second factor contributing to the generally slow increase in overall epipsammic cell numbers in sandy sediments, viz. competition for space. Indeed, very fine and fine sandy sediments often support extremely dense epipsammic communities. It is therefore not unconceivable that during prolonged periods of favourable weather conditions the sand grains in the upper layers soon become too crowded and growth is limited. The absence of sharp decreases in cell numbers might be attributed to different factors. First, various studies have shown that many epipsammic diatoms can survive a long time under adverse conditions (prolonged periods of burial in dark, sometimes even anoxic, deeper sediment layers). Second, the absence of severe storms during the sampling period might be responsible for the persistence of dense epipsammic diatoms communities in the very fine and fine sandy sediments. Third, it might be that grazing on epipsammic communities is less important than in epipelic communities.

The same adaptations which allow epipsammic diatoms to survive burial in deeper sediment layers probably also allows them to co-oexist with dense epipelic populations in silty sediments.

Although a considerable part of the observed variation in epipelic and epipsammic diatom communities (42.5 % and 30.5 % respectively) can be related to changes in the above-mentioned environmental factors (viz. sediment composition, salinity and climatic factors), variation partitioning indicates that especially in the epipsammon there still is a considerable part of the variation (8.4 %) which is spatially structured but can not be related to the measured sediment characteristics, salinity or elevation. This purely spatial variation could be caused by overlooked or unmeasurable environmental variables, but also by other, mainly biotic processes such as contagious biological processes (e.g. clonal population expansion) or infections by e.g. chytrids, which can locally wipe out entire populations.

The high **diversity** in benthic diatom communities might also be caused by the constant **physical disturbance** of the sediments, which promotes species diversity by keeping the number of organisms of each species low and thus reducing the intensity and importance of direct interspecific competition for resources. The most important disturbing factors for benthic diatom communities in intertidal sediments are the wind- and tide-induced sediment disturbance. Communities dominated by epipsammic diatoms are usually more diverse and have a lower dominance than those dominated by epipelic ones. This could be due to the fact that in dense epipelic mats interspecific competition, which is known to reduce diversity, can be high. Sediments dominated by epipsammic diatoms are usually characterized by stronger physical disturbance, which prevents the occurrence of strong organizing processes.

Apart from the disturbance hypothesis, there might be another factor which could promote the co-occurrence of a high number of epipsammic species at any one station, namely **microhabitat heterogeneity**. The existence of distinct micro-spatial distribution patterns within single sand grains indicates that microhabitat heterogeneity is important in structuring epipsammic diatom communities and hence that the number of distinct habitats available for colonization by specialized taxa is higher than generally assumed.

Little is known about the exact life strategies of benthic diatom species in estuarine (and coastal) sediments. However, as the results of this study reveal, the specific life form composition of a benthic diatom community has important ecological implications: not only do different life forms react in a different way to changing conditions in the abiotic environment, but their specific life strategies might also involve different behaviour when confronted with various allo- and autogenic biological constraints.

1. Introduction

1.1. General introduction and aims

Macro-tidal estuaries such as the Westerschelde, a heavily polluted and eutrophicated estuary in the Southwest Netherlands, are often characterized by the presence of extensive intertidal sand- and mudflats. The superficial sediments of these flats usually support dense (cyano)bacterial and protist populations, which play an important role in the production and mineralization processes in the sediments and in the estuarine ecosystem as a whole (Heip *et al.* 1995). The protist communities mainly consist of micro-algae, flagellates and ciliates. Although micro-algae are usually considered to be photoautotrophic, little is known about their full nutritional capacities. Organotrophy and phagotrophy have been shown to be important ways of acquiring the elements necessary for growth in many micro-algal species (Nygaard & Tobiesen 1993, Nilsson 1995, Skovgaard 1996).

Diatoms (Bacillariophyta) are a dominant component of sediment-inhabiting protist communities in estuarine and marine environments (cf. Admiraal 1984, Cariou-Le Gall & Blanchard 1995).

The taxonomy of many estuarine diatoms, both benthic and planktonic, is only little known. This is partly due to shortage of specialized literature on diatoms from brackish waters. Most existing taxonomic information is scattered and often confusing. In addition, the epipsammic diatom fraction has been largely overlooked (ignored?) due to their small size and often inconspicuous life-form [i.e. in close association with individual sediment particles (see below)].

The taxonomy of estuarine species has long been plagued by force-fitting of taxa to existing freshwater and marine species. For example, *Cyclotella choctawhatcheeana*, a brackish-water planktonic diatom, was recently described from a lagoon in Florida (*Prasad et al.* 1990). Since its description, it has been reported from estuaries and saline lakes worldwide and now appears to be one of the most common estuarine *Cyclotella* species in many areas (cf. Håkansson *et al.* 1993). Before it was usually identified as *C. caspia* or *C. meneghiniana*. Other examples include taxa which are usually identified as *Amphora pediculus*, *A. copulata*, *Achnanthes lemmermannii* and many more. It goes without saying that the general lack of taxonomic information on estuarine diatoms jeopardizes the reliability of published ecological and biogeographical information (cf. Wood & Leatham 1992).

Force-fitting also has the disadvantage that it inevitably leads to the overestimation of the range of morphological variability of species. This leads to lumping of taxa which in its turn leads to a loss of ecological information.

The benthic* diatom community is usually divided in two major components, viz. the epipelon which consists of the free-living diatoms and the epipsammon which comprises the diatoms that live attached to the substratum (i.c. sand grains). The epipelon consists of larger, highly motile species, while the epipsammic diatoms are usually small, immobile or only slowly moving (Round *et al.* 1990). The distinction between both groups is, as expected, not clearcut, and this has prompted some authors to contest the use of these terms (De Jonge 1985). However, as will be shown in this study, both terms are still useful in ecological research if slightly redefined.

The epipelon can easily be separated from the sediment by suspension. In addition, the

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* Note that the term benthic diatoms here in the introduction does not include the tychoplanktonic component, while throughout the present study we have included this component with the epipelon (see chapter 2 for remarks on terminology).

development of the lens-tissue technique (by Eaton & Moss 1966), which allows to separate a large part of the live epipelon from the sediments, has strongly favoured research on epipelic communities over epipsammic ones. Despite the fact that epipsammic diatoms are often numerically dominant in estuarine sediments (Riznyk 1973, Rao & Lewin 1976, Witkowski 1991, Sabbe 1993, Nilsson 1995) and have even been shown to constitute an important part of benthic diatom biomass (Cadée & Hegeman 1974, Sundbäck 1983, Asmus & Bauerfeind 1994), very little is known about their ecology.

The patchy distribution of intertidal benthic diatom assemblages at different scales has long been recognized (e.g. Hustedt 1939, Brockmann 1950, Round 1960), although some studies indicated that in certain environments the diatom communities were strikingly homogeneous (e.g. Amspoker 1977). Numerous studies have since been made on the spatial and seasonal distribution of estuarine diatom assemblages, predominantly in European and North American estuaries. However, as already mentioned most of these studies are restricted to the epipelic diatom fraction (e.g. Riaux 1983, Admiraal *et al.* 1984, Sullivan & Moncreiff 1988, Oppenheim 1991, Underwood 1994).

By relating the distribution of the diatom assemblages to measured environmental variables, a procedure which was much aided by the strongly increased use of multivariate methods during the last two decades, possible explanations for the observed patterns are sought (e.g. Van Tongeren *et al.* 1992, Douglas & Smol 1995). The spatial distribution of estuarine diatom assemblages has thus been related to gradients in sediment grain size (e.g. Amspoker & McIntyre 1978, Oh & Koh 1995), salinity, organic matter (e.g. Witkowski 1991), intertidal elevation (e.g. Sullivan 1982, Hemphill 1995), etc. Seasonality has been attributed to changes in climatic factors such as temperature, light climate and intensity (e.g. Admiraal & Peletier 1980, Sabbe 1993), and grazing pressure (e.g. Taasen & Høisæter 1981, Peletier 1996). However, few studies are as yet available which attempt to explain the observed patterns with the aid of experiments (see review of Admiraal 1984 and references therein, Sundbäck *et al.* 1996 and references therein).

The spatial and temporal structuring of biological communities is usually interpreted in terms of two major classic ecological models: the environmental control model and the biological control model. The environmental control model assumes that the biological processes are mainly regulated by the abiotic environment (e.g. salinity, availability of food resources), while according to the biological control model biological interactions such as predation and competition are the main structuring forces in biological communities. However, it is becoming increasingly clear that both groups of controlling factors may contribute to structuring the communities, and that their relative importance can vary with time and scale (Borcard & Legendre 1994, Pinel-Alloul *et al.* 1995). It is now also recognized that other factors, which are not included in the above-mentioned models, can play an important role. Examples of such factors are historical events and disturbances of various kinds (including anthropogenic ones).

In assessing what factors influence the structure of communities, it is possible to quantify what part of the variance in the biological data can be related to measured environmental variables. However, one then assumes that most ecologically important factors have been included in the analysis. In reality, important environmental factors may have been overlooked (or cannot be measured for various reasons). In addition, it is almost impossible to measure the importance of biotic processes such as competition or behavioural responses to chemical cues (cf. Hansson 1996). However, if one assumes that these unmeasured factors have a spatially structuring influence on biological communities, it is possible to get an idea of their importance by explicitly including purely spatial structures in the ecological analyses (cf. Legendre 1993). With the aid of the recently introduced variance partitioning technique (Borcard *et al.* 1992), it is possible to partition the variation in the species data into independent components: pure spatial, pure environmental, spatially structured environmental and unexplained. By analogy with the spatial structure of biological communities, it is possible to include purely temporal variables. This allows to assess the potential role of other factors than the seasonal changes in the measured abiotic parameters in the temporal dynamics of biological communities.

The paucity of data on the composition and ecology of the benthic diatom flora of the Westerschelde estuary (cf. chapter 1.3) prompted the present study. A preliminary analysis of the composition and spatial distributional patterns of the benthic diatom communities of the Westerschelde estuary (Sabbe 1990, Sabbe & Vyverman 1991) revealed that (1) distinct patterns existed in the distribution of these communities and (2) that the systematics of these estuarine diatoms are incompletely known. The results of this study also hinted at the quantitative importance of the epipsammic diatom community in the Westerschelde estuary.

In 1991, we started an extensive study on the structural aspects, both taxonomic and ecological, of the benthic diatom communities of the Westerschelde estuary, with the emphasis on the little-known epipsammic diatom communities.

A large part of this study has been devoted to a detailed systematic account of the observed diatom flora. Most taxa were studied using advanced light microscopy and scanning electron microscopy. Detailed morphometric analyses were performed on selected taxa. When necessary, type material and material from other (including non-European) localities was studied in order to check the identity of some taxa. On numerous occasions, live and fixed (non-oxidized) material was studied in order to document plastid structure and to obtain detailed information on micro-habitat occupation.

Special attention was paid to common and widespread problematic taxa (such as representatives of the genera *Anorthoneis*, *Opephora*, *Amphora*, *Fragilaria* s.l. and *Navicula* s.l.) and species complexes (e.g. the *Amphora coffeaeformis*/*A. acutiuscula*, the *Navicula perminuta* and the *Navicula apiculata* clusters).

Detailed autecological information on most taxa was drawn from the ecological analyses (see below) and incorporated into the systematic account. This information includes data on their seasonal dynamics and their occurrence along gradients of salinity and sediment grain size.

The ecological part of this study mainly focuses on the spatial and seasonal structural dynamics of the diatom communities. Apart from a description of these communities and their distributional patterns, an attempt is made to assess what factors control their structuring. In this respect, we opted for quantitative (i.e. absolute) and not semi-quantitative (i.e. relative) cell counts as the latter can seriously distort ecological information (Thomas 1979). Notwithstanding the fact that biomass measurements derived from pigment (mainly chlorophyll *a*) analyses are much less time-consuming, these data do not allow for much resolution from a structural point of view (Cariou-Le Gall & Blanchard 1995).

We tried to describe the spatial and temporal structure of the diatom communities as completely as possible by entering purely spatial and temporal structures. We then assessed which part of this structure could be related to the measured environmental parameters and which part could not; the latter part then allowed to construct hypotheses and recommendations for future research.

In summary, the main research questions addressed in this study can be formulated as follows:

1. Which taxa are the intertidal benthic diatom communities of the Westerschelde estuary composed of?
2. Which communities can be distinguished, and what are their distributional patterns, both in space

and time?
3. What are the relationships between the measured abiotic factors and the observed patterns and to what extent can these be generalized to the whole benthic diatom community?
4. What hypotheses can be generated from a detailed multivariate analysis of the spatial and temporal distribution patterns of the communities in relation to estuarine benthic diatom ecology and population dynamics?

1.2. The Westerschelde estuary

1.2.1. General characteristics

1.2.1.1. Morphology

The River Schelde has its source in St-Quentin (North France) and discharges into the North Sea near Vlissingen (The Netherlands) after 355 km. Its catchment basin is about 19500 km². The tidal part of the Schelde [between Gent (Belgium), where the tidal regime is stopped by a sluice complex, and Vlissingen, about 160 km] constitutes a typical coastal plain estuary which runs through North Belgium (Flanders) and the Southwest Netherlands (Zeeland). It consists of two parts: the Belgian part, the Zeeschelde, which roughly comprises the freshwater tidal and oligohaline reaches, and the Dutch part, the Westerschelde, which consists of the meso-, poly- and euhaline zones of the estuary.

The present morphology of the estuary was largely formed during the Dunkirk III transgression (between 1000 and 1200 A.D.) as part of a larger estuarine area in the Southwest Netherlands. Only in the 16th century the Westerschelde became an important navigation channel. Since then, its course has been stabilized by different regulation works (dike construction, land reclamation) and dredging activities. More details on the origin and morphological evolution of the Schelde estuary can be found in Coen (1988).

Nowadays the Westerschelde estuary consists of a complex and dynamic system of flood and ebb channels and large intertidal areas (saltmarshes, mud and sand flats and shoals). In the major part of the estuary there are two parallel channels separated by shoals. The total supra- and intertidal area amounts to 13.756 ha (10.581 ha intertidal mud and sand flats, 3.175 ha inter- and supratidal saltmarshes), which is about 45 % of the total surface area of the Westerschelde estuary (Meire *et al.* 1995). The percentage intertidal area gradually increases from the mouth to the inner estuary.

1.2.1.2. Hydrology

The average discharge into the Westerschelde estuary is about 100 m³/s. Seasonal fluctuations in discharge are usually large, with high values in winter (on average 180 m³/s with peak discharges up to 600 m³/s) and low values in summer (on average 50 m³/s, with minimal values of 10 m³/s in dry periods, Ysebaert *et al.* 1993). However, as the Schelde is a typical ‘rain river’, large inter- and intra-annual fluctuations can occur as well, depending on precipitation.

The Schelde estuary is a macrotidal estuary. In the Westerschelde, the tidal range lies between 4 m (near the mouth) and 5 m (near the Dutch-Belgian border). During each tidal cycle, 50.000 m³/s water enters and leaves (augmented with the river discharge) the estuary near its mouth in Vlissingen. As the river discharge is very low compared to the total tidal prism, the residence time of water in the Westerschelde estuary is very long (up to 75 days, Heip 1989, Soetaert & Herman 1995), which is high compared to some other European tidal estuaries such as the Elbe and Gironde (Brockmann 1992, Castel 1992).

Most of the Westerschelde estuary is completely mixed; only in the eastern part (upstream of Baalhoek) mixing is only partial and small horizontal and vertical gradients (in salinity, suspended matter, nutrients) exist (Heip 1989, Herman & Heip 1996).

1.2.1.3. Water column characteristics

Due to the long water residence time in the estuary, the dilution of seawater is gradual. This results in a rather stable (both in space and time) and very gradual salinity gradient. The main salinity zones are shown in Fig. 1: salinity in the Westerschelde estuary roughly ranges between 33 ‰ (at the mouth) and 10 ‰ (at the Dutch-Belgian border). During one tidal cycle, the salinity zones remain more or less in the same position. The largest fluctuations occur in the easternmost part of the Westerschelde, between Bath and Zandvliet, where the salinity gradient is steepest. Long-term changes in salinity, caused by fluctuating river discharges, can also occur. They are most pronounced in the oligohaline and freshwater tidal ranges. For example, during the warm and dry summer of 1994, salinity values increased to about 18 ‰ in the eastern part of the Westerschelde, while in the winters of 1993/94 and 1994/95 salinity was only about ± 3 ‰ (Meire *et al.* 1995).

The Westerschelde estuary receives a large amount of particulate matter (clay and silt), both from the sea (0.6 x 10^6 tonnes/year) and from the river (about 0.7-1.0 x 10^6 tonnes/year, Oenema *et al.* 1988 and references therein). Fine material of continental origin (and associated pollutants, cf. Heip 1989) mainly settles in the eastern part of the Westerschelde estuary (especially in the Land van Saeftinghe saltmarsh, Van Eck 1991, Van Maldegem *et al.* 1993), while a large part of the marine sediments are deposited in the western part of the Westerschelde. A turbidity maximum, which moves up and down with the tides, resides in the upper reaches of the Schelde estuary (salinity < 5 ‰). However, in some years this zone is not distinct. More detailed information on biogeochemical processes in this zone are given by Herman & Heip (1996). The high load of particulate matter has major consequences for the underwater light climate and hence also for phytoplankton (and microphytobenthos) production and population dynamics (see below).

The Westerschelde estuary runs through one of the most densily populated and industrialized regions of Europe and is heavily polluted due to the discharge of untreated wastes [e.g. about 100.000 tonnes of organic C per year, mainly of anthropogenic origin (Wollast 1988)] and toxic substances. The high organic loading causes near-anoxic conditions in the water column in the oligohaline and limnetic reaches of the Schelde estuary throughout the year, which strongly influences other biogeochemical processes (such as nutrient dynamics, grazing, etc. - see below).

Nutrient concentrations are naturally high in estuaries (McLusky 1989). In addition, the Schelde estuary receives a high load of nutrients and organic material from agricultural, urban and industrial sources, which causes nutrient concentrations to be higher than in other European estuaries (Boderie *et al.* 1993, Van Spaendonck *et al.* 1993). The biogeochemistry of nutrients is strongly affected by the longitudinal redox gradient present in the Schelde estuary. Denitrification occurs in the anoxic freshwater tidal and oligohaline reaches, followed by nitrification in the upper estuary (prior to oxygen regenaration). Most nitrogen is thus oxidized from ammonia to nitrate and than leaves the system to the sea. Nitrogen is mainly lost due to denitrification of nitrate to N_2 in the water column of the upper estuary, by burial (see below) and by uptake by phytoplankton in the lower estuary (although this uptake appears to be negligible in the total N budget, Soetaert & Herman, 1995). Phosphorus geochemistry is governed by both inorganic (possible coprecipitation with colloidal iron in summer, 'phosphate buffering' in winter) and biological processes (uptake by phytoplankton blooms). Dissolved silicate shows a more or less conservative behaviour in winter but is largely removed from the water column by spring and summer diatom blooms (Boderie *et al.* 1993). More information on nutrients and their biogeochemistry in the Schelde estuary can be found in Boderie *et al.* (1993), Kromkamp *et al.* (1995) and Soetaert & Herman (1995).

1.2.1.4. Sediment characteristics

Extensive inter- and supratidal areas are present in the Westerschelde estuary, about three quarters of which are intertidal sand and mud flats. Due to natural processes (currents, river discharge, tides and climatic events such as storms) and antropogenic activities (dregding, diking) the intertidal area is a very dynamic environment. Apart from seasonal variations in sediment characteristics (cf. this study), long-term morphological changes (e.g. position and elevation of flats) take place (Van Maldegem *et al.* 1993, Ruitenbeek 1995). A general trend in the Westerschelde estuary is the gradual elevation of saltmarshes in the eastern part of the Westerschelde (cf. Van Maldegem *et al.* 1993) due to sedimentation of (polluted) fluvial particulate matter.

The Westerschelde subtidal sediments mainly consist of fine sand (125-250 μm)(Claessens 1988). In the intertidal area however, the exact grain size composition can vary considerably depending on local hydrodynamic conditions (De Jong & De Jonge, 1995; this study). Fig. 2 (after Van Maldegem *et al.* 1993) shows the percentage of mud (particles < 63 μm) in the inter- and subtidal areas of the Westerschelde. Especially in the saltmarshes and in sheltered places along the banks of the estuary, sediments can be very muddy. The shoals are usually less muddy, although locally high percentages of mud can be found (this study). In chapter 5.1.3., the sediment composition along the studied transects is discussed in detail.

Intertidal sediments are a significant component in the carbon and nitrogen cycles in estuaries: intense biogeochemical processes take place both in the oxygenated upper and in the anaerobic deeper layers. First-order estimates for the Schelde estuary indicate that they may account for about 14 % and 30 % of the total estuarine loss of nitrogen and carbon, respectively (Middelburg *et al.* 1995). Due to the accumulation and mineralization of organic matter in shallow-water sediments, nutrients in interstitial water of both sub- and intertidal areas are always higher than in the water column (De Pauw 1975 and references therein, Nienhuis 1993).

1.2.1.5. Ecology

The Westerschelde is an extremely heterotrophic system: 80 % of the carbon respired is imported into the system, mainly from the freshwater tidal reaches, the river Schelde and its tributaries. There is also some import of organic matter from the sea. In comparison, locally produced organic carbon (less than 20 %) is relatively unimportant (Heip & Herman 1995).

Due to the high input of organic matter (waste water) from the Schelde basin, heterotrophic bacterial production rates in the upper reaches of the Schelde are extremely high (amongst the highest values reported in the literature!, cf Goosen *et al.* 1995). Throughout the year, bacterial growth and respiration cause oxygen depletion in the water column in the Zeeschelde and the easternmost part of the Westerschelde, which has major consequences for higher trophic levels (Hamerlynck *et al.* 1993). Whether these bacteria are intensily grazed upon by heterotrophic protists is still unclear, although preliminary results based on the comparison of bacterial growth rates and residence time and the presence of high numbers of the latter protists (Goosen *et al.* 1995) suggest that microbial food interactions might be an important constituent of the estuarine food web.

According to model estimates, net primary production in the water column is severely light-limited and even impossible in the eastern part of the estuary due to high turbidity combined with strong vertical mixing (unfavourable mixing depth/euphotic depth ratio). However, this limitation might not be as substantial as expected from many published estimates of respiration rates and compensation depths, which might be too high (Kromkamp & Peene 1994). Nutrients are generally not limiting, although in the most seaward part of the estuary, silicate can become slighty limiting during diatom blooms (Van Spaendonck *et al.* 1993, Soetaert & Herman 1995). In the eastern part of the Westerschelde, chemosynthetic fixation of carbon by nitrifying bacteria exceeds primary production by phytoplankton (Heip & Herman 1995).

Phytoplankton species composition is dominated by coastal diatom species (mainly *Skeletonema costatum* and *Thalassiosira* spp.) in the polyhaline reaches, while in the oligohaline and freshwater tidal reaches the phytoplankton is composed of green algae (*Nannochloris coccoides* Naumann, *Monoraphidium* and *Scenedesmus* spp.), freshwater diatoms (*C. scaldensis*, *C. meneghiniana*), Cyanobacteria (*Oscillatoria* spp.) and Euglenophyceae (Muylaert & Sabbe 1996a, Muylaert & Sabbe, subm.).

Primary production by benthic algae (model estimates) amounts to about 60 % of the pelagic primary production in the Westerschelde (Soetaert & Herman 1995). Generally, nutrients do not appear to be limiting benthic primary production (Kromkamp *et al.* 1995), although nutrients and CO_2 could become limiting in dense microbial mats (Barranguet & Peene 1996). De Jong *et al.* (1990) found that nutrient supply is not limiting the growth rate of microphytobenthos in the Oosterschelde.

Between June and September *Ulva* and *Enteromorpha* spp. (amongst others) can become locally very abundant on some sandflats (Terneuzense Pas, Platen van Hulst, Rug van Baarland, Platen van Ossenisse, Baalhoek - Sabbe, unpubl.) However, according to Nienhuis (1992) macro-algal vegetation (both on hard and soft substrates) and seagrasses only play a marginal role in the total carbon budget of primary producers, as high turbidity and exposure to waves and tides prevents invasion of potential habitats.

Marine and brackish saltmarshes constitute about a quarter of the total inter- and supratidal area in the Westerschelde and represent about the same amount of the total primary producer carbon budget of the estuary (Nienhuis 1992).

The structure of the food web in the Westerschelde is mainly determined by the carbon sources described above and by the abiotic conditions (e.g. anoxia) in the different reaches of the estuary. Hummel *et al.* (1988) hypothesized that two separate food chains are present in the Westerschelde, a photo-autotrophic coastal food chain in the most seaward part and a heterotrophic chain in the eastern part. This hypothesis was confirmed and refined by Hamerlynck *et al.* (1993), who indicated that in the middle reaches of the estuary a 'nutrient-rich desert' is present, i.e. in this zone there is an excess of nutrients and primary production is high but the higher trophic levels do not seem to be able to exploit this food source (due to high current velocities?). The presence of two food chains can be inferred from the distribution of the dominant animal groups in the estuary [zooplankton (Soetaert & Van Rijswijk 1993), hyperbenthos (Mees *et al.* 1993), macrobenthos (Ysebaert *et al.* 1993) and epibenthos and fish (Hamerlynck *et al.* 1993)], which are all characterized by different communities in the meso- and poly/euhaline sections of the estuary [for more details, see Hamerlynck *et al.* (1993)].

1.2.1.6. Conclusion

The Schelde estuary takes a unique position amongst European macrotidal estuaries because of the very long water residence time (resulting in a very stable salinity gradient) and the extremely high organic (and other) pollution, which causes record heterotrophic bacterial production rates. This production results in water column and sediment anoxia with major biochemical and ecological consequences for the whole estuary and adjacent coastal waters.

More general information on the Schelde estuary can be found in De Pauw (1975), Moerland (1987), Meire *et al.* (1992), Meire *et al.* (1995), Heip & Herman (eds. - 1995) and in Heip *et al.* (1995).

1.2.2. A concise history of microphytobenthos and phytoplankton research in the Schelde estuary

To date, relatively little is known about the composition and ecology of the diatom communities of the Schelde estuary. Moreover, most information concerns planktonic diatoms; virtually nothing is known about the benthic diatom flora of this estuary.

The earliest information on diatoms of the Schelde estuary was gathered by Van Heurck at the end of the 19th century, witness the large collection of slides from the Schelde [collected between Antwerpen and Vlissingen] in the Van Heurck Diatom Collection in Antwerpen (AWH) and the numerous references to the Schelde estuary in his 'Synopsis des Diatomées de Belgique' (Van Heurck 1880-1885) and 'A treatise on the Diatomaceae' (Van Heurck 1896)(a complete list of all species reported from the Schelde estuary by Van Heurck is given in Van Meel 1958). Van Heurck mainly deals with the presence or absence of diatom species in the Schelde estuary as well as in other localities. To our knowledge, no papers specifically dealing with the diatom flora of the Schelde estuary were published by Van Heurck.

During the first part of the 20th century, studies on diatoms from the Schelde estuary are rare and scattered (Conrad & Kufferath 1912, Van Goor 1923)(cf. Van Meel 1958). The first systematic study of the phytoplankton of the Schelde estuary (mainly from stations around Antwerpen) is made by Van Meel in 1958. It is worth noting that most algological studies on brackish waters in Belgium published in this century deal with landlocked creeks (remainders of tidal creeks from earlier trans- and regressions)(e.g. Conrad & Kufferath 1954, Van Meel 1949, 1958, Caljon 1983), while only few papers are dedicated to tidal brackish water systems. Louis *et al.* (1975) provided some information on the phytoplankton of the freshwater tidal part of the Schelde in their study of Belgian rivers and canals.

De Pauw (1975) made a comprehensive study of the plankton (including the phytoplankton) of the Schelde estuary. Although the phytoplankton smaller than 50 µm was not quantitatively sampled, this study offers the first ecological survey of the netplankton communities of the Schelde estuary.

From then on, more papers appear on different aspects of the phytoplankton communities of the Schelde estuary, e.g. on biomass and production (e.g. Jackson & De Visscher 1975, Van Spaendonck *et al.* 1993, Soetaert *et al.* 1994, Kromkamp *et al.* 1995), structural aspects (Bakker & De Pauw 1974, Rijstenbil 1993, Muylaert 1994, Van Kerckvoorde 1996, Muylaert & Sabbe, subm., Muylaert *et al.* subm.) and systematics of selected diatom groups (Muylaert & Sabbe 1996a, 1996b).

To our knowledge, the first studies specifically dedicated to benthic diatoms from the Schelde estuary only appeared in the last decade. Vos (1989) reported on the isolation of intertidal benthic diatoms from a mudflat near the Dutch-Belgian border in order to study the micro-contaminant content in these organisms (see also Stronkhorst *et al.* 1994). Spatial and seasonal microphytobenthos biomass dynamics have been studied since 1989 (Directoraat-Generaal Rijkswaterstaat, Rijksinstituut voor Zee, Middelburg, The Netherlands). The results of this monitoring program were reported by de Jong & de Jonge (1994)[see also de Jong & de Jonge (1995)]. The composition, spatial distribution and temporal dynamics of intertidal benthic diatom communities of the Westerschelde were studied by Sabbe & Vyverman (1991), Sabbe (1993), Sabbe *et al.* (1995) and Sabbe & Vyverman (1995). The systematics and spatial distribution of intertidal protist communities of the freshwater tidal and oligohaline reaches of the Schelde estuary were studied by Van Nieuwerburgh (1996). Preliminary results on microphytobenthic production in the Westerschelde estuary can be found in Kromkamp *et al.* (1995). Estimates on the contribution of microphytobenthos production to total primary production in the Westerschelde estuary are given by Nienhuis (1993) and Soetaert & Herman (1995).

No extensive search was made for papers dealing with micropalaeontology in the area of the Westerschelde estuary; some cores from the lower Schelde basin were studied by Denys & Verbruggen (1989).

1.3. Diatoms and the benthic environment

Intertidal benthic diatoms live in an environment which is not only characterized by steep vertical gradients and horizontal patchiness (on different scales) in chemical and physical factors, but which can also be subject to strong and sometimes sudden changes in these gradients. Oenema *et al.* (1988) characterized intertidal areas as semi-terrestrial, i.e. hydrosphere, lithosphere and atmosphere interact in this complex environment. In addition, this habitat is also strongly influenced by biological processes. Physically, biological activity can either disrupt (e.g. burrowing activities of macrofauna) or stabilize (e.g. through excretion of extracellular substances by the diatoms themselves, cf. Paterson *et al.* 1990) the sediments. Biological processes are also largely responsible for the establishement of the above-mentioned gradients (e.g. through bacterial activity, oxygen production, possible nutrient depletion in dense microalgal layers, etc.). The steepness of the physical, chemical and biological gradients are strongly influenced by the nature of the sediment.

Profiles of concentrations in chemical compounds in sediments show that strong vertical gradients exist. Below a certain depth (a few mm's in silty sediments to many meters) oxygen is depleted through aerobic decomposition of organic material. Below this zone, several other compounds are used as terminal electron-acceptor, the ones with the higher capacities to accept electrons first, so that their concentrations also diminish with increased sediment depth (cf. Patterson *et al.* 1989 and references therein). For example, sulphur is reduced to sulphides which cause the sediment to become black below the oxygenated zone. These sulphides can inhibit growth or kill diatom species, although certain species are able to survive high amounts of sulphides and can even grow in their presence (Admiraal & Peletier 1979a). The latter may be due to lower grazing and competitive pressure in high sulphide/low oxygen environments (Kennett & Hargraves 1985).

In order to grow and survive, most diatoms need light and nutrients. Moreover, growth is dependent on several additional, often species-specific conditions: active growth is only possible within certain ranges of e.g. temperature and salinity (cf. Admiraal 1984 and references therein).

The depth of the photic zone strongly depends on the nature of the sediments: in silty sediments, the photic zone is much shallower (tenths of a mm) than in sandy sediments (several mm). Moreover, the nature and condition (e.g. wet or dry) of the sediment also influences other light characteristics such as its spectral composition and the amount of backscattering (Kühl & Jørgensen 1994). In addition, layers of micro-algae can considerably change the spectral composition of the light in the lower layers of the photic zone due to the specific absorption of wavelengths (Ploug *et al.* 1993). There are strong indications that benthic diatoms can maintain photosynthesis at very low light quantities and can adapt to changes in the light climate (Sundbäck *et al.* 1996 and references therein).

Inorganic nutrients (as P, N or Si) are usually abundant in estuarine sediments, although nutrient limitation (e.g. inorganic C but also silicate) can occur in dense layers of microalgae (Admiraal 1984 and references therein). However, not much is known about this phenomenon or the factors influencing its occurrence. Several experiments have shown that the addition of inorganic nutrients to water overlying sediment cores can stimulate microalgal growth (cf. Nilsson *et al.* 1991, Nilsson & Sundbäck 1991, Sundbäck & Snoeijs 1991), while others indicate that nutrients are not limiting in intertidal environments (Admiraal *et al.* 1982). It has also been shown that benthic diatoms can take up organic compounds (such as dissolved free amino acids, cf. Nilsson 1995 and references therein, Tuchman 1996), a phenomenon which also appears to vary from one species to the other. Experiments have shown that while some species are strictly autotrophic, others are photoheterotrophic, while still others can grow on organic substrates in the dark (Admiraal &

Peletier 1979b).

Grain size composition influences the amount of interstitial space (porosity) and thus other important factors such as water content (Patterson *et al.* 1989 and references within). Silty sediments, with a high water content, are cohesive, which means that they will be less easily eroded than would be expected on the basis of their size alone (McLusky 1989); in addition, they are often stabilized by the micro-organisms themselves (cf. above). Sandy sediments are generally characterized by high saturated pore water flow (m's/day) due to large pore sizes. This permits rapid drainage of interstitial water from the upper layers at low tide. In muddy sediments, this pore water flow is very low (mm's/day) due to the much smaller pore sizes (Oenema *et al.* 1988). Water-logged sediments are also less sensitive to rapid changes in salinity [e.g. as a consequence of heavy rainfall (Wieser 1975) or strong insolation (Oppenheim 1991)] and temperature. In sandy beaches in temperate areas, temperature can range between 8 and 22 °C in the upper mm's of the sediment on a summer day (Wilson 1983).

The sediment also has a direct influence on benthic diatom communities: sand grains act as a substratum for epipsammic diatoms and influence community composition and microscale distribution patterns through their microtopography, while it has also been shown that sand grain mineralogy can influence colonization by diatoms (e.g. through possible release of inhibiting ions, Krejci & Lowe 1986).

Another important factor influencing diatom growth and distribution is grazing. Species from almost all major faunal groups inhabiting estuaries have been shown to graze on diatoms: ciliates (Patterson et al. 1989), meiofauna (such as copepods and nematodes, cf. Plante-Cuny & Plante 1984), amphipods (Sundbäck & Persson 1981), prawns (Newell *et al.* 1995), fish (Almeida *et al.* 1993) and even birds (Meininger & Snoek 1992).

In natural assemblages, it is very hard to disentangle the numerous intercorrelated (and possibly also interacting) factors which influence the distribution of benthic diatoms. Unfortunately, it is as yet impossible to do experiments with benthic micro-algae without altering the benthic environment in one way or another (cf. Nilsson & Sundbäck 1991). In addition, the study of benthic protist communities is still seriously hampered by the fact that many phenomena and processes can only be studied at too low a resolution to give a realistic picture of what is actually experienced by the individual organisms in the sediment. Although recently some important breakthroughs have been realized, mainly by the development of microprobes for measurement of e.g. oxygen, pH and irradiance, there are still no adequate methods to directly assess processes such as nutrient limitation in dense microbial communities.

More detailed information on the intertidal and interstitial habitat can be found in Admiraal (1984) and Patterson *et al.* (1989) respectively.

2. Terminology

2.1. General

Zeeschelde: the Belgian part of the Schelde estuary, which roughly comprises the freshwater tidal and oligohaline reaches

Westerschelde: the Dutch part of the Schelde estuary, which consists of the meso-, poly- and euhaline zones of the estuary.

Estuarine gradients:
1. We followed the classification system of estuarine divisions proposed by McLusky (1993). The different terms involved are listed in Table 1.
2. All Westerschelde stations have been allocated to different sediment classes (=SC, see chapter 3.2.6. for more details). Samples belonging to these classes are referred to as sandy (SC 1), silty sandy (SC 2), sandy silty (SC 3) or silty (SC 4). However, in the systematical part (chapter 4), we have used a slightly different terminology in order to be able to be more specific about the autecological requirements of the epipsammic taxa. These terms are: silty (with high silt percentage and a low amount of sand, as opposed to the following 3 terms), very fine sandy, fine sandy and medium sandy. If a taxon is said to be typical of e.g. fine sandy sediments, it means that its abundance is positively related to the amount of fine sand in the samples (cf. chapter 5.3).

2.2. Ecological terms

Epipelon: 'diatoms that live freely on and in sediments' (Round *et al.* 1990), 'pennate diatoms with well-developed motility which allows migration into the sediment' (Admiraal 1984).

In this study the term epipelon is used *sensu* Round *et al.* (1990); it is a collective term for **all taxa that live in loose association with the sediment, i.e. including (mainly larger) motile pennate diatoms but also immotile taxa such as araphids and centrics**. It thus refers to taxa that are traditionally classified as epipelic (cf. Admiraal 1984) and tychoplanktonic. In this study, epipelic taxa are also referred to as free-living taxa. The epipelon includes life-forms 5-7 and some taxa of life-form category 4 (see chapter 3.4.3. for more details on the life-forms).

Epipsammon: 'attached diatom communities growing on sandgrains' (Round *et al.* 1990), 'largely immobile diatoms fixed firmly to their substratum' (Admiraal 1984).

In this study the term epipsammon is used in a slightly different sense, viz. those **taxa that live in close association (either attached or free-living) with *individual* sediment particles**. These taxa can also move through the sediment but their travel speeds are much lower than of the epipelic motile diatoms. Moreover, when moving upwards (to the sediment surface) they move from sandgrain to sandgrain (Harper 1969). In contrast to Admiraal (1984) the epipsammon in our definition also includes the numerous small motile taxa that live in the micro-environment created by the topography of individual sandgrains. The epipsammon includes the life-form categories 1-3 and some taxa of category 4.

Community: This term is used here in its most general sense, i.e. any assemblage of populations of living organisms in a prescribed area or habitat (Krebs 1985, Snoeijs 1995).

Microhabitat: a small place in the general habitat (= the locality or external environment in which an organism lives)(Holmes 1979). We mainly use this term in a spatial sense: for example, a crevice and a plateau on a sandgrain are two different microhabitats.

2.3. Abbreviations

For labels of stations, environmental parameters and taxa see Tables 3, 7 and 18 respectively. Some commonly used abbreviations are given in Table 2.

3. Materials & Methods

3.1. Sampling

Thirty-two sampling stations along a total of 11 intertidal transects were selected from 109 stations that are sampled monthly in a microphytobenthos biomass (as chlorophyll *a*) monitoring program which was started in 1989 by the Directoraat-Generaal Rijkswaterstaat, Rijksinstituut voor Zee, Middelburg, The Netherlands. All sampling stations are situated in the Westerschelde proper, i.e. between the North Sea and the Dutch-Belgian border. Mainly eu-, poly- and mesohaline stations have been sampled, while oligohaline and freshwater tidal stations (which are situated in the Zeeschelde, cf. chapter 1) have not been sampled in this study. The sampling stations were selected in order to cover the entire range in salinity and sediment type in the Westerschelde estuary. The exact location of the stations and transects is shown in Fig. 3. The main characteristics of each sampling station are listed in Table 3. The stations are labelled with 2 letters (referring to the name of the transect location) and the station number. This label can be extended with two letters referring to the sampling month*.

Sediment samples were taken monthly between October 1991 and October 1992, either by access from the river banks (bank transects) or by boat [shoals (e.g. Hooge Platen, Molenplaat) or bank transects which are not easily accessible from the river bank (e.g. Konijnenschor)]. Almost all 32 stations were sampled monthly (Table 4). However, a few transects could not be sampled on all occasions due to adverse weather (storm, mist) or unfavourable tides.

Sediment samples were taken at low tide by pushing a perspex cylinder (diameter 22 mm) into the sediment and removing the top 10 mm from the core. This procedure was repeated five times (within 1 m²) to compensate for microscale differences in diatom composition and abundance; the five cores were then combined to yield one composite sample for each sampling station. Samples were then fixed with 4%-formalin. These samples were used for quantitative analysis of the benthic diatom communities (see below). Throughout the sampling period a number of sediment samples were taken for observations on live material.

On each sampling occasion, surface (10 mm) sediment samples were taken for physical and chemical analysis of the sediment and interstitial water. The following parameters were determined:

- grain size distribution
- water content
- interstitial water salinity
- organic carbon and nitrogen content

Data on air temperature, irradiance, wind speed and precipitation were obtained from the monthly bulletins of the Royal Dutch Meteorological Institute (K.N.M.I.) and the Belgian Royal Meteorological Institute (K.M.I.). The water column parameters, the exact station coordinates and the station elevation data were made available by kind permission of Dr. D. J. de Jong (Directoraat-Generaal Rijkswaterstaat, Rijksinstituut voor Zee, Middelburg, The Netherlands).

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* OA: October (1991); NO: November; JA: January; FE: February; MA: March; AP: April; ME: May; JN: June; JL: July; AU: August; SE: September; OB: October (1992).

3.2. Environmental parameters

Additional information on units and labels of the environmental parameters is summarized in Table 7.

3.2.1. Climatic parameters: air temperature, irradiance, wind speed and precipitation

Air temperature, irradiance, average wind speed and precipitation were measured at Vlissingen (The Netherlands), at the mouth of the Westerschelde estuary. Maximal wind speed was measured at Deurne near Antwerpen (Belgium), about 20 km east of the easternmost transect in the estuary (Appelzak).

Irradiance values are the global irradiance values, which are the sum of both the direct and diffuse irradiance (cf. monthly bulletins K.N.M.I). Two measures of both air temperature and irradiance were used, referring to the values measured in the week or month preceding sampling. Both measures were then related to the biological data and evaluated. Air temperature values concern the average values of the week and month preceding sampling, irradiance values the total of the values measured in the week and month preceding sampling.

Wind speed was introduced as both the average wind speed in the week preceding sampling and the maximal value recorded in that week. Precipitation concerns the total precipitation in the month preceding sampling.

3.2.2. Water column parameters: salinity, temperature, transparancy

Monthly measurements of these variables were made at 10 pelagic stations along the longitudinal axis of the Westerschelde. The position of these stations is shown in Fig. 4. In the multivariate analyses (see chapter 5.3.) each intertidal station was assigned the value of the water column parameter of the nearest pelagic station. The measurements were made in the same week as the sediment sampling campaign.

3.2.3. Physical sediment parameters: grain size distribution, water content

Size analysis of the sediment was performed with a Coulter Counter (LS100), which yields a continuous size distribution of the sediment particles. By adopting a grade scale [i.c. the Wentworth scale (Buchanan & Kain 1971, see Table 5)], we can then assess what volume percentage is present in each size class. The following partcle size classes were distinguished: clay, silt, very fine sand, fine sand, medium sand and coarse sand (see Table 5 for more details).

Water content of the sediment was measured by the water loss on a wet/dry weight basis. Wet sediment was collected in pre-weighted containers, weighted and left to dry for several days at about 60 °C (cf. Oppenheim 1991), after which it was weighted again.

3.2.4. Chemical sediment parameters: interstitial water salinity, organic carbon and nitrogen content

Sediment samples from the top 10 mm of each station were collected and allowed to settle for several hours (or centrifuged). The salinity of the interstitial water was then measured with a hand refractometer. Organic carbon and nitrogen content were measured on oven dried (60 °C) sediment samples using a Nitrogen Analyzer 1500 (Series 2, Carlo Erba Instruments).

3.2.5. Morphological parameter: station elevation

Station elevation data were obtained from a monthly sedimentation/erosion monitoring program of the intertidal area in the Westerschelde estuary (Directoraat-Generaal Rijkswaterstaat, Rijksinstituut voor Zee, Middelburg, The Netherlands) for the Molenplaat (stations 1-4), Konijnenschor and Baalhoek transects. For most other stations (except those from the Hooge Platen transect), approximate measurements were performed in summer 1994. The elevation of the Hooge Platen stations was estimated from contour maps.

3.2.6. Elevation and sediment classes

In order to statistically analyse trends in environmental parameters (chapter 5.1.) and some general structural characteristics of the diatom communities (chapter 5.2.) the sampling stations were allocated to 4 sediment classes (SC1-4) and 4 elevation classes (EC1-4).

The 4 sediment classes were distinguished on the basis of the percentage clay and silt content (i.e. particles < 63 µm) of the samples (SC1: < 10 %; SC2: 10-20 %; SC3: 20-30 %; SC4: > 30 %). Samples belonging to these classes are referred to as sandy, silty sandy, sandy silty and silty respectively [except in the systematical part (chapter 4), cf. also chapter 2.1.]. If the clay and silt content of a station was variable throughout the year, it was assigned to that sediment class to which most of the samples from that station belonged. Note that the yearly average clay and silt content value of some stations does not fall within the sediment class it has been assigned to (Table 3). This is mainly due to the fact that in some stations large fluctuations in silt content occurred. For example, in station 2 of the Konijnenschor (KS 2), the amount of clay and silt ranged from 6.8 % in January to 34.6 % in September; the extremely low January value thus considerably lowered the average value, while all other samples from that station had much higher values (between 24.1-34.6 %) than the January ones.

The elevation classes are, in relation to the mean tidal level (MTL): EC1: > 0.5 m; EC2: 0-0.5 m; EC3: -0.5-0 m; EC4: < -0.5 m. The assignment of stations to the sediment and elevation classes is shown in Tables 3 and 6.

3.3. Sample preparation and counting

3.3.1. Sample preparation and quantitative counts

Part of the homogenized composite sediment samples was oven-dried at 60 °C. One gram sediment dry weight (SDW) of each sample was then oxidized with hydrogen peroxyde (27 %) and acetic acid (99 %)(Schrader 1973). Subsequently the sediment was washed 3 to 4 times with distilled water and diluted to a final volume of 50 ml. After thorough homogenization a subsample of 50 µl was taken with a micropipette, transferred to a coverslip and air-dried. Permanent preparations were made with Naphrax mounting medium.

On each coverslip the diatom valves in a transect of known surface area were counted. For each slide a minimum area of 5000 by 100 µm was counted. Counts were continued beyond this minimum area until at least 400 valves were counted. In some samples, diatom densities were very low; a maximum of ten transects of 5000 by 100 µm was then scanned for diatoms. The transect counts were extrapolated to the total surface area of the dried drop*. Thus the total number of

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* Special care was taken to make sure that shape of all dried drops was circular to elliptical. By measuring the short (a) and the long radius (b) of the circle/ellipse the exact surface area of the drops could then be calculated (πab).

cleaned valves (and hence frustules) in one gram SDW could be calculated.

3.3.2. Living-dead counts

On 31 occasions [23 samples from Baalhoek taken between 18 March 1991 and 10 May 1991 (cf. Sabbe 1993), 6 samples (January, July and September) from the Platen van Hulst (PH2), and the Terneuzense Pas (TE1) and 2 samples (May, September) from the Appelzak (AZ1)], a part of the fixed sample was stained with Bengal Rose, which allows to distinguish between empty frustules and those with a cell content (the latter are considered to be alive or only recently dead and will henceforth be referred to as living diatoms). After homogenization, a small subsample was transferred to a coverslip, air-dried and mounted in Naphrax. The percentage of living cells in a count of 200 frustules was calculated for the dominant taxa (when recognizable) and/or life-forms (see chapter 3.4.3.). The latter grouping appeared to be necessary as many cells could not be identified to species or even genus level due to the presence of clay and silt particles and organic detritus, or due to their attached life-form. It was, however, always possible to assign all cells to one of the life-forms. The corresponding counts on the permanent (cleaned) preparations could then be corrected using the living/dead diatom ratios. This yielded the total number of living diatoms per gram SDW.

3.3.3. Statistical testing of the cleaning and counting method

The reliability of the cleaning and counting procedure was tested by statistically analyzing 4x4 replicate counts of one sample taken at Baalhoek (station 1) on 19 April 1991. At the time of sampling, this station supported rich epipsammic and epipelic diatom populations (for more details, see Sabbe 1993). After homogenization of the dried sediment, four 1 gram SDW samples were oxidized and for each gram four replicate counts (four different 50 µl subsamples) were made. One-way analysis of variance was performed on the log-transformed counts for the three dominant epipsammic taxa, viz *Achnanthidium delicatulum* (Kützing) Grunow, *Opephora guenter-grassii* (Grunow) Sabbe & Vyverman and *Catenula adhaerens* Mereschkowsky, the total cell count and the counts of the attached and freeliving diatom fractions. No significant differences were found between the replicate counts ($p < 0.05$) of the four 1 gram samples for the counts of *Achnanthidium delicatulum* and *Opephora guenter-grassii*, the total number of valves and the epipsammic and epipelic diatom fractions. However, the counts for *Catenula adhaerens*, a species that builds ribbon-like colonies of variable size on sandgrains, did show significant ($p = 0.05$) differences.

Replicate counts were made for ten other samples (from ten different sampling dates - for more details see Sabbe 1993). These usually did not differ by more than 10-15 % (cf. Admiraal *et al.* 1982).

3.4. Identification

3.4.1. Light microscopy (LM)

Cleaned material was examined using a Leitz Diaplan microscope with Differential Interference Contrast (DIC) optics. Microphotographs were made using a Wild Phtotoautomat MPS 45 on Agfapan APX 25 films (LM) and a Mamiya 6x7 on Agfapan APX 100 films (SEM). Live and fixed material was examined for information on life-form, plastid structure, colony formation and microhabitat.

3.4.2. Scanning electron microscopy (SEM)

Sample preparation for SEM required a more drastic preparation method to ensure sufficiently clean material. The above-mentioned cleaning method according to Schrader (1973) often gave problems with detrital material which hampered observations of ultrastructural details of diatom valves. The samples for SEM were therefore treated with nitric (70 %) and sulphuric acid (99 %) and gently heated for 30 minutes. SEM examination was performed with a Jeol JSM-840 at 15 kV.

3.4.3. Life-forms

The life-form of each taxon was assessed through microscopical examination of fresh or fixed material or (for rare taxa) drawn from the literature (mainly Denys 1991a, Vos & De Wolf 1993, Round *et al.* 1990). Nine categories were distinguished (cf. also Sundbäck 1983):

1. ***Adnate***: these diatoms are tightly appressed to the sand grain surface by their valve face (mainly monoraphid taxa such as many *Achnanthes* and all *Cocconeis* and *Anorthoneis* taxa, but also most representatives of the biraphid genus *Fallacia*) or by their girdle (the colony forming biraphid diatoms *Catenula adhaerens* and *Biremis lucens*).
2. ***Stalked***: includes mainly araphid diatom taxa (e.g. *Opephora* and *Fragilaria* spp.) which are attached to the sand grains by means of (usually) short stalks.
3. ***Motile < 10 µm***: small, mostly biraphid taxa (mainly *Amphora* and *Navicula*) which live in close association with sand grains.
4. ***Motile 10-20 µm***: this group mainly includes representatives of the genera *Amphora*, *Navicula* and *Nitzschia*.
5. ***Motile > 20 µm***: this group mainly conprises the larger taxa belonging to *Amphora*, *Diploneis*, *Navicula* and *Nitzschia*.
6. ***Tychoplankton***: includes mainly centric (belonging to the Cymatosiraceae and the genera *Cyclotella* and *Thalassiosira*) and araphid diatom taxa (e.g. *Rhaphoneis* and *Delphineis*). Note that the exact life-form of many of these taxa is little known and that some may concern truly planktonic taxa.
7. ***Interstitial***: this group includes only a few species, viz *Anaulus uniseptatus*, *Leyanella arenaria* and *Cymatosira* sp. 1, which occur in the interstitial space between sediment particles in sandy sediments.
8. ***Plankton***: includes truly planktonic species (e.g. *Coscinodiscus* spp.)
9. ***Epiphyton***: comprises taxa which lived attached to macro-algae and higher plants; in our material it mainly concerns taxa that have been washed in from vegetated areas (e.g. *Ctenophora pulchella*).

The exact life-form of each taxon is given in Table 18. More detailed information can also be found in the autecological description for each taxon (chapter 4). Both planktonic and epiphytic taxa were eliminated from the ecological analyses; these categories have therefore only been introduced in the systematic part (chapter 4.2, Table 18).

Diatoms belonging to life-forms 1-3 have been assigned to the epipsammon, life-forms 5-7 to the epipelon. The assignment of diatoms from life-form 4 to the epipsammon or epipelon differs from species to species (cf. Table 18). For more details, see chapter 4.

3.5. Diversity

Hill's diversity numbers of the order 0, 1, 2 and +∞ (Hill 1973), were calculated for each sample* . N_0 is equal to the total number of species present in the sample (= species richness), N_1 is the inversed natural logarithm of the Shannon-Wiener diversity index, N_2 is the reciprocal of Simpson's dominance index, $N_{+\infty}$ (the dominance index) is the reciprocal of the proportional abundance of the commonest species (Begon *et al.* 1990, Heip *et al.* 1988).

N_0 misses the information that species are rare or common, and is especially hard to interpret when oxidized material has been counted (even after selective reduction of the number of taxa, see previous footnote), as it is not sure whether the rare taxa present were actually alive at the time of sampling, or washed in from another habitat. We therefore refrained from using this index as it proved too ambiguous to interpret the trends. N_1 and N_2 share the feature that the higher their value, the more equitable the communities are (the higher the eveness). It is important to keep in mind that a species-rich but inequitable community can have a lower N_2 than a species-poor but equitable community. The lower N_2 of a community, the more it is dominated by one or a few species. Finally, the lower $N_{+\infty}$, the more the community is dominated by one species.

3.6. Data analysis

After the initial examination of some structural features of the data set, mainly using correlation analysis and graphical displays, a detailed analysis was done with different multivariate methods and associated statistical techniques. First, (canonical) ordination techniques were used to describe the benthic diatom communities present in the Westerschelde and their spatial and temporal structuring in relation to the abiotic environment. Second, a more quantitative approach (variation partitioning) was used to assess the relative contribution of different sets of variables to explaining the variation in the species data and to examine the spatial and temporal structure of the data set in further detail. In addition, weighted averaging was used to determine species optima and tolerances for selected environmental variables.

Summary information on the data sets used in these analyses can be found in Table 8; they are discussed in more detail in chapter 5.3.1.

3.6.1. Data transformation

Data transformations were performed on both the species and environmental data sets which were used in statistical (Pearson correlation analysis, analysis of variance) and multivariate (PCA, RDA - see below) analyses. All species data (counts of absolute cell numbers per g SDW) were log transformed [log (x+1)](cf. Jongman *et al.* 1987). Skewed environmental variables were transformed using the same logarithmic transformation. Variables with other distribution types (e.g. bimodal) were not transformed. Table 7 lists which environmental variables have been transformed. In the program CANOCO 3.1, which was used for the multivariate analysis, the environmental variables are automatically standardized to mean 0 and variance 1 (Ter Braak 1988).

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* Note that the data set used to calculate these values was not the full species data set but the species included in data set 3 (which is a reduced data set, cf. chapter 5.3.1), which comprises 89 taxa. However, for the calculation of the diversity indices, we did not omit *Cyclotella atomus*, *C. caspia*, *C. meneghiniana*, *C. choctawhatcheeana*, *Thalassiosira angulata*, *T. curviseriata*, *T. proschkinae* and *Thalassionema nitzschiodes*. The data set for the calculation of the diversity indices thus comprises 97 taxa.

3.6.2. Correlation and graphical analysis

The main trends in absolute cell abundance (including those of the different life-forms) and diversity were studied using correlation analysis (Pearson correlation coefficient). They were summarized with the aid of Box-Whisker plots which allow to make inferences about the significance of the observed trends (Wilkinson 1990, Gätje 1992) by comparing the confidence intervals (95 %) around the medians. However, apart from all statistically significant trends, some non-significant trends can still be informative. For example, the seasonal trend in ISW salinity for the whole estuary (Fig. 12) does not reveal any significant differences between the different months, as the salinity range covered by each month by far exceeds the changes in salinity between months. If every station would be plotted separately (and providing replicate samples were available), significant temporal trends would probably emerge. These graphs can therefore still be informative.

Three-dimensional (3D) surface plots were constructed to display trends in cell numbers, diversity and environmental parameters along two environmental gradients simultaneously. The surfaces were fitted to the XYZ coordinate data according to the distance-weighted least squares smoothing procedure. Analysis of variance (ANOVA) was used to study trends within the 3D trend surfaces by comparing between the sets of samples (used to construct the trend surfaces).

3.6.3. Weighted averaging regression

Weighted averaging regression is a method which allows to estimate optima and tolerances for taxa along single environmental gradients. It is implemented using the computer program WACALIB 3.1 (Line & Birks 1990). This approach was used, in combination with ordination analyses, to assess the autecological requirements of the observed taxa.

3.6.4. Multivariate analysis

(after Jongman *et al.* 1987, ter Braak 1994, ter Braak & Verdonschot 1995)

A common feature of data used in ecological research is that they are multivariate, i.e. each statistical sampling unit (i.c. a diatom sample) is characterized by many attributes (e.g. taxa and environmental measurements). Ecological datasets are therefore bulky and complex, showing a considerable amount of noise, redundancy, internal relationships (e.g. between species) and outliers (Gauch 1982).

Multivariate methods make such data easier to handle. These methods can be divided into 3 groups: indirect gradient analysis (ordination), direct gradient analysis (regression analysis) and classification (cluster analysis)(Jongman *et al.* 1987). The direct methods use species and environment data in a single, integrated analysis; the indirect methods use the species data only (ter Braak 1994). Recently, it has become common practice to use multivariate techniques to study the spatial and temporal variation in diatom communities (e.g. Snoeijs 1994, 1995, Douglas & Smol 1995, Vyverman *et al.* 1995, 1996, Pan & Stevenson 1996).

3.6.4.1. Ordination

Introduction

Ordination techniques arrange sites along axes on the basis of data on species composition (usually relative or absolute cell abundances). The underlying hypothesis is that species are not randomly distributed but react to their environment, both biotic and abiotic. The variation in the species data then reflects the variation in the environment. Without knowing the environmental variables, one may therefore still attempt to reconstruct such variables from the species data alone. The ordination axes can be viewed as hypothetical environmental variables, which can then be compared to the measured environmental variables by means of statistical methods. In canonical (or constrained) ordination, which is a multivariate form of regression analysis, axes based on the variation in species composition are still constructed, but with the constraint that the axes have to be a function of the supplied environmental data.

Direct and indirect ordination techniques can be further subdivided on the basis of the underlying model they use for the species responses along environmental gradients. Two major response models can be distinguished: linear and non-linear response models. Relationships between species and the environment are usually non-linear: species abundances are often unimodal function of the environmental variables. However, when samples have been taken along a section of an important gradient, the observed response function is not unimodal but monotonically decreasing or increasing. Therefore the use of linear methods is often still appropriate. The choice of the adequate ordination technique is important as it has major consequences for the reliability of the results of the ordination (see below).

Classification techniques can be divided in two major groups: agglomerative and divisive methods. Agglomerative methods start with individual objects and combine them into groups, according to a similarity measure; divisive methods start with all objects as a group and divide them into subsequently smaller groups. The latter techniques pay more attention to large differences in the dataset, while in agglomerative techniques 'local' similarities prevail.

As nowadays community variation is usually being considered as largely continuous, it seems inappropriate to partition the objects into discrete groups. However, a classification of communities can sometimes provide a useful summary for large datamatrices, particularly when complemented by an ordination (Digby & Kemp 1987).

A widely used classification program is TWINSPAN (Two Way INdicator SPecies ANalysis). This program, however, is actually a hybrid technique based on the partitioning of the first axis of a correspondence analysis (Jongman *et al.* 1987, Mees *et al.* 1993).

Ordination analyses: practical procedure

The program CANOCO 3.12 (version April 1991)(ter Braak 1988, 1990) was used to perform all ordinations. The species data set was first screened in order to eliminate rare, non-benthic and allochtonous taxa from the analyses. This yielded several data sets of different size (number of taxa and samples) which were compared to assess the influence of these eliminations on the ordinations. The definitive ordinations which were used to describe the diatom communities and their spatial and temporal structuring were performed on the most reduced set of taxa (see below).

The choice of the appropriate ordination method (linear or unimodal) was assessed by running a preliminary Detrended Correspondence Analysis (DCA, Hill & Gauch 1980) as recommended by Jongman *et al.* (1987). The output of this analysis provides a check on how unimodal the data are by listing the standard deviation (s.d.) length of the ordination axes. If this length is less than 2 s.d., most of the species response curves will be monotonic, in which case linear methods are most appropriate. When the length of the gradient is larger than 2 s.d., unimodal methods are used. The linear methods available in the CANOCO 3.12 are Principal Components Analysis (PCA) and its canonical form Redundancy Analysis (RDA), the unimodal methods are Correspondence Analysis (CA, and its detrended form DCA) and Canonical Correspondence Analysis (CCA). More information on the application of these techniques and interpretation of the output can be found in Jongman *et al.* (1987), Palmer (1993), ter Braak (1994) and ter Braak & Verdonschot (1995). The interpretation of ordination diagrams follows specific rules which depend on the choice of the method (linear or unimodal). Some very general rules for the interpretation of the diagrams we have produced are given in chapter 5.3.3.

The environmental variables used in the ordination analyses include all 22 variables from Table 7 and 6 temporal variables. The temporal variables were introduced as dummy variables (cf. Jongman *et al.* 1987, Snoeijs 1989, Martin & Bouchard 1993) to represent the month in which the samples were taken. The values of these dummy variables can only take the value of 0 or 1; there are as many dummy variables as there are months in the data set used. For example, the dummy variable for the month March takes the value 1 for the samples from March and 0 for the samples from other months.

Removal of multicollinearity and non-significantly contributing independent variables

In data sets with a large number of environmental variables two problems commonly occur. First, many variables display relationships amongst each other. Second, many environmental variables do not contribute significantly to explaining the variability in the species data set but artificially increase the explained variation by mere chance (cf. Borcard *et al.* 1992). The first phenomenon is termed multicollinearity (Jongman *et al.* 1987, Pinel-Alloul *et al.* 1995). It affects the stability of canonical coefficients in a constrained ordination (Jongman *et al.* 1987, cf. also Wilkinson 1990) and thus jeopardizes the interpretation of the output. Only when multicollinear variables have been removed from the analyses one can interpret the significance of the contribution of the remaining variables to the ordination axes. The second phenomenon leads to an overestimation of the explained variance in canonical ordinations. It is therefore advisable to select a minimal subset of independent variables that explain the species data about as well as the full set (ter Braak 1990). In order to obtain this minimal, highly significant subset of variables, two procedures are used:

(1) Highly multicollinear variables are removed from the ordination analysis by looking at their variance inflation factor (VIF)(ter Braak 1988). If this value is higher than 20, the variables are eliminated from the active analysis.

(2) Forward selection of environmental variables is a multivariate extension of univariate stepwise multiple regression (forward option)(cf. Wilkinson 1990) and is available as an option in constrained ordination analyses in CANOCO 3.12 (ter Braak 1990). At each step of the forward selection, the 'best' variable (i.e. the variable which adds most to the total explained variance in the species data) is added. The statistical significance of the effect of each variable can be tested by a Monte Carlo permutation test. Note however that due to the collinearity problem many environmental variables may display equal variance contribution to the total variation in species composition, but only one will be chosen by the forward selection procedure. So, the best subset of environmental variables is not unique (cf. Pinel-Alloul *et al.* 1995). For more details on this method, see e.g. ter Braak (1990), Økland & Eilertsen (1994), ter Braak & Verdonschot (1995).

We combined both methods in our analyses: first we removed variables with a high inflation factor, than we ran a RDA with forward selection and only retained those variables that contributed significantly to the ordination. The remaining environmental variables were analyzed passively, i.e. their correlations with the ordination axes were computed after the computations for the ordination (Van Tongeren *et al.* 1992, Snoeijs 1995).

From the canonical coefficients and the intra-set correlations between the environmental variables and the ordination axes it is possible to assess the relative contribution of the different environmental variables to the RDA axes. The significance of the contribution of the selected environmental variables to each axis was judged by an approximate *t*-test [if the (absolute) t-values of the canonical axes are smaller than 2.1, they do not contribute significantly (ter Braak 1988, Duff & Smol 1995)]. Only variables that are strongly correlated to an axis (i.e. intra-set correlations > 0.50) were judged important. Note that other, intercorrelated variables might also have a significant intra-set correlation, but if this is lower than 0.50 we did not take them into account. This way, the most important variables related to the species data were determined for each axis.

3.6.4.2. Variation partitioning

The technique of variation partitioning is based on partial canonical ordination analyses, and can be performed using Canonical Correspondence Analysis (Borcard *et al.* 1992, Økland & Odd 1994, Heikkinen & Birks 1996) or Redundancy Analysis (ter Braak & Wiertz 1994).

Variation partitioning (Borcard *et al.* 1992) is a technique which allows to decompose (partition) the variation in a species-sample data matrix (i.e. the total sum of squares in the species data) on different sets of explanatory variables. Variation partitioning thus provides quantification and statistical testing of the variation explained by different sets of variables. Moreover, it allows to assess what fraction of the variation explained by two variable sets is shared by both. Separate analyses would not allow the quantification of this fraction (cf. Fig. 5).

Partitioning the variation in a species data set (using Redundancy Analysis) on two sets of explanatory variables (U) and (T) proceeds as follows (cf. Borcard *et al.* 1992 and Økland & Eilertsen 1994):

1. Select those variables in (U) and (T) that contribute significantly (Monte Carlo permutation test, 99 permutations, $p<0.05$) to explaining the variation in the species data set (forward selection procedure in CANOCO, cf. above). The variation explained (VE) by these selected variables is denoted U and T respectively (VE = sum of all canonical eigenvalues, shown in the ordination output of the CANOCO program*). Note that multicollinear variables are not eliminated as the canonical coefficients do not have to be interpreted (cf. above).
2. Assess the amount of variation explained by (T) which is not shared by (U), i.e. T/U, by performing a partial RDA on (T) with the significant variables of (U) as covariables.
3. Calculate the amount of variation shared by (T) and (U), i.e. $U \cap T$, by subtracting T/U from T.
4. Calculate the amount of variation in (U) which is not shared by (T) (= U/T) by subtracting $U \cap T$ from U.
5. $T \cup U$ is equal to the sum of T/U and U (or U/T and T).
6. The amount of unexplained variation is $1-(T \cup U)$.

Note that it is important that prior to calculating the amount of variation explained by a variable set, it is important to select only those variables that contribute significantly to the analysis.

The measured environmental variables were grouped into different sets. In some analyses these were subdivided into smaller subsets (Table 9): within the physical and chemical variable set, three subsets were distinguished: sediment (comprising all sediment characteristics), salinity (with water column and interstitial water salinity and transparancy, which is strongly related to the estuarine salinity gradient) and the single morphological parameter elevation.

An additional set of explanatory variables consisting of spatial variables was introduced in the variation partitioning analysis. These were added to explicitly include purely spatial structures into

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* Note that when CCA is used, the sum of all canonical eigenvalues has to be divided by the total inertia (which is always = 1 in RDA) to yield the fraction of variance explained.

the model (Legendre 1993). Variation partitioning can then be used to assess what part of the spatial variation in the species data can be related to the measured environmental variables. Note that the inclusion of purely spatial variables is analogous to the introduction of purely temporal variables (cf. above) into the environmental data matrix.

The spatial matrix was constructed following the recommendations of Legendre (1990, see also Legendre 1993). It contains all the terms of a polynomial trend surface regression of the form $z = b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3$, where x and y are the geographic coordinates of the sampling stations (see Table 10 for labels). The number of higher order polynomials to be included is a compromise. On the one hand, including the higher powers of x and y increases the number of parameters to be fitted and so it produces a better-fitting map (including more complex features like patches or gaps, Borcard *et al.* 1992, Heikkinen & Birks 1996). The inconvenient of including many higher power parameters is that they become more and more difficult to interpret ecologically (Legendre & Fortin 1989); for this reason no higher order polynomials than the 3rd have been included. On the other hand, by keeping the number of polynomials low, only the large-scale spatial structures of the species data can be captured (Borcard & Legendre 1994). Small-scale structures (mainly small-scale autocorrelation effects caused by contagious biological processes such as infections or clonal reproduction, but also small-scale environmental patchiness) are not captured by this method.

In this study, variation partitioning was used to assess the relative importance of the different (sets of) variables (listed in Table 9) in explaining the variation in the species data. In our analyses, we followed the procedure proposed by Pinel-Alloul *et al.* (1995) who carried out 4 statistical analyses in order to assess the variation patterns in their data set. In addition, prior to these analyses the contribution of single variables to explaining the variation in the species data was examined (cf. Økland & Odd 1994). The four different approaches proposed by Pinel-Alloul *et al.* (1995) are:

1. A **global** approach which involves all explanatory variables. This approach is mainly used to assess whether all variable (sub)sets contribute significantly to explaining the variation in the species data;
2. **Independent** approaches in which the independent influence of the different (sub)sets of variables on the total variation in the species data is assessed;
3. **Differential** approaches. These analyses are used to quantify the amount of covariation between the different variable (sub)sets. They also allow to test the significance of the additional contribution of a given variable (sub)set in explaining the variation in the species data allowing for the contribution of another variable (sub)set;
4. An **additive** approach in which the results of the independent approaches are combined in order to construct the best final predictive model (i.e. the one with the lowest amount of unexplained variation) taking the results of the other approaches into account.

The contribution of single variables allows to assess the influence of the individual variables on community structure and dynamics. This information cannot be derived from the analyses on the different (sub)sets of variables, although an indication of their importance can also be deduced from the RDA ordination diagrams (chapter 5.3).

The combination of the above-mentioned approaches provides detailed insight into the relative contribution of the different variable (sub)sets in explaining the variation in the various species data sets. Special attention is paid to the contribution of the spatial and temporal variable sets in the different data sets and their relationship with the measured environmental variable sets.

Variation partitioning is especially useful when used in combination with the more traditional use of ordination analyses (cf. above, see chapter 5.3): while the latter gives more detailed information on the structural features of the species data set, the former is more adequate in quantifying the contributions of the different variables (and variable sets) and the amount of covariation between them. However, the most attractive feature of variation partitioning certainly lies in the possibility to assess the amount of purely spatial variation in the species data set.

4. Systematical part

4.1. Introduction

Table 18 lists all diatom taxa observed during this study and provides details of their exact life-form and data set affiliations. For more information on the different life-forms, see chapter 3.4.3. More information on the data set affiliation is given in chapter 5.3.1.

We have adopted the classification system proposed by Round *et al.* (1990, cf. Hartley *et al.* 1996). In the following chapter, the taxa are arranged in alphabetical order within each family and genus.

As the identity of many common estuarine benthic diatoms is still only little known, we have provided a detailed morphological and autecological description for many taxa observed during the cell counts. For each taxon the following information is given:

- **Name + author**
- Reference to the illustrations
- **Most commonly used synonyms**
- **References** to papers with:
  (1) the original description/illsutration of the taxon
  (2) illustrated (LM or SEM) description of its type material
  (3) good (preferably illustrated) descriptions of the taxon
- **Morphological description** with
  (1) cell dimensions: **L** (length in µm), **W** (width of the valve in µm), **W(P)** (width in girdle view), **S** (number of striae in 10 µm), **S(D)** (number of striae in 10 µm on dorsal side of the valve in dorsiventral cells), **S(V)** (number of striae in 10 µm on ventral side of the valve in dorsiventral cells), **S(R)** (number of striae in 10 µm on the valve with a raphe-sternum in heterovalvar cells), **S(P)** (number of striae in 10 µm on the valve without a raphe-sternum in heterovalvar cells), **D** (diameter of the valve of centric diatoms), **F** (number of fibulae in 10 µm in representatives of Bacillariales), **A** (number of areolae in 10 µm in centric valves). Note that when the number of valves measured is not explicitly stated, n = 20. Stria and areolar densities in centric diatoms have been measured as recommended by Ross *et al.* (1979); for pennate diatoms, the recommendations given by Schoeman & Archibald (1976-80) have been followed.
  (2) a detailed morphological light microscopical (LM) and scanning electron microscopical (SEM) description of the cells. This usually consists of a description of the cleaned frustules, although in some cases information on the plastid structure and colony formation is given.
- **Remarks** (on morphology, systematics and nomenclature)
- **Biogeography & Ecology**: This section contains information on the biogeography and ecology [life-form, spatial and seasonal distribution in relation to the measured environmental parameters (mainly sediment type and salinity)] of the taxon. The ecological information is mainly drawn from the ordination analyses and from weighted averaging regression (cf. chapter 3.6.3.). The results from the latter analyses are given in Table 39. When we refer to a taxon as being 'common', this usually means that it is included in data set 3; 'rare' refers to taxa which do not belong to the latter group, while ‘very rare’ indicates that only a few valves belonging to that taxon have been found. Unless the identity of a taxon was unmistakable, the use of published

data on its autecology and biogeography was restricted to those that provided illustrations and/or descriptions which allow unambiguous identification.

- **Label**: the 8-character label given to the species in the ordination diagrams. The label usually refers to the latin binomial of each taxon, i.e. the first four letters refer to the genus while the last four letters refer to the specific epithet.

Not all taxa have been treated in detail. For many well-known truly planktonic species (e.g. *Coscinodiscus*, *Stephanodiscus* and *Skeletonema* spp.) we refer to published descriptions. Likewise, rare taxa which posed no taxonomical problems were not described in detail. Finally, some taxa were too rare in our material to allow unambiguous identification (e.g. *Cymbella* sp., *Entomoneis* spp., *Gomphonema* spp.): these taxa have not been described at all but are only included in the species list (Table 18) where they indicated with an asterisk.

In addition to our own material, we also studied herbarium material (usually type material) in order to verify some identifications. A list of the material examined during this study is given in the table below.

Authority/locality	Material
Cleve et Möller slide n° 255, Hourdel (France)	AWH n° II 9 A12
Cleve et Möller slide n° 155, Balearic Islands	AWH n° II 6 B 5
Frenguelli, Cabo Guardian, Santa Cruz (Argentina)	Frenguelli 379 n° 5, UNLP
Frenguelli, Riacho San Blas (Argentina)	Frenguelli 388 n° 3, UNLP
Grunow, Kalkbay, Cape Town (South Africa)	Grunow slide n° 790, AWH n° VI 41 B10
Van Heurck, Ile de Mors (Denmark)	Types du Synopsis, n° 280, BR
Salah, Blakeney Point, Norfolk (Great Britain)	BM 36399-36402 and 36405-36407
Hustedt, Miang Besar (Borneo)	BRM N 15/51
Hustedt, Leybucht 10301, Leysand (Germany)	BRM N 12/36 (R. M. n° 1136)
Hustedt, Sandplate Memmert 12342 (Germany)	BRM 397/75 (R. M.)
Møller, Præstø Fiord, Denmark	C Møller A XII a 1
Foged, Mbwa maji south of Dar-es-Salaam, Tanzania, 'visceral contents from Holothurian on sandy bottom' (Foged 1975)*	C Foged 35/68*
Grunow, Lysekil, Bohuslan (Sweden)	Grunow slide n° 2106, W

AWH, Van Heurck Diatom Collection, Antwerp (Belgium); UNLP, Collection of the Divisíon Ficología de la Facultad de Ciencias Naturales y Museo de la Universidad Nacional de La Plata (Argentina); BR, National Botanical Garden, Meise (Belgium); BM, Natural History Museum, London (Great Britain); BRM, Friedrich-Hustedt-Arbeidsplatz für Diatomeenkunde, Bremerhaven (Germany); C, Botanical Museum, University of Copenhagen (Denmark); W: Naturhistorisches Museum Wien, Botanische Abteilung (Austria)

* examined by A. Witkowski (cf. Sabbe *et al.* 1995)

We also studied some samples (collected by W. Vyverman) from different estuarine and marine localities in Papua New Guinea and South Australia. In cooperation with A. Witkowski some *B. lucens* material from the Gulf of Gdansk (Baltic Sea, Poland) was studied.

Terminology used in the description of the structures of the silicious cell wall is based on Anonymous (1975), Ross *et al.* (1979), Hendey (1964: valve outlines and structural types), Cox & Ross (1980) and Round *et al.* (1990: cingulum and raphe structures). The terminology used in the description of plastid structure and other cytological characteristics is mainly derived from the studies of Mann (e.g. 1994a) and Cox (e.g. 1988b, 1996).

Figures are referred to with a combination of the plate and figure number (e.g. Fig. 2-3 = Plate 2, figure 3).

4.2. Systematic list

DIVISIO BACILLARIOPHYTA

CLASS COSCINODISCOPHYCEAE

Subcl. Thalassiosirophycidae

Ordo Thalassiosirales

Fam. THALASSIOSIRACEAE Lebour

Thalassiosira Cleve 1873

Genus description: Hasle 1973, Round *et al.* 1990

Thalassiosira is a well-studied genus thanks to the detailed studies (usually involving the type material) of Hasle and Fryxell (cf. the reference list given in Krammer & Lange-Bertalot 1991, Prasad *et al.* 1993 and Muylaert & Sabbe 1996a). Hasle & Syvertsen (1996) provide a key for the marine representatives of this genus.

Some species of this predominantly marine planktonic genus are major components of phytoplankton assemblages in estuarine waters (cf. Belcher & Swale 1986, Sancetta 1990). A detailed account of the most common *Thalassiosira* species from the spring phytoplankton of the Schelde estuary is given by Muylaert & Sabbe (1996a). For completeness, we here repeat the morphological descriptions of some *Thalassiosira* species in addition to those of others. Furthermore, in addition to information on their spatial distribution in the water column of the estuary, the present study pays attention to their spatial and temporal distribution in the intertidal sediments of the Westerschelde. A striking feature of the occurrence of *Thalassiosira* species in estuaries is that there seem to be large differences between the dominant taxa in the water column and in the benthos: some common taxa are exclusively found in the water column and were hardly ever present in the sediments (e.g. *T. pacifica* Gran & Angst); other taxa were exclusively observed in sediment samples (*T. decipiens*), and yet other taxa occur in large numbers both in the plankton and benthos (e.g. *T. proschkinae*). This indicates that some species have adopted a distinct benthic or tychoplanktonic life-form and are not only present as empty valves in the sediment (cf. also *Thalassiosira cedarkeyensis* Prasad, Prasad *et al.* 1993).

The following list is definitely not exhaustive: several other *Thalassiosira* taxa were sometimes found in the sediment, but as these did not occur in the counts, we have not included them in the list below.

Thalassiosira angulata (Gregory 1857) Hasle 1978a [Figs 1-1,1-2, 33-1]

Synonyms:

Orthosira angulata Gregory 1857

References:

(1) Gregory 1857
(2) Hasle 1978a
(3) Hasle 1978a, Hasle & Syvertsen 1996, Muylaert & Sabbe 1996a

Morphology:

D: 13-26 (16 ± 4.1); A: 8-11 (9.7 ± 1.1)

LM - Cells connected by mucus threads forming chains of up to 6 cells. The areolae are usually arranged in an eccentric pattern and become smaller towards the margin of the valve. Near the margin and on the mantle, the areolae are arranged in radial rows. A marginal ring of fultoportulae [3-3.5 (3.2 ± 0.2) in 10 µm], one marginal rimoportula (which is usually placed closer to one fultoportula, Fig 1-1, arrowed) and one central fultoportula are present.

SEM - The external tubes of the marginal fultoportulae possess 'cap-like' structures at their ends. This structure is very reminiscent of the 'flared skirt' structure on the fultoportulae in *T. nordenskioeldii* Cleve.

Remarks: *Thalassiosira angulata* closely resembles *T. decipiens*, from which it can mainly be distinguished in areolar density, the position of the rimoportula, the cap-like structures at the end of the fultoportulae, the radial arrangement of the areolae near the valve margin and its autecology (for more details see Muylaert & Sabbe 1996a).

Biogeography & Ecology: *T. angulata* is common in the plankton in the middle and lower reaches of the Schelde estuary. It was regularly found in low numbers in silty sediments throughout the Westerschelde estuary.

THALANGU

Thalassiosira bramaputrae (Ehrenberg 1854) Håkansson & Locker 1981

Synonyms:

Stephanodiscus bramaputrae Ehrenberg 1854
Coscinodiscus lacustris Grunow in Cleve & Grunow 1880
Thalassiosira lacustris (Grunow) Hasle 1977

References:

(1) Ehrenberg 1854
(2)
(3) Hasle & Lange 1989, Håkansson & Locker 1981

Morphology:

LM & SEM - A detailed description of this species is given by Hasle & Lange (1989).

Biogeography & Ecology: Only a few valves belonging to this freshwater species were found in our sediment samples; they are most probably washed in from the river.

THALBRAM

Thalassiosira curviseriata Takano 1981 [Figs 1-14,1-15,1-16,1-17, 33-6, 33-7]

References:

(1) Takano 1981
(2) Takano 1981
(3) Takano 1980, 1981, Hallegraeff 1984, Bérard-Therriault *et al.* 1987, Hasle & Syvertsen 1996

Morphology:

D: 5-10 (n=20); A: about 27 (n=2)

LM - Valves round but usually giving a pentagonal or hectagonal appearance in LM due to the 'flattening' of the valve face/mantle junction around the marginal fultoportulae [(4?-)5-6 per valve]. The latter bear wings, although in some specimens these have eroded because of the acid treatment of the samples. In the centre of the valve, two (sometimes one?) fultoportulae are present. A (rimo?)portula is present in the marginal ring of fultoportulae, close to one fultoportula. The areolae are very small; the areolation pattern is radial with secondary, curved, tangential rows to fasciculate.

SEM - Only external valve views were observed. Valve face concentrically curved with a steep mantle and a central depression. The marginal fultoportulae have wings (although they are only still partially present in the specimen in Fig. 33-6); one or two fultoportulae are present in the central valve depression. Inbetween these fultoportulae, two large puncta are visible (Fig. 33-7). The opening of a (rimo?)portula can be seen close to a marginal fultoportula (Fig. 33-6). In some specimens, most of the outer valve face is covered with small granules, while in other specimens these granules appear to be absent. The areolae are only visible near the valve margin and in the central depression. The structure of the cingulum is unclear: the copulae appear to be very thick.

Remarks: *T. curviseriata* appears to be closely related to *T. teleata* Takano (Takano 1980): the only good distinguishing feature between the two taxa would be the shape of the wings, a feature which we were not able to observe in our material. We have allocated our specimens to *T. curviseriata* because in most specimens (see however Fig. 33-6) two central fultoportulae were present (*T. teleata* would only possess one). The relationship between both taxa needs further study. The presence of granules on the external valve face seems to be variable, from only a few granules inbetween the areolae to a dense cover (Takano 1981, Hallegraeff 1984, Bérard-Therriault *et al.* 1987, this study).

Biogeography & Ecology: *T. curviseriata* and *T. teleata* have been reported from coastal plankton (forming chain-like or mucilagineous colonies) in Japan (Takano 1980, 1981), Australia (Hallegraeff 1984), the Atlantic coast of North America (benthic material - Bérard-Therriault *et al.* 1987) and Europe (this study). This taxon was one of the more common *Thalassiosira* taxa present in silty sediments throughout the Westerschelde estuary. We also found it in Salah's sediment samples from Blakeney Point (England)(Figs 33-14, 33-15).

THALCURV

Thalassiosira decipiens (Grunow 1878) Jørgensen 1905 [Figs 1-3, 1-4, 1-5, 33-2]

Synonyms:

Coscinodiscus eccentricus var.? *decipiens* Grunow 1878

References:

(1) Grunow 1878
(2) Hasle 1978a
(3) Hasle 1978a, 1979, Bérard-Therriault *et al.* 1987, Cooper 1995a, Hasle & Syvertsen 1996, Muylaert & Sabbe 1996a

Morphology:

D: 8.7-16.2 (13.2 ± 2.3); A: 10-13 (11.5 ± 1)

LM & SEM - Plastids more or less reniform, about 6 per cell. The living cells are often associated with sediment and detrital particles (Fig 1-5). The areolation pattern is eccentric. The areolae become smaller towards the valve margin. A marginal ring of fultoportulae [4-6 (5 ± 0.6) in 10 µm, n=4], one marginal rimoportula (whose position is exactly between two fultoportulae in the marginal ring) and one central fultoportula are present.

Remarks: See *T. angulata*

Biogeography & Ecology: *T. angulata* is a typical marine, planktonic species (Hasle 1978a), whereas *T. decipiens* is most often recorded from shallow, coastal and estuarine environments and seems to be a tychoplanktonic (or even benthic) species (Drebes 1974, Belcher and Swale 1986, Bérard-Therriault *et al.* 1987, Cooper 1995a). *T. decipiens* was the most common (up to 1.2 x 10^6 cells/g SDW) *Thalassiosira* species in silty stations throughout the estuary, but was never found in the plankton of the Schelde (Muylaert & Sabbe 1996a).

THALDECI

Thalassiosira eccentrica (Ehrenberg 1841) Cleve 1904

Synonyms:

Coscinodiscus eccentricus Ehrenberg 1841

References:

(1) Ehrenberg 1841
(2) Fryxell and Hasle 1972
(3) Fryxell and Hasle 1972, Hasle & Syvertsen 1996, Muylaert & Sabbe 1996a

Morphology:

D: 28-52 (37 ± 8.4); A: 8-10 (9 ± 0.8)

LM/SEM - The areolation pattern is eccentric; the areolae diminish in size towards the valve mantle. Two marginal rings of fultoportulae and one marginal rimoportula can be distinguished. In addition to one sub-central fultoportula, adjacent to the central areola, numerous fultoportulae occur scattered over the valve face. On the valve mantle several rings of spines are present.

Biogeography & Ecology: *Thalassiosira eccentrica* is common in the plankton of the middle and lower reaches of the Schelde estuary (Muylaert & Sabbe 1996a). It was only rarely found in the intertidal sediments.

THALECCE

Thalassiosira leptopa (Grunow in Van Heurck 1883) Hasle & Fryxell 1977

Synonyms:

Coscinodiscus (*lineatus* var.?) *leptopus* Grunow in Van Heurck 1883
Coscinodiscus leptopus Grunow in Rattray 1890

References:

(1) Van Heurck 1883
(2) Hasle & Fryxell 1977
(3) Hasle & Fryxell 1977, Hasle & Syvertsen 1996

Morphology:

L: 36.2; A: 9 (n=1)

LM - Areolation pattern linear; the areolae are smaller on the valve mantle. No portulae are present in the valve face.

Biogeography & Ecology: *Thalassiosira leptopa* is present in plankton samples from the Atlantic, Pacific and Indian ocean but is apparently absent from colder waters (Hasle & Fryxell 1977). Only a few valves belonging to this species were found in our sediment samples.

THALLEPT

Thalassiosira nordenskioeldii Cleve 1873

References:

(1) Cleve 1873
(2) Hasle 1978a
(3) Hasle 1978a, Hasle & Syvertsen 1996

Morphology:

D: 9-23 (14 ± 3.8)(n=11)

LM & SEM - Cells connected by mucus threads to form chains of up to 24 cells. Areolation pattern fasciculate. One marginal ring of fultoportulae [4-6 (5 ± 0.6) in 10 µm, n=12], one central fultoportula and a marginal rimoportula are present. The centre of the valve face is depressed. The valve mantle is wide which gives the frustules their typical, octangular shape in girdle view. The outer openings of the marginal fultoportulae are surrounded by a 'flared skirt' (cf. Hasle 1978a). This structure can also easily be distinguished in LM.

Biogeography & Ecology: *Thalassiosira nordenskioeldii* is commonly reported from the plankton of the North Sea, especially in early spring (February-April)(Meunier 1915) but was rare in the Schelde estuary proper (Muylaert & Sabbe 1996a). The distribution of this species is restricted to the northern cold water region and temperate waters (Hasle & Syvertsen 1996). Only a few valves belonging to this (fragile) species were found in our sediment samples.

THALNORD

Thalassiosira proschkinae Makarova 1979

[Figs 1-6, 1-7, 1-8, 33-4, 33-5]

Synonyms:

Thalassiosira spinulata Takano 1981
Thalassiosira proschkinae var. *spinulata* (Takano) Makarova 1988

References:

(1) Makarova *et al.* 1979
(2) Makarova *et al.* 1979
(3) Takano 1981, Belcher and Swale 1986, Feibicke *et al.* 1990, Krammer and Lange-Bertalot 1991, Hasle & Syvertsen 1996, Muylaert & Sabbe 1996a

Morphology:

D: 7-8 (7.5 ± 0.5); A: 16-22 (19 ± 2.1)(n=8)

LM & SEM - In living cells, four chloroplasts can be distinguished (Fig. 1-6). The areolation pattern is radial to eccentric. This species is characterized by a marginal ring of fultoportulae, one subcentral rimoportula and a central fultoportula.

Remarks: Although *Thalassiosira proschkinae* is a distinct and easily recognizable species, it might have often been overlooked or misidentified because of its minute size and association with sediment and detrital particles (cf. Figs 1-6, 33-4). There is no doubt that in our counts we have assigned other minute *Thalassiosira* species (which do not have a subcentral rimoportula) to *T. proschkinae*, although the majority of valves belonged to the latter species.

Biogeography & Ecology: *Thalassiosira proschkinae* was only described in 1979 from the Black Sea but has since been reported as a dominant component of planktonic [Takano 1981, Belcher and Swale 1986, Feibicke *et al.* 1990, Krammer and Lange-Bertalot 1991, Snoeijs 1993, Hasle & Syvertsen 1996] and benthic [Bérard-Therriault *et al.* 1987, Sabbe & Vyverman 1991 (as Spec. 1), Snoeijs 1993, Underwood 1994, as *Coscinodiscus* sp. 1] assemblages in brackish waters worldwide (cf. also *Cyclotella choctawhatcheeana*). In the Schelde estuary, it is extremely abundant in the polyhaline and mesohaline reaches (Muylaert & Sabbe 1996a). *T. proschkinae* was the most commonly found *Thalassiosira* species in the intertidal sediments. In many other studies on intertidal brackish water sediments or other benthic habitats, *T. proschkinae* valves are found (cf.

above). A detailed ecological survey of this species (Feibicke *et al.* 1990) showed that there might be an autochtonous population in benthic habitats. At present, the common occurrence of this species in these habitats is not well understood: either *T. proschkinae* is a typical tychoplanktonic species (specially adapted for this life form, see below), or certain stages in its life cycle are benthic, or its presence is mainly due to sedimentation from the water column. In this respect, it is worth mentioning that, at least in the Schelde estuary, the girdle of most cells is covered with sediment and detrital material, which could cause the cells to sink quicker to the sediment. This phenomenon is also known from other *Thalassiosira* species and might play a role in retaining the cells of this brackish water species in the brackish reaches of the estuary (cf. Muylaert & Sabbe 1996a).

T. proschkinae is a typical brackish water species, which does not occur in freshwater or marine environments (Feibicke *et al.* 1990, Snoeijs 1993, Muylaert & Sabbe 1996a). In this respect, the association of this species with sediment particles could also be a way to promote the retention of this species in the upper and inner reaches of estuaries.

THALPROS

***Thalassiosira* cf. *simplex* Hustedt 1956**

[Figs 1-9, 1-10]

References:

(1) Hustedt 1956
(2) Simonsen 1987
(3) Hasle 1978b

Morphology:

D: 16-16.2; A: 17-18

LM - Valves very flat (both the valve centre and marginal ring of fultoportulae are simultaneously in focus). Areolation pattern irregularly radial with short secondary curves. Near the valve margin, a distinct ring of fultoportulae (10-11 in 10 μm) is present.

Remarks: This taxon belongs to the species complex around *Thalassiosira rudolfii* (Bachmann) Hasle, *T. faurii* (Gasse) Hasle and *T. simplex* Hustedt (cf. discussion in Hasle 1978b). However, due to the rarity of this taxon no specimens could be studied in SEM; it is therefore at present impossible to make a positive identification of this species. *T. rudolfii* and *T. faurii* would have three subcentral fultoportulae, which we can not distinguish in our LM illustrations. Our specimens most closely resemble *T. simplex* in size and dimensions, but this species appears to have a distinctly convex valve (cf. Simonsen 1987). Our valves closely resemble the *T. simplex*? specimens illustrated in Hasle (1978b, Figs. 70-71).

Biogeography & Ecology: *Thalassiosira simplex* was described from a brackish Venezualan lagoon (salinity 1 ‰). The *T. simplex*? specimens illustrated in Hasle (1978b) are from North American rivers and lakes, while Archibald (1983) illustrated a similar diatom (identified as *T. rudolfii*) from the Sundays river in South Africa. *T.* cf. *simplex* was only sporadically found in our material.

THALCFSI

Thalassiosira tenera Proschkina-Lavrenko 1961 [Figs 1-11, 1-12, 1-13, 33-3]

References:

(1) Proschkina-Lavrenko 1961
(2)
(3) Hasle & Fryxell 1977, Hasle & Syvertsen 1996

Morphology:

D: 11.2-20.8; A: 12.5-16.5 (n = 5)

LM - Areolation pattern linear. The valve face areolae become slightly smaller towards the valve face margin. The valve margin is characterized by short but very distinct radial ribs, 25-29 in 10 µm. A ring of fultoportulae (about 5 in 10 µm) is present.

SEM - Valve face flat, mantle shallow (note however that the valve appears to have collapsed). Near the valve margin, small radial ribs are present. Every 5th to 7th rib, a small spine-like structure (eroded external opening of marginal fultoportulae) can be seen. A fultoportula is present inside the central areola.

Remarks: *Thalassiosira tenera* is characterized by the linear areola pattern and the shape of the marginal fultoportulae (Hasle & Syvertsen 1996).

Biogeography & Ecology: *T. tenera* is a cosmopolitan (exclusive polar regions) coastal species, which is often found in brackish water (see list in Hasle & Fryxell 1977, and also Belcher & Swale 1986, Bérard-Therriault 1987, Hasle & Syvertsen 1996). It has not yet been reported from the plankton of the Schelde estuary (Muylaert & Sabbe 1996a), but valves were regularly found in silty sediment samples.

THALTENE

Fam. SKELETONEMATACEAE Lebour

Skeletonema Greville 1865

Genus description: Round *et al.* 1990

Skeletonema costatum (Greville) Cleve is a common component of the phytoplankton assemblages in the marine and brackish parts of the Schelde estuary, while *S. subsalsum* (Cleve-Euler) Bethge is present (though less common) in the plankton of the freshwater tidal and brackish reaches (Muylaert & Sabbe, in press). However, the fragile *Skeletonema* valves were only rarely present in the sediment samples from the Westerschelde.

Fam. STEPHANODISCACEAE (Fricke) Round

Cyclotella Kützing ex Brébisson 1838

Genus description: Round *et al.* 1990

In recent studies on the systematics of the genus *Cyclotella* (e.g. Schoeman & Archibald 1980, Håkansson 1982, Lange & Syvertsen 1989, Håkansson 1990, Wendker 1991, John & Economou-Amilli 1991, Håkansson *et al.* 1993, Håkansson & Kling 1994, Nikiteeva & Likhoshway 1994, Scheffler 1994) the following morphological features of the frustule are usually regarded to be of taxonomic importance: the form and arrangement of the marginal striae, all features (e.g. number, shape, satellite pores) of the central and marginal fultoportulae and the rimoportula(e), the shape and size of the alveoli and the structure of the central area. Other features, such as the presence and the structure of spines and granules are known to be more variable and are therefore considered to be less important (Round *et al.*, 1990).

Cyclotella species are often reported in high numbers from benthic habitats (cf. also *Thalassiosira* spp., Denys 1991b). Whether this is mainly due to sedimentation of dense blooms from the water column (as it appears to be the case with *C. atomus*) or whether they actually form part of the living benthic community requires further investigation.

Cyclotella atomus Hustedt 1937 [Figs 2-1, 2-2, 2-3, 34-1, 34-2]

References:

(1) Hustedt 1937-38
(2) Simonsen 1987, Krammer & Lange-Bertalot 1991, Snoeijs & Potapova 1995
(3) Schoeman & Archibald 1976, Krammer & Lange-Bertalot 1991, Snoeijs & Potapova 1995

Morphology:

D: 5-7.5

LM - Valves circular, marginal zone narrow with about 14-15 costae in 10 µm. Every third to fourth costa appears to be thickened. The central part is rather structureless; one subcentral portula is visible.

SEM - Valve face flat, mantle shallow. Central part of valve face flat and structureless except for the external opening of the subcentral fultoportula. Radial rows (6-7 per stria) of areolae are found on low ridges in the marginal zone; the striae become wider towards the valve margin. The interstriae are situated in shallow furrows. The external openings of the marginal fultoportulae are visible in the valve face/mantle transition. Internally, fultoportulae (with 2 satellite pores each) are present on every third to fifth costa. The subcentral fultoportula has 2 to 3 satellite pores. A small rimoportula is present on the costa opposite the subcentral fultoportula; its slit-like internal opening is obliquely orientated. In a number of specimens some costae are partly covered by a central lamina. The cingulum consists of 3 (?) copulae.

Remarks: Genkal & Kiss (1993) described a new variety of *Cyclotella atomus*, viz. *C. atomus* var. *gracilis* Genkal & Kiss, which can be distinguished from the nominate variety in having a distinct central lamina. However, this feature is variable in our material, even within one valve. The true identity of *C. atomus* needs further study, as up to now little is known about the morphological variability of this species: some published illustrations of this taxon show specimens with slightly different morphological features (cf. Sabater & Klee 1990).

Biogeography & Ecology: *C. atomus* was described from lakes in Sumatra and Java, and has subsequently been reported worldwide (cf. references in Snoeijs & Potapova 1995), mainly from rivers and oligohaline waters (cf. Belcher & Swale 1978). In our benthic material, *Cyclotella atomus* was most abundant in winter and spring in the meso- and oligohaline reaches of the Westerschelde.

CYCLATOM

Cyclotella cf. ***caspia*** Grunow 1878

[Figs 2-19, 2-20, 2-21]

Synonyms:

Cyclotella kuetzingiana var.? *caspia* Grunow in Van Heurck 1882

References:

(1)	Grunow 1878
(2)	Krammer & Lange-Bertalot 1991, Håkansson *et al.* 1993
(3)	Krammer & Lange-Bertalot 1991, Håkansson *et al.* 1993, Hasle & Syvertsen 1996

Morphology:

D: 9.7-18.7

LM - Valves circular. The central part is distinctly tangentially undulated and has little structure. In some specimens, a row of portulae, placed in a semi-circle, is visible in the central part (Fig. 2-21). Marginal area wide, with 20-25 striae in 10 µm.

Remarks: Only a few valves belonging to this taxon were found. Unfortunately, no SEM observations could yet be made so the true identity of this taxon and its relationship to seemingly closely related species, such as *C. choctawhatcheeana*, remains unclear. There is little doubt that some other taxa, such as *C. litoralis* Lange & Syvertsen (see below)(Fig. 3-3), have been identified as *C.* cf. *caspia* during the cell counts.

Biogeography & Ecology: According to Hasle & Syvertsen (1996) *Cyclotella caspia* is a euryhaline species from the northern temperate region. However, given the numerous misidentifications of this taxon (see Håkansson *et al.* 1993), it is not sure whether this characterization is correct. In the Schelde estuary, it was regularly present in silty samples in the polyhaline reaches.

CYCLCFCA

Cyclotella choctawhatcheeana Prasad 1990 [Figs 10-10, 10-11, 10-12, 10-13, 34-3, 34-4]

Synonyms:

Cylotella hakanssoniae Wendker 1991

References:

(1) Prasad *et al.* 1990
(2) Prasad *et al.* 1990
(3) Wendker 1991, Krammer & Lange-Bertalot 1991, Håkansson *et al.* 1993, Cooper 1995a, b, Carvalho *et al.* 1995

Morphology:

D: 8.1-13.1

LM - Valves circular. Central area slightly tangentially undulated, caliculate. Usually, a few portulae are visible in one half of the central part. Marginal zone with 15.5-20 striae in 10 µm.

SEM - Valve face tangentially curved, caliculate. The external openings of subcentral fultoportulae (see below) can be seen in the raised part of the central valve face. The valve face curves gently towards its margin but then curves abruptly into a shallow mantle. The external openings of the marginal ring of fultoportulae are situated on the latter transition, while an incomplete ring of small granules (spines?) is present above the ring of fultoportulae. The interstriae are slightly ridged. Internally, a few (often 4) subcentral fultoportulae (with 3 satellite pores each) are present in one half of the central part. Marginal fultoportulae (with 2 satellite pores each) are present on every second to fourth costa. A small rimoportula (with vertical slit-like internal opening) is present on a costa opposite the subcentral fultoportulae. The cingulum appears to consist of numerous copulae.

Remarks: The story of *C. choctawhatcheeana* is quite comparable to that of *Thalassiosira proschkinae* (see there). After being described in 1990 (Prasad *et al.* 1990), it soon appeared to be one of the most widespread *Cyclotella* species in brackish waters, both in estuaries (e.g. Cooper 1995b) and inland saline lakes (Carvalho *et al.* 1995). No less than 5 detailed papers have been dedicated to the morphology and (paleo-)ecology of this species (Prasad *et al.* 1990, Wendker 1991, Håkansson *et al.* 1993, Cooper 1995b, Carvalho *et al.* 1995). It also appears that *C. choctawhatcheeana* has often been referred to as *C. caspia* in the literature (Håkansson *et al.* 1993 and references therein).

Biogeography & Ecology: *C. choctawhatcheeana* is a cosmopolitan and often dominant species in brackish waters, both coastal and inland. It is probably mainly a planktonic species but is also often found in benthic and periphytic samples (see references in Håkansson *et al.* 1993). *C. choctawhatcheeana* has dramatically increased in abundance in Chesapeake Bay (USA) in the last 50 years (Cooper 1995b), which according to the author can be ascribed to recent anthropogenic changes in the area (eutrophication, turbidity, changes in freshwater input).
C. choctawhatcheeana is common in the plankton of the oligo- and mesohaline reaches of the Westerschelde estuary; it occurs in chains as in the type material from Choctawhatchee Bay (Prasad *et al.* 1990). Note that in the Baltic area (Wendker 1991, Håkansson *et al.* 1993) chain-building was never observed. *C. choctawhatcheeana* was commonly found in silty sediments.

CYCLCHOC

Cyclotella meneghiniana Kützing 1844 [Figs 2-14, 2-15, 2-16, 35-1, 35-2]

References:

(1) Kützing 1844
(2) Håkansson (1990)
(3) Lowe 1975, Schoeman & Archibald 1980, Håkansson 1982, Battarbee *et al.* 1984, Håkansson 1990

Morphology:

LM & SEM - *C. meneghiniana* was described in detail by Lowe (1975), Schoeman & Archibald (1980), Håkansson (1982), Battarbee *et al.* (1984), and Håkansson (1990).

Remarks: For remarks and comparison with *C. scaldensis*, see there.

Biogeography & Ecology: *Cyclotella meneghiniana* is known to prefer brackish waters (Hustedt 1930) or eutrophic waters with high conductivity (Håkansson 1990) and appears to be very common in the freshwater tidal reaches of estuaries (Filardo & Dunstan 1985, De Sève 1993). *Cyclotella meneghiniana* was mainly found in silty sediments in the mesohaline reaches of the estuary. As *C. atomus*, it was more abundant in the colder months. See also *C. scaldensis*.

CYCLMENE

Cyclotella radiosa (Grunow 1882) Lemmermann 1900

Synonyms:

Cyclotella comta var. *radiosa* Grunow in Van Heurck 1882

References:

(1) Van Heurck 1882
(2) Krammer & Lange-Bertalot 1991
(3) Krammer & Lange-Bertalot 1991, Snoeijs & Potapova 1995

Morphology:

D: 14.2-28.5

LM - Valves circular. Central part flat, irregularly delimited and perforated by numerous puncta. The marginal zone is rather wide, with 16-18 striae in 10 µm. Every third to fifth costa appears to be thickened.

Biogeography & Ecology: *Cyclotella radiosa*, a planktonic species from eutrophic waters, was only rarely found in our sediment samples. It is rare in the plankton of the freshwater tidal part of the Schelde estuary (Muylaert, pers. comm.).

CYCLRADI

Cyclotella scaldensis Muylaert & Sabbe 1996 [Figs 2-17, 2-18, 34-5, 34-6]

References:

(1) Muylaert & Sabbe 1996b
(2) Muylaert & Sabbe 1996b
(3) Muylaert & Sabbe 1996b

Morphology:

D: 16.3-33.8 (20.3 ± 4.3, n = 29)

LM - Valves circular. The central area is transversely undulate and distinctly colliculate, the colliculae being radially arranged near the margin of the central area. The marginal zone has 7.2-11.2 (8.5 ± 1.0, n = 27) striae in 10 µm; the striae and costae are crossed by a hyaline ring. Fultoportulae are present near the valve margin at the end of 30 to 75 % of the costae; 1 to 9 fultoportulae can be seen in the raised part of the central valve face. Careful focussing also reveals the presence of one large marginal rimoportula.

SEM - As the whole valve face is externally covered by a dense sheet of granules, it is difficult to be certain about the areolation of the marginal zone. We therefore use the term 'ridges' and 'furrows' (instead of striae and interstriae) to indicate the exact position of certain structures. The marginal zone consists of ridges separated by furrows. The shape of the ridges is rectangular. Areolae perforate the cell wall in the marginal zone; their exact location, on the marginal ridges, can only be seen in broken valves. Whether the striae become wider towards the valve margin (as in *C. meneghiniana*, cf. Håkansson & Kling 1994) is impossible to assess. Granules cover the entire outer valve surface and sometimes form dendritic silica structures. Spines are present at the end of some furrows on the valve face - valve mantle junction. They are conical and have a buttressed base. On the valve mantle, below some furrows, the external openings of fultoportulae can be seen; they are short and tubular and surrounded by a more or less structureless aggregation of silica. The external opening of the rimoportula consists of a large nodule and is also situated below a furrow in the marginal zone, though slightly closer towards the valve centre than the openings of the fultoportulae.

The internal central area is smooth. The central fultoportula(e) have 3 satellite pores each and are more or less arranged in a semicircle. Their number appears to increase with valve diameter. The costae in the marginal area are partially covered by a central lamina. Fultoportulae with 3 satellite pores each are present on every second to fifth costa (or on 30 to 75 % of all costae). They are more densely spaced when the valves are larger. The marginal rimoportula is placed on a costa opposite the central fultoportula(e). It is large and has a twisted stalk, which causes its internal slitlike opening to be obliquely orientated. The valvocopula is as broad as the valve mantle (cf. Muylaert & Sabbe 1996b, Fig. 15). The first copula is much smaller and open. The second copula is as broad as the valvocopula and has a ligula that fits in the opening of the first copula. The third copula is as broad as the second and is also open. The opening of the third copula is covered by the ligula of the fourth and last copula, which again is narrow. The openings in the copulae are arranged in a dextral pattern (Fryxell *et al.* 1981). The external surface of the cingulum is completely covered with small granules, similar to but smaller than the ones on the valves.

Remarks: *C. scaldensis* closely resembles *C. meneghiniana*, especially in LM. However, it differs from the latter species in the following respects: (1) the central area is distinctly colliculate; (2) the alveolar openings are smaller (relative to the radius of the valve) due to the presence of an internal central lamina; (3) the marginal fultoportulae are only present on 30 to 75 % of the costae; (4) the marginal rimoportula is large and twisted and has a distinct, knob-like external opening. Other striking differences between the two species concern the external ornamentation of the valve: the valves and the cingulum in *C. scaldensis* are covered by a dense layer of small granules, while the marginal spines have a distinctly different shape than the ones in *C. meneghiniana* and are never accompanied by minor spines. Although the latter features might not be of great taxonomic value, they appeared to be very stable within the studied populations.

C. scaldensis can easily be distinguished from some other common estuarine *Cyclotella* species: apart from being larger, it differs from *C. atomus*, *C. choctawatcheeana* and *C. caspia* Grunow, in having three instead of two satellite pores on the marginal fultoportulae (Lowe 1975, Genkal & Kiss 1993, Håkansson *et al.* 1993).

For a more complete discussion of this species and its relationship to similar species, see Muylaert & Sabbe (1996b).

Biogeography & Ecology: *C. scaldensis* is the most abundant diatom species in the spring phytoplankton communities of the freshwater and oligohaline tidal reaches of the Schelde estuary (Muylaert & Sabbe 1996b). It was also found in the intertidal sediments of the Westerschelde but as no distinction was made between this species and *C. meneghiniana*, it is impossible to assess whether the spatial and seasonal distribution of these species in the sediments is different.

CYCLMENE

Cyclotella striata (Kützing 1844) Grunow 1880

[Figs 3-1, 3-2, 35-3, 35-4]

Synonyms:

Coscinodiscus striatus Kützing 1844

References:

(1) Kützing 1844
(2)
(3) Lange & Syvertsen 1989, Krammer & Lange-Bertalot 1991, Hasle & Syvertsen 1996, Håkansson 1996

Morphology:

D: 23.7 - 28.1 (n=2)

LM - Valves circular. Central part transversely undulate and colliculate. Marginal area rather narrow, with alveoli which are partly covered by a central lamina. Costae 11-12 in 10 µm. A marginal fultoportula appears to be present on every second to third fultoportula.

SEM - Valve face strongly transversely undulate and colliculate. In the marginal area, radial striae are present in shallow furrows, while the interstriae are slightly ridged. The striae are composed of two main rows of distinct areolae, adjacent to the ridged interstriae, and one (or more?) very short rows of smaller areolae. Long spines are sometimes present on the interstriae on the valve face/mantle junction. When occurring on the same interstria, the spines are situated above the external openings of the marginal fultoportulae (Fig. 35-4). The external opening of the rimoportula is a large, twisted nodule (Fig. 35-4, arrowed). Internally, the valve is characterized by the presence of marginal chambers with coarse and costate interstriae (cf. Lange & Syvertsen 1989). The marginal fultoportulae are situated on the second to fourth interstria (always on a costate interstria); every fultoportula has 3 satellite pores. There are two alveoli per marginal chamber (note that not all coarse interstriae form marginal chambers!). No central fultoportulae are visible. The marginal rimoportula is large and has a twisted, slit-like internal opening.

Remarks: *Cyclotella striata* specimens from the type locality (Cuxhaven, Elbe estuary, Germany) have been described in detail by Håkansson (1986, 1996) and Lange & Syvertsen (1989). Our specimens correspond well to the specimens from Cuxhaven and were therefore identified as *C. striata*.

The valve shown in Fig. 3-3 clearly belongs to the *C. striata*-complex (cf. Håkansson *et al.* 1993). They probably belong to *C. litoralis* Lange & Syvertsen (syn. *C. striata* var. *baltica*, Håkansson *et al.* 1993, Håkansson 1996).

Biogeography & Ecology: *C. striata* is a brackish-marine species from the northern temperate region (Hasle & Syvertsen 1996). It was only rarely found in the Westerschelde sediments, but is present in the plankton of the brackish and marine reaches of the Schelde estuary (Muylaert 1994).

CYCLSTRI

Cyclotella sp. 1

[Figs 2-7, 2-8, 2-9]

Morphology:

D: 4.6-5 (n=3)

LM - Valves circular. Marginal zone narrow, finely striated (23-27 striae in 10 µm). About every sixth costa appears to be thickened. The central area is structureless; one subcentral portula is present.

Remarks: This small *Cyclotella* species is very reminiscent of *C. atomus* but has a much finer structure. It also resembles a small *Cyclotella* species reported from Chesapeake Bay by Cooper (1995a), but this taxon also has a coarser structure (12-18 striae in 10 µm).

Biogeography & Ecology: *Cyclotella* sp. 1 was mainly found in silty sediments in the polyhaline reaches of the estuary. Unlike *C. atomus* and *C. meneghiniana*, it does not appear to be more abundant in winter and spring.

CYCLSP01

Cyclotella sp. 2

[Figs 2-4, 2-5, 2-6]

Morphology:

D: 6.9 (n=1)

LM - Valves circular. Central part raised and slightly tangentially undulated, with bumps and hollows. Marginal zone wide (occupying almost half the valve width), finely striated (23-27.5). No thickened striae are visible. A ring of spines or granules seems to be present near the valve margin.

Biogeography & Ecology: Valves belonging to this taxon were only rarely found in silty sediments throughout the estuary.

CYCLSP02

Cyclostephanos Round 1987

Genus description: Theriot *et al.* 1987, Round *et al.* 1990

A few valves belonging to *Cyclostephanos dubius* (Fricke) Round were observed in the sediment samples. *C. dubius* is a truly planktonic species in slightly brackish waters (Krammer & Lange-Bertalot 1991). For a detailed description, see Krammer & Lange-Bertalot 1991.

Stephanodiscus Ehrenberg 1845 (Ehrenberg 1846)

Genus description: Round *et al.* 1990

Three species, viz. *Stephanodiscus hantzschii* Grunow, *S. medius* Håkansson and *S. parvus* were regularly observed in our sediment samples. All three species are common in the plankton of freshwater tidal reaches and the tributaries of the Schelde (Muylaert 1994, Muylaert *et al.*, subm.). As they do not occur in brackish or marine waters, the presence of single valves in the sediments of the Westerschelde estuary is due to sedimentation of dead valves imported from the river. For more information on this genus, we refer to Krammer & Lange-Bertalot (1991) and the references therein.

Thalassiocyclus Håkansson & Mahood 1993

Genus description: Håkansson & Mahood 1993

This genus was recently established to accomodate the diatom originally described as *Stephanodiscus lucens* (Hustedt 1957), which combines characteristics of both *Stephanodiscus* and *Thalassiosira*.

Thalassiocyclus lucens (Hustedt 1939) Håkansson & Mahood 1993 [Fig. 3-4]

Synonyms:

Stephanodiscus lucens Hustedt 1939
Cyclotella lucens (Hustedt) Simonsen 1987

References:

(1) Hustedt 1939
(2) Simonsen 1987, Håkansson & Mahood 1993
(3) Krammer & Lange-Bertalot 1991, Håkansson & Mahood 1993

Morphology:

A detailed morphological description of this species can be found in Håkansson & Mahood (1993).

Biogeography & Ecology: *T. lucens* was only rarely observed in our sediment samples; it is very rare in the plankton of the Schelde estuary (Muylaert, pers. comm.). *T. lucens* was originally described as an oligohalobous species from sediments in the Ems estuary (Hustedt 1939), and has subsequently been reported from estuaries in Europe (Krammer & Lange-Bertalot 1991, this study) and North America (Håkansson & Mahood 1993).

STEPLUCE

Subcl. Coscinodiscophycidae

Ordo Melosirales

Fam. MELOSIRACEAE Kützing

Melosira Agardh 1824

Genus description: Round *et al.* 1990, Krammer & Lange-Bertalot 1991

Melosira nummuloides Agardh 1824

References:

(1)	Agardh 1824
(2)	
(3)	Krammer & Lange-Bertalot 1991, Snoeijs 1993, Hasle & Syvertsen 1996

Morphology:

A detailed description of this species can be found in Krammer & Lange-Bertalot (1991).

Biogeography & Ecology: *Melosira nummuloides* is a common and widespread epilithic, epiphytic and planktonic species in brackish and marine waters (Krammer & Lange-Bertalot 1991, Snoeijs 1993). Only a few valves were found in the Westerschelde sediments. *M. nummuloides* is common in the plankton of the oligohaline part of the Schelde estuary (Muylaert, pers. comm.).

MELONUMM

Fam. HYALODISCACEAE Crawford

Podosira Ehrenberg 1840

Genus description: Round *et al. 1990*

Podosira stelliger (Bailey 1854) Mann 1907

Synonyms:

Hyalodiscus stelliger Bailey 1854

References:

(1)	Bailey 1854
(2)	
(3)	Hendey 1964

Morphology:

A description of this species is provided by Hendey (1964).

Remarks: According to Round *et al.* (1990), *Podosira stelliger* should be returned to its original genus.

Biogeography & Ecology: *Podosira stelliger* is a common marine tychoplanktonic species. It usually lives attached to a substratum but is also found in the plankton. It was frequently present in silty sediment in the polyhaline reaches of the estuary.

PODOSTEL

Ordo Paraliales

Fam. PARALIACEAE Crawford

Paralia Heiberg 1863

Genus description: Round *et al.* 1990, Crawford *et al.* 1990

Paralia sulcata (Ehrenberg 1838) Cleve 1873

Synonyms:

Gaillonella sulcata Ehrenberg 1838
Melosira sulcata (Ehrenberg) Kützing 1844

References:

(1) Ehrenberg 1838
(2)
(3) Crawford 1979, Roelofs 1984, Cooper 1995a, Hasle & Syvertsen 1996

Morphology:

A detailed morphological description of this species can be found in Crawford (1979).

Remarks: Cooper (1995a) pointed out that the brackish-marine diatom which is usually reported as *Paralia sulcata* might actually have been confused with *P. marina* (W. Smith) Heiberg, as *P. sulcata* would be a fossil species.

Biogeography & Ecology: *Paralia sulcata* is found both in the benthos and plankton of coastal areas and estuaries (cf. Hasle & Syvertsen 1996); it is probably cosmopolitan. *P. sulcata* is often considered as a benthic diatom ('bottom form'), which easily becomes resuspended into the water column (Hendey 1964, Denys 1991b, Prasad *et al.* 1993). According to Roelofs (1984), the abundance of *P. sulcata* increases with increasing salinity in estuarine inlets. In the Schelde estuary it is rarely observed in the plankton (Muylaert, pers. comm.), while it is common in silty sediments throughout the year.

PARASULC

Pseudopodosira Jousé in Proschkina-Lavrenko 1949

Genus description: Proschkina-Lavrenko 1949, Olshtynskaja 1990

Pseudopodosira westii (W. Smith 1856) Sheshukova-Poretzkaya & Gleser 1964

Synonyms:

Melosira westii W. Smith 1856

References:

(1) W. Smith 1856
(2)
(3) Olshtynskaja 1990

Morphology:

A detailed morphological description of this species can be found in Olshtynskaja (1990).

Biogeography & Ecology: *Pseudopodosira westii* is a common marine species in the North Sea (Hendey 1964). In the Schelde estuary, it was frequently found in silty sediments in the polyhaline reaches of the estuary.

PSEUWEST

Ordo Aulacoseirales

Fam. AULACOSEIRACEAE Crawford

Aulacoseira Thwaites 1848

Genus description: Round *et al.* 1990, Krammer & Lange-Bertalot 1991

Aulacoseira ambigua (Grunow in Van Heurck 1882) Simonsen 1979

Synonyms:

Melosira crenulata var. *ambigua* Grunow in Van Heurck 1882

References:

(1) Van Heurck 1882
(2)
(3) Simonsen 1979, Krammer & Lange-Bertalot 1991

Morphology:

LM & SEM description: Krammer & Lange-Bertalot 1991, Cox 1996

Biogeography & Ecology: See *A. granulata*

AULAAMBI

Aulacoseira granulata (Ehrenberg 1843) Simonsen 1979

Synonyms:

Gallionella granulata Ehrenberg 1843

References:

(1) Ehrenberg 1843
(2)
(3) Simonsen 1979, Krammer & Lange-Bertalot 1991, Cox 1996

Morphology:

LM & SEM description: Krammer & Lange-Bertalot 1991, Cox 1996

Biogeography & Ecology: Both *Aulacoseira ambigua* and *A. granulata* are typical planktonic species in eutrophic freshwaters (Cox 1996). The rare specimens found have been washed in from the river basin and freshwater tidal reaches of the Schelde.

AULAGRAN

Ordo Coscinodiscales

Fam. COSCINODISCACEAE Kützing

Coscinodiscus Ehrenberg 1838

Genus description: Round *et al.* 1990, Hasle & Syvertsen 1996 (and references therein)

Complete valves belonging to *Coscinodiscus* species were only sporadically found in our sediment samples. However, often small parts of the valves were found but these could usually not be identified to species level. Moreover, *Coscinodiscus* is a marine planktonic genus (Hasle & Syvertsen 1996), and therefore its occurrence in the sediments is solely due to sedimentation from the water column.

A few valves of *Coscinodiscus denarius* A. Schmidt, *C. jonesianus* (Greville) Ostenfeld and *C. marginatus* Ehrenberg were encountered during the counts. For a detailed description of these species, we refer to Hustedt (1930), Hendey (1964) and Hasle & Syvertsen (1996).

Fam. AULACODISCACEAE (Schütt) Lemmermann

Aulacodiscus Ehrenberg 1844

Genus description: Round *et al.* 1990, Hasle & Syvertsen 1996

Aulacodiscus argus (Ehrenberg 1844) A. Schmidt 1886

Synonyms:
Tripodiscus argus Ehrenberg 1844

References:
(1) Ehrenberg 1844
(2)
(3) Hendey 1964, Hasle & Syvertsen 1996

Morphology:
LM & SEM description: Hasle & Syvertsen 1996

Biogeography & Ecology: Only a few valves belonging to this coastal planktonic species were found in our sediment samples.

AULAARGU

Fam. HEMIDISCACEAE Hendey emend. Simonsen

Actinocyclus Ehrenberg 1837

Genus description: Round *et al.* 1990, Hasle & Syvertsen 1996

Actinocyclus normanii (Gregory 1859) Hustedt 1957 f. ***normanii*** / f. ***subsalsus*** (Juhlin-Dannfelt 1882) Hustedt 1957 [Fig. 3-8]

Synonyms:
Coscinodiscus normanii Gregory in Greville 1859
Coscinodiscus subsalsus Juhlin-Dannfelt 1882

References:

(1) Juhlin-Dannfelt 1882
(2)
(3) Hasle 1977, Kiss *et al.* 1990, Krammer & Lange-Bertalot 1991, Snoeijs & Vilbaste 1994, Hasle & Syvertsen 1996

Morphology:

D: 21.9-41.2 (n=2)

LM & SEM description: Hasle (1977)

Remarks: *Actinocyclus normanii* f. *normanii* and *A. normanii* f. *subsalsus* are closely related morphologically and only differ in size (although there is a certain overlap) and ecology (Hasle 1977): while *A. normanii* f. *normanii* mainly occurs in marine and brackish waters, *A. normanii* f. *subsalsus* would be most abundant at lower salinities and would also occur in fresh water (Hasle 1977). However, more recently many authors do not distinguish between both forms, mainly because no difference in salinity preference is found (cf. Kiss *et al.* 1990, Rehbehn *et al.* 1993 and references therein) but also because there appears to be a large overlap in size (Kiss *et al.* 1990).

Biogeography & Ecology: *A. normanii* (both forms) was only rarely found in the sediment samples. Rehbehn *et al.* (1993) investigated the distribution of *A. normanii* in the plankton of 5 German estuaries and found that it mainly occurred in the freshwater tidal reaches of these estuaries. *A. normanii* appeared to be very well adapted to the strongly changing light conditions in these turbid and dynamic reaches.

A. normanii is regarded as an indicator of water pollution or eutrophication (cf. Kiss *et al.* 1990 and references therein). However, its invasive appearance in the Danube river in Hungary in 1988 could not be explained by eutrophication, as the Danube had already been hypertrophic for years (Kiss *et al.* 1990).

Actinocyclus normanii (both forms) are present in low numbers in the freshwater tidal reaches of the Schelde estuary and its tributaries (Muylaert *et al.*, subm.). Only a few valves were found in the intertidal sediments of the Westerschelde estuary.

ACTINONO/ACTINOSU

Actinocyclus octonarius Ehrenberg 1838

Synonyms:

Actinocyclus ehrenbergii Ralfs in Pritchard 1861

References:

(1) Ehrenberg 1838
(2)
(3) Hendey 1964, Hasle & Syvertsen 1996

Morphology:

D: 31.5-86 (n=2)

LM & SEM description: Hasle & Syvertsen 1996

Biogeography & Ecology: Only a few valves of this cosmopolitan species were found; it is common in the plankton of coastal areas.

ACTIOCTO

Fam. HELIOPELTACEAE H. L. Smith

Actinoptychus Ehrenberg 1843

Genus description: Round *et al.* 1990

Actinoptychus senarius (Ehrenberg 1838) Ehrenberg 1843

Synonyms:

Actinocyclus senarius Ehrenberg 1838

References:

(1) Ehrenberg 1838
(2)
(3) Bérard-Therriault *et al.* 1987, Snoeijs & Potapova 1995, Hasle & Syvertsen 1996

Morphology:

D: 15.6-48-7 (-74.4)

LM & SEM: see Hasle & Syvertsen 1996

Remarks: No original description of this easily recognizable species is given.

Biogeography & Ecology: *Actinoptychus senarius* is a cosmopolitan, tychoplanktonic species (Hendey 1964); it is common in both plankton and silty intertidal sediments throughout the Westerschelde estuary (Muylaert & Sabbe, subm.).

ACTPSENA

Actinoptychus splendens (Shadbolt 1854) Ralfs in Pritchard 1861

Synonyms:

Actinosphaenia splendens Shadbolt 1854

References:

(1) Shadbolt 1854
(2)
(3) Hendey 1964, De Wolf & Denys 1993

Morphology:

LM & SEM: Hendey 1964

Biogeography & Ecology: The distribution and ecology of this tychoplanktonic, cosmopolitan species is discussed in De Wolf & Denys 1993.

ACTPSPLE

Subcl. Biddulphiophycidae

Ordo Triceratiales

Fam. TRICERATIACEAE (Schütt) Lemmermann

Auliscus Ehrenberg 1843

Genus description: Round *et al.* 1990

Auliscus sculptus (W. Smith 1853) Ralfs in Pritchard 1861

Synonyms:

Eupodiscus sculptus W. Smith

References:

(1) W. Smith 1853
(2)
(3) Hendey 1964

Morphology:

D: 28.9-44.5 (n=2)

LM - Valves broadly elliptical. Two distinct ocelli are present on both sides of the valve. A complex, radiate pattern of ridges and rows of areolae covers the whole valve face except for the centre.

SEM - Only one internal valve view was observed. Valve face curved. The internal view reveals a distinct 8-shaped depression in the centre of the valve. Internally, the areolae are covered with domed vela (cf. Round *et al.* 1990).

Remarks:

Biogeography & Ecology: *Auliscus sculptus* is a benthic species which lives attached to sand grains (cf. SEM illustrations in Vos 1986). It was very rare in our material.

AULISCUL

Cerataulus Ehrenberg 1843

Genus description: Round *et al.* 1990

Cerataulus radiatus (Roper 1859) Ross in Hartley 1986

Synonyms:

Biddulphia radiata Roper 1859
Cerataulus smithii Ralfs in Pritchard 1861

References:

(1) Roper 1859
(2)
(3) Hendey 1964, Hartley 1986

Morphology:

A description of this species is given by Hendey (1964).

Biogeography & Ecology: Only a few valves belonging to this coastal, tychoplanktonic (?) species were found in our material (cf. Denys 1991b).

CERARADI

Odontella Agardh 1832

Genus description: Round *et al.* 1990, Hasle & Syvertsen 1996

Odontella aurita (Lyngbye 1819) Agardh 1832

Synonyms:

Diatoma aurita Lyngbye 1819
Biddulphia aurita (Lyngbye) Brébisson 1838

References:

(1) Lyngbye 1819
(2)
(3) Takano 1984, Hasle & Syvertsen 1996

Morphology:

A detailed morphological description of this species can be found in Hendey (1964) and Takano (1984).

Biogeography & Ecology: *Odontella aurita* is a common coastal species, which is usually attached in long chains to a substratum (Hendey 1964). It is probably cosmopolitan (Hasle & Syvertsen 1996). *O. aurita* is common in silty sediment samples of the Westerschelde and appears to be more abundant in the polyhaline reaches.

ODONAURI

Odontella rhombus (Ehrenberg 1841) Kützing 1849

Synonyms:

Zygoceros rhombus Ehrenberg 1839
Biddulphia rhombus (Ehrenberg 1839) W. Smith 1856

References:

(1) Ehrenberg 1841
(2)
(3) Hasle & Syvertsen 1996

Morphology:

A detailed morphological description of this species can be found in Hendey (1964).

Biogeography & Ecology: *O. rhombus* is a common coastal species in the North Sea (Hendey 1964). In the Westerschelde sediments, it was much rarer than *O. aurita* and *O. rostrata*.

ODONRHOM

Odontella rostrata (Hustedt 1939) Simonsen 1987 [Figs 3-11, 3-12, 35-5]

Synonyms:

Biddulphia rostrata Hustedt 1939

References:

(1) Hustedt 1939
(2) Simonsen 1987
(3) Sar 1989

Morphology:

L: 19.7; W: 12.7 (n=1)

LM - Valves elliptical with rostrate apices. The valves are strongly convex with an elevation in the centre of the valve. Near both apices, a horn-like elevation is present. In the central elevation, two long spine-like structures can be seen in some specimens, although they have disappeared in many valves. The areolae are radial, about 20 in 10 µm. Numerous ribs connect the central elevation with the lower part of the valve.

SEM - Only external valve views were observed. Valves strongly convex. The valve margin has a distinct, recurved rim. The central elevation can be either pronounced (Fig. 35-5) or indistinct. The horn-like elevations bear ocelli but these can not be distinguished in our material (cf. however Sar 1989). The spine-like structures are the external tubes of two rimoportulae (cf. Sar 1989). The external openings of the areolae are covered with domed occlusions. Apart from the radial ribs connecting the central area with the lower part of the valve, a more or less developed network of ribs lies inbetween the areolae. Numerous small spines are present on the intersections of these ribs. At least three wide, punctate copulae are present.

Remarks: Although the domed occlusions of the areolae were described as vela by Sar (1989), they look more like rotae (cf. Sar 1989, Fig. 3). In that case, they would be identical to the occlusions of *O. aurita* (cf. Takano 1984, Fig. 8). The relationship between both species needs further study, as the main distinguishing features seem to concern valve shape and the presence of ribs. It is also not sure whether these species belong in the genus *Odontella* (cf. also Round *et al.* 1990), given the structure of the areolae, which are occluded by rotae and do not appear to be loculate as characteristic for the genus *Odontella*.

Biogeography & Ecology: *O. rostrata* has been reported from sediments along the North Sea coasts (Hustedt 1939, this study) but also from brackish waters in Africa (Compère 1991) and from oceanic plankton samples in the South Atlantic Ocean (Sar 1989). Its exact life-form is unknown, as it is present in plankton samples but is also often found in benthic environments (cf. *O. aurita*). Its distribution within the estuary is similar to that of *O. aurita*.

ODONROST

Triceratium Ehrenberg 1839 (Ehrenberg 1841)

Genus description: Round *et al.* 1990

Triceratium favus Ehrenberg 1839

References:

(1) Ehrenberg 1841
(2)
(3) Hendey 1964

Morphology:

A description of this species is given by Hendey (1964).

Biogeography & Ecology: *Triceratium favus* is a common marine coastal species in the North Sea (Hendey 1964). It was very rare in the Westerschelde sediments.

TRICFAVU

Fam. PLAGIOGRAMMACEAE De Toni

Dimeregramma Ralfs in Pritchard 1861

Genus description: Round *et al.* 1990

Dimeregramma minor (Gregory 1857) Ralfs in Pritchard 1861

[Figs 3-13, 3-14,]

Synonyms:

Denticula minor Gregory 1857

References:

(1) Gregory 1857
(2)
(3) Hustedt 1927, Poulin *et al.* 1984a, Round *et al.* 1990, Cooper 1995a, Snoeijs & Potapova 1995

Morphology:

L: 11.2-36.9; W: 5.4-8.7; S: 10-13.5 (large form)
L: 7.5-8.7; W: 3.7-4.4; S: 13-17 (small form)

LM - Valves lanceolate with sometimes slightly produced, rounded apices. Axial area narrowly lanceolate, often more or less transapically expanded in the centre of the valve. Striae radiate, composed of distinct, roundish areolae. At both poles, a hyaline area is present.

SEM - Only an internal valve view (of the small form) was observed. Valve face rather curved in transapical section, gradually merging into the mantle. Areolae round, occlusion type not visible. At both poles, a large apical pore field is present. Cingulum structure unknown.

Remarks: Two different forms, which apparently only differ in size and stria density, were observed: a small and a large form. At first sight, these appear to correspond to two varieties, viz. the nominate variety and *Dimeregramma minor* var. *nana* (Gregory) Van Heurck 1885. However, the published data (Hustedt 1927, Hendey 1964) on these taxa do not correspond to the two Westerschelde forms: *D. minor* usually has 9-10 str./10 µm and var. *nana* about 14 str./10 µm (Hustedt 1927). Other reports of the latter variety do not correspond to each other (Poulin *et al.* 1984a: 12 str./10 µm, John 1983: 12-14 str./10 µm). Cooper (1995a) did not distinguish between these two varieties as intermediate forms were present. The relationship between the two forms is as yet unclear and requires further study. We did not distinguish between both forms in the cell counts.

Biogeography & Ecology: *Dimeregramma minor* is apparently cosmopolitan (Hendey 1964, Navarro 1982, John 1983, Poulin *et al.* 1984a, Cooper 1995a). In the Schelde estuary, it was mainly present in sandy sediments in the polyhaline reaches, where it grows attached to sandgrains by a short stalk.

DIMEMINO

Plagiogramma Greville 1859

Genus description: Round *et al.* 1990

Plagiogramma staurophorum (Gregory 1857) Heiberg 1863

[Figs 35-6, 35-7]

Synonyms:

Denticula staurophora Gregory 1857

References:

(1) Gregory 1857
(2) Hasle *et al.* 1983
(3) Round *et al.* 1990, Snoeijs & Potapova 1995

Morphology:

L: 13.1-22.5; W: 4.8-6.2; S: 12-14.5

LM - Valves lanceolate, apices cuneate to rounded. Axial area absent; centrally a plain area, surrounded by distinct ribs, is present. Striae parallel to radiate, composed of large, more or less square to rectangular areolae. The poles are devoid of areolae.

SEM - Valve face more or less flat, curving rather abruptly into the mantle. Centrally, a plain fascia is present. Internally, this area is enclosed between two distinct, transapical ribs (pseudosepta, cf. Round *et al.* 1990) and the valve margin. The areolae are occluded by cribra which lie near the outer valve surface. Internally, the striae (except for the ones adjacent to the fascia) are separated by thickened virgae. At both poles, a large apical pore field is present. A marginal ring of spines is present on the valve face margin. Cingulum structure not observed.

Remarks: The stria density of our specimens is distinctly higher than the values reported in the literature (cf. Hustedt 1927, John 1983, Snoeijs & Potapova 1995).

Biogeography & Ecology: An apparently cosmopolitan (cf. John 1983) species which usually grows in short, ribbon-like colonies on sandgrains. It shows a clear preference for fine sandy sediments; its abundance appears to be independent of the amount of silt in the sediments. In the Baltic area it is absent below 10 ‰, which is in accordance with our observations: *Plagiogramma staurophorum* is mainly found in the polyhaline reaches.

PLAGSTAU

Ordo Biddulphiales

Fam. BIDDULPHIACEAE Kützing

Biddulphia Gray 1821

Genus description: Round *et al.* 1990

Biddulphia alternans (Bailey 1851) Van Heurck 1885

Synonyms:

Triceratium alternans bailey 1851

References:

(1) Bailey 1851
(2)
(3) Hendey 1964

Morphology:

A description of this species is given by Hendey (1964).

Biogeography & Ecology: The marine tychoplanktonic species *Biddulphia alternans* was only sporadically found in our sediment samples (cf. Denys 1991b).

BIDDALTE

Ordo Anaulales

Fam. ANAULACEAE (Schütt) Lemmermann

Anaulus Ehrenberg 1844

Genus description: Round *et al.* 1990

Anaulus uniseptatus Salah 1955 [Figs 3-5, 37-1]

References:

(1) Salah 1955
(2) This study (specimen from type locality)
(3) Salah 1953, Hendey 1964

Morphology:

L: 5-12.5; W: 2.5-3.7 (Westerschelde, n=2)

L: 8.6; W: 2.3 (Blakeney Point, n=1)

LM - Valves elliptical to lanceolate with cuneate-obtuse apices. A distinct transverse costa crosses the centre of the valve. No areolae are visible. At both apices, a raised pore-like opening can be seen.

SEM - Only one internal valve view was observed. The internal valve face, which is not perforated, appears to be slightly curved on both sides of the central transverse costa. At both apices, an ocellus-like structure is present; no closing plates are visible. Only one non-porous copula is present in this specimen.

Remarks: Hendey (1964) pointed out that this species might not belong to the genus *Anaulus*, which is probably heterogeneous and in need of revision (Round *et al.* 1990). ***Anaulus uniseptatus*** does not possess a rimoportula and has only one transverse costa (cf. *A. creticus* Drebes & Schulz, Round *et al.* 1990).

Biogeography & Ecology: To our knowledge, *A. uniseptatus* has previously only been reported from the type locality (Blakeney Point on the English North Sea coast). It was only rarely present in the polyhaline reaches of the estuary; its occurrence appears to be rather independent of the silt content of the sediment. We have characterized it as an interstitial species by analogy with other small centric diatoms such as *Cymatosira* sp. 1 and *Leyanella arenaria*, although it could also be epipsammic.

ANAUUNIS

Eunotogramma Weisse 1855

Genus description: Round *et al.* 1990

Eunotogramma dubium Hustedt 1939

[Fig. 3-6]

References:

(1) Hustedt 1939
(2) Simonsen 1987
(3) Simonsen 1987, Garcia-Baptista 1993b

Morphology:

L: 10-13.1; W: 2-3.5

LM - Valves semi-arcuate, with rounded apices. Valve face crossed by 2-5 transapical cross-bars.

Biogeography & Ecology: *Eunotogramma dubium* was described by Hustedt (1939) from intertidal sandflats in the German Wadden Sea. It is commonly reported from sandy sediments worldwide (Garcia-Baptista 1993b, this study).

EUNODUBI

Subcl. Lithodesmiophycidae

Ordo Lithodesmiales

Fam. LITHODESMIACEAE Round

Lithodesmium Ehrenberg 1839 (Ehrenberg 1841)

Genus description: Round *et al.* 1990, Hasle & Syvertsen 1996 (and references therein)

Lithodesmium undulatum Ehrenberg 1839

References:

(1) Ehrenberg 1841
(2)
(3) Hasle & Syvertsen 1996

Morphology:

A description of this species is given by Hasle & Syvertsen 1996.

Biogeography & Ecology: Only a few valves of this marine planktonic species were found in the sediments.

LITHUNDU

Subcl. Cymatosirophycidae

Ordo Cymatosirales

Fam. CYMATOSIRACEAE Hasle, von Stosch & Syvertsen

The discovery of flagellate male gametes in four species belonging to the genera *Cymatosira*, *Plagiogrammopsis*, *Leyanella* and *Arcocellulus* and the structure of the auxospore envelope prompted the foundation of the family Cymatosiraceae Hasle, von Stosch & Syvertsen (Hasle *et al.* 1983). This family comprises two existing genera, viz. *Cymatosira* and *Campylosira*, and seven new genera, viz. *Plagiogrammopsis* (formerly in *Plagiogramma*), *Brockmanniella*, *Minutocellulus*, *Leyanella*, *Arcocellulus*, *Papiliocellulus* and *Extubocellulus* (Hasle *et al.*, 1983, Round *et al.* 1990, Gardner & Crawford 1994).

In the Schelde estuary sediments, we found three distinct, small forms which could not be allocated to any known taxon. However, many Cymatosiraceae exhibit extreme stadial variation, expressed in changes in size, shape, cingulum structure, valve curvature and areolation pattern and loss of certain structures (such as pili, spinulose areas and marginal ridges)(Hasle *et al.*, 1983). This causes cells belonging to opposite ends of the size spectrum to be morphologically dissimilar. Moreover, changes in the environment (e.g. temperature) can cause changes in valve structure, so that different morphological forms of one species can exist. We have now entered these unknown forms (taxa?) as undescribed species of the genus we believe they belong to. However, further investigations, which fall outside the scope of the present study, are necessary to assess whether these forms truly concern discrete taxa or whether they form part of the form spectrum around an already described species.

Representatives of the Cymatosiraceae are widespread and common in marine and estuarine environments. Most have been described from and are usually found in sediments but they also appear in the (nano)plankton of shallow seas and estuaries (Hasle *et al.*, 1983). Whether they prefer a benthic or pelagic habitat in nature is as yet not well known (e.g. *Cymatosira belgica*, Denys 1995 and references therein).

Table 19 compares the distinguishing features of some problematic taxa observed during this study. In addition to the taxa described below, we also found very small valves of taxa that belong to the Cymatosiraceae (e.g. *Plagiogrammopsis* sp. 1, cf. Table 19, Fig. 36-4). Unfortunately, the material was too rare to allow identification or even proper description of these taxa.

Brockmaniella Hasle, von Stosch & Syvertsen 1983

Genus description: Hasle *et al.* 1983, Round *et al.* 1990

Brockmanniella brockmannii (Hustedt 1939) Hasle, von Stosch & Syvertsen 1983

[Figs. 3-9, 3-10, 37-2]

Synonyms:

Plagiogramma brockmannii Hustedt 1939
Plagiogramma parallelum Salah 1955
(?) *Cymatosira capensis* Giffen 1975

References:

(1)	Hustedt 1939
(2)	Simonsen 1987
(3)	Hasle *et al.* 1983, Round *et al.* 1990, Gardner & Crawford 1994, Hasle & Syvertsen 1996

Morphology:

L: 8.5-21.2; W: 3.1-5; (14.5-)16-20

LM - Colonial, forming long ribbon-like colonies. Valves linear to elliptical with broadly rounded apices. Each valve has a large, square to rectangular fascia. The areolae are placed in transapical, curved rows.

SEM - Valve face flat, curving gently into a shallow mantle. The fascia is raised externally; a process is present on one side of the fascia. Areolae round, occluded by vela. Spines are present along the valve margin. Two raised ocelluli are present at the valve apices; they are diagonally opposed.

Remarks: A detailed description of this species is given in the above-mentioned papers. The genus *Brockmaniella* is characterized by the presence of a fascia, marginal spines and a subcentral rimoportula and the absence of pili and pseudosepta.

Brockmaniella brockmannii appears to be conspecific with *Plagiogramma parallelum*, which was described by Salah (1955) from Blakeney Point (England). Specimens from his material are illustrated in Figs. 3-9 and 3-10: they have more or less parallel valve margins and are slightly broader (viz. 5-6 µm) than most reported dimensions [however, Gardner & Crawford (1994) mention a width of 7 µm for *B. brockmannii*]. As shape and dimension fall within the range of morphological variation of *B. brockmannii*, both species are most probably conspecific.

According to Hasle *et al.* (1983), *B. brockmannii* is also conspecific with *Cymatosira capensis*, described by Giffen (1975) from Saldanha bay (South Africa). The latter species, however, does not appear to have the large central area which is typical of *B. brockmannii*. It remains to be assessed whether this area was not observed by Giffen or whether it is truly absent, in which case *C. capensis* might still constitute a separate species.

Biogeography & Ecology: *Brockmanniella brockmannii* is a common species in sediments and plankton in North Europe (Hasle & Syvertsen 1996) but was also found in samples from Florida (USA) and is probably much more widespread (Round *et al.* 1990). It is common in silty sediments in the polyhaline reaches of the Westerschelde estuary, which is in accordance with its occurrence in the plankton of these reaches (Muylaert, pers. comm.).

BROCBROC

Campylosira Grunow ex Van Heurck 1885

Genus description: Hasle *et al.* 1983, Round *et al.* 1990

Campylosira cymbelliformis (A. Schmidt 1874) Grunow in Van Heurck 1881

[Figs 3-7, 36-1, 36-2]

Synonyms:

Campylosira alexandrica Salah 1955

References:

(1) A. Schmidt *et al.* 1874
(2)
(3) Hasle *et al.* 1983

Morphology:

L: 11.9-33.7; W: 4.4-6; S: 13-15 puncta in 10 µm

LM - Valves semi-lanceolate with usually produced, rostrate-capitate to apiculate apices. Areolae scattered over the valve face, in larger specimens arranged in longitudinal rows (Fig. 3-7). In the centre, a small offset circular hyaline area can be present. A distinct ring of spines is present along the valve face margin.

SEM - Only internal valve views were observed. Valve face slightly curved, gently merging into a rather shallow mantle. Areolae round, occluded by hymenate (?) vela. An offset process is present in the centre, on the curved side of the valve. An distinct, raised ocellulus is present at both apices. Externally, a marginal ring of interlocking spines is present (Fig. 36-2). Cingulum structure not observed.

Remarks: Our specimens are on average smaller than those reported in the description of this species in Hasle *et al.* (1983)(viz. 11.9-33.7 µm versus 20-55 µm). The smallest specimens correspond (both in size and shape) to *Campylosira alexandrica*, which according to Hustedt (1957), concerns *C. cymbelliformis* specimens at the lower end of the size range.

Biogeography & Ecology: *Campylosira cymbelliformis* is a common, cosmopolitan benthic or tychopelagic species (Hasle *et al.* 1983, Garcia-Baptista 1993b). In the Westerschelde, it was usually present in low numbers in silty sediments.

CAMPCYMB

Cymatosira Grunow 1862

Genus description: Hasle *et al.* 1983, Round *et al.* 1990

Cymatosira belgica Grunow in van Heurck 1881

References:

(1) Grunow in Van Heurck 1881
(2)

(3) Hasle *et al.* 1983, Round *et al.* 1990, Hasle & Syvertsen 1996

Morphology:

L: 6.9-23.7; W: 2.7-5; S: 9-12 puncta in 10 µm

LM - Valves lanceolate with rounded to slightly produced apices. In the centre of the valve, a apically elongate, hyaline area is sometimes present. Along the valve margin, the areolae are arranged in longitudinal rows. In the centre, they are more randomly scattered. Spines are present along the valve margin.

Remarks: A detailed description of this species and the genus *Cymatosira* in general can be found in Hasle *et al.* (1983) and Round *et al.* (1990). The areolar density appears to be a very constant feature of *Cymatosira belgica*: our measurements (9-12 areolae/10 µm) exactly matches the description in Hasle *et al.* (1983). Our smallest specimens are smaller than the reported range (viz. 10-40 µm, Hasle & Syvertsen 1996).

Biogeography & Ecology: *Cymatosira belgica* is a common, cosmopolitan species (Hendey 1964, Hasle *et al.* 1983, Podzorski & Håkansson 1987, Cooper 1995a). In the Westerschelde estuary, it was one of the most abundant and characteristic species in silty sediments, where it was always found together with *Delphineis minutissima* and *Thalassiosira proschkinae* (e.g. Underwood 1994, Denys 1995). *C. belgica* is found throughout the whole estuary.

CYMABELG

Cymatosira sp. 1

[Figs 4-12, 4-13, 4-14, 36-3]

Morphology:

L: 2.5-10; W: 1.5-2.5; W(P): 4.4; S: 19-24

LM - Valves very small, elliptical to lanceolate, with rounded to cuneate apices. No special features are visible due to the small size. There are no distinct hyaline areas. The areolae are arranged in longitudinal rows along the valve margin and are more irregularly placed in the centre of the valve. In girdle view, the cells are rectangular. The cingulum appears to be composed of numerous copulae.

SEM - Only external valve views were observed. The valve face is curved (centrally convex) and gently slopes into a rather deep mantle. The centre of the valve is distinctly bulged; no fascia is present. At each pole, a raised ocellulus is present; they open slightly laterally, in opposite directions. They each have about 3 to 4 porelli. The areolae are occluded by external cribra, usually with one or two pores. In one specimen (not illustrated) two small marginal spines can be seen.

Remarks: This taxon was provisionally assigned to the genus *Cymatosira* because of the absence of a fascia and the position of the ocelluli. However, the presence of marginal spines and a subcentral process could not yet be ascertained.

Biogeography & Ecology: This taxon probably belongs to the interstitial flora of sandy sediments:

in the Westerschelde estuary it was only found in fine and medium sandy sediments (in contrast with *C. belgica* which occurs in silty sediments). It is most abundant during the summer months.

CYMASP01

Leyanella Hasle, von Stosch & Syvertsen 1983

Genus description: Hasle *et al.* 1983, Round *et al.* 1990

Leyanella arenaria Hasle, von Stosch & Syvertsen 1983 [Figs 4-15, 36-6]

References:

(1) Hasle *et al.* 1983
(2) (?) Hasle *et al.* 1983
(3) Hasle *et al.* 1983, Round *et al.* 1990

Morphology:

L (radius of curvature): 11.2; W: 2.5; S: 21 puncta in 10 µm (n=2)

LM - No complete frustules were observed in the cleaned material. Valves strongly curved and slightly triundulate in girdle view. Two pili protrude from near the apices on the external side of a convex valve; they are about as long as the valve. In valve view, the valve again appears to be strongly curved along the apical axis. Longitudinal rows of areolae are present along the valve margin; in the centre they are less numerous and scattered, or absent.

SEM - Valve face strongly curved in apical direction but also slightly in transapical direction. Two finely porous marginal ridges are present along the valve margins. Two complete pili (i.e. they possess a reflexed first branch, cf. Hasle *et al.* 1983) are present on the convex valve (= the pilus valve). The pilus bases are attached near two externally raised ocelluli. Two longitudinal rows of areolae run underneath the marginal ridges. Their occlusion type is not clear, but the vela appear to be convex externally. The areolae on the valve face are irregularly scattered and few in number. Cingulum structure unknown.

Remarks: A detailed description of this species is given in Hasle *et al.* (1983). Our specimens slightly differ from theirs in having a higher areolar density (20-21 versus 15-17 areolae in 10 µm).

Biogeography & Ecology: *Leyanella arenaria* was described from sandflats in the German Wadden Sea and is characterized as an interstitial species (Hasle *et al.* 1983), which is in accordance with its distribution in the Westerschelde estuary where it is mainly found in medium sandy sediments. It has been recorded by Ricard (1987) as a tychoplanktonic and benthic species and was also found by Denys (1991a) in Holocene deposits of the Belgian coastal plain.

CYMASP01

Plagiogrammopsis Hasle, von Stosch & Syvertsen 1983

Genus description: Hasle *et al.* 1983, Round *et al.* 1990, Gardner & Crawford 1994

Plagiogrammopsis minimum (Salah 1955) Sabbe comb. nov. prov.

[Figs 4-6, 4-7, 4-8, 4-9, 36-7, 36-8]

Synonyms:

Plagiogramma minimum Salah 1955

References:

(1)	Salah 1955
(2)	this study
(3)	Salah 1955, Colijn & Nienhuis 1978, Denys 1991a, Sabbe & Vyverman 1991, Cooper 1995a

Morphology:

L: 6.4-16(-27!); W: 1.9-3.2; W(P): 4-4.6; S: (11-)12-14(-16)(n=26)

LM - Valves lanceolate with rounded, sometimes slightly produced apices (note that a single, extremely large (recent post-auxospore?) valve has valves that are slightly curved at the apices). The centre of the valve is slightly but distinctly constricted; a pseudoseptum is present. No sterna are visible. The areolae are arranged in longitudinal rows, parallel to the valve margin; they are interrupted at the central constriction. Note also that no areolae are present at the apices. In girdle view the frustules are more or less rectangular, centrally slightly constricted, with slightly raised but blunt apices. The number of copulae could not be assessed.

SEM - Valve face curved, merging almost imperceptibly with a rather deep mantle. Internally, a pseudoseptum runs from margin to margin in the central fascia. On one side of this pseudoseptum, and slightly offset, a process is visible, which opens externally via a short tube. The areolae are only distinctly longitudinally aligned along the valve margin; on the rest of the valve, their pattern is less regular. They are more or less round and occluded by external, cribrate vela (with about 8-10 pores each). Externally, spinules can be present on the cribra. At each pole, a raised ocellulus is present; they open laterally in opposite directions. A marginal ring of rather long, thin spines is present.

Remarks: *Plagiogramma minimum* does not belong to the genus *Plagiogramma* but to the genus *Plagiogrammopsis*. Although no pili or colony formation were observed, this transfer is justified as all other features of this taxon fit the description of the genus *Plagiogrammopsis* (viz. presence of pseudoseptum, long spines, distinctly laterally opening ocelluli and an external cribrum with spinules). The similar genus *Brockmanniella* does not possess a pseudoseptum or external cribra with spinules.

Biogeography & Ecology: *Plagiogrammopsis minimum* has been reported from the North Sea area (Colijn & Nienhuis 1978, as *Plagiogramma* sp. 1, Vos 1986, Denys 1991a, this study) and North America (Cooper 1995a). In the Westerschelde estuary, *P. minimum* is restricted to fine sandy sediments in the poly- to euhaline reaches, where it is most abundant in summer. It is not sure whether this species is interstitial or epipsammic.

PLAGMINI

Plagiogrammopsis sigmoideum (Salah 1955) Sabbe comb. nov. prov.

[Figs 4-1, 4-2, 4-3, 4-4, 4-5]

Synonyms:

Plagiogrammopsis mediaequatus Gardner & Crawford 1994

References:

(1) Salah 1955
(2) this study
(3) Salah 1955, Gardner & Crawford 1994

Morphology:

L: 7.7-20; W: 2.2-3; W(P): 6.9; S: 14-16

LM - Valves lanceolate with slightly produced to rostrate apices. The valves are sometimes slightly sigmoid (hence the epithet). In the centre, a distinct, more or less roundish fascia is present. The areolae are arranged in longitudinal rows, parallel to the valve margins. The fascia appears distinctly convex in girdle view.

Remarks: This species differs from *Plagiogrammopsis vanheurckii* in the absence of a pseudoseptum, the presence of a wing on the pili (not observed in this study) and the less pronounced apical elevations (cf. Fig. 4-5)(Gardner & Crawford 1994). Although we have not been able to obtain SEM images of this species, there is little doubt that it is conspecific with *P. mediaequatus*, which was recently described from the British Isles (Gardner & Crawford 1994): they are identical in LM and have the same dimensions and stria density. Their descriptions and arguments show that *P. sigmoideum* belongs to the genus *Plagiogrammopsis*.

Biogeography & Ecology: *P. sigmoideum* was described from intertidal sediments in Blakeney Point (England). It was then reported (as the synonym *P. mediaequatus*) from various localities around the British Isles. It has also been reported from Holocene deposits of the Belgian coastal plain (Denys 1991a). In the Westerschelde, it was common in silty sediments in the middle and lower reaches of the estuary.

PLAGSIGM

Plagiogrammopsis vanheurckii (Grunow in Van Heurck 1881) Hasle, von Stosch & Syvertsen 1983

[Fig. 36-5]

Synonyms:

Plagiogramma vanheurckii Grunow in Van Heurck 1881

References:

(1) Grunow in Van Heurck 1881

(2)
(3) Hasle *et al.* 1983, Round *et al.* 1990, Gardner & Crawford 1994, Hasle & Syvertsen 1996

Morphology:

L: 11.2-25; W: 3-4; S: 12-17 (vnl. 13-14)

LM - Valves lanceolate, usually with produced, capitate to apiculate apices. In girdle view, the valves are rectangular, with elevated apical and central parts. In the centre of the valve, a distinct pseudoseptum is present in the middle of a more or less rectangular fascia. A ring of spines is visible along the valve margin. The areolae form longitudinal striae.

SEM - Valve face curved, merging almost imperceptibly with a shallow mantle. In the centre of the valve, a distinct fascia, extending from margin to margin, is present. Internally, a transapical pseudoseptum runs across this fascia. The areolae are round and externally occluded by convex cribra. Ocelluli are present at both apices: they are distinctly raised and open laterally, in opposite directions. Just inside the marginal rows of areolae, a ring of spines is present. The spines are long and flexible and tend to 'stick together' (Fig. 36-5). A process is present in the ring of spines (on one valve of each frustule, cf. Hasle *et al.* 1983). The valve without the process bears two incomplete pili (i.e. without reflexed first branches and spinulose areas), inserted at the apices. The cingulum structure is not very clear.

Biogeography & Ecology: *Plagiogrammopsis vanheurckii* is a cosmopolitan, common species in coastal waters, both in the sediments and in the (tycho)plankton (Denys 1991, Hasle & Syvertsen 1996). It was common in silty sediments throughout the estuary.

PLAGVANH

Incertae sedis sp. 1

[4-16, 4-17, 37-3, 37-4]

Morphology:

L: 5.7-15.6; W: 2.2-3.5; S: ± 23-29 puncta in 10 μm

LM - Cells forming ribbon-like colonies. Valves semi-elliptical with cuneate to rostrate apices. No sternum or fascia is present. The valve surface is covered with scattered, irregularly distributed, tiny areolae.

SEM - Valve face more or less flat to curved (in transpapical direction); sometimes, the central part appears to be raised (Fig. 37-3). The mantle is shallow. No hyaline areas are present. Simple linking spines are present along the valve face margin; in some specimens these are bifurcate at their apices. The valve face is perforated by numerous scattered, small poroids. Occlusion type unknown, absent? At each pole a raised ocellulus is present; externally, they are surrounded by a distinct rim. They are diagonally opposed to one another in a clockwise direction. The structure of the cingulum is not very clear: it is rather deep and appears to be composed of numerous copulae.

Remarks: In LM, this taxon can easily be confused with *Catenula adhaerens*, which has a similar

shape and dimensions but is more robust and has no scattered areolae but (indistinct) striae.
This taxon was originally assigned to the genus *Brockmaniella* which it superficially resembles: it has (1) rather flat cells with a slightly convex centre bordered by shallow depressions; (2) two offset, laterally opening ocelluli; (3) no pili and no pseudoseptum. However, it differs from *Brockmanniella brockmannii* in the absence of a fascia, the structure of the spines and the areolae, and the apparent absence of subcentral processes.

The apparent isovalvy, the simple structure of the areolae (poroids without apparent vela) and the absence of a central area point to a position of this taxon in the subfamily Extubocelluloideae (Hasle *et al.* 1983), which has only one genus, *Extubocellulus* Hasle, von Stosch & Syvertsen. However, our taxon does not seem to belong to *Extubocellulus*, as it has a different pervalvar/apical axis length ratio and a marginal ring of spines. It should probably be placed in a new genus in this subfamily.

Biogeography & Ecology: This unknown taxon was rather common in fine sandy sediments in the poly- and euhaline reaches of the estuary. Unlike *Cymatosira belgica* and *Brockmaniella brockmannii* it was usually not found in silty sediments, which might indicate that it has an interstitial or even epipsammic life-form. We found valves belonging to this taxon in Hustedt's material from from the German Wadden Sea (BRM N12/36, Leybucht, Leysand).

BROCSP01

CLASS FRAGILARIOPHYCEAE

Subcl. Fragilariophycidae

Ordo Fragilariales

Fam. FRAGILARIACEAE Greville

Over the fragilarioid diatoms (*Synedra* s.l. and *Fragilaria* s.l.) much controversy exists (Cox 1993): while Krammer & Lange-Bertalot (1986-1991) advocate the maintenance (and amplification) of a large genus *Fragilaria* s.l., Williams & Round (1986, 1987) and Round *et al.* (1990) have divided *Fragilaria* s.l. into several new or re-established genera. The main features of most genera belonging to the Fragilariaceae which were observed during this study are listed in Table 20. New genera of fragilarioid diatoms have been described since, e.g. *Desikaneis* (Prasad & Livingston 1993), *Psammosynedra* (Round 1993), *Synedropsis* (Hasle *et al.* 1994) and *Fossula* (Hasle *et al.* 1996), indicating a general trend towards a more refined classification at the genus level in this group. In this study we follow the classification system proposed by Round *et al.* (1990). However, further investigation is needed to elucidate the relationships between some of the new or resurrected genera, especially between *Martyana*, *Staurosira*, *Staurosirella*, *Punctastriata* and *Pseudostaurosira*.

Ctenophora (Grunow 1862) Williams & Round 1986

Genus description: Williams & Round 1986, Round *et al.* 1990

Ctenophora pulchella (Ralfs ex Kützing 1844) Williams & Round 1986

Synonyms:

Synedra pulchella Ralfs ex Kützing 1844
Fragilaria pulchella (Ralfs ex Kützing 1844) Lange-Bertalot 1980

References:

(1) Ralfs ex Kützing 1844
(2) Williams & Round 1986
(3) Williams & Round 1986, Round *et al.* 1990, Snoeijs 1993

Morphology:

L: 43.1; W: 6.2; S: 16 (n=1)

LM - Valves lanceolate, apices slightly rostrate. Axial area narrow, linear; central area broad, more or less circular, delimited by two curved ribs. Striae punctate, opposite, parallel to slightly radiate near the apices. In the central area, the striae are only lightly visible.

Remarks: This species was transferred to the new, monotypic genus *Ctenophora* by Williams & Round (1986)(see also Round *et al.* 1990).

Biogeography & Ecology: Only a few valves of this epiphytic, cosmopolitan (Williams & Round 1986) species were found in our material.

CTENPULC

Fragilaria Lyngbye 1819

Genus description: Williams & Round 1987, Round *et al.* 1990

Note that we follow the narrow concept of the genus *Fragilaria*, i.e. sensu Williams & Round 1987, non sensu Krammer & Lange-Bertalot 1991.

Fragilaria used to be a very large genus, which is now (although not generally) interpreted in a much narrower sense. However, as with *Navicula* (see discussion) it is still difficult to place many old and new taxa, which used to belong to the genus *Fragilaria* s.l., as the identity of and the relationships between some new and resurrected genera in the Fragilariaceae is still insufficiently known. It may therefore be necessary to establish new genera to accomodate taxa that still belong to *Fragilaria* s.l. but which cannot be incorporated in any of the existing fragilarioid genera. For example, Flower *et al.* (1996) described a new genus, *Stauroforma* Flower, Jones & Round, which hitherto comprises only two species. Although the description of new genera based on only one or few species is contested, it often appears that soon after many more new species are transferred to these genera [e.g. *Nupela* Vyverman & Compère (cf. Lange-Bertalot 1993, Lange-Bertalot & Moser 1995), *Biremis* (Sabbe *et al.* 1995, Vyverman *et al.* 1997), *Plagiogrammopsis* (Gardner & Crawford 1994, this study)].

A number of species we have assigned to *Fragilaria* certainly do not belong to *Fragilaria* s.s.: it is then explicitly stated.

Fragilaria cf. *atomus* Hustedt 1931 sensu Snoeijs *et al.* (1991)

[Figs 5-13, 5-14, 5-15, 5-16, 5-17, 38-6, 38-7, 38-8, 38-9, 39-1]

Synonyms:

Martyana atomus Snoeijs 1991
Fragilaria virescens var. *subsalina* f. *oviformis* Cleve-Euler 1953, sensu Poulin *et al.* 1984, (?) sensu Cleve-Euler 1953

References:

(1) Hustedt 1931
(2) Simonsen 1987
(3) Poulin *et al.* 1984a, 1986, Kuylenstierna 1989-90, Snoeijs *et al.* 1991, Witkowski & Lange-Bertalot 1993, Lange-Bertalot 1993a

Morphology:

L: 6.2-12.1; W: 1.6-3.1; S: 19-22

LM - Valves isopolar (elliptical) to heteropolar (ovate), head pole broadly rounded, foot pole rounded to cuneate to slightly produced, rostrate. Axial area absent or (partly) present, then very narrow, often eccentric. Striae parallel, punctate (usually very indistinct in LM). Sometimes short striae are present. Note that although in most valves the striae run uninterrupted from margin to margin, in some specimens the striae are alternate. In some frustules, one valve has opposite striae and the other valve alternate striae (Fig. 5-16 and 5-17).

SEM - Valve face flat, gently curving into a the mantle. Striae composed of small, round to slightly apically elongate poroids (occlusion type unknown), usually uniseriate but in some valves locally biseriate (Fig. 38-6, cf. also Snoeijs *et al.* 1991, Figs. 6, 12, 16 and 17). In some frustules, one valve has uniseriate striae while the other valve has biseriate ones (cf. Snoeijs *et al.* 1991, Fig. 12). The head pole is perforated by more or less randomly distributed poroids (Fig. 38-9) or by short, radiate rows of poroids, which do not differ from the valve areolae (Fig. 38-6). At the foot pole, a small, indistinct apical pore field seems to be present (Fig. 38-7). At the head pole, a distinct step (cf. Snoeijs *et al.* 1991) is usually present. The cingulum appears to consist of at least two non-porous copulae (Fig. 38-8).

Remarks: Our specimens correspond to the description of *Fragilaria atomus* given by Witkowski & Lange-Bertalot (1993), Snoeijs *et al.* (1991, as *Martyana atomus*) and Poulin *et al.* (1986, as *Fragilaria virescens* var. *subsalina* f. *oviformis*). We have therefore tentatively assigned our specimens to *Fragilaria atomus* (sensu Snoeijs *et al.* 1991). However, the identity of this species is not very clear. To our knowledge, no SEM study has yet been made of Hustedt's type material. Our specimens are attached to the substratum by means of a small mucilage stalk apparently secreted by the foot pole apical pore field (cf. also Snoeijs *et al.* 1991), while Hustedt's *Fragilaria atomus* forms ribbon-like colonies ('zu dicht geschlossenen Bändern verbunden', Hustedt 1931). It is not unlikely that we are dealing with two distinct but closely related taxa. This can only be verified by (SEM) examination of the type material.

Our specimens also closely resemble *Fragilaria cassubica* Witkowski (Witkowski & Lange-Bertalot 1993, cf. also Fig. 5-26). However, the latter differs in size (9-20 µm), stria density (15-18 str./10 µm) and shape (it always has a distinctly elongate foot pole) from our specimens. In addition, spines are occasionally present in *F. cassubica*; these have never been observed in our *F. atomus*. Whether these (slight) differences are significant to make a distinction between both species remains to be assessed. In addition, the relationship between our taxon and *Fragilaria gedanensis* Witkowski (see below) has to be investigated. During the cell counts, valves corresponding to the latter species have always been included in *Fragilaria* cf. *atomus*.

Neither *Fragilaria atomus* nor *F.* cf. *atomus* belong to *Fragilaria* s.s. Snoeijs *et al.* (1991) transferred *F. atomus* (and *F. schulzii*) to *Martyana* but this transfer is unclear and requires further study (see also *Martyana martyii*).

It is important to point out that the diatom illustrated in Krammer & Lange-Bertalot (1991) and which is most probably identical to our *Fragilaria* cf. *atomus*, does not concern *F. subsalina* but *F. cassubica* (cf. Lange-Bertalot 1993a). This has already led to some incorrect reports of *F. subsalina* (e.g. Cooper 1995a).

Biogeography & Ecology: *Fragilaria* cf. *atomus* occurs in the epipsammon of very fine to fine sandy sediments throughout the estuary. As already mentioned, it grows attached to the substratum by a short mucilage stalk. True colony formation has never been observed. As with other stalked species, its distribution within the estuary appears to be independent of the silt content of the sediment.

FRAGCFAT

Fragilaria capensis Grunow 1863 [Figs 4-25, 4-26, 4-27, 4-28, 4-29, 4-30, 4-31, 37-6, 37-7, 37-8]

Synonyms:

Fragilaria improbula Witkowski & Lange-Bertalot 1995

References:

(1)	Grunow 1863
(2)	Krammer & Lange-Bertalot 1991 (lectotype), Witkowski *et al.* 1995, this study
(3)	Krammer & Lange-Bertalot 1991, Witkowski *et al.* 1995

Morphology:

L: 7.5-28.7 (40); W: 2.7-5.2; W(P): 5-6.2; S: 13-15; 18-20 puncta in 10 µm (cingulum) (isotype population, n=35, Grunow slide 790, Kalkbay, Cape Town, South Africa)
L: 5.2-15; W: 3.5-5; W(P): 5.6-8.7; S: 13.5-15 (16); 20 puncta in 10 µm (cingulum)(Westerschelde populations)

LM - Valves elliptical with rounded apices to lanceolate with cuneate sub-rostrate to rostrate apices. Axial area linear, narrow. Striae always alternate, distinctly punctate. In girdle view, the valves are rectangular. The number of copulae is not clear. In most specimens, the cingulum displays two to three rows of distinct puncta. In the isotype material, a large valve which probably also belongs to this species, was found (Fig. 4-31). It is very large compared to the rest of the specimens and has a slightly excentric axial area; it might concern a recent post-auxospore valve.

SEM - Valve face flat, at almost right angles with the rather deep mantle. The axial area is narrow. The striae consist of small, round areolae. Both internally and externally, the areolae are separated by slightly raised virgae and vimines. As in *Fragilaria eichornii*, small structures, which are quite reminiscent of the mantle plaques (cf. Round *et al.* 1990, p. 346, *Fragilaria*), are present around the valve margin. At both poles, a characteristic, rather small and round pore field is present. In all studied specimens these pore fields consist of three short (2 to 3 puncta) apical rows of small puncta. The pore fields are slightly depressed, both internally and externally. The cingulum was only observed in one specimen: it consists of at least two copulae, which each possess two rows of puncta. The advalvar margin of the valvocopula is scalloped and fits on to the costal framework.

Remarks: Examination of an isotype slide of *Fragilaria capensis* (Grunow slide 790, AWH slide VI 41 B10) shows that there is no doubt that the Westerschelde specimens belong to this species. Comparison of the descriptions and illustrations of *Fragilaria capensis* and *F. improbula* (Witkowski *et al.* 1995) indicate that they are conspecific. The main distinguishing features (as given by the authors) are the shape of the valve and valve ends, the number of rows of areolae on the mantle, the dimensions and the stria density. Both in the isotype population and the Westerschelde material, small elliptical, larger lanceolate forms (with rostrate apices) and intermediate forms were present. The number of rows of areolae on the mantle in *F. capensis* is not 1 or 2 but amounts up to 4 or more (as shown in their own Fig. 13, Witkowski *et al.* 1995), as in *F. improbula*. Finally, the different dimensions of both species merely reflect that they occupy both halfs of the size range of a single species. All illustrated specimens of *F. improbula* have 12-15 striae in 10 µm, which is almost identical to the stria density range in *F. capensis*. Possibly, the finer specimens concerned elliptical forms of *F. eichornii* (see below). In addition, the SEM illustrations of *F. improbula* show that there are no ultrastructural differences with *F. capensis*: the presence of only one apical pore field in *F. improbula* cannot be verified.

Witkowski *et al.* (1995) already pointed out the resemblance of *Fragilaria eichornii* and *F. capensis*. It is clear that both species do not belong to *Fragilaria* s.s. (Williams & Round 1987): they have no rimoportulae or spines (they do not form ribbon-like colonies), have more simple apical pore fields and have a different, very typical cingulum structure. Moreover, both species are marine to marine-brackish (while *Fragilaria* s.s. is mainly a freshwater genus). Their exact generic affinity is hard to assess for the time being, given the current poor knowledge on many araphid genera formerly belonging to *Fragilaria* s.l. (e.g. *Staurosira*, *Staurosirella*, *Punctastriata* and *Pseudostaurosira*)(cf. also Table 20).

Specimens which possibly also belong to *F. capensis* were reported by Hustedt (1955) from Beaufort (USA) as *Trachyneis acuminata* Peragallo (they may, however, also belong to *Fragilaria* sp. 2, see below). Any which way, it is certain that at least some further reports of *Fragilaria capensis* as *Trachyneis acuminata* (e.g. Navarro 1982, Podzorski & Håkansson 1987, (?) Cooper 1995a) are (directly or indirectly) based on Hustedt's (possibly incorrect) description. We have not yet been able to obtain the original description of the latter species but Hustedt himself points out that his specimens differ from *T. acuminata* sensu Peragallo in stria density and coarseness of punctation.

Biogeography & Ecology: *Fragilaria capensis* has been reported from the Atlantic coast of North America (Navarro 1982, (?) Hustedt 1955, (?) Cooper 1995a, all as *Trachyneis acuminata*), from the Philippines (Podzorski & Håkansson 1987, as *Trachyneis acuminata*), from Africa (Grunow 1863, Witkowski *et al.* 1995), from Yemen (Witkowski *et al.* 1995, as *Fragilaria improbula*) and from Europe [both the Baltic area (Witkowski *et al.* 1995, as *Fragilaria improbula*) and the North Sea coast (England, in Salah's material from Blakeney Point, and The Netherlands, this study], and can thus be considered as a cosmopolitan species.

F. capensis is found in the epipsammon of fine sandy sediments, where it lives attached to sandgrains by means of unusually long mucilage stalks. It is more frequent at higher salinities.

FRAGCAPE

Fragilaria capucina Desmazières 1825 [Fig. 7-2]

References:

(1) Desmazières 1825
(2)
(3) Williams & Round 1987, Krammer & Lange-Bertalot 1991

Morphology:

L: 27.5; W: 5; S: 16-17

LM - Valves elliptical with slightly produced, more or less rostrate apices. Axial area narrowly lanceolate, central area transapically expanded, on one side of the valve reaching to the valve margin. Striae marginal, radiate.

Biogeography & Ecology: Only a few valves belonging to this freshwater species were found in our material.

FRAGCAPU

Fragilaria eichornii Witkowski & Lange-Bertalot 1995 [Figs 4-18, 4-19, 4-20, 4-21, 4-22, 37-5, 38-1]

References:

(1) Witkowski *et al.* 1995
(2) Witkowski *et al.* 1995
(3) Witkowski & Lange-Bertalot 1993, Witkowski *et al.* 1995

Morphology:

L: 6.9-14; W: 2.5-3.1; S: 20-22

LM - Valves almost elliptical (small specimens) to distinctly clavate (larger specimens), always (though sometimes only slightly) heteropolar. The large specimens have a rounded head pole and a produced foot pole. Axial area linear, very narrow. Striae invariably alternate, parallel throughout the valve. They are distinctly punctate. In girdle view, the frustules are cuneate, the cingulum is characterized by two rows of distinct puncta (about 25 in 10 µm).

SEM - Only internal valve views were observed. Valve face flat, at right angles with the rather deep mantle. The central sternum is narrow. The striae are separated by slightly raised virgae and are composed of round poroids; no occlusions are visible. Both at the head and foot pole, a 'pore field', consisting of apically elongate slits (Fig. 37-5), is present.

Remarks: The specimens from the type population are on average larger and wider than the Westerschelde specimens (Witkowski *et al.* 1995). No small, almost elliptical specimens were present in the type population. Note that the stria density of the illustrated specimens (about 19 str./10 µm)(cf. also Witkowski & Lange-Bertalot 1993, Figs. 5n-r) does not fully correspond to the one mentioned in the description (15-19 str./10 µm). The presence of spines could not be verified in our material. In the valves observed, a pore field was present at both poles, and not only at the foot pole (cf. Witkowski *et al.* 1995).

Fragilaria eichornii does not belong to *Fragilaria* s.s. (Williams & Round 1987) but appears to be closely related to *Fragilaria capensis* (see above).

Biogeography & Ecology: *Fragilaria eichornii* was described from brackish, sandy sediments in the Gulf of Gdansk (Baltic Sea). In the Westerschelde estuary, it was mainly found in fine sandy sediments, especially in the polyhaline reaches.

OPEPSPEA

Fragilaria cf. *gedanensis* Witkowski 1993 [Figs 5-11, 5-12, 39-3]

References:

(1) Witkowski 1993

(2) Witkowski 1993
(3) Witkowski 1994, Witkowski & Lange-Bertalot 1993

Morphology:

L: 6.2-9; W: 2.1-3.1; S: 12-21(!)

LM - Valves ovate to clavate; head pole broadly rounded, foot pole cuneate to slightly produced. Axial area narrow to indistinct. Striae parallel (to radiate near the apices), opposite. Cingulum structure unknown.

SEM - Valve face flat, gently curving into the mantle. Sternum usually indistinct, very narrow. The striae are composed of roundish to apically elongate areolae. Within one stria, the areolae become smaller towards the valve margin and the central sternum. Each areola (except the smaller, roundish ones) is crossed by a small central rib, which seems to protrude from the vimines (Fig. 39-2). Thus, the areolae are divided in two parts, which sometimes gives the impression that the striae are biseriate (cf. Witkowski 1993). These parts are (obviously) always opposite each other and are occluded by a velum of unknown type. The head pole is perforated by numerous roundish puncta, which are distributed randomly or are arranged in radiate rows (Fig. 39-2). At the foot pole, a second pore field is present, though it is much less distinct . The cingulum appears to be composed of at least two non-porous, (?) open copulae.

Remarks: The identity of *Fragilaria gedanensis* (which does not belong to *Fragilaria* s.s.) is not very well circumscribed. It is mainly characterized by the opposite striation and the ultrastructure of the areolae. Our specimens are structurally identical to the ones illustrated in the type description of this species (Witkowski 1993, Figs. 16-18). The main difference lies in the stria density, which is much higher in most of our specimens (up to 21 str./10 µm). The type description gives 9-14 str./10 µm, although densities up to 18 str./10 µm can be measured in the illustrated valves (e.g. Witkowski 1993, Fig. 18). The high stria densities make it often impossible to distinguish between our *F. gedanensis* specimens from *Fragilaria* cf. *atomus* in the LM; the only difference lies in the ultrastructure of the areolae: in *F. gedanensis*, small ribs, protruding from the vimines are present, whereas in *F.* cf. *atomus*, this is never the case. In addition, the poroids of the (pseudo?)biseriate striae in *F. gedanensis* are always opposite, while in the biseriate striae of *F.* cf. *atomus*, the poroids are alternate (cf. Fig. 38-6, 39-1 and Snoeijs *et al.* 1991, Fig. 17). A *F. gedanensis* specimen illustrated in Witkowski & Lange-Bertalot (1993, Fig. 3q) has alternate poroids within the striae and therefore probably do not belong to *F. gedanensis*. The ultrastructure of the areolae of the latter species is actually very reminiscent to the one of *Opephora guenter-grassii* and *O. mutabilis* (Sabbe & Vyverman 1995), which are also characterized by small ribs protruding from the vimines.

A detailed study of a large number of valves of *F. gedanensis* is necessary to assess its relationship with both *F.* cf. *atomus* and *Opephora guenter-grassii.* All three species have overlapping size and stria density ranges, which makes it very hard to distinguish between them in LM. *Opephora guenter-grassii* usually has alternate striae but opposite striation has also been observed (cf. Sabbe & Vyverman 1995) so this character seems to be of dubious taxonomic value, within this taxon at least.

Biogeography & Ecology: *Fragilaria gedanensis* was described from the Gulf of Gdansk in the Baltic Sea and can be found throughout the (brackish) Baltic area (Witkowski & Lange-Bertalot 1993). Our report constitutes the first record of this species outside this area. During the cell counts, no distinction was made between this taxon and *Fragilaria* cf. *atomus*. It was therefore impossible to assess its ecological requirements, except that it occurs as a stalked epipsammic species in brackish to marine sediments.

FRAGCFAT

Fragilaria schulzii Brockmann 1950 [Figs 5-7, 5-8, 5-9, 5-10, 38-11]

Synonyms:

Fragilaria virescens var. *oblongella* f. *clavata* Grunow in Van Heurck 1881
Opephora schulzii (Brockmann) Simonsen 1962
Martyana schulzii (Brockmann) Snoeijs 1991

References:

(1)	Brockmann 1950
(2)	Brockmann 1950
(3)	Poulin *et al.* 1984a, Snoeijs *et al.* 1991, Witkowski & Lange-Bertalot 1993

Morphology:

L: (5-)10-21.2; W: 3.1-5; S: 15.5-17

LM - Valve shape elliptical, isopolar to heteropolar. Apices (broadly) rounded, sometimes produced. Axial area indistinct (only visible as a thin strip) to absent. Striae parallel throughout the valve, indistinctly punctate. Cingulum structure not observed.

Remarks: *Fragilaria schulzii* seems to be closely related to *F. atomus*, from which it can only be distinguished in size and stria density. In addition, the head pole in *F. schulzii* is devoid of striae but has a small pore field, whereas in *F. atomus* radiate striae are usually present instead of a pore field (cf. Snoeijs *et al.* 1991). *F. schulzii* seems to be a well circumscribed species: it is larger and has a less dense striation than most similar taxa, such as *F. atomus* and *F.* cf. *subsalina*. However, in some case the distinction between *F. atomus* and *F. schulzii* appears to be problematic (cf. Kuylenstierna 19989-90, Cooper 1995a).
Fragilaria schulzii does not belong to *Fragilaria* s.s. The transfer of this species to the genus *Martyana* is doubtful and requires further study (see also *Martyana martyi*).

Biogeography & Ecology: *Fragilaria schulzii* was described by Brockmann (1950) from the German Wadden sea coast and has been reported from localities throughout Europe (e.g. Kuylenstierna 1989-90, Sabbe & Vyverman 1991, Gätje 1992) and North America [Poulin *et al.* 1984a (as *Fragilaria virescens* var. *oblongella* f. *clavata*), Cooper 1995a]. In the Westerschelde estuary, it was mainly found in fine sandy sediments. As most stalked species, it appears to be rather insensitive to higher amounts of silt.

FRAGSCHU

Fragilaria* cf. *subsalina (Grunow 1881) Lange-Bertalot 1993

[Figs 5-1, 5-2, 5-3, 5-4, 5-5, 38-3, 38-4, 38-5]

Synonyms:

Fragilaria virescens var. *subsalina* Grunow in Van Heurck 1881

References:

(1) Grunow in Van Heurck 1881
(2)
(3) Stabell 1981, Krammer & Lange-Bertalot 1991, Lange-Bertalot 1993a, Snoeijs *et al.* 1991

Morphology:

L: 6-15.9; W: 2.5-3.7; S: (19-)20-21.5

LM - Valves isopolar, sometimes very slightly heteropolar. Axial area only visible as a very narrow line, sometimes eccentric. Striae parallel, usually opposite but often locally alternate (Fig. 38-3); their structure is indistinct in LM. Both poles are devoid of striae. Cingulum structure unknown.

SEM - Valve face flat, curving rather gently into the mantle. The central sternum (= axial area) is visible as a thin strip of silica. In some specimens, small spines are present on the virgae, on the valve face-mantle transition. The striae are composed of roundish to transapically elongate areolae, occluded by a velum. At both poles, a large apical pore field is present; they have a semi-arcuate shape and consist of radiate rows of small puncta. Internally, the striae lie between raised virgae. The cingulum was not observed.

Remarks: *Fragilaria* cf. *subsalina* does not belong to *Fragilaria* s.s. It was described by Grunow in Van Heurck (1881). His illustrations show a more or less isopolar valve without a central sternum, about 17.5 µm long and 4 µm wide. It has about 20 striae in 10 µm. A detailed description of this species was given by Stabell (1981): it shows a diatom with 17-18 striae in 10 µm, rather large marginal spines and (?) no apical pore fields (cf. also Rao & Lewin 1976). Lange-Bertalot (1993a) pointed out that the true identity of *Fragilaria subsalina* is uncertain as the type material has not yet been examined. Note that the diatom illustrated in Krammer & Lange-Bertalot (1991) as *F. subsalina* is not true *F. subsalina* (i.e. sensu Grunow) but represents *Fragilaria cassubica* (see also *F.* cf. *atomus*).

We have tentatively identified our specimens as *Fragilaria* cf. *subsalina*, on the basis of valve shape (isopolar), presence of marginal spines and stria density and pattern (cf. also Snoeijs *et al.* 1991). Unlike Stabell (1981), we did observe two large apical pore fields. Examination of the type material is necessary to establish the true identity of this species, and whether it belongs to *Fragilaria* s.s. or not (like our specimens).

Biogeography & Ecology: During the cell counts, no distinction was made between this taxon, *Fragilaria* cf. *atomus* and *F. gedanensis*. We were therefore unable to assess its exact ecological requirements. Due to the uncertain identity of *Fragilaria subsalina*, it is impossible to give information on its biogeography.

FRAGCFAT

Fragilaria sp. 1

[Figs 7-4, 7-5, 7-6, 41-3, 41-4]

Morphology:

L: 3.7-12; W: 1.3-2.2; S: (16?-)19-22

LM - Valves lanceolate-elliptic with cuneate, rarely produced and rounded apices. Axial area narrow, linear. Striae distinct, alternate.

SEM - Valve face curved in transapical section, merging gradually into the mantle. The striae are composed of roundish areolae, which typically become smaller from the central sternum to the valve margin. The occlusion type is not very clear: the vela are probably connected to the vimines by means of small ribs (Fig. 41-4). This is very reminiscent of the occlusion type in *Pseudostaurosira perminuta* (cf. Sabbe & Vyverman 1995, Figs. 56, 60), which is volate. Unfortunately, no internal valve views could be observed. No apical pore fields or spines could be distinguished. Cingulum structure unknown.

Remarks: This taxon is characterized by its minute size and the structure of the areolae, which typically become smaller towards the valve margin. It is quite reminiscent of *Fragilaria exiguissima* Archibald (1966), though this species has a higher stria density (28 str./10 µm).
Fragilaria sp. 1 does not belong to the *Fragilaria* s.s. Further research is needed to assess its generic affinities.

Biogeography & Ecology: Surprisingly, this araphid diatom was always found in silty sediments throughout the estuary, although it was also found in sandy beach sediments on the Belgian coast (Blondeel 1996). We have therefore characterized it as a tychoplanktonic species, although its exact life-form is as yet unknown.

FRAGSP01

Fragilaria sp. 2

[Figs 4-23, 4-24, 38-2, 38-10]

References:

(1)
(2)
(3) (?) Hustedt 1955

Morphology:

L: 18.7-21.9; W: 3.7; S: 12

LM - Valves lanceolate with capitate-produced apices. The valves are very often heteropolar: one of the poles is more produced than the other one. Axial area narrowly lanceolate, absent at poles. Striae opposite, parallel throughout the valve and distinctly punctate. A ring of spines is visible along the valve margin in some specimens (Fig. 4-24); the spines seem to be placed on the virgae. Cingulum structure unknown.

SEM - Only one internal valve view was observed. Valve face flat, at almost right angles with a very shallow mantle. The striae consist of small round poroids, which lie in a groove between the raised virgae and axial area. Their occlusion type is unknown. The striae do not extend far on the mantle: only a single areola is present on the mantle. Along the valve margin, simple spines are present (Fig. 38-10). A small apical pore field is present at one pole (the other pole is not visible in the single specimen observed).

Remarks: This taxon has probably been confused with *Fragilaria capensis* during the cell counts. However, it differs from that species in several respects, viz. the presence of spines, the shallow mantle with only one areola and the heteropolarity of the valves. *Fragilaria* sp. 2 does not belong to *Fragilaria* s.s. It is possible that the diatom identified as *Trachyneis acuminata* by Hustedt (1955) is conspecific with *Fragilaria 'scalaris'*. The valves in his illustrations are distinctly heteropolar.

Biogeography & Ecology: Although this taxon was very rare in our counts, it had been observed on previous occasions (Sabbe 1990) and appears to have a peculiar distribution in Westerschelde estuary: while it is very rare in most stations, it was abundant on one single small sandy shoal near the mouth of the estuary.

Fragilariforma Williams & Round 1988

Genus description: Williams & Round 1987, 1988, Round *et al.* 1990, Williams 1996a

Fragilariforma virescens (Ralfs 1843) Williams & Round 1988

Synonyms:

Fragilaria virescens Ralfs 1843
Neofragilaria virescens Williams & Round 1987

References:

(1) Ralfs 1843
(2)
(3) Krammer & Lange-Bertalot 1991, Williams & Round 1987, Williams & Round 1988, Williams 1996

Biogeography & Ecology: Only a few, presumably washed in valves of this freshwater species were found

FRAGVIRE

Martyana Round 1990

Genus description: Round *et al.* 1990

Martyana martyi Round 1990 [Figs 6-8, 6-9, 6-10, 6-11, 40-1, 40-3]

Synonyms:

Opephora martyi Héribaud 1902
'*Fragilaria leptostauron* var. *martyi* (Héribaud) Lange-Bertalot 1991' (invalidly published)
Fragilaria martyi (Héribaud) Lange-Bertalot 1993
Further synonymy: see Witkowski *et al.* 1995/96

References:

(1) Héribaud 1902
(2)
(3) Round *et al.* 1990, Krammer & Lange-Bertalot 1991, Snoeijs *et al.* 1991, Lange-Bertalot 1993a, Witkowski *et al.* 1995/96

Morphology:

L: 7.5-25.6(-42.2?); W: 6.2-13.7; W(P): 6-16.9; S: 5-6.5(-9.5?)

LM - Valves lanceolate to elliptical, isopolar or slightly heteropolar. Apices broadly rounded to cuneate. Central sternum linear to narrowly lanceolate. In LM, the striae *appear* to be composed of large, elliptical alveoli, which are alternate. The cingulum is composed of 5-6 curved copulae.

SEM - Valve face flat, gently curving into the mantle. The striae are composed of slit-like areolae. No occlusions are visible. Large apical pore fields, composed of apical rows of small puncta, are present at both poles (Fig. 40-3); in some specimens, however, only one apical pore field can be observed (Fig. 40-1). No spines are present. The cingulum is composed of 5 curved, non-porous, split copulae.

Remarks: Much controversy exists over the validity of the genus *Martyana* Round (Round *et al.* 1990). This genus was established to accomodate for one species, *Opephora martyi*, and can be distinguished from *Fragilaria* and related genera in the absence of spines and rimoportulae, the structure of the striae (with slit-like areolae), the presence of a large apical pore field at the foot pole and a characteristic 'step' at one pole. Snoeijs *et al.* (1991) transferred two more species to this new genus, viz. *Fragilaria atomus* and *Opephora schulzii* (see there), on the basis of the above-mentioned characteristics. The main difference with *Martyana martyi* lies in the structure of the striae, which are not slit-like as in the latter species.

According to other authors (Krammer & Lange-Bertalot 1991, Lange-Bertalot 1993b, Witkowski *et al.* 1995/96), *Martyana* constitutes a superfluous genus. However, as *Opephora martyana* does not belong in the genus *Opephora* (cf. also Sabbe & Vyverman 1995), they transferred it to *Fragilaria* s.l. (i.e. sensu Krammer & Lange-Bertalot 1991). In a detailed study of *Fragilaria martyi* (Witkowski *et al.* 1995/96) they show that some features evaluated as important for the independent position of the genus *Martyana*, are insufficient as they can vary within the species, viz. presence of marginal spines and the 'step' at the head pole (see also above).

We agree with Witkowski *et al.* (1995/96) that there are problems with the exact identity of the genus *Martyana*. For example, in the Westerschelde material we usually found valves with two apical pore fields, while according to the genus description *Martyana* only has one. It thus appears that most problems with the genus *Martyana* are due to an insufficient generic description, which might need to be slightly emended, and to the uncertain identity of some widespread fragilarioid taxa, such as *Staurosirella pinnata* (Ehrenberg) Williams & Round and *S. leptostauron* (Ehrenberg) Williams & Round. We believe that *Martyana martyi* does constitute an entity which can be separated from other members of the Fragilariaceae (especially in the ultrastructure of the areolae) and have therefore retained this taxon in the genus *Martyana*. However, the generic allocation of *Fragilaria atomus* and *F. schulzii* to *Martyana* is more problematic and requires further study.

Biogeography & Ecology: *M. martyi* is an cosmopolitan, epipsammic, stalked species in very fine to fine sandy sediments, mainly in the inner and upper reaches of the estuary. This is in accordance with published information on its distribution in freshwater and slightly brackish water environments (Witkowski *et al.* 1995/96 and references therein). *M. martyi* appeared to be more abundant in colder months.

MARTMART

Meridion Agardh 1824

Genus description: Round *et al.* 1990

Meridion circulare (Greville 1823) Agardh 1831

Synonyms:
Echinella circularis 1822

References:

(1) Greville 1823
(2)
(3) Williams 1985, Krammer & Lange-Bertalot 1991

Biogeography & Ecology: Only a few valves of this epiphytic freshwater species were found.

MERICIRC

Opephora Petit 1888

Genus description: Round *et al.* 1990, Sabbe & Vyverman 1995

The genus *Opephora* has long been abused to accommodate many heteropolar fragilarioid diatoms. However, recently its identity has been re-assessed (Round *et al.* 1990): it is now limited to those taxa which are related to the type of the genus, *O. pacifica*, while others which only superficially resemble this species were moved to other genera (e.g. *Opephora martyi* Héribaud).

Some authors have questioned the maintenance of the genus *Opephora* (Krammer & Lange-Bertalot, 1986-1991). This is mainly because it was originally established on the basis of LM characteristics which would not suffice the creation of a new genus today. However, evidence from our own observations and other studies (Sullivan, 1979; Round *et al*, 1990) has shown that specimens of the type of the genus from widely dispersed localities consistently show the same alveolar ultrastructure (cf. description of *Opephora pacifica*). Notwithstanding that this *a posteriori* characteristic was not (or rather could not be) recognized by Petit (1888) and has, in recent descriptions, acquired greater taxonomic weight than the original discriminating features given by Petit (1888), it remains characteristic of the *typus generis* and should be treated as such. The same combination of features (the unique areolar ultrastructure plus the other characteristics of the *typus generis*) is to our knowledge not known in taxa from any other genus and strongly favours the preservation of the genus *Opephora*.

The genus *Opephora* in the Westerschelde estuary was studied in detail (Sabbe & Vyverman 1995). In addition, representatives of this genus were also studied in herbarium material[1] and in samples collected in Australia (Hopkins estuary, Victoria). Large parts of this paper have been reproduced below, albeit in a slightly modified version.

Opephora guenter-grassii (Witkowski & Lange-Bertalot 1993) Sabbe & Vyverman 1995

[Figs 5-27, 5-28, 5-29, 5-30, 5-31, 5-32, 5-33, 5-34, 5-34, 39-3, 39-4]

Synonyms:

Fragilaria guenter-grassii Witkowski & Lange-Bertalot 1993

References:

(1) Witkowski & Lange-Bertalot 1993
(2) Witkowski & Lange-Bertalot 1993
(3) Witkowski & Lange-Bertalot 1993, Witkowski 1994, Sabbe & Vyverman 1995

Morphology:

Westerschelde:	L: 3.7-20 (8.7 ± 2.9); W: 1.8-3.1 (2.3 ± 0.3); S: 12-16 (13.7 ± 1.1)(n=68)
Somme (Hourdel):	L: 7.5-13.7 (10.6 ± 1.7); W: 2.5-3.7 (3.0 ± 0.5); S: 12-16 (13.6 ± 1.0)(n=28)
Blakeney Point:	L: 4.7-12.5 (8.7 ± 2.0); W: 1.6-3.1 (2.4 ± 0.3); S: 12-17 (13.5 ± 1.5)(n=32)
Hopkins:	L: 5.1-8.7 (7.3 ± 1.4); B: 1.9-2.5 (2.3 ± 0.3); S: 12-14 (13.2 ± 0.8)(n=5)

LM - In living material, one large plastid, which appears bilobed in girdle view, can be observed. The cells are either solitary or form short radiating or chain-like colonies (in which the cells are attached to each other at their apices). The valves are usually heteropolar, the ends rounded to cuneate. In girdle view, the frustules are 2.2-5.9 µm wide and more or less cuneate. The shape of the axial area is variable, ranging from linear to narrowly lanceolate. The striae are parallel at the centre, parallel to convergent at the poles; their arrangement is usually alternate, although valves with opposite striae or a mixed striation pattern could also be observed. They are not visibly cross-lineolate and are not crossed by a marginal longitudinal crossbar.

SEM - The valve face is flat to rounded, gradually sloping into the mantle. Interlocking spines were never observed. The striae consist of elongated areolae which, both internally and externally, are crossed by a more or less complex network of narrow ribs (often eroded), which seem to protrude

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[1] Cleve et Möller slide n° 255, Hourdel (France)(AWH n° II 9 A12), Frenguelli 379 n° 5, Cabo Guardian, Santa Cruz (Argentina)(UNLP), Frenguelli 388 n° 3, Riacho San Blas (Argentina)(UNLP), Grunow slide n° 790, Kalkbay, Cape Town (South Africa)(AWH n° VI 41 B10), Van Heurck, Types du Synopsis, n° 280, Ile de Mors (Denmark)(BR), Salah's material from Blakeney Point, Norfolk (Great Britain)(BM 36399-36402 and 36405-36407), Hustedt's material from Miang Besar (Borneo)BRM N 15/51

from the vimines. Apical pore fields are present at both poles, the one at the foot pole usually being more developed. No rimoportulae are present. The structure of the cingulum is not very clear: it seems to be composed of at least 4 copulae.

Remarks: Our specimens have a larger size range than the holotype specimens described by Witkowski & Lange-Bertalot (1993)(namely 3.7-20 µm versus 4.5-7 µm respectively) and are usually heteropolar in valve view (cf. Witkowski & Lange-Bertalot (1993) more often elliptic). The latter may be a size-related effect, comparable to those reported by e.g. Geitler (1932), Tropper (1975) and Cox (1993) for other diatom taxa. The 9-12 str./10 µm given in the type description (Witkowski & Lange-Bertalot 1993) does not correspond with that of the illustrated type specimens (about 12-14 str./10 µm), which is closer to our observations.

This species was originally described as a *Fragilaria* species (and not as an *Opephora* species) because it does not possess a marginal rib or spines (Witkowski & Lange-Bertalot 1993). However, nor are these two features typical for the genus *Opephora* (as asserted in the type description of *Fragilaria guenter-grassii*). Therefore they cannot be a sound basis for the exclusion of *O. guenter-grassii* from *Opephora*.

This species seems to be closely related to *Opephora mutabilis*, from which it differs in size and stria density (although there is a considerable overlap between the two species, the average values for all localities are consistently and distinctly different), in the absence of a longitudinal, marginal crossbar and spines, in the width of the sternum (which tends to be broader in *O. guenter-grassii*), in the arrangement of the striae [sometimes totally or partly opposite, Fig. 5-27], and in habit (no ribbon-like colony-formation, probably due to the lack of spines).

In LM this species can easily be confused with the recently described species *Fragilaria gedanensis* Witkowski (cf. Witkowski 1993; Witkowski & Lange-Bertalot 1993). According to the type description (Witkowski 1993) this species always has opposite (or slightly alternating) striae. However, the taxonomic value of this feature is uncertain as frustules were found in the Westerschelde material with a mixed striation pattern on a single valve. The ultrastructure of the striae is not clearly defined. In some specimens (cf. Witkowski 1993, Fig. 18) the striae are very like those of *O. guenter-grassii*, while in other specimens the striation pattern resembles that of *F. atomus* Hustedt (syn. *Martyana atomus* Snoeijs), which are sometimes biseriate over part of the valve (cf. Witkowski & Lange-Bertalot 1993, Fig. 2j; Snoeijs *et al.* 1991, Figs 12 and 17). The occurrence of a similar phenomenon (i.e. a locally aberrant striation within one valve) prompted Lange-Bertalot (1989, 1993) to reject the new genus *Punctastriata* Williams & Round. The taxonomic significance of such characteristics clearly needs further investigation.

Biogeography & Ecology: *Opephora guenter-grassii* is a common and often dominant component of epipsammic assemblages in the Westerschelde estuary (up to 16 x 10^6 cells per gram SDW, relative abundance 40 %). Its spatial distribution within the estuary is rather independent of both salinity and the silt content of the sediment (providing sandgrains are present). It occurs as solitary cells or short, radiating colonies on the surface of sandgrains.

O. guenter-grassii has been reported as an epipsammic species from brackish and marine habitats in Europe (e.g. Rincé 1990, as *O. perminuta*; Sabbe 1993, as *O.* cf. *perminuta*; Witkowski & Lange-Bertalot 1993), North America (Navarro 1982; as *O. pacifica*), Australia, Southeast Asia and South America (Sabbe & Vyverman 1995) and thus appears to be cosmopolitan.

OPEPGUEN

Opephora marina (Gregory 1857) Petit 1888 [Figs 6-6, 6-7, 40-9, 40-10]

Synonyms:

Meridion (?) *marinum* Gregory 1857
Sceptroneis marina (Gregory) Lagerstedt 1876
Thalassiothrix marina (Gregory?) Grunow in Van Heurck 1881
Grunoviella marina (Gregory) Peragallo & Peragallo 1897-1908

References:

(1) Gregory 1857
(2)
(3) Hustedt 1931, Ricard 1987, Rincé 1990

Morphology:

L: 18.7-21; W: 4.4-5; S: 10-11

LM - Valves clavate, always distinctly heteropolar. Head pole broadly rounded, foot pole produced, rostrate. Axial area broad, clavate. The striae are marginal and appear to be composed of at least one alveolus; they are more or less radiate throughout the valve.

SEM - Only a single internal valve view was observed. Valve face flat, gradually merging into the mantle. Each stria is composed of a single round to elliptical (transapically elongate) alveolus. These are occluded (internally) by complex, flat vela (cribra or rotae?) of the same type as in *Opephora naveana* Le Cohu (cf. Sabbe & Vyverman 1995). Apical pore fields of a weakly developed ocellulimbus type are present at both apices; they consist of several apically orientated rows of small puncta. Cingulum structure unknown.

Remarks: Although our specimens are smaller and have a higher stria density than the specimens from the type description and Hustedt's description, there is little doubt that they belong to this species. Similar, smaller forms were observed by Poulin *et al.* (1984) and Kuylenstierna (1989-90). Rincé (1990) reported even smaller specimens with about 8-16 str./10 µm from the Loire estuary (France), but as no illustrations are provided it is impossible to assess whether his specimens truly concern *Opephora marina*. Witkowski (1994) observed similar small forms in the Gulf of Gdansk (Poland) and states that they might belong to *Opephora marina* var. *minuta* Cleve-Euler (1953). However, the type material of this taxon has not yet been investigated and therefore its identity and relationship with similar forms such as *Pseudostaurosira perminuta* and *Opephora guenter-grassii* are still unknown. Indeed, Witkowski's (1994) Pl. 12, Fig. 18 is very reminiscent of *Opephora naveana* (cf. Sabbe & Vyverman 1995) but has a broader central sternum. Clearly, these forms need further study.

Opephora marina displays all features that are characteristic of the genus *Opephora* (cf. Sabbe & Vyverman 1995), viz. absence of rimoportulae, occlusion type and habitat, and should therefore be placed in this genus.

Biogeography & Ecology: *Opephora marina* was originally described from Lamlash bay on the Scottish West Coast (Gregory 1857) but is probably cosmopolitan (cf. e.g. Hustedt 1931, Poulin *et al.* 1984, Rincé 1990). In the Westerschelde, it was very rare in sandy sediments near the mouth of the estuary.

OPEPMARI

Opephora mutabilis (Grunow 1879) Sabbe & Vyverman 1995

[Figs 5-18, 5-19, 5-21, 5-22, 5-23, 5-24, 5-25, 39-7]

Synonyms:

Sceptroneis mutabilis Grunow (*marina* var?) in Cleve & Möller 1879
Sceptroneis marina var ?? *parva* Grunow in Van Heurck 1881
Grunoviella parva (Grunow) Peragallo & Peragallo 1897-1908
Opephora parva (Grunow) Krasske 1939
O. olsenii Møller 1950
(?) *O. horstiana* Witkowski 1994

References:

(1) Cleve & Möller 1879
(2) Sabbe & Vyverman 1995 (isotype)
(3) Sundbäck 1987, Witkowski 1994, Sabbe & Vyverman 1995

Morphology:

Westerschelde:	L: 3.7-19.4 (10.4 ± 3.2); W: 2.5-5.0 (3.2 ± 0.6); S: 8-16 (10.2 ± 2.1)(n=39)
Somme (Hourdel):	L: 7.6-18.1 (13.0 ± 2.6); W: 3.1-5.0 (4.1 ± 0.6); S: 9-13 (10.9 ± 1.0)(n=30)
Blakeney Point:	L: 7.0-11.5 (9.1 ± 1.9); W: 2.5-5.0 (3.6 ± 1.2); S: 9-14 (11.2 ± 2.5)(n=4)
Hopkins:	L: 7.7-18.1 (13.4 ± 2.8); W: 2.5-3.7 (3.3 ± 0.4); S: 9-14 (11.9 ± 1.8)(n=18)

LM - The isotype slide contains only solitary valves whereas small, ribbon-like colonies (of 2 to several cells) were present in the Westerschelde material. In girdle view, the frustules are rectangular. The plastid structure was not observed. The valves are always heteropolar (ovate to clavate). The axial area is usually very narrow, occasionally slightly lanceolate. The valvar ends are rounded to cuneate (at the footpole only). The striae are coarse, parallel at the centre, parallel to convergent at the poles, and usually alternate throughout the valve. In larger specimens, the striae appear to be clearly cross-lineolate. Most valves have a distinct longitudinal ring of spines along the valve margin.

SEM - A thorough SEM description of this species (as *O. olsenii*), which closely fits the specimens observed in this study, is given by Sundbäck (1987).

Remarks: The average dimensions for each locality compare well and match the description of this species by Sundbäck (1987), except that the maximum stria density values are higher (up to 16 striae in 10 µm) in our measurements. Although different opephoroid taxa were present on the isotype slide, the population illustrated in Figs 14, 15, 20, 22, 23, 25 and 26 (in Sabbe & Vyverman 1995) was selected as the isotype of *O. mutabilis* because of its close match with the description (9-10 striae in 10 µm) and illustrations of *S. marina* var. ?? *parva* in Van Heurck (1881). In original editions of this work, the illustrations show a more or less distinct areolar substructure (cross-lineolation ?). However, the marginal ring of spines is not illustrated in the original drawings.

O. mutabilis, O. guenter-grassii, O. naveana and *O.* sp. 1 appear to be closely related. The relationship between these taxa and similar taxa such as *Pseudostaurosira shiloi* (Lee, Reimer &

McEnery) Hallegraeff & Burford (Hallegraeff & Burford 1995) requires further study.

The nomenclatural history of *Opephora mutabilis* and *Pseudostaurosira perminuta* is closely linked. VanLandingham (1978)[and to our knowledge most other authors since Peragallo & Peragallo (1897-1908)] referred to *Sceptroneis marina* var. ?? *parva* Grunow and *S.* ? *marina* var. ?? *perminuta* Grunow (Van Heurck, 1881) as the first records of *O. parva* and *O. perminuta*. The descriptions of these taxa in Van Heurck (1881) consist of some illustrations (Pl. XLV, Figs 18-20 and 36 respectively) and the accompanying legends, which mention the stria density (9-10 and 15 in 10 µm respectively) of both taxa and the fact that they occur together in the same locality (Hourdel, France). Both taxa were also described in Peragallo & Peragallo (1897-1908), where reference is made to the same locality, Hourdel, and to a slide (n° 155, Cleve & Möller). In the Van Heurck Diatom Collection we found a Cleve et Möller slide labelled Hourdel (nr. 255), which contained the two taxa. We consider this slide an isotype, while the corresponding Cleve & Möller slide nr. 255 in the Grunow Diatom Collection in Vienna carries the holotypes of both taxa.

However, two years before the descriptions in Van Heurck (1881), a list (made by Grunow) of the diatom species on slide nr. 255 ('Hourdel, embouchure de la Somme') was published in Cleve & Möller's Diatoms (part V (1879), Cleve & Möller 1877-1882). This list contains the following entry: '*Sceptroneis (marina* var. ?) *mutabilis* Grunow (*Fragilaria mut.* form. 10 str. in 0.01 mm) common. var. *minuta* Grunow. 15 str. in 0.01 mm.' As the descriptions in Van Heurck (1881) and Cleve & Möller (1879) correspond to each other and no other opephoroid diatoms were mentioned in the species list of slide n° 255, the entries in both works must refer to the same taxa. However, the entries in Cleve & Möller (1879) represent the oldest legitimate names and therefore have priority. They are also reported in VanLandingham (1978)['*Sceptroneis mutabilis* Grunow in Cleve & Möller 1881, nr. 255 (*marina* var.?)' and '*S. mutabilis* var. *minuta* Grunow in Cleve & Möller 1881, nr. 255 (*marina* var.?)], though for reasons unknown to the author, their use is not recommended. Moreover, the connection between the descriptions in Cleve & Möller (1879) and Van Heurck (1881) was not made. Peragallo & Peragallo (1897-1908) also mentioned *Sceptroneis mutabilis* Grunow ?? as a possible (note the question marks) synonym of *Grunoviella parva* (Grunow) Peragallo & Peragallo (syn. *Sceptroneis marina* var. *parva*).

In Van Heurck (1881), Grunow placed both taxa as varieties of *Sceptroneis marina* (although with some reserve: notice the question marks in *S. marina* ?? var. *parva* and *S.* ? *marina* var. ?? *perminuta*) because of their resemblance to *S. marina* (Gregory) Lagerstedt (now *Opephora marina* (Gregory) Petit). He also changed the epithet *minuta* to *perminuta*.

Peragallo & Peragallo (1897-1908) transferred *S. marina* var. ?? *parva* and *S. ?* marina var. ?? *perminuta* to the genus *Grunoviella* and raised them to specific rank (*G. parva* (Grunow) Peragallo & Peragallo and *G. perminuta* (Grunow) Peragallo & Peragallo). Besides *S. marina* var. ?? *parva*, *Fragilaria mutabilis* var. ? *cuneata* and *S. mutabilis* ?? are given as synonyms.

Frenguelli (1938) transferred *G. perminuta* to the genus *Opephora* (*O. perminuta* (Grunow) Frenguelli, while Krasske (1939) did the same for *G. parva* (*O. parva* (Grunow) Krasske). VanLandingham (1971), however, does not recommend the use of the latter entry. Finally, we transferred *O. perminuta* to the genus *Pseudostaurosira* and reinstated the first specific epithet of *O. parva*, i.e. *mutabilis* (Sabbe & Vyverman 1995).

Biogeography & Ecology: In the Westerschelde estuary, *Opephora mutabilis* is a common epipsammic, stalked species, although it is much rarer than *Opephora guenter-grassii*. As with the latter species, the distribution of *O. mutabilis* in the estuary appeared to be rather independent of the amount of silt in the sediments and salinity. *O. mutabilis* typically forms short, ribbon-like colonies, which are attached to sandgrains with a mucilage stalk.

O. mutabilis is a cosmopolitan, epipsammic and epiphytic species from predominantly brackish environments in Europe (e.g. Sundbäck 1987, Kuylenstierna 1989-90, Wendker 1990, Gätje 1992), North America (Poulin *et al.* 1984a), Southeast Asia (Podzorski & Håkanson 1987), Australia (Sabbe & Vyverman 1995) and Africa (Compère 1991; as *O. pacifica*).

OPEPMUTA

Opephora naveana Le Cohu 1988 [Figs 5-20, 39-5, 39-6]

Synonyms:

Fragilaria opephoroides Takano 1988 (this entry is not a real synonym as the name was not validly published)

References:

(1)	Le Cohu 1988
(2)	Le Cohu 1988
(3)	Le Cohu 1988, Takano 1988, Witkowski 1994

Morphology:

L: 7.5-12.2 (9.5 ± 1.8); W: 2.7-3.7 (3.1 ± 0.3); S: 13-15 (13.4 ± 0.7)(n=7)

LM - The LM features of this species are very similar to those of *Opephora mutabilis*, from which it can only be distinguished by its more robust appearance, the number of striae (on average higher in *O. naveana*) and the (often indistinguishable) alveolar nature of the striae.

SEM - The valve face is flat and clearly separated (often at an angle of almost 90 degrees) from the mantle by a prominent, longitudinal bar. Simple spines are present on this bar interrupting the striae, though in most specimens they seem to disappear. The striae are composed of at least 2 large alveoli, one on the valve face and one (rarely two) on the mantle. The striae are sunk below the level of the virgae externally, internally and are always alternate. The sternum is linear to slightly lanceolate. The alveoli are occluded by a complex, flat cribrum, which seems to be composed of densely intertangled volae, sometimes connected to the alveolar wall by a few small ribs. In a specimen from the Braakman (a land-locked creek off the Westerschelde estuary) these ribs are more numerous. Two apical pore fields are present; that at the foot pole is larger. The pore field at the head pole is often situated on the mantle. The cingulum is composed of at least 6 open copulae.

Remarks: This species was, prior to the description of Le Cohu (1988), also described by Takano (1988) as *Fragilaria opephoroides*. However, only an iconotypus was indicated and therefore, according to articles 8.3, 37.1 and 37.3 of the ICBN (Greuter *et al.* 1994) this entry is invalid. Some specimens clearly belong to *Opephora naveana*. The structure of the cribra with the numerous small ribs protruding from the alveolar walls, bending inwards and ending blindly in the alveoli is an unmistakable feature of this species (cf. Le Cohu 1988, Takano 1988). The identity of the majority of the Westerschelde specimens is however more problematic. They differ slightly from the type description (Le Cohu 1988) in the structure of the cribra, which lack the small ribs.

This species is probably closely related to *O. mutabilis*. In the LM, it is often hard to distinguish *O. naveana* from the smaller and more delicate specimens of *O. mutabilis*. The main distinguishing feature between the two species is an electron microscopical one: only the stria structure (no cross-lineolation, different areolar occlusions) can be used to make a positive identification of the two species. Both possess two apical pore fields so this feature cannot be used to separate them (cf. Le Cohu, 1988). Further research is needed to assess whether two different occlusion types are involved or variation of the same structure, and whether or not *O. mutabilis* and *O. naveana* are conspecific.

Biogeography & Ecology: Due to the problematic LM identification of *O. naveana*, its ecological preferences are still unclear. A similar diatom was observed by Witkowski (1994, as *Opephora* sp. 1) and Witkowski et al. (1995, Fig. 27, as *Fragilaria brevistriata*) in the Baltic area. *O. naveana* was described as a freshwater species from the Kerguelen Islands (Le Cohu 1988) but also appears to occur in brackish and marine sediments in Japan (Takano 1988), Europe and Australia (Sabbe & Vyverman 1995).

OPEPMUTA

Opephora pacifica (Grunow) Petit 1888 [Figs 6-1, 6-2, 6-3, 6-4, 6-5, 41-5]

Synonyms:

Fragilaria pacifica Grunow 1862

References:

(1)	Petit 1888
(2)	Lange-Bertalot 1989, Sabbe & Vyverman 1995 (isotype material)
(3)	Sabbe & Vyverman 1995

Morphology:

Westerschelde:	L: 13.0-48.5 (23.0 ± 12.5); W: 4.0-7.7 (5.7 ± 1.5); 6-9 (7.3 ± 1.0)(n=7)
Kalkbay:	L: 11.2-46.2 (23.2 ± 8.5); W: 6.5-8.5 (5.6 ± 1.8); 6.5-8.5 (7.4 ± 0.7)(n=35)

LM - No living material was observed. The valves are usually heteropolar, although some isopolar ones were present in the isotype material. The valve apices are broadly rounded to cuneate. The striae are parallel to slightly radiate towards the apices and somewhat alternate. The axial area is narrow. In girdle view, the frustules are more or less rectangular. The cingulum appears to be composed of about 4 copulae which are strongly curved at the apices. One of these (the valvocopula ?) is very wide. Neither a marginal crossbar nor spines were present.

SEM - This species was rare in the Westerschelde material and only one specimen was observed in the SEM. Notwithstanding the poor quality of the material, some important features can be distinguished, viz. the wide valvocopula, the absence of a marginal crossbar and spines and the nature of the occlusions, which seem to be composed of small ribs protruding from the alveolar walls and then bending inwards.

Remarks: In Lange-Bertalot (1989) reference is made to two different slides in the Grunow collection [Grunow slides nr. 790 (Kap der Guten Hoffnung) and nr. 1737 (Samoa)] as containing *Fragilaria pacifica*. It is argued that Grunow's '*Opephora*-Sippen' have spines on the mantle edge and thus do not differ from *O. mutabilis* (cf. Krammer & Lange-Bertalot 1986-1991). However, in the van Heurck Diatom Collection a hand-written book is present ('Grunow - Diatomées', no references), containing a list of Grunow slides (n° 30-2130). A species list is given for each slide. The list for nr. 790 mentions *Fragilaria pacifica* (underlined), whereas the list for nr. 1737 does not. Moreover, Grunow (1863) makes no mention of the latter locality in his second description of *F. pacifica*. In other words, the *Opephora* species from Samoa, referred to by Lange-Bertalot (1989) as *O. pacifica*, were not identified as *F. pacifica* by Grunow. Judging from the illustrations in Lange-Bertalot (1989, Tafel VII, Fig. 14-17), spines only occur in the specimens from Samoa. These actually resemble '*O. pacifica*' valves illustrated in Navarro (1982, Pl. 12, Figs 5, 6). These possess a marginal crossbar but seem to differ from *O. mutabilis* in size and stria density and are therefore probably a different taxon. None of the numerous specimens that we observed on the isotype slide possesses spines.

On the basis of our own observations we therefore believe that *Opephora pacifica* is distinctly different from the above-described *Opephora* species in size, stria density and type of areolar occlusions. In addition, it differs from *O. mutabilis* and *O. naveana* in the absence of a marginal crossbar and spines. The specimens that we observed in the Westerschelde estuary are identical to those illustrated in Sullivan (1979) and Round *et al.* (1990) and probably represent true *O. pacifica*.

Biogeography & Ecology: *O. pacifica* is very rare (only at one occasion up to 0.3 x 10^6 cells per gram SDW) in sandy sediments in the mouth of the estuary. It is a cosmopolitan, marine, epipsammic and epiphytic species: it has been reported from North America (e.g. Sullivan, 1979), South America, Europe and South Africa (Sabbe & Vyverman 1995).

OPEPPACI

Opephora sp. 1

[Figs 5-36, 5-37, 5-38, 5-39, 5-40, 39-8, 39-9, 39-10, 40-2]

References:

(1)
(2)
(3) Takano 1986

Morphology:

L: 6.2-31.7; W: 3.4-5; S: 13-14.5(-15)

LM - Cells forming ribbon-like colonies, up to 5 or more (?) cells long. Valves elliptical, isopolar to heteropolar, with broadly rounded to cuneate apices. Axial area very narrow, linear. Striae parallel in the centre to radiate at the apices, non-punctate, alternate. In some specimens, a distinct longitudinal ring of spines can be seen along the valve margin.

SEM - Valve face flat, merging rather gradually with the shallow mantle. The striae are composed of (slightly) apically elongate areolae and lie between raised virgae. The areolae are internally occluded by complex vela; externally, small ribs, by means of which the vela appear to be attached to the vimines, are visible. Interlocking spines are present on a marginal crossbar on the valve face-mantle junction; they are either simple and rather small or longer and sometimes spathulate. A very typical feature of this taxon is the presence of small, granule-like 'spines' on the vimines between the areolae. At both poles, a pore field is present: one of these is large and consists of apical rows (of puncta? - not clearly visible), separated by wavy ridges. The other one is much smaller and is composed of a few rather randomly placed puncta. The cingulum is composed of 5-6 open, non-porous copulae.

Remarks: There is little doubt that this taxon belongs to the species group around *Opephora mutabilis* and was therefore placed in the genus *Opephora* (cf. Sabbe & Vyverman 1995). It is indeed very similar to the latter species, which also forms ribbon-like colonies (presence of marginal spines), has the same complex areolar occlusions and almost identical pore fields. However, *Opephora* sp. 1 differs from *O. mutabilis* in several respects: (1) the valves of *O. mutabilis* are always heteropolar, while *O.* sp. 1 valves are usually more or less isopolar, more elliptical; (2) the number of striae in 10 µm in *O.* sp. 1 falls within the stria density range of *O. mutabilis* but is on average higher, viz. 13-14 versus 10-12 in the latter (measured on several different populations, cf. Sabbe & Vyverman 1995); (3) *O.* sp. 1 always has one small 'spine' on most vimines of the valve, while this is not the case in *O. mutabilis*. However, in some specimens of *O. mutabilis* (cf. Sundbäck 1987, Fig. 37, Witkowski 1994, Pl. 11, Fig. 4, Sabbe & Vyverman 1995, Fig. 62), small 'spines' can be seen on the vimines, though there are usually more than one (up to three) and are only present on the mantle; (4) the marginal spines never have accompanying, small, basal spines. Whether these differences are stable and sufficient to distinguish between both taxa still has to be verified through study of a larger number of specimens from different populations.

Opephora sp. 1 is also reminiscent of *Fragilaria flavovirens* Takano (1986), though this resemblance appears to be only superficial, as there are differences in stria density (16-18 in *F. flavovirens*), number of areolae present on the mantle (usually one in large specimens of *F. flavovirens*), the structure of the apical pore fields (two identical pore fields in *F. flavovirens*) and occlusion type (rotae in *F. flavovirens*). *F. flavovirens* does not belong to *Fragilaria* s.s. and requires further study.

Biogeography & Ecology: *Opephora* sp. 1 is a common species in fine to medium sandy in the lower reaches and the mouth of the estuary. It was also observed in Salah's material from Blakeney Point (England).

OPEPSP01

Pseudostaurosira Williams & Round 1987

Genus description: Williams & Round 1987, Round *et al.* 1990, Sabbe & Vyverman 1995

Pseudostaurosira was established by Williams & Round (1987) to accomodate for the species group around *Pseudostaurosira brevistriata* (Grunow) Williams & Round (syn. *Fragilaria brevistriata* Grunow); the same species group is recognized as a 'Sippencomplex' by Krammer & Lange-Bertalot (1986-1991). *Pseudostaurosira* is characterized by sparse marginal areolae, a (usually) wide sternum and complex, branched areolar occlusions. Our investigations of *P. perminuta* show that its frustule morphology shows intermediate features between *Staurosira* (number of marginal areolae) and *Pseudostaurosira* (areolar ultrastructure). Therefore, these genera either ought to be combined or have their diagnoses reconsidered and modified. The latter is common practice in systematics: for example, the recent discovery of a new species belonging to the genus *Plagiogrammopsis* has prompted Gardner & Crawford (1994) to emend the description of this genus. As all taxa belonging to *Pseudostaurosira* share a similar, complex type of areolar occlusions, which differs from the occlusion type in *Staurosira,* we advocate the maintenance of a separate genus *Pseudostaurosira*. This genus would then also include taxa with more than 2 marginal areolae and a variable sternum shape.

Pseudostaurosira brevistriata(Grunow in Van Heurck 1885) Williams & Round 1987

[Fig. 6-18]

Synonyms:

Fragilaria brevistriata Grunow in Van Heurck 1885

References:

(1) Grunow in Van Heurck 1885
(2)
(3) Williams & Round 1987, Round *et al.* 1990, Krammer & Lange-Bertalot 1991, Witkowski *et al.* 1995

Morphology:

L: 20.2-21.2; W: 3.7-4.6; S: 14-14.5

LM - Valves elliptical with more or less rostrate apices. Central sternum very broad. Striae marginal, short, more or less radiate throughout the valve.

Remarks: According to the type description of *Fragilaria geocollegarum* (Witkowski *et al.* 1995), our specimens cannot belong to this species as they are much larger. The true identity of *Fragilaria brevistriata* appears to be only little known, given the variety of forms that are identified as this species [e.g. compare Williams & Round (1987) with Witkowski *et al.* (1995)]

Biogeography & Ecology: Only a few valves of this cosmopolitan freshwater species (Krammer & Lange-Bertalot 1991) were found. They were most probably washed in from the catchment basin.

PSEUBREV

Pseudostaurosira perminuta(Grunow in Van Heurck 1881) Sabbe & Vyverman 1995

[Figs 6-12, 6-13, 6-14, 6-15, 6-16, 6-17, 40-4, 40-5, 40-6]

Synonyms:

Sceptroneis ? *marina* var. ?? *perminuta* Grunow in Van Heurck 1881
Sceptroneis mutabilis var. *minuta* Grunow (marina var.??) in Cleve & Möller 1879
Grunoviella perminuta (Grunow) Peragallo & Peragallo 1897-1908
Opephora perminuta (Grunow) Frenguelli 1938
Fragilaria neoelliptica Witkowski 1994
(?) *Fragilaria construens* var. *subsalina* Hustedt 1925

References:

(1) Grunow in Van Heurck 1881
(2) Sabbe & Vyverman 1995
(3) Sabbe & Vyverman 1995, Witkwoski 1994

Morphology:

Westerschelde:	L: 6.2-16.2 µm (10.4 ± 2.7); W: 2.2-4.1 µm (3.0 ± 0.5); S: 14-18 (16.0 ± 0.8)(n=30)
Somme (Hourdel):	L: 5.6-17.5 µm (10.6 ± 3.1); W: 2.5-4.1 µm (3.6 ± 0.3); S: 15-18 (16.7 ± 0.7)(n=30)
Blakeney Point:	L: 7.2-16.2 µm (11.6 ± 2.4); W: 2.2-4.4 µm (3.2 ± 0.7); S: 14-17 (15.7 ± 0.9)(n=10)

LM - Only solitary valves were found on the isotype slide (Cleve & Möller nr. 155, AWH). In samples from the Westerschelde estuary, small colonies consisting of two to six cells were present. The plastid structure is unknown. The valves are usually more or less heteropolar (ovate to clavate), rarely isopolar (elliptic). The valve ends are rounded to cuneate. In girdle view, the frustules are rectangular, 3.1-6.2 µm broad. The striae are parallel to slightly radiate in the centre, becoming more radiate at the apices; they are usually more or less alternate. The average stria density matches the original description (15 str./10 µm) in Cleve & Möller (1879) and is almost identical to that in the original illustration of this species in Van Heurck (1881), where 16 striae can be counted in 10 µm. The shape of the axial area is quite variable, narrowly to broadly lanceolate, often occupying almost half the valve width. Moreover, because of the variable length of the striae (within one valve), it is usually irregular. In some specimens, the striae appear to be interrupted by a prominent, marginal ring of spines. Teratological forms were quite common.

SEM - The valve face is flat with a gradual transition to the mantle. In most specimens, a prominent ring of simple spines is present on the margin of the valve face, invariably interrupting the striae (on the vimines). They are sometimes more or less spathulate, though shape can be quite variable, even within one frustule. The spines are accompanied by smaller granules on both sides of the marginal ring of spines. The striae comprise circular to elliptical areolae (about 45-60 in 10 µm), which diminish in size away from the valve face margin. The areolae are occluded internally by a velum of the volate type. Externally, a small rib (by which the vola is probably attached to the areolar wall) is sometimes visible. In most specimens however, these structures are lost. Apical pore fields are present at both apices. The foot pole field is usually larger and more regular, consisting of a few rows of poroids, often separated by a wavy ridge. No rimoportulae are present. The cingulum consists of several (up to 10) open, ligulate copulae, which are curved at the apices. The valvocopula is wide.

Remarks: *Pseudostaurosira perminuta* shows some resemblance to *Staurosira elliptica* (Schumann) Williams & Round (syn. *Fragilaria elliptica*). The true identity of the latter is unclear however (Hustedt, 1931-1959; Williams & Round, 1987), as SEM examination of the type material has not been made (cf. Krammer & Lange-Bertalot, 1986-1991). We agree with Krammer & Lange-Bertalot (1986-1991) that specimens of *S. elliptica* described by Haworth (1975) are more closely related to *Staurosira construens* Ehrenberg (syn. *Fragilaria construens* (Ehrenberg) Grunow). They differ from *S. elliptica* sensu Archibald (1983), sensu Poulin *et al.* (1984a) and sensu Krammer & Lange-Bertalot (1986-1991). *Pseudostaurosira perminuta* differs from Haworth's specimens in having additional granules, in the constant position of the intercostal spines and the variable shape of the axial area and valve (usually more opephoroid). The main points of difference in the descriptions of Archibald (1983) and Poulin *et al.* (1984a) are the granules and the presence of several areolae below the ring of spines. The specimens described by Krammer & Lange-Bertalot (1986-1991) have much more coarsely punctate striae.

P. perminuta also resembles, and could possibly be conspecific with, *Fragilaria construens* var. *subsalina* Hustedt (Simonsen, 1987; Krammer & Lange-Bertalot, 1986-1991). As no SEM study of the type material of the latter has been made yet (Krammer & Lange-Bertalot 1986-1991) and no data are available on its morphological variability, we prefer to maintain them as two taxa. *S. elliptica* sensu Poulin *et al.* (1984a) shows a great resemblance to *F. construens* var. *subsalina*.

Finally, *Pseudostaurosira perminuta* shows great affinity with *P. zeilleri* (Héribaud) Williams & Round (syn. *Fragilaria zeilleri* Héribaud) and its varieties in several respects [cf. type material descriptions in Serieyssol (1988)], viz.: the structure of the internal areolar occlusions, the variable shape of the axial area [cf. *F. zeilleri* var. *elliptica* Gasse (Gasse 1980)], the presence of several areolae below the marginal ring of spines (only *F. zeilleri* var. *nitzschioides* Héribaud; Serieyssol, 1988). The main differences are the presence of the granules and a higher stria density in *P. perminuta*.

For the nomenclatural history of *Pseudostaurosira perminuta*, see *Opephora mutabilis*.

Biogeography & Ecology: *Pseudostaurosira perminuta* seems to prefer higher salinities than e.g. *Opephora guenter-grassii* and *O. mutabilis*, with which it often co-occurs. Although *P. perminuta* is present in the mesohaline stations it reaches higher abundances (up to 0.7 x 10^6 cells per gram SDW) in the poly- and euhaline stations. As *O. mutabilis*, *P. perminuta* forms short, ribbon-like colonies which are probably attached to sandgrains. *Pseudostaurosira perminuta* has hitherto only been reported as a benthic (most probably epipsammic) species from brackish and marine sediments in Europe (Witkowski 1994; this study).

PSEUPERM

Staurosira Ehrenberg 1843

Genus description: Williams & Round 1987, Round *et al.* 1990

Staurosira construens Ehrenberg 1843 [Figs 6-19, 6-20]

Synonyms:

Fragilaria construens (Ehrenberg) Grunow 1862

References:

(1) Ehrenberg 1843
(2)
(3) Williams & Round 1987, Round *et al.* 1990, Krammer & Lange-Bertalot 1991

Morphology:

LM - Valves lanceolate to cruciform with cuneate apices, lanecolate with triundulate margins (forma *triundulata*) or slightly panduriform with rostrate apices (f. *binodis* (Ehrenberg) Hustedt). Axial area very narrow, linear (Fig. 6-19) to broader, lanceolate-elliptical (Fig. 6-20). Striae slightly radiate throughout the valve.

Remarks: Both *Staurosira construens* and its forms *triundulata* and *binodis* were found.

Biogeography & Ecology: *Staurosira construens* is a freshwater species (except for its var. *subsalina* Hustedt) and was very rare in our samples; it is probably washed in from the catchment basin.

STAUCONS+STAUCOTR

Synedra Ehrenberg 1830

Genus description: Williams & Round 1986, Round *et al.* 1990

Synedra acus Kützing 1844

Synonyms:

Fragilaria ulna (Nitzsch) Lange-Bertalot var. *acus* (Kützing 1844) Lange-Bertalot 1980

References:

(1) Kützing 1844
(2)
(3) Williams & Round 1986, Krammer & Lange-Bertalot 1991, Snoeijs & Potapova 1995

Biogeography & Ecology: Only one valve belonging to this epiphytic (or free-living) diatom species was found; it was probably washed in from the upper and freshwater tidal reaches of the estuary. In the Baltic, it occurs in salinities up to 6 ‰ (Snoeijs & Potapova 1995), which is outside the salinity range of the sampling stations in the Westerschelde estuary.

SYNEACUS

Tabularia (Kützing 1844) Williams & Round 1986

Genus description: Williams & Round 1986, Round *et al.* 1990

Tabularia fasciculata (Agardh 1812) Williams & Round 1986 [Fig 40-8]

Synonyms:

Diatoma fasciculatum Agardh 1812
Synedra fasciculata (Agardh) Kützing 1844
Fragilaria fasciculata (Agardh) Lange-Bertalot 1980 p.p.
Further synonymy, see Snoeijs 1992, 1993

References:

(1) Agardh 1812

(2) Snoeijs 1992 (lectotype)
(3) Williams & Round 1986, Krammer & Lange-Bertalot 1991, Snoeijs 1992, 1993

Morphology:

L: 34.7-43.7; W: 5.5-7.5; S: 14 (n=2)

LM - Valves lanceolate, apices cuneate. Central sternum broad, lanceolate. Striae marginal, parallel to radiate (at the apices). Their structure is indistinct. At both poles, a portule is visible.

SEM - Valve face flat, gradually merging into a shallow mantle. The striae are composed of two large areolae (only the valve face one is visible, cf. Snoeijs 1993), crossed by small apically orientated ribs. A rimoportula is visible at one pole only (Fig. 40-8). Two apical pore fields of unknown type are present. Cingulum structure unknown.

Remarks: The *Tabularia fasciculata*-complex is a complicated and highly variable group: Snoeijs (1993) recognized 4 discrete *fasciculata*-forms in material from the Baltic Sea. Our specimens correspond well to the description of *T. fasciculata* given by Snoeijs, but at least one specimen (Fig. 40-8) has only one rimoportula, while *T. fasciculata* usually has two per valve. This specimen therefore might belong to *Tabularia* cf. *laevis* (cf. Snoeijs 1993).

Biogeography & Ecology: Only a few valves belonging to this epiphytic species were found. According to Krammer & Lange-Bertalot (1991), *Tabularia fasciculata* is a typical brackish water species, which can also be found in marine and freshwater environments. Snoeijs (1993) found that in the Baltic it is most abundant close to the Swedish West Coast (where it is dominant, cf. Kuylenstierna 1989-90) and becomes rarer with declining salinities.

SYNEFASC

Ordo Rhaphoneidales

Fam. RHAPHONEIDACEAE Forti

Delphineis Andrews 1977

Genus description: Andrews 1977, Round *et al.* 1990

Delphineis minutissima (Hustedt 1939) Simonsen 1987

[Figs 6-21, 6-22, 6-23, 6-24, 41-1]

Synonyms:

Rhaphoneis minutissima Hustedt 1939

References:

(1) Hustedt 1939
(2) Simonsen 1987
(3) this study

Morphology:

L: 4.6-21.3; W: 3.1-7.6; S: (14-)16-20

LM - Two or more small, girdle-appressed plastids are present (Figs 6-21, 6-22). Valves broadly elliptical with broadly rounded apices to lanceolate with cuneate apices. Axial area narrow, linear, expanded into small circular areas at both poles. At the top of these areas, two small puncta are often visible. Two portules are visible, one at each pole. Striae radiate, composed of rather large, roundish areolae. A marginal ring of spines is visible in some specimens. Girdle shallow.

SEM - Valve face flat, gradually sloping into a shallow mantle. Striae composed of roundish areolae, occluded by rotae. Note the presence of two small puncta in the central sternum, near the apices, and the rimoportula and its external, roundish opening. On the valve face-mantle junction, a marginal ring of small spines is present.

Remarks: Simonsen (1987) transferred this species, described by Hustedt (1939) as *Rhaphoneis minutissima*, to the genus *Delphineis* Andrews (see Round *et al.* 1990).

Biogeography & Ecology: Together with *Cymatosira belgica* and *Thalassiosira proschkinae*, *D. minutissima* was the most abundant and characteristic taxon in silty sediments throughout the estuary. It is often found associated with small sediment or detritus particles, which probably get easily suspended in to the watercolumn. We therefore classified it as a tychoplanktonic species. However, Denys (1995b) pointed out that it will readily grow on the surface of sandgrains and thus adopts a truly epipsammic life-form.
D. minutissima has been reported from marine and brackish sediments worldwide (Hustedt 1939, 1955, De Jonge 1985, Cooper 1995a), often still as *Rhaphoneis minutissima* (Denys 1991a, 1995b, Juggins 1992, Vos & De Wolf 1993).

DELPMINU

Delphineis surirella (Ehrenberg 1841) Andrews 1981 [Figs 7-3, 41-2]

Synonyms:

Zygoceros surirella Ehrenberg 1841
Rhaphoneis surirella (Ehrenberg) Grunow in Van Heurck 1881

References:

(1) Ehrenberg 1841
(2)
(3) Hustedt 1927, Andrews 1981, Poulin *et al.* 1984a, Round *et al.* 1990, Riaux-Gobin 1991, Hasle & Syvertsen 1996

Morphology:

L: 9.4-30; W: 6.9-17.2; S: 8.5-12

LM - Plastids not observed. Valve morphology identical to that of *Delphineis minutissima* except for size and stria density.

SEM - Valve face flat, curving rather gently into a shallow mantle. Central sternum linear, narrow. At both poles, two small puncta are visible in the central sternum. At both poles, a rimoportula is present on one side of these puncta. Externally, they open into a small, simple pore. Along the valve face margin, a more or less distinct rib is present. The striae are composed of roundish areolae, occluded by rotae. Cingulum structure unknown.

Biogeography & Ecology: According to Andrews (1981)(see also Hasle & Syvertsen 1996), *Delphineis surirella* is restricted to cool and temperate seas. *D. surirella* was common in silty sediments, but unlike *D. minutissima*, it is more restricted to higher salinities.

DELPSURI

Delphineis surirella var. *australis* (Petit 1877) Andrews 1981 []

Synonyms:

Rhaphoneis fasciolata var. *australis* Petit 1877
Rhaphoneis surirella var. *australis* (Petit 1877) Grunow in Van Heurck 1881

References:

(1) Petit 1877
(2)
(3) Hustedt 1927

Morphology:

LM - Valves identical to the nominate variety except for the central sternum which is much wider, more or less panduriform.

Biogeography & Ecology: Only a few valves belonging to this variety were observed in the estuary.

DELPSUAU

Rhaphoneis Ehrenberg 1844

Genus description: Round *et al.* 1990

Rhaphoneis amphiceros (Ehrenberg 1840) Ehrenberg 1844 [Fig. 7-1]

Synonyms:

Cocconeis amphiceros Ehrenberg 1840

References:

(1) Ehrenberg 1840
(2)
(3) Hustedt 1927, Round *et al.* 1990, Hasle & Syvertsen 1996

Morphology:

L: 14.4-66.9; W: 12.5-23.7; S: 6.5-8

LM - Plastids numerous, discoid (Fig. 69-19). Valves lanceolate to elliptical, with rostrate apices. Central sternum narrowly lanceolate. Striae punctate and radiate, composed large, round areolae.

SEM - Only internal valve views were observed. Valve face flat, gradually curving into a shallow mantle. The round areolae are occluded by rotae which consist of (two) small, concentric rings of silica. Two apical pore fields are present; they consist of about 5 apical rows of small puncta. Near these pore fields, small rimoportulae, and in the observed valve also an isolated punctum, are present. Cingulum structure unknown.

Remarks:

Biogeography & Ecology: This unmistakable and probably cosmopolitan species is common in the plankton and benthos of marine and brackish, coastal areas. In the Westerschelde estuary, it is common both in the plankton and in silty sediments. *Rhaphoneis amphiceros* is probably cosmopolitan (Hasle & Syvertsen 1996).

RHAPAMPH

Ordo Thalassionematales

Fam. THALASSIONEMATACEAE Round

Thalassionema Grunow ex Hustedt 1932

Genus description: Hallegraeff 1986, Round *et al.* 1990

Thalassionema nitzschioides (Grunow 1862) Van Heurck 1896 [Figs 7-7, 40-7]

Synonyms:

Synedra nitzschioides Grunow 1862
Thalassiothrix nitzschioides Grunow in Van Heurck 1881

References:

(1) Grunow 1862
(2)
(3) Hallegraeff 1986, Snoeijs & Vilbaste 1994, Moreno-Ruiz & Licea 1995, Hasle & Syvertsen 1996

Morphology:

L: 7.5-38; W: 2.5-3.4; S: 10-13

LM - Valves linear with broadly rounded apices. Axial area broad, linear. Striae marginal, short.

SEM - Valve face flat in the centre, marging gradually into the mantle. Central sternum broad. The 'striae' consist of a single, marginal areola. A small triangle is suspended by small bars above its outer opening. Cingulum structure not observed.

Remarks: The Westerschelde specimens are at the smaller end of the size range compared to other published descriptions (Hallegraeff 1986, Snoeijs & Vilbaste 1994, Hasle & Syvertsen 1996).

Biogeography & Ecology: *Thalassionema nitzschioides* is a common neritic diatom species which is cosmopolitan but appears the be absent from both the Arctic and Antarctic (Hasle & Syvertsen 1996). It forms zig-zag or stellate colonies. In the meso- and polyhaline reaches of the Westerschelde estuary, it is a common component of the phytoplankton assemblages (Muylaert, pers. comm.). This is in accordance with its distribution in the Baltic area where it can be commonly found in brackish water down to salinities of 6 ‰ (Snoeijs & Vilbaste 1994). *Thalassionema nitzschioides* was common in silty sediments throughout the estuary.

THALNITZ

CLASS BACILLARIOPHYCEAE

Subcl. Bacillariophycidae

Ordo Lyrellales

Fam. LYRELLACEAE Mann

Petroneis Stickle & Mann 1990

Genus description: Round *et al.* 1990

This genus was originally included in *Navicula* but differs from the latter 'in almost every respect except the central position of the raphe' (Round *et al.* 1990), especially in the structure of the plastids (butterfly or X-shaped) and the areolae.

Petroneis humerosa (Brébisson 1856) Stickle & Mann 1990 [Figs 7-16, 7-17]

Synonyms:

Navicula humerosa Brébisson 1856

References:

(1) Brébisson 1856
(2)
(3) Round *et al.* 1990, Hendey 1964

Morphology:

L: 50.4-60; W: 24.7-26.9; S: 10

LM - Valves broadly linear with rostrate apices. Axial area rather broad, central area transapically expanded. Raphe straight, central raphe endings straight, expanded, apparently lying in a spathulate groove. Terminal raphe endings deflected to the same side. Striae distinctly punctate (about 15 in 10 µm), radiate throughout the valve (to slightly parallel near the apices). In the centre, some shortened striae are present; alternating with longer ones.

Biogeography & Ecology: *Petroneis humerosa* was very rare in fine and medium sandy sediments in the lower reaches and the mouth of the estuary. However, in the Baltic area it is present, albeit in low numbers, across the whole salinity gradient (Snoeijs & Vilbaste 1994). Hendey (1964) characterizes it as a . *P. humerosa* has been reported from Europe (references above), South America (Garcia-Baptista 1993b) and probably elsewhere.

PETRHUME

Ordo Cymbellales

Fam. ANOMOEONEIDACEAE Mann

Dickieia Berkeley ex Kützing 1844

Genus description: Cox 1985, Mann 1994a

See Table 21 for a comparison with similar genera formerly belonging to *Navicula* s. l.

Dickieia subinflata (Grunow in Cleve 1883) Mann 1994

[Figs 7-8, 7-9, 42-8]

Synonyms:

Navicula subinflata Grunow in Cleve 1883
Navicula sleensis Simonsen 1959

References:

(1) Cleve 1883
(2)
(3) Simonsen 1959, Hustedt 1962, Witkowski 1991a, 1994, Mann 1994a, Snoeijs & Vilbaste 1994, Cooper 1995a

Morphology:

L: 13.7-21.8; W: 5.5-7.4; S: 19-21 (n=5)

LM - Valves broadly elliptical to linear, apices broadly rounded. Raphe-sternum narrow but distinct, central area transapically expanded, fascia/(?)stauros-like. Raphe straight, central raphe endings straight, pore-like. Terminal raphe endings simple, apparently straight. Striae radiate throughout the valve, the central ones are always curved. They are distinctly punctate. In the centre, some short striae are sometimes present near the valve margin.

SEM - Only external valve views were observed. Valve face flat, gently curving into a rather deep mantle. Raphe-sternum raised, raphe straight. Central raphe endings straight, pore-like. Terminal raphe endings straight, simple. Terminal fissures strongly hooked in the same direction. They are long, curve back towards the centre and continue for a short distance along the valve margin. The striae consist of round poroids; no occlusions are visible. The poroids around the central area and alongside the raphe-sternum are often slightly larger than the other ones. In the fascia (or stauros?), either no striae or a few short ones (near the valve margin) are present. The cingulum consists of six open, slightly curved copulae. Each copula bears one or two rows of poroids. The valvocopula bears short rows of tiny poroids.

Remarks: The first valid entry of this name was not in Cleve & Möller (1882)(cf. VanLandingham 1975, Mann 1994), as no description or illustration was provided, but in Cleve (1883). Mann (1994a) transferred this species from *Navicula* to the resurrected genus *Dickieia*. Cox (1985) gave a detailed LM and SEM description of this species. Our specimens differ from hers in the deflection of the terminal fissures, opposite in her specimens, in the same direction in ours (cf. also Hustedt 1962).

Biogeography & Ecology: *Dickieia subinflata* is a common, brackish-marine species along the coasts of the North Atlantic and Arctic Ocean, the North Sea, the Baltic Sea and the Adriatic Sea (Hustedt 1962, Cox 1985, Witkowski 1994, Cooper 1995a). In the Westerschelde estuary, it was rare in fine sandy sediments, mainly in the mesohaline section of the estuary.

DICKSUBI

Dickieia sp. 1

[Figs 7-10, 7-11, 7-12, 7-13]

Morphology:

L: 12.5-23.1; W: 3.1-5; S: 13-25

LM - One plastid, consisting of two valve-appressed plates, connected by a girdle-appressed bridge containing a lenticular pyrenoid. The plates are both divided into two lobes by a transapical split in the centre of the valve. Valves linear to linear-lanceolate, apices broadly rounded. Axial area narrow, central area transapically expanded but sometimes absent (in smaller specimens). Raphe straight, raphe-sternum distinct, narrow. Central raphe endings close together, simple. Terminal raphe endings not visible. Striae more or less parallel (to slightly radiate) throughout the valve. In the centre they are distinctly more widely spaced than near the apices. Sometimes short striae are present in the central area along the valve margin. Their structure is indistinct.

Remarks: The above-mentioned striae density values indicate that there are large differences in stria density within one valve (centre versus apical region). However, we also found some very fine specimens; it is not sure whether two forms (taxa?) are involved.

This taxon probably belongs to the genus *Dickieia* (Mann 1994a). However, unlike in this genus, the two valve-appressed plates of the plastid are not K-shaped: there is no longitudinal indention beneath the raphe.

The general appearance of *Dickieia* sp. 1 is very reminiscent of *D. ulvacea*, from which it can be distinguished in size (they are consistently smaller and narrower!), stria density and plastid shape (cf. Cox 1985). The valves of *Dickieia* sp. 1 also appear to be more robust than the ones of *D. ulvacea*. *D*. sp. 1 is also very similar to *Dickieia expecta* (VanLandingham) Mann (syn. *Navicula aberrans* Simonsen *non* Cleve-Euler), but differs from this species in not being asymmetrical about the apical axis and in the structure of the striae, which are not distinctly punctate in *D*. sp. 1. The interrelationship between *D. ulvacea* and *D. expecta* is not very clear and needs further investigation; Cox (1985) postulated that *D. expecta* might be a form at the bottom of the size range of *D. ulvacea*. Whether *D*. sp. 1 belongs to one of these taxa is therefore not clear yet: it seems, however, that we are dealing with a different, more robust taxon, which is closely related to the above-mentioned *Dickieia* species.

Biogeography & Ecology: *Dickieia* sp. 1 was rare in silty to fine sandy sediments, mainly in the middle and lower reaches of the Westerschelde estuary.

DICKSP01

Staurophora Mereschkowsky 1903

Genus description: Round *et al.* 1990

This genus was described by Mereschkowsky (1903b). Mann (1996) pointed out that the name can only be used if it is conserved against *Staurophora* Wildenow, a redundant name for a group of liverworts. For practical reasons, we decided to use this name for the time being, nothwithstanding the nomenclatural problems, as it allows us to make the distinction between *Stauroneis* and the species belonging to *Staurophora*.

Staurophora is characterized by its plastid structure (one plastid with two valve-appressed, K-shaped plates and a central pyrenoid), the presence of a distinct stauros, the structure and shape of the raphe and the raphe endings.

Staurophora is very reminiscent of *Stauroneis* in cleaned material, but differs from this genus in the structure of its plastids and the raphe (Stickle & Mann 1988, Round *et al.* 1990, Mann 1996). It is also very similar to the recently resurrected genus *Dickieia* (Mann 1994a, where it is compared to different naviculoid genera but not to *Staurophora*), the only difference being the presence of a stauros in *Staurophora* [in *Dickieia*, there is no stauros (cf. Ross *et al.* 1979), the central striae are usually more widely spaced - however, see *D. subinflata*], and the shape and structure of the central raphe endings [compare Cox (1985) and Mann (1994a) for *Dickieia* to Round *et al.* (1990) for *Staurophora*]. No information could be found on the type of auxosporulation in *Staurophora*, which may be an additional distinguishing feature between these two genera. The relationship between both genera needs further study (see also remarks on *Dickieia subinflata*). See Table 21 for a comparison with similar genera

Staurophora cf. *salina* (W. Smith 1853) Mereschkowsky 1903

[Figs 8-1, 8-2, 8-3, 8-4, 8-5, 41-6, 41-7, 41-8]

Synonyms:

Stauroneis salina Smith 1853

References:

(1) W. Smith (1853)
(2) Cox (1988a)
(3) Hendey 1964, Cox 1988a, Hustedt 1939, 1959, Krammer & Lange-Bertalot 1986

Morphology:

L: (16.9?) 29.4-59; W: (5?)6-13.3; S: 18-22 (-24)

LM - One plastid, consisting of two valve-appressed, K-shaped plates. These are connected one one side by an girdle-appressed isthmus in which a pyrenoid is visible. The latter appears to be rather rectangular in Fig. 8-5, but in the majority of specimens it is more or less lenticular and sometimes has a layered structure. Valve shape is quite variable, from elliptical with broadly rounded to cuneate-subrostrate apices, to distinctly lanceolate, often with slightly produced apices. Axial area narrow but distinct, often (always?) broader on one side of the valve. Central area dilated into a distinct stauros, becoming wider towards the valve margin though never reaching the latter (Fig. 8-2). Raphe straight, central raphe endings pore-like, terminal raphe endings straight, terminal fissures hooked in the same direction. Striae radiate to slightly convergent near the apices. Their structure is indistinct. Each valve has at least 2 copulae.

SEM - Valve face gently curved in transapical section, mantle rather deep. Raphe-sternum well-developed, both internally and externally. In the centre, a distinct stauros is present (Figs 41-6, 41-8). Internally, the raphe fissure opens laterally, except in the centre and near the apices. However, no accessory rib is present. The central raphe endings are expanded on the outside and strongly hooked on the inside. The terminal raphe endings are straight and end in a small helictoglossa on the inside. Externally, the terminal fissures appear to be strongly hooked in the same direction. The uniseriate striae consist of small poroids, occluded by a hymen on the inside. In Fig. 41-7, at least 3 copulae are visible.

Remarks: This taxon clearly belongs to the species group around *Staurophora salina*. The type description and illustration of this species (as *Stauroneis salina*) describe an elliptical-lanceolate diatom (L: 40.6-55.8 µm; S: 17.7 str./10 µm) with a 'linear' stauros (Smith 1853). In the illustration (Pl. XIX, Fig. 188) it can be seen that this stauros is more or less rectangular and does not reach the valve margin. A valve from the type slide (BM 23622, cf. Hendey 1964) is illustrated in Cox (1988a, Fig. 44): the stauros appears to slightly widen towards the valve margin (cf. also Hendey 1964). However, it is worth noticing that this specimen has 21-22 str./10 µm! Krammer & Lange-Bertalot (1986) illustrate two specimens from a Van Heurck slide (Type du Synopsis 44). These specimens measure 33.3 µm and 36.3 µm, while their description states 50-110 µm (this dimension is even used as a distinguishing feature in the key to *Stauroneis*!). From these examples, it should be clear that only little is known about the true identity of this species and its morphological variability. Many similar taxa have been described, e.g. *Staurophora amphioxys* (Gregory) Mann (syn. *Stauroneis gregorii* Ralfs in Pritchard), *Staurophora wislouchii* (Poretzky & Anisimova) Mann, *S. elata* (Hustedt) Mann, *Stauroneis dubitabilis* Hustedt (syn. *S. gregorii* var. *densestriata* Hustedt) and *Stauroneis marina* Hustedt. All these taxa are very similar (at least at first sight); they only slightly differ in valve shape (from linear to lanceolate, with or without slightly produced apices), size (always between 23 and 85) and stria density (always around 20 str./10 µm), stria pattern (radiate to parallel), stauros shape and size (rectangular or widening towards the valve margin, reaching the latter or not). However, the differences are always slight, and all species have been collected from brackish water and marine sites, mostly coastal, sometimes in inland saline lakes. Whether the differences are consistent and the variation patterns stable, is hard to assess. It is not sure what the earlier researchers actually saw [cf. above for *Staurophora salina*, cf. also Hustedt's descriptions and the photographs in Simonsen (1987)]. A thorough study of the type material of all these taxa is necessary to eliminate any nomenclatural redundancy and assess their taxonomic significance.

Our specimens are very similar to the *Staurophora salina* specimen illustrated in Cox (1988a). Therefore, and also because this name is commonly used for similar diatoms in many studies, we have tentatively identified them as such. Whether or not our own material consists of different morphotypes, has not been assessed.

Biogeography & Ecology: Diatoms belonging to the *Staurophora salina*-complex (cf. species mentioned above) are found in brackish and marine sites worldwide, both coastal and inland (e.g. Hustedt 1939, Rao & Lewin 1976, John 1983, Garcia-Baptista 1993b, ...). In the Westerschelde estuary it was mainly present in rather silty sediments, almost exclusively in the mesohaline reaches.

STAUSALI

Fam. CYMBELLACEAE Greville

Placoneis Mereschkowsky 1903

Genus description: Mereschkowsky 1903, Cox 1987

This genus consists of naviculoid diatoms mainly characterized by the structure of the plastids (one plastid consisting of two valve-appressed, connected X-shaped plates) and the areolae (with internal occlusions of the vola-type). For a more thorough description and comparison to *Navicula* s.s. see Cox 1987.

Placoneis clementis (Grunow 1882) Cox 1987 [Figs 7-14, 7-15]

Synonyms:

Navicula clementis Grunow 1882

References:

(1) Grunow 1882
(2)
(3) Krammer & Lange-Bertalot 1986, Cox 1987, Kuylenstierna 1989-90, Round *et al.* 1990, Juggins 1992

Morphology:

L: 11.5-18.6; W: 6.4-7.8; S: 13-16.5

LM - One plastid, consisting of two valve-appressed, X-shaped plates (Fig. 7-14). Valves elliptical with produced, usually subrostrate apices. Axial area narrow, central area transapically expanded, somewhat rectangular. Two distinct pores, both on the same side of the raphe, are present near the central raphe endings. The raphe is straight, with a distinct raphe-sternum. The central raphe endings are straight; the structure of the terminal raphe endings is unclear. The striae are strongly radiate throughout the valve; in the centre, the striae are shortened. Their structure is indistinct.

Biogeography & Ecology: *P. clementis* is a species from electrolyte-rich to brackish waters (Cox 1996), which is in accordance with its (rare) occurrence in the mesohaline reaches of the Westerschelde estuary.

PLACCLEM

Fam. GOMPHONEMATACEAE Kützing

Gomphonema Ehrenberg 1832

Genus description: Round *et al.* 1990

Gomphonema is a common benthic freshwater genus. In the Westerschelde sediments, only a few isolated valves belonging to *Gomphonema olivaceum* (Hornemann) Brébisson and the species complex around *Gomphonema angustatum* (Kützing) Rabenhorst/*G. parvulum* (Kützing) Kützing. There is no doubt that these valves were washed in from the river.

Ordo Achnanthales

Fam. ACHNANTHACEAE Kützing

Achnanthes Bory 1822

Genus description: Round *et al.* 1990

In most recent major diatom floras (e.g. Hustedt 1927-66, Krammer & Lange-Bertalot 1986-91), *Achnanthes* comprises all monoraphid diatoms which do not possess the set of features which characterizes *Cocconeis* Ehrenberg and related taxa (*Campyloneis* Grunow, *Anorthoneis* Grunow and the epizoic genera *Bennettella* Holmes and *Epipellis* Holmes)(Krammer & Lange-Bertalot 1991). However, Round *et al.* (1990) split up *Achnanthes* s.l. into three seperate genera, viz. *Achnanthes* s.s., *Achnanthidium* and *Eucocconeis*. The latter two taxa are resurrected genera which were described in the last century (Küzting 1844, Cleve 1895). Krammer & Lange-Bertalot (1991) recognize *Achnanthidium* at the subgeneric level; in their opinion, this subgenus also comprises *Eucocconeis*. Note also that Hustedt in his diatom flora (1927-1966) wrongly applies the name *Achnanthidium* to the *Achnanthes brevipes* group (Round *et al.* 1990)*.

Clearly, the resurrection of the genera *Achnanthidium* and *Eucocconeis* raises a lot of questions and causes a lot of nomenclatural problems (cf. Lange-Bertalot 1993b). However, the distinction between *Achnanthes* s.s. and *Achnanthidium* seems to be justified (Czarnecki & Edlund 1995, Lange-Bertalot 1993). Moreover, there are strong indications that *Achnanthidium* itself is a heterogeneous genus (Krammer & Lange-Bertalot 1991, Round *et al.* 1990, see also the footnote on this page!). The main features of Achnanthes, Achnanthidium (sensu Round et al. 1990), Anorthoneis and Cocconeis are given in Table 22.

Achnanthes amoena Hustedt 1952

[Figs 8-6, 8-7, 42-1]

Synonyms:

Achnanthes biceps sensu *Takano* (1979)
A. orientalis Hustedt 1933 non Petit 1904
A. triconfusa VanLandingham 1967

References:

(1) Hustedt 1952
(2) Simonsen 1987
(3) Gotoh 1979, Takano 1979, Lange-Bertalot & Krammer 1989, Krammer & Lange-Bertalot 1991, Chang 1992, Snoeijs 1993, Cooper 1995a, Reimer 1996

Morphology:

L: 12-15.7; W: 3.8-5; S(R): 25-26.5; S(P): 16.5-19 (n(P) = 2, n(R) = 2)

LM - Plastid structure not very clear: there appears to be one H-shaped plastid. Valves broadly

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* Just recently, Round & Bukhtiyarova (1996) redefined the genus *Achnanthidium* and created 4 new genera to accommodate for some members of *Achnanthidium* s.l. (i.e. sensu Round *et al.* 1990). However, there was no time left to properly incorporate this information into this study.

elliptical with rostrate apices. Axial area of the P-valve (= valve without raphe) is narrowly lanceolate. The striae are slightly radiate throughout the valve and are crossed by a hyaline area on both sides of the axial area. The R-valve (= valve with raphe) has a narrow raphe-sternum; the raphe is straight, with straight, slightly expanded central raphe endings. The striae on this valve are also slightly radiate throughout the valve; they are not interrupted. Note also that the stria density on the P-valve is considerably lower than the one on the R-valve (cf. Hustedt 1952, Chang 1992).

SEM - The valve face of the P-valve is flat, gradually sloping into the mantle. The (central) sternum is broader in the centre. The striae are interrupted by lateral sterna and consist externally of very narrow, slit-like areolae; no occlusions are visible.

Remarks: *Achnanthes amoena* was described on the basis of only a few specimens found in the 'Kamerun-Lagune' (Hustedt 1952). A more thorough description was given by Krammer & Lange-Bertalot (1991) and Chang (1992). *A. amoena* appears to be a very variable species, both in size and stria density.

We only found a few valves which correspond to the above-mentioned descriptions. However, the specimens described by Chang (1992) are quite different from ours: the areolae of the P-valve are much broader; the ones inside the lateral sterna are distinctly roundish. Our specimens more closely resemble the specimens illustrated in Krammer & Lange-Bertalot (1991). See also the remarks on *Achnanthes lemmermannii* var. *obtusa*.

Biogeography & Ecology: The autecology of this species is not very clear; it is not unlikely that different forms (taxa?) are involved. *A. amoena* was originally described from a saline lagoon in Cameroon, but it could have been washed in from freshwater (Hustedt 1952). Chang (1992) and Krammer & Lange-Bertalot (1991) reported it from brackish and marine sites. Snoeijs (1993) observed this species in the Baltic area, where it is common at salinities of 5-6 ‰. Here it occurs in the epilithon and epiphyton, attached to the substratum by a short mucilage stalk. However, Krammer & Lange-Bertalot also described this as common in 'elektrolytreichen' freshwater. This is in accordance with the observations of this species from North America [see references in Reimer (1996)], where it appears to be a dysphotic freshwater species. It seems, however, that these forms do not concern true *A. amoena* [cf. illustrations in Reimer (1996), which shows specimens with distinctly punctate striae].

In the Westerschelde estuary, *A. amoena* was mainly found in fine sandy sediments. Live specimens were with certainty observed at salinities of about 18 ‰, so it also occurs at higher salinities than observed by Snoeijs (1993).

ACHNAMOE

Achnanthes bahusiensis (Grunow 1880) Lange-Bertalot 1989

[Figs 9-28, 9-29, 9-30, 9-31, 9-32, 9-33, 43-4, 43-6, 43-7]

Synonyms:

Navicula minuscula var. *bahusiensis* Grunow in Van Heurck 1880
Navicula bahusiensis (Grunow) Grunow 1884

References:

(1) Grunow in Van Heurck 1880
(2) Krammer & Lange-Bertalot 1991 (lectotypus)
(3) Lange-Bertalot & Krammer 1989, Krammer & Lange-Bertalot 1991, Snoeijs & Potapova 1995, Witkowski 1994

Morphology:

L: 15-24.7; W: (4?-)5.6-7.5; S(R): 26-30(n=3); S(P): 29-37

LM - One plastid, appressed to one side of the girdle, with plates extending under the valves. These plates can consist of one or two lobes (Fig. 9-28), in other specimens their structure is more complicated (Fig. 9-29). However, it is not sure whether the latter form, which is rare, is the normal condition of the plastid. Valves broadly elliptical to lanceolate with subrostrate to distinctly rostrate or even slightly rostrate-capitate apices. The axial area of the P-valve is very narrow, sometimes slightly broader in the centre of the valve. The striae on this valve are slightly radiate in the centre to radiate at the poles. Their structure is indistinct. The raphe-sternum of the R-valve is narrow but distinct. The raphe is straight, the central raphe endings are slightly expanded and close together. The terminal part of the raphe is not visible. In the centre, a distinct punctum (possibly a stigma? cf. Fig. 9-30) is present on one side of the central nodule. The central area is roundish on the opposite side of the punctum, and has a rectangular or irregular shape on the side of the punctum. The striae on this valve are radiate throughout the valve. Their structure is indistinct. Note that the stria density on the R-valve is considerably lower than the one on the P-valve.

SEM - Valve face flat, curving abruptly into a very shallow mantle. The striae on the P-valve (only internal valve views) are biseriate (to multiseriate, cf. Fig. 43-6, arrowed) near the margin; however, towards the central sternum, the puncta merge and form apically elongate areolae. The striae are separated by costate virgae. On the central sternum, 'raphe vestiges' (cf. Sterrenburg 1988) can be seen in some valves (Fig. 43-6). The structure of the R-valve is quite different from the one of the P-valve. The raphe is straight, with expanded central and simple terminal raphe endings. Terminal fissures appear to be present but this is not very clear. The larger part of the striae consists of round poroids, occluded on the inside by hymenate vela. The marginal areolae are larger and transapically elongate, as are the areolae alongside the raphe-sternum in the centre of the valve; especially around the central area, they can be quite long. Internally, the striae are separated by costate virgae. Internally, the isolated punctum (or stigma) appears to be covered by a hooded structure, which is partly eroded in Fig. 43-7; its external opening is much smaller. The cingulum seems to consist of at least two shallow copulae.

Remarks: As Snoeijs already pointed out (Snoeijs & Potapova 1995), this species does not belong to *Achnanthes* s.s. (*sensu* Round *et al.* 1990).

A. bahusiensis has probably been described several times under different names, such as *Navicula bremeyeri* var. *rostrata* Hustedt, *N. abstrusa* Hustedt, *N. observanda* Simonsen, *Achnanthes punctifera* Hustedt, *A. tenuis* Hustedt, *A. wellsia* Reimer (= *A. solea* Hustedt), *A. modica* Hustedt, *A. heterostriata* Hustedt and *A. pseudosolea* Simonsen [see Krammer & Lange-Bertalot (1991) and Witkowski (1994)]. Most of these taxa only slightly differ from one another in shape and striation density and pattern. Whether it concerns discrete taxa or whether they represent different forms of one and the same species is hard to assess without investigating their morphological variability. For a more thorough discussion of this group, see Lange-Bertalot & Krammer (1989) and Krammer & Lange-Bertalot (1991). The specimens from the Westerschelde estuary differ from most published descriptions of this species in having distinctly rostrate to rostrate-capitate. The P-valves are identical to the *N. abstrusa* specimens illustrated in Simonsen (1987).

Biogeography & Ecology: It is not sure whether *Achnanthes bahusiensis* is an epipsammic species (cf. Snoeijs & Potapova 1995). On several occasions we observed free-living, highly motile cells. *A. bahusiensis* was mainly present in fine sandy to medium sandy sediments throughout the Westerschelde estuary. Living cells were observed in the mesohaline section, which is in accordance with its distribution in the Baltic area (Snoeijs & Potapova 1995).

ACHNCFBA

Achnanthes cf. *bremeyeri* Lange-Bertalot 1989

[Figs 9-24, 9-25, 9-26, 9-27]

Synonyms:

(?) *Navicula bremeyeri* Hustedt 1939

References:

(1) Lange-Bertalot & Krammer 1989
(2) Lange-Bertalot & Krammer 1989
(3) Krammer & Lange-Bertalot 1991

Morphology:

L: 11.9-12.5; W: 4.2-4.9; S(R): 34-35 (n=2); S(P): 30-31 (n=1)

LM - Valves broadly elliptical, apices broadly rounded. Apart from this feature, the lower stria density and the less radiate striae on the R-valve, the valves of this species are identical to the ones of *Achnanthes bahusiensis*.

Remarks: *Achnanthes bremeyeri* differs from *Achnanthes bahusiensis* in having broadly rounded apices which are never produced and a higher stria density (about 40 str./10 µm)[See Lange-Bertalot & Krammer (1989) for a more thorough discussion of this species]. Our specimens do not completely correspond to the description of *A. bremeyeri*, as they have considerably less than 40 str./10 µm.

Achnanthes bremeyeri most probably does not belong in *Achanthes* s.s. (cf. above - *Achnanthes bahusiensis*). As long as no SEM examination of this species has been made, its generic allocation can not be assessed with certainty.

Biogeography & Ecology: Only a few valves belonging to this taxon were observed.

ACHNCFBA

Achnanthes brevipes Agardh 1824

References:

(1) Agardh 1824
(2)
(3) Lange-Bertalot & Krammer 1989, Krammer & Lange-Bertalot 1991, Snoeijs & Vilbaste 1994

Morphology:

L: 61.7; W: 18.6; S: 8.5

For a detailed LM and SEM description of this unmistakable species, we refer to Lange-Bertalot & Krammer (1989).

Remarks: Only a few valves of this epiphytic/epilithic species were found in our sediment samples.

Biogeography & Ecology: *Achnanthes brevipes* is a common, cosmopolitan marine and brackish water species, usually epiphytic or epilithic. Only a few valves were observed in our sediment samples.

ACHNBREV

Achnanthes lemmermannii Hustedt 1933 **var.** ***obtusa*** Hustedt 1939

[Figs 8-8, 8-9, 8-10, 8-11, 42-2, 42-7]

Synonyms:

Achnanthes biasolettiana Grunow var. *linearis* Grunow

References:

(1) Hustedt 1939
(2) Simonsen 1987
(3) Van Heurck 1884-1887 (Types du Synopsis nr. 11), Cleve 1895, Lange-Bertalot & Krammer 1989, Krammer & Lange-Bertalot 1991

Morphology:

L: 10-12.9; W: 4.4-4.6; S(R): 24-26.5; S(P): 21.5-23.5(centre)/23.5-24 (poles)(n=5)

LM - Valves broadly elliptical to linear with subrostrate to rostrate apices. R-valve with narrow but distinct raphe-sternum, which is broader in the centre. Raphe straight, central raphe endings slightly expanded, close together and lying in a distinct, often slightly transapically expanded central nodule. Striae radiate throughout the valve, sometimes slighty further apart in the centre. P-valve with a distinct, narrowly lanceolate, central sternum. Lateral sterna absent or only very slightly visible (Fig. 8-8). Striae radiate throughout the valve, sometimes distinctly more widely spaced in the centre (Fig. 8-9). The structure of the striae on both valves is indistinct.

SEM - The valve face (both R- and P-valve) is flat, curving abruptly into a shallow mantle. Raphe-sternum narrow, transapically expanded in the centre. Raphe straight, central raphe endings only slighty expanded, terminal fissures deflected (hooked?) in the same direction. The striae consist of 'alveoli' (cf. Chang 1992, the use of the term alveolus here is not completely appropriate), which are not interrupted by lateral sterna and are occluded by what seems to be a hymenate velum. Internally, the raphe and its endings are straight and coaxial.

Remarks: *Achnanthes lemmermannii* var. *obtusa* was described by Hustedt (1939) from intertidal flats in the German Wadden Sea. According to Krammer & Lange-Bertalot (1991), this taxon is conspecific with *A. biasolettiana* var. *sublinearis* (which was described from the Schelde estuary near Antwerpen). As these authors already pointed out, *A. lemmermannii* var. *obtusa* has nothing to do with the nominate variety *A. lemmermannii* var. *lemmermannii*, whose identity is not clear (see also the remarks for this species). Neither is it related to *A. biasolettiana*. The relationship between *A. lemmermannii* var. *obtusa* and *A. amoena*, of which it is quite reminiscent, ought to be studied. The main difference with the latter species lies in the stria density and pattern, which is very similar on both valves (the difference in stria density between the R- and P-valve is not as marked as in *A. amoena*).

Biogeography & Ecology: During the counts no distinction was made between this taxon, *Achnanthidium bahusiensis* and *Achnanthes* cf. *bremereyi*. Its autecology is therefore impossible to assess.

ACHNCFBA

Achnanthes parvula Kützing 1844

[Figs 9-22, 9-23]

Synonyms:

Achnanthes brevipes var. *parvula* (Kützing) Cleve 1895

References:

(1) Kützing 1844
(2)
(3) Lange-Bertalot & Krammer 1989, Krammer & Lange-Bertalot 1991

Morphology:

L: 19.4; W: 6.2; S: 14 (n=1)

LM - Only one R-valve was observed. Valve elliptical with slightly cuneate apices. Raphe-sternum narrow, central area transapically expanded up to the valve margin. Striae radiate throughout the valve. They consist of large, round areolae. The raphe is straight. The central raphe endings are expanded, pore-like; the terminal raphe endings are deflected in the same direction.

Remarks: Only one valve belonging to this species was found.

ACHNPARV

Achnanthes submarina Hustedt 1956 [Figs 8-12, 8-13]

Synonyms:

Achnanthes biceps Hustedt 1959
Achnanthes breenii Archibald 1966
Achnanthes pseudobiceps Håkansson 1974

References:

(1) Hustedt 1956
(2) Simonsen 1987
(3) Hustedt 1956, Lange-Bertalot & Krammer 1989, Krammer & Lange-Bertalot 1991, Snoeijs & Vilbaste 1994

Morphology:

L: 11-12.5; W: 5-5.6; S(P): ± 25; S(R): ± 28

LM - Valves elliptical with capitate apices. P-valve with a narrow axial area at the poles, widening into a large, lanceolate hyaline area in the centre of the valve. Striae radiate in the centre, becoming parallel at the apices. In the centre, the striae are slightly more widely spaced; short marginal striae may be present. The R-valve has a narrow raphe-sternum and a transapically expanded, roundish central area. Raphe straight; central raphe endings slightly expanded; terminal raphe endings not visible. The stria pattern is similar to the one of the P-valve.

Remarks: *Achnanthes submarina* was also described as *A. breenii* from lake Nhlange, about half a mile away from the coast of Natal, South Africa (Archibald 1966).

Biogeography & Ecology: This species was only very rarely found in the sediment samples of the Westerschelde estuary. It was described by Hustedt (1956) from brackish water in Venezuela, where it occurred in large numbers. In Europe, it appears to be much rarer (cf. Krammer & Lange-Bertalot 1991) and is also found in fossil material. This species appears to be cosmopolitan in brackish water sediments and near coasts (cf Krammer & Lange-Bertalot 1991).

ACHNSUBM

Achnanthes sp. 1 [Figs 10-1, 10-2, 10-3]

Morphology:

L: 10.5-12.5; W: 6.9-8.7; S(R): 29 (n=1); S(P): 27-28.5

LM - Valves broadly elliptical with cuneate apices. Both valves are distinctly curved about the median transapical plane. R-valve with narrow raphe-sternum and distinct central nodule. The central area is very small and roundish. The central raphe endings are slightly expanded to pore-like and rather close together; the terminal raphe endings could not be observed. The striae have a delicate structure and are only barely visible: they are radiate throughout the valve. The central sternum of the P-valve appears very wide and elliptical in some specimens (Figs 10-2, 10-3), while in other specimens it is narrower. The striae on this valve are distinct in the marginal and apical zone, while in the centre of the valve their structure is less clear (more delicate?); they are radiate throughout the valve. The cingulum was not observed but appears to be very shallow, as could be assessed through careful focussing of some frustules.

Remarks: This taxon (and especially the structure of the P-valve) is quite reminiscent of *Achnanthes subsalsa* Petersen but differs in the structure of the R-valve, which has no distinct, more or less rectangular central area as in *A. subsalsa*.
Achnanthes sp. 1 most probably does not belong in *Achnanthes* s.s. However, SEM examination of the valve structure and examination of living material is necessary before its generic affiliations can be assessed.

Biogeography & Ecology: This taxon was very rare in medium sandy sediments in the lower reaches and the mouth of the estuary.

ACHASP01

Fam. COCCONEIDACEAE Kützing

Anorthoneis Grunow 1868

Genus description: Sterrenburg 1988, Round *et al.* 1990, Hein 1991

A small genus, comprising about 9 (legitimate) species, which is very reminiscent of *Cocconeis* but differs from the latter in the eccentricity of the raphe system and the absence of projections on the valvocopula. Common features include the presence of a rapheless (P-valve) and a raphe (R-valve) valve, the very low pervalvar height, the shape of the internal central raphe endings.

Anorthoneis is typically reported as an epipsammic or epiphytic genus from marine littoral sediments worldwide. The identity of most species is discussed in Sterrenburg (1988). However, while the larger species (*A. excentrica* (Donkin) Grunow, *A. eurystoma* Cleve) are relatively well known, the identity of the smaller specimens is still problematic, especially the relationships between *Anorthoneis tenuis* Hustedt, *A. pulex* Sterrenburg and *A. vortex* Sterrenburg. The identity of the first species is not discussed in Sterrenburg (1988), although it is very similar to the two new species he described.

During the cell counts, we found four different valve types which were assigned to *Anorthoneis*: two P-valves and two R-valves. We therefore assumed that we were dealing with two different morphotypes or two different taxa. The acid treatment of the samples caused the frustules to fall apart. Therefore, it was not easy to find the matching P- and R-valves. The distinction between both taxa was finally based on the observation of a single complete frustule in SEM (Fig. 44-1) and on the fit of the dimensions of the measured specimens (Table 23).

While trying to identify the observed taxa, we found that the existing descriptions of similar *Anorthoneis* species (viz. *A. tenuis*, *A. pulex* and *A. vortex*) are insufficient or at least confusing.

Anorthoneis cf. *pulex* Sterrenburg 1988 [Figs 10-4, 10-5, 10-6, 10-7, 10-8, 44-1, 44-2, 44-3]

Synonyms:

(?) *Cocconeis tenuis* Hustedt 1939

References:

(1) Sterrenburg 1988 (1987?)
(2) Sterrenburg 1988 (1987?)
(3) Sterrenburg 1987, 1988, Hein 1991, Hustedt 1939, 1955, Simonsen 1987

Morphology:

Dimensions: see Table 23. Note the high variability in stria density on both valves.

LM - Valves broadly elliptical, with broadly rounded apices. The P-valves are characterized by a usually large (about ½ of the valve width), slightly asymmetrical (both in shape and position on the valve) hyaline area. In a few rare cases, 'faint' areolae (which are not as distinct as the ones closer to the margin) are present in this hyaline area. Often, raphe vestiges are present on the P-valves (Fig. 10-5). The striae are radiate throughout the valve. Sometimes, a few short striae are present at the valve margin (Fig. 10-5). The R-valve is much more delicate than the P-valve. It is characterized by an eccentric raphe system, a narrow raphe-sternum and the presence of a small, more or less round central area. The raphe is straight or more or less curved (Fig. 10-6). The central raphe endings are distinct and are separated by a distinct central nodule. The terminal raphe endings are situated at a distance of the valve margin. The striae are radiate throughout the valve. They are only distinct near the valve margin (see below). A few short striae can be present.

SEM - The valve face is flat but often has a submarginal ridge (P-valve) or depression (R-valve); the mantle is extremely shallow. Externally, the central raphe endings are straight and only slightly expanded, while internally they are slightly expanded and non-coaxial, slightly deflected in opposite directions. The terminal raphe endings are straight and more or less expanded both internally and externally. Internally, they are surrounded by a distinct helictoglossa. No terminal fissures are present. The striae of the P-valve are uniseriate and consist of large, roundish poroids, which are occluded by hymenate vela. The striae on the R-valve consist of much smaller poroids. Near the valve margin, the striae become biseriate, and are separated internally by costate virgae. This probably explains the distinctness of the striae in the marginal zone as compared to the central zone. Note that every stria of the R-valve ends in a single, more or less elliptical punctum (only visible in internal views). The cingulum is very shallow and consists of 5 to 6 non-porous copulae (Fig. 44-1).

Remarks: The P-valves of this taxon are very reminiscent of the P-valves of *Anorthoneis pulex* (Sterrenburg 1988). The main difference lies in the structure of the R-valve, which, judging from the illustrations and description in Sterrenburg (1988), is similar to the one of the P-valve but with a raphe system. However, we suspect that his Figs. 19-21 might actually depict complete frustules: the raphe system seen would then not belong to the valve with the coarse areolae visible in these figures, but to a hardly visible R-valve. As only a P-valve is shown in SEM, it is impossible to assess whether our suspicion is justified or not, until the type material of this species has been investigated in SEM. Moreover, we suspect that a similar thing has happened with the illustrations of the holotype material of *Cocconeis tenuis* (cf. below). The P-valves of this species are also identical to our specimens. As the epithet *tenuis* is already taken (*Anorthoneis tenuis*, Hustedt

1955), *A. pulex* would be a legitimate name and *Cocconeis tenuis* its synonym. See also the discussion below.

Biogeography & Ecology: Specimens belonging to this taxon were also reported from Chesapeake Bay (USA)(as *Anorthoneis* cf. *tenuis*, Cooper 1995a) and the Oosterschelde estuary (The Netherlands)(as *Cocconeis tenuis*, Vos 1986).
No distinction was made between the three described *Anorthoneis* taxa during the cell counts. *Anorthoneis* spp. are a typical component of the adnate epipsammic community in medium sandy sediments in the polyhaline reaches and the mouth of the estuary.

ANORSPEC

Anorthoneis cf. *tenuis* Hustedt 1955

[Figs 10-9, 10-10, 10-11, (?) 10-12, (?) 10-16, 44-4, 44-5, 44-6]

References:

(1) Hustedt 1955
(2) Simonsen 1987
(3) Hein 1991, Hustedt 1955, Simonsen 1987

Morphology:

Dimensions: see Table 23

LM - Valve shape as in *A.* cf. *pulex*. The main differences with this taxon in LM are: (1) the much smaller size or even absence of the central hyaline area and the more frequent presence of the 'faint' areolae in this area on the P-valve; (2) the distinct difference in stria density between the marginal zone and the rest of the P-valve. Note that the marginal striae are not merely a continuation of the central striae with some short inserted striae but that the stria pattern at the margin is rather 'independent' of the central one; (3) the stria density on the R-valve (measured along the raphe-sternum) is significantly lower than at the valve margin, where numerous short striae are present.

SEM - The ultrastructure of the valve is similar to the one of *A.* cf. *pulex*. No additional distinguishing features between both taxa could be found in SEM. The raphe vestiges appear to be present either as a line of small puncta (externally, Fig. 44-5) or as a faint line (internally, Fig. 44-4). The main distinction between the P-valves of both taxa is the presence of single, transapically elongate areolae (rarely two together) inserted amongst the striae along the valve margin in *A.* cf. *tenuis* (cf. above). These form a marginal ring of small and large areolae. Note also that the central hyaline area of the P-valve is visible internally but not externally in the examined specimens. This could explain the presence of the 'faint areolae' in this area, which would then consist of areola-like depressions on the valve exterior.

Remarks: The stria density of the specimens measured is lower (12-16 versus 18-20 str./10 µm) than the one reported for the single holotype specimen in Hustedt (1955). For a more thorough discussion, see below.

Biogeography & Ecology: This taxon was reported by Cooper (1995a) from Chesapeake Bay (USA). Autecology see *A.* cf. *pulex*.

ANORSPEC

Anorthoneis vortex Sterrenburg 1988

[Figs 10-14, 10-15]

References:

(1) Sterrenburg 1988
(2) Sterrenburg 1988, Hein 1991
(3) Sterrenburg 1988, Hein 1991

Morphology:

L: 13.7-15; W: 12.1-12.2; S: 19.5-22

LM - Only P-valves were observed. Valves elliptical, with broadly rounded apices. Axial area very narrow, in the centre dilated to an asymmetrical, more or less round central area. Striae radiate throughout the valve; they are distinctly curved and also form curved lines in other directions (cf. 10-14).

Remarks: The illustrated specimens are from Salah's material from Blakeney Point (England), but similar valves were observed in our own material from the Westerschelde. They correspond to the description of *Anorthoneis vortex* (Sterrenburg 1988)(although they are slightly smaller), which was described from the Dutch North Sea coast. For a more detailed discussion, see below.

Biogeography & Ecology: See *A.* cf. *pulex*

ANORSPEC

General remarks on the three observed Anorthoneis taxa

In Table 23 the main morphological and some ecological features of the three above-mentioned taxa are compared to each other and to the published descriptions of *Anorthoneis tenuis, A. pulex, A. vortex, A. dulcis* and *Cocconeis tenuis*.

The distinction between these taxa (forms?) is quite precarious and difficult, which is due to a number of factors. A major problem in the identification of the smaller *Anorthoneis* species is the fact that it is usually very difficult to observe the raphe valve, mainly because of the low pervalvar height of the frustules (cf. Sterrenburg 1988) but also because the raphe valve is often only lightly silicified. A good illustration of this problem is the exact identity of the raphe valve of *Cocconeis tenuis* Hustedt. The holotype specimen of this species [illustrated in Simonsen (1987), Pl. 375, Figs. 1-4] consists of only one valve according to Simonsen, but of two valves (i.e. a complete frustule) according to Hustedt (see also below). Therefore, it is almost impossible to assess the structure of the complete frustule without SEM examination of the material. A second problem can be ascribed to the contradictions and incompleteness in the existing descriptions. For example, the stria density of *A. pulex* is 21-24 according to Sterrenburg (1988), 24-28 according to Hein (1991) and 18-22 according to our own measurements. Note that all measurements were made on the same set of photographs (viz. Figs 16-23, Sterrenburg 1988)! A third important factor obscuring the identity of these taxa is the fact that in some cases only very little material has been studied (e.g. *Cocconeis tenuis*, *Anorthoneis tenuis*). The latter species was described on the basis of a single P-valve.

A last source of confusion is the fact that very little is known about the morphological variation in most taxa (with few exceptions, e.g. *Anorthoneis vortex*). The variation patterns of features of presumed taxonomic importance, such as the size and shape of the central hyaline area, the presence of areolae on the mantle, the nature of the striae in the marginal zone and the presence of short and 'faint' striae, are largely unknown. For example, we did find some 'intermediate' specimens (Figs. 10-13, 10-16) that we were unable to assign to any of the above-described taxa.

Given these problems, it is hard to assess what the relationships are between the above-mentioned small *Anorthoneis* specimens: do they concern morphological forms of one or two taxa, or do they concern true species? To provide an answer to this question, it will be necessary to make a detailed LM and SEM study of a large number of (complete!) frustules (including the type materials) from different localities. Until then, we maintain the distinction between the forms observed.

Cocconeis Ehrenberg 1837

Genus description: Krammer & Lange-Bertalot 1991, Round *et al.* 1990

This complex genus can be distinguished (see Table 22) from *Achnanthes* and *Achanthidium* in plastid number (*Achnanthes*) and shape (*Achnanthidium*), the ultrastructure of the poroids (*Achnanthes*), the internal shape of the central raphe endings (*Achnanthes*), the structure of the cingulum (especially the valvocopula) and life-form (Round et al. 1990). Additional distinguishing features are the submarginal hyaline ring, the presence of a loculiferous ring, little or no curvature along the apical axis, the tendency to be elliptical in outline (Kreis & Stoermer 1979). For a more detailed description, see Krammer & Lange-Bertalot (1991, and references therein).

Cocconeis peltoides Hustedt 1939

[Figs 11-1, 11-2, 11-3, 11-4, 43-5, 44-1, 44-2, 44-3]

References:

(1) Hustedt 1939
(2) Simonsen 1987
(3) Hendey 1964, Giffen 1975, Kuylenstierna 1989-90, Wendker 1990, Juggins 1992, Sabbe 1993, Snoeijs & Vilbaste 1994, Witkowski 1994

Morphology:

L: 9.6-20; W: 6-10; S(P): 15-19.5; S(R): 12-20 along the raphe-sternum, up to 50 near the valve margin.

LM - Valves elliptical with broadly rounded apices. R-valve very fragile, raphe-sternum narrow, distinct, central area absent. Raphe straight, central raphe endings slightly expanded, straight. Striae parallel in the centre, radiate towards the apices. The stria density is much lower in a lanceolate area alongside the raphe-sternum than near the margin. P-valve much more robust than R-valve, central sternum narrowly lanceolate, sometimes broader in the centre of the valve. On both sides of the central sternum, a narrow, lateral hyaline area is present.

SEM - The valve face of the R-valve is flat, curving into a very shallow mantle. The valve margin itself consists of a distinct rib (Fig. 45-1). The raphe lies in an externally very indistinct raphe-sternum. Internally, the raphe-sternum is raised. Externally, the central raphe endings are only slightly expanded and straight, the terminal ones are very pore-like but very small. There are no terminal fissures. Internally, the central raphe endings are slightly expanded, non-coaxial, slightly deflected in opposite directions. The striae consist of small round poroids, internally occluded by hymenes (Fig. 43-5). Near the valve margin, they sometimes merge and become transapically elongate (Fig. 45-3). Note that close to the raphe, the striae are biseriate; these than become uniseriate and extend to the valve margin. About halfway between the raphe and the valve margin, these long striae are 'joined' by shorter striae. The P-valve is much more robust and has a central sternum, which is narrow externally (due to the presence of ribs, which extend into the sternum, Fig. 45-2) and lanceolate internally (Fig. 43-5). The lateral hyaline areas correspond to two raised (cf. Fig. 45-2) sections of the valve, so the latter is M-shaped in transapical section. The striae are uniseriate and consist of distinct, round poroids, which are internally occluded by hymenate vela. *The striae are externally separated by more or less distinctly costate virgae.* The structure of the shallow cingulum is not clear.

Biogeography & Ecology: *Cocconeis peltoides* is a common adnate species throughout the Westerschelde estuary. It is a common species in sandy sediments throughout Northern and Western Europe (see references above). It is also reported from North America [Chesapeake Bay, USA (Cooper 1995) and Beaufort, USA (Hustedt 1955 - no illustrations)] and from South Africa (Giffen 1975), but the latter two reports have to be critically checked. See also the discussion of *Cocconeis* sp. 2.

COCCPELT

Cocconeis cf. *placentula* Ehrenberg 1838 [Figs 11-11, 11-12, 46-5, 46-6]

References:

(1) Ehrenberg 1838
(2)
(3) Krammer & Lange-Bertalot 1991, Snoeijs 1993

Morphology:

L: 6.9-8.7(-12.9); W: (3.9-)4.2-5(-6.2); S(P): (24-)28-36; S(R)(n=2!): 22.5-27

LM - Valves elliptical, with broadly rounded apices. R-valve with very narrow raphe-sternum and a distinct submarginal ring of silica. The raphe is straight, the central and terminal raphe endings are not distinguishable. The striae are radiate throughout the valve, except in the centre where they are more or less parallel. R-valve with narrow, linear central sternum. Stria orientation as on R-valve; they consist, however, of distinct, transapically elongate areolae. The ribs inbetween the striae form wavy, longitudinal lines across the striae. The stria density on the P-valve is usually higher than the one on the R-valve.

SEM - Only P-valves were observed. The valve face is flat, curving rather gently into a very shallow mantle. The transapically elongate areolae are slit-like externally and wider on the inside, where they are occluded by hymenate vela. The structure of the shallow cingulum is not very clear: at least two copulae seem to be present.

Remarks: This taxon largely corresponds to the description of *Cocconeis placentula* (cf. Krammer & Lange-Bertalot 1991). However, there are some slight differences, viz. size and stria density (see below), the absence of a (small) central area, and its autecology [*C. placentula* is a typical freshwater-brackish water species (Juggins 1992, Snoeijs 1994), while our specimens were also thriving in poly- and euhaline environments - see also the discussion of this species in Cooper (1995a), which indicates that the reported salinity preferences of this species differ from paper to paper, probably due to misidentifications]. We therefore hesitate to make a positive identification of this taxon as *C. placentula*.

We also have problems in assigning our specimens to one of the existing varieties as listed in Krammer & Lange-Bertalot (1991). Their stria density is intermediate between *C. placentula* var. *placentula* and *C. placentula* var. *tenuistriata* Geitler.

Biogeography & Ecology: *Cocconeis* cf. *placentula* is a common epipsammic taxon in fine sandy sediments throughout the estuary.

COCCCFPL

Cocconeis placentula Ehrenberg 1838 **var. *euglypta*** (Ehrenberg 1854) Grunow 1884

[Fig. 11-13]

Synonyms:

Cocconeis euglypta Ehrenberg 1854

References:

(1) Ehrenberg 1854
(2)
(3) Krammer & Lange-Bertalot 1991, Cooper 1995a

Morphology:

L: 15.6; W: 8.4; S(P): 15.5 (n=1)

LM - Valves elliptical, with broadly rounded apices. R-valve not observed. P-valve with narrow, linear central sternum. Each striae is composed of 2-4(-5?) transapically elongate areolae. The vimines are more or less longitudinally aligned and form about 3 slightly wavy longitudinal lines on both sides of the central sternum. Note that the central striae are slightly more widely spaced.

Biogeography & Ecology: This taxon was common in slightly more silty sediments and has a higher salinity optimum than *Cocconeis* cf. *placentula*.

COCCPLEU

Cocconeis stauroneiformis (W. Smith 1853) Okuno 1957 [Fig. 11-18]

Synonyms:

Cocconeis scutellum var. ß W. Smith 1853

Cocconeis scutellum Ehrenberg 1838 var. *stauroneiformis* (W. Smith 1853) Rabenhorst 1864

References:

(1) W. Smith 1853
(2)
(3) Okuno 1957, Krammer & Lange-Bertalot 1991, Snoeijs 1993

Morphology:

L: 14.4-20; W: 9.4-11.8; S(R): 10; S(P): 12 (note: only one P- and one R-valve!)

LM - Valves elliptical with rounded to slightly cuneate-obtuse apices. R-valve with narrow raphe-sternum. Raphe straight, central raphe endings slightly expanded, straight. A distinct submarginal silicious ring is present. The striae are parallel in the centre to radiate towards the apices; the central striae are further apart ('stauros?'). The P-valve has a narrow central sternum. The striae have the same striation pattern as on the R-valve. No submarginal ring is present. The 'stauros' is not as distinct as on the R-valve.

Biogeography & Ecology: Only a few valves belonging to this taxon were found in the Westerschelde estuary.

COCCSTAU

Cocconeis sp. 1 [Figs 11-5, 11-6, 11-7, 11-8, 11-9, 11-10, 45-4, 45-5]

Morphology:

L: 7.2-9.6; W: 3.5-5.6; S(P): 17-21(-22.5); S(R): ± 20-23.5(-26?) alongside the raphe to ± 50 along the margin

LM - Valves elliptical, apices broadly rounded. R-valve with very narrow raphe-sternum; central raphe endings very close together. Striae indistinct, radiate. P-valve much more robust; central sternum more or less wide, lanceolate, very often with 'raphe vestiges' (e.g. Fig. 11-5). Striae distinct, radiate throughout the valve, especially near the apices.

SEM - The valve face of the only lightly silicified R-valve is flat and curves more or less gently into a shallow mantle. This valve has a structure which is very similar to the one of the P-valve of *Cocconeis peltoides*, viz. uniseriate 'long' striae which stretch from the valve margin to the raphe, where they become biseriate, and 'short' striae inbetween the 'long' striae along the valve margin. The raphe is straight, the central raphe endings are only slightly expanded externally; internally, they are non-coaxial, deflected in opposite directions. The valve face of the (more robust) P-valve is flat and curves rather abruptly into a shallow mantle. The central sternum is lanceolate and rather wide in the centre. Externally, raphe vestiges can be seen in some specimens. Note also numerous small transapical ribs in this area. The striae are situated in the marginal zone; they are uni- to biseriate, composed of round to apically elongate poroids. Most striae begin and end in one single poroid; each stria has also one pore on the mantle or valve face-mantle junction (Fig. 45-4). The poroids are internally occluded by hymenate vela. The structure of the shallow cingulum is unknown.

Remarks: *Cocconeis* sp. 1 is reminiscent of small specimens of *Cocconeis peltoides* (cf. structure of R-valve), but has a completely different P-valve structure, in addition to differences in dimensions and stria density.

Biogeography & Ecology: This taxon was also reported by Juggins (1992) from the Thames estuary (note that his description mentions a lower stria density (14 str./10 µm) while the illustration shows a specimen with 16-17 str./10 µm). *Cocconeis* sp. 1 was common in fine sandy sediments throughout the estuary.

COCCSP01

Cocconeis sp. 2

[Figs 10-17, 10-18, 10-19, 10-20, 10-21, 10-22, 45-7, 45-8]

Synonyms:

(?) *Cocconeis pusilla* Archibald 1966

References:

(1)
(2)
(3) Archibald 1966

Morphology:

L: 6.6-8.7; W: 3.7-5; S(P): 25.5-32; S(R): 29-32(and more?) along the raphe, to ± 70 along the margin

LM - Valves elliptical, with broadly rounded apices. The P-valve has a more or less narrowly lanceolate central sternum, which is sometimes transapically expanded in the centre of the valve (Figs 10-16, 10-17, 10-18). In some specimens, distinct raphe vestiges can be distinguished. The striae are mostly radiate throughout the valve, sometimes parallel in the centre. In many specimens, the striae are more widely spaced in the centre of the valve than at the poles. The R-valve is very lightly silicified; its structure is almost indistinguishable in the LM. The raphe is straight, the central raphe endings are close together, separated by a distinct central nodule.

SEM - The valve face of the R-valve is flat, curving rather gently into a shallow mantle. The structure of the R-valve is very similar to the one of *Cocconeis peltoides* and *C.* sp. 1. The main differences are, apart from size and striation density, the structure of the striae in the marginal zone (i.e. the zone between the valve margin and a line running about halfway between the latter and the raphe), viz. 'merged' into transapically elongated lines, and the structure of the striae along the raphe, viz. not consisting of two areolae but of one apically elongate areola. The striae on this valve are composed of small poroids, internally occluded by hymenate vela. The raphe is straight, the central raphe endings are straight and only slightly expanded externally, non-coaxial and deflected to opposite directions internally. The P-valve face is flat, curving gently into a shallow mantle. The central sternum is usually characterized by distinct raphe vestiges. The uniseriate striae consist of small, round poroids, which are internally occluded by hymenate vela. The structure of the shallow cingulum is unknown but seems to be composed of at least two copulae.

Remarks: *Cocconeis* sp. 2 is reminiscent of both *C. peltoides* and *C.* sp. 1 but differs from both species in, amongst others, size and stria density, the absence of lateral hyaline areas (*C. peltoides*), the uniseriate striae and the absence of poroids on the mantle (*C.* sp. 1).
Cocconeis sp. 2 might be conspecific with *Cocconeis pusilla* (Archibald 1966) but this species has to be studied before any conclusions can be drawn.

The resemblance of the structure of the R-valve of *Cocconeis peltoides*, *C.* sp. 1 and *C.* sp. 2 is remarkable. Moreover, these R-valves lack a feature which is typical of most representatives of the genus *Cocconeis*, viz. the distinct submarginal ring of silica.

Biogeography & Ecology: Unlike *Cocconeis peltoides* and *C.* sp. 1, *C.* sp. 2 is common in very fine sandy to silty sediments throughout the estuary. This taxon was also found in Salah's material from Blakeney Point, England. It is probably also present in brackish water sediments in Papua New Guinea, but a thorough SEM examination of this material is necessary before this can be unambiguously assessed.

COCCSP02

Cocconeis sp. 3

[Figs 11-16, 11-17]

Morphology:

L: 7.7-8.7(-16.9?); W: (3.1?-)5-5.6; S: (26.5-)28-32(-34.5)

LM - Valves elliptical with broadly rounded apices. Only P-valves were observed. They have a typical, broadly lanceolate central sternum. In the middle of this sternum, a slight apical line can be seen. The striae are restricted to a submarginal zone; they are parallel in the middle and radiate throughout the rest of the valve.

Remarks: Whether the single larger specimen (see dimensions above) also belongs to *Cocconeis* sp. 3 has to be checked. This taxon has a very constant size and stria density range.
The general appearance of the P-valve of this taxon is very reminiscent of the P-valve of *Cocconeis pelta* A. Schmidt. However, this species is larger and has a significantly lower stria density.

Biogeography & Ecology: *Cocconeis* sp. 3 is rare in sandy sediments throughout the estuary.

COCCSP03

Cocconeis sp. 4

[Figs 11-14, 11-15, 45-6]

Morphology:

L: 14-16.2; W: 9.5-11.2; S(P): 18-19 (n=3)

LM - Valves elliptical with cuneate-obtuse apices. Only P-valves were observed. Central sternum veru narrow, linear, in the centre very slightly transapically expanded. The striae are more or less radiate throughout the valve. They have about 26 areolae in 10 µm. The submarginal area of the valve is distinctly raised, except at the apices. The marginal zone is devoid of areolae.

SEM - Only P-valves were observed. Valve face markedly concave in transapical section; the valve face curves abruptly into a shallow (?) mantle. The central sternum is very narrow and is only distinct in the centre of the valve, where it is broader. The striae are composed of more or less round areolae. The external valve face (except the centre of the valve) is characterized by superimposed, short and long ridges, both in the apical and transapical system, inbetween the areolae. A raised, distinct ring of silica is present in the submarginal area. The mantle possesses a ring of small droplet-like warts. The cingulum structure is not very clear but the cingulum seems to be composed of three shallow copulae, of which at least one is open (Fig. 45-6).

Biogeography & Ecology: The distribution of this taxon in the estuary is identical to that of *C.* sp. 3.

COCCSP04

Cocconeis sp. 5

[Figs 11-20, 11-21, 11-22, 11-23, 11-24, 11-25]

Morphology:

L: 10-13.7(-20?); W: 6-8.7(-12.5?); S(P): (7.5?-11.2?-)13-13.5 (centre); marginal ribs (see below): 16-18

LM - Valves elliptical with rounded to cuneate-obtuse apices. R-valve with narrow raphe-sternum. Raphe straight to slightly curved, central raphe endings simple, straight, close together. No striae are visible in LM. P-valve with narrow, linear central sternum. A more or less distinct submarginal rib is present. On the inside of this rib, the areolae are large, more or less rounded to transapically elongate and separated by vimines which form wavy longitudinal lines. Small ribs seem to protrude from the outside of the submarginal rib (separating one row of marginal areolae?). These ribs sometimes appear to be forked (Figs. 11-25). Note that the marginal ribs are more densily placed than the virgae on the inside of the submarginal rib.

Remarks: Apart from the typical forms described above, we also found some larger specimens with distinctly forked marginal ribs (Figs. 11-20) and a lower stria density (about 10 to 7 striae/10 µm along the central sternum). Other specimens did not have a distinct submarginal ring. Whether all these forms belong to the same taxon is hard to assess without SEM and requires further study. In Hustedt's material from Miang Besar, Borneo (Hustedt slide N 15/51), we found some similar specimens, both R- and P-valves (Fig. 11-21, 11-22) . These, however, have a higher stria density on the P-valve (about 17-18 str./10 µm along the central sternum).

Biogeography & Ecology: Valves which probably also belong to this taxon were observed in Grunow's material from Kalkbay (South Africa), Hustedt's material from Miang Besar (Borneo) and Salah's material from Blakeney Point (England). A taxon which is probably conspecific with

Cocconeis sp. 5 was also reported by Cooper (1995a, Figs. 31a-c) as *Rhaphoneis* ? cf. *tenuis* Hustedt (Hustedt 1952, Simonsen 1987) from sediment cores from Chesapeake Bay (USA). *Cocconeis* sp. 3 is indeed quite reminiscent of *Rhaphoneis tenuis* (which probably concerns a P-valve of a *Cocconeis* species, cf. Simonsen 1987), but there are some marked differences, especially in the structure of the central sternum and the marginal zone.

COCCSP05

Fam. ACHNANTHIDIACEAE Mann

Achnanthidium Kützing 1844

Genus description: Round *et al.* 1990

For general remarks, See *Achnanthes*.

Achnanthidium delicatulum s.l. Kützing 1844 [Figs 9-1, 9-2, 9-3, 9-4, 9-5, 9-6, 9-7, 9-8, 9-9, 9-10, 43-3]

Synonyms:

Achnanthes delicatula (Küzting) Grunow in Van Heurck 1880

References:

(1) Kützing 1844
(2) Krammer & Lange-Bertalot 1991 (*neotypus*)
(3) Lange-Bertalot & Krammer 1989, Krammer & Lange-Bertalot 1991, Tropper 1975, Kuylenstierna 1989-90,

Morphology:

L: 10-23; W: 5-10: S(R): 11-16; S(P): 11-19

LM - One plastid, appressed to one side of the girdle, with (usually bilobed) plates extending under the valves. These lobes often extend as far as the opposite side of the girdle. Valves elliptical to lanceolate, apices usually slightly produced, subrostrate. The raphe (R-valve) is straight with straight, slightly expanded central raphe endings. The raphe-sternum is usually rather narrow but sometimes lanceolate to rhombic; central area usually more or less transapically expanded, roundish. The central sternum on the P-valve is more variable in shape, from narrow and linear to (broadly) lanceolate or rhombic. On one side of the raphe, a hyaline area is often present (due to the presence of widely spaced striae). The striae on both valves are more or less radiate, though less so (to parallel in the centre) on the P-valve.

SEM - Valve face flat, abruptly curving into a shallow mantle. Raphe-sternum distinct, raphe straight. Central raphe endings pore-like, more or less hooked. Terminal fissures bent in the same direction, ending in a slightly expanded punctum (or depression?). P-valve as R-valve (without raphe and associated structures). Striae multiseriate (up to 4 or 5 rows of poroids near the margin). The striae in the centre of the R-valve, are distinctly wedge-shaped (this is not as marked on the P-valve). Cingulum shallow, probably three open, non-porous copulae. Internally, the striae are separated by costate virgae. The central raphe endings are non-coaxial and straight; the terminal raphe endings are simple and straight.

Remarks: *Achnanthidium delicatulum* was originally described from a brackish site in the German Wadden Sea (Wangerooge). As the type material appears to be lost, Lange-Bertalot (in Ruppel & Lange-Bertalot 1980) designated a neotype (viz. Van Heurck, Types du Synopsis 234 - BM 26545). The taxonomy and nomenclature of the taxon group around *A. delicatulum* ('Der *Achnanthes delicatula*-Sippenkomplex') is extremely complicated [for a thorough discussion, see Krammer & Lange-Bertalot (1991)]. We have applied the name *Achnanthidium delicatulum* in its broadest sense (i.e. sensu latissimo, Krammer & Lange-Bertalot 1991, p. 70), although we are fully aware that this name covers many different morphological types present in our material. Individual valves could be assigned to the different varieties described in Krammer & Lange-Bertalot (1991); some of these (e.g. *Achnanthes delicatula* var. *engelbrechtii* (Cholnoky) Lange-Bertalot, *A. delicatula* var. *hauckiana* (Grunow) Lange-Bertalot) are illustrated in the illustrations.

A thorough revision of this ecologically important and widespread group of diatoms is necessary to assess the taxonomic significance of the different morphological forms comprised in *A. delicatulum* sensu latissimo, in other words whether we are dealing with distinct taxa or a continuous range of forms (cf. Tropper 1975, Wendker 1990).

Biogeography & Ecology: In the Westerschelde estuary, *Achnanthidium delicatulum* sensu latissimo was one of the most common adnate species in very fine to fine sandy sediments; it appears to be indifferent to higher amounts of silt in the sediment. It appears to be more abundant in the mesohaline reaches of the estuary, but this relationship could be spurious because of the predominance of slightly less coarsely grained sediments in the inner reaches of the estuary (see chapter 5.1.3.3.). *A. delicatulum* is an extremely common and apparently cosmopolitan diatom in waters with high conductivity and in brackish (and marine?) waters. It is usually identified as *Achnanthes delicatula* or *A. hauckiana* Grunow and their varieties (e.g. Archibald 1983, John 1983, Kuylenstierna 1989-90, Wendker 1990, Gätje 1992, Sabbe 1993, Snoeijs 1993 and Witkowski 1994). Although *Achnanthes hauckiana* is a commonly used name for specimens from brackish sites, it is not sure whether these, despite their very similar LM appearance, have anything to do with the specimens from the type locality (see Krammer & Lange-Bertalot 1991).

ACHNDELI

Achnanthidium lanceolatum Brébisson ex Kützing 1849 [Figs 9-19, 9-20, 9-21]

Synonyms:

Achnanthes lanceolata (Brébisson) Grunow in Cleve & Grunow 1880

References:

(1) Kützing 1849
(2)
(3) Lange-Bertalot & Krammer 1989, Krammer & Lange-Bertalot 1991

Morphology:

L: 7.8-14.2; W: 3.4-6.7; S: 13-15.5

Remarks: Only a few valves belonging to this freshwater species were found. The considerable morphological variation of this taxon is illustrated and discussed in Krammer & Lange-Bertalot (1991).

Biogeography & Ecology: *A. lanceolatum* has been reported as an epipsammic diatom from the freshwater tidal areas of the Thames estuary (Juggins 1992). The few specimens we observed in the Westerschelde estuary were therefore most probably washed in from the freshwater tidal reaches or tributaries.

ACHNLANC

Achnanthidium sp. 1

[Figs 9-17, 9-18, 43-8, 43-9]

References:

(1)
(2)
(3) Witkowski 1994

Morphology:

L: 6.6-8.7; (3.7-)4-5; S(R): 18.5-22(-24?); S(P): 16-18(-19)

LM - Valves elliptical, apices broadly rounded. Raphe-sternum (R-valve) narrow, central area absent. Raphe straight, central raphe endings slightly expanded, straight. P-valve with narrow central sternum; central area unilaterally expanded to the valve margin (cf. *Achanthidium lanceolatum*, but without 'hufeisenformige Fleck', cf. Round *et al.* 1990). Striae radiate, more markedly on the R-valve.

SEM - Only P-valves were observed. Valve face flat, rather abruptly curving into a very shallow mantle. Striae multiseriate (up to 3 to 4 rows of poroids near the valve margin), wedge-shaped (especially in the centre of the valve). Internally, the striae are separated by costate virgae. Cingulum shallow (number of copulae unknown).

Remarks: This taxon differs from the taxon group around *A. lanceolatum* in the absence of a depression in the lateral hyaline area of the P-valve and in stria density. It probably belongs to the taxon group around *A. delicatulum* (cf. Witkowski 1994, Pl. 18, Fig. 4). We are as yet not sure what the taxonomic status of this taxon should be. However, as it was consistently distinct from the many forms of *A. delicatulum* and as it has a slightly different autecology, we believe it warrants taxonomic recognition.

Biogeography & Ecology: *Achnanthidium* sp. 1 is common in fine sandy sediments in the Westerschelde estuary. Unlike *A. delicatulum*, it is usually not found in very fine sandy sediments or sediments with higher amounts of silt. *Achnanthidium* sp. 1 was also found in the Gulf of Gdansk (Baltic Sea)(Witkowski 1994) and in the Thames estuary (Juggins 1992, as *Achnanthes* sp. 2).

ACHNSP01

Achnanthidium sp. 2

[Figs 9-11, 9-12, 9-13, 9-14, 9-15, 9-16, 43-1, 43-2]

References:

(1)
(2)
(3) Lange-Bertalot & Krammer 1989, Krammer & Lange-Bertalot 1991, Witkowski 1991,

Morphology:

L: 6.5-12.5; W: 3.7-4.4; S(R): 17-19.5; S(P): 16-20

LM - Plastid structure not very clear but appears to be similar to the plastid shape of *Achnanthidium delicatulum*. Valves elliptical to lanceolate, with produced (subrostrate to rostrate) apices. R-valve with narrow raphe-sternum, straight raphe and a small, transapically expanded central area. P-valve with narrowly lanceolate central sternum. The striae are radiate throughout the valve (on both valves). Note that the there is no significant difference in stria density between the R- and the P-valve.

SEM - Valve face slightly curved in transapical section, no mantle can be distinguished. Raphe straight, central raphe endings straight, only slightly expanded. The terminal fissures are bent (unknown whether this is in the same direction or not). The striae are uni- (near the central sternum) to biseriate (near the margin) and consist of small, alternating poroids, which are internally occluded by a velum of the hymenate type. Externally, a third row of only a few 'poroids' long can be seen in the striae. However, it is not sure whether 'poroids' actually penetrate the valve, as they are never visible on the inside of the valves [note however the internal valve view in Kuylenstierna (1989-90, Pl. 34, Fig. 336), where a third row of poroids is clearly visible]. On the R-valve, the striae are distinctly wedge-shaped near the centre of the valve. Internally, the striae are separated by costate virgae. The cingulum is shallow and consists of two non-porous, open copulae, one of which (the valvocopula?) is much wider than the other one (Figs. 43-1, 43-2).

Remarks: *Achnanthidium* sp. 2 can be distinguished from *A. delicatulum* by its size and stria density (which is higher on average) and the structure of the striae (only 2, rarely 3 (?) rows of poroids). This taxon is very common in brackish sediments in Europe and is usually identified as *Achnanthes* (cf.) *lemmermannii* Hustedt (Sundbäck 1983, Kuylenstierna 1989-90, Witkowski 1994. Lange-Bertalot & Krammer 1989, Wendker 1990, Krammer & Lange-Bertalot 1991, Gätje 1992, Juggins 1992). *A. lemmermannii* has only with certainty be observed in the type locality, a freshwater site (the Wumme River in the vicinity of Bremen)(Lange-Bertalot & Krammer 1989). The confusion surrounding this taxon was actually started by Hustedt himself, who reported it as very common in brackish-marine, intertidal flats in the German Wadden Sea (Hustedt 1939). He postulated that the type specimens of *A. lemmermannii* might have been imported from coastal areas. This would not be completely unlikely, although he reported it as not rare in the type material. Moreover, the specimens from the Westerschelde [and the brackish ones illustrated in Krammer & Lange-Bertalot (1991, Pl. 26, Figs 33-40)] differ from *A. lemmermannii* in having (sub)rostrate (not capitate) apices, the presence of short striae in the centre of the valve of most specimens and in their autecology. Only a thorough SEM examination of the type material of *A. lemmermannii* would give a decisive answer about the relationship between both taxa. Until then, it it better to keep them separate and to not use the name *A. lemmermannii* for the brackish and marine taxa.

Biogeography & Ecology: This epipsammic taxon is very common in the Westerschelde estuary: it is mainly found in fine and medium sandy sediments and has a higher salinity optimum than *Achnanthidium delicatulum* and *A.* sp. 1. It has also been reported from brackish and marine sediments throughout Europe (see above) and in Chili (Krammer & Lange-Bertalot 1991).

ACHNSP02

Achnanthidium sp. 3

[Figs 8-14, 8-15, 8-16, 8-17, 8-18, 42-3, 42-6]

References:

(1)
(2)
(3) Kuylenstierna 1989-90, Sundbäck & Snoeijs 1991

Morphology:

L: 4.4-8.7; W: 2.2-3.7; S(P): 26-32(-36); S(R): about 32 (n=1!)

LM - Valves elliptical to lanceolate with cuneate to rounded apices. Raphe-sternum very narrow, central raphe endings close together, hardly distinguishable. Terminal raphe endings lie at some distance of the apical valve margin. Central sternum of the P-valve very narrow. Striae parellel to radiate in the centre of the valve, to radiate towards the apices. the central striae are sometimes more widely spaced.

SEM - Valve face flat, curving rather abruptly into a shallow mantle. The P-valve has a very narrow central sternum. The striae are composed of two rows of poroids. Internally, the striae are separated by costate virgae. No R-valves were observed with certainty.

Remarks: This taxon most probably belongs to the genus *Achnanthidium* judging from the structure of the P-valve.

Biogeography & Ecology: There is little doubt that this taxon is conspecific with some specimens from the West Coast of Sweden, illustrated in Sundbäck & Snoeijs (1991, as *Achnanthes* cf. *delicatissima* Simonsen) and Kuylenstierna (1989-90, as *Achnanthes* sp. C). They have a similar valve shape, size range and stria density and have striae that consist of two rows of poroids. Whether this taxon is conspecific with *Achnanthes delicatissima*, as suggested by Sundbäck & Snoeijs (1991), remains unclear until the type material of this species has been investigated. Simonsens taxon is slightly larger and broader and has a significantly higher stria density on the P-valve (more than 40) than on the R-valve, which is not in accordance with our observations and those of Kuylenstierna (1989-90).

Achnanthidium sp. 3 has been found in sediment samples from the Westerschelde estuary, Blakeney Point (England) and the Swedish West Coast (cf. references above). In the Westerschelde estuary, it is mainly found in medium sandy sediments in the lower reaches and in the mouth of the estuary.

ACHNSP03

Achnanthidium sp. 4

[Figs 8-19, 8-20, 8-21, 42-4, 42-5]

Morphology:

L: 6.2-7.5; W: 2.9-3.7; S(R): 45-55 (n=2)

LM - Valves lanceolate-rhombic with blunted apices. R-valve with more or less distinct raphe-sternum and central nodule. P-valve with distinct central sternum. The structure of both valves is very delicate: no striae can be distinguished in LM.

SEM - Only R-valves were observed. The valve face is flat, curving into a very shallow mantle. The raphe is straight and lies in a narrow raphe-sternum, which is raised on the inside of the valve. The central raphe endings are straight and simple (both internally and externally), the terminal raphe endings are straight. In Fig. 42-5, a bent terminal fissure can be seen. The striae are radiate throughout the valve and consist of alveoli which run uninterrupted from the valve amrgin to the raphe-sternum. They are occluded by a hymenate velum. Note that short striae are often present in the centre of the valve.

Remarks: The identity of this small diatom is not clear. It is characterized by its delicate structure, the typical lanceolate-rhombic shape and the structure of the striae and can thus be distinguished from *Achnanthidium* sp. 3, which often occurred in the same samples.

Biogeography & Ecology: The distribution of this taxon in the Westerschelde estuary is almost identical to that of *Achnanthidium* sp. 3.

ACHNSP04

Ordo Naviculales

Subordo Neidiineae

Fam. BERKELEYACEAE Mann

Berkeleya Greville 1827

Genus description: Cox 1975a, 1975b, Round et al. 1990

Berkeleya rutilans (Trentepohl in Roth 1806) Grunow 1880

Synonyms:

Conferva rutilans Trentepohl in Roth 1806
Amphipleura rutilans (Trentepohl in Roth 1806) Cleve 1894

References:

(1) Trentepohl in Roth 1806
(2)
(3) Cox 1975b, Lobban 1985, Snoeijs 1993

Morphology:

L: 25.6; W: 5; S: 23 (n=1)

LM & SEM description: a detailed description of this species is given by Cox (1975a).

Biogeography & Ecology: Single valves of this tube-dwelling species were regularly found in low numbers in our sediment samples, mainly in silty sediments in the mesohaline section of the estuary. *Berkeleya rutilans* has been recorded from numerous localities worldwide [e.g. the Pacific coast of North Americ (Lobban 1984, 1985), Europe (Cox 1975a, Houpt 1994), etc.].

BERKRUTI

Lunella Snoeijs 1996

Genus description: Snoeijs 1996

See Table 21 for a comparison with similar genera

***Lunella* sp. 1** [Figs 12-1, 12-2, 12-3, 12-4, 46-1, 46-2]

References:

(1)
(2)

(3) Snoeijs 1996

Morphology:

L: 7.7-8.7; W: 2.5-2.7; S: 22-25 (note, however, that they are often more widely spaced on the dorsal side, with values between 18-25 str./10 µm)

LM - Valves more or less elliptical, asymmetrical about the apical plane (dorsal margin convex, ventral margin more or less straight), and in some specimens also about the transapical plane (Figs 12-1, 12-2). Apices cuneate to cuneate-obtuse. Axial area narrow, central area absent; the central nodule is usually distinct. Raphe straight, central raphe endings straight, slightly expanded to pore-like. Striae parallel to radiate near the apices; the central striae on the dorsal side are more widely spaced, usually only in the centre of the valve but in some specimens throughout the valve (Fig. 12-4).

SEM - Valve face more or less flat, at almost right angles with a deep mantle. Raphe-sternum narrow, slightly raised (Fig. 46-1). Raphe very slightly curved; terminal raphe endings slightly expanded and slightly deflected to the dorsal side. Terminal raphe endings bent to the ventral side. The striae consist of one row of more or less round areolae, occluded by a velum. The areolae adjacent to the raphe-sternum on the dorsal side are slighly apically elongate and larger than the other areolae. The cingulum consists of at least 3 slightly curved, punctate copulae. No internal valve views were obtained.

Remarks: The monospecific genus *Lunella* was recently described by Snoeijs (1996); it is probably closely related to *Parlibellus* but differs from this genus in its 'catenuloid' cell construction (i.e. with an asymmetrical valve face and the girdle equally deep on the dorsal and ventral side) and the lower number of copulae (3-4). Although no internal valve views were observed, our specimens were assigned to *Lunella* on the basis of the above-mentioned features. For more information on the genus *Lunella* and its relationship with other raphid diatom genera, see Snoeijs (1996).

Lunella sp. 1 differs from *Lunella bisecta* in stria density (22-25 in *Lunella* sp. vs. 50-57 in *L. bisecta*) and the absence of a more refractive central band. In *Lunella* sp. 1, the striae are clearly visible in LM. Other distinguishing features are the shape of the central raphe endings (slightly deflected towards the dorsal not ventral side), the position of the raphe which is slighty less eccentric and the presence of areolar occlusions (note however that these may have been eroded in *L. bisecta*).

Biogeography & Ecology: *Lunella bisecta* Snoeijs, the type of the genus, was described from epipilithic mucilage communities in the northern Baltic sea (5 ‰). It was relatively most abundant in late winter in water temperatures of 0 °C. *Lunella* sp. 1 is especially common in fine sandy sediments and occurs throughout the estuary.

NADISP05

Parlibellus Cox 1988

Genus description: Cox 1988a

This genus is characterized by the two butterfly-shaped chloroplasts, more or less circular areolae, a raphe terminating well before the valve apices and numerous open copulae. Some of its members are tube-dwelling (Cox 1988a).

See Table 21 for a comparison with similar genera

Parlibellus plicatus (Donkin 1873) Cox 1988

[Figs 12-14, 12-15, 46-7]

Synonyms:

Navicula plicata Donkin 1873 non Ehrenberg 1858

References:

(1) Donkin 1873
(2)
(3) Krammer & Lange-Bertalot 1986, Cox 1988a, Kuylenstierna 1989-90

Morphology:

L: 43.4-67.5; W: 8.7-10.6; S: 20-22 (n=3)

LM - Plastids 2, each lying against the girdle, typically butterfly-shaped (Fig. 12-14). Valves linear, apices broadly rounded. Axial area distinct, rather narrow, central area more or less circular. Raphe more or less straigt, central raphe endings straight, expanded, terminal raphe endings close to the apices, deflected? Striae finely punctate, slightly radiate throughout the valve (to convergent near the apices?). The striae in the centre of the valve are slightly more widely spaced.

SEM - Only one internal valve view was observed. The striae consist of small, round poroids. Raphe opens in a rather wide, apparently slightly asymmetrical raphe-sternum.

Remarks: Only a few valves belonging to this species was found. Its striation density is about 20-21 str./10 µm, which is close to the upper limit given by Cox (1988a) and Krammer & Lange-Bertalot (1986) for this species.

Biogeography & Ecology: *Parlibellus plicatus* is a common species on sandy shores, especially around the North Sea (Cox 1988a, Kuylenstierna 1989-90, Krammer & Lange-Bertalot 1986). It was not found during the cell counts.

Parlibellus sp. 1

[Fig. 12-11]

Morphology:

L: 21.2-23.7; W: 5; S: 32-33 (n=2)

LM - Valves lanceolate, apices slightly cuneate. Axial area narrow, central area absent. Raphe straight, raphe sternum distinct, elevated. A distinct central nodule is present. Central raphe endings straight, expanded. Terminal raphe endings terminating before the valve apices, deflected in the same direction. Striae finely punctate, parallel in the centre to slightly convergent towards the apices. Note the central striae which are slightly more widely spaced. The cingulum is very wide and consists of numerous copulae.

Remarks: This taxon resembles *Navicula* sp. (Kuylenstierna 1989-90, Pl. 58) but has a higher striation density (32-33 str./10 µm versus about 20 str./10 µm in *Navicula* sp.). Although no SEM images of this taxon could be made its general appearance (cf. raphe, stria and cingulum structure) seems to suggest that it belongs to *Parlibellus*.

Biogeography & Ecology: This taxon was usually common (though never in high numbers) in fine sandy sediments throughout the Westerschelde estuary.

PARLSP01

Parlibellus sp. 2

[Figs 12-6, 12-7, 12-8, 12-9, 12-12, 12-13, 47-5]

References:

(1)
(2)
(3) Cleve & Grunow 1880, Hustedt 1939, 1959, 1962, Brockmann 1950, Simonsen 1960, 1987, Giffen 1975, Krammer & Lange-Bertalot 1986, Mann 1988, Kuylenstierna 1989-90, Witkowski 1991a

Morphology:

L: 16.2-33.6; W: 4.7-7.5; S: 18-22(-24?)

LM - Plastids two, girdle appressed, butterfly-shaped (sometimes only slightly) with extensions under the valves (Figs 12-6, 12-7, 12-8, 12-9). Droplets are present between the centre and the apices, inbetween the two plastids. Note the centrally positioned nucleus with a nucleolus (Fig. 12-7). Valves elliptical, rarely slightly inflated in the centre, apices broadly rounded. Axial area narrow, central area slightly transapically expanded, more or less elliptical. Raphe straight, central raphe endings distant (separated by a distinct central nodule), expanded. Terminal raphe endings deflected (to the same side?). Striae more or less radiate throughout the valve (to slightly parallel near the apices); their structure is indistinct. In the centre, they are more widely spaced, usually more so on one side of the valve. Sometimes a few short striae are visible in the centre of the valve (Figs 12-2, 12-13). Cingulum wide with numerous copulae (up to 9).

SEM. Only external valve views were observed. Valve face flat, gently curving into the rather deep mantle. Raphe straight, central raphe endings straight, opening into a spathulate groove. Terminal fissures strongly hooked (to the same side?). Striae uniseriate around the centre, biseriate throughout the rest of the valve. On one side of the valve, a fascia (or stauros?) is present. An isolated punctum is present. It is not sure, however, whether this is a constant feature of this taxon.

Remarks: There is little doubt that this taxon belongs to the species group around *Navicula protracta*, which belongs to the Naviculae microstigmaticae sensu Hustedt (1962). Mann (1988) pointed out that this species might belong to *Parlibellus* (see further). We were hesitant, however, to assign this taxon to *N. protracta* mainly because of the presence of short striae in the centre of the valve and the biseriate striae. Unfortunately, no internal valve views could be observed in SEM, so we do not know whether *Parlibellus* sp. 1 has pseudosepta at the poles like *N. protracta* (Mann 1996). *Parlibellus* sp. 1 is also very reminiscent of *Stauroneis legleri* Hustedt (Hustedt 1959, Simonsen 1987), a species which was described of inland saline lakes in Austria. *S. legleri* almost certainly does not belong to *Stauroneis*. Further study (with examination of live material of *S. legleri*) is required to assess the relationship between both taxa.

Recently, two genera, viz. *Parlibellus* (Cox 1988a) and *Dickieia* (Mann 1994), have been (re)-established to accomodate for some members of this group (see further). *Parlibellus* sp. 1 certainly does not belong to *Navicula* s.s.: it differs from the latter in plastid shape, cingulum structure and the ultrastructure of the areolae, which are round instead of apically elongate. *Dickieia* spp. possess only one plastid with two K-shaped, valve-appresses lobes; therefore *Parlibellus* sp. 1 cannot belong to this genus. However, it does possess features which are characteristic of the genus *Parlibellus* (viz. the butterfly-shaped plastids, the wide cingulum with numerous copulae and the small, round areolae) and was therefore allocated to this genus, although it does exhibit some features which have, to our knowledge, not been observed before in members of this genus, viz. the biseriate striae and the presence of long terminal fissures.

The species group around *Navicula protracta* has, to our knowledge, not been revised yet [although some studies do exist on the systematics of some species, cf. *N. protracta*, Mann 1988]; it contains several taxa which are very similar to *Parlibellus* sp. 1, such as *Navicula protracta*, *N. protractoides* Hustedt (see Cox 1987), *N. crucicula*, *N. pseudoinflata* Giffen, *N. subinflatoides* Hustedt, *N. utlandshoerniensis* (= *N. manifesta* Hustedt non Marsson), *Dickieia excepta* (VanLandingham) Mann (= *N. aberrans* Simonsen non Cleve-Euler) and *D. subinflata* (Grunow in Cleve) Mann. Little is known about the morphological variability within this species group, which is necessary to assess the relationship between these taxa and *N.* cf. *protracta*. For a more thorough discussion of the interrelationships in this group, see Hustedt (1962), Krammer & Lange-Bertalot (1986), Cox (1987, 1988a) and Mann (1988, 1994a, 1996).

Biogeography & Ecology: All the above-mentioned taxa have been reported from brackish and marine localities throughout Europe. An unidentified diatom which is very similar to *Parlibellus* sp. 1 was found in the Nordre Älv estuary on the Swedish West coast (Kuylenstierna 1989-90, as *N.* sp. R). *Parlibellus* sp. 2 is restricted to the mesohaline reaches of the Westerschelde estuary, where it is one of the most abundant epipelic diatom taxa in silty sediments. It is most abundant in late winter, early spring.

PARLSP02

Fam. DIADESMIDACEAE Mann

Luticola Mann 1990

Genus description: Round *et al.* 1990

Luticola cohnii (Hilse 1860) Mann 1990 [Fig. 46-4]

Synonyms:

Stauroneis cohnii Hilse 1860
Navicula mutica var. *cohnii* (Hilse) Grunow in Van Heurck 1880
Navicula cohnii (Hilse) Lange-Bertalot 1985

References:

(1) Hilse 1860
(2)
(3) Archibald 1983, Lange-Bertalot & Bonik 1978, Krammer & Lange-Bertalot 1986

Morphology:

L: 10-22.5; W: 5-7.5; S: 20-24

LM - Valves elliptical with rounded, often slightly produced apices. Axial area rather wide, slightly asymmetrical; central area transapically elongated, almost reaching the valve margin. A distinct stigma is present somewhat halfway between the valve margin and the central nodule, or closer to the latter. Raphe slightly curved, central raphe endings expanded, pore-like, deflected in the same direction, away from the valve side with the stigma. Terminal raphe endings deflected in the same direction as the central raphe endings. Striae consist of radiate rows of distinct, roundish puncta.

SEM - No internal valve views were observed. Valve face flat, with a sharp transition to the rather shallow margin. Raphe slightly curved, central raphe endings deflected, terminal fissures strongly hooked, in the opposite direction of the central and terminal raphe endings. Striae consist of more or less round areolae (± 20 in 10 µm); no occlusions are visible. On the valve margin one distinct longitudinal row of transapically elongated puncta is present.

Remarks: *Luticola cohnii* has been studied in detail by Lange-Bertalot & Bonik (1978) and Archibald (1983). Our specimens display most features which are characteristic of this species: unlike in *Luticola mutica* (Kützing) Mann, (1) the central raphe endings are deflected in the opposite direction of the stigma, (2) the position of the stigma is closer to the central raphe endings than to the valve margin and (3) the central raphe endings are not as sharply deflected as described for *L. mutica*. The ecological distinction between these two taxa is not very clear: according to Krammer & Lange-Bertalot (1986) *Luticola cohnii* is much rarer but this could be due to misidentifications. We decided to assign our specimens to *Luticola cohnii*, although their striation density is slightly higher than described for this species (viz. 20-24 str./10 µm versus 15-20 str./10 µm in *L. cohnii*).

Biogeography & Ecology: Although *Luticola cohnii* has been reported as a rare species from subaerial habitats worldwide (Krammer & Lange-Bertalot 1986) and from brackish waters in Europe (this study, Denys 1991a), South Africa (Archibald 1983) and North America (Patrick & Reimer 1966), its ecological characterization and geographical distribution remain uncertain due to possible mix up with *Luticola mutica* (and vice versa). See also *L. mutica*.

LUTIMUTI

Luticola mutica (Kützing 1844) Mann 1990 [Fig. 12-5]

Synonyms:

Navicula mutica Küzting 1844

References:

- (1) Küzting 1844
- (2) Krammer & Lange-Bertalot 1986 (isotypes)
- (3) Archibald 1983, Lange-Bertalot & Bonik 1978, Krammer & Lange-Bertalot 1986, Round *et al.* 1990

Morphology:

L: 16.6; W: 6.3; S: 20 (n=1)

LM - Valves elliptical, sometimes with triundulate margins, with produced, rostrate apices. Axial area slightly asymmetrical; central area transapically elongated. A stigma is present somewhat halfway between the valve margin and the central nodule. Raphe slightly curved, central raphe endings expanded, pore-like, apparently only slightly deflected in the same direction, away from the stigma. Terminal raphe endings deflected in the same direction. Striae consist of radiate rows of distinct puncta.

Remarks: Both valves found show features typical of *L. mutica*, viz. the distinctly rostrate apices and the triundulate margins. However, the central raphe endings curve away from the stigma (Fig. 12-5) and one specimen had up to 24 str./10 μm. Clearly, this species group needs more investigation.

Biogeography & Ecology: *Luticola mutica* is a cosmopolitan, common diatom in fresh and (slightly) brackish waters (Archibald 1983, John 1983, Krammer & Lange-Bertalot 1986, Round et al. 1990, Gätje 1992). During the cell counts, we did not distinguish between *L. cohnii* and *L. mutica*. Valves belonging to these species were rarely found in the mesohaline section of the estuary. As we never observed live cells, they might have been washed in from the freshwater tidal part of the estuary or the rivers (cf. Juggins 1992). See also *L. cohnii*.

LUTIMUTI

Fam. SCOLIOTROPIDACEAE Mereschkowsky

Biremis Mann & Cox 1990

Genus description: Round *et al.* 1990

The diatom genus *Biremis* D.G. Mann *et* E.J. Cox (Round *et al.* 1990) was established to accommodate a small group of naviculoid diatom species which were distributed between *Amphora* (*A. digitus* A. Schmidt and *A. ridicula* Giffen), *Pinnularia* (*P. ambigua* Cleve and *P. fritschii* Salah) and *Mastogloia* (*M. baculus* Hustedt). The main feature of this genus is its peculiar stria structure; internally this consists of two incompletely separated, transapically elongate chambers, which open externally by 2 longitudinal rows of foramina, one near the valve margin and one near the usually wide raphe-sternum (Round *et al.* 1990, Sabbe *et al.* 1995). Most representatives have been described from brackish and marine sediments. However, recently five new freshwater *Biremis* species were discovered in Tasmanian mountain lakes (Vyverman *et al.* 1997).

See Table 21 for a comparison with similar genera.

Biremis ambigua (Cleve 1895) Mann 1990

[Figs 14-1, 14-2, 14-3, 46-3, 46-8]

Synonyms:

Pinnularia ambigua Cleve 1895

References:

(1) Cleve 1895
(2)
(3) Cox 1990, Sabbe *et al.* 1995

Morphology:

LM & SEM - A detailed description of this species can be found in Cox (1990); it is extensively compared to *B. lucens* in Sabbe *et al.* (1995).

Biogeography & Ecology: *Biremis ambigua* is a common and widespread epipelic diatom (John 1983, Podzorski & Håkansson 1987, Cox 1990, Sabbe *et al.* 1995). In the Westerschelde estuary, it is mainly found in rather sandy sediments (median grain size optimum is higher than that of the epipsammic *B. lucens*!, cf. Table 39); it appears to occur throughout the estuary.

BIREAMBI

Biremis lucens (Hustedt 1942) Sabbe, Witkowski & Vyverman 1995

[Figs 14-4, 14-5, 14-6, 14-7, 14-8, 14-9, 14-10, 47-1, 47-2]

Synonyms:

Navicula lucens Hustedt 1942
Fallacia lucens (Hustedt) Mann 1990

References:

(1) Hustedt 1942
(2) Simonsen 1987, Sabbe *et al.* 1995
(3) Sabbe *et al.* 1995

Morphology:

Hustedt's holotype of *Navicula lucens* was studied on BRM slide N 15/52 (labelled 'Miang Besar, Borneo 4'). In addition, specimens belonging to this species were studied in material from Europe [The Netherlands (Westerschelde estuary), England (Blakeney Point, BM slides 36399-36402, 36405-36407), Poland (Gulf of Gdansk, Baltic Sea)], Australasia [the Hopkins estuary (Victoria, Australia) and an outlet of Lake Nagada (Madang Province, Papua New Guinea)] and Africa [C slides of Foged's material (35/68) from Mbwa maji south of Dar-es-Salaam, Tanzania, 'visceral contents from Holothurian on sandy bottom' (Foged 1975)].

A detailed morphometric study of this material revealed the presence of two distinct morphological types in the material from Europe. The main differences between them lie in stria density, valve and raphe sternum shape (see below). As we did find any other LM or SEM characteristics that can be used to distinguish both morphotypes, we use the term '*B. lucens* complex' in the morphological description below.

LM - The cells of the *Biremis lucens* complex contain two chloroplasts which are slightly indented both near the centre and the apices; each has a pyrenoid. No valvar views of the live cells were observed. However, careful focussing revealed that each chloroplast consists of 2 plates lying against the girdle and most probably connected to each other by the pyrenoid: the chloroplasts would therefore be H-shaped in valvar view. Near the centre two droplets are visible. In freshly divided cells the typical shape is not present.

In some populations of the *Biremis lucens* complex, the valves may be slightly constricted or inflated in the centre. One valve of the holotype specimen is constricted between the apex and the centre though this seems to be a teratological form. In girdle view, the frustules are rectangular and often more or less constricted centrally. The striae are short and marginal, slightly radiate in the centre to convergent near the apices. In oblique or girdle view they appear to be composed of two large foramina, one near the valve margin and one adjacent to the raphe-sternum. The latter is usually wide. The raphe is straight, the central raphe endings are straight and slightly expanded.

SEM - The raphe-sternum is more or less plain and flat, and the transition between the valve face and the mantle is gradual. The striae consist of two round to slightly apically elongated foramina. These form two longitudinal rows, one near the valve margin and one on the face-mantle transition, which are separated by a longitudinal hyaline region. The raphe is straight with expanded central raphe endings. The terminal fissures are strongly hooked in the same direction and end near the marginal row of foramina.

Internally, the raphe-sternum is plain. The polar raphe endings terminate in distinct helictoglossae and the central raphe endings are slightly raised. A bipartite cribrum lies between each pair of foramina; the cribra are separated by indistinct ribs. In eroded specimens it can be seen that the latter are indeed ribs and not septa, i.e. they are only connected to the valve interior between the foramina. Thus two longitudinal chambers are formed, which open externally by the foramina and internally by narrow slits in the cribra near the foramina.

The cingulum is composed of at least 6 open copulae, all of which have two (often incomplete) longitudinal rows of small pores. However, the latter feature is not always visible.

Size and dimensions of the two European morphotypes are shown in the table below, where they are compared to the type material and the studied non-European material.

	N	LENGTH (MM)	WIDTH (MM)	STR./10 MM	VALVE SHAPE	RAPHE-STERNUM SHAPE
Morphotype 1	98	7.6-20.0 μ = 11.8	2.5-4.5 μ = 3.5	14.0-17.0 μ = 15.1	Elliptical to lanceolate; apices rounded to cuneate	Usually lanceolate, in larger specimens elliptical
Morphotype 2	198	11.2-25.0 μ = 16.0	3.0-5.0 μ = 4.0	11.0-13.0 μ = 12.0	Elliptical; apices broadly rounded, rarely slightly	Elliptical with cuneate apices
Borneo (type)	7	11.2-15.0 μ = 12.9	3.5-4.7 μ = 3.8	16.0-17.0 μ = 16.4	Elliptical to lanceolate; apices rounded to cuneate	Lanceolate, sometimes elliptical with cuneate
Tanzania, Papua New Guinea, Australia	56	8.8-25.5 μ = 15.4	3.7-5.6 μ = 4.4	12.0-16.0 μ = 13.8	Elliptical; apices rounded	Lanceolate to rhombic

Analysis of Westerschelde samples from different localities and different seasons revealed that the discontinuity between the two morphotypes was stable, both in space and time. For more details on this morphometric analysis we refer to Sabbe *et al.* (1995).

Remarks: *Biremis lucens* was originally illustrated in A. Schmidt's Atlas der Diatomaceenkunde (1934), pl. 400, figs 30-32, but because Hustedt failed to give a description, this does not constitute valid publication of the name. A valid description of *B. lucens* with full reference to the illustrations in A. S. Atlas is given in Hustedt (1942), which therefore constitutes the first valid publication of the basionym (cf. Simonsen 1987). It also precedes Salah's (1953) description which has incorrectly been considered as the first valid publication of the basionym (Hartley 1986, Round *et al.* 1990). A further description of the species was given by Hustedt (1927-66). Mann (in Round *et al.* 1990) incorrectly transferred this species to the genus *Fallacia* Stickle *et* Mann.

Biremis lucens is very similar to *B. ambigua*, which has been described in detail by Cox (1990). However, it differs from the latter in size, stria density, chloroplast morphology and ecology. *B. ambigua* is usually larger, has on average 8 never more than 9 striae in 10 µm. The chloroplasts of *B. ambigua* are more H-shaped in girdle view, with an indentation under the valve rather than opposite the polar girdle region as in *B. lucens*. In addition, *B. ambigua* is a solitary, epipelic species, while *B. lucens* is usually colonial and epipsammic.

The morphometric analysis of the *Biremis lucens* populations from the Westerschelde estuary revealed a striking bimodality in the frequency distribution of the stria density data. This discontinuity appeared to be stable, both in space and time. We therefore decided to distinguish between two morphotypes in the Westerschelde area, one of which has on average 12 (Figs 14-4, 14-5, 14-6, 14-7), the other 15 striae in 10 µm (Figs 14-8, 14-9, 14-10). Unfortunately, this distinction on the basis of stria density could not be supported by other, independent morphological evidence. On the one hand, the observed differences in valve and raphe-sternum shape were not quantified in this study and therefore do not constitute objective evidence for the existence of the morphotypes. On the other, it is unlikely that additional morphological proof will be found in the electron microscope, given the relative simplicity of the *Biremis lucens* valves. However, the autecology and the biogeographical distribution of the two morphotypes does support their distinction (cfr. also below). Although they were sympatric in most Westerschelde stations, they displayed different and independent spatial and seasonal distribution patterns (cf. Figs 54 and 55 in Sabbe *et al.* 1995). Moreover, morphotype 2 was significantly more abundant in more silty sediments and at lower salinities, whereas morphotype 1 appeared to be the dominant, and often only, morphotype in stations with coarse sandy sediments. The distribution of the latter morphotype, however, was not significantly related to the studied environmental parameters. Both morphotypes could consistently be distinguished in samples from the other European localities, which shows that they are stable across a wide geographical range. Moreover, the dominance of morphotype 2 in the fine-grained sediments of the brackish Gulf of Gdansk (salinity about 8 ‰) confirms its ecological preferences based on the observations on the Westerschelde material. However, the morphotypes were not with certainty observed in the non-European material. Other, yet insufficiently known morphological variation patterns exist in this material (cf. the table above).

Notwithstanding the fact that the recognition of both morphotypes is mainly based on a single morphological feature, it is clear that we are dealing with stable, discontinuous morphological variation, supported by ecological and biogeographical evidence. In addition, further analysis of valve and raphe-sternum shape could possibly reveal additional objective differences in the morphology of the two morphotypes.

It could be argued that the morphological differences are too small to distinguish between two morphotypes. However, previous studies have shown that seemingly insignificant but stable differences in valve morphology can have a genetic basis (Hasle 1978, Mann 1989b, Medlin *et al.* 1991). In some of these studies, the combination of morphological and molecular or genetic research consequently led to the description of new species (e.g. *Thalassiosira guillardii* Hasle; *Skeletonema pseudonana* Medlin). This indicates that it is worth recognizing and describing small but stable morphological differences in diatom species.

Biogeography & Ecology: *Biremis lucens* was originally described by Hustedt from silt samples ('Schlammprobe') from the coast of Borneo and was later characterized as a tropical marine species (Hustedt 1942, 1927-66). The type slide contains only a few valves, all of which seem to belong to morphotype 1. *Biremis lucens* was consequently reported from brackish and marine localities in Africa and Europe (Cholnoky 1963, Denys 1991a, Giffen 1975, Salah 1953, Sabbe and Vyverman 1991, Sabbe 1993). Moreover, unidentified or wrongly identified specimens that most probably belong to this species have been found in recent and fossil material from Europe (e.g. Denys and Verbruggen 1989, as *Pinnularia ambigua*; Kuylenstierna 1990, Pl. 65, Figs 802-803). The cosmopolitan nature of the *B. lucens* complex is confirmed in this study: specimens were observed in material from Europe, Africa and Australasia. However, it is not clear whether the different morphological forms are cosmopolitan: morphotype 1 is present in samples from Europe (The Netherlands, Poland and England) and possibly Asia (Borneo, the type material). Morphotype 2 was observed with certainty only in samples from Europe, although it might be present in the material from Tanzania. In addition, in the European localities we never found valves that corresponded to those from Tanzania, Papua New Guinea and Australia.

The *B. lucens* morphotypes are epipsammic, growing either as solitary cells or (most often) in short, ribbon-like colonies of up to 6 cells on the surface of sand-grains. The cells are attached to the sandgrains by their girdle in a manner reminiscent of the colonies of *Catenula adhaerens* Mereschkowsky (Sundbäck & Medlin 1986). *B. ambigua* clearly occupies a different ecological niche and is a typical epipelic species (cf. also Cox 1990).

The general occurrence of the *B. lucens* complex within the estuary is positively related to median grain size (with a preference for fine sand) and is slightly negatively related to the silt content of the sediment. The observations from the Westerschelde estuary are partly confirmed by studies in the Gulf of Gdansk, where the taxon was rare in sandy beach sediments dominated by epipsammic species such as *Achnanthes delicatula* and *Opephora mutabilis* (Grunow) Sabbe *et* Vyverman. However, it also frequently occurred (relative abundance up to 2 %) in sublittoral (water depth 5 m), fine-grained sediments, dominated by epipelic species (Witkowski, pers. comm. in Sabbe *et al.* 1995). No live material from the other localities was observed.

In the Westerschelde estuary the *Biremis lucens* complex is most abundant in the inner and middle estuary but thriving populations were also found in more saline waters (up to 33 ‰). This observation agrees with what is found elsewhere: the salinity in the Gulf of Gdansk is now 8 ‰, while the salinity at the sampling sites in Lake Nagada and in the Hopkins estuary fluctuates strongly (10-20 ‰ and 1-34 ‰ respectively). Other reports include brackish-water (Cholnoky 1963) and marine localities (Giffen 1975, Hustedt 1927-66, Salah 1953).

The relationship between the spatial and seasonal distribution of the morphotypes and the environmental parameters was investigated using multiple regression techniques. The spatial distribution of morphotype 1 could not be significantly explained by the measured environmental variables. The abundance of morphotype 2, however, appeared to be significantly related to the silt content of the sediment and the water column salinity. Multiple regression yielded the following, highly significant equation: (Abundance morphotype 2) = 4.76 + 0.11 (Silt content) - 0.15 (WC salinity), $R^2 = 0.72$ and $F = 11.5$ ($p < 0.01$) for 2 and 9 degrees of freedom. This equation explains

66 % ($R^2_{adj} = 0.66$) of the variation in the abundance data of this morphotype. The beta-values of the two environmental variables are 0.69 and -0.67 respectively, which indicates that they are almost equally important. No other combinations of environmental variables could significantly explain the spatial variation in the abundance data of morphotype 2. Fig. 54 (in Sabbe *et al.* 1995) shows the abundance of the two *Biremis lucens* morphotypes, the percentage silt content and the water column salinity at 12 different stations along the longitudinal estuarine axis (for more details on sample sets, see Sabbe *et al.* 1995). Both morphotypes occurred at most stations. The trends in silt content and the abundance of morphotype 2 are in close agreement, while the relationship between water salinity and the abundance of this morphotype seems to be mainly caused by its high abundance in station 12. Note that although no significant relationships were found between the measured environmental variables and morphotype 1, this morphotype appears to be dominant in the stations with the lowest silt content.

The seasonal variation in cell numbers of both morphotypes, water column salinity and silt content of the sediment at one brackish water station (sample set 2) is shown in Figure 55 (in Sabbe *et al.* 1995). No significant trend was found in the cell numbers of morphotype 1. Its abundance exhibited small fluctuations throughout the study period. The cell numbers of morphotype 2 did show a significantly decreasing pattern ($R^2 = 0.38$, $F = 5.52$, $p < 0.05$) during the study period and were lowest during the summer months. However, multiple regression revealed no significant relationships between this decrease and the change in salinity or sediment characteristics over time. Data from localities other than the Westerschelde estuary were insufficient to allow an assessment of the ecological range of the morphological types at those localities.

BIRELUCE

Biremis sp. 1

[Figs 14-12, 14-13, 14-14]

References:

(1)
(2)
(3) Witkowski 1994

Morphology:

L: 18.4-26.2; W: 3.7-4.4; S: (12-)13(-14)

LM - Plastids two; their structure is identical to the one of the plastids of *Biremis lucens*. Valves linear, apices broadly rounded. Valve flat, curving rather abruptly into the mantle (?). Raphe-sternum narrow, central area only slightly transapically expanded, more or less elliptical. Raphe straight, central raphe endings expanded, terminal raphe endings invisible. Striae radiate throughout the valve; their structure is indistinct but seems to be alveolate. The cingulum consists of numerous, porous copulae.

Remarks: The plastid structure (only observed, not illustrated) and LM appearance of this taxon indicate that it belongs to the genus *Biremis*. Note that the raphe-sternum is narrow, which is unusual within this genus.

Biogeography & Ecology: This taxon was recorded by Witkowski (1994) from the Gulf of Gdańsk

(Baltic Sea) and was also found in Hustedt's material from the German Wadden Sea (Memmert, L. 12342). *Biremis* sp. 1 was rare in rather sandy sediments in the mseohaline reaches of the estuary.

BIRESP01

Subordo Sellaphorineae

Fam. SELLAPHORACEAE Mann

Fallacia Stickle & Mann 1990

Genus description: Round *et al.* 1990

The genus *Fallacia* is mainly characterized by the presence of a hyaline lyre (consisting of two depressed lateral sterna) and a conopeum which covers the striae partly or completely. In addition, it can be distinguished from *Navicula* (in which its representatives were formerly placed) in plastid structure and reproductive features (cf. Round *et al.* 1990). Except for *Fallacia forcipata* and *F. tenera*, which are both epipelic, *Fallacia* taxa are typical components of the epipsammic community in fine and medium sandy sediments. Especially in the latter group many undescribed taxa appear to be present.

See Table 21 for a comparison with similar genera.

Fallacia aequorea (Hustedt 1939) Mann 1990 [Figs 13-1, 13-2, 13-3, 47-3, 47-4]

Synonyms:

Navicula aequorea Hustedt

References:

(1) Hustedt 1939
(2) Simonsen 1987
(3) Hustedt 1939, Hustedt 1962, Hendey 1964

Morphology:

L: 6.9-14.4; W: 4.3-5.5; S: 25-29(-32?)

LM - Valves elliptic to linear elliptic, apices rounded. Axial area narrow, central area of variable size and shape (from circular to more or less square), usually with irregular margins, often extending into narrow, apparently rudimentary lateral sternums (Figs 13-1, 13-2). Raphe straight, central raphe endings straight, widely spaced, with a distinct linear central nodule. Apical raphe endings distant from the valve apices. Striae (often indistinctly) punctate, parallel to radiate.

SEM - Valve face flat, gently curving into a shallow margin. The striae consist of round areolae, occluded by a velum (of the hymenate type?). Conopeum rather narrow (Fig. 47-4), only extending as far as the first longitudinal row of areolae next to the raphe. The conopeum covers a slightly depressed, H-shaped lyra. Unlike in many other *Fallacia* species (cf. *F. tenera*, *F. cryptolyra*, ...) no areolae are present within the area enclosed by the lateral sterna. Internal and external raphe endings straight, internal polar raphe endings end in a small helictoglossa. External terminal fissures absent.

Remarks: The stria density in our specimens appears to be slightly higher than the one reported by Hustedt (1939; 22-25 str./10 µm), although the lectotype and other specimens illustrated in Simonsen (1987) all have about 25-26 str./10 µm. Moreover, some *Fallacia aequorea* specimens reported as *Navicula misella* Hustedt from the North American Atlantic coast (Hustedt 1955) also have a higher stria density (28 str./10 µm)(cf. Simonsen 1987).

Biogeography & Ecology: This species has been reported from the North Sea (Hendey 1964, Sabbe 1993, De Jonge 1985, Hustedt 1939, Salah 1953) and from the North American Atlantic (as *Navicula misella* p.p., cf. Simonsen 1987, Cooper 1995a) and Pacific coasts (Rao & Lewin 1976). The specimens from the Mediterranean (Cholnoky 1961) belong to another taxon. *Fallacia aequorea* seems to be absent from the Baltic area. It is common in fine sandy sediments throughout the Westerschelde estuary, especially in the polyhaline reaches.

FALLAEQU

Fallacia amphipleuroides (Hustedt 1955) Mann 1990 [Fig. 13-4]

Synonyms:

Navicula amphipleuroides Hustedt
(?) *Fallacia fenestrella* (Hustedt) Mann
(?) *Navicula fenestrella* Hustedt
Navicula escorialis Simonsen

References:

(1) Hustedt 1955
(2) Simonsen 1987 (lectotype)
(3) Håkansson & Stabell 1977, Hustedt 1955, 1962, Navarro 1982

Morphology:

L: 10; W: 5; S: 17-19 (n=1)

LM - Valves elliptical, apices rounded. Axial and central area very broad. Striae marginal, short. Raphe branches slightly curved. The central raphe endings are far apart but connected by a rib-like central nodule.

Remarks: Only one valve of this species was found. It has a somewhat less dense striation than the type specimens (20-24 str./10 µm). VanLandingham (1975) considers both *Fallacia fenestrella* (syn. *Navicula fenestrella*) and *Navicula escorialis* (two taxa which Hustedt (1962) himself regarded as synonyms of each other) as synonyms of *F. amphipleuroides*. Håkansson & Stabell (1977) consider *F. fenestrella* as a distinct species because it has a straight raphe and an absent 'median rib' (= rib between the central raphe endings). The illustrations of the lecto- and isolectotype material of *F. amphipleuroides* and *F. fenestrella* (cf. Simonsen 1987) demonstrate that it is not easy to distinguish between these taxa: the two specimens which Hustedt himself marked and named as two separate species (Simonsen 1987, Plate 619, Figs 19 and 20) might be conspecific.

The relationship between *Navicula wuestii* Simonsen (which probably also belongs to the genus *Fallacia*) and *Fallacia amphipleuroides* is less clear. Hustedt (1962) pointed out the ressemblance of *N. wuestii* to *F. fenestrella* but also to *F. teneroides* (Hustedt) Mann, which is distinctly different from *F. fenestrella*.

Biogeography & Ecology: This species has been found in North America (Hustedt 1955, Navarro 1982), Europe (Hustedt 1962, Håkansson & Stabell 1977, Kuylenstierna 1989-90) and South Africa (Cholnoky 1968, Giffen 1975). Cholnoky (1961) reported this species from the Mediterranean Sea but his specimens probably concern *Fallacia florinae* (Möller) Witkowski.

Fallacia cryptolyra (Brockmann 1950) Stickle & Mann 1990 [Figs 13-5, 13-6, 13-7, 48-2, 48-7, 48-8]

Synonyms:

Navicula cryptolyra Brockmann 1950
Navicula praestoeensis Møller 1950
Fallacia cassubiae Witkowski 1991b
(?) *Lyrella phyllohordae* Guslakov 1992

References:

(1) Brockmann 1950
(2) Brockmann 1950, Krammer & Lange-Bertalot 1986
(3) Hustedt 1931-1959, Hargraves & Levandowsky 1971, Håkansson & Stabell 1977, Krammer & Lange-Bertalot 1986, Witkowski 1991b, Witkowski 1994, Snoeijs & Potapova 1995

Morphology:

L: 6.9-12.1; W: 3.7-5; S: 26-40 (and more?)

LM - Valves elliptical with broadly rounded apices. Axial area very narrow, central area more or less expanded into a roundish area with iregular margins. The raphe branches are straight to slightly curved and distinct; the central raphe endings are expanded, the terminal ones are distinct, lying at some distance from the valve margin. The striae are parallel in the centre to radiate towards the apices; they are interrupted by a lyre-shaped hyaline area (but note that at least in some specimens areolae appear to be present in the lateral areas). The lyre can be more or less distinct: sometimes a distinct H-shaped lyre is present (with strongly curved lateral areas), while in other specimens the lyre is indistinct to almost invisible.

SEM - Valve face flat, curving gently into a shallow mantle. Raphe-sternum and conopeum indistinguishable in external view. The raphe is slightly curved. The central raphe endings are expanded, the terminal fissures are bent in the same direction. Internally, the terminal raphe endings end in distinct helictoglossae. The lyre-shaped canal formed by the lateral depressions (Fig. 48-8) and the conopeum open to the outside via 4 openings, two on each side of the terminal fissures. In some specimens, additional openings were present besides the central raphe openings, but these could have been created by erosion of the conopeum. The conopeum is finely porous. The striae consist of small areolae. Two different morphological types appear to be present: one form has small poroids, occluded by (hymenate?) vela, the other has larger areolae (also occluded by hymenate vela), especially alongside the conopeum margin. However, it is not clear what the relationship is between these forms or whether the appearance of the areolae in SEM might be misleading due to the presence of marginal finger-like extensions of the conopeum (cf. Round *et al.* 1990). In an internal view, the areolae all appear to have the same size; the striae are interrupted by the lateral sterna. In some specimens, the striae are shortened in the centre of the valve (Fig. 48-2; cf. also Hargraves & Levandowsky 1971, Snoeijs & Potapova 1995). Note that the lyre is asymmetrical: on one side one longitudinal row of areolae is present, on the other two. The cingulum is composed of one or two non-porous, shallow copulae.

Remarks:

	Fallacia cryptolyra	*Fallacia cassubiae*	*Fallacia clepsidroides*
description	Brockmann 1950, Krammer & Lange-Bertalot 1986	Witkowski 1991b, Witkowski 1994	Witkowski 1994, Snoeijs & Potapova 1995
dimensions	L: 8-11; W: 5 (Br. 1950) L: 8-15; W: 5-6 (Kr. & LB. 1986)	L: 8-11; W: 4-5.5	L: 8-12; W: 3.5-5.5
stria density (str./10 µm)	27-29 (Br. 1950) 24-25 (Kr. & LB. 1986)(on figs: 26-27)	25-27	21-24
lyre	'sehr schmall', interrupted in centre, strongly curved, rather indistinct in LM (Br. 1950)	indistinct in LM, asymmetrical	very distinct in LM, not asymmetrical
central area	'nicht erkennbar' (Br. 1950), 'undeutlich begrentzt' (Kr. & LB. 1986)	somewhat expanded	square
cingulum	?	one copula	one copula
conopeum	?	with finger-like extensions	Appears to have entire margins and to be rsetricted to the lateral areas (no finger-like extensions)
other			peculiar finger-like extensions *inside* the lyre

During the counts, we have interpreted *F. cryptolyra* in its broadest sense, i.e. we have included all small '*F. cryptolyra*'-like forms in this taxon. However, given the high morphological variability of our specimens, both in LM and SEM, it is not unlikely that different taxa are involved. Published accounts also witness the high heterogeneity in this complex (Sundbäck & Snoeijs 1991, Cooper 1995a). Various '*F. cryptolyra*'-like species have been described (e.g. *Navicula suspirii* Cholnoky 1961, *F. cassubiae*, *F. clepsidroides*) but it is clear that further study is required to assess the relationship between these taxa. Especially the identity of *F. cryptolyra* is little known: the type material of this species ought to be studied in detail (SEM!).

F. cassubiae appears to be conspecific with *F. cryptolyra*. The main distinguishing features given by Witkowski (1991b, 1994) are size, stria density and appearance of the lyre in LM. However, there is overlap, both in size and stria density (cf. Table above); moreover, the appearance of the lyre in *F. cryptolyra* is not 'distinct' (Witkowski 1991b, 1994), but indistinct ('Lyrastreifen treten (...) wenig hervor', Brockmann 1950). The list of differences in SEM features is irrelevant in the light of the absence of SEM studies on the type material of *F. cryptolyra*.

Fallacia clepsidroides does appear to be a distinct species, although some of its features need further study, e.g. the small finger-like extensions inbetween the areolae within the lyre (cf.

Witkowski 1994, Pl. 26, Fig. 11) and the exact structure of the conopeum (does it really have an entire margin or is the conopeum eroded?).

Biogeography & Ecology: *F. cryptolyra* s.l. is particularly common in the epipsammon of medium sandy sediments in the eu- and polyhaline reaches of the estuary. It has been reported from predominantly brackish sediments in Europe (e.g. Brockmann 1950, Snoeijs & Potapova 1995), North America (Hargraves & Levandowsky 1971, Cooper 1995a), Africa (Archibald 1966) and probably elsewhere.

FALLCRYP

Fallacia florinae (Møller 1950) Witkowski 1993 [Fig. 13-8]

Synonyms:

Navicula florinae Møller 1950
Navicula sibayiensis Archibald 1966

References:

(1) Møller 1950
(2) Witkowski 1993
(3) Møller 1950, Hustedt 1964, Hendey 1964, Archibald 1966, Witkowski 1993, 1994

Morphology:

L: 10-11.9; W: 6.2-6.6; S: 28-29 (centre) to 33 (near apices)

LM - Valves elliptical, apices rounded. Axial and central area broadly lanceolate. A lyra-shaped area surrounding the raphe branches can be ditinguished. The raphe branches are slightly curved; the central nodule is thickened. Central raphe endings straight. The striae, which are more widely placed at the centre, are more or less radiate throughout the valve.

Remarks: Only a few valves of this species, which has been described in detail by Witkowski (1993), were found. They slightly differ from his description in having a somewhat denser striation. *Fallacia florinae* is almost certainly conspecific with *Navicula sibayiensis*, which was described from coastal (freshwater (?) and brackish-water) lakes in Natal (South Africa)(Archibald 1966).

Biogeography & Ecology: This species has been reported from the Baltic and the North Sea coasts (cf. references above and Denys 1991a), Africa (Archibald 1966, as *Navicula sibayiensis*) and Australia (John 1983) and appears to be cosmopolitan. In the Westerschelde estuary it was very rare.

FALLFLOR

Fallacia forcipata (Greville 1859) Stickle & Mann 1990 [Figs 13-28, 13-29]

Synonyms:

Navicula forcipata Greville 1859

References:

(1) Greville 1859
(2)
(3) Krammer & Lange-Bertalot 1986, Hendey 1964, Kuylenstierna 1989-90, Peragallo & Peragallo 1897-1908

Morphology:

L: 17.5-35; W: 8.7-14.4; S: 17.5-23

LM - Valves elliptical to linear-lanceolate, apices rounded. Central area rectangular, transapically expanded (though not beyond the lateral sterna). Lateral sterna constricted in the centre of the valve. Raphe sternum well developed, raphe straight. Central raphe endings straight, pore-like, incrassate. Terminal fissures hooked (in the same direction). Striae punctate, parallel to convergent in the centre (cf. Fig. 13-28), radiate towards the apices. Central striae sometimes shortened.

Remarks: Several varieties of *Fallacia forcipata* have been described (cf. Peragallo & Peragallo 1897-1908, VanLandingham 1975); they mainly differ in size and stria density. Some of these have already been re-established to species rank (e.g. *Fallacia nummularia* (Greville) Mann), others probably should have their rank altered from variety to species (e.g. *Navicula forcipata* var. *versicolor*, cf. Peragallo & Peragallo 1897-1908). Our specimens have a high stria density and should therefore, according to Peragallo & Peragallo 1897-1908, be placed in *Navicula forcipata* var. *densestriata* A. S. Schmidt. They are, however, much smaller than stated in most known descriptions of this variety. However, as to our knowledge, only little is known about the variability within this species (cf. Kuylenstierna 1989-90) we decided not to distinguish between *Navicula forcipata* var. *densestriata* and the nominate variety.

Biogeography & Ecology: Kuylenstierna (1989-90) reported similar small specimens from the Nordre Älv estuary on the Swedish West coast. *Fallacia forcipata* is a rather rare epipelic species in fine sandy sediments in the middle and lower reaches of the Westerschelde estuary (cf. also Colijn & Dijkema 1981). *F. forcipata* s.l. is a cosmopolitan taxon.

FALLFORC

Fallacia pygmea (Kützing 1849) Stickle & Mann 1990 [Fig. 13-27]

Synonyms:

Navicula pygmea Kützing 1849

References:

(1) Kützing 1849
(2) Schoeman and Archibald 1980

(3) Simonsen 1975

Morphology:

L: 23.7; W: 8.7; S: 25 (n=1)

LM - Valve elliptic, apices cuneate-obtuse. Axial area narrow, central area square, laterally expanded (beyond the lateral sterna). Lyra narrowly lanceolate. Raphe branches slightly curved, central raphe endings straight, expanded. Striae more or less radiate throughout the valve, distinctly punctate (about 30 puncta in 10 µm).

Remarks: A thorough description of this species was given by Schoeman and Archibald (1980). This species can be distinguished from other similar representatives of the genus *Fallacia* in having distinctly punctate striae and a central area which is transapically expanded beyond the lateral sterna.

Biogeography & Ecology: *Fallacia pygmea* is commonly reported from estuarine and marine sediments worldwide (e.g. Schoeman & Archibald 1980, John 1983, Gätje 1992, Kuylenstierna 1989-90, Garcia-Baptista 1993). It was very rare in the sediment samples from the Westerschelde estuary but might be more abundant in the oligohaline and freshwater tidal reaches (cf. Gätje 1992).

Fallacia tenera (Hustedt 1937) Mann 1990

[Figs 13-9, 13-10, (?) 13-11, (?) 13-12, 47-7]

Synonyms:

Navicula dissipata Hustedt in A. Schmidt 1936
Navicula tenera Hustedt 1937
Further synonymy, see Schoeman & Archibald 1979

References:

(1) Hustedt 1937-38
(2) Schoeman & Archibald 1976-80, Simonsen 1987
(3) Schoeman & Archibald 1976-80, Krammer & Lange-Bertalot 1986

Morphology:

L: 8.1-14.4; W: 4-6.6; S: 17.5-22.5 (and more?)

LM & SEM - A detailed description of the frustule morphology of this species is given by Schoeman & Archibald (1976-80). Our specimens fully correspond to their description. Note that the finger-like marginal extensions of the conopeum appear to be 'held' in the areolae by two (or more) small spine-like structures protruding from the transapical walls of the areolae.
Single plastid H-shaped, with two marginal, girdle-appressed lobes and a rather wide isthmus, lying under one valve. At least one pyrenoid is visible in the isthmus. Note that in one specimen, the isthmus has two small lobes extending apically.

Remarks: Some small specimens (Figs 13-11, 13-12) which probably do not belong to *F. tenera* have been lumped with this species during the counts. These forms were mainly present in sandy sediments in the mouth of the estuary.

Biogeography & Ecology: *Fallacia tenera* is a widespread and common epipelic species and has been reported from Europe (e.g. Snoeijs & Potapova 1995), Africa (Schoeman & Archibald 1976-80), Australasia (Hustedt 1937-38, John 1983) and America (Cooper 1995a). In the Westerschelde estuary, it is common in different sediment types, mainly in the meso- and polyhaline reaches.

FALLTENE

Fallacia sp. 1

[Figs 13-15, 13-16, 13-17, 47-6]

Morphology:

L: 9.7-19.4; W: 6.2-8.1; S: 22.5-27

LM - Valves elliptic (never lanceolate), apices rounded. Axial area narrow, sometimes more or less transapically expanded in the largest specimens (Fig. 13-15). Central area square to rectangular, though never extending further laterally than the branches of the hyaline lyre. The shape of the latter is lanceolate; in larger specimens the lyra is constricted near the central area. Raphe straight, central raphe endings straight, expanded, more or less widely spaced (especially in the larger specimens). Striae more or less radiate throughout the valve; their structure is indistinct.

SEM - Valve face flat. A conopeum (which is broken near the lateral sterna in Fig. 47-6) seems to cover the whole valve surface. Raphe straight, central raphe endings expanded, terminal fissures hooked in the same direction. The H-shaped lyra is lanceolate, somewhat depressed. The structure of the striae is unclear. The cingulum consists of two (?) open, ligulate copulae.

Remarks: This diatom was originally assigned to *Fallacia pygmea*. Our identification was mainly based on the small specimens of *Fallacia pygmea* illustrated in Krammer & Lange-Bertalot (1986, Pl. 65, Figs. 4-6), which are typical of freshwater environments. However, on the basis of the above-mentioned descriptions we have to conclude that, despite some superficial similarities in shape, size and striation density, *Fallacia* sp. 1 does not belong to *F. pygmea*. It mainly differs from this species in the structure of the striae, which are not distinctly punctate, and the shape of the central area, which is not transapically dilated. Note that as in *F. pygmea*, the conopeum covers the whole valve surface.

Biogeography & Ecology: *Fallacia* sp. 1 was rare in fine and medium sandy sediments throughout the estuary.

FALLSP01

Fallacia sp. 2

[Figs 13-22, 13-23, 13-24, 13-25, 48-4, 48-5, 48-6]

Morphology:

L: 6.2-10.1(-12.9?); W: 3.7-4.6(-5?); S: (26.5-)28-32

LM - Valves elliptical, apices rounded. Axial and central area very broad (taking up more than three quarters of the valve width). Raphe straight, with distinct central and terminal nodules. A ring of short marginal striae is present. Note however that in some specimens, faint striae are visible up to the raphe-sternum.

SEM - Valve face flat, mantle shallow. A distinct, finely porous conopeum with parallel margins and with short extensions (opposite the marginal striae) surrounds the raphe branches. External central raphe endings straight, not expanded; the terminal fissures are both deflected to the same side. Internally, both the apical and central fissures are straight and end in a small helictoglossa. Each stria consists of one areola near the lyre, and one (rarely two) marginal, transapically elongated areola, occluded by a velum. This is only visible in internal views, as externally the extensions of the conopeum cover the inner row of areolae. In some specimens, each pair of areolae is internally connected by a groove. Cingulum structure unclear; at least one well-developed copula is present (Figs 48-5, 48-6).

Remarks: This taxon is very reminiscent of *Fallacia amphipleuroides* but has a higher stria (always more than 26 str./10 µm) and longitudinal rows of areolae on both sides of the raphe (in addition to the marginal striae). The latter also appears to be present *in F. fenestrella* (Hustedt) Mann (Hustedt 1962) but again the stria density is significantly higher in *F.* sp. 2.

The relationship between *Fallacia* sp. 2 and *F.* sp 4 needs further study.

Biogeography & Ecology: *Fallacia* sp. 2 is a common epipsammic species in medium sandy sediments in the lower reaches and the mouth of the Westerschelde estuary. *Fallacia* sp. 2 was also found in Hustedt's material from the German Wadden Sea (Leybucht 10301, Leysand).

FALLSP02

Fallacia sp. 3

[Figs 13-13, 13-14, 48-1, 48-3]

Morphology:

L: 7.5-9; W: 3.7-4.4; S: 24-28 (-30 ?)

LM - Valves elliptical to linear, with a more or less 'angular' outline. Valve margins in the centre almost parallel. Apices blunted. Axial area narrow; central area small. Raphe branches slightly curved; central raphe endings straight, slightly expanded. Polar raphe endings indistinct. Striae parallel to slightly radiate at the poles; their structure is indistinct. The central striae appear to be somewhat shortened in the centre. Two (indistinct) longitudinal lines cross the striae on each side of the raphe, one near the valve margin and one more or less parallel to the raphe branches.

SEM - Valve face flat, mantle more or less shallow. The valve face margin and the mantle are separated by a ridge that is especially pronounced near the valve apices. On the valve mantle, a row of transapically elongated areolae is present; in the centre these areolae are round. Note that areolae are also present on the mantle of thevalve apices. The raphe sternum is elevated above the valve face. The raphe branches are slightly curved, the central raphe endings straight and the terminal fissures hooked in the same direction. A distinct, finely porous conopeum stretches from the raphe sternum to about 1/2 of the valve (cf. longitudinal line in LM)(note, however, that the width of the conopeum in *Fallacia* can be quite variable as was shown by Hallegraeff & Burford 1996). This conopeum easily breaks (probably because of the acid treatment) along the edge of the raphe sternum (Fig. 48-3). Its margins are more or less entire and usually slightly constricted in the centre of the valve. The striae extend from the marginal ridge to the conopeum and are partially covered by the latter. They consist of a few (up to four?) round areolae, which are occluded by a velum. Spine-like structures are present on the virgae just inside the conopeum margin. The cingulum consists of at least one non-porous copula.

Remarks: This taxon superficially resembles *Fallacia carpenteriae* Hallegraeff & Burford (Hallegraeff & Burford 1996) in having a distinct marginal ridge but differs from this species in life-form (epipsammic vs. nanoplanktonic), size (L: 7.5-9 vs. 2.9-3; W: 3.7-4.4 vs. 1.7), stria density (24-28 vs. 50 striae/ 10 µm) and other aspects of its structure.

Biogeography & Ecology: *Fallacia* sp. 3 is a common epipsammic diatom in medium sandy sediments in the lower reaches and the mouth of the estuary. It was also found in sandy beach sediments along the Belgian coast (Blondeel 1996).

FALLSP03

Fallacia sp. 4

[Figs 13-18, 13-19, 13-20, 13-21]

Morphology:

L: 5.6-11; W: 3.7-5; S: 26-30

LM - Valves elliptical, apices broadly rounded. Axial area narrow, central area indistinct. Raphe branches slightly curved, central raphe endings expanded, pore-like and close together (but separated by a distinct central nodule). Terminal raphe endings more or less straight, not reaching the apical valve margin. Striae more or less radiate throughout the valve, especially near the apices. The striae are crossed by a line which runs more or less parallel with the valve margin. Sometimes the space between this line and the raphe is covered by a conopeum-like structure, which makes it impossible to distinguish the striae in this area (e.g. Fig. 13-19).

Remarks: Although this taxon is quite common, it was not observed with certainty in SEM. It is therefore suspected that it may have been confused with another taxon in SEM, e.g. *Fallacia* sp. 2, which has similar dimensions. In these small *Fallacia* taxa, it is often hard to associate LM features with structures visible in SEM.

Biogeography & Ecology: *Fallacia* sp. 4 was rare in medium sandy beach sediments in the lower reaches and the mouth of the estuary. It has also been found in Salah's material from Blakeney Point (England) and Hustedt's material from the German Wadden Sea (Leybucht; Leysand, BRM slide N12/36), which indicates that has probably been overlooked or misidentified in other studies.

FALLSP04

Sellaphora Mereschkowsky 1902

Genus description: Mann 1989a, Round *et al.* 1990

Sellaphora was re-established and separated from *Navicula* s.l. on the basis of the structure of the plastids, the areolae and the raphe (cf. Round *et al.* 1990).
See Table 21 for a comparison with similar genera.

Sellaphora pupula (Kützing 1844) Mereschkowsky 1902

Synonyms:
Navicula pupula Kützing 1844

References:

(1) Kützing 1844
(2)
(3) Krammer & Lange-Bertalot 1986, Mann 1989a, Cox 1996

Morphology:
L: 20.5; W: 6.6; S: 21

LM & SEM: see Krammer & Lange-Bertalot 1986, Mann (1989a, b)

Remarks: *S. pupula* comprises a large number of morphological distinct types ('phenodemes') which appear to be reproductively isolated (Mann 1989b).

Biogeography & Ecology: *S. pupula* is a common and widespread epipelic species in electrolyte-rich freshwaters (Cox 1996). Only one (broken) valve was found in our material; there is no doubt that this valve has been washed in from the river.

SELLPUPU

Fam. PINNULARIACEAE Mann

Caloneis Cleve 1894

Genus description: Cleve 1894, Krammer & Lange-Bertalot 1986, Round *et al.* 1990

According to Round *et al.* (1990), there is no satisfactory basis for separating the genera *Caloneis* and *Pinnularia*. Notwithstanding, there is much variation within the *Pinnularia/Caloneis* complex (cf. Cox 1988), but new generic splits will not be along the traditional generic boundaries (Round *et al.* 1990, Stidolph 1995).

Caloneis amphisbaena (Bory 1824) Cleve 1894 f. *subsalina* (Donkin 1871) Van der Werff & Huls 1960

[Fig. 15-3]

Synonyms:

Navicula subsalina Donkin 1871
Caloneis subsalina (Donkin 1871) Hendey 1951

References:

(1) Donkin 1871
(2)
(3) Hendey 1964, Edgar 1980, Krammer & Lange-Bertalot 1986, Snoeijs 1993, Snoeijs & Potapova 1995

Morphology:

L: 37.5-44.1; W: 16.9-19: S: 16-18 (n=2)

LM - One plastid consisting of two large, girdle-appressed lobes, which are only connected beneath one valve via a narrow isthmus (Fig. 15-3). Two large droplets, one associated with each plastid lobe, are present. Valves elliptical with subrostrate to rostrate apices. Raphe-sternum rhombic; raphe straight, central raphe endings pore-like and slightly deflected in the same direction. Terminal raphe endings strongly hooked in the same direction (opposite to the one of the central raphe endings). Striae radiate to convergent at the apices; no areolae are visible. The striae are crossed by two longitudinal lines.

Remarks: The plastid structure of our specimens is slightly different from the one illustrated in Cox (1988b, 1996): while our specimens have a narrow central isthmus connecting the two girdle-appressed lobes, such a structure is not present in Cox's specimens. This could indicate that the presence of an isthmus is a variable feature within this species or that we are dealing with two different taxa. Further studies on a large number of specimens are needed to assess this phenomenon.

Biogeography & Ecology: *Caloneis amphisbaena* f. *subsalina* is a common and widespread species in electrolyte-rich and brackish waters (Cox 1996). It is probably cosmopolitan (Krammer & Lange-Bertalot 1986): it was rare in silty sediments in the Westerschelde estuary.

CALOAMSU

Caloneis africana (Giffen 1966) Stidolph 1995

[Fig. 15-1]

Synonyms:

Caloneis brevis (Gregory 1857) Cleve 1984 var. *distoma* Grunow 1880 f. *africana* Giffen 1966

References:

(1) Giffen 1966
(2)
(3) Stidolph 1995

Morphology:

L: 42.9-53.8; W: 16.5-19.4; S: 16

LM - Valves elliptical with subrostrate apices. Axial area narrow, asymmetrical; central area transapically expanded, round and asymmetrical. Raphe straight, central raphe endings pore-like, terminal raphe endings strongly hooked in the same direction. Striae radiate to parallel at the apices; no areolae are visible. A longitudinal line crosses the striae near the valve margin.

Remarks: We have assigned the illustrated specimen to *Caloneis africana* on the basis of its large sickle-shaped terminal raphe endings, which is the main characteristic to distinguish between this species and the similar species *Caloneis crassa* (Gregory) Ross (Stidolph 1995). However, given the fact that *Caloneis crassa* has also been reported from the Westerschelde estuary (Stidolph 1995), it is not unlikely that these two species have been confused during the cell counts.

Biogeography & Ecology: *Caloneis africana* is a common, cosmopolitan species from marine and estuarine habitats, while *C. crassa* appears to be much less common and has so far only been reported from the Northern hemisphere (Stidolph 1995). *C. africana/C. crassa* was rare in sandy sediments throughout the Westerschelde estuary.

CALOCRAS

Pinnularia Ehrenberg 1843

Genus description: Krammer & Lange-Bertalot 1986, Round *et al.* 1990

Pinnularia cruciformis (Donkin 1861) Cleve 1895

[Fig. 14-15]

Synonyms:

Navicula cruciformis Donkin 1861

References:

(1) Donkin 1861
(2)
(3) Hendey 1964, Hartley *et al.* 1996

Morphology:

L: 41.2; W: 12.5; S: 11 (n=1)

LM - Valve broadly linear, with broadly rounded apices. Axial area narrow, central area transapically expanded, rectangular. Raphe branches curved, central raphe endings expanded, rather close together; terminal raphe endings not visible. Striae radiate in the centre to convergent towards the apices. A longitudinal line runs alongside the raphe-sternum on at least one side of the valve.

Biogeography & Ecology: *Pinnularia cruciformis* is a marine epipelic species, probably mainly from sandy sediments (Kuylenstierna 1989-90). It has been reported from Europe (Hendey 1964, Kuylenstierna 1989-90). Only a few specimens were found in our material.

PINNCRUC

Pinnularia krookiformis Krammer 1992 [Fig. 12-10]

Synonyms:

Pinnularia krockii sensu Krammer & Lange-Bertalot 1986

References:

(1) Krammer 1992
(2) Krammer 1992
(3) Krammer & Lange-Bertalot 1986, Krammer 1992

Morphology:

L: 19.7; W: 4.4; S: 21.5

LM - Valves broadly elliptic with capitate apices. Axial area narrow, central area transapically expanded, rhombic. Central raphe endings expanded, slightly deflected in the same direction. Terminal fissures hooked in the same direction. Striae radiate in the centre to convergent near the apices.

Remarks: This species closely resembles *Pinnularia krookii* (*krockii*). However, the latter species has distinctly triundulate valve margins and is not wider in the centre than at the apices. In addition, *P. krookii* is a species from electrolyte-poor waters in nordic-alpine environments, while *P. krookiformis* is a brackish-water species (cf. Krammer & Lange-Bertalot 1986, Krammer 1992).

Biogeography & Ecology: *Pinnularia krookiformis* occurs in both inland and coastal brackish waters in Europe [Kuylenstierna 1989-90 (as *P. krockii*), Krammer 1992]. It was very rare in the Westerschelde stations.

PINNKROO

Pinnularia stauntonii (Grunow in Cleve & Möller 1878) Cleve 1895 [Figs 14-16, 15-2, 49-3]

Synonyms:

Allioneis stauntonii Grunow in Cleve & Möller 1878

References:

(1) Donkin 1861
(2)
(3) Peragallo & Peragallo 1897-1908, Hartley *et al.* 1996

Morphology:

L: 36.5-56.2; W(P): 18.7; S: 8-11 (n=2)

LM - Only frustules in girdle view were observed. Frustules rectangular, slightly constricted in the centre. The raphe appears to be strongly curved, with the central raphe endings distinctly deflected to one side (Fig. 14-16). The central raphe endings are pore-like. The shape of the central area appears to be more or less circular, reaching the valve margin on one side of the valve but not on the other. The striae are strongly radiate in the centre to strongly convergent near the apices. The cingulum consists of one (or two?) unperforated copulae.

SEM - Valve face strongly convex, merging imperceptibly with a deep mantle. Raphe-sternum narrow, shape of central area uncertain. Note the presence of a distinct apically elongated depression on one side of the central nodule. Raphe strongly curved, with hooked terminal fissures and central raphe endings slightly deflected in the same direction and expanded. Striae multiseriate, composed of usually three rows of poroids.

Biogeography & Ecology: *P. stauntonii* has been reported from the North Sea coasts and the Atlantic coasts of Scotland (Peragallo & Peragallo 1897-1908, Cleve 1895). In the Westerschelde estuary, it was occasionaly found in sandy sediments in the lower estuary and near the mouth.

PINNCSTA

Subordo Diploneidineae

Fam. DIPLONEIDACEAE Mann

Diploneis Ehrenberg ex Cleve 1894

Genus description: Round *et al.* 1990

This is an easily recognizable genus with a typical valve structure (mainly characterized by the presence of longitudinal canals). However, it appears to be in need of thorough revision, witness the presence of two or more constant morphotypes in most British *Diploneis* species, while the distinction between at least some common marine species and varieties appears to be less evident (Droop 1994, 1996). We have as yet not been able to perform a critical morphological analysis of the *Diploneis* taxa from the Westerschelde to investigate this phenomenon and have largely followed Krammer & Lange-Bertalot (1986) for their identification and nomenclature. Note that the width values in the descriptions refer to the largest cell width.

Diploneis aestuarii Hustedt 1939 [Fig. 15-9]

Synonyms:

(?) *Diploneis vacillans* var.? *minuta* (Grunow 1880) Cleve 1894

References:

(1) Hustedt 1939
(2) Simonsen 1987
(3) Simonsen 1987

Morphology:

L: 12.5-17.5(-24.5); W: 5-6.5(-8.1); S: (14-)16-18.5

LM - Valves elliptical to linear, usually slightly constricted in the centre, with broadly rounded to cuneate-obtuse apices. Axial area narrow, linear, central area not transapically expanded. Raphe straight, central raphe endings slightly expanded. Longitudinal canals narrow, parallel. Striae radiate throughout the valve; their structure is indistinct in LM.

Remarks: *Diploneis aestuarii* might be conspecific with *Diploneis vacillans* var. *minuta* (Grunow) Cleve (Van Heurck 1880, Pl. 9, Fig. 9, Cleve 1894), which has the same size, shape and stria density. Examination of the type material (*D. vacillans* var. *minuta* was described from a marine site in Belgium) is needed to assess their relationship.

Biogeography & Ecology: *Diploneis aestuarii* is one of the most abundant *Diploneis* species in the Westerschelde estuary. It has been reported from estuarine and marine mudflats in Europe (Hustedt 1939, Sabbe 1993) and North America (Cooper 1995a). *D. aestuarii* was rare to common in silty sediments, especially in the polyhaline reaches of the estuary.

DIPLAEST

Diploneis didyma (Ehrenberg 1841) Cleve 1894 [Fig. 49-1]

Synonyms:

Navicula didyma Ehrenberg 1841

References:

(1) Ehrenberg 1841
(2)
(3) Krammer & Lange-Bertalot 1986, Snoeijs 1993

Morphology:

L: 25-51.2; W: 13.1-18.7; S: 8.5-11

LM - Valves elliptical with broadly rounded apices, more or less constricted centrally. Axial area linear, narrow, central area rectangular, not transapically elongated. Longitudinal canals become more narrow towards the apices. The striae are radiate throughout the valve and consist of 1 to 5 areolae.

SEM - Only external valve views were observed. Valve face flat, gradually sloping into a shallow mantle. The central raphe endings are straight and pore-like; the terminal fissures are hooked in the same direction. Each longitudinal canals open externally by a row small round pores; these pores are larger near the apices. The external openings of the areolae are transapically elongate. No occlusions are visible (possibly eroded).

Remarks: Droop (1994) reports the existence of 3 different morphotypes within the British populations of this species, which, by analogy with the *Diploneis smithii* s.l. complex, might constitute different species.

Biogeography & Ecology: *Diploneis didyma* is, together with *D. aestuarii*, the most common *Diploneis* species in the Westerschelde estuary; however, unlike the latter it was especially abundant in very fine to fine sandy sediments. It is mainly found in the inner and middle reaches of the estuary. *Diploneis didyma* is common and widespread in estuarine and marine sediments worldwide (e.g. John 1983, Compère 1991, Snoeijs 1993, Cooper 1995a)

DIPLDIDY

Diploneis interrupta (Kützing 1844) Cleve 1894

Synonyms:

Navicula interrupta Kützing 1844

References:

(1) Kützing 1844
(2)
(3) Krammer & Lange-Bertalot 1986, Snoeijs 1993

Morphology:

L: 47, 3; W: 18; S: 9.5

LM & SEM description: Krammer & Lange-Bertalot 1986

Remarks:

Biogeography & Ecology: Only a few frustules belonging to this presumably cosmopolitan species (Krammer & Lange-Bertalot 1986) were found.

DIPLINTE

Diploneis litoralis (Donkin 1871) Cleve 1894

[Figs 22-1, 22-2]

Synonyms:

Navicula littoralis (*litoralis*) Donkin 1871

References:

(1) Donkin 1871

(2)
(3) Snoeijs & Vilbaste 1994, Witkowski 1994

Morphology:

L: 41.4-50; W: 21.7-26.2; S: 11-12

LM - Two apically elongated, girdle-appressed plastids, with lobes extending under the valve faces. These lobes are only separated by very narrow slits (Fig. 22-2). Valves broadly elliptical with rounded apices. Axial area narrowly linear, central area rectangular, not transapically expanded. Raphe straight, terminal raphe endings deflected in the same direction. Longitudinal canals narrow, parallel. The striae are composed of double rows of alternating pores; they are radiate throughout the valve.

Remarks: As for *D. didyma*, two distinct morphotypes are present in British material; these might constitute separate species (Droop 1994).

Biogeography & Ecology: Only a few valves belonging to this predominantly marine *Diploneis* species (Denys 1991a) were found in our samples. The live specimen illustrated in Fig. 22-2 is from a medium sandy beach on the Belgian coast.

DIPLLITT

Diploneis oblongella (Naegeli 1849) Cleve-Euler 1922

Synonyms:

Diploneis ovalis var. *oblongella* (Naegeli) Cleve 1894

References:

(1) Naegeli in Kützing 1849
(2)
(3) Krammer & Lange-Bertalot 1986, Witkowski 1994

Morphology:

LM & SEM description: see Krammer & Lange-Bertalot 1986

Biogeography & Ecology: Only a few valves belonging to this freshwater species were found in the Westerschelde estuary.

DIPLOBLO

Diploneis ovalis (Hilse 1861) Cleve 1891

Synonyms:

Pinnularia ovalis Hilse in Rabenhorst 1861

References:

(1) Hilse in Rabenhorst 1861
(2)
(3) Krammer & Lange-Bertalot 1986

Morphology:

LM & SEM description: see Krammer & Lange-Bertalot 1986

Remarks: Only a few valves of this freshwater species were found in the Westerschelde estuary.

DIPLOVAL

Diploneis papula (A. S. Schmidt 1875) Cleve 1894 [Figs 15-4, 15-5, 15-6, 15-7, 15-8, 49-2]

Synonyms:

Navicula papula A. Schmidt 1875

References:

(1) A. Schmidt 1875
(2)
(3) Hustedt 1930, Salah 1953, Giffen 1970

Morphology:

L: 13.7-16.2; W: 7.7-8.7; S: 16-18 (Westerschelde)
L: 15-22.5; W: 9.4-10.1; S: 16-17 (Blakeney Point, n=2)

LM - Valves elliptical with broadly rounded apices. Axial area linear, longitudinal canals semi-lanceolate to semi-rhombic. Central area roundish to rectangular (slightly transapically expanded); the central nodule is very distinct. Raphe straight, central raphe endings straight, pore-like. Striae radiate throughout the valve. They are interrupted by a longitudinal line on both sides of the raphe.

SEM - Only one external valve view was observed. Valve face flat, gradually sloping into a shallow mantle. The external openings of the longitudinal canals are round and appear to be occluded by a velum. They lie in two rather irregular longitudinal lines which curve around the central nodule. The raphe is straight. The central raphe endings appear to be slightly deflected in the same direction; the terminal fissures are strongly hooked in the same direction. The central nodule is surrounded by a distinct, ring-like depression. The striae consist of one (near the apices) or two transapically expanded areolae; no occlusions are visible (possibly eroded). Within each stria, the areolae are separated by a short bar which lies slightly lower than the valve surface; these bars are longitudinally aligned and form the lines crossing the striae on both sides of the raphe.

Remarks: Hustedt's description of *Diploneis papula* mentions 10-14 str./10 µm, although Giffen (1970) reported specimens with 15-16 str./10 µm and Salah's specimens from Blakeney Point (England) have up to 18 striae/10 µm (Salah 1953).

Biogeography & Ecology: *Diploneis papula* has been reported from Samoa and Mexico (Cleve 1894), the Philippines (Podzorski & Håkansson 1987) and the Mediterranean (Peragallo & Peragallo 1897-1908, Hustedt 1930, this study - Cleve & Möller slide n° 155 from the Balearic Islands) and elsewhere. Although the latter author described this species as a typical species of warmer seas, it also appears to occur in colder waters, e.g. in South Africa (Giffen 1970) and in the North Sea (this study, Salah 1953, Droop 1994). It is worth noticing that all specimens recorded from the latter sites (e.g. Figs 15-5, 15-6) were characterized by a higher stria density than those reported from the warmer localities (cf. Fig. 15-8). Droop (1994) reported 6 different morphotypes of *D. papula* in British material (cf. also discussion *D. smithii*). *D. papula* was rare in sandy sediments in the Westerschelde estuary.

DIPLPAPU

Diploneis smithii (Brébisson 1856) Cleve 1894 var. *dilatata* (Peragallo 1908) Terry 1908

[Fig. 16-1]

Synonyms:

Navicula smithii Brébisson var. *dilatata* Peragallo

References:

(1) Peragallo in Tempère & Peragallo 1908
(2)
(3) Krammer & Lange-Bertalot 1986, Droop 1994, Snoeijs & Vilbaste 1994

Morphology:

L: 28.7-28.9; W: 18; S: 10-11 (n=2)

LM - Valves elliptical to broadly lanceolate, apices always broadly rounded. Axial area and longitudinal canals lanceolate, central area transapically expanded. Striae radiate throughout the valve; they consist of double rows of alternating pores.

Remarks: This variety was separated from the nominate variety on the basis of shape and size of both the valve and the central area.

Biogeography & Ecology: Only a few valves belonging to this species were observed in the Westerschelde material. *Diploneis smithii* and its varieties belong to the most common estuarine and marine *Diploneis* species worldwide (cf. Kuylenstierna 1989-90, Cooper 1995a and references therein, Droop 1994, 1995).

DIPLSMDI

Diploneis smithii var. *pumila* (Grunow 1882) Hustedt 1937

[Fig. 16-2]

Synonyms:

Navicula ovalis var. *pumila* Grunow 1882

References:

(1) Grunow 1882
(2)
(3) Krammer & Lange-Bertalot 1986

Morphology:

L: 18-21.2; W: 8.7-9; S: 15 (n=2)

LM - Valves elliptical, apices broadly rounded. Axial area and longitudinal canals landeolate, central area small, not transapically expanded. Striae radiate throughout the valve; each consists of a double row of alternating pores.

Biogeography & Ecology: This taxon was very rare in the Westerschelde material (cf. *Diploneis smithii* var. *dilatata*).

DIPLSMPU

Subordo Naviculineae

Fam. NAVICULACEAE Kützing

Cymatoneis Cleve 1894

Genus description: Round *et al.* 1990

Cymatoneis sp. 1

References:

(1)
(2)
(3) Round *et al.* 1990

Morphology:

L: 13; W: 5.5; S: 19 (n=1)

LM - Valves elliptical with subrostrate apices. Two distinct longitudinal folds are present in the valve face. The axial area is narrow, the raphe is straight with slightly expanded central raphe endings and distinct, elongate and expanded terminal raphe endings. The striae are radiate to convergent at the apices.

Remarks: This taxon could not be assigned to any commonly reported *Cymatoneis* species. However, no extensive literature search could yet be carried out.

Biogeography & Ecology: This species was only rarely found in the sampling stations but appears to be more common on certain (sandy) shoals in the Westerschelde which were not studied in the study (Sabbe, unpublished data). Most representatives of this genus are found in the epipelon of subtropical and tropical sandy sediments. As we have never observed living specimens in the Westerschelde, it is not unlikely that it concerns fossil, resuspended material.

CYMTSPEC

Navicula Bory 1822

Genus description: Cox 1979, Round *et al.* 1990, Mann 1994a

The extremely large genus *Navicula* s.l. (sensu Hustedt 1931-1959 and Krammer & Lange-Bertalot 1986) has recently been split up into many resurrected and new genera; only the taxa that correspond to the type of the genus (*Navicula tripunctata* (Müller) Bory, cf. Cox 1979) are now considered true *Navicula* (s.s.). *Navicula* is characterized by linear areolae, two girdle-appressed plastids (with an elongate, rod-like pyrenoid each) and a characteristic type of raphe system (Mann 1994a). See Table 21 for a comparison with similar genera

Given the enormous size of the genus *Navicula* s.l., this new generic concept has considerable consequences for diatom taxonomy and its users; this problem is discussed in more detail in chapter 6.3.

Notwithstanding the (re-)introduction of numerous genera, it appears that yet more natural species groupings can be distinguished within *Navicula*. One such group is the species complex around *Navicula crucifera* Grunow, *N. apiculata* Brébisson and *N. scoliopleura* A. Schmidt. Its distinctness was already appreciated by earlier diatomists: it roughly corresponds to the group Retusae (cf. Peragallo & Peragallo 1897-1908). Representatives of this group usually appear under names as *Navicula crucifera* (Hendey 1964, Van der Werff & Huls 1957-74), *N. apiculata* (which, according to Patrick & Reimer (1966), is conspecific with *N. crucifera*)(Kuylenstierna 1989-90) and its varieties and forms [*N. apiculata* f. *minima* A. Schmidt, which VanLandingham (1975) includes in the nominate variety, and *N. apiculata* var. *minima* (Grunow) Hustedt (Hustedt 1939)], *N. scoliopleura* (Van der Werff & Huls 1957-74, Kuylenstierna 1989-90), *N. bipustulata* Mann (Witkowski 1991a) and its synonym *N. subapiculata* (Grunow) Hustedt (Hustedt 1939, 1955, Møller 1950, Giffen 1966), and some other varieties of *N. cancellata* Donkin, such as *N. cancellata* var *apiculata* (Gregory) Peragallo & Peragallo. Considerable confusion seems to exist regarding the correct identity of many representatives of this group. However, even a detailed LM study of this group would probably suffice to clarify most taxonomic and nomenclatural problems.

The following taxa belonging to this species complex were observed in the Westerschelde estuary: (?) *N. abscondita*, *N. accedens*, *N. cancellata*, *N. bipustulata*, *N.* cf. *bipustulata*, *N. starmachioides*, *N.* sp. 3, *N.* sp. 5, *N.* sp. 6, (?) *N.* sp. 13. All these species have more or less the same valve shape, characterized by a somewhat linear valve outline with subrostrate to rostrate-capitate apices and a deep mantle. The valves are slightly arcuate in girdle view. The deep mantle appears to be responsible for the variable aspect of the valves in LM: when the valves are lying at a slant or on their mantle, one gets an oblique or girdle view of the valve (see Figs 17-19, 17-6). The striae are distinct and composed of apically elongate areolae. The central raphe endings are usually close together while the apical ones are situated at some distance of the valve margin and lie in a well-developed terminal nodule. Usually no terminal fissures are present (Figs 50-2, 50-5, 50-7).

The plastid structure in this group appears to be constant, viz. two plate-like girdle-appressed plastids which are usually arranged diagonally across from one another (see *N. bipustulata*, *N. starmachioides*).

What taxonomic status this group should be given remains an open question. On one hand, they display a stable *combination* of features which appears to be absent in other *Navicula* spp. (valve shape, structure of the terminal nodule and raphe system, distinctly diagonal plastid configuration); on the other hand, they do possess most features characteristic of the type of the genus *Navicula* (cf. above). Further information on cytological and reproductive features of this species complex is needed before its taxonomic status (subgeneric?) can be assessed in relation to *Navicula*.

Navicula abscondita Hustedt 1939

(Figs 17-7, 17-8, 49-4)

References:

(1) Hustedt 1939
(2) Krammer & Lange-Bertalot (1985), Simonsen 1987 (lectotype)
(3) Hustedt 1939, Krammer & Lange-Bertalot 1985, 1986

Morphology:

L: 24.4-33; W: 5.2-6.3; S: 13.5-15

LM - Valves lanceolate, apices cuneate, slightly produced. The valve margins are usually distinctly parallel in the centre of the valve. Axial area narrow, central area small, roundish. Raphe straight, distinct, central raphe endings close together, situated in an elliptical, distinct central nodule. Terminal raphe endings expanded and deflected in the same direction. Striae more or less parallel (to slightly radiate) in the centre to convergent towards the apices. Their structure is indistinct.

SEM - Valve face flat, gently curving into a more or less deep mantle. Raphe-sternum well-developed especially in the centre, where a conopeum-like structure is present. Raphe straight, opening laterally, except in the centre and at the apices. Terminal nodules pronounced, raised; terminal fissures more or less hooked, probably deflected to the same side. Striae lineolate, the central ones are shortened and separated by distinct costae.

Remarks: Our specimens correspond to Hustedt's protologue. However, we cannot agree with Simonsen's (1987) lectotypification: only the specimens in his illustrations 16 and 17 (Pl. 378)[slide 267/3, 'Linke n° 31', which Hustedt mentions as the main locality (sehr häufig)] correspond to the type description. Although *N. abscondita* is not as 'häufig' in this slide as Hustedt indicated (Simonsen 1987), these are the only valves that correspond to the type description. The specimens in the other illustrations (Simonsen 1987, Pl. 378, 11-15), which Simonsen has proposed as the lectotype, have a much higher striation density (about 19-20 str./10 µm) and lack the small central area. A similar, to our knowledge hitherto undescribed taxon (or form), was observed in the Westerschelde and is described elsewhere as *Navicula* sp. 8. We believe it would be better to select slide 267/3 (Hamburger Sand, Leybucht, 31) as the lectotype slide for *Navicula abscondita*.

Moreover, some other specimens from Simonsen (1987), viz. Pl. 380, figs. 11-12 (from the lectotype slide of *Navicula flagellifera* Hustedt) and Pl. 381, figs. 3-4 (from the lectotype slide of *Navicula pavillardii* Hustedt) seem to represent valves which probably belong to *N. abscondita*: they differ from *N. flagellifera* in the indistinctness of the stria ultrastructure and the different aspect of the valve apex, and from *N. pavillardii* in the striation pattern (striae are not distinctly lineolate and more parallel throughout the valve) and in the presence of a small central area.

Navicula abscondita differs from *N. duerrenbergiana* (see below) in having a larger, more distinct central nodule, a small roundish central area and striae with an indistinct ultrastructure. *N. abscondita* actually strongly resembles *N. ramossissima* (Agardh) Cleve (cf. Kuylenstierna 1989-90, Pl. 59, fig. 742, from Agardh's (iso- or lecto?)type material). Further study of the type material is needed to clarify the affinities between these two taxa.

Biogeography & Ecology: This species has been reported from the European Atlantic (Hustedt 1939, Brockmann 1950, this study) and the Mediterranean coasts (cf. Simonsen 1987, pl. 380, figs. 3-4, as *N. pavillardii*). The specimen illustrated in Kuylenstierna (1989-90, Pl. 58, fig. 735, as *N.* cf. *abscondita*) seems to belong to another taxon as it has a different valve shape and lacks the typical roundish central area.

N. abscondita was rare in silty sediments in the middle and lower reaches of the Westerschelde estuary.

NAVIABSC

Navicula accedens Hustedt 1954

[Figs 17-4, 17-5, 50-1]

References:

(1)	Hustedt 1954
(2)	Simonsen 1987
(3)	Hustedt 1954

Morphology:

L: 31.3; W(P): 8.1 (in the centre of the valve); S: 13 (n=1)

LM - In the LM, only girdle views of this species were observed. Valve views are illustrated in Simonsen (1987). Frustules rectangular in girdle view, in the centre they are constricted. Axial area narrow, central area more or less rectangular. Raphe-sternum distinct, central and terminal nodules well-developed. The terminal raphe endings are situated at some distance from the valve margin (Fig. 17-4). Striae slightly radiate in the centre to convergent near the apices. They are distinctly lineolate (about 24 areolae in 10 µm). Both in the centre and near the apices, three to four shortened striae are present. Cingulum structure unknown.

SEM - Only one frustule of this apparently delicate diatom was observed (external view). The valve face is curved, with a gradual transition into the deep mantle. Raphe more or less straight, lying in a pronounced raphe-sternum. Central raphe endings very close together, not expanded; terminal raphe endings slightly bent in the same direction, slightly expanded, lying in a distinct, raised terminal nodule. The striae consist of apically elongate areolae. At the valve apices, some slit-like openings can be seen.

Remarks: *N. accedens* belongs to the species complex around *N. apiculata* (cf. above).

Biogeography & Ecology: *N. accedens* has been described from sandy sediments in Cresswell, on the east coast of England (Hustedt 1954). To our knowledge, this is the first report of this species outside the type locality. Only a few valves of this species were found in the Westerschelde material.

It is worth noticing that specimens, which probably also belong to this species, have been reported from sandy beach sediments in Brazil (Garcia-Baptista 1993b). They were incorrectly identified as *Navicula cancellata*. Whether it truly concerns *N. accedens* remains unclear, as her specimens are distinctly narrower than the ones reported by Hustedt (1954), and they have a higher stria density.

Only a few valves belonging to this species were observed in the Westerschelde estuary.

Navicula arenaria Donkin 1861 var. *rostellata* Lange-Bertalot 1985

[Figs 16-13, 16-14, 16-15, 49-5, 49-6]

Synonyms:

Navicula rostellata Kützing 1844 sensu Brockmann 1950, Cleve-Euler 1953, Hendey 1964, (?) Peragallo & Peragallo 1897-1908
(?) *Navicula normalis* Hustedt 1955

References:

(1) Krammer & Lange-Bertalot 1985
(2) Krammer & Lange-Bertalot 1985
(3) Peragallo & Peragallo 1897-1908, Hustedt 1955, Hendey 1964, Lange-Bertalot 1980b, Krammer & Lange-Bertalot 1985, Kuylenstierna 1989-90

Morphology:

L: 25-44.4; W: 6.2-11.6; S: 10-13

LM - Plastids two, girdle-appressed; two crystal-like structures are associated with the central nucleus and the plastids. Valves linear to linear-lanceolate with produced, subrostrate to rostrate apices. Axial area narrow, central area transapically expanded, of variable shape (roundish to rectangular), usually about 1/2 of the valve width. Raphe straight, central raphe endings expanded to pore-like, close together. Central nodule distinct. Terminal raphe endings deflected in the same direction. Striae radiate in the centre to convergent near the apices; their structure is indistinct in the LM.

SEM - Valve face only flat along the raphe-sternum, gently curving into the mantle. Raphe-sternum distinct, externally expanded in the centre. Internally, the raphe lies in an raised, distinct rib, and opens laterally, except in the centre and near the apices, where distinct, slightly deflected (in the same direction) helictoglossae are present. An accessory rib lies alongside the raphe-sternum. In the centre, this rib is depressed. Externally, the central raphe endings are close together and hooked (in the same direction). The terminal raphe endings are deflected in the same direction (opposite to the one of the central raphe endings), while the terminal fissures are strongly hooked (in the same direction, opposite to the one of the terminal raphe endings). The striae consist of apically elongate areolae, occluded internally by a hymen. Externally, they are slit-like and more or less longitudinally aligned.

Remarks: There is no doubt that our specimens, despite some slight differences in size and stria density, belong to this taxon. Lange-Bertalot (1980b) reported on the confusion that exsists as to the true identity of *Navicula rostellata*. *N. rostellata* from marine environments (Brockmann 1950, Hendey 1964, Ricard 1977) is usually identical to our taxon. When it is reported from freshwater environments, it usually concerns an entirely different diatom (with distinctly deflected central pores and lineolate striae), which Lange-Bertalot (1993b) refers to as *Navicula viridula* (Kützing) Ehrenberg var. *rostellata* (Kützing) Cleve. Until Kützing's type material has been studied, this seems to be a satisfactory solution and it is better to avoid using the name *Navicula rostellata*.

Peragallo & Peragallo (1897-1908) use the name *Navicula viridula* var. *rostellata* in the text and *N. rostellata* in the legend to the plates for a diatom which resembles *N. arenaria* var. *rostellata* (their stria density of 10-12 str./10 µm is more in accordance with our observations). *N. arenaria* var. *rostellata* is also reminiscent of *N. normalis* (Hustedt 1955, Simonsen 1987), which is almost identical in structure but has distinctly lineolate striae [but cf. Brockmann (1950, Pl. 1, Fig. 4), where *N. arenaria* var. *rostellata* is also clearly lineolate].

Biogeography & Ecology: *Navicula arenaria* var. *rostellata* is one of the most abundant epipelic species in silty sediments and seems to prefer higher salinities. It is a typical component of the spring diatom communities.

N. arenaria var. *rostellata* is a common and widespread species on all North Sea coasts (Krammer & Lange-Bertalot 1986). Its geographic distribution is little known (as *N. rostellata* in

Rao & Lewin 1976 and Garcia-Baptista 1993b?)

NAVIARRO

Navicula bipustulata Mann 1925 [Figs 17-14, 17-19, 17-20, 17-21, 19-5, 50-2, 50-3]

Synonyms:

Navicula cancellata var. *subapiculata* Grunow 1880
Navicula cancellata f. *minor* Schulz 1926
Navicula subapiculata Hustedt 1939
Navicula scoliopleura sensu Van der Werff & Huls 1957-74

References:

(1) Mann 1925
(2)
(3) Hustedt 1939, 1955, Møller 1950, Witkowski 1991a, 1994

Morphology:

L: 20-27.5, W: 4.3-5.6, W(P): 9.3-11.5, S: 11.5-13

LM - Two girdle-appressed plastids are present, diagonally opposite each other. Valves linear-elliptical with produced, rostrate apices. Axial area narrow, central area more or less rectangular. Raphe slightly curved but usually appears distinctly curved due to the orientation of the apically curved valve in the preparations. Raphe-sternum distinct. Central raphe endings close together, straight, expanded, lying in a more or less thickened central nodule. Terminal raphe endings deflected in the same direction, lying in a well-developed central nodule at some distance from the valve margin. Striae radiate in the centre, convergent towards the apices. In the centre of the valve one or two short striae are present. The structure of the striae is indistinct. Frustules in girdle view more or less rectangular and centrally constricted (Fig. 17-14). Central and terminal nodules pronounced. Cingulum structure unclear, one wide valvocopula (and one more copula?) are visible.

SEM - Valve face more or less flat, gently sloping into a deep mantle. Raphe slightly curved, central raphe endings as in LM, apical raphe endings bent, lying in a distinctly thickened terminal nodule. No terminal fissures are visible. Internally, the raphe lies in a raised raphe sternum. The thickened central nodule is clearly visible. Helictoglossae are present at the terminal raphe endings. The striae consist of apically elongate areolae; internally occluded by hymenes.

Remarks: Despite some small differences in stria density and the indistinct ultrastructure of the striae in the LM we have assigned our specimens to *N. bipustulata*. The characteristic valve shape, with the distinct, well-developed apices, can clearly be seen in Fig. Fig. 17-20; *N. bipustulata* belongs to the species complex around *N. apiculata* (cf. above). This taxon has been reported from different localities but has been given different names. In a study on the benthic algal flora of an estuary on the Swedish West coast (Kuylenstierna 1989-90) it appears under the names *Navicula apiculata* Brébisson (Pl. 52, figs. 588-590) and *N. scoliopleura* A. Schmidt (Pl. 56, figs. 683-684). The illustrated specimens cannot belong to these taxa as *N. apiculata* does not possess a distinct central area [cf. e.g. Brébisson 1854, Schmidt *et al.* 1874-1959, Peragallo & Peragallo 1897-1908 (as *N. crucifera* var. *apiculata* (Brébisson) Peragallo & Peragallo), Van Heurck 1896] and *N. scoliopleura* is much larger (about 78 µm long), with about 4 to 5 striae in 10 µm (cf. original illustration in Schmidt *et al.* 1874-1959). However, Kuylenstierna's identification is based on the description of *N. scoliopleura* in Van der Werff & Huls (1957-74), where this species is wrongly represented by a *N. bipustulata* specimen. Another similar species, *N. crucifera* Grunow, shows great affinity with *N. apiculata*. Patrick & Reimer (1966) consider these two taxa as conspecific. It is evident that the type material of all these species has to be examined to clarify their taxonomy and nomenclature.

Biogeography & Ecology: This species has been reported from different European localities (Schmidt *et al.* 1874-1959, Hustedt 1939, Møller 1950, Kuylenstierna 1989-90, this study) and probably also occurs on the North American Atlantic coast (Hustedt 1955). In the Westerschelde estuary, *N. bipustulata* is a common epipelic species in fine sandy sediments; it has a rather low salinity optimum (Table 39). It is most abundant in early spring.

NAVIBIPU

Navicula* cf. *bipustulata Mann 1925

[Figs 17-15, 17-16, 17-17, (?) 17-18]

Morphology:

L: 17.5-27.5, W: 3.7-5, S: (12-)13

LM - This diatom is almost identical to *N. bipustulata* (size, striation density) but has distinctly lineolate striae and more expanded central raphe endings.

Remarks: This taxon might be conspecific with *N. bipustulata* but more valves have to be examined before the relationship between both taxa can be assessed. We distinguished between both taxa because of the distinct lineolate nature of the striae in *N.* cf. *bipustulata*.

Biogeography & Ecology: *N.* cf. *bipustulata* is much rarer than *N. bipustulata* but appears to be found in the same environments.

NAVICBIP

Navicula digitoradiata (Gregory 1856) Ralfs in Pritchard 1861

[Fig. 19-11]

Synonyms:

Pinnularia cuprinus Gregory 1856

References:

(1) Gregory 1856
(2)
(3) Krammer & Lange-Bertalot 1986, Kuylenstierna 1989-90

Morphology:

L: 38; W: 11.4; S: 12 (n=1)

LM - Two girdle-appressed plastids. Two (four?) small droplets are visible near the plastids, just before and after the central cytoplasmatic bridge. Valves linear-lanceolate, apices rounded. Axial area narrow though distinct, central area transapically expanded, more or less round. Central raphe endings straight, expanded, pore-like. Terminal raphe endings deflected in the same direction. Striae strongly radiate in the centre to slightly convergent near the apices. Their structure is indistinct. In the centre, some short striae alternate with longer ones.

Remarks: Only large specimens were observed. These are so typical that they can hardly be mistaken for any other species. See also Krammer & Lange-Bertalot (1986) for a discussion of the smaller specimens, the varieties and forms of this species.

Biogeography & Ecology: *Navicula digitoradiata* is a rare epipelic species in fine sandy sediments in the lower reaches and the mouth of the Westerschelde estuary. It appears to be common and widespread in brackish and marine sediments throughout Europe (Krammer & Lange-Bertalot 1986, Snoeijs & Vilbaste 1994, Hartley et al. 1996) and has also been reported from Africa (Archibald 1983) and the Pacific and Atlantic coasts of North America (Rao & Lewin 1976, Cooper 1995a).

NAVIDIGI

Navicula diserta Hustedt 1939

[Figs 18-10, 18-11, 18-12, 18-13, 18-14, 18-15, 18-16, 18-17, 18-18, 51-1, 51-2, 51-3, 51-6]

References:

(1) Hustedt 1939
(2) Simonsen 1987, (?) Krammer & Lange-Bertalot 1985, 1986
(3) Hustedt 1939, Simonsen 1987, Archibald 1983, Krammer & Lange-Bertalot 1985, 1986, Kuylenstierna 1989-90 (Pl. 58, Figs. 718-719), Witkowski 1994

Morphology:

Westerschelde	L: 8.7-11.2, W: 3.1-3.7, S: 14.5-17.5 (mainly 16-17)
Leybucht (Leysand)	L: 8.7-10.2; W: 2.5-3.5; S: 14-18 (mainly 16)
Memmert	L: 7.7-12.5; W: 2.5-3.7; S: 14.5-18.5 (mainly 16)

LM - Valves lanceolate-elliptic, with obtuse cuneate to more or less blunted apices. Axial area narrow, central area of variable shape and size, from more or less large and rectangular (Figs 18-14, 18-15) to small and roundish (e.g. Fig. 18-16), but most often irregularly shaped due to the presence of one or more shortened striae (e.g. Fig. 18-18). The latter are sometimes only shortened on one side of the valve. Raphe straight, central raphe endings expanded to pore-like, sometimes slightly deflected in the same direction (cf. Fig. 18-15), apical pores distinct, expanded, deflected in the same direction. Central and terminal nodules usually well-developed. Striae usually more or less parallel to radiate to convergent towards the apices. Stria structure most often indistinct, sometimes distinctly lineolate.

SEM - Valve face flat, with a rather gradual transition into the mantle. Raphe straight, central raphe endings distinctly pore-like, often more or less deflected in the same direction. Terminal fissures strongly hooked in sharp angles. Internal raphe fissures opening laterally, except at the central and polar raphe endings. Internal central raphe endings straight, not expanded, terminal pores with well developed helictoglossae. Externally, a distinct but small conopeum is always present near the centre of the valve; it is transapically expanded near the central raphe endings and extends along the raphe branches (though not as far as the apices), where a rudimentary conopeum can also be present (Fig. 51-6). The striae are composed of slit-like, apically elongate areolae, which are internally occluded by a hymenate (but often eroded) velum. The areolae are usually apically aligned, though in most valves some are orientated in different directions, most often near the poles. On the mantle, at least 1 and up to 3 longitudinal rows of areolae are present. The cingulum is composed of 3 (or more) strongly curved copulae; the valvocopula is very wide and appears to be strongly curved near the apices.

Remarks: Small lanceolate, naviculoid cells with shortened central striae are often very abundant and widespread in estuarine and marine sediments (Kuylenstierna 1989-90, Witkowski 1994, ...). These small forms are usually referred to as *N. perminuta*, but also as *N. diserta* and *N. hansenii.* In the Westerschelde material, it appeared that several distinct forms were present. This had also been found by other authors working in the Baltic area (e.g. Kuylenstierna 1989-90 and Witkowski 1994). At first sight these forms closely resemble each other in LM. However, LM and SEM examination of a large number of valves from the Westerschelde estuary showed that several different forms could consistently be distinguished, both in LM and SEM.

We therefore decided to study the type material of the three above-mentioned taxa to assess whether they concerned the same diatom or whether they were different. According to Krammer & Lange-Bertalot (1986, see also Lange-Bertalot 1993b), *N. perminuta, N. diserta* and *N. hansenii* (amongst others, cf. Krammer & Lange-Bertalot 1985) are synonyms.

The following observations were made on the type materials:

(1) Grunow's type material of *Navicula perminuta* could not be studied as the preparation was damaged (no coverslip). However, specimens from the type slide are illustrated in Krammer & Lange-Bertalot (1985, 1986). These concern a diatom which corresponds well with the original illustrations in Van Heurck (1880-1885). The only differences lie in size (up to 14 µm in Krammer & Lange-Bertalot 1986). Note the high stria density (20-21 str./10 µm), the variable size of the central area and its shape (always rectangular). It is worth noticing that it appears that *N. perminuta* has been described from a epiphyton sample (Grunow lists *Licmophora* spp., *Striatella* sp., ... as co-occurring species)

(2) The search for the type material of *Navicula diserta* is very confusing, which is partly caused by Hustedt himself. Hustedt indicated the Leybucht (Leysand and Kopersand) as the type locality for this species. However, he placed the name *N. diserta* on a slide from another locality, viz. a sandflat near Nessmersmiel which is situated about 20 km east of the Leybucht. This slide (N6/23), which was made in 1940 (after his 1939 publication), was then interpreted by Archibald (1983) and Krammer & Lange-Bertalot (1985, 1986) as the designated type slide for this species. Simonsen (1987) correctly designated another BRM slide N12/36 (from Leysand, Leybucht) as the lectotype for *N. diserta* because a *N. diserta*-like specimen is marked (= encircled) by Hustedt on this slide (cf. Simonsen 1987, Pl. 379, Figs. 39-40). No other slide from Leybucht material in BRM has marked specimens or the name *N. diserta* mentioned. Other similar specimens marked by Hustedt were present on BRM slide 397/75 from a sandflat in Memmert (not Leybucht!).

However, there are some problems with Simonsen's lectotypification. The illustrated lectotype specimen (our Fig. 18-7) has no lineolate striae, which is the main feature of this species according to Hustedt. On examining slide N12/36, we noticed that at least two (possible more) different forms were present. One form corresponds well to the description of *N. diserta* and is identical to the specimens (from Memmert) illustrated in Simonsen (1987), Pl. 379, Figs. 41-43. The lineolate nature of the striae can not be well distinguished in his illustrations, partly because they are not very clear, but also because some specimens of this form do not show this feature very well. We have provided new illustrations of this form in Figs 18-13 and 18-14, where the lineolate nature of the striae is clearly visible. The second form (the one illustrated in on Pl. 379, Figs. 39-40, cf. also our Fig. 18-7) can be distinguished from the first in the shape of the valve (which is more convex in transapical section) and the position of the central raphe endings, which are closer together. This difference is very hard to detect in the illustrations provided by Simonsen; the main problem lies in the fact that his illustration of form 2 concerns a valve from the bottom end of the size range of an otherwise distinct form. Specimens of form 2 from slide N12/36 never had lineolate striae.We therefore consider the first form as true *N. diserta*.

Form 1 is described below in detail as *N. diserta*. Material from the type locality was studied in LM and SEM (Figs 51-1and 51-2); in addition, numerous specimens of this taxon were also studied in material from other localities (see there). Form 2 concerns a species which was recently described from the Baltic Sea by Witkowski & Lange-Bertalot, viz. *Navicula starmachioides*. A detailed description of this species is given below. On comparing the descriptions of *Navicula diserta* and *N. starmachioides*, it will become clear that both species are very different: *N. starmachioides* actually belongs to the species complex around *N. apiculata* (see above), whereas *N. diserta* does not. *N. starmachioides* appears to be closely related to *N.* sp. 3 (see there).

(3) The type material of *N. hansenii* was studied on a slide from the Møller collection (C). Again, different morphological forms were present in this slide. These forms are illustrated in Kuylenstierna (1989-90) and correspond to the two valves illustrated by Møller in his type description (Møller 1950). One form is large and rather coarse (Kuylenstierna 1989-90, Pl. 58, Figs. 712-714, with about 12-14 str./10 μm), the other is smaller and finer (Kuylenstierna 1989-90, Pl. 58, Figs. 715-171, with about 16-20 str./10 μm). However, neither of these two forms corresponds well to the type description of *N. hansenii*, which apparently gives an average stria density value (16) between these two forms! On a card that is present in his card-file, Møller later added some photographs which illustrate his concept of this species and which comprises both forms. Apparently he regarded both forms as *N. hansenii* and gave a concise (i.e. averaged?) description. Whether both forms actually belong to the same taxon is hard to assess and requires a detailed morphometric analysis of the type slide. A puzzling note added by Møller on his card concerns the relationship between *N. diserta* and *N. hansenii*: he mentions that *N. diserta* differs in having distinctly lineolate striae. This is very odd as *almost all* specimens of *N. hansenii* in the type slide have distinctly lineolate striae, a feature which is not mentioned in the type description of the latter species.

More research is needed to further assess the identity of the three above-mentioned taxa; it is as yet unclear how the morphological variation within Møller's concept of *N. hansenii* should be interpreted. However, some (preliminary) conclusions can already be drawn:

1. *Navicula perminuta* has a higher stria density than *N. diserta*. Moreover, there are some other differences, mainly in the shape of the valve and the shape and structure of the central area and the centre of the valve. In the Westerschelde, we found a form that corresponds well with *N. perminuta* (sensu type specimens illustrated in Krammer & Lange-Bertalot 1985, 1986); we have therefore decided to refer to this form as *Navicula* cf. *perminuta* (see there). A detailed

description of this taxon (see there) and comparison with *N. diserta* is given (see *N. diserta*). Note also that both taxa had a completely different ecology in the Westerschelde estuary! Further study on the type material of *N. perminuta* is needed before any further conclusions concerning its relationship with *N. diserta* can be drawn.

2. *N. diserta* appears to be a distinct species; it is widespread (see above) and common. However, its morphological variability is as yet insufficiently known. Note also that both Kuylenstierna (1989-90, as N. sp. U) and Witkowski (1994, as *N.* cf. *perminuta*) distinguished a form which is identical to our *N. diserta*. This adds further proof to our statement that we are dealing with a distinct species.
3. *N. hansenii* is rather reminiscent of *N. diserta* but differs in several respects, e.g. in the shape of the central area which is always rectangular (although it is sometimes almost absent in some specimens from the type slide). It is also worth noticing that *N. hansenii* was described from what looks to be a epiphytic sample (dominated by *Synedra* and *Licmophora* spp.); as it was very abundant in this sample it seems that this is its main niche, and not in the epipsammon as *N. diserta*. The main problem lies in the exact identity of *N. hansenii*, which has to be further studied. It is not unlikely that *N. hansenii* is conspecific with *N. perminuta*; it is almost impossible to distinguish between small forms of *N. hansenii* and the illustrations of type material of *N. perminuta*. Note also that both species were described from the western Baltic, and that both appear to occur in epiphytic material.
4. The significance of the presence of lineolate striae is unclear. While it is certain that in some circumstances it can be a good indicator of the spacing of the individual areolae within a stria, it is also a feature which can be influenced by the condition (i.e. eroded or not) of the diatom valves. This feature did allow us to identify Hustedt's *N. diserta*, but already within one slide both specimens with and without lineolate striae were present. In the Westerschelde, most specimens had no distinctly lineolate striae. We have therefore paid special attention to other features which might aid the identification of this species, e.g. the shape of the central area and the structure of the centre of the valve (see *N. diserta*).

The table below lists the characteristics of our concept of *N. diserta*, *N. starmachioides* and *N. perminuta*. The identity of *N. hansenii* is as yet uncertain.

	Navicula perminuta	*Navicula diserta*	*Navicula hansenii*	
description	Grunow in Van Heurck 1880	Hustedt 1939	Møller 1950	Møller, date unknown, post-1950**
type material	Coll. Grunow 2106 (damaged!)(W)	BRM N12/36 (R. M. n° 1136. Leybucht 10301, Leysand-1939. H. 2.)	C A XII a no. 1	
photographic illustration of type material	Krammer & Lange-Bertalot 1985, 1986	this study	Kuylenstierna 1989-90 (Pl. 58, Figs. 712-714), this study	
dimensions (µm)	L: 8.5-12; W: 2.5-3.5*	L: 11; W: 2-3	L: 10-20; W: 2.5-4	L: 7.5-19; W: 2-4.5
stria density (str./10 µm)	about 20*	14-18	16	14-18
shape	valves lanceolate with cuneate to cuneate-obtuse apices*	valves linear-lanceolate with 'stumpf gerundeten, nicht vorgezogen Enden'	valves linear-lanceolate, apices 'cuneate rounded' with 'pointed poles'	cf. Møller 1950
central area	transapically expanded due to shorter central striae or more or less absent*	transapically expanded due to shorter central striae	rectangular due to shortened central striae	cf. Møller 1950
axial area	narrow*	very narrow	narrow but distinct	cf. Møller 1950
striae	slightly radiate to convergent near apices*	slightly radiate, distinctly lineolate	parallel to slightly radiate to convergent near apices	slightly radiate to convergent near apices*

* Deduced from illustrations

** This information was obatined from annotations made by Møller on a card from his card-index (Nielsen, pers. comm.). The information on this card consists of a Danish description (identical to the one in Møller 1950) but also some photographs (with legend) made by Møller long after 1950 (Nielsen, pers. comm.). From this card it appears that Møller's concept of *N. hansenii* was much broader than in his original description.

N. diserta mainly differs from *N.* cf. *perminuta* in the following respects: (1) it has a stria density which is on average lower; (2) it is less variable in shape and especially size; (3) the shape of the central area is more variable, while in *N. perminuta* it is always distinctly rectangular; (4) the presence of a rudimentary conopeum; (5) the central raphe endings are always distinctly pore-like; (6) the terminal fissures are usually hooked in a more angular way.

Biogeography & Ecology: *Navicula diserta* is one of the most common small motile epipsammic species throughout the Westerschelde estuary. It is especially abundant in fine sandy sediments.
N. diserta has with certainty been observed in samples from Europe [Somme estuary (France), Westerschelde estuary (The Netherlands), Belgian coast (Blondeel 1996), Wadden Sea (Germany), English North Sea coast (Blakeney Point, Norfolk), Baltic Sea (Kuylenstierna 1989-90, as *N.* sp. U, Witkowski 1994, as *N.* cf. *perminuta*)] and South America (Riacho San Blas, Argentina).

NAVIDISE

Navicula duerrenbergiana Hustedt 1934 [Fig. 16-12]

Synonyms:

Navicula stundlii Hustedt 1959

References:

(1)	A. Schmidt *et al.* (1874-1959), Pl. 393, fig. 8-9.
(2)	Simonsen 1987
(3)	Krammer & Lange-Bertalot 1985, 1986, Kuylenstierna 1989-90, Snoeijs 1993

Morphology:

L: 28.7; W: 5.6; S: 15

LM - Valves lanceolate, apices cuneate. Axial area narrow, central area indistinct. Raphe straight, central raphe endings extremely close and small, often indistinct. Terminal raphe endings hooked, deflected in the same direction. Striae lineolate (about 33 areolae in 10 µm), parallel to slightly radiate in the centre, becoming more radiate between the centre and the apices and then again parallel at the apices.

Remarks: As Kuylenstierna (1989-90) already pointed out, this species probably belongs in another genus than *Navicula*. However, whether it belongs to e.g. *Haslea* Simonsen or *Craticula* Grunow can only be determined after thorough SEM examination and study of live material.

Biogeography & Ecology: According to Krammer & Lange-Bertalot (1986) this species has only been reported from saline inland waters in Europe and Israel and from the Spanish mediterranean coast but they (rightly) suspected that it is much more widespread on seacoasts. Since the publication of their flora, it has also been found on the West and East coast of Sweden (Kuylenstierna 1989-90, Snoeijs 1989) and on the Dutch North Sea coast (this study).

Only a few valves belonging to this species were found in the Westerschelde samples. However, colonies of this tube-dwelling were observed on others sandflats (Rug van Baarland) in the middle reaches of the estuary.

NAVIPAVI

Navicula finmarchica (Cleve & Grunow 1880) Cleve 1895 var. *acuta* Salah 1955

[Figs 16-3, 16-4, 16-5, 16-6, 54-4]

Synonyms:

Stauroneis finmarchica Cleve & Grunow 1880

References:

(1)	Cleve & Grunow 1880
(2)	
(3)	Kuylenstierna 1989-90, Salah 1955, Hendey 1964, Archibald 1983, Snoeijs & Vilbaste 1994, Witkowski 1994

Morphology:

L: 12.9-23.7; W: 6.2-8.5; S: 15-18.5

LM - Plastids two, girdle-appressed, arranged symmetrically opposite each other. Each plastid is accompanied by two small droplets. Valves lanceolate, apices slightly produced (cuneate subrostrate). Axial area narrow, cenral area small, rectangular. Raphe more or less straight, raphe-sternum distinct. Note that one side of the raphe-sternum of each raphe branch is curved. The central raphe endings are close together and more or less pore-like. The striae are radiate throughout the valve; the two central striae are shortened. Two lateral sterna interrupt the striae. Sometimes they are distinctly hyaline, but most often the striae are still visible in this area.

SEM - Only an internal valve view was observed. Valve face flat, mantle very shallow. Raphe straight, central raphe endings thickened and raised. Terminal raphe endings straight; a distinct helictoglossa is present at each pole. Longitudinal ribs are visible on both sides of the raphe and the central nodule. The striae are composed of roundish areolae, occluded by a (hymenate?) velum. A H-shaped hyaline area interrupts the striae. In each valve apex, two isolated puncta are present.

Remarks: The Westerschelde specimens have a higher stria density than the one reported for *N. finmarchica* by Cleve & Grunow (1880) and Hendey (1964), viz. 15-18.5 str./10 µm versus 12-14 str./10 µm and 11-13 str./10 µm respectively. They are also smaller than their specimens (12.9-23.7 µm versus 30-42 µm and 28-40 µm respectively). Salah (1955) found similar small specimens at Blakeney Point (England) and described them as a new variety, *N. finmarchica* var. *acuta* (14-16 µm long, 16-18 str./10 µm)(cf. Figs 63-25, 64-18). Whether this variety and the nominate variety form part of a continuum, as our observations (which seem to bridge the gap in size and stria density between both varieties) might suggest, is hard to assess on the basis of the information at hand. As we did not observe any specimens that completely correspond to the original description, we decided to allocate our specimens to Salah's variety until further research is carried out.

Navicula finmarchica probably does not belong to *Navicula* s.s. (cf. also Snoeijs & Vilbaste 1994) though its true generic allocation is not clear yet (*Lyrella*?).

The specimens illustrated in Archibald (1983) probably do not belong to this species, as they are much narrower and have a different central area and lyre structure.

Biogeography & Ecology: *N. finmarchica* var. *acuta* is a rare epipelic species in rather silty sediments, especially in the mesohaline section of the estuary. *N. finmarchica* is usually considered as an Arctic marine diatom (cf. Witkowski 1994).

NAVIFIAC

Navicula flanatica Grunow 1860

[Figs 20-11, 20-12, 20-13, 20-14, 52-6]

Synonyms:

Navicula ammophila Grunow var. *flanatica* (Grunow) Cleve 1895
Navicula cancellata Donkin var. *scaldensis* Van Heurck 1885

References:

(1) Grunow 1860
(2)
(3) Krammer & Lange-Bertalot 1985, 1986, Kuylenstierna 1989-90, Archibald 1983, Snoeijs & Potapova 1995, Peletier 1996

Morphology:

L: 17.5-30.9; W: 5-7.2; S: 12-13.5(-14)

LM - Two girdle-appressed plastids, slightly diagonally opposite, with large lobes extending under the valves, almost covering the whole valve face. Nucleus central. Valves lanceolate, apices slightly produced, cuneate to subrostrate. Axial area narrow, central area absent to slightly transapically expanded. Raphe straight, central raphe endings straight, expanded, pore-like, close together. Terminal raphe endings deflected in the same direction. Striae distinctly lineolate, radiate in the centre to convergent towards the apices. The central striae are often more widely spaced.

SEM - Only external valve views were observed. Valve face more or less curved in transapical section. Raphe-sternum distinct and raised. Central raphe endings straight, central nodule slightly transapically expanded. Terminal nodules well-developed, terminal fissures hooked (in the same direction, which is opposite to the one of the terminal raphe endings). Striae consist of slit-like areolae, which are longitudinally aligned. No occlusions are visible externally. The central striae are sometimes shorter (Fig. 52-6).

Remarks: The Westerschelde specimens are almost invariably smaller than the ones reported in the literature (cf. Krammer & Lange-Bertalot 1985, 1986, Hendey 1964, Kuylenstierna 1989-90) and have a slightly higher stria density. Archibald (1983) described almost identical specimens from South Africa, where he identified them as *Navicula ammophila* Grunow. He points out that his specimens compare well with Grunow's concept of this species (as present in Grunow's slide 2822a). Consequently, our specimens could also belong to *N. ammophila* (*sensu* Archibald 1983, *sensu* Grunow 1882). However, further study is necessary to clarify the true identity of *N. ammophila*, as many reports of this species seem to refer to different taxa [cf. Krammer & Lange-Bertalot (1985), where an example of Hustedt's concept of this species is illustrated in Pl. 22, Figs. 6-7, and Krammer & Lange-Bertalot (1991), where Van Heurck's concept is represented in Pl. 71, Figs 14-15]. Therefore we prefer to refer to our specimens as *Navicula flanatica* for the time being, as up to now this seems to be the most commonly used name for these forms (cf. Krammer & Lange-Bertalot 1985, 1986, Kuylenstierna 1989-90, Brockmann 1950, Gätje 1992, Witkowski 1994).

Biogeography & Ecology: *Navicula flanatica* is a common epipelic species throughout Europe (cf. references above) and has also been reported from North America (Cooper 1995a). *N. flanatica* is one of the most abundant epipelic species in the Westerschelde: it is restricted to silty sediments, mainly in the mesohaline zone, and reaches its highest abundance in late winter-early spring. This pattern is in accordance with the occurrence of this species in other brackish and marine sediments in Europe (Colijn & Dijkema 1981, Juggins 1992, Gätje 1992 and references therein, Peletier 1996). Although this has been attributed to a negative tolerance to high temperatures (Admiraal 1984), it appears that other factors must be regulating the dynamics of this species, as it has also been found in summer assemblages (Peletier 1996).

NAVIFLAN

Navicula gregaria Donkin 1861 [Figs 21-7, 21-8, 21-19, 53-3, 53-4]

Synonyms:

(?) *Navicula gregalis* Cholnoky 1963
(?) *Navicula wetzelii* Hustedt 1927 (cf. Lange-Bertalot 1993b)
(?) *Navicula gratissima* Hustedt 1944 (cf. Lange-Bertalot 1993b)
(?) *Navicula acephala* Schoeman 1973

References:

(1) Donkin 1861
(2) Schoeman & Archibald 1978 (slide from type locality)(BM 11987, not BM 11927 as in Patrick & Reimer 1966)
(3) Cox 1987, 1995a, b, Lange-Bertalot 1993b, Krammer & Lange-Bertalot 1986, Schoeman & Archibald 1978, Archibald 1983, Kuylenstierna 1989-90, Snoeijs & Vilbaste 1994

Morphology:

L: 24.4-39.4; W: 6.2-8.1; S: 16.5-18

LM - Two girdle-appressed plastids, slightly diagonally opposed. Unlike in Cox (1995a), the plastids are not as distinctly diagonally offset, nor is the cytoplasmatic bridge diagonal. Our *N. gregaria* plastids are similar to the ones illustrated in Kuylenstierna (1989-90) for this species. As in his specimens, there are also four conspicuous droplets visible, two against each plastid. The valves are lanceolate with produced to rostrate apices. Axial area narrow, central area transapically expanded (size and shape variable), usually asymmetrical. Raphe straight, central raphe endings expanded and pore-like, slightly deflected in the same direction. Central nodule distinctly unilaterally thickened, adding to the asymmetrical appearance of the valve centre. Terminal raphe endings expanded, pore-like, deflected in the same direction (opposite to the one of the central raphe endings). Striae punctate (about 30 areolae in 10 µm), slightly radiate in the centre to convergent towards the apices.

SEM - Valve face flat, curving into a shallow mantle. Raphe straight, external central raphe endings pore-like, deflected in the same direction. External terminal fissures hooked. Internally, a distinct accessory rib runs along one side of the slightly raised raphe-sternum. Centrally, a distinct unilateral thickening of this rib is visible. The internal raphe fissures open laterally (away from the accessory rib), though only slightly so in the centre and at the apices. Here, distinct helictoglossae are present. Striae composed of apically elongate areolae, slit-like on the outside, broader on the inside. No occlusions are visible (probably eroded during preparation). On the outside, the areolae are distinctly longitudinally aligned; these longitudinal striae curve around the central area.

Remarks: Brockmann (1950), Hendey (1964) and Vos (1989a) mistook this species for *Navicula phyllepta*, which has different features (cf. also Krammer & Lange-Bertalot 1986, Cox 1995a).
Cox (1987) pointed out that different forms can be distinguished within the 'old' *Navicula gregaria*: she distinguished three forms, which differ both morphologically and ecologically. *Navicula gregaria* A ('good' *N. gregaria*, Cox 1987) is 26-30 µm L, 7-8 µm W and has 14-16 distinctly

punctate striae in 10 µm and is found in brackish sites. *N. gregaria* B differs from this taxon in being smaller (18-26 µm L, 5-6 µm W), having more rostrate apices, a higher striation density (18-22 str./10 µm) and a less distinct stria punctation (Cox 1987). *N. gregaria* B occurs in freshwater but extends into brackish water. (For the description of *N. gregaria* C, a freshwater form, see Cox 1987). However, in Cox (1995b), it is questioned whether this distinction into separate forms (taxa?) is possible, on the basis of experimental studies with *N. gregaria* clones (which shows that freshwater clones are euryhaline). Morphological shifts occur when freshwater forms are grown at higher salinities. This seems to be in accordance with Lange-Bertalot's (1993b) observations, which do not allow a clear distinction between the different forms, and our own observations on the Westerschelde specimens, which have 16.5-18 (distinctly punctate) striae in 10 µm, are about 24-39 µm long and 6-8 µm wide. Even some smaller forms, which we believe might belong to *Navicula gregaria* (see below, *N. gregaria* form 1), still have the same stria density and distinctly punctate striae. For further discussion of the occurrence of different morphological forms of *Navicula gregaria*, see below.

The type material of suspected synonyms (cf. above) should be compared to *Navicula gregaria*. Also, its relationship with *N. litoris* Salah (cf. Fig. 21-14), which is very similar to *N. gregaria* but has straight central raphe endings, has to be investigated.

A last remark concerns the typification of *Navicula gregaria*, which has been made quite confusing (cf. Lange-Bertalot 1993b and Cox 1995a). For a more detailed discussion on this matter, see Cox (1995a).

Biogeography & Ecology: *Navicula gregaria* is one of the most common epipelic species in brackish-water sediments in Europe (Cox 1987, Wendker 1990, Gätje 1992, Peletier 1996) and has also been reported outside Europe (e.g. Garcia-Baptista 1993b). It is one of the most abundant epipelic species in silty sediments in the mesohaline reaches of the Westerschelde estuary; it is slightly more abundant in late spring and summer, which is in accordance with the temperature optimum (15 °C) for this species recorded by Hickmann (1982) and its seasonal occurrence in the Elbe estuary (Gätje 1992).

NAVIGREG

Navicula gregaria f. 1

[Figs 21-1, 21-2, 21-3, 21-4, 21-5, 21-6, 53-1, 53-2]

References:

(1)
(2)
(3) Schoeman & Archibald 1978, Lange-Bertalot 1993b

Morphology:

L: 10-19.4; W: 4.4-6; S: (16-)17-19(-20)

LM - Valves lanceolate, apices cuneate obtuse, often slightly produced (apparently this feature is size-dependent, the larger, the more produced). Axial area narrow, central area transapically expanded, usually asymmetrical. Raphe straight, central raphe endings straight (e.g. Fig. 21-3) to slightly deflected (e.g. Fig. 51-4), central nodule unilaterally thickened (always into the larger side of the central area). Terminal raphe endings expanded, slightly deflected in the same direction.

Striae distinctly punctate (about 25-30 str./10 µm), radiate in the centre, convergent towards the apices.

SEM - Valve face flat, mantle shallow. Raphe straight, central raphe endings expanded, slightly deflected in the same direction. Terminal fissures hooked (both in a direction opposite to the one of the central raphe endings). Internally, a distinct accessory rib, which is slightly thickened in the centre, is present. The raphe fissure opens laterally (away from the accessory rib), except in the centre and near the apices (where a distinct helitoglossa is present). Striae composed of apically elongate, longitudinally aligned areolae. These are broader on the inside. No occlusions are visible (probably eroded during preparation).

Remarks: There is no doubt that this diatom concerns a form closely related to (or even conspecific with) *Navicula gregaria*. The main morphological differences are valve apex shape (no distinctly produced apices), the *on average* higher stria density, the less distinct thickening of the accessory rib, and the little or not deflected central pores. The apical shape could be a consequence of the smaller size of *Navicula gregaria* form 1 [comparable to the phenomenon observed in *Navicula genustriata* Hustedt (Denys & Carter 1989, Fig. 48)]. However, Schoeman & Archibald (1983) found that the shape of the apices is not size-dependent in *Navicula gregaria*. We have decided to treat *Navicula gregaria* and its f. 1 as separate entities because they seem to occupy a different ecological niche (see below).

Navicula gregaria f. 1 is very similar to *Navicula namibica* Rumrich & Lange-Bertalot (Lange-Bertalot 1993b), which was recently described from electrolyte-rich desert wells in Namibia. The only obvious difference between our Westerschelde specimens and *N. namibica* lies in the central raphe endings, which are more or less deflected in our specimens, while they are straight in *N. namibica*. This form is also reminiscent of *N. litoris* (cf. *N. gregaria*); further study is needed.

Biogeography & Ecology: In contrast to *Navicula gregaria*, which is typical of silty sediments in the mesohaline reaches, *N. gregaria* f. 1 is characteristic of fine sandy sediments throughout the estuary. It is most abundant in the spring diatom communities.

NAVIGRF1

Navicula margino-nodularis Salah 1953 [Figs 17-1, 17-2, 17-3]

Synonyms:

Navicula subfortis Hustedt 1954

References:

(1) Salah 1953
(2)
(3) Salah 1953, Hustedt 1954, Simonsen 1987

Morphology:

L: 16.2-23.7; W: 6.2-10; S: 11-13.5

LM - Valves (often broadly) elliptical, apices broadly rounded to rostrate. Axial area narrow, central area round to transapically expanded, more or less elliptical. Raphe slightly curved, central raphe endings slightly expanded, more or less straight, terminal raphe endings slightly expanded, more or less curved in the same direction. Terminal nodule distinct, surrounded by a row of elongate puncta. Striae distinctly lineolate (± 22 areolae in 10 µm), strongly radiate in the centre, radiate or convergent towards the apices (both striation patterns can occur within one valve, Fig. 17-3).

Remarks: Salah (1953) mentions 9 str./10 µm in the type description but on his illustrations about 12 str./10 µm can be counted. Hustedt's description and dimensions correspond to our own measurements. This species is mainly characterized by the distinct terminal nodules (cf. also Salah 1953). Our specimens do not always possess rostrate apices (as already indicated by Hustedt 1954). It is not sure whether this species belongs to *Navicula* s.s.; SEM examination is necessary to determine its generic affinities.

Biogeography & Ecology: This rare species has been reported from sandy sediments on the Scottish (Hustedt 1954), English (Salah 1953) and Dutch coasts (this study). *N. margino-nodularis* was very rare in fine sandy sediments in the Westerschelde estuary.

NAVIMARG

Navicula meniscus Schumann 1867

[Figs 19-10, 49-7]

Synonyms:

Navicula peregrina [Ehrenberg] Kützing var. *meniscus* (Schumann) Grunow in Van Heurck 1880

References:

(1) Schumann 1867
(2)
(3) Krammer & Lange-Bertalot 1985, 1986, Hendey 1964, Kuylenstierna 1989-90, Cox 1987, Lange-Bertalot 1993b, Witkowski 1994, Snoeijs & Potapova 1995

Morphology:

L: 43.7-62.5; W: 13.5-15; S: 8(-9)

LM - Valves lanceolate, apices broadly rounded, often blunted, sometimes slightly produced. Axial area narrow on one side, slightly broader on the other. Central area more or less rectangular, slightly asymmetrical. Raphe straight, central raphe endings straight, pore-like to forked. The central nodule is slightly expanded. Terminal raphe endings deflected in the same direction. Striae (strongly) radiate in the centre (except for the 2 or 3 central striae) to parallel-convergent near the apices. They consist of transapically elongate areolae (22-24 in 10 µm); the ones alongside the raphe system are slightly broader and sometimes even roundish. Valve width and stria density are remarkably constant within different populations of this species and even compare very well with some literature reports [cf. width 13.5-15.5 µm and 7-8 striae in 10 µm in Snoeijs & Potapova (1995)].

SEM - Only an external valve view was observed. Valve face flat, curving abruptly into the mantle. Raphe straight, central raphe endings T-shaped to forked (one side of the T is distinctly hooked). Terminal fissures strongly hooked. Striae composed of transapically alongate areolae; no occlusions are visible externally. The areolae near the raphe and the valve face margin are somewhat broader. The areolae of the short, central striae become smaller (to round) towards the central area. The cingulum consists of at least one wide copula.

Remarks: *Navicula meniscus* can be confused with the following species: *N. peregrina* (Ehrenberg) Kützing, *N. rhynchocephala* Kützing s.s., *N. rhynchotella* Lange-Bertalot, *N. slesvicensis* Grunow in Van Heurck and *N. kefvingensis* (Ehrenberg) Küzting. It differs from *N. peregrina sensu* Lange-Bertalot (1993b) in having a higher stria and areolar density [5-6 str./10 µm and 18-20 areolae in 10 µm for *N. peregrina*; however, compare with Krammer & Lange-Bertalot (1986) who give 5-7 str./10 µm and 18-25 areolae in 10 µm for *N. peregrina*]. Moreover, *N. peregrina* possesses a distinct, raised raphe-sternum (Lange-Bertalot 1993b, Pl. 67, Figs. 4-6), which is lacking in *N. meniscus*. *N. rhynchocephala* s.l. (= *sensu* auct. non Lange-Bertalot 1993b) has been split up in two separate taxa, viz. *N. rhynchocephala* s.s. (= sensu Lange-Bertalot 1993b) and *N. rhyncotella* (cf. also Cox 1987 and Witkowski 1994). The main difference between both taxa lies in the valve width (8.5-10 µm versus 10-16 µm respectively), the shape of the central raphe endings (clearly hooked in *N. rhynchotella*), the raphe-sternum (distinctly raised in *N. rhynchocephala*) and ecology [freshwater (*N. rhynchocephala*) versus brackish water (*N. rhynchotella*)]. Both species differ from *N. meniscus* in having distinctly produced to rostrate apices.

Navicula slesvicensis and *N. kefvingensis* have a denser lineolation (> 25 areolae in 10 µm); *N. slesvicensis* is also narrower (< 11 µm), while *N. kefvingensis* has a slightly lower stria density (7-7.5 str./10 µm), and, judging from the illustrations in Lange-Bertalot (1993b) is broader (> 16.5 µm). Lange-Bertalot (1993b) also remarks that both species also differ from *N. meniscus* in having hooked central raphe endings, which would not be present in *N. meniscus*. However, our specimens do possess hooked central raphe endings (Fig. 2874). It is clear that further study is needed to assess the relationship between all the above-mentioned taxa. Especially detailed examination of the type material is necessary (but cf. Lange-Bertalot 1993b, p. 117).

Biogeography & Ecology: *Navicula meniscus* is common in the late winter-early spring assemblages in fine sandy sediments, especially in the middle and lower reaches of the Westerschelde estuary. Note also that is has a very low elevation optimum: it was always most abundant in the lower intertidal zone. *N. meniscus* is a common epipelic species in Europe (Cleve 1895, Witkowski 1994).

NAVIMENI

Navicula microdigitoradiata Lange-Bertalot 1993

[Figs 20-4, 20-5, 20-6, 20-7, 20-8, 20-9, 20-10, 53-5, 53-6]

Synonyms:

Navicula cincta f. *minuta* Van Heurck 1885

References:

(1) Van Heurck 1885
(2) Lange-Bertalot 1993b
(3) Carter 1979, Krammer & Lange-Bertalot 1986, 1991, Kuylenstierna 1989-90, Lange-Bertalot 1993b, Snoeijs & Potapova 1995

Morphology:

L: 13.7-30; W: 3.7-6.2; S: 14-20(-22)

LM - Two girdle-appressed plastids, arranged symmetrically about the apical plane. Valves lanceolate with cuneate apices. Axial area narrow. Sometimes (always?) there appears to be a short rib running parallel with the raphe in the centre of the valve (43-24, 52-26). Central area roundish to elliptical, usually small. Raphe more or less straight (to slightly curved), central raphe endings straight (to slightly deflected in the same direction, cf. 43-24, 52-26), expanded. Terminal raphe endings deflected (in the same direction?). Striae from strongly radiate in the centre to parallel-convergent towards the apices. Their structure is indistinct. In the centre, one to several short striae are present.

SEM - Only internal valve views were observed. Valve face curved. Raphe seems slightly curved. The raphe fissures open laterally, except in the centre and at the poles, where distinct helictoglossae are present. Central raphe endings straight, terminal raphe endings strongly deflected in the same direction. An accessory rib, interrupted in the centre of the valve, runs on one side the raphe-sternum. This rib is connected to the internal costae, except near the apices (Fig. 53-6). The striae are composed of apically elongated, internally hymenate areolae.

Remarks: This species was described as *Navicula cincta* f. *minuta* by Van Heurck (1885, Types de Synopsis 83) and is probably also conspecific with *Navicula digitoradiata* var. *minima* Cleve-Euler (1953). Lange-Bertalot (1993b) described it as a nomen novum and status novus. It appears to be a very variable species (cf. our own specimens) and further (SEM) study is necessary to assess whether or not we are dealing with one single or several different taxa.

Our specimens differ from the ones described by Lange-Bertalot (1993b) in having a higher striation density (up to 21-22 str./10 µm). We are not sure whether some more delicate specimens (cf. Fig. 20-10) also belong to this taxon. It was often hard to decide whether some specimens should be identified as *Navicula microdigitoradiata* or *N. phyllepta.*

Biogeography & Ecology: *N. microdigitoradiata* has been reported from brackish-water and marine sites in Europe, both from the Atlantic and Mediterranean coasts (e.g. Lange-Bertalot 1993b, Kuylenstierna 1989-90, this study). It is common in silty sediments throughout the Westerschelde estuary and is typical of the spring assemblages.

NAVIMICR

Navicula cf. *mollis* (W.M. Smith 1856) Cleve 1895 [Figs 20-16, 20-17, 20-18, (?) 20-15, 50-4, 51-7]

Synonyms:

Schizonema mollis W.M. Smith 1856
Navicula ramosissima var. *mollis* (W.M. Smith) Hendey 1964

References:

(1) W.M. Smith 1856
(2) Krammer & Lange-Bertalot 1991(b)
(3) Peragallo & Peragallo 1897-1908, Archibald 1983, Lobban 1983, 1984, Krammer & Lange-Bertalot

1985, 1986, Krammer & Lange-Bertalot 1991

Morphology:

L: (12.5-)14.2-27; W: 3.7-6.2; S: 13-16

LM - Valves linear-lanceolate/elliptical with cuneate apices. Axial area narrow, central area of variable size and shape though usually more or less rectangular. Raphe straight, central raphe endings straight, expanded to pore-like, terminal raphe endings more or less hooked in the same direction. The central nodule is distinct in most (though not all!, cf. Fig. 20-15) specimens (whether or not the two forms, with and without the distinct central nodule, belong to the same taxon is as yet unclear). Further study is required to elucidate this question. Striae parallel to slightly radiate in the centre of the valve to convergent near the apices. Their structure is indistinct.

SEM - Valve face curved. Raphe straight, central raphe endings straight and pore-like. Terminal nodule distinct, terminal fissures strongly hooked in the opposite direction as the terminal raphe endings. Striae composed of apically elongated areolae, externally slit-like, internally broader and occluded by a velum. The internal raphe fissuers open laterally, except in the centre and near the poles. A distinct helictoglossa is present at the poles. The raphe rib seems to be accompanied by an accessory rib, but the latter can only clearly be distinguished in the centre, where it is interrupted (arrow!), and at the apices. The rest of this rib seems to coincide with the raphe rib. A semi-circle of internally small but externally apically elongated puncta is present near the apical margin. Cingulum consists of at least one, rather wide, unperforated copula.

Remarks: This species has been provisionally identified as *Navicula* cf. *mollis* on the basis of a combination of the following characteristics: (1) size and stria density, (2) the parallel to slightly radiate striation pattern in the centre of the valve and (3) the distinctly hooked terminal fissures. However, they differ from *Navicula mollis* [cf. specimen from type slide (Coll. Roper 2680 = BM 22905), Krammer & Lange-Bertalot 1991] in shape (distinctly lanceolate in the type specimens), the shape of the central area, which is usually more or less rectangular in our specimens (versus round in *N. mollis*) and the height of the mantle (which appears to be higher in *N. mollis*: note the different aspect of the valve margin in the LM). In addition, *Navicula mollis* is mainly known as a tube-dwelling diatom (cf. Lobban 1984), while our taxon has a different ecology (see below). Our specimens most closely resemble the valves illustrated in Archibald (1983, Pl. 17, 302-304) and Krammer & Lange-Bertalot (1986, fig. 27, 8).

Navicula cf. *mollis* is also reminiscent of *N. tripunctata* (O. F. Müller) Bory (but differs in size and striation density) and *N. recens* (Lange-Bertalot) Lange-Bertalot (whose striation pattern is distinctly radiate in the centre of the valve).

Clearly, the species group around *N. tripunctata*, including the above-mentioned species, needs further study. Therefore, whether the literature reports of *N. mollis* (e. g. Krammer & Lange-Bertalot 1986, 1991, Cholnoky 1961, Giffen 1963, 1970, Lobban 1985, ...) refer to the same taxon is difficult to assess.

Biogeography & Ecology: *Navicula* cf. *mollis* is common in fine sandy sediments, especially in the polyhaline reaches and the mouth of the estuary. It is most abundant in the summer months.

NAVICFMO

Navicula orthoneoides Hustedt 1955 [Fig. 54-1]

References:

(1) Hustedt 1955
(2) Simonsen 1987
(3) Hustedt 1952, 1962, Sterrenburg & Sterrenburg 1991

Morphology:

L: 17.7-22.1; W: 12.5-16.2; S: 20.5 (n=2)

LM - Valves broadly elliptical, apices broadly rounded. Axial area distinct, more or less narrow, central area very small. Raphe straight, central raphe endings straight (however see below), slightly expanded. Terminal raphe endings straight, they lie at some distance of the valve margin. Striae distinctly punctate, strongly radiate throughout the valve. In the centre a few short striae are present. Along the valve margin and near the central nodule, some transapically elongate areolae can be seen.

SEM - Only an internal valve view was observed. Valve face flat, mantle very shallow. Raphe-sternum distinct, raised. Raphe straight. Central raphe endings slightly deflected in opposite directions (?), terminal raphe endings surrounded by distinct helictoglossae. Areolae roundish, occluded by hymenate vela.

Remarks: Sterrenburg & Sterrenburg (1991) give a detailed account of this species, which does not belong to *Navicula* s.s. *N. orthoneoides* seems to show some (superficial?) affinity with the recently described genus *Cavinula* Mann & Stickle, which however is apparently restricted to freshwater (Round *et al.* 1990). Examination of live material is necessary to assess this relationship.

Biogeography & Ecology: Dense populations of this cosmopolitan species were found on sandy beaches on the Dutch North Sea coast. It was also reported from North America (East and West coast) and from the Seychelles and Tanzania (Sterrenburg & Sterrenburg 1991, Hustedt 1955, Coste & Ricard 1984, Foged 1975). In the Westerschelde estuary, *N. orthoneoides* was very rare on sandflats in the middle reaches and lower of the estuary. It was also present in samples from sandy beaches on the Belgian coast, which is in accordance with its distribution along the Dutch coast (Sterrenburg & Sterrenburg 1991).

NAVIORTH

Navicula palpebralis Brébisson ex W. Smith 1853 [Figs 19-7, 53-7]

References:

(1) W. Smith 1853
(2)
(3) Hendey 1964

Morphology:

L: 26.2-40 (-57.8); W: 12.5-14.4 (-20.1); S: 10-11 (-12)

LM - Plastids two, girdle-appressed, symmetrically arranged about the apical plane. Two conspicuous droplets are visible near one of the plastids. Valves lanceolate, apices cuneate, sometimes slightly produced, subrostrate. Axial and central area distinct, forming a lanceolate to rhombic hyaline area. Central raphe endings straight, expanded and pore-like; terminal raphe endings deflected in the same direction. Striae radiate throughout the valve; in the centre some short striae are present. Their structure is indistinct.

SEM - Only an external valve view was observed. Valve face transapically undulate, at the margins gently curving into a shallow mantle. A distinct, raised raphe-sternum is visible (transapically expanded near the central pores). Thus, in the lanceolate, hyaline area (cf. LM), two 'subareas' can be distinguished: the raised raphe-sternum and a depressed area, into which the marginal striae extend as slight depressions of the valve face. The central raphe endings are straight and expanded; the terminal fissures are hooked in the same direction. The slightly costate striae are composed of apically elongate areolae; no occlusions are visible externally.

Remarks: Numerous infraspecific taxa of *Navicula palpebralis* have been described (cf. VanLandingham 1975). However, Hendey (1964) pointed out that *N. palpebralis* is an extremely variable species and therefore doubts whether any clear cut divisions can be substantiated. This requires careful morphological analysis of a large number of specimens from various sites (cf. Droop 1994).

Biogeography & Ecology: *N. palpebralis* is a common epipelic species in silty, very fine and fine sediments throughout the Westerschelde estuary. It is a typical component of the spring assemblages. It is common and widespread throughout Europe (e.g. Hendey 1964, Witkowski 1994) and has also been reported from North America (Cooper 1995a) and probably elsewhere.

NAVIPALP

Navicula* cf. *perminuta Grunow in Van Heurck 1880 non Ostrup 1913

[Figs 18-22, 18-23, 18-24, 18-25, 18-26, 18-27, 51-4, 51-5, 51-6]

Synonyms:

Navicula cryptocephala var. *perminuta* (Grunow) Cleve 1895
(?) *Navicula hansenii* Møller 1950(?)
(?) *Navicula dulcis* Patrick 1959 non Krasske 1939
(?) *Navicula taedens* Cholnoky 1968
(?) *Navicula pseudoincerta* Giffen 1970
(?) *Navicula mendotia* VanLandingham 1975
(?) *Navicula rusticensis* Lobban 1984

References:

(1) Grunow in Van Heurck 1880
(2) Krammer & Lange-Bertalot 1985, 1986
(3) Archibald 1983, Lobban 1984, Krammer & Lange-Bertalot 1985, 1986, Kuylenstierna 1989-90, Lange-Bertalot 1993b, Snoeijs 1993, Witkowski 1994

Morphology:

L: 6-15; W: 2.5-4; S: (16-17.5-)18-22(-24)

LM - This taxon was often found in short, ribbon-like colonies. Valves lanceolate to slightly elliptical in small forms, apices cuneate obtuse. Axial area narrow, central area distinctly rectangular due to the presence of two shorter striae in the centre of the valve. Raphe straight. Central raphe endings straight, slightly expanded; terminal raphe endings distinct, deflected in the same direction. Striae usually slightly radiate to convergent near the apices (in smaller specimens the striae are more parallel in the centre). Their structure is usually indistinct but are sometimes lineolate.

SEM - Valve face flat, curving quite sharply into the mantle (which is at an almost right angle to the valve face). Raphe straight, central raphe endings expanded but usually small, terminal raphe fissures strongly hooked (in the same direction). Internally, the raphe fissures open laterally, except in the centre and at the apices, where a distinct helictoglossa is present. The striae are composed of slit-like areolae, internally occluded by a hymenate velum. The areolae are usually longitudinally aligned but in the centre and near the apices they are often placed obliquely. On the mantle, one distinct marginal ring of areolae is present. The structure of the cingulum is unclear: at least 3 copulae appear to be present.

Remarks: The exact identity of *N. perminuta* is unclear and requires further study. Little is known about the morphological variation of this species. For a more thorough discussion on the type material of *N. perminuta* and a comparison of this species with *N. diserta* and *N. hansenii*, see *N. diserta*.

Biogeography & Ecology: Diatoms identical to our *Navicula* cf. *perminuta* have been reported from the Baltic area [Snoeijs 1993, Kuylenstierna 1989-90 (as *N. perminuta*, including *N.* sp. K?), Witkowski 1994 (only his Pl. 32, Figs 12 and 14, not Fig. 13 which is *N. diserta*)]. They are reported to be very common in sediments but also in epilithic and epiphytic communities. Given the uncertain idenity of this taxon, it is hard to assess its geographical distribution. We found *N.* cf. *perminuta* also in Salah's material from Blakeney Point. For example, *N. perminuta*-like diatoms have been reported from South Africa by Giffen (1970, 1973, as *N. hansenii*) and Archibald (1983), but on the basis of their illustrations it is impossible to assess whether we are dealing with the above-described *N.* cf. *perminuta* or another, similar taxon.

In the Westerschelde estuary *N.* cf. *perminuta* was one of the most abundant taxa in silty sediments; it is slightly more abundant at higher salinities. It usually formed small ribbon-like colonies, which are very similar to those illustrated in Giffen (1973, as *N. hansenii*) from epiphytic samples. Note that his *N. pseudoincerta* (Giffen 1970), which he later synonymyzes with *N. hansenii*, was described from sand. Further study (on live material) is needed to assess whether the reports from sediments and epiphyton concern the same taxon (see also *N. diserta*: the type material of both *N. perminuta* and *N. hansenii* concerns epiphytic samples).

NAVIPERM

Navicula phyllepta Kützing 1844

[Figs 20-1, 20-2, (?) 20-3, 52-3]

Synonyms:

Navicula lanceolata var. *phyllepta* (Küzting) Van Heurck

References:

(1)	Kützing 1844
(2)	Lange-Bertalot 1980 (lectotype), Krammer & Lange-Bertalot 1986, Cox 1995a
(3)	Krammer & Lange-Bertalot 1985, 1986, Lange-Bertalot 1993b, Kuylenstierna 1989-90, Riaux & Germain 1980, Cox 1995a

Morphology:

L: 13.1-25; W: 4.1-7; S: 18-24

LM - Two girdle-appressed plastids. Valves lanceolate with cuneate to slightly produced, subrostrate apices. Axial area narrow, central area small, more or less round. Raphe straight, central raphe endings straight, expanded, close together. Terminal raphe endings deflected in the same direction. Striae finely lineolate, radiate in the centre (the central 3 to 4 striae are shorter) to convergent near the apices.

SEM - Only external valve views were observed. Valve face flat, mantle shallow. Raphe sternum well-developed, raised. Central raphe endings straight, terminal fissures strongly hooked. Striae composed of apically elongate, slit-like areolae. In most observed specimens (cf. also Riaux & Germain (1980), Pl. 1, Fig. 4, as *Navicula gregaria*), but not in all (cf. Kuylenstierna 1989-90, Krammer & Lange-Bertalot 1985), the vimines (cf. Cox & Ross 1980) are thickened. However, these thickenings do not connect across the interstriae (as in *Craticula*, cf. Round *et al.* 1990), or only near the valve apices (Fig. 52-3).

Remarks: This species has often been confused with *Navicula gregaria* (see there). Our specimens differ from the ones illustrated in Krammer & Lange-Bertalot (1986)(and most other literature reports) in being on average smaller and in having a considerably higher stria density (cf. Witkowski 1994).

Biogeography & Ecology: *Navicula phyllepta* is a very common epipelic diatom in brackish and marine sediments in Europe (cf. references above). As *N. gregaria* and *N. flanatica*, it is typical for silty sediments in the inner reaches of the estuary. It reaches its maximum abundance in late spring, early summer. This contradicts its seasonal occurrence in the Elbe estuary, where it is a typical winter species (Gätje 1992).

NAVIPHYL

Navicula salinicola Hustedt 1939

[Figs 18-38, 18-39, 18-40, 18-41]

References:

(1)	Hustedt 1939
(2)	Simonsen 1987 (lectotype)

(3) Peragallo & Peragallo 1897-1908, Krammer & Lange-Bertalot 1985, 1986, Simonsen 1987

Morphology:

L: 5.7-13.7; W: 2.5-3.1; S: 17.5-22

LM - Valves elliptical, apices rounded. Axial area narrow, central area absent or only very slightly transapically expanded (due to the presence of one or more shorter striae). Raphe straight, central raphe endings straight, slightly expanded. Terminal raphe endings deflected in the same direction. Striae slightly radiate to parallel in the centre, to slightly convergent near the apices. Their structure is indistinct.

Remarks: Originally, we identified this taxon as *Navicula incertata* Lange-Bertalot (syn. *N. incerta* Grunow *in* Van Heurck 1880 *non* Ehrenberg 1837), which strongly resembles *N. salinicola*. Krammer & Lange-Bertalot (1985, 1986) and Lange-Bertalot (1993b) discuss the affinities between both species and conclude that they are most probably conspecific. In Lange-Bertalot (1993b), specimens of *N. incertata* from the most diverse habitats (from estuaries in the North of Spain to terrestrial habitats in high altitude rainforest in Venezuela!) indicate that the ecological concept of this taxon is very broad.

The original type material of *N. incertata* has, to our knowlegde, never been investigated. The original illustration (Grunow in Van Heurck 1880) and description (Grunow in Van Heurck 1885) and the description in Krammer & Lange-Bertalot (1985, 1986) mention a stria density of about 15 and 13-16 str./10 µm respectively. *Navicula salinicola*, on the other hand, has a stria density of about 17-20 str./10 µm (Hustedt 1939, Krammer & Lange-Bertalot 1986). Given these densities, which are quite close together, one would be inclined to regard thes two taxa as conspecific. However, all measured specimens from the Westerschelde estuary have a stria density of about 17-22 str./10 µm [cf. also the lectotype specimens in Simonsen (1987), Pl. 381, Figs. 11-15, not Figs. 16-20, cf. Lange-Bertalot 1993b]. As long as it cannot be shown that there is a continuous range in stria density between 13 and 22 str./10 µm within specimens in a natural assemblage or a culture, it cannot be concluded that *N. salinicola* and *N. incertata* are conspecific. Whether Simonsen's (1987) choice of lectotype material is justified, remains to be assessed.

Biogeography & Ecology: *N. salinicola* was mainly found in very fine sandy to silty sediments in the inner and middle reaches of the estuary (cf. low salinity optimum, Table 39). As for other small *Navicula* spp. (cf. *N.* cf. *perminuta*) it is hard to assess the exact geographical distribution of this species on the basis of published data alone *N. salinicola*-like specimens are commonly reported from estuarine and marine habitats in e.g. Europe (Krammer & Lange-Bertalot 1986) and North America (Cooper 1995a, as *N. incerta*).

NAVISALI

Navicula starmachioides Witkowski & Lange-Bertalot 1996 nom. nov. pro *N. starmachii* Witkowski & Lange-Bertalot 1994 non Kaczmarska 1976

[Figs 18-1, 18-2, 18-3, 18-4, 18-5, 18-6, 18-7, 18-8, 18-9, 50-7]

References:

(1) Witkowski 1994
(2) Witkowski 1994
(3) Witkowski 1994, Metzeltin & Witkowski 1996

Morphology:

L: 8.7-21.9; W: 2.5-3.7(-4.7?); S: (13-)14-18.5

LM - Plastids two, girdle-appressed, arranged asymmetrically about the apical plane. Frustules in girdle view almost rectangular; they are constricted in the centre. Valves elliptical to lanceolate, apices rounded to rostrate. Axial area narrow, distinct; central area rectangular. Raphe appears slightly curved. Central raphe endings close together, straight, expanded (pore-like). Central nodule roundish, distinct. Terminal raphe endings deflected in the same direction, lying in a distinct terminal nodule. In specimens with rostrate apices, they are seen to lie at some distance from the apical valve margin. Striae slightly radiate in the centre to convergent towards the apices. The cingulum appears to consist of at least one wide copula.

SEM - Valve face more or less flat, gently curving into the mantle, which is rather deep. Raphe curved, especially near apices; central raphe endings very close, slightly deflected to the same side. Terminal raphe endings clearly deflected in the same direction. No terminal fissures present. Terminal nodules well-developed. The striae consist of apically elongated, slit-like areolae.

Remarks: *Navicula starmachioides* was only recently described from brackish-water sediments in the Baltic Sea (Witkowski 1994). Our specimens are slightly different from the type specimens: they are usually smaller and have a higher average stria density. Our specimens also have more parallel striae. Small specimens belonging to this species can easily be confused with other small *Navicula* species such as *N. diserta* (cf. Simonsen 1987, Pl. 379, Figs. 39-40). See also *N. diserta* and *N.* sp. 3.

Biogeography & Ecology: *Navicula starmachioides* has up to now only been reported from the Baltic area. We have observed it in samples from the Westerschelde estuary but also in Salah's material from Blakeney Point (England) and Hustedt's material from the German Wadden Sea (see *Navicula diserta*). It thus appears to be common on all North Sea coasts.
In the Westerschelde estuary, *N. starmachioides* was common in different sediment types, mainly in the mesohaline section of the estuary. This is in accordance with its occurrence in the brackish Baltic Sea. It is a typical component of spring assemblages.

NAVISTAR

Navicula sp. 1

[Figs 18-28, 18-29, 18-30, 18-31, 18-32, 19-6, 52-1]

References:

(1)
(2)
(3) Lange-Bertalot 1993b, Witkowski 1994

Morphology:

L: 7.5-15; W: (3.5-)3.7-4.4; S: (15-)16-18.5(-19.5)

LM - Two girdle-appressed plastids, arranged asymmetrically about the apical plane. Valves lanceolate, apices cuneate obtuse to cuneate. Axial area narrow, central area usually roundish. Raphe straight, central raphe endings straight, slightly expanded, separated by a distinct, rectangular central nodule. Terminal raphe endings expanded, slightly deflected in the same direction. Striae sometimes parallel though usually more or less radiate in the centre to convergent towards the apices. Their structure is indistinct.

SEM - Only internal valve views were obtained. Valve face flat, gently curving into a shallow mantle. Internal raphe sternum well developed; the raphe fissures open more or less laterally, except in the centre and at the terminal nodules. A thickening of the raphe-sternum occurs in the centre (central nodule) but not to such an extent as Round *et al.* (1990) described for the genus *Navicula* s.s., nor did we observe an accessory rib along the raphe. Terminally, a small helictoglossa is present. The striae consist of slightly rectangular areolae; internally these are occluded by a hymenate velum. Semicircles of small puncta are present around the terminal nodules.

Remarks: This species is very reminiscent of the recently described *Navicula germanopolonica* Witkowski & Lange-Bertalot (Lange-Bertalot 1993b) but differs from the latter in having a higher areolation density (about 40-50 in 10 µm versus 25-28 in 10 µm for *N. germanopolonica*). Accordingly, the lineolate nature of the striae could not be observed in the LM (unlike in *N. germanopolonica*, cf. Lange-Bertalot 1993b, pl. 45, Figs. 1-5). Sundbäck (1981, as *Navicula* typ I and 1983, as *Navicula* sp. 1) and Kuylenstierna (1989-90, as *Navicula* sp. C) both reported a taxon similar to *Navicula* sp. 1 from the Swedish west coast. However, their specimens have clearly lineolate striae and therefore most probably belong to *N. germanopolonica*, although they both have a higher number of striae in 10 µm (viz. 18-22).

Biogeography & Ecology: *Navicula* sp. 1 is one of the most common epipsammic diatoms in fine sandy sediments throughout the Westerschelde estuary.

NAVISP01

Navicula sp. 2

[Figs 18-42, 18-43, 18-44, 18-45, 52-5]

References:

(1)
(2)
(3) Hustedt 1939, Simonsen 1987, Sundbäck 1981, Lange-Bertalot & Rumrich 1981, Hendey 1964, Witkowski 1994

Morphology:

L: 7.5-13.1(-17.8); W: 4.4-6; S: 16-18(-20?)

LM - Valves lanceolate, apices cuneate obtuse. Axial area narrow, central area more or less developed, of variable shape and size. Raphe straight; central raphe endings straight, slightly expanded, separated by a small though distinct, rectangular central nodule. The terminal raphe endings are expanded and deflected towards the same side. Striae radiate in the centre to slightly convergent near the poles. In the centre, one to several shortened striae are present.

SEM - Only external valve views were observed. Valve face flat, curving into a shallow mantle. Raphe-sternum more or less wide, central raphe endings strongly hooked in the same direction, opening into a spathulate groove. Terminal raphe endings slightly deflected in the same direction (opposite to the one of the central raphe endings), terminal fissures strongly hooked in the same direction as the central raphe endings. Striae consist of apically elongate areolae. In the centre, a few shortened striae are present. Note the presence of a few punctae around the terminal nodules. The cingulum consists of at least one, shallow copula.

Remarks: This taxon is characterized by its striation pattern in the centre of the valve, viz. strongly radiate, often curved striae. Most often these are alternatingly short and long. *N.* sp. 2 was also observed by Sundbäck (1981, as *N.* cf. *biskanteri*, and 1983, as *N.* sp. 5) on the Swedish West coast. *Navicula* sp. 2 is very reminiscent of *Navicula biskanterae* Hustedt [Hustedt 1939 (as *N. biskanteri* Hustedt), 1962] but differs from this species in the number of striae in 10 µm (which, according to Hustedt's protologue, is about 24). Also, the drawings of Hustedt (1939, 1962) show a diatom with a distinctly less radiate striation pattern in the centre of the valve. The latter is quite remarkable as Simonsen's lectotype specimens (from Memmert, a locality indicated by Hustedt in the protologue) all have distinctly radiate striae. It remains to be seen whether Simonsen's lectotype specimens truly concern *N. biskanterae*. Another similar species is *N. paul-schulzii* Witkowski & Lange-Bertalot which was recently described from the Baltic Sea (Witkowski 1994). However, comparison of this species with *N. biskanterae* shows that it is identical to Simonsen's lectotype specimens of *N. biskanterae* (Simonsen 1987). Before these taxa can be synonymyzed, the true identity of *N. biskanterae* has to be assessed. *Navicula* sp. 2 differs from *N. paul-schulzii* in stria density and pattern and in the shape and curvature of the central and terminal raphe endings.

Biogeography & Ecology: *N.* sp. 2 was an abundant epipsammic taxon in fine and especially medium sandy sediments, mainly in the middle and lower reaches of the estuary.

NAVISP02

Navicula sp. 3

[Figs 18-36, 18-37]

Morphology:

L: 7.5-14.4; W: 21.-2.9; W(P): 2.2-5.2; S: (19-)22-23(-25)

LM - Valves linear-lanceolate, apices cuneate. Axial area narrow, central area rectangular. Raphe more or less straight, central raphe endings appear straight; they are close together, pore-like. Terminal raphe endings expanded, slightly deflected in the same direction. Terminal nodules distinct. Striae parallel to convergent towards the apices.

Remarks: This taxon is just like a miniature version of *Navicula starmachioides* (see there), which itself seems to be a small form of *N. bipustulata*: they mainly differ from each other in size and stria density. Whether it concerns 3 different species or three closely related forms is difficult to assess and needs further investigation. The presence of small, possibly intermediate forms between *Navicula starmachioides* and *N. bipustulata* (e.g. Fig. 18-1) seems to suggest that these two taxa are related. On the other hand though, these three taxa seem to be distinct enough: their morphological variability seems to be restricted to certain size and stria density limits.

Biogeography & Ecology: *Navicula* sp. 3 is common in silty, very fine and fine sandy sediments throughout the estuary.; it appears to have an identical distribution to *N. starmachioides*.

NAVISP03

Navicula sp. 4

[Figs 18-33, 18-34, 18-35, 52-2]

Morphology:

L: 7.5-11.2; W: (2.7-)3.7-4.6(-5); S: (19-)21-22.5(-24)

LM - Valves lanceolate, apices cuneate; sometimes slightly produced. Axial area extremely narrow, central area small, more or less orbicular, sometimes slightly asymmetrical. Raphe straight, central raphe endings straight, only slightly expanded; central nodule distinct, rectangular. Terminal raphe endings straight or only slightly deflected to the same side. Striae slightly radiate (to parallel) throughout the valve, except near the apices where they are always parallel. Their structure is indistinct.

SEM - Only internal valve views were observed. Valve face flat, mantle shallow. Internal raphe sternum distinct, raised. The raphe fissures open more or less laterally, except in the centre and at the apices. No accessory rib is present (cf. *Navicula* sp. 1). The central raphe fissures are straight and close together. At the terminal raphe endings, a helictoglossa is present. Striae are composed of slightly elongated, hymenate areolae.A semicircle of small areolae is present along the apical margin.

Remarks: This taxon differs from *Navicula* sp. 1 in its striation pattern (which is more parallel) and density (which is higher).

Biogeography & Ecology: *Navicula* sp. 4 is an epipsammic species but appears to prefer coarser sediments than *N.* sp. 1 and also has a higher salinity optimum (note however that this could be due to the occurrence of medium sand in the estuary).

NAVISP04

Navicula sp. 5

[Figs 17-11, 17-12, 17-13, 50-5, 50-6]

Morphology:

L: 15.6-19.2, W: 3.7-5.4, S: (13-)14-14.5

LM - Valves elliptical with slightly produced apices. The valves usually lie in oblique view (cf. *N. bipustulata*). Axial area narrow, central area more or less rectangular. Raphe straight, raphe-sternum well-developed. Central raphe endings close together, straight, expanded; terminal raphe endings more or less straight, expanded. Central and especially terminal nodule well-developed. The terminal raphe endings lie at some distance of the apical valve margin. Striae distinctly lineolate (about 25 areolae in 10 µm), radiate in the centre to slightly convergent near the apices.

SEM - Only external valve views were observed. Valve face flat in the centre, more or less gently curving into the rather deep valve mantle. Raphe straight, raphe sternum slightly raised. Central raphe endings close together, only slightly deflected to the same side. Terminal raphe endings more or less straight (rather wavy than bent) and expanded, terminal nodule distinct, raised. No terminal fissures visible. Note the presence of a few apically orientated, slit-like areolae at the valve apices (Fig. 50-6). The striae consist of apically elongated areolae, although around the central area some pore-like and some more or less transapically orientated areolae are present.

Remarks: *Navicula* sp. 5 differs from *N. bipustulata* in valve shape, size and stria density. Its striae are also always distinctly lineolate in LM.

Biogeography & Ecology: *Navicula* sp. 5 was rare in fine sandy sediments in the middle reaches of the estuary. It appears to have a rather peculiar distribution as it was observed in large numbers on another sandflat in the estuary (which was not sampled in this study)(Sabbe, unpubl.).

NAVISP05

Navicula sp. 6

[Figs 17-9, 17-10]

Morphology:

L: 16.6-19, W: 4.1-5, S: 14-14.5

LM - Valves elliptical-lanceolate with produced, subrostrate apices. Axial and central area narrow. Raphe straight, raphe sternum distinct. Central raphe endings close together, straight, slightly expanded. Terminal raphe endings distinctly expanded and pore-like, deflected in the same direction. The terminal raphe endings lie at some distance from the apical valve margin. The striae are distinctly lineolate (about 24-25 areolae in 10 µm), radiate in the centre. No shortened striae are present in the centre of the valve.

Remarks: This taxon is very reminiscent of *Navicula* sp. 5. The two taxa were kept separate because *Navicula* sp. 6 has no transapically expanded central area. However, it is not unlikely that they are conspecific.

Biogeography & Ecology: *Navicula* sp. 6 was also observed together with *N.* sp. 5 (see there).

NAVISP06

Navicula sp. 7

[Figs 18-20, 18-21, 52-4]

References:

(1)
(2)
(3) Giffen 1975, Sundbäck 1982, Kuylenstierna 1989-90, Snoeijs & Potapova 1995

Morphology:

L: 7.7-13.7; W: 4.1-5.6; S: 15-17.5(-18.5)

LM - Valves lanceolate with more or less rounded to slightly produced apices. Axial area narrow, central area roundish, often more developed on one side of the valve. Raphe straight, central raphe endings straight, expanded (pore-like), separated by a well-developed, rectangular central nodule. Terminal raphe endings expanded, slightly deflected to the same side. Striae distinctly lineolate, parallel to radiate in the centre of the valve, convergent near the apices. The areolae are apically aligned, thus creating longitudinal striae which are curved around the central area.

SEM - Only external views were observed. Valve face flat, curving into a shallow mantle. Raphesternum indistinct except in the centre where a conopeum-like structure is present near the central pores (cf. *Navicula diserta*). The latter structure extends towards the apices about halfway the length of the raphe branches. Raphe straight, central raphe endings pore-like and straight. Terminal fissures strongly hooked in the same direction. The striae consist of widely spaced, apically elongated, slit-like areolae (about 23 in 10 µm, maybe more?). The cingulum consists of at least 3 to 4 copulae, which are slightly curved at the apices (Fig. 52-4).

Remarks: As *Navicula* sp. 1, this taxon strongly resembles *Navicula germanopolonica* (Lange-Bertalot 1993b). The main difference lies in the shape of the central area (which is more variable in *N. germanopolonica*), the striation pattern (which is centrally more radiate in *N. germanopolonica*) and the conopeum-like, lateral extensions along the raphe (which only occur in *N.* sp. 7)(cf. Lange-Bertalot 1993b, Pl. 45: Figs. 6-7).

Similar diatoms were also reported by Sundbäck (1981), Kuylenstierna (1989-90) and Snoeijs & Potapova (1995). They were identified as *Navicula viminoides* Giffen (Giffen 1975). As for shape, size and the presence of the conopeum-like raphe structure, *N.* sp. 7 is indeed very reminiscent of specimens of *N. viminoides sensu* Sundbäck (1981, cf. also Snoeijs & Potapova 1995). However, it differs in stria density (about 12 str./10 µm in *N. viminoides*) and maybe also in the structure of the central area, which is reported to be 'absent or variously lanceolate through failure of the ends of some of the middle striae' instead of distinctly circular as in *N.* sp. 7 (Giffen 1975).

Biogeography & Ecology: *Navicula* sp. 7 is a common epipsammic species in fine sandy to very fine sandy sediments in the mesohaline reaches of the Westerschelde estuary.

NAVISP07

Navicula sp. 8

[Figs 21-9, 21-10, 21-11]

References:

(1)
(2)
(3) Hustedt 1939, Krammer & Lange-Bertalot 1985, 1986, Simonsen 1987

Morphology:

L: 15-23.7; W: 3.7-5; S: (17.5-)18-20.5

LM - Valves lanceolate; they give the impression of being only weakly silicified. The valve face appears to be very flat, with a shallow mantle. Apices slightly produced (to cuneate-subrostrate). Axial and central area narrow. Raphe straight, raphe-sternum distinct; the latter is constricted inbetween the central raphe endings. These are close together, expanded and pore-like. Terminal raphe endings slightly deflected in the same direction, expanded. Terminal and central nodules pronounced. Striae indistinct, parallel throughout the valve or slightly radiate in the centre to slightly convergent towards the apices.

Remarks: This taxon is illustrated in Simonsen (1987, Pl. 378, fig. 11-15, as *Navicula abscondita*) and is probably as yet undescribed. For a more detailed discussion, see under *N. abscondita*. Both taxa are actually quite similar at first glance and are often sympatric (cf. also Hustedt 1939). Further research is needed to assess their relationship [maybe similar to the one described by Cox (1985) for *Dickieia ulvacea* Berkeley ex Kützing (syn. *Navicula ulvacea* (Berkeley ex Kützing) Cleve) and *Navicula subinflatoides*?].

Biogeography & Ecology: *Navicula* sp. 8 is rare in different sediment types, mainly in the mesohaline reaches of the Westerschelde estuary.

NAVISP08

Navicula sp. 9

[Figs 16-9, 16-10, 54-2, 54-3]

Morphology:

L: 11.2-25.6; W: 3.1-6.6; S: 19-21.5 (-24?)

LM - Valves lanceolate, apices cuneate to subrostrate. Axial area very narrow on one side, (apparently) wider on the other side (merging with a longitudinal hyaline area). Central area transapically expanded but vaguely delimited, connected to lateral hyaline areas. Raphe straight, central raphe endings expanded and pore-like, terminal raphe endings curved. Striae slightly radiate to slightly convergent near the apices. They are crossed by rather irregularly shaped and placed lateral hyaline areas.

SEM - Valve face flat, at almost right angles to the shallow mantle. The raphe is straight, the external central raphe endings are conspicuously droplet-like and curved; the terminal fissures are hooked in the same direction, opposite to the one of the central raphe endings. Internally, a distinct accessory rib is present; the terminal raphe endings end in a helictoglossa. The structure of the striae is peculiar: only a few curved, longitudinal lines of slit-like areolae are present. In addition, a distinct, complete marginal ring of slit-like areolae is present on the mantle. Note also that there is always one longitudinal, centrally interrupted line of areolae alongside the raphe. Internally, the areolae are occluded by domed vela. The cingulum appears to be composed of at least one, non-porous copula.

Remarks: This taxon could not be assigned to any known species and probably concerns an undescribed species.

Biogeography & Ecology: *Navicula* sp. 9 was very rare in medium sandy sediments in the mouth of the estuary. It was also present in samples from beach sediments along the Belgian coast (Blondeel 1996). It thus appears to be a typical species of marine sandy sediments.

NAVISP09

Navicula sp. 10

[Figs 20-19, 20-20, 21-20, 21-21]

Morphology:

L: 17.2-31.9; W: 4.5-7.5; (12-)12.5-14.5(-15)

LM - Plastids two, girdle-appressed, arranged symmetrically about the apical plane. two conspicuous droplets are present fore and aft the central cytoplasmatic bridge. Valves linear-lanceolate to lanceolate. The valve face appears very flat in LM (compare to *Navicula flanatica*); the mantle seems to be very shallow. Apices slightly produced, cuneate to subrostrate. Axial area narrow, central area small, often asymmetrical, more or less rectangular (due to shortening of one or more central striae) or absent. Raphe straight, central raphe endings close, expanded to pore-like. Terminal raphe endings hooked (!) in the same direction. Striae lineolate, parallel to slightly radiate, convergent near the apices.

Remarks: This taxon differs from *Navicula flanatica* in usually having a distinct central area and parallel striae. It also resembles *Navicula* cf. *mollis* but differs from this species in having distinctly lineolate striae.

Biogeography & Ecology: *Navicula* sp. 10 is a common epipelic taxon in different sediment types, especially in the polyhaline reaches of the estuary. It is a typical component of late winter/early spring epipelic diatom assemblages. It is also present in Salah's material from Blakeney Point on the English East coast (BM 36407).

NAVISP10

Navicula sp. 11

[Figs 19-8, 19-9]

Morphology:

L: 17.2-17.4; W: 3-3.7; S: 18-21 (n=2)

LM - Valves linear-elliptical, apices broadly rounded. Axial area narrow, central area broad, more or less square. Raphe straight, central raphe endings slightly expanded; wide apart. Terminal raphe endings expanded and deflected in the same direction. Striae radiate in the centre to convergent near the apices. Their structure is indistinct.

Remarks: Only a few valves belonging to this taxon were found.

NAVISP11

Navicula sp. 12

[Figs 16-7, 16-8, 54-5]

References:

(1)
(2)
(3) Vos 1986, Blondeel 1996

Morphology:

L: 15-22.9; W: 5.7-7.5; S: 18-20

LM - Valves elliptical, apices rostrate to rostrate-capitate. Valve face flat, mantle extremely shallow. Axial area narrow, central area absent. Raphe straight, central raphe endings straight, pore-like. Terminal raphe endings slightly deflected in the same direction. Striae punctate, parallel to radiate towards the apices. On each side of the raphe, two to four distinct, parallel longitudinal striae are present; they curve around the central nodule. On both sides of the central nodule, one to three transapically elongated, distinct areolae are present.

SEM - Only internal valve views were observed. The valve face is very flat, the mantle is extremely shallow. The raphe-sternum is well-developed and appears to have an accessory rib; the raphe-fissure opens laterally. The internal central raphe endings are straight, the terminal ones are also more or less straight and end in a distinct helictoglossa. The striae are composed of somewhat round areolae, occluded by a (hymenate?) velum. Near the margins and alongside the raphe, the areolae are slightly apically elongated, while on both sides of the central nodule, distinctly transapically elongated areolae are present. The cingulum structure is unknown.

Remarks: This taxon probably does not belong to *Navicula* s.s. More detailed examination of plastid and frustule structure is needed before its generic allocations can be assessed.

Biogeography & Ecology: *Navicula* sp. 12 was rare in different sediment types in the poly- and euhaline reaches of the Westerschelde estuary. This taxon has hitherto also been reported from the Oosterschelde (Vos 1986), which until the middle of the 20th century used to be a part of a larger river delta just north of the Westerschelde estuary, but which nowadays constitutes a tidal inlet of the North Sea. It was also common in sediment samples from sandy beaches along the Belgian coast (Blondeel 1996).

NAVISP12

Navicula sp. 13 [Figs 19-1, 19-2, 19-3, 19-4]

Morphology:

L: 14.4-20; W: about 4.5; S: 17-24

LM - Frustules in girdle view linear, with broadly rounded apices. Plastids two, girdle-appressed, asymmetrically arranged about the apical plane. It was also observed that the plastids were always brightly green and not yellowish brown as in most diatoms. Two conspicuous droplets accompany each plastid. Valves lanceolate with rostrate apices, though usually lying in girdle view. The valves appear to be strongly convex in transapical section; the mantle is deep. Raphe branches curved in girdle view. Central raphe endings very close together, pore-like. Terminal raphe endings lie at some distance of the apical valve margin. Striae parallel to convergent near the apices. The central ones are sometimes slightly more widely spaced. Their structure is indistinct. The cingulum appears to be composed of one wide copula.

Remarks: This taxon was almost without exception observed in girdle view. It might belong to the species complex around *N. apiculata* (cf. above); further research is needed.

Biogeography & Ecology: *Navicula* sp. 13 is common in different sediment types in the Westerschelde estuary and is more abundant in the mesohaline stations.

NAVICSAL

Navicula sp. 14 [Figs 19-12, 19-13, 19-14]

Morphology:

L: 13.7-18.7; W: 4.4-5; W(P): 6.9; S: 20-24

LM - Valves lanceolate, slightly curved along the apical axis. Apices cuneate. The valves usually lie in a slightly tilted position, more or less yielding a girdle view of the valve. Axial area narrow, central area small, rectangular. Raphe straight, central raphe endings expanded to pore-like, deflected in opposite directions. Terminal raphe endings not visible. Striae parallel in the centre, but strongly radiate throughout the rest of the valve. The cingulum seems to consist of at least one, wide copula (Fig. 19-13).

Remarks: This easily recognizable taxon could not be identified with the consulted literature. It probably does not belong to *Navicula* s.s.

Biogeography & Ecology: *Navicula* sp. 14 was rare in the Westerschelde estuary; nothing is known about its ecological requirements.

NAVISP14

Navicula sp. 15 [Figs 21-12, 21-13]

Morphology:

L: 13-16; W: 4.6-5; S: 15.5-17.5

LM - Valves lanceolate, apices cuneate, slightly produced. Axial and central area extremely narrow. Raphe curved (?), central raphe endings very close together, straight, expanded. Striae distinctly lineolate, radiate in the centre to convergent near the apices.

Biogeography & Ecology: *Navicula* sp. 15 was common in silty sediments throughout the Westerschelde estuary; it was most abundant in spring.

NAVISP15

Trachyneis Cleve 1894

Genus description: Round *et al.* 1990

Trachyneis aspera (Ehrenberg 1840) Cleve 1894

Synonyms:

Navicula aspera Ehrenberg 1840

References:

(1) Ehrenberg 1841
(2)
(3) Hartley *et al.* 1996

Morphology:

L: 49.5; W: 9.5; S: 14 (n=1)

LM & SEM - Frustules rectangular with constricted centre in girdle view. Two rectangular, girdle-appressed plastids with serrated margins. For a complete LM and SEM description of this species, see Hendey (1964) and Round *et al.* (1990).

Biogeography & Ecology: *Trachyneis aspera* is an common epipelic species in Europe (Hendey 1964, Kuylenstierna 1989-90), North America (Cooper 1995a), South East Asia (John 1983, Podzorski & Håkansson 1987). In the Westerschelde estuary, it was mainly found in sandy sediments near the mouth of the estuary.

TRACASPE

Fam. PLEUROSIGMATACEAE Mereschkowsky

Gyrosigma Hasall 1845

Genus description: Cardinal *et al.* 1989, Round *et al.* 1990, Sterrenburg 1991

The systematics of the diatom genera *Gyrosigma* and *Pleurosigma* (see below) are treated in detail in an ongoing series of publications by Sterrenburg (1990-1995).

Gyrosigma acuminatum (Kützing 1833) Rabenhorst 1853

Synonyms:

Frustulia acuminatum Kützing 1833
Gyrosigma spenceri (Quekett 1848) Griffith & Henfrey 1856

References:

(1) Kützing 1833
(2) Sterrenburg 1995
(3) Sterrenburg 1994, 1995, Snoejs & Vilbaste 1994

Morphology:

L: 80-82.5; W: 11.2; S: 23-25 (long.), 23-24 (transverse)(n=2)

LM - Valves sigmoid-oblong, apices rounded. Axial area narrow, raphe sigmoid. The pore-like central raphe endings lie in a slightly transapically expanded central nodule. The terminal fissures could not be observed. Both longitudinal and transverse striae can be observed; the longitudinal ones are absent near the valve margin.

Remarks: As the type material of *G. spenceri* fully matches the more slender specimens of *G. acuminatum*, *G. spenceri* is a later synonym of *G. acuminatum* (Sterrenburg 1994). However, this does not mean that the numerous reports of *G. spenceri* from brackish and marine localities would actually concern *G. acuminatum* specimens, as this species mainly occurs in freshwater or brackish waters. It is more likely that they concern some other, yet undescribed or undefinable taxa. For a thorough discussion on these taxa, see Sterrenburg (1995).

Biogeography & Ecology: *Gyrosigma acuminatum* is a common epipelic species from electrolyte-rich to brackish waters (Cox 1996). Only a few damaged valves were found in our material.

GYROACUM+GYROSPEN

Gyrosigma fasciola (Ehrenberg 1841) Griffith & Henfrey 1856

Synonyms:

Ceratoneis fasciola Ehrenberg 1841

References:

(1) Ehrenberg 1843
(2)
(3) Krammer & Lange-Bertalot 1986, Kuylenstierna 1989-90

Morphology:

L: 78.5; W: 10.5; S: 25 (transverse) (n=1)

LM - See Krammer & Lange-Bertalot 1986.

Biogeography & Ecology: *Gyrosigma fasciola* is a common epipelic species in Europe (Krammer & Lange-Bertalot 1986, Hartley *et al.* 1996), North America (Cardinal *et al.* 1986) and elsewhere. It was generally rare in our material but could become locally dominant (Sabbe, unpubl.).

GYROFASC

Pleurosigma W. Smith

Genus description: see references *Gyrosigma*

Pleurosigma aestuarii (Brébisson in Kützing 1849) W. Smith 1853

Synonyms:

Navicula aestuarii Brébisson ex Kützing 1849
Pleurosigma angulatum var. *aestuarii* (Brébisson) Van Heurck 1880

References:

(1) Kützing 1849
(2)
(3) Kuylenstierna 1989-90

Morphology:

L: 84.5-90; W: 20.6-21; S: 21 (diagonal), 19-21 (transverse).

LM - Valves sigmoid-lanceolate, apices rostrate. Axial area narrow, raphe sigmoid. Central raphe endings close together, pore-like, lying in a distinct, circular to elliptic central nodule. The striation pattern consists of three systems of transverse and oblique lines which cross each other at an angle of about 57°. However, at the apices, this pattern shifts into a pattern with two systems of lines (longitudinal and transverse).

Remarks: The relationship between *Pleurosigma aestuarii* and *P. angulatum* (sensu W. Smith, cf. Sterrenburg 1990) is not very clear. Van Heurck (1880, cf. also Patrick & Reimer 1966, Cardinal *et al.* 1989, Kuylenstierna 1989-90) considered *P. aestuarii* as a variety of *P. angulatum*: the nominate variety would have a slightly coarser striae and rounded, non-rostrate produced apices.

Biogeography & Ecology: *P. aestuarii* is a common epipelic species in Europe (Kuylenstierna 1989-90, Hartley *et al.* 1996), North and South America (Atlantic coasts, Cardinal *et al.* 1986, Sterrenburg 1991), In the Westerschelde estuary, it was rare in silty sediments in the polyhaline and euhaline reaches.

PLEUAEST

Fam. STAURONEIDACEAE Mann

Craticula Grunow 1868

Genus description: Round *et al.* 1990

Craticula cuspidata (Kützing 1833) Mann 1990

Synonyms:

Frustulia cuspidata Kützing 1833
Navicula cuspidata (Kützing 1833) Kützing 1844

References:

(1) Kützing 1833
(2)
(3) Krammer & Lange-Bertalot 1986, Round *et al.* 1990

Morphology:

LM & SEM description: Krammer & Lange-Bertalot 1986

Biogeography & Ecology: Only one valve belonging to this predominantly freshwater species was found.

CRATCUSP

Ordo Thalassiophysales

Fam. CATENULACEAE Mereschkowsky

Amphora Ehrenberg ex Kützing 1844

Genus description: Round *et al.* 1990, Mann 1994b

> 'Es ist sicher, dass gerade die kleinen marinen *Amphora*-arten einer gründlichen Revision bedürfen, ...' (Aleem & Hustedt 1951)
>
> 'Such a decision, however, should await the much needed revision of the Section *Halamphora*...' (Sullivan 1979)
>
> '...yet another taxon which emphasizes the need of a thorough revision of the *A. acutiuscula-coffeaeformis* complex' (Archibald 1983)

Amphora is a large and heterogeneous genus with predominantly marine representatives which is in need of thorough revision (Krammer & Lange-Bertalot 1986, Round *et al.* 1990, Mann 1994b). Cleve (1895) recognized 9 subgenera within the genus *Amphora*, but recent evidence based on cytological and reproductive studies has shown that these subgenera themselves are heterogeneous and therefore do not constitute a sound basis for revision (Mann 1994b).

Several species complexes in this genus are very complicated, e.g. the *Amphora coffeaeformis-acutiuscula* complex. During this study a number of taxa belonging to this cluster were found, viz. comprises *Amphora coffeaeformis* and its varieties, *A.* cf. *exigua*, *A.* cf. *delicatissima*, *A.* cf. *subacutiuscula*, *A. tenerrima*, *A.* sp. 3, *A.* sp. 6 and *A.* sp. 7. In SEM they all appear to have a similar structure: the dorsal striae are usually biseriate near the raphe and become uniseriate towards the dorsal margin. However, the (transapical) length of the biseriate part is variable, and it is uncertain whether this feature varies within or between taxa. The dorsal striae are sometimes crossed by a longitudinal crossbar or, more often, by shorter apically orientated ribs. This ultrastructural uniformity makes it hard to assess the apparent high variability in size and striae density. Whether we are dealing with numerous separate taxa or only a few, highly variable ones, can only be determined through culture studies and/or comparing the ultrastructure of different populations from different localities. Given the widespread and common occurrence of representatives of this group in brackish and marine environments, their confusing taxonomy and, as a consequence, complicated nomenclature, a thorough revision of this group is needed. The problems surrounding this species complex are treated in more detail in chapter 6.3.1.1.

Many representatives of the genus *Amphora* appear to be most abundant in summer (see below), while most other epipelic taxa have their maximum abundance in spring.

The terminology used in the descriptions of the *Amphora* species below is based on Schoeman & Archibald (1976-80) and Krammer (1980).

Amphora coffeaeformis (Agardh) Kützing 1844

[Figs 25-15, 25-16, 27-1, 27-2, 57-4, 57-5]

Synonyms:

Frustulia coffeaeformis Agardh
Amphora salina W. Smith
For a more complete synonymy list, see Archibald & Schoeman 1984.

References:

(1) Agardh 1827
(2) Archibald & Schoeman 1984
(3) Bérard-Therriault *et al.* 1986, Krammer & Lange-Bertalot 1986, Schoeman & Archibald 1987b

Morphology:

L: 27.5-50; W: 5-6.2; S(D): 16-20(-24?); S(V): 22-32(-44?) (n=9)

LM - Frustules elliptical with broadly rostrate apices. Plastid H-shaped; they consist of two large lobes lying against the dorsal girdle and connected in the centre. Two droplets are associated with each lobe; two droplets are also present inbetween the lobes, fore and aft the central bridge (not visible in Figs 27-1, 27-2). Dorsal margin convex, ventral margin straight but usually slightly concave. Axial and central area narrow, raphe more or less striaght. Central raphe endings expanded, slightly bent to the dorsal side, terminal raphe endings deflected to the ventral side. A longitudinal line (= dorsal conopeum margin, see below) runs alongside the raphe. Dorsal striae radiate; their structure is indistinct. Ventral striae distinct in some specimens but barely visible in others; they are always interrupted in the centre.

SEM - Valve face flat; the dorsal mantle is at right angles to the valve mantle. External raphe fissures accompanied by a dorsal accessory rib running the whole length of the raphe. A wide dorsal conopeum is present. Central raphe endings slightly expanded, terminal fissures deflected to the dorsal side. Dorsal striae biseriate, ventral striae uniseriate (?). Internally, the position of the conopeum is visible as a longitudinal fold running alongside the raphe. The terminal raphe endings end in a helictoglossa; a dorsal flap hides the central raphe endings. Cingulum wide, consisting of numerous open, punctate copulae.

Remarks: On account of the numerous observations of this species from the most diverse localities, one gets the impression that this is one of the most common brackish-water *Amphora* species. However, Archibald & Schoeman (1984), in their excellent revision of this species, already indicated that many old and recent reports are incorrect due to misinterpretations of its identity. They presented a new and more comprehensive concept of *A. coffeaeformis*, based on a LM and SEM study of the type material. In our study, only valves fitting this description were assigned to this species. Especially the non-punctate structure of the dorsal striae in LM appears to be a typical feature of this species (cf. also Krammer & Lange-Bertalot 1986).

Biogeography & Ecology: *Amphora coffeaeformis* is commonly reported from brackish and marine sites worldwide. However, as Archibald & Schoeman (1984) point out, many reports (especially the ones without good illustrations) are not trustworthy. Given the current status of this species as being one of the most common brackish-water *Amphora* taxa, surprisingly few specimens of this species were observed in the Westerschelde estuary. Here it was mainly present in silty sediments throughout the estuary. It was most abundant in summer.

AMPHCOFF

Amphora coffeaeformis* var. *aponina (Kützing 1844) Schoeman & Archibald 1984

[Figs 25-17]

Synonyms:

Amphora aponina Kützing

References:

(1) Kützing 1844
(2) Archibald & Schoeman 1984
(3) Schoeman & Archibald 1987b

Morphology:

L: 16.6-25; W: 3.1-3.7; S(D) 19-22(-24?)

LM - Valves semi-lanceolate with capitate apices. Dorsal striae radiate; their structure is indistinct. The ventral striae could not be resolved in LM.

Remarks: Cleve (1895) considered this taxon as a synonym of *A. coffeaeformis* (cf. also Van Landingham 1967). Schoeman & Archibald (1984) however found some subtle differences between these taxa and consider *A. aponina* as a variety of *A. coffeaeformis*.
The smaller specimens are very reminiscent of *Amphora tenerrima*; further study is needed to elucidate the relationships between both taxa.

Biogeography & Ecology: Only a few valves belonging to this taxon were observed.

AMPHCOAP

Amphora copulata (Kützing) Schoeman & Archibald 1986 [Figs 23-17, 23-18]

Synonyms:

Frustulia copulata Kützing 1833
Amphora libyca Ehrenberg
Amphora affinis Kützing

References:

(1) Kützing 1833
(2) Lee & Round 1988 (SEM), Schoeman & Archibald 1986c (LM)
(3) Krammer & Lange-Bertalot 1986, Lee & Round 1988, Schoeman & Archibald 1986c, Snoeijs 1993

Morphology:

L: 21.2-32.5; W: 6.2-7.2; S: 15-16 (n=2)

LM - Valves semi-elliptical. Dorsal margin convex, ventral margin straight. Raphe (slightly ?) biarcuate. Dorsal striae parallel in the centre, radiate at the poles, composed of several areolae. A more or less square to rectangular central area is present on the dorsal valve face. It is separated from the raphe by one (?) row of areolae. Ventral striae radiate in the centre, convergent at the poles, interrupted in the centre.

Remarks: Our specimens fully match the description given in Schoeman & Archibald (1986c).

Biogeography & Ecology: Only a few valves of this widespread freshwater species were found (see also *A.* cf. *copulata*).

AMPHCOPU

Amphora cf. *copulata* [Figs 23-15, 23-16, 23-19, 23-20, 23-21, 23-22, 23-23, 23-24, 56-1, 56-2, 56-3]

Morphology:

L: 14.7-45; W: 3.7-7.7; S(D): 14.5-18; S(V): 13.5-18

LM - Plastids H-shaped, lying against the ventral girdle, with 4 lobes projecting dorsally. Two droplets lie in the centre between the lobes. Valves semi-elliptical to slightly semi-arcuate. Apices rounded. Dorsal margin convex, ventral margin straight to concave. Raphe bi-arcuate, central raphe endings more or less straight to slightly dorsally deflected. Dorsal striae parallel in the centre to radiate at the apices. They consist of transapically elongated areolae (which are visisble depending on the orientation of the valve). Usually a prominent longitudinal, hyaline bar is present in the proximal dorsal valve face, though in some specimens this seems to be lacking. In other valves, a small lanceolate hyaline area can be present in the middle of this hyaline bar. The ventral striae consist of one or two elongated puncta; in the latter case they are separated by a longitudinal hyaline area (cf. *Amphora pulchella*). In most cases, the ventral striae are interrupted in the centre.

SEM - The ventral and proximal dorsal valve face lie in one plane, clearly separated from the distal dorsal area by a prominent longitudinal rib. Central raphe endings dorsally deflected, terminal fissures hooked to the dorsal side. A prominent dorsal conopeum is present. On the ventral side, a conopeum is only slightly developed at the apices and sometimes also in the centre (Fig. 56-2). On the proximal dorsal valve face, a hyaline area, which fades into an irregular rib towards the apices and is sometimes transapically expanded in the centre, can be distinguished; in smaller specimens this hyaline bar is absent (or hidden by the conopeum?, Fig. 56-3). In the distal dorsal area, the striae are composed of several (up to 5 or more) transapically elongated areolae. The ventral striae consist of 1 (to 2, cf. Fig. 56-1) elongated, slit-like areolae. The cingulum consists of 4 open (?) copulae.

Remarks: *A.* cf. *copulata* is a variable taxon: especially the shape of the longitudinal hyaline bar is very variable. Whether we are dealing with a morphological continuum or whether distinct morphological forms can be discerned is impossible to assess on the basis of the material hitherto examined. *A.* cf. *copulata* appears to be closely related to *A. copulata* and *A.* cf. *helenensis* (see there). The main difference between *A.* cf. *copulata* and the type of *A. copulata* (cf. Lee & Round 1988, Figs. 1-6) lies in the ventral area, which has a well-developed conopeum in the latter, and its ecology (*A. copulata* is a freshwater species). *A.* cf. *copulata* closely resembles form C of Lee & Round (1988), which has a similar, rudimentary ventral conopeum.

A. cf. *copulata* is probably related to *A. copulata* in a similar way as the various freshwater forms (of hitherto unknown taxonomical rank) of this species (cf. Lee & Round 1988). A similar phenomenon could also be observed in the cluster of forms around *A. pediculus* (see there). Information on the possible occurrence of different forms of these species in brackish and marine habitats is to our knowledge non-existent. Whether we are dealing with separate taxa (species or varieties) or mere phenotypical variation of one and the same taxon remains unknown until further studies are carried out.

Similar *A. copulata*-like taxa were also found in Hustedt's (marine) material from Borneo (BRM slide N15/51, Miang Besar, Borneo 4) and the German wadden Sea (BRM N12/36), in Canada (Bérard-Therriault *et al.* 1986; as *A. libyca* = *A. copulata*), in the Caspian Sea (Karayeva 1987; as *A. proteus* Gregory f. *ambigua* Proschkina-Lavrenko), in Great Britain (Hartley *et al.* 1996) and in South Africa (Giffen 1963; as *A. javanica*, which is probably a misidentification [cf. the original illustration in A. Schmidt (1874-1859)]. Especially the last is very reminiscent of our forms but has a slightly lower stria density (12 versus 13.5-18).

Biogeography & Ecology: *Amphora* cf. *copulata* is rare in different sediment types, mainly in the mesohaline reaches of the Westerschelde estuary.

A. copulata is usually characterized as a freshwater species from waters with moderate to high electrolyte content (Krammer & Lange-Bertalot 1986, Cox 1996). The forms we have grouped in *A.* cf. *copulata* (and which are very closely related to *A. copulata*) are without doubt brackish-water species: thriving populations were found in the meso- and polyhaline reaches of the Westerschelde estuary (cf. also references from other localities). *A.* cf. *copulata* appears to be cosmopolitan (cf. above). Similar specimens have also been reported from brackish and marine localities worldwide (cf. references listed above, Cooper 1995a, Fig. 109).

AMPHCFCO

Amphora cymbamphora Cholnoky 1960

[Figs 21-15, 21-16]

Synonyms:

Amphora natalensis Cholnoky 1960
Amphora novaeguineae Cholnoky 1963

References:

(1) Cholnoky 1960
(2)
(3) Archibald 1983, Kuylenstierna 1989-90

Morphology:

L: 16.9-23.2; W: 3.7-4.4; S(D): 17-19; S(V): 17.5-20

LM - Valves semi-lanceolate to almost semi-rhombic; apices slightly produced, cuneate to subrostrate. Dorsal margin convex, ventral margin straight. Raphe straight to slightly bi-arcuate, close to the ventral margin. Central raphe endings close together, expanded. Dorsal striae parallel to slightly convergent near the apices; the central one(s) can be slightly shorter. Ventral striae short, not interrupted in the centre.

Remarks: Our specimens are identical to the ones Archibald (1983) described as being 'atypical', although they are still identified as *Amphora cymbamphora* (cf. also Kuylenstierna 1989-90 who observed similar specimens). *Amphora ramsbottomi* Salah (Salah 1955) and *A. macilenta* Gregory (1857, see also Peragallo & Peragallo 1897-1908) are very reminiscent of *A. cymbamphora* (and were described prior to the latter species) but have a lower stria density.

A. cymbamphora probably forms part of the species complex around *Amphora angusta* Gregory, comprising a.o. *A. ramsbottomi*, *A. tenarescens* Cholnoky, *A. cymbamphora*, *A. macilenta*, *Seminavis ventricosa* (Gregory) Garcia-Baptista (Garcia-Baptista 1993b). More species might have to be transferred to the recently established genus *Seminavis* Mann (Round *et al.* 1990).

Biogeography & Ecology: *A. cymbamphora* has been reported from Europe (Kuylenstierna 1989-90, this study), Africa (Cholnoky 1960, Archibald 1983) and South East Asia (as *A. novaeguineae*, Cholnoky 1963). In the Westerschelde estuary, *A. cymbamphora* was common in silty to fine sandy sediments in the polyhaline reaches. It was most abundant in summer.

AMPHCYMB

Amphora* cf. *delicatissima Krasske 1930

[Figs 26-5, 26-6, 26-7,]

Synonyms:

Amphora coffeaeformis var. *perpusilla* Grunow 1884

References:

(1) Krasske 1930
(2) Krammer & Lange-Bertalot 1986
(3) Krammer & Lange-Bertalot 1986

Morphology:

L: 9.7-19.5; W: 2.5-5; S(D): 28-34

LM - This taxon closely resembles *Amphora* sp. 2 but is on average slightly larger, often has a flattened dorsal margin and does not have the typical curves (which run from the ventral margin to the central nodule in *A.* sp. 2).

Remarks: This taxon might have to be united with *A.* sp. 2 but this will have to await SEM study of *A.* cf. *delicatissima*. We tentatively identified this taxon as *A. delicatissima* on the basis of the illustrations of this species in Krammer & Lange-Bertalot 1986.

Biogeography & Ecology: *Amphora* cf. *delicatissima* was common in fine to medium sandy sediments throughout the Westerschelde estuary.

AMPHCFDE

Amphora cf. *exigua* Gregory 1857 [Figs 25-7, 25-8, 25-9, (?) 25-10, 25-11, 58-5]

References:

(1) Gregory 1857
(2)
(3) Archibald 1983, Bérard-Therriault *et al.* 1986, Hendey 1964, Peragallo & Peragallo 1897-1908

Morphology:

L: 20-32.5; W: 4.6-5.9; W(P): 8.7-10.6; S(D): (11?-)15-18; S(V): (17?-)21-24(-26)

LM - Valves semi-elliptical, apices rostrate-capitate to capitate. Ventral margin more or less straight, dorsal margin, which is very prominent in LM, convex. In most specimens, a distinct dorsal conopeum can be seen. Dorsal striae parallel to radiate in the centre, radiate at the apices. Their structure is indistinct. Ventral striae interrupted in the centre. the cingulum is composed of numerous, punctate (16-17 puncta in 10 µm) copulae.

SEM - Dorsal valve mantle and face distinctly separated, at nearly 90 degrees from each other. Internally, the terminal raphe endings end in a helictoglossa, while in the centre the raphe endings are covered by a small flap, emanating from the dorsal side of the raphe. Dorsal striae biseriate, though usually ending in a single areaola near the dorsal margin. Ventral striae composed of one or more (Fig. 58-5) large puncta, occluded by a velum-like structure. In the centre they are absent or present and very small.

Remarks: It appears that during the counts two similar forms have been united under the name *Amphora* cf. *exigua*, viz. a more delicate form which is described above (e.g. Fig. 25-8), and a second, more robust form (Fig. 25-11). The latter mainly differs from the finer form in stria density (S(D): 11-13, S(V): 17-18) and is the form which corresponds best to the original description of Gregory (1857). There *Amphora exigua* was mainly negatively characterized ['It has no striking features, (...)'].

The main problem with *Amphora exigua* is that it is 'figured by Gregory in a manner which admits of no thrustworthy identification' (Cleve 1895). Therefore, as long as the type material has not been examined, we refrain from making a positive identification. While the original material is described as having 11 str./10 µm, this measure has already gone up to 12-14 in Cleve (1895) and 12-18 in Peragallo & Peragallo (1897-1908). Archibald (1983) illustrates *A. exigua* specimens with distinctly more widely spaced central striae. In general, it seems that the name *Amphora exigua* is used for robust *A. coffeaeformis*-like diatoms with striae with indistinct structure in LM.

A. cf. *exigua* closely resembles *A. coffeaeformis* but differs from it in stria density (which is on average higher in the latter) and the ultrastructure of the ventral striae (one or several puncta, occluded by a velum, instead of a uni- or biseriate row of areolae). It is also reminiscent of *A. tumida* Hustedt (Hustedt 1956, Simonsen 1987) but this species usually has a centrally inflated ventral margin and has a finer structure.

The distinction between this taxon and (supposedly) related taxa such as *A. coffeaeformis* and *A.* sp. 6 is obscured by the apparent existence of intermediate forms. In LM, small, less delicate specimens of *A. coffeaeformis* can hardly be distinguished from *A.* cf. *exigua* (compare Figs 25-8 and 25-15). On the other hand, we found several specimens (both in LM and SEM) which appeared to be an intermediate form between *A.* cf. *exigua* and *A.* sp. 6, the only difference with the *A.* cf. *exigua* specimens lying in the structure of the dorsal striae, which are distinctly punctate near the dorsal margin (see also introduction to the genus *Amphora*).

Biogeography & Ecology: As for *A. coffeaeformis* it is hard to assess the geographical distribution of this taxon given its uncertain identity. *A.* cf. *exigua* was common in different sediment types and was most abundant in the polyhaline reaches of the Westerschelde estuary. It was most abundant in summer.

AMPHCFEX

Amphora graeffeana Hendey 1973 nom. nov. pro *A. graeffii* Grunow sensu Cleve 1895 non *A. graeffii* Grunow in A. Schmidt 1875

[Figs 24-8, 24-9, 24-10]

Synonyms:

(?) *Amphora graeffii* Grunow 1875 var. *minor* Peragallo & Peragallo 1897-1908

References:

(1) A. Schmidt *et al.* (1874-1959)
(2)
(3) Peragallo & Peragallo 1897-1908, Hustedt 1955, Simonsen 1962, John 1981, 1983, Bérard-Therriault *et al.* 1986, Schoeman *et al.* 1986, Karayeva 1987, Kuylenstierna 1989-90

Morphology:

L: 30-35; W: 6.2-6.5; S(D): 24-25; S(V) 23-26

LM - Valves semi-lanceolate, apices slightly produced. Raphe straight to slightly bi-arcuate. Central raphe endings straight, expanded. The central nodule is slightly transapically expanded. A semi-lanceolate hyaline area lies adjacent to the raphe on the dorsal side. The dorsal striae are radiate throughout the valve and are crossed by a longitudinal hyaline line which runs more or less parallel to the dorsal valve margin. On the ventral side, very short striae are present right next to the raphe; they are interrupted in the centre.

Remarks: Diatoms with a semi-lanceolate dorsal hyaline area and a longitudinal line crossing the dorsal striae have been identified as a.o. *Amphora truncata* Gregory, *A. graeffii* Grunow (= *A. grevilleana* Gregory, see Schoeman *et al.* 1986), *A. exsecta* Grunow in Schmidt 1875, *A. graeffii* var. *minor* Peragallo & Peragallo, *A. beaufortiana* Hustedt, *A. graeffeana* and *A. australiensis* John. The differences between these species mainly concern size, stria density and the presence/absence and exact position of striae on the ventral side of the valve. The Westerschelde specimens correspond most closely to *A. graeffeana*. This species is probably conspecific with *A. graeffii* var. *minor*, in which case the name *A. graeffeana* should be used (Schoeman *et al.* 1986). The only difference lies in the striation pattern on the ventral side of the valve: the ventral striae in *A. graeffeana* are restricted to the apical region (cf. also *A. beaufortiana* sensu Karayeva 1987), while in our specimens they are interrupted in the centre only. Our specimens also closely resemble *A. australiensis* and *A. truncata* which both have an identical ventral striation pattern but have a lower stria density on the dorsal side (Gregory 1857, John 1981). If *A. truncata* appears to be conspecific with *A. graeffeana* the former name would be the oldest correct name.

A. beaufortiana does not possess ventral striae and has a coarser structure (Hustedt 1955, Simonsen 1987). However, Simonsen (1962) points out that *A. beaufortiana* from the Baltic Sea is an extremely variable species: he observed a continuum in size (30-100 µm) and stria density (19-27 str./10 µm) but apparently never observed ventral striae.

Further study of type material and the morphological variability of these taxa is needed to resolve the taxonomical and nomenclatural problems in this complex.

Biogeography & Ecology: *A. graeffeana* was very rare in the Westerschelde stations. The above-mentioned taxa have been described and reported from brackish and marine localities worldwide (Europe, North America, Australia, references see above).

AMPHGRAE

Amphora cf. *helenensis* Giffen 1973

[Figs 23-10, 23-11, 23-12, 23-13, 23-14]

References:

(1) Giffen 1973
(2)
(3) Giffen 1973, Archibald 1983, Kuylenstierna 1989-90

Morphology:

L: 14.4-21.2; W: 3.7-4.4; S(D): 20-23; S(V): 18.5-19.5 (n=4)

LM - Valves semi-elliptical. Dorsal margin convex, ventral margin striaght to concave. Raphe slightly bi-arcuate; central raphe endings more or less straight, slightly expanded. Ventral striae parallel to radiate, interrupted in the centre. Dorsal striae parallel (in the centre) to radiate (near the apices). An longitudinal, semi-arcuate hyaline area is present on the proximal valve face.

Remarks: *Amphora* cf. *helenensis* from the Westerschelde has a slighhtly higher stria density than the *A. helenensis* type specimens (Giffen 1973). *A.* cf. *helensis* belongs to the species complexes around *A. copulata* and *A. pediculus*, but SEM examination of the material is necessary to assess to which cluster it belongs. It was kept separate from *A.* cf. *copulata* because of its finer structure and the striation pattern on the ventral valve side (viz. one row of transapically elongate areolae). *A.* cf. *helenensis* is very reminiscent of *A. proteus* f. *ambigua* (Karayeva 1987), which has an even finer structure, and *A.* cf. *helenensis* sensu Kuylenstierna (1989-90). A thorough study of the type material of the above-mentioned taxa and an assessment of their morphological plasticity is needed to clarify the relationships within this complicated species cluster. The smaller specimens of *A.* cf. *helenensis* is also quite reminiscent of our *A.* cf. *pediculus* form B; there is little doubt that both taxa have been mixed up during the counts. Their relationship needs further study.

Biogeography & Ecology: Kuylenstierna (1989-90) and Karayeva (1987, as *Amphora proteus* f. *ambigua*) observed similar valves in their material from the Swedish West Coast and the Caspian Sea respectively. We also observed *Amphora* cf. *helenensis* in Hustedt's material from the German Wadden Sea (Leybucht)(BRM N12/36). In the Westerschelde, this taxon was rare; its ecological requirements are uncertain.

AMPHCFHE

Amphora hybrida (Grunow in Van Heurck 1880) Grunow in Van Heurck 1884 (?)

[Figs 24-1, 24-2, 24-3, 24-4]

Synonyms:

Amphora angulosa var. *hybrida* 1880
Amphora castellata Giffen 1963
For a complete synonymy, see Archibald & Schoeman (1985)

References:

(1)	Van Heurck 1880
(2)	Archibald & Schoeman 1985
(3)	Archibald & Schoeman 1985, Karayeva 1987, Kuylenstierna 1989-90, Wendker 1990

Morphology:

L: 26.2-46.2; W: 3.7-6; S(D): 20-23; S(V): about 32

LM - Valves semi-lanceolate, subrostrate to rostrate. Dorsal margin convex, ventral margin more or less straight. A conopeum is present on the dorsal side of the raphe (Fig. 73-26). Dorsal striae radiate throughout the valve; they are crossed by a characteristic longitudinal hyaline bar which runs more or less parallel to the dorsal valve margin. Ventral striae present but indistinct.

Remarks: A detailed taxonomical and morphological description of this species is given by Schoeman & Archibald (1984, as *A. castellata*) and Archibald & Schoeman (1985). Our specimens differ from the type and other specimens illustrated in these papers in the shape of the apices, which are never capitate, and the outline of the dorsal valve margin, which is never constricted centrally. Note that the specimens from Salah's material from Blakeney Point (England)(Fig. 24-4) do have capitate apices. The latter specimen is identical to *Amphora bacillaris* sensu Peragallo & Peragallo (1897-1908)(cf. also Hartley *et al.* 1996, Pl. 15, Fig. 8). However, the identity of the latter taxon is unclear as the original description is not clear and Cleve's (1895) concept of this species is different from Peragallo & Peragallo's (1897-1908): according to Cleve (1895) there is no longitudinal hyaline bar on the dorsal valve side. The type material of *A. bacillaris* should be studied to reveal the true identity of this species and its relationship with *A. hybrida*.

Biogeography & Ecology: *Amphora hybrida* is a cosmopolitan, epipelic species from brackish and marine sediments in Europe [Belgium (coast + Schelde estuary, Van Heurck 1880-1885, this study), Sweden (Kuylenstierna 1989-90), England (Archibald & Schoeman 1985, this study), France (Peragallo & Peragallo 1897-1908), Germany (Wendker 1990), Azerbaijan (Karayeva 1987)], Africa (Giffen 1963, Schoeman & Archibald 1984), South America (Garcia-Baptista 1993b) and probably elsewhere. In the Westerschelde, it was mainly found in the inner reaches of the estuary and thus appears to be a typical brackish-water species.

AMPHHYBR

Amphora laevis Gregory 1857 **var.** ***laevissima*** (Gregory 1857) Cleve 1895 [Fig. 22-10]

Synonyms:

Amphora laevissima Gregory 1857

References:

(1) Gregory 1857
(2) Schoeman & Archibald 1986a (Figs. 24-28 - proposed type)
(3) Gregory 1857, Cleve 1895, Peragallo & Peragallo 1897-1908, Bérard-Therriault *et al.* 1986, Schoeman & Archibald 1986a

Morphology:

L: 33.7; W: 8.7; S(D): 33

LM - Valves semi-elliptical with slightly produced apices. Dorsal margin convex, slightly constricted in the centre; ventral margin undulate. Raphe strongly bi-arcuate, lying in a distinct rib. Central raphe endings close together, slightly expanded. A stuaros is present on the dorsal side of the valve. Dorsal striae only barely visible; ventral striae not visible (or absent?).

Remarks: See *A. laevis* var. *perminuta*

Biogeography & Ecology: Only a few valves belonging to this taxon were found.

AMPHLAEV

Amphora laevis **var.** ***perminuta*** [Grunow in Van Heurck 1884 (?)] Cleve 1895

[Figs 22-4, 22-5, 22-6, 22-7, 22-8, 22-9]

Synonyms:

Amphora laevissima Gregory 1857 var. *perminuta* [Grunow in Van Heurck 1884 (?)] Cleve 1895
(?) *Amphora exilissima* Giffen 1967

References:

(1) Van Heurck 1884-1887
(2) Schoeman & Archibald 1986a (Figs. 22-23 - material from type locality)
(3) Gregory 1857, Peragallo & Peragallo 1897-1908, Bérard-Therriault *et al.* 1986, Schoeman & Archibald 1986a

Morphology:

L: 7.5-16.9(-33.7?); W: 1.9-4.6(-8.7?); S(D): 30-34

LM - Frustules broadly elliptical with blunted apices. Plastids H-shaped, with the bridge lying against the dorsal girdle and lobes extending towards the ventral side of the frustules. Two large droplets lie on both sides of the bridge; sometimes there are also other, smaller droplets present. Valves semi-lanceolate. Dorsal margin convex, ventral margin bi-arcuate (Fig. 22-4) or (depending on orientation of valve) straight to slightly convex (e.g. Figs 22-6, 22-9). Raphe shape as ventral margin. Central raphe endings straight. Dorsal striae parallel to radiate throughout the valve; they can often not be distinguished. Ventral striae not visible (or absent). A distinct stauros is present on the dorsal side of the valve.

Remarks: Both *Amphora laevis* and *A. laevissima* (= *A. laevis* var. *laevissima* (Gregory) Cleve 1895) were described by Gregory in 1857. Two varieties, *A. laevissima* var. *perminuta* Grunow in Van Heurck 1884 (= *A. laevis* var. *perminuta* (Grunow) Cleve 1895) and *A. laevis* var. *minuta* Cleve 1895 (1895) were consequently described at the end of the 19th century. The main differences between these taxa lie in size and stria density. Most reports of *Amphora laevis* concern relatively large (40-90 µm) diatoms with about 23-24 striae in 10 µm (e.g. Peragallo & Peragallo 1897-1908, Bérard-Therriault *et al.* 1986, Schoeman & Archibald 1986a), which is well in accordance with Gregory's (1857) original description. *Amphora laevis* var. *laevissima* has a higher stria density [26-30 str./10 µm on the dorsal side, 27-32 (but often invisible) on the ventral side]. *A. laevis* var. *perminuta* or *A. laevis* var. *minuta* both have 'very delicate striae' (Cleve 1895), but var. *minuta* is larger (35 µm) than var. *perminuta* (12-19 µm long, Peragallo & Peragallo 1897-1908)(Cleve 1895).

However, several authors already pointed out that it is not always easy to distinguish between the above-mentioned taxa: Bérard-Therriault *et al.* (1986) suggested that *A. laevis* var. *perminuta* and var. *minuta* might belong to the same taxon, while Schoeman & Archibald (1986) suspect that *A. laevis* var. *laevissima* and the nominate variety might have to be united.

Giffen (1967) described a small *Amphora* species, *A. exilissima* Giffen, from brackish waters in South Africa. The main difference with *A. laevis* var. *perminuta* would lie in its size (9-10 µm). However, as we observed a size continuum down to 7.5 µm in the latter taxon in the Westerschelde material, it seems that both taxa ought to be united.

Biogeography & Ecology: *Amphora laevis* and its varieties appear to be cosmopolitan [Europe (cf. references above), Africa (Giffen 1967), North (Bérard-Therriault *et al.* 1986) and South (Garcia-Baptista 1993b) America]. In the Westerschelde, *Amphora laevis* var. *perminuta* is common in different sediment types in the poly- and euhaline reaches.

AMPHLAPE

Amphora lineolata Ehrenberg 1838

[Figs 27-3, 27-4]

References:

(1) Ehrenberg 1838

(2)

(3) Peragallo & Peragallo 1897-1908, Bérard-Therriault *et al.* 1986, Krammer & Lange-Bertalot 1986, Snoeijs & Vilbaste 1994

Morphology:

L/ 44.6; W: 7.2; S(D/V): 21

LM & SEM - Plastids two, for and aft. A detailed morphological description of this species can be found in Krammer & Lange-Bertalot (1986).

Biogeography & Ecology: Only a few specimens belonging to this cosmopolitan brackish-water species were found (cf. Krammer & Lange-Bertalot 1986, Bérard-Therriault *et al.* 1986).

AMPHLINE

Amphora* cf. *longa Hustedt 1955 nom. nov. pro *A. elegans* Peragallo 1893 in Tempère & Peragallo 1889-1895 non *A. elegans* Gregory 1857 [Figs 24-11, 24-12, 24-13, (?) 24-14]

References:

(1) Tempère & Peragallo 1889-1895
(2)
(3) Peragallo & Peragallo 1897-1908, Hustedt 1955, Bérard-Therriault *et al.* 1986, Hendey 1973

Morphology:

L: 32-42.3; W: 4.6-5.1; S: 29-30 (transverse), about 30 (longitudinal)

LM - Valves narrowly lanceolate, slightly asymmetrical. Dorsal margin straight or slightly constricted in the centre to convex, ventral margin more or less straight or slightly constricted to convex. Raphe straight to slightly bi-arcuate, close to the ventral margin. Dorsal transverse striae parallel to slightly radiate at the poles and very finely punctate, longitudinal striae parallel to the raphe system. The central 'stauros' appears to be made up by 3-5 distinct, more widely spaced striae, both dorsally and ventrally. Ventral striae parallel. Central area absent.

Remarks: The specimens from the Westerschelde and Blakeney Point (England) differ from the other; above-mentioned descriptions in size (length 32-42 µm versus 60-100 µm) and striae density [29-30 str./10 µm versus 20-25 in Hendey (1973), Peragallo & Peragallo (1897-1908) and Bérard-Therriault *et al.* (1986)].

Biogeography & Ecology: To our knowledge, *A. longa* has only been reported from Europe (Peragallo & Peragallo 1897-1908, Hendey 1973) and the Atlantic coast of North America (Hustedt 1955, Bérard-Therriault *et al.* 1986). Only a few specimens belonging to this species were observed in the Westerschelde estuary.

AMPHLONG

Amphora margaritifera Cleve 1895 [Fig. 21-24]

Synonyms:

Amphora cruciata Östrup 1897
Amphora interrupta Heiden in Heiden & Kolbe 1928
Amphora maletractata Simonsen 1992 nom. nov. pro *A. interrupta* Heiden in Heiden & Kolbe 1928 non *A. interrupta* Pantocsek 1886

References:

(1) Cleve 1895
(2)
(3) Heiden & Kolbe 1928, Bérard-Therriault *et al.* 1986, Simonsen 1992

Morphology:

L: 27.5; W: 5.9; S(D/V): 11

Lm - Valve semi-elliptical with rostrate apices. Ventral margin more or less straight, dorsal margin convex. Raphe more or less straight, central raphe endings slightly deflected to the dorsal side. Dorsal striae composed of two distinct areolae, separated by a rather wide longitudinal sternum. In the centre, the dorsal striae are interrupted by a transapical hyaline band (stauros? fascia?). The ventral striae probably only consist of one areola each.

Remarks: This diatom is usually identified as *Amphora interrupta* (which is a homonym), but comparison of the type material (Simonsen 1992) with *A. margaritifera* shows that both species are most probably identical. Although *A. margaritifera* has a lower stria density than *A. interrupta* [8-11 (cf. Cleve 1895, Pl. III, Fig. 30-31) versus 11-16.5 (Simonsen 1992, Pl. 67), it seems that the stria density is rather variable (cf. Simonsen 1992, type *A. interrupta*).

Biogeography & Ecology: *A. margaritifera*, which was described from the Galapagos Islands, has been reported from the South Polar Ocean (Heiden & Kolbe 1928), the east coast of North America (Bérard-Therriault *et al.* 1986), Europe [Kuylenstierna 1989-90, Hartley et al. 1996 (as *Amphora* sp., Pl. 25, Fig. 9), this study] and the Philippines (Podzorski & Håkansson 1987). Only one valve of this marine species was found in the Westerschelde material.

AMPHMARG

Amphora montana Krasske 1932

[Figs 21-17, 21-18]

Synonyms:

A. submontana Hustedt

References:

(1) Krasske 1932
(2) Krammer & Lange-Bertalot 1986
(3) Krammer & Lange-Bertalot 1986

Morphology:

L: 12.5; W: 3

LM - Valves semi-elliptical to slightly arcuate, apices rostrate to rostrate-capitate. Dorsal margin convex, ventral margin bi-arcuate. Raphe slightly bi-arcuate, central raphe endings dorsally deflected. A distinct dorsal stauros is present. Dorsal striae only slightly visible near the stauros. Ventral striae only visible near the centre, where they are more widely spaced.

Biogeography & Ecology: Only a few valves of this freshwater species were found in the oligohaline part of the estuary.

Amphora ostrearia Brébisson in Kützing 1849 **var. *belgica*** Grunow in Van Heurck 1885

[Fig. 22-3]

Synonyms:

(?) *Amphora litoralis* Donkin 1858

References:

(1) Van Heurck 1885
(2) Schoeman & Archibald 1986a (holotypes *Amphora ostrearia* and *A. litoralis)*
(3) Krammer & Lange-Bertalot 1986

Morphology:

L: 32.3-41.2; W: 6.2-8; S(V/D): 14-15

LM - Valves semi-elliptical to semi-arcuate. Dorsal margin convex to bi-arcuate (depending on orientation of the valve), ventral margin distinctly bi-arcuate. Raphe bi-arcuate. Dorsal and ventral striae radiate in the centre to convergent near the apices. The striae consist of more or less round areolae. The central ventral striae are shorter. On the dorsal side, a distinct stauros is present.

Remarks: *Amphora ostrearia* has several varieties (cf. Peragallo & Peragallo 1897-1908). *A. ostrearia* var. *belgica* and *A. ostrearia* var. *lineata* Cleve seem to be very closely related, the only differences lying in size (30-50 µm versus 50-80 µm respectively) and stria density (16-17 versus 12-13 str./10 µm). As our specimens have 14-15 str./10 µm and are smaller than 50 µm we have assigned them to *A. ostrearia* var. *belgica*. Both varieties actually more closely resemble *A. litoralis* (which according to VanLandingham 1967 is a synonym of *A. ostrearia*) than the type of *A. ostrearia*. The *A. litoralis* valves shown in Schoeman & Archiobald (1986a) are, some minor differences in size and stria density excepted, identical to our *A. ostrearia* var. *belgica* specimens. Comparison of the type of A. litoralis with the above-mentioned varieties should point out whether *A. litoralis* should be re-established or not (cf. Schoeman & Archibald 1986a).

Biogeography & Ecology: Only a few specimens belonging to this taxon were found.

AMPHOSTR

Amphora ovalis (Kützing 1833) Kützing 1844

References:

(1) Kützing 1833
(2) Schoeman & Archibald 1986 (LM), Lee & Round 1987 (SEM)
(3) Krammer & Lange-Bertalot 1986, Schoeman & Archibald 1986c, Lee & Round 1987

Morphology:

L: 42.8; W: 10.8; S(D): 10; S(V): 11 (n=1)

LM & SEM - A thorough description of this species can be found in Lee & Round 1987.

Remarks: The specimens found in the Westerschelde belonging to this species completely match the description given by Schoeman & Archibald (1986c).

Biogeography & Ecology: Only one valve of this freshwater species was found in the oligo-/mesohaline part of the estuary.

Amphora* cf. *pediculus (Kützing 1844) Grunow 1875 in Schmidt et al. 1874-1959

[Figs 23-1, 23-2, 23-3, 23-4, 23-5, 23-6, 23-7, 23-8, 23-9, 56-4, 56-5, 56-6, 56-7, 56-8, 57-1]

Synonyms:

Cymbella? *pediculus* Kützing 1844
Amphora ovalis var. *pediculus* (Kützing) Van Heurck 1885
For a more complete synonymy list, see Schoeman & Archibald 1978

References:

(1) Kützing 1844
(2) Schoeman & Archibald 1978
(3) Schoeman & Archibald 1978, Lee & Round 1989, Snoeijs 1993

Morphology:

Two distinct forms appeared to be present in the Westerschelde material: they could only be distinguished with ease in SEM. The LM description given below therefore concerns '*A.* cf. *pediculus* s.l.', while the SEM description is given for both forms separately (cf. also Lee & Round 1989).

L: 5.4-16.2; W: 2.2-4; S(D): 22-28; S(V): 20-26

LM - Frustules broadly elliptical. Valves semi-elliptical, apices cuneate. Raphe straight to slightly curved, central raphe endings straight, not expanded. Dorsal striae radiate; their structure is indistinct. Ventral striae radiate in the centre to convergent near the apices. Central area always transapically expanded to the ventral side, sometimes transapically expanded to the dorsal side (with intermediate forms). Depending on the orientation of the valve, a longitudinal hyaline bar can be seen on the dorsal side of the valve.

SEM -

Form 1 - L: 7.5-8, W: 2.2; S(D): 23.5-27; S(V): 23-25.5 (n=3)

Ventral and proximal dorsal valve face flat, lying in one plane; distal dorsal valve face almost at right angles to the rest of the valve face. Raphe slightly bi-arcuate. Central raphe endings more or less straight; terminal fissures strongly dorsally deflected. A conopeum is only rudimentary developed near the apices on the dorsal side of the raphe. The ventral 'striae' are composed of a single elongated punctum, occluded by a velum. The dorsal striae consist of two puncta, separated by a longitudinal hyaline bar. The central area is always transapically expanded on the ventral side of the valve, while on the dorsal side it can be present or absent. When present, it often has a small punctum-like depression near the central nodule. The presence of this depression can vary within one frustule (Fig. 2443). The cingulum consists of 3 copulae.

Form 2 - L: 8.7-16.2; W: 3-4; S(D): 25-28; S(V): 22-26

This form differs from form 1 in the following respects: (1) size (on average larger and broader); (2) the presence of a dorsal conopeum which runs the whole length of the raphe branches; on the ventral side, a rudimentary conopeum can be present on the ventral side near the apices; (3) the striae on both the proximal and distal dorsal valve face are composed of two areolae; especially in larger specimens these are slit-like on the outside. Internally, the areolae are always more or less elliptical and occluded by a velum; (4) the longitudinal hyaline bar separating the proximal and distal valve face is more pronounced, especially on its distal side, which has a conopeum-like appearance. In some specimens, it merges with the dorsal conopeum near the apices.

Both forms possess a transapically expanded central area, both on the ventral and dorsal side. However, on the dorsal side it ususally does not reach the longitudinal hyaline bar. There are strong overlaps in size and stria density between both forms.

Remarks: The main differences between the *Amphora pediculus* and *A. copulata* clusters are: (1) In *A. pediculus* the ventral areolae extend as close to the centre as do the raphe slits, and (2) the raphe branches are never strongly curved in *A. pediculus*. Our forms therefore belong to the *A. pediculus* cluster.

Our form 1 differs from the lectotype of *Amphora pediculus* (Schoeman & Archibald 1978) in the structure of the central area: in the type specimens the central area is always transapically expanded and always reaches the bar separating the distal and proximal dorsal valve face. In addition, the stria density of form 1 is situated in the upper part of the stria density range of the type of *A. pediculus*.

Form 1 is virtually identical to *Amphora pediculus* - form B described in Lee & Round (1989), a morphological form often reported from rivers in Britain. A literature search yielded more specimens which are very similar to our form 1. Snoeijs (1993) shows an *Amphora pediculus* valve from brackish water in the Baltic which, apart from a slightly more developed conopeum, is identical to our specimens.

Our form 2 closely resembles form A of Lee & Round (1989), but in some of our specimens the areolae are much more slit-like, as in their form E. A valve similar to our form 2 was reported from a Swedish estuary by Kuylenstierna (1989-90, as *A.* cf. *helenensis*).

There is little doubt that *A.* cf. *pediculus* form 1 and 2 belong to the *A. pediculus* cluster. This 'species', which Lee & Round (1989) have shown to consist of a group of presumably closely related morphological forms, is considered to be a common and typical freshwater species (cf. Krammer & Lange-Bertalot 1986). However, *Amphora pediculus* is also often reported from brackish environments (e.g. Karayeva 1987, Sabbe & Vyverman 1991, Snoeijs 1993, Witkowski 1994, this study). Whether these brackish forms also belong to *Amphora pediculus* or whether they constitute separate species can not yet be assessed. However, at first sight there seems to be very little difference between some brackish and freshwater forms [e.g. compare Snoeijs 1993 (nr. 10) with Lee & Round 1989 (Figs. 16-17)].

Apart from form 1 and 2, we sometimes observed yet other small 'pediculoid' *Amphora* specimens, which we were unable to study in more detail during this study. Some of these forms occurred in marine sediments from the mouth of the estuary (Fig. 23-5) and were also found in Salah's material from Blakeney Point (England)(Fig. 23-6). As these 'pediculoid' specimens are usually identified as *A. pediculus*, little research has been done on the identity of these small forms.

Biogeography & Ecology: As already mentioned, *Amphora pediculus* is usually reported from freshwater environments, but has often been reported from brackish habitats. *Amphora* cf. *pediculus* was the most widespread *Amphora* species in the Westerschelde samples and occurred in 70 % of all samples. It was mainly found in fine and medium sandy sediments throughout the estuary.

AMPHCFPE

Amphora pulchella Peragallo & Peragallo 1898 [Figs 24-5, 24-6, 55-1, 55-2, 55-3, 55-5]

References:

(1) Peragallo & Peragallo 1897-1908
(2)
(3) Peragallo & Peragallo 1897-1908, Hartley 1986, Hartley *et al.* 1996

Morphology:

L: 29-45; W: 5.4-7.7; S: 12-17 (n=5)

LM - Valves more or less elliptical to semi-elliptical. Raphe straight to slightly curved. Dorsal striae composed of roundish areolae; interstriae distinct. A longitudinal hyaline bar crosses the dorsal striae close to the raphe system. A small arcuate structure can be seen on the dorsal side of the central nodule (Fig. 24-6). Ventral striae radiate in the centre, convergent at the apices. They consist of 2 (or near the apices up to 4) elongated puncta, arranged in two longitudinal rows separated by a broad hyaline area. The ventral striae are interrupted in the centre. Due to the orientation of the valves in the LM, the ventral valve face can often not be seen. Thus the dorsal and ventral views of the valve can be quite different, in some cases even giving the impression that we are dealing with two separate taxa.

SEM - Two rather different external valve views were observed: one valve appears to be slightly eroded (Fig. 55-1), while the other one is intact (Fig. 55-2). A distinct, rather wide conopeum is present on the dorsal side and covers the longitudinal dorsal sternum (when intact); on the ventral side it is only developed in the centre and at the poles. The central raphe endings are slightly dorsally deflected; the terminal fissures are hooked to the dorsal side. The virgae on the dorsal valve face are extremely well-developed and almost touch one another; the areolae and vimines are sunk beneath the outer valve surface and are only barely visible in intact valves (Fig. 55-2). The areolae are more or less round and are occluded by a velum-like structure (Fig. 55-5). The longitudinal hyaline crossbar is situated on the same level as the virgae. The ventral striae are composed of 2 (to 4) elongated puncta (Fig. 55-2). Internally, the areolae are slightly sunk below the internal valve face level. The raphe endings could not be observed in detail; no helictoglossae appear to be present. A short, apical groove lies inbetween the central raphe endings. On the dorsal side, a small nodule (also visible in LM) is present. The structure of the cingulum is unknown: only one, non-punctate copula was observed.

Remarks: The only difference between our specimens and the ones described in Peragallo & Peragallo (1897-1908) lies in size (29-45 versus 60 µm length). The valve depicted in their illustration Pl. 44, Fig. 19 (as *A.* sp.? *A. pulchella* var?) might concern a ventral valve view of this species (cf. above). *A. pulchella* can be distinguished from *Amphora arenicola* (Grunow) Cleve by its smaller size, the dorsal hyaline bar and the typical striation pattern on the ventral valve face (Peragallo & Peragallo 1897-1908). *Amphora pulchella*-like diatoms have been reported by Kuylenstierna (1989-90, Figs 399, 435) and Hartley *et al.* (1996, Pl. 25, Fig. 1).

Biogeography & Ecology: *Amphora pulchella* has to our knowledge only been reported from Europe (Peragallo & Peragallo 1897-1908, Hartley 1986, this study). In the Westerschelde it was only occasionally found in medium sandy sediments.

AMPHPULC

Amphora cf. *subacutiuscula* Schoeman 1972

[Figs. 26-8, 26-9, 26-10, 26-11, 26-12, 26-13, 26-14, 26-15, 26-16, 57-2, 57-6]

Synonyms:

(?) *Amphora margalefii* Tomàs 1990 var. *lacustris* Sanchez-Castillo

References:

(1) Schoeman 1972
(2)
(3) Archibald 1983

Morphology:

L: 8-30.4; W: 2.2-6; S(D): 28-36 (between apices and centre), about 22-26 in the centre; S(V): 28-32 and more?

LM - Frustules elliptical with slightly produced apices. Plastids H-shaped. Valves semi-lanceolate, apices cuneate to rostrate. Dorsal margin convex, ventral margin straight to slightly inflated in the centre, rarely undulate. Raphe arcuate, central raphe endings close together, separated by a distinct central nodule. Dorsal striae parallel in the centre to radiate near the apices; the central ones are more widely spaced. The ventral striae are only barely visible.

SEM - Ventral valve face rather wide, more or less flat, dorsal valve face curved. Central raphe endings close together, dorsally deflected. Internally, the central raphe endings are hidden by a small silicious flap protruding from the dorsal side. Terminal fissures deflected to the dorsal side. A distinct dorsal conopeum is present. The dorsal striae are biseriate, finely punctate. The ventral striae are uniseriate; they are more widely spaced and shorter in the centre of the valve. The cingulum is composed of 5 copulae.

Remarks: This taxon is mainly characterized by the more widely spaced central striae (especially dorsally) and the indistinct structure of the ventral valve face. Our specimens are identical to the *A.*

subacutiuscula valves described by Archibald (1983), except for a small difference in size range [8-30 µm (Westerschelde) versus 16-30 µm (Archibald 1983)]. However, as the author pointed out that the true identity of *A. subacutiuscula* is uncertain, we refer to this taxon as *A.* cf. *subacutiuscula.*

The relationship between *A. margalefii* var. *lacustris* (see Sanchez-Castillo 1993), which was described from brackish lakes in Southern Spain and *Amphora* cf. *subacutiuscula* needs further study; they might be conspecific.

At first we thought that the larger specimens (e.g. Fig. 26-15) belonged to a different taxon, but except for size we could not find any other differences with the smaller specimens and therefore consider them as belonging to the same, apparently highly variable taxon.

Biogeography & Ecology: *Amphora* cf. *subacutiuscula* was common in fine sandy sediments throughout the Westerschelde estuary. Its occurrence seems to be rather independent of the presence of higher amounts of silt in the sediment. This taxon has been reported from Africa (Archibald 1983) and Europe (this study). Similar specimens were also observed by Kuylenstierna (1989-90, as *Amphora* sp. C, Fig. 445).

AMPHCFTE

Amphora cf. *sublaevis* Hustedt 1955

[Fig. 24-7]

Synonyms:

Amphora abludens Simonsen 1962

References:

(1) Hustedt 1955
(2) Simonsen 1987
(3) Hustedt 1955, Simonsen 1960, Bérard-Therriault *et al.* 1986, Kuylenstierna 1989-90

Morphology:

L: 26.9; W: 4.1; S: 29

LM - Valves semi-lanceolate, apices slightly produced, subrostrate. Dorsal valve margin convex, ventral margin straight. Raphe slightly bi-arcuate, central raphe endings straight, separated by a distinct central nodule. Terminal raphe endings deflected to the ventral margin. A wide, semi-lanceolate sternum is present on the dorsal side of the raphe. The dorsal striae are marginal, radiate. No striae appear to be present on the ventral side of the valve. It is not clear whether a central stauros is present or not.

Remarks: As the stria density is lower (about 30 str./10 µm) than in the type specimens of both *A. sublaevis* (about 40 str./10 µm) and *A. abludens* (38 and more str./10 µm) we have refrained from making a positive identification as *A. sublaevis* (note however that Bérard-Therriault *et al.* 1986 mention 26-40 str./10 µm for their *A. abludens* specimens).

A. abludens was originally separated from *A. sublaevis* on the basis of the presumed absence of the semi-lanceolate hyaline area in the latter, but Simonsen (1987) pointed out that Hustedt's drawing of this species (Hustedt 1955, Pl. 13, Fig. 14) was incorrect and that such a sternum is present indeed.

Biogeography & Ecology: *Amphora sublaevis* appears to be present in material from Europe (e.g. this study) and North America (Hustedt 1955, Bérard-Therriault *et al.* 1986). Only a few specimens were found in the Westerschelde material.

Amphora tenerrima Aleem & Hustedt 1951

[Figs 26-17, 26-18, 26-21, 26-22, 26-23, 26-24, 26-25, 58-6, 58-7, 58-8]

References:

(1) Aleem & Hustedt 1951
(2)
(3) Hustedt 1955

Morphology:

L: 10-19.5; W: 2.5-3.7; S(D): 19.5-26(-28); S(V): 36-38

LM - Frustules broadly elliptical with broadly rostrate apices. Plastids H-shaped with the two lobes almost touching, sometimes almost butterfly-shaped. Valves semi-elliptical, apices rostrate to slightly capitate. In larger specimens the dorsal margin is more or less parallel to the ventral one. The latter is usually slightly inflated, either in the centre (Fig. 26-21) or between the centre and the apices (e.g. Fig. 26-22). Dorsal striae parallel to radiate in the centre, distinctly radiate at the apices. Ventral striae not visible in the LM. A distinct dorsal conopeum is often visible as a narrow line running parallel to the raphe.

SEM - The dorsal conopeum is well developed and is especially broad just below the valve apices; it is also visible from the interior of the valve. The terminal fissures are distinctly dorsally deflected, the central raphe endings only slightly. The dorsal striae are biseriate. At the valve face-mantle margin, they are crossed by a longitudinal bar, which is very distinct in some valves but barely noticeable in others. Towards the dorsal margin, the striae become uniseriate (Fig. 58-8). The ventral striae consist of one or more, often very narrow, elongated puncta, occluded by a velum. In the centre, they are very short, thus creating a central area. The structure of the cingulum is not very clear: several copulae are present, each bears two rows of puncta.

Remarks: Some slight differences in dimensions and stria density excepted, the specimens from the Westerschelde completely match the original description (Aleem & Hustedt 1951). The relationship of this species with both *A. delicatissima* Krasske and *A. tenuissima* Hustedt is not very clear. *A tenuissima* is reported to have 36 striae in 10 µm on the dorsal side, although on the LM illustration of this species (selected by Simonsen 1987) we could only count up to 30 striae in 10 µm. It is not unlikely that the frustule selected by Simonsen belongs to *A. tenerrima* (which is also present in Hustedt's Beaufort material, cf. Hustedt 1955) and not to *A. tenuissima*. A thorough EM study of the type material of the latter taxon is necessary to distinguish between these taxa.

Our specimens resemble the SEM illustrations of this species in Kennet & Hargraves (1984) but differ in size and stria structure, which is punctate in their specimens. Bérard-Therriault *et al.* (1986) reported *A. tenerrima* from an estuary in Québec. Their specimens differ from ours in the ultrastructure of the striae, which are clearly punctate in their specimens (cf. also Kuylenstierna 1989-90). Lee & Reimer (1984) described *A. tenerrima* as occurring endosymbiontic in foraminifera. However, the striation in these specimens is extremely dense (judging from their illustrations up to 44-58/10 µm on the dorsal side and up to 75 on the ventral side !). This would suggest a closer affinity with *A. delicatissima*, although even that species does not have such a high stria density.

Biogeography & Ecology: *A. tenerrima* has been reported from Europe (Aleem & Hustedt 1951), North America (Hustedt 1955, Bérard-Therriault *et al.* 1986) and South Africa (Archibald 1983). The distribution of this species in the Westerschelde estuary is almost identical to that of *Amphora* cf. *subacutiuscula*.

AMPHTENE

Amphora wisei (Salah 1955) Simonsen 1962

[Figs 21-23, 55-4, 55-6]

Synonyms

Amphora turgida Gregory 1857 var. *wisei* Salah 1955

References:

(1) Salah 1955
(2)
(3) Simonsen 1962, Bérard-Therriault *et al.* 1986, Pankow 1990

Morphology:

L: 9.2-12.9; W: 2.9-3.7; S(D): 16-20

LM - Valves semi-elliptical with capitate, dorsally deflected apices. Dorsal margin convex, more or less striaght in the centre. Ventral margin straight to slightly bi-arcuate. The raphe lies right next to the ventral margin. A dorsal conopeum is usually visible. Dorsal striae parallel to radiate; their structure is indistinct. Ventral striae not visible.

SEM - Valve face flat, dorsal mantle shallow. Ventral valve face very narrow; the ventral 'striae' consist of one punctum each. Raphe more or less straight, central raphe endings straight, close together. Internal terminal raphe endings straight, separated by a small longitudianl rib (double helictoglossa?). The internal terminal raphe endings end in a helictoglossa; the external terminal fissures are probably dorsally deflected. Dorsal conopeum well-developed; internally, the conopeum margin is visible as a longitudinal hyaline line interrupting the dorsal striae. On the ventral side of this line, the striae consist of two areolae only; they appear to be occluded by a velum. Dorsally, the striae are biseriate (although certain parts consist of only one punctum each). Externally, the structure of the striae is unclear. The cingulum appears to be composed of numerous open (?) copulae.

Remarks: *Amphora wisei* appears to be closely related to *Amphora turgida* Gregory and related species. However, to our knowledge it can not be confused with any other known *Amphora* species. Its size and dimensions are remarkably constant.

Biogeography & Ecology: *Amphora wisei* was rare in the Westerschelde sediments. It has been reported from different brackish and marine localities in Europe (Baltic area: Simonsen 1962, Witkowski 1994; Great Britain: Salah 1955; The Netherlands: Daemen *et al.* 1982, this study) and North America (Bérard-Therriault *et al.* 1986).

AMPHWISE

Amphora sp. 2

[Figs 26-1, 26-2, 26-3, 26-4, 54-6]

Morphology:

L: 10.4-15; W: 2.5-3.6; S(D): 27-36 (and more?); S(V): 48-49

LM - Valves semi-lanceolate, apices rostrate-capitate to capitate. Dorsal margin convex, ventral margin straight to slightly undulate. Raphe straight to slightly arcuate. Two curved lines run from the ventral margin to the central nodule, giving the valves a very characteristic appearance. Dorsal striae parallel to radiate (near the apices), finely punctate, usually more widely spaced in the centre. Ventral striae not visible.

SEM - Dorsal valve face curved, ventral valve face flat. The raphe is straight to slightly bi-arcuate and has an accessory rib on the dorsal side. In the centre, the raphe (not the central raphe endings!) abruptly curve to the dorsal side. The terminal fissures are strongly hooked to the dorsal side. A dorsal conopeum is present; the longitudinal canal it encloses opens to the outside via two apical openings. The dorsal striae are composed of small areolae (about 30 in 10 µm). It is possible that the striae are biseriate near the raphe, but as they are hidden by the conopeum it is not possible to assess this. The ventral 'striae' are situated along the ventral margin; they consist of one slightly transapically elongated punctum each.

Remarks: *Amphora* sp. 2 belongs to the species complex around *A. coffeaeformis* and *A. acutiuscula* (cf. introduction to the genus *Amphora*): it can be distinguished from similar taxa such as *Amphora tenerrima*, *A.* sp 6 and especially *A.* cf. *delicatissima* and *A.* sp. 5 in the structure of the raphe in the centre of the valve and in its dimensions (size, stria density).

This taxon is reminiscent of *A. tenuissima*, which was described by Hustedt (1955) from Beaufort (U.S.A). However, until the type material of this species has been studied it is impossible to assess the true identity of this species [note that the specimen illustrated in Simonsen (1987) most probably represents *A. tenerrima* - see there].

Biogeography & Ecology: *Amphora* sp. 2 was also found in Salah's material from Blakeney Point (England)(BM 36402). In the Westerschelde estuary it was typically found in medium sandy sediments in the mouth and polyhaline reaches of the estuary.

AMPHSP02

Amphora sp. 3

[Figs 22-11, 22-12, 22-13]

Morphology:

L: 8.7; W: 1.9; S(D): 25-26

LM - Valves semi-elliptical, apices slightly protracted, rounded. Dorsal margin convex, ventral mrgin more or less straight. Dorsal striae parallel to slightly radiate near the apices. Ventral striae indistinct.

Remarks: It is not sure whether this diatom belongs to *Amphora*; it could also belong to the recently described genus *Lunella* (Snoeijs 1996). However, no SEM observations could be made to ascertain this.

Biogeography & Ecology: Only a few valves belonging to this taxon were found.

AMPHSP03

Amphora sp. 4

[Figs 22-14, 22-15, 22-16, 55-7]

References:

(1)
(2)
(3) Hustedt 1955, Archibald 1983

Morphology:

L: 6.2-14.4; W: 1.9-2.7; S(D): about 54; S(V) about 59 (Fig. 5823)

LM - Valves semi-elliptical with distinctly capitate apices. Dorsal margin convex, ventral margin more or less straight to slightly convex. The raphe system can not be distinguished from the ventral margin; central raphe endings appear expanded and are separated by a distinct central nodule. Striae not visible in LM!

SEM - Valve face flat to slightly transapically convex, separated from the dorsal mantle by a conspicious rigde. The dorsal conopeum is narrow. Raphe branches straight, central raphe endings slightly deflected to the dorsal side. Terminal fissures strongly hooked to the dorsal side. The dorsal striae are visible as radiate lines; no areolae can be seen. The ventral striae are hard to distinguish, even in SEM. Each 'stria' consists of a single, transapically elongated punctum. The cingulum consists of several punctate copulae.

Remarks: Archibald (1983, Pl. 5, Fig. 137) illustrated an almost identical valve which he identified as *Amphora tenuissima* (Hustedt 1955), although he adds that his specimens 'are not identical to this taxon, but more closely fulfill the diagnosis of this species than any other *Amphora* known to the author at present'. *Amphora* sp. 4 from the Westerschelde differs from both Hustedt's and Archibald's taxa in having a much higher stria density: it was never possible to resolve the striae in LM as in Hustedt's and Archibald's taxa. Note again that the true identity of *A. tenuissima* is unknown; the specimen from the type locality illustrated in Simonsen (1987) most probably concerns *A. tenerrima* and not *A. tenuissima*.

Biogeography & Ecology: *Amphora* sp. 4 was rare in medium sandy sediments in the mouth and polyhaline reaches of the estuary.

AMPHSP04

Amphora sp. 5 [Figs 25-12, 25-13, 25-14, 58-3, 58-4]

Morphology:

L: 14.5-21; W: 3.7-5; S(D): 20-27; S(V): 51-55

LM - Valves semi-lanceolate, apices distinctly capitate. Ventral margin more or less straight, dorsal margin convex. Raphe straight, central raphe endings slightly expanded. Dorsal striae composed of distinct puncta (especially on the distal valve face and mantle), radiate throughout the valve and sometimes slightly more widely spaced in the centre. Ventral striae not visible in the LM.

SEM - Valve face flat, gently curving into the dorsal mantle. Dorsal conopeum well-developed; it forms a longitudinal canal which opens to the outside large openings at the apices. Both the central and dorsal raphe endings are dorsally deflected. The dorsal striae are biseriate on the proximal dorsal valve face but become a single row of puncta towards the dorsal margin. The predominantly marginal ventral striae consist of a single, small, more or less elongated punctum. They are interrupted at the centre. The cingulum consists of 5-7 (and more?) open copulae; each bears at least one row of small puncta.

Remarks: The main distinguishing characteristics of this taxon are the characteristic valve shape (with distinctly capitate apices) and the extremely delicate ventral striation. This taxon slightly resembles *A.* cf. *acutiuscula* sensu Karayeva (1987) in its dimensions and stria density, but the valve shape of our specimens is distinctly different.

Biogeography & Ecology: *A.* sp. 5 is common in different sediment types, mainly in the inner and middle reaches of the Westerschelde estuary. It was most abundant in summer.

AMPHSP05

Amphora sp. 6 [Figs 25-1, 25-2, 25-3, 25-4, 25-5, 25-6, (?) 25-10, 58-1, 58-2, (?) 57-3, (?) 57-7]

References:

(1)
(2)
(3) Archibald 1983, Bérard-Therriault *et al.* 1986, Krammer & Lange-Bertalot 1986, Karayeva 1987, Wendker 1990, Garcia-Baptista 1993b, Snoeijs & Potapova 1995

Morphology:

L: 12.5-22.5 µm; W: 3.5-5.2 µm; S(D): 17-23; S(V): 24-32

LM - Frustules broadly elliptical with broadly rostrate apices. Plastids H-shaped. Valves semi-elliptical, apices rostrate. Ventral margin slightly inflated between the centre and the apices; dorsal margin convex. Dorsal striae distinctly punctate, parallel in the centre, radiate near the apices. Ventral striae not punctate. Central area slightly developed on the ventral side. In some specimens a dorsal conopeum is visible.

SEM - The central raphe endings are slightly, the apical ones distinctly dorsally deflected. On the distal dorsal valve face, the striae are composed of distinct puncta (about 30 in 10 µm). Near the raphe, they are biseriate. In some specimens the latter is hardly visible due to the presence of a well-developed conopeum. The ventral striae are composed of one, more or less elongated alveolus, occluded by a velum. The cingulum consists of several (up to 6 or more) open, punctate copulae (Fig. 58-1)

Remarks: This taxon was originally identified as *Amphora acutiuscula* Kützing 1844. However, when one compares various descriptions of this species by different authors, it appears that considerable confusion exists as to its true taxonomical identity. Archibald (1983) studied the type material (Kützing material nr. 252 - BM 18173) of *A. acutiuscula* and concluded that it is confusing as three different forms are present in the type slide. Moreover, none of these has distinctly punctate striae, a feature which is regarded as being typical of *A. acutiuscula* (cf. Archibald 1983, Bérard-Therriault *et al.* 1986, Krammer & Lange-Bertalot 1986, Snoeijs & Potapova 1995). This means that what is usually named *A. acutiuscula* does not correspond to the original type material. We therefore decided not to use this name until its taxonomy has been thoroughly studied. The confusion around this taxon might have been introduced by Van Heurck (1880-85)(cf. Krammer & Lange-Bertalot 1986, Pl. 151, Fig. 6' for an illustration of Van Heurck's concept of *A. acutiuscula*).

Amphora sp. 6 closely resembles the taxa illustrated in Archibald (1983, Figs. 490-492, as *A. acutiuscula*), Bérard-Therriault *et al.* (1986, Figs. 5 and 6, as *A. acutiuscula*), Witkowski (1994, Figs. 1 and 6, as *A. acutiuscula* and *A. holsatica* respectively) and Snoeijs & Potapova (1995, nr. 209, *A. acutiuscula*). However, our specimens are usually smaller, have a higher stria density and are not distinctly capitate. In the SEM they clearly differ in the width of the 'biseriate part' of the dorsal striae and the (relative) size of the puncta, which are much smaller in the Westerschelde material.

It is also reminiscent of *A. holsatica* Hustedt (cf. Simonsen 1987, pl. 132; fig. 13) but differs from that species in having a higher stria density and smaller size, and a different valve shape and stria structure (cf. also Snoeijs & Potapova 1995).

Amphora sp. 6 appears to be very closely related to *Amphora tenerrima*. Especially the smaller specimens are very similar. They were mainly distinguished on the basis of the nature of the striae, which are always distinctly punctate in *A.* sp. 6. *A.* sp. 6 also has a lower average stria density, both dorsally and ventrally. Finally, the distinct longitudinal bar crossing the dorsal striae does not seem to be present in *A.* sp. 6.

Biogeography & Ecology: This taxon was also found in Salah's material from Blakeney Point, Great Britain (Fig. 57-15). In the Westerschelde estuary we mainly found this taxon in the mesohaline reaches, where it was common in different sediment types. Note that unlike many other epipelic *Amphora* species it did not show a distinct summer abundance peak.

AMPHSP06

Catenula Mereschkowsky 1903

Genus description: Round *et al.* 1990

The true identity of this genus, which is mainly known through one of its two representatives, *Catenula adhaerens* (cf. Round et al. 1990), is only little known as the type of the genus, *C. pelagica*, has not yet been studied in detail (Snoeijs 1996).

Catenula adhaerens (Mereschkowsky 1901) Mereschkowsky 1902 [Fig. 21-22]

Synonyms:

Navicula adhaerens Mereschkowsky 1901
Amphora sabyii Salah 1955

References:

(1) Mereschkowsky 1901
(2)
(3) Sundbäck & Medlin 1986

Morphology:

L: 12.3-18; W: 2-2.5 (n=7); S: 27.5 (n=1)

LM & SEM - A detailed morphological description of this species was given by Sundbäck & Medlin (1986).

Remarks: In LM, *Catenula adhaerens* closely resembles representatives of the genus *Lunella* (see there). However, both *Lunella bisecta* (Snoeijs 1996) and *Lunella sp.* (see below) have copulae with rows of poroids, striae which are continuous across the valve face-mantle junction and do not have transapically elongated areolae on their mantle (cf. Sundbäck & Medlin 1986).

Biogeography & Ecology: *Catenula adhaerens* is one of the most common epipsammic species throughout the Westerschelde estuary and typically forms ribbon-like colonies on the surface of sandgrains. It is especially abundant in fine to very fine sandy sediments; its occurrence appears to be insensitive to the amount of silt in the sediment.
It has been reported from brackish and marine sites worldwide, e.g. Europe (cf. Sundbäck & Medlin 1986 and references therein) and North America [both Pacific (Rao & Lewin 1976, as *Amphora staurophora*, Amspoker 1977, as *Amphora sabyii*) and Atlantic coasts (Cooper 1995a)].

CATEADHA

Ordo Bacillariales

Fam. BACILLARIACEAE Ehrenberg

Bacillaria Gmelin 1791

Genus description: see Round *et al.* 1990

Bacillaria paxillifer (O. F. Müller 1786) Hendey 1951 [Fig. 27-9]

Synonyms:

Vibrio paxillifer O. F. Müller 1786
Bacillaria paradoxa Gmelin 1788

References:

(1) O. F. Müller 1786
(2)
(3) Krammer & Lange-Bertalot 1988, Snoeijs 1993

Morphology:

L: 90.8-99; W: 7; F: 6-10; S: 21.5-24 (n=2)

LM - Cells forming motile colonies. Valves narrowly lanceolate, apices cuneate to sligthly produced. Canal raphe central not eccentric, fibulae not interrupted centrally. Striae finely punctate.

Remarks: *Bacillaria paxillifer* builds motile colonies in which the diatoms slide to and fro with respect to each other (cf. Round *et al.* 1990, Kapinga & Gordon 1992a, b).

Biogeography & Ecology: Only a few valves belonging to this species were found in our material. *B. paxillifer* is a common epipelic species in marine sediments worldwide (Archibald 1983, Krammer & Lange-Bertalot 1988, Cooper 1995a).

BACIPARA

Denticula Kützing 1844

Genus description: see Round *et al.* 1990

Denticula subtilis Grunow 1862 [Fig. 27-7]

References:

(1) Grunow 1862
(2) Krammer & Lange-Bertalot 1988 (lectotype)
(3) Krammer & Lange-Bertalot 1988

Morphology:

L: 13; W: 5; F: 7; S: not visible in LM

LM - Valves lanceolate, apices cuneate. Fibulae long, spanning the valve transapically. Striae invisible.

Remarks: *Denticula subtilis* has a higher stria density than *D. tenuis* Kützing, which has striae that are clearly visible in LM. During the cell counts, no distinction was made between both taxa.

Biogeography & Ecology: *Denticula subtilis* is commonly reported from brackish and electrolyte-rich freshwaters (Krammer & Lange-Bertalot 1988). Only a few valves of this species were found in the Westerschelde material.

DENTTENU

Denticula tenuis Kützing 1844

[Fig. 27-6]

References:

(1) Kützing 1844
(2)
(3) Krammer & Lange-Bertalot 1988

Morphology:

L: 8.7; W: 3.1; F: 8; S: 24

LM - Valves lanceolate, apices cuneate. Fibulae long, spanning the valve transapically. Between each fibula, 2-3 striae are visible.

Remarks: See *Denticula subtilis*.

Biogeography & Ecology: *Denticula tenuis* is a litoral freshwater species in waters of moderate electrolyte content (Cox 1996). The rare valves found in our material could possible have been washed in from the river basin.

DENTTENU

Hantzschia Grunow 1877

Genus description: Mann 1980, Round *et al.* 1990, Lange-Bertalot 1993b

The genus *Hantzschia* is a natural group but is very difficult to define. The only character that appears to be common to all *Hantzschia* species **and** is absent from *Nitzschia* is the division type, i.e. a cell with hantzschioid symmetry (i.e. the raphes are on the same side of the frustule) gives rise to two daughter cells also of hantzschioid symmetry. When hantzschioid *Niztschia* cells divide, they never breed true, i.e. one cell will be of nitzschioid (i.e. raphes on opposite sides of the frustule) and the other of hantzschioid symmetry (Mann 1980 and references therein). Apart from this character, which is impossible to assess in oxidized material, there are several other features which are generally common in *Hantzschia* species but which also occur in *Nitzschia* species, viz. (1) valve symmetry (asymmetrical about the apical plane and with the raphe usually on the less convex side); (2) plastid structure; (3) cingulum structure; (4) offset form of the internal raphe central endings; (5) terminal fissures curved towards the distal margin and (6) angle between the distal mantle and the valve face (perpendicular or obtuse)(see Mann 1980 for more details).

Many *Hantzschia species*, including the three species described below (*H. distinctepunctata*, *H. marina* and *H. virgata*) are known to display a lot of infraspecific (?) variation (cf. Mann 1981, Mann (in prep.) announced in Droop 1994). In *H. virgata* and *H. distinctepunctata*, the infraspecific variation is discontinuous (Mann 1981, Garcia-Baptista 1993a), which raises the question whether these forms can still be regarded as infraspecific forms or taxa or whether they warrant recognition at the species level (see also chapter 6.3.).

In our material we regularly found taxa with the typical hantzschioid valve symmetry. Unfortunately, due to the rarity of these taxa, we were unable to study them in SEM. Therefore, as valve symmetry was the only character we could observe, we have here listed these taxa as *Hantzschia/Nitzschia* spp. until further studies can be done.

Hantzschia* cf. *distinctepunctata (Hustedt 1921) Hustedt in A. Schmidt 1921

[Figs 29-5, 29-6]

Synonyms:

Hantzschia amphioxys (Ehrenberg 1841) Grunow in Cleve & Grunow 1880 var. *distinctepunctata* Hustedt 1921

References:

(1) Hustedt 1921
(2) Simonsen 1987, Compère 1990
(3) Mann 1980, Krammer & Lange-Bertalot 1988, Compère 1990, Garcia-Baptista (1993a, b), Lange-Bertalot 1993b

Morphology:

L: 28.9-31.2; W: 3.7; S: 19-20; F: 10 (n=2)

LM - Valves linear-lanceolate, asymmetrical about the apical plane; apices capitate. Proximal valve margin slightly constricted, distal margin convex. Each fibula ends in an interstria; the central fibuale are more widely spaced. The striae are distinctly punctate, uniseriate.

Remarks: Although this taxon corresponds well to the general description of *H. distinctepunctata*, it is considerably smaller and has a higher stria density than most specimens reported in the literature. Due to the rarity of the taxon, it was impossible to assess whether it belongs to the morphological complex around *H. distinctepunctata* (see below) or whether it is a separate, as yet undescribed species. *H. distinctepunctata* is a highly variable species: Garcia-Baptista (1993a, b) recognized 3 different morphological forms within this species.

Biogeography & Ecology: *H. distinctepunctata* was described from the (inland) River Voi in

Kenya (Schmidt 1921) but has since also been reported from estuarine and marine localities in Europe (Mann 1980), Africa (Archibald 1983, Compère 1990), South America (Garcia-Baptista 1993b), the Indo-Pacific region (John 1983, Lange-Bertalot 1993b) and other localities (see references in Garcia-Baptista 1993a). Only a few specimens belonging to this species were observed in the Westerschelde material.

HANTDIST

Hantzschia marina (Donkin 1858) Cleve in Cleve & Grunow 1880

[Figs 28-2, 28-3, 28-4, 28-5, 59-1]

Synonyms:

Epithemia marina Donkin 1858

References:

(1)	Donkin 1858
(2)	
(3)	Krammer & Lange-Bertalot 1988, Garcia-Baptista 1993a, b

Morphology:

L: 50-60; W: 7.5; S/F: 7-8 (n=2)

LM - There are two more or less rectangular plastids; they are appressed against the proximal side of the girdle, with lobes (4 per plastid, two below each valve) extending to the distal side. The nucleus is situated inbetween the two plastids on their distal side. The valves are semi-lanceolate, asymmetrical about the apical plane and have more or less capitate apices. The less convex side is slightly constricted in the centre. Each biseriate stria (with the puncta in quincunx) is separated by a distinct transapical ridge (see below). The number of these ridges is equal to the number of fibulae. The cingulum consists of several punctate copulae.

SEM - Only an external valve view was observed. Valve face convex, gradually merging into the distal valve mantle. The striae are separated by prominent ridges; the areolae are reniform (note that in Fig. 59-1 only one row of areolae of each biseriate stria is visible). The raphe is interrupted centrally; on the distal side of the central nodule a small, conopeum-like structure is visible.

Remarks: Only two *Hantzschia* species have two rows of areolae separated by ridges, i.e. *Hantzschia marina* and the recently described *H. psammicola* Garcia-Baptista (Garcia-Baptista 1993a,b). The two species can easily be distinguished by the shape of the areolae (reniform in *H. marina*, round in *H. psammicola*) and by the ratio fibulae/transapical ridges (1 in *H. marina*, < 1 in *H. psammicola*). To our knowledge, *H. psammicola* has not yet been reported outside the type locality in Brazil.

Biogeography & Ecology: *Hantzschia marina* is a common epipelic species on sandy sediments in Europe (Hendey 1964). In the Westerschelde estuary, it was rare in medium sandy sediments in the mouth of the estuary. Its geographical distribution needs further study: it was *not* observed by e.g. Rao & Lewin (1976), Cooper (1995a), Poulin *et al.* (1990), Archibald (1983), John (1983) and

Podzorski & Håkansson (1987). The only reports we have found so far are from Europe only.

HANTMARI

Hantzschia virgata (Roper 1858) Grunow in Cleve & Grunow 1880 **var. *virgata***

[Figs 29-7, 59-2]

Synonyms:

Nitzschia virgata Roper 1858
Hantzschia insolita Giffen 1967

References:

(1)	Roper 1858
(2)	
(3)	Krammer & Lange-Bertalot 1988, Mann 1981

Morphology:

L: 74.1; W: 10; S: 11-12 (distal valve face); F: 6-7

LM - Valves linear to lanceolate, asymmetrical about the apical plane. The proximal valve margin is constricted in the centre, the distal margin is slightly convex. The apices are rostrate each fibula ends in an interstria; the central ones are more widely spaced. The striae are distinctly punctate, uniseriate. The stria density on the distal valve face and mantle is lower than on the proximal valve face and mantle.

SEM - Only an external valve view was observed. Valve face strongly curved, merging imperceptibly with the rather deep mantles. Striae uniseriate on the distal part of the valve; the stria density becomes much denser on the proximal part of the valve and mantle. A few copulae with 2 (3?) rows of areolae each are visible.

Remarks: *Hantzschia virgata* can be confused with *H. distinctepunctata* but in the latter species the ratio striae/fibulae is < 2, while in *H. virgata* it is > 2 (Krammer & Lange-Bertalot 1988). For a detailed discussion of this species and its infraspecific variation, see Mann (1977, 1980, 1981). We have assigned our specimens to variety *virgata* on the basis of the 'doubling' of the striae within the interspaces of the fibulae.

Biogeography & Ecology: *Hantzschia virgata* is a common epipelic species in estuarine and marine sandflats (Mann 1981). It has been reported from Europe (Krammer & Lange-Bertalot 1988), North (Round 1970) and South America (Garcia-Baptista 1993b) and Africa (Giffen 1967). Only a few specimens were found in the Westerschelde material.

HANTVIRG

Hantzschia/Nitzschia sp. 1

[Fig. 27-8]

Morphology:

L: 12.5; W: 3.4; S: 26; F: 14 (n=1)

LM - Valves broadly linear in the centre; the apices are cuneate to subrostrate. The whole valve is asymmetrical about the apical plane. The middle fibulae are not more widely spaced; each fibula spans one stria. The striae are distinctly punctate.

Biogeography & Ecology: Only a few specimens belonging to this taxon were observed in our samples from the Westerschelde.

HANISP01

Hantzschia/Nitzschia sp. 2

[Figs 26-6, 26-7, 26-8]

Morphology:

L: 11.2-16.2; W: 1.6-2, F: 9-10 (n=3)

LM - Valves semi-lanceolate, apices cuneate. The raphe system lies near the straight valve margin, which gives the valve a *Cymbellonitzschia*-like appearance. The central fibulae are not more widely spaced. No striae can be seen in LM.

Remarks: *Hantzschia/Nitzschia* sp. 2 is very reminiscent of a diatom (identified as *Cymbellonitzschia diluviana* Hustedt) reported by John (1983) from the Swan River estuary (Australia). This taxon is also slightly reminiscent of a *Hantzschia* sp. illustrated in Kuylenstierna (1989-90, Pl. 70, Figs 879-881) but that taxon is much larger and has distinctly more widely spaced central fibulae. Salah (1955) described a *Cymbellonitzschia* species (*C. hossamedinii* Salah) from Blakeney Point (England), but that species has striae that can be resolved in LM.

Biogeography & Ecology: *Hantzschia/Nitzschia* sp. 2 was rare in medium sandy sediments in the mouth of the estuary.

HANISP02

Hantzschia/Nitzschia sp. 3

[Fig. 28-1]

Morphology:

L: 50; W: 5; S/F: 17 (n=1)

LM - Valve semi-lanceolate with capitate produced apices. The raphe system is situated on the straight valve margin. The number of fibulae, which are indistinct, is probably identical to the number of striae. A distinct central nodule can be distinguished. No individual areolae can be distinguished in LM.

Remarks: This taxon resembles an unidentified *Nitzschia* species illustrated in Hartley *et al.* (1996, Pl. 194, Fig. 5) but that diatom has less fibulae than striae.

Biogeography & Ecology: Only a few valves belonging to this taxon were found.

HANISP03

Nitzschia Hassall 1845

Genus description: Round *et al.* 1990, Mann 1986

Nitzschia is a large and difficult genus which is, despite the appearance of comprehensive identification works for this genus (cf. Krammer & Lange-Bertalot 1986), in need of thorough revision (Mann 1986). Recently, several new or re-established genera have been separated from *Nitzschia*, e.g. *Psammodictyon* and *Tryblionella* (Round *et al.* 1990).

The distinction between many *Nitzschia* species is precarious, especially in the section 'Lanceolatae' ('The taxonomically most problematic group of diatoms', Lange-Bertalot 1977), a very large species group which is mainly negatively characterized by the absence of features which characterize other sections of the genus *Nitzschia* (e.g. conopeum, central position of the raphe system, ...)(Krammer & Lange-Bertalot 1988). Most likely, many species within this section are superfluous, due to the insufficient knowledge about phenotypic morphological variability of these *Nitzschia* species.

As many *Nitzschia* species are fragile, it is certain that their cell numbers are underestimated due to the destruction of valves during acid treatment of the samples.

Nitzschia cf. *aequorea* Hustedt 1939

[Figs 29-3, 29-4]

References:

(1) Hustedt 1939
(2) Simonsen 1987
(3) Simonsen 1987, Krammer & Lange-Bertalot 1988

Morphology:

L: 31.2-37.5; W: 5-5.6; S: about 30; F: 11 (n=2)

LM - Valves lanceolate wih slightly capitate apices; valves not constricted in the centre. Middle fibulae not more widely spaced. Striae barely visible, finely punctate.

Remarks: There is little doubt that this species belongs to the species complex around *N. aequorea* and *N. agnita* (see also *N.* cf. *rosenstockii*). The main problem with this complex is that many superfluous species have been described (e.g. by Cholnoky) or that species have been described on the basis of only a few specimens. In addition, the type material appears to be lost in many cases (Krammer & Lange-Bertalot 1988). As only a few specimens of *N.* cf. *aequorea* were observed in our material, it was impossible to fully assess its true identity.

Biogeography & Ecology: Only a few specimens belonging to this taxon were observed in the Westerschelde material. *Nitzschia aequorea* was desrcibed from the German Wadden Sea but has also been reported from inland waters (e.g. Compère 1991).

NITZCFAE

Nitzschia brevissima Grunow in van Heurck 1881

[Figs 29-9, 29-10]

Synonyms:

Nitzschia obtusa W. Smith 1853 var. *brevissima* (Grunow) Van Heurck 1885

References:

(1) Grunow in Van Heurck 1881
(2) (?) Krammer & Lange-Bertalot 1988
(3) Germain 1986, Krammer & Lange-Bertalot 1988, Kuylenstierna 1989-90

Morphology:

L: 32-36.2; W: 6.2; S: > 36; F: 6-8 (n=2)

L: Valves linear, constricted in the centre and with rostrate-capitate apices. Striae not visible in LM, fibulae distinct.

Biogeography & Ecology: *Nitzschia brevissima* is a common and supposedly cosmopolitan species from brackish water (Archibald 1983, Germain 1986), especially at low salinities (Krammer & Lange-Bertalot 1988). It was only rarely found in the Westerschelde samples.

NITZBREV

Nitzschia commutata Grunow in Cleve & Grunow 1880

[Figs 29-1, 29-2]

References:

(1) Cleve & Grunow 1880
(2)
(3) Krammer & Lange-Bertalot 1988

Morphology:

L: 55-76; W: 6-6.2; S: 16-19; F: 7-9 (n=3)

LM - Valves more or less linear but asymmetrical about the apical axis due to subrostrate apices which are slightly curved in the distal direction and the proximal valve margin which is constricted in the centre. The distal valve margin is more or less straight or only slightly concave. The fibulae end in one interstria; the central ones are distinctly more widely spaced. The striae are uniseriate and consist of distinct punctae, 18-20 in 10 µm.

Remarks: We have identified this taxon as *Nitzschia commutata*, although both the number of striae and the number of fibulae is lower than given for this species in Krammer & Lange-Bertalot (1988).

Biogeography & Ecology: *Nitzschia commutata* is an epipelic species from brackish and electrolyte-rich waters wordlwide (Archibald 1983, Krammer & Lange-Bertalot 1988, Compère 1991, Cox 1996). Only a few valves of this species were found in our material.

NITZCOMM

Nitzschia* cf. *dissipata (Kützing 1844) Grunow 1862 [Figs 30-1, 30-2, 30-3, 30-4]

Synonyms:

Synedra dissipata Kützing 1844

References:

(1) Kützing 1844
(2)
(3) Schoeman & Archibald 1976, Krammer & Lange-Bertalot 1988, Kuylenstierna 1989-90

Morphology:

L: 12.5-43.7; W: 2.5-5.2; W(P): 5.9-8.1; F: 6-9

LM - Two girdle-appressed plastids, fore and aft, with lobes emanating from the margins. Frustules more or less rectangular in girdle view. Note that no wing-like expansions can be seen near the apices. Valves (often very narrowly) lanceolate, apices slightly capitate. The canal raphe lies more or less in the centre of the valve. The central fibulae are not more widely spaced. The striae cannot be resolved in LM.

Remarks: It is possible that different forms of small *Nitzschia dissipata*-like taxa have been lumped together in *N.* cf. *dissipata*. Some of the smaller specimens (Figs 30-3, 30-4) are very reminiscent of N. *dissipata* (as illustrated in Krammer & Lange-Bertalot 1988, T. 11, Figs 4-5). They also resemble *N. incrustans* Grunow, a species which was described from brackish water in the harbour of Dieppe (France) but has hardly ever been reported since (cf. Krammer & Lange-Bertalot 1988, Kuylenstierna 1989-90). The latter species, however, appears to have a very wide cingulum, consisting of numerous copulae, while our (living) specimens have a narrow girdle. Before detailed studies have been made on the identity and interrelationships of *N. dissipata* and similar taxa, it is impossible to identify these forms with certainty. For the time being we decided to refer to them as *N.* cf. *dissipata.*

Biogeography & Ecology: Similar small forms were described from marine localities on the Swedish West coast by Kuylenstierna (1989-90, as *Nitzschia* sp. D). *Nitzschia* cf. *dissipata* was rare in the Westerschelde; its ecological requirements are unknown.

NITZCFDI

Nitzschia dubia W. Smith 1853 [Fig. 31-9]

References:

(1) W. Smith 1853
(2) Krammer & Lange-Bertalot 1988
(3) Krammer & Lange-Bertalot 1988, Kuylenstierna 1989-90, Snoeijs & Potapova 1995

Morphology:

L: 50-78.8; W(P): 19-20; S: 23-26; F: 11-13 (n=3)

LM - Only cells in girdle view were observed. Two girdle-appressed (lobes of?) plastids are visible (Fig. 31-9). The frustules are more or less rectangular, slighlty constricted centrally; the apices are broadly rounded. The individual valves (also in girdle view!) are more or less linear to lanceolate and asymmetrical about the apical plane; their apices are rostrate and curved towards the cingulum. All fibulae end in one interstria; the central fibulae are slightly more widely spaced. No individual punctae can be distinguished in the striae. The cingulum is rather narrow and appears to be composed of numerous narrow copulae.

Remarks: We have identified our specimens as *Nitzschia dubia* on the basis of the central constriction of the frustule, which is not as pronounced as in similar species such as *N. bilobata* and *N. hybrida* (Krammer & Lange-Bertalot 1988).

Biogeography & Ecology: *Nitzschia dubia* is a common epipelic taxon in brackish waters (Cox 1996). It is been reported in Europe (e.g. Hendey 1964, Snoeijs & Potapova 1995, Cox 1996, Hartley *et al.* 1996). It was very rare in the Westerschelde material.

NITZDUBI

Nitzschia cf. *frustulum* (Kützing 1844) Grunow in Cleve & Grunow 1880 [Figs 28-10, 28-11, 28-12, 28-13, 28-14, 60-3, 60-4, 60-5]

Synonyms:

Synedra frustulum Kützing 1844

References:

(1) Kützing 1844
(2) Krammer & Lange-Bertalot 1988 (lectotype)
(3) Krammer & Lange-Bertalot 1988, Wendker 1990a, b

Morphology:

L: (4.4-) 7.5-11.2; W: (1.9-) 2.2-2.7; S: 25-32 (34.5), mostly 26-28; F: 12-14.5

LM - Valves lanceolate, apices cuneate, sometimes slightly produced. Raphe marginal, fibulae distinct, sometimes more widely spaced in the centre. Striae distinct, uniseriate, slightly curved near the apices.

SEM - Valve face flat, canal raphe marginal. External raphe fissures appears to be continuous from pole to pole, the terminal fissures are hooked towards the proximal side. Internally, a distinct, raised central nodule is present, as well as two small helictoglossae at the terminal raphe endings. The striae are composed of small, round, poroids, about 44-48 in 10 µm. No occlusions are visible. The interstriae are slightly costate internally. A single line of areolae is present between the raphe and the proximal valve margin.

Remarks: The morphology of this taxon has been discussed in detail by Wendker (1990a). According to this author, there is a morphological continuum between *Nitzschia frustulum* and *N. inconspicua* Grunow, two species which are usually only distinguished on the basis of the shape of the valve apex (cuneate to subrostrate in *N. frustulum*, broadly rounded in *N. inconspicua*) and their autecology (brackish waters vs. freshwater respectively). However, Kuylenstierna (1989-90) found that in his material from the Swedish West coast *N. frustulum* always had one row of areolae on the mantle near the raphe, while *N. inconspicua* always had two, a feature which had not been reported before (cf. Krammer & Lange-Bertalot 1988, Wendker 1990a). Together with the shape of the valve apex and the brackish habitat, this additional feature supports the identification of our specimens as *N. frustulum*.

However, many questions remain as to the true identity of our specimens. The species complex around *N. frustulum* is very complicated and as yet little is known about the morphological variation within this complex (see however Wendker 1990a). The size range of our specimens compares well with those of specimens from Chesapeake Bay (L: 6-10 µm, W: 2-3, F: 10-15 and S: 20-30, Cooper 1995a). For the time being, we therefore refer to our specimens as *N.* cf. *frustulum* until further resaerch has been carried out.

Biogeography & Ecology: *Nitzschia* cf. *frustulum* is the most abundant *Nitzschia* species in the Westerschelde estuary, although possibly other abundant, more fragile epipelic *Nitzschia* species are underestimated in the oxidized cell counts. It is mainly found in fine sandy sediments and is slightly more abundant in the polyhaline reaches of the estuary. *Nitzschia frustulum* is commonly reported from brackish waters worldwide (e.g. Wendker 1990b, Snoeijs 1993, Witkowski 1994, Cooper 1995a).

NITZCFFR

Nitzschia hybrida Grunow in Cleve & Grunow 1880

References:

(1) Cleve & Grunow 1880
(2)
(3) Krammer & Lange-Bertalot 1988

Morphology:

A detailed description of this species is given by Krammer & Lange-Bertalot 1988.

Biogeography & Ecology: Only a few specimens belonging to this species were found in the Westerschelde material.

NITZHYBR

Nitzschia minutula (*lanceola* var.?) Grunow in Cleve & Grunow 1880 non Grunow in Van Heurck 1881 (69-5)

[Fig. 29-9]

References:

(1) Cleve & Grunow 1880
(2)
(3) Krammer & Lange-Bertalot 1988

Morphology:

L: 17.5; W: 4.7; S/F: 17.5 (n=1)

LM - Valves lanceolate, apices cuneate. The number of striae is identical to the number of fibulae. The striae are finely punctate.

Remarks: Only a few valves of this species were found. It belongs to the species complex around *Nitzschia compressa* var. *vexans* (Grunow) Lange-Bertalot, which is discussed in detail in Krammer & Lange-Bertalot (1988) and Archibald (1983). We have assigned our specimens to *N. minutula* (*lanceola* var.?) on the basis of the illustrations of this species in Krammer & Lange-Bertalot (1988). It mainly differs from closely related species such as *N. siliqua* Archibald and *N. compressa* var. *vexans* in valve shape and stria structure. However, the true identity of *N. minutula* (*lanceola* var.?) is as yet unclear (cf. VanLandingham 1978) and requires further study.

Biogeography & Ecology: Only a few specimens belonging to this species were found; its ecological requirements are unknown.

NITZMINU

Nitzschia nana Grunow in Van Heurck 1881

References:

(1) Van Heurck 1881
(2)
(3) Krammer & Lange-Bertalot 1988

Morphology:

L: 27.5; W: 3.7; F: 12-13; S: > 28 (n=1)

LM - Valves sigmoid-linear, apices rostrate. The central fibulae are more widely spaced. The striae are very fine and appear non-punctate in LM.

Biogeography & Ecology: *Nitzschia nana* was very rare in the Westerschelde stations.

NITZNANA

Nitzschia pellucida Grunow in Cleve & Grunow 1880 [Fig. 29-8]

References:

(1) Cleve & Grunow 1880
(2)
(3) Krammer & Lange-Bertalot 1988

Morphology:

L: 25; W: 3.7; F: 17 (n=1)

LM - Valve (in girdle view?) lanceolate, distinctly constricted on the side of the raphe canal, convex on the other side. Apices asymmetrically produced. Raphe canal eccentric (in this valve position). Fibulae small, more widely spaced in the centre of the valve. Striae not visible in LM.

Biogeography & Ecology: Only a few valves belonging to this brackish-water species were observed (Krammer & Lange-Bertalot 1988).

NITZPELL

Nitzschia cf. *rosenstockii* Lange-Bertalot 1980 [Figs 30-11, 30-12, 30-13, 30-14]

References:

(1) Lange-Bertalot 1980a
(2) Lange-Bertalot 1980a
(3) Lange-Bertalot 1980a, Krammer & Lange-Bertalot 1988

Morphology:

L: 8.7-21.9; W: 2.5-5 (-7.9); F: 14-18 (-20) (n=17)

LM - Valves lanceolate, with cuneate to cuneate-obtuse apices. Raphe system eccentric. Fibulae short; the central ones are not more widely spaced. The striae and copulae could not be resolved in LM.

Remarks: *Nitzschia rosenstockii* belongs to the species complex around *N. aequorea* and *N. agnita*, which comprises many brackish-water taxa (cf. Krammer & Lange-Bertalot 1988). As *N. rosenstockii* has only been reported from the type locality (a freshwater site in Sicily) and we have not been able to study its morphology in SEM, we refrain from making a positive identification.

Biogeography & Ecology: *N. rosenstockii* has been described from electrolyte-rich water in Sicily (Krammer & Lange-Bertalot 1988) but is also present in other areas, such as the Baltic Sea (Snoeijs & Kautsky 1989). *N.* cf. *rosenstockii* is a common epipelic species in silty and very fine sandy sediments of the mesohaline reaches of the Westerschelde estuary.

NITZCFRO

Nitzschia sigma (Kützing 1844) W. Smith 1853

Synonyms:

Synedra sigma Kützing

References:

(1) Kützing 1844
(2)
(3) Krammer & Lange-Bertalot 1988

Morphology:

L: 40-140.6; W: 5.4-10.4; F: 8-12; S: 20-22 (n=3)

A detailed description of this species is given by Krammer & Lange-Bertalot 1988.

Biogeography & Ecology: Only a few valves belonging to this species were found.

Nitzschia valdestriata Aleem & Hustedt 1951

[Fig. 28-15]

References:

(1) Aleem & Hustedt 1951
(2) Simonsen 1987
(3) Krammer & Lange-Bertalot 1988, Snoeijs & Vilbaste 1994

Morphology:

L: 6.9; W: 2.2; S: 24; F: 10 (n=1)

LM - Valve lanecolate, apices cuneate. Fibulae not centrally interrupted; each fibula spans two interstriae. Striae distinct, areolae not visible in LM.

Biogeography & Ecology: Only one specimen of this widespread brackish-water species (Kuylenstierna 1989-90, Cooper 1995a, Hartley *et al.* 1996) was found in the Westerschelde material.

NITZVALD

Nitzschia sp. 1

[Figs 31-7, 31-8]

Morphology:

L: 49.6-53.1; W: 6.7-7.5; S: 31-36 (and more?); F: 11-13 (n=2)

LM - Plastid structure unclear: probably two lobed plastids fore and aft; nucleus central. Valves lanceolate with capitate apices. Canal raphe more or less central. Central fibulae not more widely spaced. Striae very fine but usually visible in LM (DIC).

Remarks: This taxon was at first identified as *N. dissipata*. However, if we rigorously compare the description of this species in Krammer & Lange-Bertalot (1988) to our own than we have to exclude our specimens from *N. dissipata*: they have a lower stria density and a higher number of fibulae in 10 µm. In addition, *N. dissipata* is a freshwater species from electrolyte-rich waters. However, *N. dissipata* is also often recorded from brackish and marine localities (e.g. Schoeman & Archibald 1976 and Poulin *et al.* 1990). Whether these reports actually concern true *N. dissipata* is not certain. The species complex around this species is in need of a thorough revision.

Biogeography & Ecology: *Nitzschia* sp. 1 is common in fine sandy sediments throughout the Westerschelde estuary.

NITZSP01

Nitzschia sp. 2

[Figs 30-16, 30-17, 30-18, 30-19]

Morphology:

L: 16.2-23.7 (-36.2); W(P): 3.7-5; F: 11-16 (n=10)

LM - Only girdle views were observed, both in living and oxidized material. Two more or less rectangular to very slightly H-shaped plastids (in girdle view!), fore and aft in the cell, encompassing the central nucleus. Each plastid has a circular pyrenoid. Frustules rectangular in girdle view, sometimes very slightly constricted in the centre of the valves. Fig. 68-15A shows a frustule in oblique view. The fibulae are quite irregularly placed, the central ones are distinctly further apart. The striae and copulae could not be resolved in LM.

Remarks: This species is characterized by the distinctly more widely spaced central fibulae and the rectangular shape in girdle view. *Nitzschia* sp. 2 is very reminiscent of *Nitzschia tenuistriata* Hustedt (cf. Simonsen 1987). Unfortunately, to our knowledge, this species has never been reported since its description. Further study is needed to assess the identity of this species.

Biogeography & Ecology: *Nitzschia* sp. 2 is one of the common epipelic *Nitzschia* species in the Westerschelde estuary; it is mainly found in silty and very fine sandy sediments and is more abundant in the mesohaline reaches of the estuary.

NITZSP02

Nitzschia sp. 3

[Figs 30-7, 30-8, 30-9, 30-10]

Morphology:

L: 14.1-21.5; W: 4.1-7.5; F: 9.5-16 (mostly 12-13)(n=16)

LM - Valves broadly lanceolate; the proximal and distal valve margin are parallel due to a slight constriction of the valve margins in the centre. Apices cuneate-obtuse. Fibulae short, the middle ones are more widely spaced.

Remarks: *Nitzschia* sp. 3 is characterized by its small size, shape and more widely spaced central fibulae, but especially by the impossibility to resolve the striae in LM (DIC). This taxon possibly belongs to the species complex around *Nitzschia capitellata* Hustedt and is actually quite remeniscent of the smallest forms of this species (cf. Krammer & Lange-Bertalot 1988, Fig. 62-11). However, our specimens are almost always smaller than 20 µm, which Krammer & Lange-Bertalot mention as the lower limit of the length range of *N. capitellata.* Further study is needed to assess the relationship between *N.* sp. 3 and *N. capitellata.*

The general size and shape of *N.* sp. 3 is also similar to that of *Nitzschia laevis* Hustedt, but this species has a much lower stria density.

Biogeography & Ecology: *N.* sp. 3 was rare in silty sediments in the Westerschelde estuary.

NITZSP03

Nitzschia sp. 4

[Figs 30-5, 30-6]

Morphology:

L: 22-35; W: 3.7-5; F: 12-14 (n=4)

LM - Valves linear to lanceolate (smaller specimens) with rostrate-capitate apices. The valves are slightly constricted in the centre of the valve. The central fibulae are not more widely spaced than the rest of the fibulae. No striae are visible in LM.

Remarks: *Nitzschia* sp. 4 is quite reminiscent of *N. capitellata* Hustedt but this species has more widely spaced central fibulae.

Biogeography & Ecology: *N.* sp. 4 was rare in silty sediments in the mesohaline part of the estuary.

NITZSP04

Psammodictyon Mann 1990

Genus description: Round *et al.* 1990

Psammodictyon is closely related to both *Tryblionella* (see below) and *Nitzschia.* The main discriminating features of *Psammodictyon* are (1) the loculate structure of at least part of the valve, (2) the occurrence of typical ridges around the external raphe fissures, (3) the shape of the valve and (4) the typical quincunx arrangement of the loculi (for more details see Round *et al.* 1990).

Psammodictyon panduriforme (Gregory 1857) Mann 1990 var. *delicatulum* (Grunow in Cleve & Grunow 1880) Poulin 1990

[Figs 32-7, 32-8, 32-9, 59-4, 59-5]

Synonyms:

Nitzschia panduriformis Gregory 1857 var. *delicatula* Grunow in Cleve & Grunow 1880

References:

(1) Cleve & Grunow 1880
(2)
(3) Krammer & Lange-Bertalot 1988, Poulin *et al.* 1990

Morphology:

L: 13.5-23.7; W: 6.2-7.5; F: 11-14.5; S: 22-25 (n=7)

LM - Valves panduriform, apices slightly produced. Central fibulae more widely spaced. The striae, with areolae in quincunx, are crossed by a distinct apical fold.

SEM - Only external valve views were observed. Valve face undulate. The external raphe fissures are accompanied by a ridge on either side; the distal ridge folds over the valve face margin. The areolae open to the outside via a foramen, while internally a velum-like structure can be seen. Note that near the proximal valve margin, this typical loculate structure is replaced by simple poroids.

Remarks: We have identified our specimens as *Psammodictyon panduriforme* var. *delicatulum* on the basis of the illustrations shown in Krammer & Lange-Bertalot (1988, T. 39, Fig. 9). However, as already pointed out by the latter authors, the identity of this taxon and related taxa, such as *Psammodictyon constrictum*, *Tryblionella coarctata* (Grunow) Mann, *Psammodictyon panduriformis*, *P. mediterraneum* (Hustedt) Mann and their varieties, is far from clear. In our material, we found other valves (Figs. 32-1, 32-2) which (in LM) only differed from *P. panduriforme* var. *delicatulum* in size and striation density. During the counts, some of these valves were identified as *Tryblionella coarctata*. Note also that the *P. panduriforme* var. *delicatulum* specimens illustrated in Poulin *et al.* (1990) are quite different from the Westerschelde specimens. Clearly, further research is needed to assess the identy of these taxa and their relationship to each other.

Given the strong resemblance between *Tryblionella coarctata* and *Psammodictyon constrictum*, *P. mediterraneum* and *P. panduriforme*, it seems unlikely that this taxon belongs to *Tryblionella*: it should probably be placed in *Psammodictyon*.

Biogeography & Ecology: *P. panduriforme* var. *delicatulum* was common in silty sediments throughout the estuary.

PSAMPADE

Tryblionella W. Smith 1853

Genus description: Round *et al.* 1990

As *Psammodictyon Tryblionella* is mainly polythetically defined: a list of diagnositic combinations for this genus is given by Round *et al.* (1990).

Further research is needed to elucidate the relationships between the genera *Nitzschia, Psammodictyon* and *Tryblionella.*

Tryblionella apiculata Gregory 1857

[Fig. 60-2]

Synonyms:

Synedra constricta Kützing 1844
Nitzschia constricta (Kützing) Ralfs non (Gregory 1855) Grunow 1880
Nitzschia apiculata (Gregory 1857) Grunow 1878
Tryblionella constricta (Kützing) Poulin 1990 non Gregory 1855

References:

(1) Kützing 1844
(2) Krammer & Lange-Bertalot 1988 (lectotype)
(3) Schoeman & Archibald 1976, Krammer & Lange-Bertalot 1988, Snoeijs & Vilbaste 1994

Morphology:

L: 22.5-41.2; 6-8.7; F/S: 16-19

LM - Valves linear, apices subrostrate to rostrate. The number of striae is equal to the number of fibulae. A apical sternum crosses the striae in the centre of the valve.

Remarks: The nomenclature of the species *Tryblionella apiculata* and *Psammodictyon constrictum* (Gregory) Mann has always been very confusing (cf. also Krammer & Lange-Bertalot 1988). The table below shows the chronological history of both names and their synonyms.

Kützing 1844	*Synedra constricta*	
Gregory 1855		*Tryblionella constricta*
Gregory 1857	***Tryblionella apiculata***	
Ralfs in Pritchard 1861	*Nitzschia constricta*	
Grunow 1878	*Nitzschia apiculata*	
Grunow in Cleve & Grunow 1880		*Nitzschia constricta*
Mann in Round *et al.* 1990		***Psammodictyon constrictum***
Poulin *et al.* 1990	*Tryblionella constricta*	

The correct names are indicated in bold face. Note that *Tryblionella apiculata* was described twice.

Although *constricta* is the oldest available epithet, it cannot be used as the combination *Tryblionella constricta* already exists (Gregory 1855); therefore the transfer by Poulin *et al.* (1990) is illegitimate. The correct name for this diatom is *Tryblionella apiculata*. The diatom originally described as *Tryblionella constricta* belongs to the genus *Psammodictyon.* Note that when both species were still classified under *Nitzschia*, the diatom described by Kützing should have been named *Nitzschia constricta*, as the epithet *constricta* would have priority over *apiculata*.

According to Krammer & Lange-Bertalot (1988), *Psammodictyon constrictum* might be synonymous with *Tryblionella coarctata* (Grunow in Cleve & Grunow 1880) Mann 1990. (see below), in which case the latter name should become a synonym of *P. constrictum*. See also *T. marginulata*.

Biogeography & Ecology: *Tryblionella apiculata* is a common and widespread species in freshwater (electrolyte-rich), estuarine and marine sediments worldwide (Hendey 1964, Gerloff *et al.* 1978, Archibald 1983, Krammer & Lange-Bertalot 1988, Compère 1991, Cooper 1995a, Cox 1996). *T. apiculata* was the one of the most common epipelic representatives of the Bacillariaceae in our counts from the Westerschelde estuary (note however that this rather robust species was not affected by the acid treatment as were many fragile taxa (mainly belonging to *Nitzschia*); its importance is thus overestimated in relation to other members of the Bacillariaceae). It was present in silty sediment samples and is restricted to the mseohaline reaches of the estuary (cf. its very low salinity optimum in Table 39).

TRYBAPIC/NITZCONS

Tryblionella coarctata (Grunow in Cleve & Grunow 1880) Mann 1990 [Figs 32-1, 32-2]

Synonyms:

Nitzschia coarctata Grunow 1880

References:

(1) Cleve & Grunow 1880
(2)
(3) Krammer & Lange-Bertalot 1988, Compère 1991

Morphology:

See *Psammodictyon panduriforme* var. *delicatulum*

Remarks: Note that this species should probably belong to the genus *Psammodictyon* (see *P. panduriforme* var. *delicatulum*).

Biogeography & Ecology: *T. coarctata* was rare in rather sandy sediments in the Westerschelde estuary. It might have been confused with *Psammodictyon panduriforme* var. *delicatulum* during the cell counts.

TRYBCOAR

Tryblionella debilis Arnott in O'Meara 1873

Synonyms:

Nitzschia debilis (Arnott) Grunow in Cleve & Grunow 1880

References:

(1) O'Meara 1873
(2)
(3) Krammer & Lange-Bertalot 1988

Morphology:

L: 22.5; W: 8.2 (n=1)

LM - Valves linear-elliptical with rounded apices. In the centre of the valve, an apical strip with distinct ribs is present; the striae are not visible in LM.

Biogeography & Ecology: *Tryblionella debilis* is common in marine sediments in Europe (Krammer & Lange-Bertalot 1988), South Africa (Archibald 1983) and probably elsewhere. In the Westerschelde estuary it was very rare.

TRYBDEBI

Tryblionella granulata (Grunow 1880) Mann 1990

[Figs 31-3, 31-4]

References:

(1) Grunow in Cleve (1878) *or* Grunow (1880)
(2)
(3) Gerloff *et al.* 1978, Krammer & Lange-Bertalot 1988

Morphology:

L: 16.2; W: 10; F/S: 7 (n=1)

LM - Valves broadly elliptical with cuneate apices. The number of fibulae is equal to the number of striae. The latter consist of large, round areolae, more or less in a quincunx arrangement. However, towards the distal valve margin (cf. SEM photographs in Gerloff *et al.* 1978), these large areolae are replaced by double rows of poroids.

Remarks: A detailed SEM study of *Tryblionella granulata* and *T. punctata* (see there) should reveal whether these species belong to *Tryblionella* or to *Psammodictyon*.

Biogeography & Ecology: *T. granulata* is a common marine species on sandy sediments and has been reported from Europe (Krammer & Lange-Bertalot 1988), Africa (Archibald 1983, Compère 1991), North America (Cooper 1995) and Australia (John 1983). Only a few specimens belonging to this species were found in the Westerschelde estuary.

TRYBGRAN

Tryblionella hungarica (Grunow 1862) Mann 1990 [Fig. 32-5]

Synonyms:

Nitzschia hungarica Grunow 1862

References:

(1) Grunow 1862
(2)
(3) Krammer & Lange-Bertalot 1988, Snoeijs & Potapova 1995

Morphology:

L: 51.2; W: 6.9; F: 8-9; S: 15-16

LM - Valves linear, slightly constricted centrally, with subrostrate apices. Fibulae ending in one or two interstriae; the central ones are slightly further apart. Striae non-punctate, crossed by a rather narrow sternum in the centre of the valve.

Remarks: See *Tryblionella marginulata.*

Biogeography & Ecology: Only a few valves belonging to this species were observed in our material.

Tryblionella levidensis* var. *levidensis W. Smith 1856 [Fig. 31-1]

Synonyms:

Nitzschia levidensis (W. Smith) Grunow in Van Heurck 1881

References:

(1) W. Smith 1856
(2)
(3) Archibald 1983, Krammer & Lange-Bertalot 1988, Poulin *et al.* 1990, Snoeijs & Vilbaste 1994

Morphology:

L: 20.6; W: 10; transapical ribs: 10 (n=1)

LM - Valves broadly linear with cuneate apices. The valve is crossed by numerous transapical ribs. In the centre of the valve, a distinct apical fold is present (usually visible as a distinct zigzag-line through the presence of the transapical ribs).

Biogeography & Ecology: Only a few specimens of the nominate variety were observed in our material. *Tryblionella levidensis* var. *levidensis* is a cosmopolitan taxon (Hendey 1964, Archibald 1983, John 1983, Poulin *et al.* 1990, Cooper 1995a) in estuarine and marine sediments, but also in electrolyte-rich freshwaters (Cox 1996).

TRYBLELE

Tryblionella levidensis* var. *salinarum (Grunow in Cleve & Grunow 1880) Sabbe comb. nov. prov.

[Fig. 31-2]

Synonyms:

Tryblionella salinarum (Grunow in Cleve & Grunow) Pelletan 1889
Nitzschia levidensis var. *salinarum* Grunow in Cleve & Grunow 1880

References:

(1) Cleve & Grunow 1880
(2)
(3) Krammer & Lange-Bertalot 1988, Snoeijs & Potapova 1995

Morphology:

L: 12.5-13; W: 8-9; transapical ribs: 11-15 (n=3)

LM - Valves elliptical with cuneate apices. The valve is crossed by numerous transapical ribs. However, no *distinct* apical fold is present in the centre of the valve.

Remarks: *Tryblionella levidensis* var. *salinarum* can be distinguished from the nominate variety in its generally smaller size, a higher number of transapical ribs in 10 µm and in the appearance of the central apical fold which does not appear as a distinct zigzag-line [Krammer & Lange-Bertalot 1988, compare also the illustrations of both taxa in Snoeijs & Vilbaste (1994) and Snoeijs & Potapova (1995) respectively]. We decided not to raise this taxon to species level (*Tryblionella salinarum* (Grunow in Cleve & Grunow) Pelletan) as for the time being we have no clear idea about the morphological variability within this species.

Biogeography & Ecology: *Tryblionella levidensis* var. *salinarum* is a common species in estuarine and marine sediments worldwide (Compère 1991, Snoeijs & Potapova 1995). Only a few valves were found in the Westerschelde material.

TRYBLESA

Tryblionella marginulata (Grunow in Cleve & Grunow 1880) Mann 1990

[Fig. 32-6]

Synonyms:
Nitzschia marginulata Grunow in Cleve & Grunow 1880

References:

(1) Grunow in Cleve & Grunow 1880
(2)
(3) Archibald 1983, Krammer & Lange-Bertalot 1988

Morphology:

L: 43.7; W: 8.7; F: 7; S: 19

LM - Valve linear-lanceolate, with subrostrate, slightly asymmetrical apices. The valve is slightly constricted centrally. The fibulae are apically elongate, spanning two to three interstriae; the central ones are slightly further apart. Striae non-punctate, crossed by an apical fold in the centre of the valve. Note the marginal sternum on the distal side of the valve, which could be an optical artefact (out of focus).

Remarks: *Tryblionella marginulata* can at first sight easily be confused with two other species which also occurred in the Westerschelde material, viz. *T. hungarica* and *T. apiculata* (cf. there). In the Table below some of their most important features are listed. *T. marginulata* is usually wider than both other species, and has fibulae which are distinctly apically elongated and often span two (or more, cf. Fig. 32-6) interstriae. *T. hungarica* can easily be distinguished from *T. apiculata* in having an unequal number of striae and fibulae.

	T. marginulata	*T. hungarica*	*T. apiculata*
Length (µm)	43-110 (Kr.& LB. 1988)	(20)35-130 (Kr.& LB. 1988) 20-110 (S. & A. 1976) 29-52 (Sn.&Pot.1995)	(1) 20-58 (Kr.& LB. 1988) 20-58 (S. & A. 1976) 31-42 (Sn. & Vil. 1994)
Width (µm)	9-17 (Kr.& LB. 1988)	(4.5)5-9 (Kr.& LB. 1988) (4)5-9 (S. & A. 1976) 4.5-8 (Sn.&Pot.1995)	(1) 4.5-8.5 (Kr.& LB. 1988) 4.5-8 (S. & A. 1976) 6-7 (Sn. & Vil. 1994)
Fibulae (nr. in 10µm)	9-14, often spanning 2 interstriae (Kr.& LB. 1988)	7-10(11), spanning 1 or 2 interstriae (Kr.& LB. 1988) 7-11 (S. & A. 1976)	(1) (14) 15-20 (Kr.& LB. 1988) (14)15-20 (S. & A. 1976)
Striae (nr. in 10µm)	19-28 (Kr.& LB. 1988)	16-20(22)(Kr.& LB. 1988) 16-18(20), 2 rows of puncta (S. & A. 1976)	(1) (14)15-20 (Kr.& LB. 1988) (14)15-20, (2)3-4 rows of puncta (S. & A. 1976)
Other	Apices only slightly produced (Kr.& LB. 1988)	apices (sub)rostrate (Kr.& LB. 1988, S. & A. 1976)	apices (sub)rostrate ((1) Kr.& LB. 1988, S. & A. 1976)

Kr.& LB. 1988 = Krammer & Lange-Bertalot 1988, S. & A. 1976 = Schoeman & Archibald 1976, Sn. & Vil. 1994 = Snoeijs & Vilbaste 1994, Sn.& Pot. 1995 = Snoeijs & Potapova 1995
(1) as *Nitzschia constricta*(Kützing) Ralfs

Biogeography & Ecology: Only a few valves belonging to *T. marginulata*. It occurs in brackish-marine and electrolyte-rich freshwaters (Krammer & Lange-Bertalot 1988).

TRYBMARG

Tryblionella navicularis (Brébisson in Küzting 1849) Ralfs in Pritchard 1861 [Figs 32-4, 60-1]

Synonyms:

Nitzschia navicularis (Brébisson in Küzting 1849) Grunow in Cleve & Grunow 1880

References:

(1) Brébisson in Kützing 1849
(2)
(3) Krammer & Lange-Bertalot 1988, Hartley *et al.* 1996

Morphology:

L: 27.5-70; W: 15-17.5; S/F: 7-8

LM - Valves broadly lanceolate; apices cuneate. The number of striae is equal to the number of fibuale. The striae are marginal and are biseriate, with areolae in quincunx. In the centre of the valve, a wide, lanceolate sternum is present. It is crossed by a series of transapical ribs which are aligned with the striae. The raphe system is eccentric, but is hardly visible in LM.

SEM - Only one external valve view was observed. Valve face flat, slightly undulate, mantle shallow. The distal valve face margin has a distinct ridge (cf. Round *et al.* 1990), while the proximal valve face margin gently curves into the mantle. Note that the areolae of the striae on the distal side are irregularly placed, while the ones on the proximal side show the typical quincunx pattern.

Biogeography & Ecology: *Tryblionella navicularis* is a widespread species in brackish and marine sediments in Europe (Krammer & Lange-Bertalot 1988). It was only rarely observed in the Westerschelde samples. The biogeography of *T. navicularis* needs further study: it was not reported by Cooper (1995a), Poulin *et al* (1990) or Rao & Lewin (1976) from North America, nor was it observed by Archibald (1983) in South Africa or by John (1983) in Australia. Podzorski & Håkansson (12987) reported it from the Philippines but it is not sure whether their illustrated specimen belong to this species.

TRYBNAVI

Tryblionella parvula (W. Smith 1853) Sabbe comb. nov. prov. [Figs 31-5, 31-6]

Synonyms:

Nitzschia parvula W. Smith 1853 non Lewis 1862

References:

(1) W. Smith 1853
(2) Krammer & Lange-Bertalot 1988
(3) Krammer & Lange-Bertalot 1988

Morphology:

L: 25.6-26.9; W: 4.9-5; F: 14-16; S: 30-32 (and more?)(n=3)

LM - Valves linear, slightly constricted in the centre. Apices rostrate. The fibulae end in one interstria each; the central ones are more widely spaced. The striae appear non-punctate in LM; they are crossed by distinct apical fold in the centre of the valve.

Remarks: Our specimens have a slightly higher fibula and stria density than mentioned in Krammer & Lange-Bertalot (1988). This species belongs to the genus *Tryblionella*.

Biogeography & Ecology: *T. parvula* has up to now only been reported from the type locality (brackish water in England)(Krammer & Lange-Bertalot 1988). In the Westerschelde, it was mainly present in silty and very fine sandy sediments in the mesohaline reaches of the estuary. It was most abundant in the stations of the Konijneschor transect.

TRYBPARV

Tryblionella punctata W. Smith 1853

Synonyms:

Nitzschia punctata (W. Smith) Grunow 1878
(?) *Pyxidicula compressa* Bailey 1851
(?) *Nitzschia compressa* (Bailey) Boyer 1916
Tryblionella compressa (Bailey 1851) Poulin 1990 sensu Poulin et al. (1990)

References:

(1) W. Smith 1853
(2)
(3) Krammer & Lange-Bertalot 1988, Poulin *et al.* 1990, Snoeijs & Vilbaste 1994

Morphology:

L: 33.7-50.1; W: 17.2-21.1; F/S: 7.5-9 (n=3)

LM - Valves broadly elliptical with cuneate apices. The number of fibulae is equal to the number of striae. A distinct apical fold crosses the striae in the centre of the valve.

Remarks: See also *Tryblionella granulata.*

Biogeography & Ecology: *T. punctata* is a common species from marine sandy sediments in Europe (Krammer & Lange-Bertalot 1988, Hartley *et al.* 1996), North America (Poulin *et al.* 1990, Cooper 1995a), Australia (John 1983) and probably elsewhere.

TRYBCOMP

Ordo Surirellales

Fam. SURIRELLACEAE Kützing

Petrodictyon Mann 1990

Genus description: Round *et al.* 1990

Petrodictyon gemma (Ehrenberg 1841) Mann 1990 [Fig. 59-3]

Synonyms:

Surirella gemma Ehrenberg 1839

References:

(1) Ehrenberg 1841
(2)
(3) Paddock 1978, Archibald 1983, Round *et al.* 1990, Hartley *et al.* 1996

Morphology:
L: 102.8; W: 44.7; S: 21

LM - Valves obovate with cuneate apices. Central sternum very narrow. The valve is characterized by distinct transapical costae (2-4 in 10 µm) and finely punctate, radiate striae.

SEM - Only an internal valve view was observed. Valve face more or less flat, at right angles to the mantle. The transapical costae are widest at the valve face/mantle junction (near the raphe). Inbetween each costa, a few (2-4) small fibulae are present. The striae are uniseriate. The structure of the raphe system could not be resolved.

Remarks: *Surirella gemma* was transferred to the new genus *Petrodictyon* (Mann in Round *et al.* 1990), which differs from *Surirella* in the structure of the valve, the transapical costae and the structure of the 'central' raphe endings.

Biogeography & Ecology: *Petrodictyon gemma* is a common epipelic species in the Westerschelde estuary but was only rarely encountered in our counts [due to its much larger size (which necessitates counting at lower magnifications) but also because it was easily broken during the acid treatment]. *P. gemma* is a cosmopolitan species (Archibald 1983, Podzorski & Håkansson 1987, Hartley *et al.* 1996).

PETRGEMM

Surirella Turpin 1828

Genus description: Round *et al.* 1990

Surirella brébissonii Krammer & Lange-Bertalot 1987 [Fig. 32-3]

References:

(1) Krammer & Lange-Bertalot 1987
(2) Krammer & Lange-Bertalot 1987
(3) Krammer & Lange-Bertalot 1987, 1988, Snoeijs 1993

Morphology:

L: 21-29, W: 15.5-16.3; W(P): 17: S: 18-19; F: 4-5 (n=3)

LM - Frustules more or less clavate in girdle view, valves heteropolar, obovate. Valve apex on broad side of valve broadly rounded, the other apex is more or less cuneate. Raphe system marginal, fibulae rather long. Central sternum narrowly linear to lanceolate. Striae radiate throughout the valve. Cingulum composed of one (?) wide, non-perforated copula.

Remarks: *Surirella brébissonii* was separated from *S. ovalis* by Krammer & Lange-Bertalot (1987) on the basis of the shape of the valve and the apices, and the structure of the raphe system (especially the internal wall of the canal raphe). Most of the observed specimens were assigned to *S. brébissonii* as they had one cuneate and one rounded pole. No SEM observations could be made to confirm our identification.

Biogeography & Ecology: *S. brébissonii* occurs in waters of moderate to high electrolyte content but can also extend into slightly brackish conditions (cf. also Gätje 1992). *S. ovalis*, although more abundant in brackish and marine waters, was only once found in our material (Krammer & Lange-Bertalot 1988, Cox 1996).

SURIBREB

Surirella minuta Brébisson in Kützing 1849

References:

(1) Kützing 1849
(2) Krammer & Lange-Bertalot 1987 (lectotype)
(3) Krammer & Lange-Bertalot 1987, 1988, Snoeijs 1993

Biogeography & Ecology: Only one valve belonging to this freshwater species was found in the Westerschelde material.

SURIMINU

Surirella ovalis Brébisson 1838

References:

(1) Brébisson 1838
(2) Krammer & Lange-Bertalot 1987 (lectotype)
(3) Krammer & Lange-Bertalot 1987, 1988

Morphology:

LM & SEM: A detailed description of this species is given by Krammer & Lange-Bertalot (1987).

Remarks: See *Surirella brébissonii.*

Biogeography & Ecology: Only one valve could be assigned to this species. See also *Surirella brébissonii.*

SURIOVAL

5. Results

5.1. Abiotic factors

Correlations between the environmental variables are listed in Table 11.

*5.1.1. Climatic factors**

Monthly average air temperature at Vlissingen during the sampling period was lowest (± 3 °C) in February and gradually increased during spring to reach maximal values in August (± 18 °C)(Fig. 6b). Total monthly irradiance (J/cm², Fig. 6a) at Vlissingen during the sampling period is strongly related to seasonal differences in daylength and sun angle: maximum values were recorded in June, while the lowest values were measured in December (about 10 % of the June values). A steep increase in irradiance took place in February/March.

Precipitation (mm) was highest in November (1991 - 128 mm) and during summer 1992 (maximum value 121.7 mm)(Fig. 6c). Average wind speed (AWS - m/s) was highest in the week preceding the January sampling campaign (Fig. 7). AWS values were higher in winter/early spring and autumn than in spring and summer. Maximal wind speed values did not differ much between the different sampling campaigns (Fig. 8). Only October and November 1991 were characterized by the absence of stronger winds. In general, the whole sampling campaign was characterized by the absence of severe storms (i.e. with wind speeds up to 25 m/s - 10 Beaufort); only on one occasion (10th March 1992) wind speeds higher than 25 m/s were recorded.

In summary, the period October 1991-October 1992 was characterized by

1. a mild winter with temperatures above normal values (especially in February 1992) and the absence of long periods of severe frost;
2. a warm spring, summer and early autumn (September 1992) with temperature values well above normal values, especially in May and June. May, June and July were very sunny with irradiance values above normal;
3. an unusually cold October month in 1992 (on average 2 °C below normal values);
4. unusually high precipitation in November 1991, August 1992 and October 1992.

5.1.2. Water column parameters

5.1.2.1. Water temperature

Fig. 9b shows the seasonal evolution in water column temperature and its changes along the longitudinal axis of the estuary. The longitudinal trends are by far exceeded by the seasonal changes: temperatures are lowest in February (mean temperature about 5 °C) and highest in August (mean temperature about 21 °C) and thus roughly reflects the trends in air temperature.

From early spring until the end of summer, there is a distinct temperature gradient with lowest values at the mouth and highest values in the inner estuary. During this period, the temperature range within the estuary is about 3 °C. During the rest of the year, temperatures are roughly the

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* Note that winter refers to the months December, January and February, spring to March, April and May, summer to June, July and August and autumn to September, October and November.

same throughout the estuary, with only slightly higher values near the mouth of the estuary. However, water temperature remains distinctly higher (about 1-2 °C) at station 'Schaar van Ouden Doel' (Oudo) which lies close to the cooling water discharge point of the nuclear power plant at Doel, and also at Boei 71 (Bo71) and Lamswaarde (Lams), which are situated somewhat further downstream.

5.1.2.2. Water column salinity (WC salinity)

During the sampling period salinity ranged from ± 5 ‰ (Schaar van Ouden Doel, April 1992) to 33 ‰ (Vlissingen and Borsele Noordnol)(Fig. 9a). The stations west of Hansweert are always poly- to euhaline, while upstream from the Zuidergat station, salinity values are almost always in the mesohaline range (cf. also Fig. 1). The stations Hansweert and Hoedekenskerke can be both poly- and mesohaline. The salinity gradient is more or less stable throughout the year (in comparison with some other estuaries such as the Elbe, cf. Brockmann 1992). However, there is a trend towards a general decrease in salinity throughout the estuary in the winter months. During the sampling period, this decrease was very pronounced due to very heavy rainfall in November 1991. This caused salinity values to drop considerably throughout the estuary by the end of November 1991, except in the three most seaward stations, where a decrease in salinity only became apparent in January 1992. This is mainly due to the long residence time within the estuary proper. During spring and summer, salinity generally increased again in most stations (except for a small dip in April). Note that the salinity values in October 1992 had not yet reached the values recorded in October 1991.

5.1.2.3. Transparancy (Secchi depth)

Secchi depth within the Westerschelde estuary ranged between 0.1 m and 2.5 m. Lowest values are recorded in winter in the most upstream stations (Schaar van Ouden Doel, Boei 71), while the highest Secchi depths were recorded near the mouth of the estuary in summer (Fig. 9c). From October 1991 until March 1992, Secchi depths were low (< 0.7 m) throughout the estuary, with lowest values in February (< 0.4 throughout the estuary!). From May onwards, transparancy increases at all stations, especially near the mouth (Borsele Noordnol, Hooge Platen, Terneuzen). However, note that Secchi depth is lower at Vlissingen, the most seaward station, than at Borsele Noordnol and Hoofdplaat. In the rest of the estuary, Secchi depth roughly ranges between 0.5 m and 1 m in the summer months. In autumn 1992, values are again lower, but they have not (yet?) reached the October 1991 values.

5.1.3. Sediment parameters

5.1.3.1. Elevation

The morphological parameter elevation is slightly negatively correlated with WC and ISW salinity (Table 11). Fig. 10 shows that the highest stations (at Konijneschor and Hooge Platen) are situated near the mouth and in the inner reaches of the estuary. The lowest stations (at Terneuzen and the Platen van Hulst) lie in the middle estuary.

There are no significant differences in ISW salinity (annual average) between stations from the same intertidal transect (Fig. 11). Only stations 5 and 6 of the Molenplaat have significantly lower average salinities, but this could be due to local current patterns around this shoal.

5.1.3.2. Interstitial water salinity (ISW salinity)

ISW water salinity closely follows the estuarine WC salinity gradiënt (Fig 11, Table 3). There is a steady and stable decrease from the mouth of the estuary to the inner estuary. Highest values were recorded at Rammekenshoek (up to 35 ‰), lowest values were measured at the Appelzak stations (8 ‰). Fig. 11 also shows that the largest seasonal fluctuations in ISW salinity were recorded in the mesohaline stations (24-32), which corresponds to the larger fluctuations in WC salinity in these stations.

Fig. 12 shows the ISW salinity averaged per month for all stations. ISW salinity appears to closely follow the same general trend as WC salinity, viz. a decrease from October 1991 to January 1992, then a gradual increase towards October 1992 (with a small dip in April-June 1992). However, the high values in October 1991 are probably also caused by the fact that 5 mesohaline stations (BH and KS transects) were not sampled in this month.

ISW salinity is significantly lower in the SC 3 stations than in those of SC 2 and 4 (Fig. 13): the majority of stations of SC 3 are situated in the inner and middle reaches of the estuary (cf. Table 3).

5.1.3.3. Physical and chemical sediment parameters

Water content of the sediment ranges between 17 % (MERA1) and 73 % (APSN1)(percentage weight), median grain size between 10.3 µm (MASN2) and 361.4 µm (OARA2), clay between 0 % (RA) and 29.4 % (MASN2), silt between 0 (RA) and 63.6 % (MASN2), very fine sand between 0 % (OARA1 a.o.) and 56.05 % (JANB1), fine sand between 0.44 % (MASN2) and 76.92 % (MEMP4), medium sand between 0 (MASN2) and 70.7 % (JARA1) and coarse sand between 0 % (many stations) and 22.2 (OARA2)(note that all grain size fractions are expressed in weight percentages). Organic carbon and organic nitrogen range between 0 (e.g. JLRA2) and 2.82 % (MEAZ1) and 0 (RA, HP4, PH, MP2-4, BH3, NB3) and 0.23 % (MEAZ1) respectively.

Trends along the estuarine salinity gradient (Fig. 14)

Many of the physical and chemical sediment characteristics are correlated with ISW salinity (Table 11). Especially very fine sand (which is a more common grain size fraction in the inner estuary) and medium sand (which occurs more frequently near the mouth and in the lower estuary) are highly significantly correlated with salinity. Water content, clay, silt and organic C are weakly negatively correlated with ISW salinity, median grain size is weakly positively related to ISW salinity. Within the estuary, sediments are generally coarser near the mouth and the lower estuary than in the inner reaches.

The coarsest sediments are found at RA (median grain size > 300 µm), where the transect runs across an exposed sandy beach ridge. These are the only stations whose sediments mainly consist of medium sand (> 60 %). The other stations with a high average median grain size (> 150 µm) are HP3-4, PS1, TE1-3, PH1-3, MP3-4, 6 and NB3; they mainly consist of fine sand (> 50 %). Coarse sand is rare in all stations but RA1-2.

The clay and silt fractions roughly follow the same trend. SN2 is the siltiest station (on average > 40 %); other stations with a higher silt content are HP1, SN1, PS2-3, MP1, 5, BH1, KS1-2, NB1, AZ1, 3.

Water content is strongly related to the clay and silt content of the sediment (Table 11). Note that the water content throughout the year is most stable in sediments with a low water content, i.e. in the least silty sediments, which quickly drain at low tide to a constant low water content value. The same goes for the organic C and N content, which is constantly low in the sandy sediments consisting of fine and medium sand, while large seasonal fluctuations occur in the silty sediments.

Seasonal trends (Fig. 16)

Considerable temporal changes in physical and chemical sediment characteristics occur in some stations, while in others temporal fluctuations are only small (Fig. 14). For example, more or less strong fluctuations in median grain size occur in RA2, HP1, 3-4, SN1-2, TE2, MP2, 6, KS2 and AZ1, while in HP2, PS2-3, TE1,3, PH1, MP3-5, BH1-3 and NB1 median grain size is rather constant throughout the year (Fig. 14a). In the other stations, minor fluctuations occur. Two different types of trends can be distinguished, especially in those stations where variation is high. The first trend is a typical seasonal trend in sediment composition: median grain size increases in winter (mainly in January) and decreases in spring-summer (with lowest values between May and July). Clay and silt content of the sediment follow the opposite trend. Typical seasonal trends occur in HP1, 3-4, SN1, MP2 and AZ1 (Fig. 16). The second type of trend is largely non-seasonal and is probably part of long-term trends in sediment composition that are common in dynamic systems such as estuaries (cf. Ruitenbeek 1995). This type of trend was observed in e.g. RA2 and MP6 (Fig. 16).

Trends along the intertidal elevation gradient (Fig. 15)

Only fine sand is highly significantly correlated to elevation: most sediments with a high fine sand content (HP 4, TE 1-3, PH 1-3, NB 3) are situated in the lower intertidal zone (see also Fig. 10). Coarse sand is only slightly positively correlated to intertidal elevation, most probably due to the relatively high position of the Rammekenshoek stations.

Within the intertidal transects, there does not appear to be a common trend towards coarser sediments in the lower intertidal zone: at PH, MP, BH and NB there is an increase in median grain size with decreasing elevation, but at SN, HP, PS, TE and AZ the opposite trend exists (Fig. 14a). When median grain size is averaged per elevation class, median grain size appears to be significantly higher in the lowest elevation class (Fig. 15). However, this is mainly due to the fact that all stations in EC 4 belong to the SC 1 and SC 2 (Table 6). It is of course impossible to assess whether the absence of SC 3 and SC 4 stations in EC 4 is due to the fact that median grain size in the lower intertidal zone is generally higher, or whether this is merely an artefact in the data set caused by the selection of sampling stations.

Relationships between physical and chemical sediment parameters

Table 11 shows that two major groups of positively intercorrelated sediment factors can be distinguished; both groups are more or less negatively correlated to each other. One group consists of clay, silt, very fine sand, water content, organic C and N content, the other group comprises fine sand, medium sand and median grain size (note however that fine and medium sand are not correlated to each other!). Coarse sand is positively related to medium sand, but also to organic C and N; however, it was too rare throughout the estuary to make any definitive inferences about its relationship to other sediment factors.

5.2. General characteristics of the benthic diatom communities of the Westerschelde estuary: cell abundance and diversity

Note

1. All correlations mentioned in this chapter are significant at the p = 0.05 level. More detailed information on the exact significance level can be found in Tables 13 to 15. Significance of trends within the surface plots has been assessed using ANOVA (cf. chapter 3.6.2.); unless stated otherwise, significant trends are significant at the p = 0.01 level.
2. In the surface plots with sediment and elevation class as the X and Y coordinate data, no stations are present in the following combinations: SC 1-EC 2, SC3-EC4 and SC4-EC4. Aberrant trends in these locations on the trend surfaces have not been interpreted.
3. For taxon affiliation to the epipelon, the epipsammon and the different life-forms, see Table 18.
4. Cell numbers were calculated after elimination of all supposedly truly planktonic species and all taxa that occurred in 3 or less samples. This reduction reduced the number of taxa to 193 (cf. chapter 5.3.1.).

5.2.1. Cell numbers

5.2.1.1. Total cell numbers

Benthic diatom cell numbers in the Westerschelde estuary ranged between 0.7 x 10^6 and 120 x 10^6 cells/g SDW (Table 12). These numbers include both living and dead diatom cells, as no distinction could be made between empty and full diatom frustules in the oxidized slides. We therefore assessed the ratio dead/living cells on 31 different occasions (cf. chapter 3.3.2. for more details). This revealed that in the epipelic diatom fraction the percentage living cells could fluctuate considerably (between 12 and 90 %). However, detailed analysis of short-term fluctuations in cell numbers at one intertidal silty station (close to BH 1, cf. Sabbe 1993) revealed that trends in living/dead ratios closely followed those in cell abundance (Sabbe, unpubl.). When peak values in cell abundance were recorded, living/dead ratios were high. On other dates, the living/dead ratio was rather stable: between 40 and 60 % of the cells was alive (except for the very low value of 12 % which was recorded only once). Moreover, seasonal trends in cell abundance of free-living motile diatoms were much more pronounced than those of epipsammic ones: species bloomed and then disappeared again.

The living/dead problem did cause some concern about the reliability of the epipsammic diatom cell numbers: single valves of attached diatoms can remain attached to sandgrains. However, the epipsammic diatom fraction (all 3 life-forms) exhibited a remarkably constant living/dead ratio between stations and throughout the year. In the above-mentioned data set (Sabbe 1993) between 55-75 % of adnate frustules had a cell content, while the percentage living stalked diatoms amounted to about 90 %. Other counts (for dates, see chapter 3.3.2.) showed that also at other stations the living/dead ratios for epipsammic diatoms were stable throughout the year. However, between stations small differences did exist in the absolute value of this ratio.

Seasonal variations in absolute cell numbers for each station are given in Fig. 16. The values shown are for 7 different life-forms (1-7, plankton (8) and epiphyton (9), whose numbers were negligible anyway, are not shown).

Total cell numbers are positively correlated with all life-forms, except interstitial species (negative correlation), which are characteristic of medium sandy sediments with generally low average diatom abundances (Table 15).

Total cell numbers are negatively correlated with interstitial water salinity, wind speed and the sediment characteristics fine, medium and coarse sand and median grain size. They are positively correlated with temperature (different measures), irradiance and, especially, the sediment characteristics water content, clay, silt and very fine sand (Tables 13 and 14). The negative relationship with salinity appears to be at least partly caused by the overall low cell numbers in the stations of the Rammekenshoek beach transect (Fig. 16).

Cell numbers are significantly higher in the siltiest sediments (SC 3 and 4). Note that the larger variation (Fig. 17a) within SC 1 is mainly due to the fact that it comprises both stations that are characterized by low numbers throughout the year (RA1-2, MP3-4) and stations that have high numbers all year round (e.g. PH1-3), and that it is not due to large temporal fluctuations in cell numbers within stations. Cell numbers are highest in late spring (June) in silty sediments; the abundance peak shifts towards summer-autumn (August-October) in the more sandy sediments (Fig. 18).

The relationship between cell numbers and elevation is not very clear: values are on average higher in EC 2 but the differences between the EC's are only significant for EC 1 and EC 2 (Fig. 19a). Moreover, this relationship seems to be spurious as EC 2 also has the highest average silt content (Fig. 15c, see also below). Fig. 20 shows that within SC 1 there appears to be a pronounced increase in cell numbers towards the lower intertidal zone. However, this is at least partly due to the presence of RA1-2 (with very low overall cell numbers) in EC 1.

5.2.1.2. Epipsammic and epipelic cell numbers

Epipsammic and epipelic cell numbers ranged between 0.3×10^6 - 67.7×10^6 cells/g SDW and 0.1×10^6 - 100.5×10^6 cells/g SDW respectively (both dead and living frustules, cf. above)(Table 12). Seasonal fluctuations in epipsammic and epipelic cell numbers per station can be deduced from Fig. 16 (see further).

Epipsammic cell numbers are positively correlated with all life-forms and to the total epipelic fraction; highest correlation values are with the adnate, stalked and motile (< 10 µm) diatom fractions. Epipelic diatom numbers are negatively correlated with small motile (< 10 µm) diatoms and interstitial species, while no correlation exists with adnate diatom abundance; the most significant correlations are with large motile species (> 10 µm) and tychoplankton. Note that epipelic cell numbers are positively correlated to the stalked diatom fraction (Tables 15).

Correlations between epipelic cell numbers and the abiotic environment closely resemble the trends in total cell numbers (Tables 13 and 14). The main differences lie in the significance level of some correlations, viz. stronger correlations with all sediment characteristics (except coarse sand which is not significant) and wind speed (weekly average), and weaker correlations with temperature (different measures) and irradiance (different measures). Epipsammic cell numbers are only correlated to the sediment characteristics very fine sand, fine sand, medium and coarse sand (the latter two negative!), salinity (both measures) and the different measures of temperature and irradiance (all measures of the latter two variables - note that again the correlations are weaker than for total cell numbers). Epipsammic cell numbers are not related to silt and water content of the sediment, median grain size or wind speed. As for total cell numbers, both diatom groups are negatively correlated with salinity, although this relationship appears to be spurious and mainly related to sediment composition (medium sand characterized by overall low cell numbers is predominant near the mouth of the estuary).

Fig. 17c shows that epipsammic cell numbers are significantly lower in SC 3 and 4; note that in SC 4 the numbers are still high. Epipelic cell numbers do show a significantly increasing trend with increasing silt content (Fig. 17b).

Temporal trends in epipelic and epipsammic cell numbers are shown in Figs 18b and 18c: peak epipsammon abundance occurs in summer-autumn, while epipelon is most abundant in late spring. Note that the seasonal trends in epipsammic cell abundance occur irrespective of the silt content of the sediment and can therefore be mainly attributed to the life-form of the diatoms and not to the abiotic environment in the different sediment types. However, this phenomenon is less clear for the epipelon, where cell numbers are higher in summer in SC1 than in the other sediment classes.

Epipelic cell numbers are significantly higher in EC 2 (cf. above, the elevation class with the highest silt content)(Fig. 19b). Epipsammic abundance is highest in both the highest and lowest intertidal zone (Fig. 19c). However, only EC 1 is significantly different from EC 2 and 3. Decomposing the intertidal elevation trends into the various sediment classes reveals some striking patterns. In all elevation classes, epipelic cell numbers increase towards the sediment classes with highest silt content (Fig. 20b). However, the trend surface for the epipsammic cell numbers versus elevation and sediment class (Fig. 20c) is saddle-shaped: significant abundance peaks occur in the lower intertidal zones in SC 1 and 2, while in SC 3 and 4 cell numbers are significantly higher in the upper intertidal zone (see below).

5.2.1.3. Life-forms: cell numbers

Cell number ranges for each life-form are given in Table 12. Interstitial taxa are never very abundant. Adnate and stalked species are present in all samples, though sometimes in very low numbers; maximum values are in the same order of magnitude. Motile species do not occur in all samples; the smallest category (< 10 µm) has lower maximum abundances than the larger ones. Tychoplanktonic taxa reach the highest abundances.

Table 15 shows that most correlations between the different life-form fractions are positive. Negative correlations exist between small motile forms (< 10 µm) and interstitial taxa on the one hand and tychoplankton and the total epipelic fraction on the other. Interstitial taxa are also negatively correlated to large motile forms (> 20 µm).

The correlation trends between cell numbers of **adnate** and **small motile (< 10 µm)** taxa and the abiotic environment largely follow those of the epipsammic fraction. However, there are some interesting differences: (1) neither of these groups is related to very fine sand, which indicates that the correlation between the epipsammon and this sediment fraction is solely due to the presence of stalked diatoms on this particle size fraction; (2) the small motile fraction (< 10 µm) appears to favour slightly coarser sediments (negative correlation with silt, water content, organic C and N, and no correlation with medium sand). Note also that the latter group is not correlated to salinity nor to any of the climatic parameters.

Stalked diatoms, although attached to sediment particles, show similar correlation trends to the those of the large motile (> 20 µm) and the tychoplanktonic taxa and to the epipelic fraction in general. The main difference lies in the strength of all correlations (i.e. less significant in the stalked diatom fraction) and the absence of significant correlations with fine sand, organic N and wind speed. Both the adnate and stalked fractions are less significantly related to irradiance than the large motile diatoms (> 20 µm).

The **motile taxa between 10-20 µm** are only slightly positively correlated to clay, silt, very fine sand and water content, which is probably due to the fact that this group comprises a mixture of taxa which all differ in their degree of association with sediment particles (from epipsammic to epipelic). This is the only group which is significantly related to elevation.

Cell numbers of **large motile diatoms (> 20 µm) and tychoplankton** closely follow the correlation trends of the epipelic fraction in general. The large motile taxa (> 20 µm) differ from the other main epipelic groups (tychoplankton and part of the motile taxa 10-20 µm) in not being correlated with temperature but only with irradiance and by the stronger negative correlation with wind speed (weekly average). The tychoplanktonic taxa are only weakly correlated to the climatic parameters temperature and irradiance; they are not correlated to wind speed.

The **interstitial** group strongly differs from all other life-forms in being positively correlated to median grain size and medium sand. The latter correlation is probably responsible for the positive correlation with salinity.

Adnate diatom cell numbers are significantly higher in SC 1 and 2 than in SC 3 and 4 (< BW plots)(Fig. 21a-g). Although there is a slight increase in numbers in SC 4 (Fig 22a), numbers are still lower than in SC 1. The slight increase in **stalked** diatom numbers from SC 1 to SC 4 is not significant, notwithstanding the significant correlation with silt (cf. above). **Small motile (< 10 µm)** diatoms become significantly more abundant when the amount of silt decreases. The trends of all these epipsammic fractions along the silt content gradient are, however, more complicated than appears from the BW plots; they will be treated in more detail below.

Motile diatoms of size group **10-20 µm** are significantly more abundant in SC 4, although the increase is not as pronounced as for the **large motile** and **tychoplanktonic** taxa. **Interstitial** diatoms are mainly characteristic of SC 1. The peak in SC 4 (Fig. 22g) is solely due to the occurrence of *Cymatosira* sp. 1 in station PS 3 in autumn.

Temporal trends in cell numbers of all life-forms are shown in Figs 22(a-g). The epipsammic groups (**adnate, stalked and small (< 10 µm) motile**) all gradually increase towards late summer-autumn. **Large motile** diatoms exhibit a distinct abundance peak in spring; note the small peak in early spring in stations belonging to SC 1, which is mainly due to a single species, *Navicula meniscus*. The **motile** diatoms **between 10-20 µm** roughly follow the same seasonal trend as the large ones, at least in the more silty stations where they are most abundant. In SC 1, they exhibit a seasonal pattern which is more typical of the epipsammic groups. This is due to the fact that at least some of the common motile (10-20 µm) taxa in the latter SC are considered to have an epipsammic life-form (e.g. *Amphora* cf. *subacutiuscula*, *Navicula* sp. 7) rather than an epipelic one as most motile (10-20 µm) taxa in SC 3 and 4 (e.g. *Navicula phyllepta*). **Interstitial** taxa are only abundant in summer samples.

When considering the relative increases in abundance between the different life-forms, it appears that changes are most pronounced in the motile diatom groups, except for the group of small motile forms (< 10 µm).

As mentioned above, the only significant correlation between cell numbers and elevation was found for the motile group (10-20 µm). However, when we decompose the trends along the intertidal gradient into the different sediment classes, some surprising patterns emerge in the distributions of the epipsammic life-forms (Fig. 24). As for the total epipsammic fraction (cf. above), the trend surfaces of the adnate, stalked and small motile (< 10 µm) life-forms are more or less saddle-shaped: within SC 1, cell numbers increase towards the lower intertidal zone, while in SC 4, the opposite trend can be seen. SC 2 and 3 take a somewhat intermediate position. This shape is most pronounced for the **adnate** diatom group: the abundance peaks in EC 1 and 4 are significantly higher than in EC 2 and 3 (Fig. 23a), but do not significantly differ from one another. All trends along this surface are significant. In the **stalked** diatom group, cell numbers in EC 1 are significantly higher than in EC 2 and 3 but not significantly different from EC 4 (Fig. 23b), even given the low cell numbers in EC 1-SC 1. Most other trends along this surface plot are significant ($p<0.05$); however, no significant differences exist between EC 3 and 4 within SC 1 and between EC 1 and 3 within SC 2. No significant differences exist between **small motile (< 10 µm)** diatom cell numbers in the different elevation classes Fig. 23c. However, ANOVA indicates that some trends along the surface plot for this group (Fig. 24c) are significant: e.g. the trend from EC 1 to EC 4 *within* SC 1, from SC 1 to SC 2 *within* EC4, and the other trends around the peak in EC 4-SC 1. We can therefore conclude that for this surface the latter peak is significant.

No significant differences exist between **motile (10-20 µm)** diatom cell numbers in the different elevation classes (Fig. 23d), notwithstanding the significant correlation with elevation (cf. above). However, ANOVA indicates that significantly increasing trends along the intertidal elevation gradient occur in SC 3 and 4.

Figs 23e-f show that **large motile (> 20 µm)** diatom numbers are significantly lower in EC 3 and 4, while **tychoplanktonic** cell numbers are significantly lower in EC 1 and 4. The trend surfaces for large motile and tychoplanktonic diatoms (Figs 24e-f) are rather similar to each other, except for the drop in large motile diatom cell numbers towards the more silty stations in the lower intertidal zone. There are, however, differences between the sediment classes. For both life-forms, numbers are significantly lower in SC 1 - EC 1. Tychoplanktonic cell numbers are significantly lower in EC 1 within SC 1, 2 and 4, which to a large extent explains the slightly increasing trend with decreasing elevation in the surface plot. Whether this trend can be generalized to the intertidal zone is doubtful: no significant differences exist between EC 3 and 4 in SC 1, between EC 2 and 4 in SC 2, and there even is an significant increase in cell numbers between EC 2 and 3 in SC 3. Only in SC 4, the increase in cell numbers is significant for all values between EC 1-3. Large motile forms do not become significantly more abundant with decreasing elevation (except around the extreme low value in EC 1-SC 1). Rather surprisingly, there is a significant decrease in numbers towards the lower intertidal zone (only EC3, no stations in EC4) in SC 3 and 4, as was noted for the epipsammon.

The trends in **interstitial** diatoms can only be interpreted for SC1, as there are too many missing values in the other sediment classes. There is no significant trend along the intertidal gradient in this sediment class.

5.2.2. Diversity

Three main trends can be distinguished in the diversity of the benthic diatom communities of the Westerschelde estuary:

1. All diversity indices ($N_1 \rightarrow N_{+\infty}$) are significantly lower in the more silty sediments (SC 3 and 4)(Fig. 25a-c). No significant differences exist between SC1 and 2 and SC 3 and 4 respectively. This is also confirmed by the correlation analysis (Table 13) which shows that the diversity indices are all negatively related to clay, silt, very fine sand, coarse sand, organic C, organic N and water content, and positively to median grain size, fine sand and medium sand (note that the significant relationship with salinity might be spurious, cf. above).
2. Diversity ($N_1 \rightarrow N_{+\infty}$) decreases in late spring/summer in most samples, especially in the more silty sediment classes (SC 3-4)[cf. significant negative correlation with temperature (different measures) and irradiance (monthly average), Table 14]. However, in SC 1 no significant temporal trend is present (Fig. 26a-c).

3. Diversity ($N_1 \rightarrow N_{+\infty}$) is usually significantly higher in EC1 and 4 than in EC 2 and 3 (Fig. 28).

The diversity versus elevation trends (Fig. 28) have to be interpreted with caution: the trend surfaces shown in Fig. 27(a-c) give a more realistic picture of the real trends than the Box-and-Whisker-plots. Due to the fact that no stations are present in the more silty (and hence less diverse, cf. above) SC 3 and 4 of EC 4, the diversity values in EC 4 will generally be higher than in the other elevation classes. We therefore compared (ANOVA) the diversity values within the sediment classes to assess which trends are significant and which are not. Fig. 27(a-c) first shows that the differences between the sediment classes (cf. above) are more pronounced than those between the elevation classes. There appears to be no unequivocal trend along the intertidal gradient: (1) in SC 1 the differences between EC1 and 4 are only barely significant ($p \leq 0.05$) for $N_1 \rightarrow N_{+\infty}$; (2) in SC2 there is a small increase in diversity in EC 3, which is only just significant ($p=0.045$) for $N_{+\infty}$, and a small but significant ($p<0.01$) decrease at EC4; (3) in SC3 there is a slightly significant ($0.05<p<0.01$) decrease towards EC3; (4) in SC4 there is a significant decrease towards EC3 for N_1 and N_2, but not for $N_{+\infty}$.

5.2.3. Temporal patterns

Visual assessment of the shape of the graphs displaying the temporal variation in total cell numbers for the 7 life-form categories for the 32 individual stations led to the distinction of 4 types of seasonal patterns (Fig. 29). Table 16 lists which stations have been assigned to what seasonal types.

1. Seasonal type 1 is characterized by low cell numbers in winter and spring and a distinct summer peak (July-August). The stations belonging to this seasonal type (Table 16) are dominated by adnate and small motile (< 10 µm) diatoms, while stalked, tychoplanktonic and larger motile (> 10 µm) are rare. However, note the minor bloom of large motile (> 20 µm) diatoms (predominantly *Navicula meniscus*) in late winter to early spring. Another typical component of this seasonal type are interstitial diatom species, which are most abundant in summer.

   Note that overall cell abundance in these stations is low in comparison with the other seasonal types.
2. A steady and gradual increase in cell numbers throughout the whole sampling period (with a small peak in June) characterizes the stations belonging to seasonal type 2. Epipsammic taxa, mainly adnate and stalked forms, are most abundant,. Larger motile diatoms (> 10 µm) and tychoplanktonic taxa are more abundant in these stations than in those of seasonal type 1.
3. Seasonal type 3 groups three stations which are characterized by the absence of a consistent temporal pattern. Motile and especially tychoplanktonic taxa are more abundant than adnate and stalked taxa.
4. Seasonal type 4 is characterized by a single peak in cell numbers in June. However, this peak is mainly caused by very high numbers of tychoplanktonic taxa (especially one species, viz. *Thalassiosira proschkinae*, is very abundant). Note that the large (> 20 µm) motile diatoms reach their peak abundance one month earlier (May). Epipsammic cell numbers are very low.

Note that overall cell numbers are an order of magnitude higher in the types 2-4 than in type 1. Median grain size, silt and water content of the sediment were significantly different between all pairs of seasonal types, except between type 2 and 3 (one-way ANOVA). Means and standard deviations of these variables for the 4 seasonal types are shown in Table 17.

No marked seasonal changes in median grain size can be detected in the stations of ST 1 and 2; silt content is more or less stable in ST 1 but goes through a minimum during spring in ST 2. Water content of the sediment is more or less stable in ST 2 but goes through a spring minimum (June) in ST 1.

Temporal fluctuations in all three environmental variables are rather irregular in ST 3. This may indicate that changes in sediment composition are largely non-seasonal (as was already shown for MP 6, cf. chapter 5.1.3.3.) which could explain the absence of a consistent temporal pattern in the stations of ST 3.

The stations of ST 4 are characterized by typical seasonal changes in median grain size, silt and water content of the sediment (cf. chapter 5.1.3.3.). Median grain size is highest in winter and lowest in spring/summer; silt and water content follow the opposite trend.

5.3. Multivariate analyses

5.3.1. Data screening

Prior to the multivariate analysis, the data matrix was reduced, both in number of taxa and in number of samples. The original data matrix (**data set 0**) consisted of 360 samples (from 32 different intertidal stations) and 294 taxa (note that this number differs from the final number of taxa identified, Table 18). A first reduction concerned the number of samples. A full set of abiotic variables was available for 185 samples; these came from 6 months, viz. October 1991, January, March, May, July and September 1992. This initial data set consisting of 185 samples and 294 taxa will be referred to as **data set 1**. The other reductions concerned the number of taxa and were done in order to reduce the amount of noise and redundancy in the analyses (Jongman *et al.* 1987).

As we did not distinguish between living and dead diatom cells, allochtonous valves (mostly dead planktonic cells or empty frustules from the upper (oligohaline) and limnetic reaches of the estuary) could not be distinguished from autochtonous living cells. Therefore we decided to reduce the data set a first time by eliminating all supposedly truly planktonic species and all taxa that occurred in 3 or less samples, i.e. in less than 0.8 % of the total number of samples. The following planktonic species and/or genera were removed from the data set: *Actinocyclus* spp., *Aulacodiscus argus*, *Aulacoseira* spp., *Cerataulus radiatus*, *Coscinodiscus* spp., *Cyclostephanos dubius*, *Lithodesmium undulatum*, *Skeletonema* spp., *Stephanodiscus* spp. and *Thalassiosira nordenskioeldii* (for the exact life form of each species, see Table 18). Notwithstanding the fact that many *Cyclotella* taxa (e.g. *C. atomus* and *C. meneghiniana*) and the remaining *Thalassiosira* taxa (e.g. *T. proschkinae* and *T. decipiens*) were observed in large numbers in the water column (Muylaert, pers. comm.), they were initially not eliminated from the analyses as they also occurred in large numbers in the sediments. The elimination of taxa with a small number of occurrences (i.c. 3) is commonly applied to data sets that are based on counts of oxidized material (e.g. Vyverman 1990). This first reduction reduced the species data set to 193 taxa. This second data set will be referred to as **data set 2**.

A second reduction removed all taxa that did not reach a relative abundance of 2 % in at least one sample. This way only the more abundant taxa were kept in the analysis, while the rare taxa were eliminated. A similar kind of reduction is also commonly used in estuarine and/or benthic environments (Snoeijs & Kautsky 1989, Wilderman 1987, Laws 1988 and Gätje 1992). In addition, all *Cyclotella* species, *Thalassiosira angulata*, *T. curviseriata*, *T. proschkinae* and *Thalassionema nitzschioides* were omitted from the definite analyses. Although there are some indications that at least some of these taxa might adopt a benthic life-form (Feibicke *et al.* 1990, Denys 1991, Muylaert & Sabbe 1996), at least during some stages of their life cycle, they are mainly reported from plankton samples. We eliminated them because their valves were sometimes very abundant in the sediments and could thus have a large influence on the ordination results. The final species data set consisted of 89 taxa and will be referred to as **data set 3**.

The data set affiliation of each taxon is given in Table 18. Summary information on the different data matrices is given in Table 8.

5.3.2. Choice of the appropriate method

The standard deviations (s.d.) of the first 4 axes of a preliminary DCA (detrending by segments) are 2.1, 1.4, 1.0 and 0.6 respectively. As the s.d. value for the first axis is only slightly higher than 2.0 (the treshold for using unimodal models, cf. Jongman *et al.* 1987), we decided to use linear ordination methods, viz. PCA and RDA. Linear ordination methods provide more quantitative information than those based on a unimodal response model (Jongman *et al.* 1987).

As most of the response curves in our data appeared to be monotonic, we decided not to use classification techniques (cf. ter Braak & Wiertz 1994). Preliminary cluster and hybrid analyses (TWINSPAN - Two-Way INdicator Species Analysis) indicated that the continuous structure in our data set did not allow to make a meaningful classification of our data. Indeed, TWINSPAN is based on an initial ordination analysis made by reciprocal averaging, which is the same as correspondence analysis (CA)(Hill 1979, Jongman *et al.* 1987). This method is appropriate only when the species response curves are unimodal and not when they are monotonic.

5.3.3. Ordination results: description of communities and distribution patterns

Data set 2 and 3 were analysed using PCA and RDA; the resulting ordination outputs and diagrams were critically compared. The ordination characteristics are summarized in Table 18. The ordination analyses on both data sets yielded very similar outputs (see Table 24) and ordination diagrams (not shown). We will therefore only discuss the ordination results of the analyses on data set 3. PCA and RDA results on data set 2 were only used for autecological characterization of taxa which were incorporated in chapter 4.2.

All ordination diagrams are correlation biplots in which the correlations with the ordination axes for both the dependent and independent variables are plotted. The data were centred and standardized by species. For classes of samples, centroids were plotted (Van Tongeren *et al.* 1992). In interpreting the (RDA) ordination diagrams, the following general rules should be kept in mind:

1. Close sites in the diagram are similar in species composition, distant sites are dissimilar.
2. Species and environmental variables are represented by arrows (not shown for species to prevent crowding of the diagrams) which connect the origin of the diagram with their respective points (coordinates=ordination scores).
3. The direction of the arrow indicates the direction in which the abundance of the corresponding species (or the value of an environmental variable) increases most; the length of the arrow equals the rate of change in that direction (and thus indicates how strongly the variable is related to the displayed ordination). Note that it is the species with the largest variance (which are not always the most abundant ones!) that dominate the PCA and RDA analyses (cf. Sabbe 1993).
4. Arrows (both species and environmental arrows) that point in the same direction indicate positive correlation, arrows that are perpendicular indicate lack of correlation, and arrows that point in opposite directions are negatively correlated.

For more information on the interpretation of ordination diagrams in linear methods, see Jongman *et al.* (1987) and ter Braak (1994).

5.3.3.1. PCA data set 3

The PCA analysis on the data set 3 describes 41.6 % of the variance in the species data in 4 axes; almost half of this amount is accounted for by the 1st axis alone. The 3rd and 4th axes are less important and represent 6.6 % and 4.3 % of the species variance respectively (Table 24). The PCA ordination results will not be discussed in detail for reasons explained below.

5.3.3.2. RDA data set 3

In an RDA constrained to all 28 environmental variables (i.e. all variables from Table 7 + the 6 temporal dummy variables), 40 % of the total variance in the species data is explained. When omitting all variables that do not significantly contribute to the ordination (using the forward selection procedure in CANOCO) and all multicollinear variables, 13 variables remain in the ordination (Table 25). These still explain 34.9 % of the total variance in the species composition and abundance; 28.4 % of this variance is accounted for by the first four axes. The 1st axis represents more than half of the total variance explained, while the other axes are less important (6.4 %, 4.3 % and 2.2 % respectively, Table 25).

The first four axes, which are all statistically significant (Monte Carlo permutation test, $p \leq 0.01$), include 81.3 % of the percentage variance of the species-environment relation, i.e. the major part of the species-environment relation is represented along these axes. Moreover, all four axes have a high species-environment correlation (0.90, 0.78, 0.81 and 0.79 respectively), which indicates that there is a strong relation between the abundance and distribution of the taxa and the abiotic environment. We can therefore conclude that the measured environmental variables account for the main variation in the species data along these axes.

As expected*, the variance in the species data explained by the first 4 axes is lower in the RDA than in the PCA (Table 24). However, the overall results for the PCA and RDA analyses are very similar (cf. the high species-environment correlation, which indicates that the sample and species points have a more or less similar configuration along the first four axes). It therefore appears that no important environmental variables have been overlooked (i.e. the measured environmental variables account for the main variation in the species data). For a further description of the ordination results, we will therefore restrict ourselves to the RDA analyses, as these are superior to PCA in elucidating species-environment relationships.

From the canonical coefficients (and their approximate t-tests) and the intra-set correlations between the environmental variables and the ordination axes (Tables 25 and 26) we assessed the relative contribution of the different environmental variables to the RDA axes. For example, median grain size, silt, fine sand, salinity (both water column and interstitial water), water content and the dummy variable for October (oamo) contribute significantly to axis 1 (i.e. $|t| > 2.1$), but only silt, water content, median grain size and fine sand are highly ($R^2 > 0.50$) correlated to this axis. In the same way, the major variables related to the species data were determined for each axis.

RDA axes 1 and 2 separate sites along gradients of grain size (silt, fine sand), water content and salinity (ISW) respectively (Fig. 31). Sites characterized by low silt content (0.0-11.0 %*) and high median grain size (143.0-306.6 μm) are grouped on the right hand side of the biplot and include the following sandy stations: Rammekenshoek (RA1-2), Platen van Hulst (PH 1-3), Molenplaat stations 3 and 4 (MP 3-4) and Baalhoek station 3 (BH 3). Most samples from station Paulinaschor 1 (PS 1), Baalhoek 2 (BH 2) and Nauw van Bath 3 (NB 3) are also found on the right of the origin.

Note that the second axis is also strongly correlated to medium sand ($R^2 = 0.55$); however, this variable does not contribute significantly to this axis.

On the left hand side of the biplot we find all samples which have a higher silt content (11.1-42.5 %) and lower median grain size (63.5-143.7 μm). These include all (or at least most) samples from predominantly sandy silty and silty sites such as the Staartse Nol (SN 1-2), the Konijneschor (KS 1-2), the Appelzak (AZ 1, 3), Paulinaschor stations 2 and 3 (PS 2-3), Molenplaat stations 1, 2 and 5 (MP 1-2, 5), Hooge Platen station 1(HP 1), Baalhoek station 1(BH 1) and Nauw van Bath station 1 (NB 1).

The silty sandy stations from Terneuzen (TE 1-3), Hooge Platen stations 2-4 and Molenplaat

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* RDA is simply PCA with a restriction on the site scores (Jongman *et al.* 1987): therefore the RDA eigenvalues are usually lower.

* lowest and highest yearly average value of stations from this group - for values see Table 3.

station 6 (MP 6), take a somewhat intermediate position but are still mainly located left of the origin.

Along the second axis, most samples are arranged according to increasing salinity (from the bottom to the top of the diagram). Thus in the lower part of the biplot most samples originating from sites in the mesohaline part of the estuary (i.e. Baalhoek, Konijneschor, Nauw van Bath and Appelzak) are located, while samples from stations with highest salinity values (Rammekenshoek, Staartse Nol, Hooge Platen, Paulinaschor) are located in the top half of the diagram. Most samples from stations from the middle part of the estuary (Terneuzense Pas, Platen van Hulst, Molenplaat) are located in the centre of the diagram.

At first glance, most samples originating from one station cluster more or less together in the biplot. This is especially true for the most silty (SN 1-2, PS 1-2, MP 1 and 5) and the most sandy stations (RA 1-2, MP 3-4, PH 1-3, BH 3). However, it appears that most samples from one station are more or less dispersed along the second axis, while only few are (also) considerably scattered along the first axis (viz. samples from stations HP 1, MP 6 and NB 3). As the biplot is completely dominated by spatial distribution patterns, it is hard to discern any general temporal trends in the data along the first two axes. However, some trends do seem to exist:

1. In most stations from the mesohaline reaches (lower half of the biplot) there appears to be a shift to the top of the diagram in early spring (BH 1-3, KS 1-2) or spring-summer (NB 1, AZ 1-3).
2. Most stations from the upper half of the biplot (except the silt-less stations RA 1-2 and MP 3-4) are characterized by a shift to the lower half of the diagram in summer (July).

This indicates that mesohaline stations have a more similar assemblage structure to polyhaline stations in spring or spring-summer, while in July most polyhaline stations are more similar to mesohaline stations. As no significant shifts in salinity occur in any of the stations, it is unlikely that these shifts could be attributed to changes in salinity. This shift could possibly be attributed to certain species which, apart from having a distinct optimum along the salinity gradient, also display a distinct seasonality (e.g. *Navicula gregaria*).

Another striking feature of the biplot of the first two RDA axes is that the scatter along the second axis is more pronounced on the right hand side of the origin, i.e. in stations with a low silt content. However, it is not clear (and impossible to assess) whether this is related to differences in salinity (the Rammekenshoek stations have higher salinity values than the Platen van Hulst or the Molenplaat ones) or sediment composition, the stations (PH, BH 3, NB 3) in the bottom half of the diagram being characterized by fine rather than by medium sand (Rammekenshoek). In addition, all samples on the right hand side of the diagram belonging to one and the same transect always cluster more or less together and are rather well separated from those from other transects. On the left side of the biplot, there is considerably more overlap between the different transects.

The difference in the amount of scatter along the 2nd axis also appears from the species diagram. All silty sandy and silty stations are characterized by high numbers of tychoplanktonic and motile diatom taxa (> 10 μm) such as *Cymatosira belgica*, *Delphineis minutissima*, *Thalassiosira decipiens*, *Paralia sulcata*, *Rhaphoneis amphiceros*, *Navicula* cf. *perminuta*, *N. phyllepta* and *N. flanatica* (Fig. 31). Some taxa appear to be more common in the polyhaline silty sandy and silty stations (e.g. *N. arenaria* var. *rostellata*, *Brockmaniella brockmannii*, *Plagiogrammopsis sigmoideum*, *Odontella aurita*), while only one species, *Navicula gregaria*, appears to be typical of the mesohaline stations.

On the right hand side of the diagram, there is a considerable scatter of mainly epipsammic taxa along the second axis. As already mentioned, this is related to the estuarine salinity gradient but also to the grain size of the samples. On the positive side of the second axis, we find taxa which are characteristic of the medium sandy sediments of Rammekenshoek and also stations 3 and 4 of the Molenplaat (*Anorthoneis* spp., *Plagiogrammopsis minimum*, *Amphora* sp. 2, *Navicula* cf. *mollis*, *N.* sp. 2 and several *Fallacia* spp.). Other taxa are typical of fine sandy sediments (*Navicula diserta*, *N.* sp. 1, *Amphora* cf. *subacutiuscula*, *Biremis lucens*). *Achnanthidium* sp. 2, *A.* sp. 3, *A.* sp. 4, *Navicula* sp. 4 and *Amphora* cf. *pediculus* can be found in both sediment types. A last group of taxa is abundant in different sediment types, from sandy (e.g. NB 3) to silty (e.g. NB 1) sediments: *Fragilaria* cf. *atomus*, *Opephora mutabilis*, *O. guenter-grassii*, *Achnanthidium delicatulum* and *Catenula adhaerens*.

The scatter of samples along the 3rd axis appears to be mainly related to the salinity gradient (WC) but also to a gradient in elevation (Fig. 32). However, more detailed examination of the biplot of the 1st and 3rd axis shows that while the samples on the left hand side of the diagram are arranged (along the 3rd axis) according to decreasing salinity (all mesohaline stations are placed in the top (left) quadrant of the biplot), the samples on the right hand side of the diagram (the sandy samples) are mainly arranged according to their elevation (the most elevated samples from Rammekenshoek being placed in the top (right) quadrant of the biplot). Thus, although both elevation and WC salinity contribute significantly to the third axis, it would, at least partly, be incorrect to infer values for both variables from the biplot of the 1st and 3rd axis.

The cumulative fit for the species (Table 27) indicates that one third of the 89 taxa, including the most important ones (i.c. the most common taxa in our samples), have more than 30 % of their variance accounted for by the first 4 axes. Note that especially tychoplanktonic and motile taxa (> 10 µm) are well fitted (e.g. *Delphineis minutissima* and *Cymatosira belgica* which have about 85 % of their variance fitted along the first 4 axes). However, it appears that along the 1st axis only tychoplanktonic and motile (> 10 µm) taxa are well fitted (i.e. more than 30 % of their variance is epxplained by that axis), while the additional fit (i.e. the increase in cumulative fit) along the 2nd axis is mainly accounted for by epipsammic species (*Achnanthidium delicatulum*, *Fragilaria* cf. *atomus*, *Opephora guenter-grassii*). The additional fit for the 3rd axis is generally low; only two taxa, *Navicula gregaria* and *Parlibellus sp.* 2 appear to be well fitted in this axis (increase > ± 20 %). Both large motile taxa show a distinct salinity optimum (in the mesohaline reaches). It thus appears that the ordination along the third axis fits badly: especially the epipsammic taxa are badly represented by this axis.

The 4rd axis represents the temporal variation in the species data and is mainly related to temperature (monthly average) and the dummy variable for the month July (jlmo). The biplot of the 1st and 4rd axis (Fig. 33) shows that both on the left and the right of the origin the samples from July are situated at the top of the diagram, while the samples from October (1991) and January are placed at the bottom. The March, May and September samples take a somewhat intermediate position.

Navicula sp. 3, *N. starmachioides*, *Nitzschia* sp. 2 and several *Amphora* species (*A. laevissima* var. *perminuta*, *A. cymbamphora*, *A.* cf. *delicatissima*, *A.* cf. *exigua* and *A.* sp. 5) are positively related with this temperature axis and are most abundant in summer, while *Martyana martyi*, *Parlibellus* sp. 2, *Opephora mutabilis*, *Navicula meniscus* and *Fallacia tenera* appear to be most abundant in the colder months.

Note that the additional fit represented by the 4th axis is low for all taxa (Table 27).

It appears that, especially along the 2nd and 3rd axis, there are distinct differences between the sandy silty/silty and sandy stations, i.e. the stations dominated by free-living and attached diatoms respectively. Moreover, the cumulative fit per taxon indicates that there are differences between these two taxon groups in the amount of variation fitted along these axes: especially the epipsammic taxa appear to be badly fitted along the 3rd axis.

Due to the constraint that as much variation in the species data as possible has to be represented in a few dimensions, a single ordination on the complete data set appears to lead to a considerable loss of information or even to some inconsistencies which make the interpretation of the ordination output precarious (e.g. the position of the Rammekenshoek stations in the biplot of the 1st and 3rd axis does not correspond to the salinity gradient which is represented by the 3rd axis). It appears that the epipelic and epipsammic taxa display different variation patters which are related to different environmental factors. We therefore decided to split our taxa in two groups, an epipelic group (including 45 taxa) which we will henceforth refer to as **data set 4** and and epipsammic group (with 44 taxa) or **data set 5**.

It is worth mentioning that we initially tried to split the samples in different groups based on sediment type. However, this did not clarify the variation patterns in our data: the main variation patterns appear to be better related to the life-form composition of a community at a given locality than to the sediment type of that station.

5.3.3.3. RDA data set 4 (= 45 epipelic taxa, 185 samples)

A RDA analysis constrained to all 28 environmental variables explains 45.3 % of the variation in the epipelic species data (Table 24). After forward selection and removal of multicollinear variables, 14 variables remain in the ordination (Table 25). These still explain 41.2 % of the variation in the species data; 35.5 % is accounted for by the first 4 axes. As in the RDA on data set 3, the first axis explains about half of the total variance explained (Table 24).

All 4 axes are statistically significant ($p \leq 0.01$). As 86.2 % of the species-environment relation is represented by these axes and the species-environment correlation of each of the axes is high (0.93, 0.86, 0.81, 0.76 respectively), we can conclude that the selected environmental variables account for most of the variation in the species data along these axes.

The 1st axis is strongly negatively related to the silt and water content of the samples and positively related to the median grain size of the sediment (Fig. 34). Most free-living taxa have more or less negative loadings along the 1st axis; only a few are typical of sandy sediments (*Navicula bipustulata*, *N. meniscus*, *N. gregaria* f. 1, *N.* cf. *mollis*, *Cymatosira* sp. 1 and Incertae sedis sp. 1). Note that a number of species appears to be indifferent to the sediment type; these occur both in silty and sandy sediments (e.g. *Fallacia tenera*, *N. meniscus*, *N. palpebralis* and *N. starmachioides*). Along this axis, silty sandy, sandy silty and silty samples with high numbers of free-living taxa are separated from more sandy samples with low numbers of these diatoms. The order of samples along this axis is therefore roughly identical to the one in the RDA on data set 3 and thus still represents the main source of variation in the data set.

However, beyond the 1st axis, the differences with the RDA on the data set 3 are more pronounced. Even in samples which are dominated by free-living diatoms (i.e. on the left hand side of the biplot), marked changes occur. This indicates that the variation introduced into data set 3 by fluctuations in occurrence and abundance of epipsammic diatoms is considerable.

The 2nd axis now exclusively represents the estuarine salinity gradient. The most striking differences between the RDA on data set 4 and the RDA on data set 3 along this axis are:

1. The sandy samples from Rammekenshoek, Platen van Hulst and stations 3 and 4 of the Molenplaat are no longer separated along the second axis. These transects are all situated in the polyhaline section of the estuary, which probably explains the absence of differences in free-

living species composition between them.

2. The samples on the left hand side of the origin are clearly divided into two groups: the mesohaline ones, with positive scores on the 2nd axis, and the polyhaline samples, which mainly have negative scores. Note that this pattern closely resembles the one that is present in the left hand side of the ordination diagram of the 1st and 3rd axis of the RDA on data set 3.

The species biplot for the 1st and 2nd axis is almost identical to the one for the 1st and 3rd axis of the RDA on the data set 3 (without the epipsammic taxa). Taxa with a positive loading along the 2nd axis (i.e. taxa which prefer mesohaline conditions) include *Amphora* sp. 6, *Berkeleya rutilans, Navicula gregaria, N. flanatica, N. phyllepta, Parlibellus* sp. 2, *Staurophora salina* and others; taxa with a high negative loading include *Brockmanniella brockmannii*, *Delphineis surirella*, *Navicula arenaria* var. *rostellata*, *N.* cf. *perminuta*, *N.* sp. 10, *Odontella aurita*, *Plagiogrammopsis sigmoideum* and most free-living taxa typical of sandy sediments (cf. above).

The 3rd axis represents the temporal structural variation within the free-living fraction of the benthic diatom communities and is mainly related to temperature (and the dummy variable for the month July, R = -0.47). The temporal succession of taxa is much more pronounced when only the free-living taxa are included in the analysis (cf. RDA ordination data set 3) and shows that a distinct succession of taxa occurs within this fraction.

Fig. 35 reveals the following seasonal trends:

1. The January samples have low scores on the 3rd axis which indicates that they are mainly characterized by the absence of typical spring and summer species. Only the January samples from the Molenplaat take a somewhat unusual position amongst the March and May samples, which is mainly due to the presence of high numbers of *Navicula meniscus* and *N.* sp. 10, two species which become more abundant in the majority of stations in (early) spring.
2. All March samples have high loadings on the third axis; they are characterized by blooms of *Navicula meniscus* and *N.* sp. 10, while also *Parlibellus* sp. 2, *Navicula bipustulata* and *N. flanatica* become more abundant, though the latter three taxa mainly in the more silty samples.
3. The May samples take a somewhat intermediate position between the March and January samples; they appear to be mainly characterized by the same taxa as the March samples but in lower numbers.

   Other taxa typical of the spring diatom communities are: *Navicula arenaria* var. *rostellata*, *N. microdigitoradiata* and *N.* sp. 15 (mainly in the sandy silty and silty samples), and *Staurophora salina*, *Navicula* cf. *bipustulata*, *N. palpebralis*, *N. starmachioides*, *N. gregaria* f. 1 and *Fallacia tenera* also in the sandier sediments.
4. In July, a distinct shift of all stations takes place towards the negative side of the third axis. This shift is strongly related to increasing temperatures during the summer months. Taxa with higher abundances in summer include *Navicula gregaria* (though only in sandy silty and silty samples), *Pleurosigma aestuarii* and several taxa belonging to the genus *Amphora* (*A.* cf. *exigua*, *A. cymbamphora*, *A. coffeaeformis* and *A.* sp. 5), while in the sandy sediments higher numbers of *Plagiogramma minimum*, *Navicula* cf. *mollis*, Incertae sedis sp. 1 and *Cymatosira* sp. 1 are found. Note that several typical spring taxa have almost disappeared in the summer.
5. The samples taken in October 1991 and September 1992 take a somewhat similar position as the July samples, but their scores are on average less negative, which indicates that the community structure in these samples is already showing more resemblance to the typical winter (i.e. January) situation.

Both the 3rd and 4th RDA axes have very low eigenvalues (Table 24). However, unlike the 3rd axis, the 4th axis did not reveal any meaningful trends in community structure. Many variables (cf. Table 25) contribute significantly to this axis but only two have a high intra-set correlation, viz.

transparancy and irradiance (monthly average). Transparancy generally increases towards the mouth of the estuary and is strongly related to the estuarine salinity gradient.

The cumulative percentages fit per taxon (Table 28) indicate that the most abundant free-living taxa are well represented by the model consisting of silt, salinity and temperature (the first 3 axes of the RDA). Most tychoplanktonic species are well described by the first axis which is mainly related to silt content. Especially *Delphineis minutissima*, *Rhaphoneis amphiceros* and the centric diatoms *Cymatosira belgica*, *Paralia sulcata* and *Thalassiosira decipiens* have high fractions (between 60 and 80 %) of their variances fitted. The occurrence of tychoplanktonic species in intertidal sediments therefore appears to be strongly related to the silt content of the environment. Other tychoplanktonic (e.g. *Plagiogrammopsis vanheurckii*) and large motile taxa (e.g. *Navicula arenaria* var. *rostellata* and *N. flanatica*) have more than 30 % of their variance accounted for by the first axis. The life-form of *Fragilaria* sp. 1 is as yet unknown but its good fit along the first axis could hint at a tychoplanktonic life form.

Taxa which have a large fraction of their variance fitted along the 2nd axis (representing the salinity gradient) include *Navicula gregaria*, *Parlibellus* sp. 2 and, to a lesser degree (as a large part their variance fitted was already represented by the 1st axis), *Navicula phyllepta*, *Odontella aurita*, *Brockmaniella brockmannii* and *Plagiogramma sigmoideum* (cf. above).

The fraction of variance fitted of *Navicula* sp. 10 and *N. flanatica* strongly increases along the 3rd axis. As already mentioned, the occurrence of some other taxa is also distinctly related to seasonal changes in temperature. However, as less than 30 % of their variance is accounted for by the first 3 axes, they have not been included in Table 28.

Inluding the 4th axis in the model does not considerably increase the fraction of variance fitted of any of the taxa listed in Table 28, nor does the cumulative fit for any other taxon increase sufficiently to rise above the 30 % limit. This confirms that the information represented by the 4th axis does not contribute much to the overall result of the ordination.

5.3.3.4. RDA data set 5 (=44 epipsammic taxa, 185 samples)

The RDA ordination of 28 environmental variables (Table 24) explains 35.2 % of the variance in the species data. After removing all non-significant and multicollinear environmental variables, we obtained an ordination with 12 variables (Table 25). Five variables that were allowed to enter the RDA on data set 4, did not contribute significantly to the explanation of the variation in the epipsammic diatom fraction, viz. irradiance (ramo), temperature (monthly average), transparancy, wind (weekly average) and the dummy variable for July. However, three other variables that were not included in the RDA on data set 4 contributed significantly to explaining the variation in the epipsammic data set: the percentage of medium-sized sand in the samples, temperature (weekly average) and the dummy variable for January. The 12 selected variables explained 29.4 % of the variation in the species data; 24.8 % is accounted for by the first 4 axes. Axis 1 and 2 explain 12.1 % and 7.0 % respectively, while the 3rd and 4th axis are much less important (3.3 and 2.3 % respectively).

All 4 RDA axes were statistically significant ($p \leq 0.01$). 84.3 % of the species-environment relation is accounted for by these axes; the species-environment correlations are high, between 0.69 (1st axis) and 0.83 (2nd axis). However, the latter values are considerably lower than the ones of the RDA ordination on data set 4, especially for the first axis. This indicates that although the selected environmental variables account for most of the variation in the species data along the first 4 axes, the fit is not as good as in the data set of the epipelic taxa.

Fig. 37 and Tables 25 and 26 show that the 1st axis mainly represents a gradient in the percentage of fine sand in the samples. Silt contributes significantly to this axis, but to a much lesser degree than in the free-living data set. The 2nd axis on the other hand, does have a strong correlation with silt ($R = 0.73$), but median grain size, medium sand, salinity (ISW) and water content also independently contribute significantly to this axis.

The biplot formed by the first 2 axes shows that both the species and sample configuration are very similar to the one in the RDA on data set 3. Note that in the RDA on data set 4 (the epipelic data set), only the order of sample and species points along the 1st axis closely resembled the one of the RDA on data set 3. This indicates that the RDA on the complete data set is mainly dominated by variations in the attached diatom species data.

Almost no epipsammic species increase in abundance towards the right hand side of the biplot. The exact life-form of e.g. *Navicula salinicola* and *Eunotogramma dubium* is not very clear yet; they might not be epipsammic. The 1st axis roughly represents the gradient (from right to left) from samples with low (relative) abundances of epipsammic taxa [Staartse Nol (SN), stations 2 and 3 of the Paulinaschor (PS)] to samples that are dominated by high numbers of epipsammic diatoms. The main variation in the epipsammic data set therefore appears to be related to the abundance of taxa, and only in the second place (see below) to the species composition.

The main gradient in species composition in the epipsammic communities lies along the 2nd axis. Anti-clockwise from the top of the biplot, the sample sediment composition changes, from the sandy (beach) sediments of Rammekenshoek (mainly medium sand), through the slightly less coarse sediments of stations 3 and 4 of the Molenplaat and the sandy stations of the Platen van Hulst (predominantly fine sand) to the sediments of Baalhoek and Nauw van Bath, which range from sandy to silty. The silt content of the samples roughly increases in a similar fashion. However, we can also detect a salinity gradient along this axis. This is due to the predominance of sandflats near the mouth of the estuary and silty sandy and silty sediments in the inner estuary. It is therefore impossible to assess from the ordination diagrams whether the distribution of some epipsammic taxa (especially those typical of the most coarse-grained sediments) is mainly related to changes in sediment grain size or salinity, or both. However, on comparing selected stations with a similar sediment composition from the meso- and polyhaline reaches, we see that the occurrence of some common taxa, such as *Achnanthidium hauckiana*, *Catenula adhaerens*, *Opephora guenter-grassii* and *Pseudostaurosira perminuta*, which according to the ordination diagram are typical of lower salinities, are also present (and in abundances of the same order of magnitude) in the polyhaline reaches of the estuary. It thus appears that sediment composition is a more important factor in determining where these taxa will thrive. However, for species from medium sandy sediments it remains impossible to assess their salinity preferences as this type of sediment is completely absent from the mesohaline reaches.

A more detailed description of the taxa associated with the different sandy sediment types has been given above (chapter 5.3.3.2.); more information on the occurrence of individual taxa can also be deducted from Fig. 37 and can also be found in the systematic part (chapter 4.2.).

When we consider the different life-forms of the epipsammic diatoms, it is striking that most stalked species (*Fragilaria* cf. *atomus*, *Dimeregramma minor*, *Martyana martyi*, *Opephora guenter-grassii*, *O. mutabilis*, *O.* sp. 1 and *Pseudostaurosira perminuta*) occur in the bottom left quadrant of the ordination diagram; they lie in a strip that is almost orthogonal to the arrow for silt content, which indicates that their occurrence and abundance is independent of the amount of silt in the sediments. For example, the silty sediments of NB 1 are dominated by *Opephora guenter-grassii*. The abundance of most adnate taxa increases towards the sandy sediments; note however that a group of adnate species (including *Achnanthes amoena*, *Achnanthidium delicatulum*, *Biremis lucens*, *Catenula adhaerens*, *Cocconeis* sp. 2) take a somewhat similar position as the stalked taxa.

Surprisingly, the distribution and abundance of small motile taxa in sandy sediments is clearly negatively related to the presence of silt of the sediment. Many small motile taxa, such as *Amphora* sp. 2, several *Fallacia* spp. and *Navicula* sp. 2 and 4, are even typical of the coarsest sediments (predominantly medium sand).

The 3rd axis appears to represent an elevation gradient. However, as already mentioned in chapter 5.1.3.3., this factor is correlated to both the percentage fine sand and medium sand in the sediments. It is therefore hard to assess whether the elevation gradient actually influences species composition or whether this relationship is spurious. *Amphora* sp. 2, *Anorthoneis* spp. and *Fallacia cryptolyra* are all typical of the medium sandy sediments in the polyhaline reaches of the estuary, which belong to elevation class 1, the highest elevation class.

No environmental variables are strongly correlated ($R \geq 0.50$) to the 4th axis (Table 26), which therefore will not be discussed.

The cumulative percentages fit per epipsammic taxon (Table 29) indicate that the most important epipsammic species are well described by the model represented by the first 2 axes, while the 3rd and 4th axis do not contribute much to the total cumulative fit for these taxa. Note that the total percentage variance explained by the RDA ordination for most epipsammic taxa is considerably lower than that for the epipelic taxa (compare Tables 28 and 29).

5.3.4. Variation partitioning (VP)

VP analyses were performed on the three species data sets used in the final ordination analyses, viz. data set 3 (89 taxa), 4 (epipelon) and 5 (epipsammon)(see Table 8). Most values for data set 3 take an intermediate value between those for the epipelic and epipsammic data sets; the discussion below will therefore mainly focus on the differences between the two latter data sets.

5.3.4.1. Contribution of single environmental variables

The contribution of single variables (Table 30) was calculated by performing a hybrid RDA with each environmental variable in turn as the only constraining variable (Økland & Eilertsen 1994). The variation explained by that variable is equal to the eigenvalue of the only constrained axis.

Except for wind speed (weekly average) and the dummy variables for January and March (the latter only in data set 3), all variables contribute significantly to explaining the variation in data sets 3 and 4. However, about one third of the variables does not contribute significantly to explaining the variation in the epipsammic data set (5); these mainly include climatic (wind speed, monthly average temperature, precipitation) and temporal parameters (all except for the dummy variable for October). Note that the remaining climatic and temporal parameters are only just significant ($p \leq 0.05$). Forward selection on all variables yields a considerably higher percentage of variation (TVE) explained in the epipelic than in the epipsammic data set (cf. also chapter 5.3.3. and Table 24).

Silt content explains most of the variation in both data set 3 (14.4 %) and 4 (21.6 %), but has a much lower relative contribution to explaining the variation in the epipsammic data set (8.2 %). In the latter data set, fine sand is the best predictive variable (9.1 %). Clay and water content of the sediment, which are strongly correlated to silt, also have a high individual contribution (especially in data sets 3 and 4) but become much less important (about 1 % in all 3 data sets) when silt is already included in the analysis.

5.3.4.2. Global approach

In this approach, all explanatory variables (excluding the spatial ones) have been included in the analysis. Forward selection was then used to select the variables that significantly contribute to explaining the variation in the various species data sets. Except for the fact that multicollinear variables have not been eliminated, this approach is identical to the RDA ordinations in the previous chapter (Tables 25, 26, 31).

In all three data sets, physical-chemical, climatic as well as temporal variables have an independent and significant contribution to explaining the variation in the species data. The main difference between the epipelic and the epipsammic species data sets lies in the total amount of variation explained by the selected variables which is considerably higher in the epipelic (42.5 %) than in the epipsammic data set (30.5 %). This appears to be largely due to the fact that more climatic and temporal variables have a significant contribution in the epipelic data set (see below). Note also that medium sand has only been selected in the epipsammic data set, while transparency is included in the analysis on the epipelic data set.

5.3.4.3. Independent approaches: independent analyses of the variation explained by the different sets of explanatory variables

In this section the independent contribution of each set of explanatory variables is analysed for the three species data sets (3-5). Table 32 lists the significantly contributing variables of each different set that have been selected in the forward selection procedure. The actual contribution (percentage variance explained) of each set on the total variation in the species data is shown in Table 33 (cf. also Fig. 39).

The same physical and chemical variables are selected in the epipelic and epipsammic data sets, except for medium sand, which is only selected in the latter data set (Table 32). Only one climatic and one temporal variable are selected in the independent analyses on the epipsammic data set, while in the epipelic data set, 6 and 4 variables, respectively, are selected. Seven and eight spatial variables are selected in the epipelic and epipsammic data sets respectively.

The contribution of the physical and chemical data to explaining the total variation in the species data is highest in the epipelic data set (35.1 versus 28.6 % in the epipsammic data set). The variation explained by the physical and chemical data is also always more important than the climatic and temporal contribution (cf. Table 33). The contribution of the climatic parameters is considerably higher in the epipelic than in the epipsammic data set: 11.7 % versus 1.2 %; this is also the case with the temporal explanatory variables, although in the epipelic data set the percentage of variation explained is lower than for the climatic variables (6.5 %). This difference between the climatic and temporal contribution is mainly due to the factor water column temperature, which has a distinct spatial component (viz. the estuarine salinity gradient (see further).

The spatial variables explain 23.2 % of the variation in the epipsammic data set, while only 17.6 % of the variation in the epipelic species data can be related to these variables.

5.3.4.4. Differential approach: covariation between and within sets of explanatory variables

The amount of covariation between and within the different variable sets and subsets (or combinations thereof) was analyzed by calculating how much a certain variable (sub)set adds to the variation explained by another variable (sub)set and by testing whether this contribution is significant or not (using Monte Carlo permutation tests, 99 unrestricted permutations, Tables 34-38). By consequently comparing this value to the variation explained by both data (sub)sets independently (cf. independent approaches) it is possible to assess the amount of covariation between both sets.

Variation partitioning between and within sets of environmental variables (excl. spatial and temporal variables)(Tables 34, 35 and 37)

Within the physical-chemical set (comprising the subsets sediment, salinity and elevation), both the salinity variables and elevation give a significant additional contribution to the variance explained by the sediment parameters in all 3 data sets; the additional contribution of elevation to salinity is also significant for all species data sets. Note that elevation explains a relatively larger part of the variation in the epipsammic data set than it does in the epipelic one.

In the epipsammic data set, the additional contribution of the climatic variables is almost never significant (or only barely, p=0.03); in the epipelic data set it always is. The amount of covariation between the sediment characteristics and the climatic variables is negligible in the epipsammic (0.1 %) and small in the epipelic data set (2.7 %). However, 4.4 % of the variation explained by the climatic variables in the epipelic data set is shared with the salinity variable set; the same goes for the salinity/sediment variable set (5.1 %).

Temporal components of variation explained by different sets of explanatory variables: variation partitioning between environmental and temporal variables (excl. spatial variables)(Tables 36 and 38)

As already mentioned, the amount of variance in the species data explained by the temporal variables is low and barely significant (1.2%) in the epipsammic data set but considerable in the epipelic one (6.5%). The covariation between the temporal and physical-chemical variables is negligible in both data sets.

As expected, the variance explained by the purely temporal variables strongly overlaps with that of the climatic variables. In the epipsammic data set (and also in data set 3), the additional contribution of the temporal parameters is not (or only barely, p=0.04-0.05) significant when climatic variables have already been included in the analysis. In the epipelic data set, the additional contribution of the temporal variables is low; when the effect of the climatic parameters is partialled out, the additional contribution is not significant. However, note that more than half of the variation explained by the climatic variables has no purely temporal component but is related to salinity (cf. also above): when temporal and salinity variables are partialled out, the additional contribution of climate is not significant in all 3 data sets*. This confirms that although the main fluctuations in water column temperature are seasonal, there is also a distinct spatially structured component as the temperature also changes along the longitudinal estuarine axis (cf. chapter 5.1.2.1.).

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* When water column temperature is not included in the climatic variable set the variation explained by this set drops to 5.7 % in the epipelic data set (instead of 11.7%).

Spatial components of variation explained by different sets of explanatory variables: variation partitioning between environmental variables (incl. temporal variables) and spatial variables (Table 33, Fig. 39).

The amount of variation in the species data that is spatially structured is higher in the epipsammic (23.2 %) than in the epipelic data set (17.6 %). However, in both data sets a similar amount (12.2-12.7 %) is accounted for by spatially structured environmental variables; a large part (about one tenth) of the variation in the epipsammic species communities is spatially structured but can not be related to the measured environmental variables.

The spatial component of the sediment characteristics amounts to more than one third in the epipelic data set and more than half in the epipsammic data set. More than half of the variation in the species data of both data sets that can be related to salinity is spatially structured. The fraction in the epipelic species data that can be related to elevation has no spatial component, while about half of this fraction in the epipsammic data set is spatially structured.

As expected, the variation explained by the temporal variables in all 3 species data sets is not spatially structured. As already shown, the inclusion of water column temperature with the climatic variables introduces a spatial component in the climatic variable set which can be detected in both data set 3 and 4 (cf. above).

5.3.4.5. Additive approach

In this last approach, we included all explanatory variables that have been selected by the forward selection procedure in the independent analyses on the 4 different variable sets. An additional analysis using the forward selection procedure on this final set of variables was done to check which variables remained significant (Table 31).

It appears that the additive approach yields the highest percentage of total variance explained (TVE) in all three data sets (Table 33). However, the difference with the TVE in the global approach is very small (data set 3 and 5) to non-existent (data set 4).

5.3.4.6. Conclusion

The global approach already indicated that factors from all 4 variable sets (physical-chemical, climatic, temporal and spatial) add an independent, significant contribution to explaining the variation in the various species data sets. The additive approach, in which all variables selected in the independent approaches are combined and which gives the highest TVE, therefore appears to give a realistic picture of the relationship between the introduced variables and the variation in the various species data sets. However, as already mentioned, the increase in TVE between the global and additive approaches is almost negligible. The global approach therefore appears to be the best compromise combining the most parsimonious set of explanatory variables with an as high as possible TVE. The figures mentioned in the paragraphs below therefore refer to this approach unless stated otherwise.

The amount of unexplained variation is lowest in the epipelic species data set (Fig. 39). However, still more than half of the variation in this data set (53.3 %) remains unaccounted for. In the epipsammic data set, unexplained variation comprises more than 60 % of the total variation in the species data. Most of the explained variation in the epipelic data set can be accounted for by the measured environmental variables (in total 42.5 %). Although a considerable part of the variation explained appears to be related to seasonal changes in community structure and cell numbers, most of the variation explained is related to environmental factors such as sediment composition, salinity and elevation. A large part of the latter variation is spatially structured (cf. independent approaches). About 4 % of the variation in the epipelic species data is spatially structured but cannot be accounted for by the measured environmental parameters.

The environmentally structured variation in the epipsammic species data set is considerably lower than in the epipelic data set (30.1 %). This is partly due to the absence of distinct temporal fluctuations in this data set but also because a smaller percentage of the variation in the epipsammon can be related to the measured physical and chemical environmental variables (28.6 % versus 35.1 % in the epipelic data set). A striking feature of the epipsammic data set is that about a quarter of the variation in the species data (23.2 %) is spatially structured. Moreover, roughly half of this amount (about 10.5 % in total) concerns spatial structured variation in the species data which can not be related to gradients in the measured environmental factors. This indicates that other, as yet unknown processes play an important role in the development of spatial heterogeneity in the epipsammon of estuarine mud- and sandflats.

6. Discussion

6.1. General remarks

6.1.1. Terminology

We have slightly redefined the terms epipsammon and epipelon as we felt that the existing definitions of both terms were insufficient. Epipelon includes all diatoms that live freely on and in sediments (= epipelon sensu Round *et al.* 1990); it is emphasized that it also includes largely immotile taxa such as centric and araphid tychoplanktonic species. The epipsammon does not only include attached diatoms but also small motile species (mainly < 10 μm). The main distinction between epipsammic and epipelic now lies in the *scale* of their habitat, i.e. the scale at which they live: epipsammic species live in close association with individual particles, while epipelic species live in association with the sediment as a whole. In this respect, the diatoms that inhabit the silt layer coating sand grains are considered to belong to the epipsammon, although they might not be as firmly attached to the sand grains as e.g. stalked or adnate species (cf. De Jonge 1985).

This distinction is roughly reflected in the size range of both groups and is confirmed by their ecology: when analyzed separately, it appears that small motile taxa behave much more like adnate and stalked taxa than larger (> 20 μm) motile diatoms (cf. chapter 5.2.).

6.1.2. Methodological aspects

One of the main goals of this study was to document spatial and seasonal patterns in the taxonomic structure and the physiognomy of the benthic diatom communities of the Westerschelde estuary. This necessitates cell counts (as opposed to pigment measurements which do not attain the desired taxonomic resolution, cf. Cariou-Le Gall & Blanchard 1995).

Structural studies of microphytobenthos are still seriously hampered by the lack of universally applicable methods to quantitatively sample complete benthic diatom communities, i.e. both the free-living and attached components. The main problems lie in the quantitative isolation of the diatoms from the sediment and the distinction between living and empty (dead) frustules. The selection of an appropriate method therefore largely depends on the specific goals of a study; every method is necessarily a compromise. For example, quantitative sampling of the epipsammon inevitably requires the use of destructive methods rendering subsequent distinction between living and dead diatoms impossible (see below).

When the emphasis lies on the free-living fraction, several methods are available. Both the lens-tissue method (Eaton & Moss 1966, Colijn & Dijkema 1981, Riaux 1983, Sullivan & Moncreiff 1988, Underwood 1994) and the cover-glass technique (Oppenheim 1991) are based on the phototactic behaviour of motile, free-living species. However, both methods do not sample the epipsammon, while for the lens-tissue method it has been shown that it gives unreliable results, both quantitatively and qualitatively (de Jonge 1979). The samples obtained with this method (and with the analogous cover-glass method) will inevitably be biased towards the most motile species, which will thus be overestimated. However, both methods are especially useful to obtain clean diatom samples of free-living species for cultures or experiments (Vos 1989a).

Another method which is often used is the suspension method (Taasen & Høisæter 1981, Admiraal *et al.* 1982): after dilution of the sediment sample, the sediment is suspended and the suspension subsampled. The suspended cells can then be counted (e.g. in a counting chamber, cf. Sundbäck & Snoeijs 1991). This method is based on the assumption that most free-living cells are suspended. However, when we applied this method to sediments with a high silt content, it appeared that the free-living fraction was seriously underestimated (Van Nieuwerburgh 1996). This could probably be due to the fact that many diatoms are associated with silt accretions which sink more rapidly from the suspension than individual silt particles or diatoms.

The most effective method available to sample the free-living fraction is density gradient centrifugation using colloidal silica Ludox (de Jonge 1979, Blanchard *et al.* 1988). This method gives optimal results for quantitatively harvesting the free-living diatoms (and other micro-algae). Isopycnic centrifugation in Percoll gradients (cf. Starink *et al.* 1994), slightly modified for use in estuarine sediments, appeared effective for separating free-living protists, including ciliates, flagellates and diatoms, from an intertidal sediment (Molenplaat) in the (Hamels *et al.*, unpubl.).

The quantification of the epipsammon appears to be more problematic. None of the above-mentioned methods is adequate to quantitatively sample the epipsammon. Ultra-sonication of sediment samples appears to give good results for separating attached cells from sand grains in some freshwater and marine sediments (e.g. Round & Hickman 1971, Sundbäck & Snoeijs 1991) but did not work with the Westerschelde sediments. This is rather odd as the species composition of the diatom communities described in Sundbäck & Snoeijs (1991) is very similar to the one of the Westerschelde communities. A possible explanation could lie in the fact that their samples were collected from subtidal sediments in a virtually non-tidal area: maybe the adhesion strength of epipsammic diatoms is higher when they grow in more dynamic, intertidal sediments.

The above-mentioned density gradient centrifugation techniques are not appropriate for quantitatively sampling the epipsammon, which is only partially sampled (de Jonge 1979). Given the different adhesive capacities of epipsammic taxa it is not unlikely that especially the tightly adherent taxa will be underestimated. Microscopic examination of samples obtained with the isopycnic Percoll centrifugation revealed that only free-living diatoms were sampled. Although present in the sediments, no epipsammic diatoms were found; this again shows that density centrifugation is not effective for sampling the epipsammon.

Therefore, if one wants to analyse the population dynamics of individual epipsammic species, there is no choice but to oxidize the sediment samples. This method ensures that (1) all epipsammic frustules are separated from the sediment particles, and (2) that the organic cell contents, which obscure the taxon-specific morphological features of the silicious cell walls, are removed. However, it is evident that this method does not allow to distinguish between living and dead cells; the counts have to be corrected for empty frustules (see below).

The method we finally came up with (cf. chapter 3.3., see also Sabbe 1993) combines counts on oxidized samples and living/dead counts on Bengal Rose-stained, fixed material. The preparation of the strewn slides for the oxidized counts appeared to be almost identical to a method independently developed by Snoeijs *et al.* (1990).

The main problem remains the distinction between living and dead cells. Many cells, especially small epipsammic ones, cannot be indentified to species level. The recent re-appraisal of cytological characteristics in diatom identification (cf. Cox 1996) opens new perspectives for counts on living material but it remains an open question whether it will ever be possible to identify small epipsammic cells on the basis of living material alone. The correction factor thus usually has to be applied at a supra-specific level (e.g. one correction factor for all opephoroid, stalked taxa).

There was no time to do a living/dead count for all samples. Instead, 31 living/dead counts were made; these revealed that although the absolute cell numbers are overestimated (for order of magnitude, which depends on the specific life-form composition of a given community, see chapter 5.2.1.1.), they do give a realistic representation of the temporal trends observed during this study. Living/dead ratios of epipelic diatoms may be highly variable (cf. also Colocoloff 1975, Sundbäck 1983, Vos 1989, Underwood 1994) but as it appears that trends in the ratio of living/dead epipelic diatoms closely follow those of cell abundance (cf. also Underwood 1994) the observed trends are still trustworthy. Living/dead ratios in epipsammic diatoms are very stable throughout longer periods of time, although differences in absolute values exist between sites (probably depending on species composition and possibly also local hydrodynamics). The temporal stability of the living/dead ratios in the epipsammon was also observed by Colocoloff (1975). The observed trends in epipsammic cell abundance therefore give a realistic picture of the real patterns.

Indeed, the temporal trends based on cell counts (our data) correspond well to the seasonal biomass curves based on microphytobenthic chlorophyll *a* measurements at the same localities in the same period (October 1991-October 1992, cf. de Jong & de Jonge 1995). Therefore, although the cell numbers themselves are overestimated a careful but realistic interpretation of the observed patterns is justified. However, it is acknowledged that detailed living/dead ratios have to be known before biomass values can be inferred from the cell counts.

6.2. The abiotic environment: general trends and remarks

6.2.1. Climate

Some climatic factors that are of importance for the wax and wane of benthic diatom populations are, apart from temperature and irradiance, wind speed [which affects water column turbidity and can resuspend epipelic diatoms (de Jonge & van Beusekom 1995)] and precipitation (which through run-off influences water column salinity, turbidity and sediment composition). In general, the sampling period was characterized by a unusually warm winter and summer, the absence of severe storms and two periods of very high precipitation.

Sediment temperature was not measured. However, published data from intertidal areas in indicate that sediment temperature closely follows the seasonal trends in air temperature (Oppenheim 1991, Gätje 1992). Sediments do tend to heat up more quickly with the difference between sediment and air varying between 0°C (autumn and winter) and 8°C (cf. Oppenheim 1991). Note that in the Elbe estuary the average difference between air and sediment temperature was about 2°C (Gätje 1992). However, in beach sediments the temperature can fluctuate considerably during the tidal cycle, depending on ambient air and water temperature (cf. chapter 1.3.).

The irradiance values introduced in the environmental data set are total values summed over the week or month preceding sampling; no corrections were made to calculate the amount of irradiance actually reaching the sediments at the various stations. This value depends on the elevation of the individual stations and on the tidal regime at the stations. For example, the daily total values actually reaching the sediments in the lower intertidal zone can be up to 10 times less than the total daily irradiance (Gätje 1992).

The sampling period had two precipitation peaks, one in November 1991 and another one during the following summer. Heavy rainfall in November 1991 caused a strong shift of the estuarine salinity gradient towards the mouth of the estuary (Fig. 9) in December (except at the most marine station Vlissingen). This shift was especially pronounced in the oligo- and mesohaline reaches of the estuary where the salinity gradient is steepest. By January 1992, salinity values in these reaches were almost 10 ‰ lower than in October 1991. The summer rain did not have a dramatic effect on the salinity gradient in the Westerschelde estuary. This may be due to the various factors which prevent the rain to actually reach the estuary in summer (e.g. higher evaporation, higher uptake by vegetations, filling-up of pools and lakes which have have a lower water level in summer).

6.2.2. Water column parameters

Water column temperature roughly follows the seasonal trends in air temperature. The longitudinal water temperature trend in the Schelde estuary is rather peculiar. Normally, the temperature gradient inverts from summer (higher temperatures upstream, lower temperatures near the mouth) to winter (lower temperatures upstream, higher temperatures near the mouth). However, in the Schelde estuary, the temperature remains higher in the upper reaches due to discharge of cooling water from a nuclear power plant at Doel near the Dutch-Belgian border.

The longitudinal salinity gradient in the Westerschelde is very stable and gradual when compared with some other European estuaries (e.g. the Elbe, cf. Brockmann 1992). However, considerable long-term changes can occur: at the beginning of the sampling period a strong shift of the longitudinal salinity gradient towards the mouth of the estuary took place, causing salinity values to drop with values up to 10 ‰ at some stations (cf. above). Note however that the salinity values before this shift were unusually high, so that at the end of the sampling period salinity values had not yet reached the October 1991 values. During spring and summer, salinity values gradually increased throughout the estuary.

6.2.3. Sediment parameters

The longitudinal ISW salinity gradient closely followed the temporal and spatial trends in water column salinity. This is in accordance with published data. De Leeuw *et al.* (1991) showed that soil salinity is not significantly lower than the salinity of the inundation water until about + 2.23 MTL; all our stations are situated below this elevation limit. From + 1.0 MTL onwards, soil salinity becomes more influenced by rainfall, as the lower soils are more waterlogged and there is less exchange with the overlying water. However, the values in de Leeuw *et al.* (1991) were measured on sediment cores of 5 cm depth. It is to be expected that salinity changes in the upper mm's are more pronounced within the tidal cycle, especially in more sandy (and thus less waterlogged sediments)(cf. Admiraal *et al.* 1984 and references therein). However, during the whole sampling period, strong fluctuations in ISW salinity were only observed on one occasion at one transect (viz. the medium sandy sediments at Rammekenshoek), where salinity values were about 5 ‰ lower than usual due to heavy rainfall. No changes occurred at the more silty sediments sampled on the same day. We never observed hypersaline conditions in the intertidal sediments sampled, unlike Rasmussen *et al.* (1983, up to 50 ‰) and Oppenheim (1991, up to 160 ‰!).

In general, most Westerschelde intertidal sediments are composed of fine sand mixed with varying amounts of silt and clay. Only one station (SN 2) can be considered as extremely silty (average median grain size 63.5 µm). The distribution of different sediment types is mainly related to the degree of exposure to currents and waves: the most coarse-grained sediments (i.e. with a high median grain size and low clay and silt content) will be found in the most exposed areas. Sediment composition thus largely reflects local hydrodynamic conditions.

Median grain size is positively correlated with the salinity gradients: sediments are generally coarser in the polyhaline reaches and near the mouth of the estuary (cf. also Ysebaert *et al.* 1993). This pattern can be observed in many European estuaries (cf. McLusky 1989, Juggins 1992) and is mainly due to the stronger tidal currents in the lower reaches and the higher rate of mud deposition in the upper and inner reaches of the estuaries. More detailed analysis of the various grain size fractions indicates that especially very fine sand and medium sand are strongly correlated to the salinity gradient, medium sand being very rare in the inner reaches where very fine sand content of the sediments is much higher. However, within every salinity zone various sediment types can still be found: the most silty sediments of the Westerschelde are situated in the lower reaches (Staartse Nol), whereas more coarsely grained-sediments can also be found in the inner reaches (although they are much rarer, e.g. station 3 at the Nauw van Bath).

The observed temporal trends in sediment composition differ from station to station (cf. chapter 5.1.3.3.). At some stations the observed trends are largely seasonal and related to seasonal changes in hydrodynamics (higher river discharge and hence stronger currents in winter) and climate (more regularly stronger winds in winter), while at others no seasonal pattern can be discerned. The temporal fluctuations at the latter stations are strongly related to long-term hydrodynamical and morphological changes in the Westerschelde estuary, which are at least partly caused by the intense dredging and spoil dumping activities in the estuary (cf. Van Maldegem *et al.* 1993).

It is difficult to find a general pattern in sediment composition change along the intertidal gradient in the Westerschelde estuary. While on exposed non-estuarine beaches the sediment becomes coarser towards the upper intertidal zones (e.g. Blondeel 1996), this pattern is usually reversed in estuaries where the lower intertidal regions are generally subject to longer periods of strong tidal currents than the upper regions. This pattern is not clear in the Westerschelde estuary: while some transects become more coarsely grained towards the lower intertidal stations, others become more silty. It is impossible to assess whether some observed trends (such as the significant increase of fine sand with decreasing intertidal elevation) reflect a general trend within the estuary or whether it is a mere artefact related to the location of the sampling transects.

6.3. Taxonomic composition of the benthic diatom communities of the Westerschelde estuary

Throughout the sampling period, diatoms dominated the microphytobenthos at the sampling stations in the Westerschelde estuary. However, a preliminary survey of living material revealed the presence of a number of protist taxa belonging to other phyla (Table 40). *Chroomonas* sp. was present in sufficiently high densities in the mesohaline stations during late spring/early summer to colour the upper layers of the sediment dark green. The other taxa listed in Table 40 were much less abundant although they could become locally abundant (e.g. *Amphidinium* spp. and *Euglena deses*). Large cyanobacteria were only sporadically observed (mainly *Merismopedia glauca*) and were never dominant.

During this study of the intertidal benthic diatom flora of the Westerschelde estuary, we observed 316 diatom taxa (species and infraspecific taxa); all taxa are listed in Table 18. While 223 taxa could be identified to species (or infraspecific) level, we were not able to determine the identity of 93 taxa (about 29 % of all taxa).

Twenty-five taxa from the latter group have been provisionally assigned to a known species; they are indicated by the abbreviation ‘cf.’ in the binomial. This group mainly comprises taxa that closely resemble species whose taxonomic or autecological identity is as yet uncertain or unknown. In many cases, our specimens only differed from the type description of these species in size and stria density, but within the scope of this study it could not be ascertained whether or not they belonged to their normal morphological continuum (e.g. *Fragilaria* cf. *gedanensis*, *Cocconeis* cf. *placentula*, *Amphora* cf. *longa*). In a number of cases (e.g. *Fragilaria* cf. *atomus* and *Amphora* cf. *exigua*) we have provisionally assigned our specimens to a certain species on the basis of a published description of specimens that are *presumed* to belong to that species. However, as the type material of the species in question has not yet been checked the true identity of these taxa is still uncertain. Finally some taxa closely resemble a known species but its common occurrence in the Westerschelde estuary disagrees with its known ecological profile (e.g. *Amphora* cf. *copulata* and *A.* cf. *pediculus*); we therefore refrained from making a positive identification.

In total, 63 taxa could not be unambiguously identified; these have been given a serial number in the genus we believe they belong to. This group includes species and probably also genera which are most likely to be new to science (e.g. *Fallacia* sp. 3 and 4, *Lunella* sp. 1, Incertae sedis sp. 1) but also many species which are common and widespread but which we suspect have consistently been given the wrong name in floristic studies (e.g. *Achnanthidium* sp. 2 which in brackish areas is almost without exception identified as *Achnanthes lemmermannii*, a freshwater species). We believe the use of such names should be avoided until the true identity of these taxa has been assessed through studies of type material.

In this study we propose 8 new nomenclatural combinations; four of which have already been published, viz. *Biremis lucens* (Sabbe *et al.* 1995), *Opephora guenter-grassii*, *O. mutabilis* and *Pseudostaurosira perminuta* (Sabbe & Vyverman 1995). Four others (*Plagiogrammopsis minimum*, *P. sigmoideum*, *Tryblionella levidensis* var. *salinarum*, *T. parvula*) have been provisionally introduced and await formal publication. It mainly concerns new nomenclatural combinations in the light of the recent developments in diatom taxonomy (see below).

Although the total number of diatom taxa observed in the Westerschelde estuary during the sampling period amounts to 316, only a limited number of taxa dominated[*] the various diatom communities at the 32 sampling stations. These taxa are listed in Table 41; their importance can also be inferred from the RDA diagrams (e.g. Fig. 31). Most of these are common in many stations, while some (such as *Achnanthes amoena*, *Amphora* sp. 5, *A.* sp. 6 and *Navicula* sp. 7) were only locally abundant and were rare in the majority of stations. *Anorthoneis* spp. and *Fallacia cryptolyra* were codominant in medium sandy stations only.

The species list of the intertidal benthic diatoms from the Westerschelde estuary mainly comprises those taxa that were observed during the cell counts. It is certainly not exhaustive for the following reasons:

1. Some taxa are only locally abundant and important populations could have been overlooked as only a limited number of stations were sampled. For example, in a preliminary survey of the benthic diatom flora of the Westerschelde estuary (Sabbe 1990) we observed dense populations of *Fragilaria* sp. 2, *Navicula* sp. 5 (as *N.* sp. 24) and *Nitzschia bergii* on certain mud- and sandflats (e.g. 'Middelplaten', 'Thomaesplaat') which were not sampled during the present study.
2. We did not sample any saltmarsh sites. In Northwest Europe, saltmarshes are largely situated in the upper intertidal zone, mainly above the point of the lowest neap high tide (McLusky 1989); large parts are therefore not daily covered by the tides. It is known that the benthic diatom community of these saltmarsh sites can be very different from that of unvegetated mud- and sandflats (Hendey 1964, Kuylenstierna 1989-90, Oppenheim 1991, Nelson & Kashima 1993, Denys 1995, Hemphill-Haley 1995). This is not only due to the different position along the intertidal gradient but also to factors related to the cover by saltmarsh plants, such as temperature, light climate and soil humidity.
3. The most striking feature of the list is the absence or rarity of certain fragile epipelic species that are commonly reported from other estuaries. These species can be very abundant in the field but

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[*] i.e. they belonged to the 10 most abundant taxa in at least one sampling station.

easily disappear when the samples are treated with strong acids. For example, *Cylindrotheca* and *Chaetoceros* spp. were completely absent from the counts although they were regularly seen in relatively high numbers in live material (see also Sabbe 1993). *Nitzschia* spp. such as *N.* cf. *rosenstockii*, *N.* sp. 1 and 2, which are more fragile than other epipelic taxa, are most probably seriously underestimated. In addition, many small species which are typical of the loosely attached flora of sandy sediments, such as representatives of the genera *Attheya*, *Hustedtiella* and *Stoschiella* (cf. Crawford *et al.* 1994, Gardner *et al.* 1995) are usually destroyed when treated with acids. However, as already pointed out in the introductory chapters, the strong acid treatment was necessary to quantitatively sample the epipsammic communities, which was our primary interest. It thus has to be kept in mind that the epipelic communities described in this study are not fully representative of the *in situ* communities.

6.3.1. General remarks on diatom systematics with special emphasis on the systematics of brackish-water diatoms

The classification of diatoms is mainly based on the morphological features of their siliceous cell wall. Besides its specific shape and size the cell wall also has a complex ultrastructure which is used for diatom identification. Problems in contemporary systematics of brackish-water diatoms are mainly related the following three factors:

1. problems related to the interpretation of morphological variation patterns, and more specifically in relation to the occurrence of cryptodiversity in diatoms;
2. problems related to the lack of specialized brackish-water floras and the widespread use of European identification works in other continents, which both lead to force-fitting of taxa (cf. Tyler 1996, Vyverman 1996);
3. nomenclatural and taxonomic problems related to recent developments in diatom systematics.

Although the emphasis in the discussion below lies on brackish-water diatoms, most problems relate to diatom systematics in general.

6.3.1.1. Morphological variability in diatoms and its implications for diatom systematics

Most diatoms are characterized by a high degree of morphological variability. This is partly due to the mode of vegetative multiplication of most diatoms, which is characterized by a steady decrease in cell size until size restitution via auxosporulation. This process can also induce other morphological changes, such as modification or loss of ultrastructural features. In addition, experimental research on selected taxa has shown that frustule morphology can change under differing environmental conditions (Syvertsen 1977, Cox 1995b). It has been shown that marine and freshwater species which invade brackish-waters can have a high morphological plasticity along the salinity gradient (cf. Snoeijs 1995, Cox 1995b). These changes mainly concern size and size-related effects (e.g. apical shape) but other effects such as changes in raphe ultrastructure and areolar dimensions and structure have also been observed (cf. Cox 1995b). In both cases the morphological change is a continuous, phenotypic phenomenon without genetic base.

However, recent detailed morphometric studies have shown that (often subtle) morphological discontinuities in shape, size and ultrastructural features exist within several diatom species, both in freshwater (Mann & Droop 1996) and brackish and marine environments (Droop 1994, Medlin *et al.* 1991, Snoeijs 1992, Sabbe *et al.* 1995,). Infraspecific morphotypes can be both sympatric and allopatric. The rare hybridization experiments and molecular studies that have been performed on these morphotypes indicate that this phenomenon has a genetic base (Hasle 1978, Mann 1989, Medlin *et al.* 1991); new species have been described on the basis of this information (e.g. *Thalassiosira guillardii* Hasle, *Skeletonema pseudocostatum* Medlin). Minute morphological differences often appear to be correlated with ecological differences (e.g. Snoeijs 1992, Reynolds 1996) and may therefore indicate (genetically controlled?) sensitivity for fungal infections, production of toxins, micro-habitat selection, etc.

Hitherto little is known about this cryptic diversity in diatoms, except for the fact that it appears to be common and widespread (Mann & Droop 1996). The genetic basis of this phenomenon has so far only been demonstrated for a number of cases; temporal and spatial distributional patterns of morphotypes are largely unknown. The implications of the consistent recognition of this phenomenon are not only important for systematic and phylogenetic research on diatoms (e.g. Round 1996a), but also for the numerous applications of diatom taxonomy in e.g. water quality assessment, biogeography, palaeo-ecology and geology. Underestimating ecologically relevant diversity can lead to information loss because of the lower resolution of the applied inference models. The implications for estuarine and marine diatom biogeography are discussed in more detail below.

In the light of these observations, it is of paramount importance that original, unambiguous descriptions of the observed morphological variation patterns are provided when making floristic surveys of geographic areas. In this study, we have tried to provide complete descriptions of most taxa observed, with special attention for common and/or difficult taxa. Indeed, taxonomic problems do not only arise because a certain taxon might have been given different names (taxonomic synonyms) but also because these names were subsequently misused in later studies (cf. *A. beaufortiana*), which is often due to insufficient descriptions. A name should only be applied to a diatom when it fully matches the original type material (within certain limits of morphological variability, to be assessed by the observer). The species complex around *Amphora coffeaeformis-acutiuscula* is a good example of what can happen when names are applied to specimens when the identity of the type material to which the name was applied is uncertain. If one checks the literature for *Amphora exigua*, a species which was described in an unsufficient manner to allow unambiguous identification, it soon appears that different taxa have been given this name (e.g. compare *Amphora exigua* sensu Cleve 1895, sensu Peragallo & Peragallo 1897-1908, sensu Archibald 1983, sensu Bérard-Therriault *et al.* 1986, etc.). Another example is *Amphora coffeaeformis* (see Archibald & Schoeman 1984). Especially when it concerns (presumably!) common and widespread species (such as *Amphora coffeaeformis* and *Amphora tenerrima*) names should be used with caution in order to avoid pollution of the ecological and biogeographical record of these taxa. Therefore, when no unambiguous original description or illustrations have been provided for a certain taxon and the type material has not been studied, it is advisable not to use the name. In this respect, studies such as Schoeman & Archibald's (1984-87) work on *Amphora* type material from the British Museum, or the 'Atlas and Catalogue of the Diatom Types of Friedrich Hustedt' by Simonsen (1987) are indispensable for both taxonomic and ecological studies.

6.3.1.2. Implications of force-fitting for diatom systematics

In addition to the problems caused by the difficult interpretation of the morphological variation patterns of the diatom frustule, identification problems in estuarine diatoms are also caused by the lack of specialized brackish-water floras. As a consequence many brackish-water diatoms have been force-fitted into marine or freshwater taxa. In addition, the widespread use of European floras in other continents obscures much hidden diversity. It goes without saying that the practice of force-fitting, in combination with the use of oxidized material, obscures a lot of valuable ecological information, such as information on microhabitat and temporal distribution patterns of certain taxa. Two showpieces in this respect are *Cyclotella choctawhatcheena* and *Thalassiosira proschkinae*. Both species were only recently described (Makarova *et al.* 1979, Prasad *et al.* 1990) but have since been reported from brackish-water localities worldwide. It now also appears that many published reports of e.g. *Cyclotella meneghiniana*, *C. striata* and *Thalassiosira levanderi* from brackish-water sites actually concern these species. The fact that both species now emerge as two very common and often dominant species in estuaries indicates that there are still serious inadequacies in our knowledge of these diatoms.

However, notwithstanding this lack of specialized floras, there actually is a lot of taxonomic information on estuarine diatoms. Unfortunately, it is very scattered and incomplete, and often the illustrations provided do not allow unambiguous identification. For example, an important series of papers on estuarine and marine diatoms of South African localities was published by Cholnoky and especially Giffen (for examples see reference list) Together they described many new taxa: in the six papers by Giffen listed in our reference list no less than 75 new species were described. To our knowlegde, the type material of none of these has ever been investigated or illustrated according to modern standards. Apart from these South African studies, there is most certainly a wealth of information still hidden in still older studies [such as the (superbly illustrated) work of Peragallo & Peragallo 1897-1908, the papers of Frenguelli (1938 a.o.) on South American diatoms, Salah's (1953, 1955) new taxa from Blakeney Point, etc.], not to mention the rather inaccessible Japanese and Russian diatom literature. It thus appears that there is an urgent need for a thorough revision of published studies, providing the material is still available.

Another disadvantage of the available literature is that it is mainly concentrated on planktonic and/or free-living taxa, while epipsammic diatoms are only rarely dealt with in a systematic way.

6.3.1.3. Implications of recent developments in diatom systematics

The recent general trend towards a more refined and natural classification at the genus level in the Bacillariophyta has sparked the creation and resurrection of numerous genera, many of which were described in Round *et al.* (1990). These 'new' genera accomodate for natural groupings within 'old' genera which were often already recognized at a subgeneric level by earlier authorities (e.g. Hustedt 1931-1959). A major breakthrough in this new 'splitting' trend is the (re-)appraisal of characters which do not only relate to cell wall morphology, but to cytological (e.g. chloroplast morphology) and reproductive features, thus adding a new set of independent characters to the taxonomical datasets. In addition, molecular techniques are increasingly used in diatom taxonomy, although their application is hitherto far from widespread.

The recent splitting trend has considerable nomenclatural consequences, which make the retrieval of information from specialized diatom studies, not only for the 'end-users' of diatom taxonomy (e.g. geologists, ecologists), but even for diatom taxonomists themselves, more difficult. Such practical considerations are important and should be dealt with, e.g. by listing commonly used synonyms and by not lightly introducing new or intentionally (!) invalidly published names (e.g. '*Fragilaria leptostauron* var. *martyi*' (Héribaud) Lange-Bertalot 1991, cf. remarks in Witkowski et al. 1995/96). However, fear of possible nomenclatural chaos, which is mainly caused by insufficient knowledge of the ICBN, should never hold back taxonomic progress. Besides, the new developments in diatom taxonomy should only cause temporary problems, which will solve themselves when new comprehensive floras and identification guides will embrace the 'new' classification (e.g. Hartley *et al.* 1996, Cox 1996).

Because of differing opinions on generic boundaries and taxonomic value of characters, but also because of fear of impracticability (cf. above), the new classification proposed by Round *et al.* (1990) is not universally accepted. At present, two parallel classification systems are therefore being used, the 'new' one and a more traditional one (cf. Krammer & Lange-Bertalot 1986-1991). In some cases, the criticism on the new system seems at least partly justified (e.g. the numerous problems in *Fragilaria* s.l.): further study is needed to assess the identity of some genera and to elucidate the relationships between them.

A more worrying phenomenon concerns the present double identity of some, mainly large, genera. For example, *Navicula* s.l., which with over 20 x 10^3 names (!) is the largest genus under the ICBN (cf. Cox 1979, Kociolek 1996), has recently been split up into several new and resurrected genera such as *Biremis*, *Craticula*, *Fallacia*, *Luticola*, *Parlibellus* and *Sellaphora* (e.g. Cox 1988a, Mann 1989a, 1994, Round *et al.* 1990). The genus *Navicula* itself is now interpreted in a much narrower sense. However, as only a small fraction of the existing *Navicula* species have been studied in detail, the generic allocation of many species is still uncertain; in some cases, the creation of new genera will be necessary. *Navicula* is thus currently interpreted in two ways: *Navicula* s.s. (comprising only the species which correspond to the type of the genus, cf. Cox 1979) and *Navicula* s.l. (the 'old' concept, which contains numerous taxa which do not belong to *Navicula* s.s. but for which no 'home' has yet been found). A similar precarious situation exists in e.g. the genera *Fragilaria* and *Synedra*. In many diatom floras, one thus finds *Navicula* species which truly belong to this genus (s.s.) but also species which certainly do not belong to this genus but whose affinities are uncertain for the time being. To solve this problem, Lange-Bertalot & Moser (1994) described a new genus, *Naviculadicta*, which was intentionally created to temporarily accomodate for those *Navicula* species whose generic affiliations are as yet unknown. Kociolek (1996) criticized the creation of *Naviculadicta* as it constitutes an unnatural (= non-monophyletic) group. Although the original idea of a catch-all genus might be a good *temporary* solution, it seems that in the end the disadvantages might overrule the benefits. It is not unlikely that *Naviculadicta* will be abused to lightly describe new taxa without having to make the effort of trying to find out where the new taxon actually belongs: it would make the treshold for describing new species even lower than it already is. It would then be left to others to trace type material and continue the study. Apart from this possible problem, it seems that the typification of *Naviculadicta* might jeopardize its future (cf. Round & Mann 1996). It goes without saying that consultation of the diatomist community (e.g. via the DIATOM-L list in the Internet) might have prevented this problem. For these reasons we have decided not to use the genus *Naviculadicta*; instead, we explicitly state whether we believe a '*Navicula*' species belongs to *Navicula* s.s. or not.

6.3.2. Are most estuarine and marine diatoms cosmopolitan? - Biogeographical remarks

The taxa listed in Table 41 are also often reported as dominant constituents of intertidal and also subtidal brackish-water benthic diatom communities in areas throughout North-West Europe [cf. studies on extant and fossil material from the Danish, German and Dutch Wadden Sea and North Sea coasts (Hustedt 1939, de Jonge 1985, Vos 1986, Gätje 1992, Denys 1993, Asmus & Bauerfeind 1994), the English North Sea coast (Juggins 1992), the English West coast (Underwood 1994), the French coast (Riaux 1983), the Kattegat (Sundbäck 1983) and Baltic area (Witkowski 1991)]*.

However, it is more difficult to assess the occurrence and distribution of the diatom taxa observed in the Westerschelde estuary outside Europe. A comparison of (illustrated!) species lists from similar estuarine habitats in North America, both from the Pacific (e.g. False Bay - Rao & Lewin 1976, San Francisco Bay - Laws 1988) and Atlantic coasts (e.g. Beaufort - Hustedt 1955,

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* More detailed remarks on the geographic distribution of each taxon can be found in chapter 4.2.

Chesapeake Bay - Cooper 1995a) shows that many species, including some which are common in our samples (e.g. *Achnanthidium delicatulum*, *Catenula adhaerens*, *Cocconeis peltoides*, *Delphineis minutissima* and *Navicula flanatica*) are also present in the American material. Detailed studies of Schoeman & Archibald (1976-1980) indicate that there can be no doubt that numerous species which are common in Europe are also present in South Africa (e.g. *Amphora coffeaeformis*, *A. pediculus*, *Fallacia tenera*, *Navicula gregaria*, *Sellaphora pupula*). Our own studies indicate that most *Opephora* species found in the Westerschelde estuary are also present in Australasian material (Sabbe & Vyverman 1995). Many common taxa thus appear to be cosmopolitan. However, in most of these studies the species have been interpreted in their broadest sense (s.l.), i.e. ignoring most if not all morphological variation within the taxon as the authors perceive it. As already mentioned, recent studies have shown that this infraspecific variation can be considerable and is often discontinuous; in many cases it is very subtle.

Our studies on *Biremis lucens* have shown that within this species at least two distinct morphological forms can be distinguished; they are characterized by small but distinct differences in stria density and size (see chapter 4.2. and Sabbe *et al.* 1995). Detailed ecological analyses revealed additional differences in their autecological requirements. However, the interesting fact from a biogeographical point of view is that the two morphotypes which were consistently present in the European material (from The Netherlands, England and Poland), could not be found with certainty in non-European material from Tanzania, Papua New Guinea and Australia. The variation patterns in the African and Australasian material appeared to be different from the ones in the European material. Moreover, the specimens in the non-European material had an intermediate stria density. Unfortunately, insufficient morphometric data are as yet available to assess the significance of this phenomenon. The fact, however, that different but complementary morphological patterns exist in geographically separate localities, takes nothing away from the validity of the distinction between the two morphotypes in the European material. It could indicate that the morphological variation within traditional diatom species is more complex than previously thought. Mann (1988, 1989b) reported similar phenomena from Scottish lakes: the morphotypes of *Stauroneis phoenicenteron* Ehrenberg and *Sellaphora pupula* (Kützing) Mereschkowsky in one lake did not necessarily correspond to those in nearby lakes. Lumping these forms without thorough morphometric analysis should therefore be avoided.

In our opinion, it is therefore not unconceivable that *Biremis lucens* is not a cosmopolitan species with variable morphology, but instead consists of different morphotypes which are sympatric and have different ecological requirements (cf. the European morphotypes) or are allopatric (the European versus the non-European material). Under the influence of local environmental conditions, these could have evolved from a common *'Biremis lucens* ancestor' into distinct morphotypes.

During this study, we encountered (both in our own material and in data drawn from the literature) other similar cases of slight but persistent morphological variation between geographically separated populations (cf. also Williams 1996b). However, further study is necessary to confirm our preliminary findings.

Morphometric analysis of *Opephora mutabilis* populations from widely separated localities (e.g. Europe and Australia) reveal slight differences in size and stria density (cf. chapter 4.2.). Whether these are comparable to those observed in *Biremis lucens* is as yet unknown and requires further study.

Diploneis papula has been reported from tropical and temperate estuarine and marine localities worldwide (cf. chapter 4.2.). However, on comparing the stria density data in the descriptions, it appears that all reports from tropical and subtropical localities mention a lower stria density than in the reports from colder waters. The opposite phenomenon, viz. finer structures in tropical forms, has been reported for freshwater diatoms (Vyverman 1990). Whether different, distinct forms (with a more restricted biogeographical distribution) are involved or whether these are mere morphological forms of one and the same taxon (with different morphology induced by different environmental conditions, cf. Cox 1995b) is as yet impossible to assess and requires analysis of a large number of allopatric populations. However, it is worth mentioning that Droop (1994) found 6 distinct morphotypes of this species in British localities alone.

Subtle deviations in valve morphology (size, stria density and other characteristics) from specimens described in published studies are common throughout the literature [e.g. cf. *Petrodictyon gemma* (syn. *Surirella gemma*) in Archibald 1983].

Another indication that the estuarine and marine taxa might be much less cosmopolitan than previously thought lies in the existence of numerous species complexes which comprise seemingly similar forms, such as the *Achanthes bahusiensis* complex, the *Staurophora salina* complex, the *Navicula perminuta* complex (see chapter 4.2.). Whether the describing authors were ignorant as to the existence of previous descriptions or whether they actually did believe that the observed slight differences justified the description of new taxa is hard to assess and requires re-examination of all materials involved. At present, there is a strong tendency to lump these forms (cf. Krammer & Lange-Bertalot 1991 for *Opephora* spp. and Lange-Bertalot 1993b for the *Navicula perminuta* complex), although in some cases detailed analysis has shown that indeed different taxa are involved (e.g. Sabbe & Vyverman 1995, this study).

The above-mentioned phenomena together with the difficult identification of many brackish-water diatoms makes it hard to assess the biogeographical distribution of estuarine and marine diatoms. In the systematical part, we have referred to published reports of the described diatoms in order to get an idea about the geographical distribution of these diatoms. However, it has to be emphasized that, altough care was taken not to include unreliable observations, the reliability of many reports, especially in ecological studies, is hard to assess in the absence of good illustrations and/or detailed descriptions. At present, it is therefore impossible to make general statements about the biogeography of brackish-water and marine diatoms.

6.4. Spatial and seasonal distribution patterns in intertidal benthic diatom communities in the Westerschelde estuary: the role of the environment and the importance of community physiognomy

6.4.1. Introduction

Estuarine benthic diatom communities display a high degree of patchiness in cell abundance and community structure on different scales, from micro- (mm's to cm's) to macroscale (km's)(Round 1960, van den Hoek *et al.* 1979, Sundbäck 1983). The development of this patchiness is caused not only by gradients in abiotic factors but also by various interactions between the biota present in the sediments, ranging from grazing and bioturbation to competition and allellopathy (cf. Admiraal 1984). By analogy with these spatial patterns, temporal fluctuations in cell numbers and species composition occur under the influence of seasonal changes in the abiotic and biotic environment.

The relationships between these patterns and important abiotic environmental factors such as sediment composition, salinity, climate and elevation have been intensively studied. However, the role of biotic factors such as grazing, competition, etc. in regulating community dynamics is far less understood. It also appears that although it is possible to make certain generalizations, conclusions regarding the relative importance of these environmental factors are sometimes contradictory between studies on different estuaries. Below, we will first give a short overview of some factors that are traditionally considered to have an important structuring and regulating effect on benthic diatom communities. We then turn to the general results of the analysis of the influence of these and other factors on the present data set. Finally, the results are discussed in more detail for the various life-forms separately.

Salinity

The importance of salinity in affecting ditribution patterns of algae (and other organisms) in estuaries is well-known. Strong salinity changes in the intertidal zone, often at short time scales, make this a stressing environment in which only well-adapted species can survive (Kirst 1995). Culture experiments with intertidal estuarine benthic diatoms have shown that many may occur over wide ranges of salinity (Admiraal 1984 and references therein): only at salinities below 4 ‰ was the growth of 'marine' species affected. These experimental results have been confirmed by numerous studies on the spatial distribution of natural estuarine and brackish-water assemblages, which indicate that a distinct discontinuity in species composition (with a shift from 'marine' to 'freshwater' species) occurs at about 2-5 ‰ (e.g. Amspoker & McIntyre 1978, Wilderman 1987, Juggins 1992, Snoeijs 1994).

Sediment composition

The relationship between sediment grain size composition and the structure of benthic diatom communities is a well-established phenomenon (e.g. Amspoker & McIntyre 1978, Van den Hoek et al. 1979, Colijn & Dijkema 1981, Sundbäck 1983, Whiting & McIntyre 1985, Laws 1988, Sabbe & Vyverman 1991, Oh & Koh 1995). However, it has to be kept in mind that a gradient in sediment composition usually coincides with changes in various other factors, ranging from desiccation and nutrient content to presence or absence of certain grazers.

Elevation

Numerous studies have hinted at the possible structuring effect of tidal elevation on the composition of benthic diatom communities. However, most of these were made in salt marsh environments (e.g. Sullivan 1975 and 1982, Nelson & Kashima 1993). Hemphill-Haley (1995) showed that in intertidal environments on the Northwest Pacific coast of America, three major elevational zones could be distinguished with respect to diatom community structure: a zone below mean lower high water, a low marsh zone (up to mean higher high water) and a higher marsh zone. Within the lowest zone, which mainly encompasses intertidal flats and channel banks, no important structural differences (which could be related to intertidal elevation) were found. Similar results were found by Amspoker & McIntire (1978) and Whiting & McIntire (1985). It thus appears that the effect of tidal elevation only becomes important in the upper intertidal zone and within saltmarshes.

Nutrients

Not much is known about the structuring effect of nutrients on estuarine intertidal benthic diatom communities. This is mainly due to the fact that nutrients are generally not limiting in estuarine sediments. In fine-grained and especially silty sediments, nutrient (e.g. inorganic carbon) limitation probably only occurs at very small spatial (and temporal) scales, which makes it very hard to detect them. As already mentioned in the introductory chapters, nutrients can become limiting in dense algal mats (cf. also Admiraal 1984 and references therein). Virtually nothing is known about possible nutrient limitation in more sandy sediments (cf. chapter 1.3.).

Grazing

Although it has been shown that many sediment-inhabiting micro-, meio- and macrofauna feed on benthic diatoms, the quantitative impact of this phenomenon on the benthic diatom populations is still incompletely known. While some studies have shown that grazing pressure may actually limit micro-algal biomass (e.g. Asmus 1982, Montagna 1984, Gould & Gallagher 1990), other studies indicate that only small fractions of this biomass are assimilated by the *herbivores (e.g. Admiraal et al. 1983, De Jonge 1992)(see also below). Usually, only the larger size classes are grazed upon; the smaller cells seem to largely escape grazing (cf. Admiraal 1984 and references therein). Due to the selectivity of this feeding behaviour for certain species or valve shapes and sizes, grazing can have a structuring influence on the diatom communities (e.g. Peletier 1996). More information on the quantitative impact of grazing on benthic diatom communities can be found in Admiraal (1984).*

Climate

It goes without saying that temperature and irradiance play a key role in the development, both qualitatively and quantitatively, of benthic diatom communities. Many studies have reported on temporal distribution patterns in these communities (e.g. Oppenheim 1991, Snoeijs 1994, Cariou-Le Gall & Blanchard 1995). For a more thorough discussion of the role of temperature and light in the dynamics of estuarine benthic diatom communities, see Admiraal (1984).

6.4.2. General results

In this study, we used multivariate analyses to (1) quantify (variation partitioning) and describe (ordination diagrams) the spatial and seasonal distribution patterns of the benthic diatom communities of the Westerschelde estuary, and (2) relate them to the measured abiotic environment. In addition, we explicitly introduced purely spatial structures into our data set (using the variation partitioning approach) to account for all the spatial differences in community structure between the stations that could not be accounted for by the measured variables. By analogy, purely temporal variables were introduced as well.

Principal components analysis (PCA) and redundancy analysis (RDA) on various data sets revealed that the observed variation in benthic diatom community is largely continuous: we therefore decided against the use of classification techniques which allow to distinguish between various clusters of species and samples. The introduction of largely artificial boundaries into our data did not reveal any additional information that could not be detected using ordination analyses. The general absence of sharp discontinuities, both in space and time, in the community structure of intertidal estuarine and marine benthic diatom assemblages is now well-established (e.g. Sullivan 1982, Sundbäck 1983, Wilderman 1987). The scatter (as opposed to clustering) of taxa in the ordination diagrams indicates that there is gradual turnover in species composition along various environmental gradients.

Redundancy analysis indicated that during the sampling period the structure of the benthic diatom communities of the Westerschelde estuary was strongly related to **spatial gradients** in *sediment composition* (grain size composition and water content), *salinity* and, to a lesser degree, *elevation*. Spatial variation patterns in both the epipelic and epipsammic diatom communities are thus largely governed by the nature of the sediment and hence indirectly by the (predominantly hydrodynamical) forces that create spatial heterogeneity in the intertidal sediments. **Temporal patterns** were clearly subordinate to spatial ones. The results of our study thus confirm the importance of physical sediment properties and salinity in structuring diatom communities on estuarine sand- and mudflats.

The first gradient in silt (and water) content of the sediment separated sites with high numbers of tychoplanktonic and the larger (> 10 μm) motile taxa from sites with lower numbers of these diatoms. Along subsequent axes, sites were separated along gradients of salinity, fine and medium sand content, elevation and temperature. However, many species were not well represented by the ordination axes; considerable interspecific differences were found in the fit of species to the ordination. We therefore decided to split up the data set into smaller data sets (cf. chapter 5.3.3.2.)

A first attempt to subdivide the data set on the basis of different sediment types (as in e.g. Gätje

1992) was not helpful in clarifying the observed patterns, and therefore did not seem appropriate from an ecological point of view*. Although allocation of stations to different sediment classes is possible, it is sometimes difficult to predict the structural aspects of the diatom communities on the basis of selected sediment parameters (e.g. median grain size and silt content, the two most commonly used characteristics). We therefore decided to run separate analyses on the two main life-form groupings, viz. the epipelic and the epipsammic species groups. These analyses clearly indicated that different variations patterns existed in the epipelon and epipsammon (cf. chapters 5.3.3.3. and 5.3.3.4). This finding also confirmed earlier observations made in the framework of a study on the short-term temporal fluctuations in coexisting populations of epipelic and epipsammic diatoms (Sabbe 1993); here it was found that the fluctuations in epipsammic and epipelic populations occurred independently from one another.

In addition, special attention was paid to the relationship between between the various life-forms within the epipelon and the epipsammon and the measured environmental parameters. Athough the existence of distinct life-forms within the benthic diatom communities (and within benthic microbial communities as a whole) is widely recognized (Admiraal 1984, Round *et al.* 1990), only little is known about their spatial and temporal patterns (cf. De Jonge 1985, Nilsson 1995).

Below we will first summarize the main results of the separate multivariate analyses for the epipelon and the epipsammon. In the next chapter, the results are discussed in more detail, incorporating the results of the correlation and graphical analyses and the information on cell abundance and diversity.

The structural variation in the epipelic diatom communities, which are mainly composed of tychoplanktonic and large (> 20 µm) motile taxa, is strongly related to spatial gradients in physical and chemical characteristics of the **sediment** and to **salinity**. Together, these factors explain about 35 % of the total variation in the epipelic species data set (cf. Table 33). The morphological parameter elevation only has a small contribution to explaining the variation in the epipelic data set and is negligible when the effect of the sediment characteristics and salinity is partialled out. A distinct temporal component explains about 6.5 % and is almost completely accounted for by the introduced **climatic factors**. About 18 % of the variation in the epipelic data set is spatially structured; most of this variation is accounted for by the measured environmental variables. About **4 % of the spatial variation** remains **unaccounted for** by the measured variables. In total, nearly half (about 47 %) of the variation in the epipelon is accounted for by the introduced environmental, temporal and spatial variables. The other half of the variation is unexplained. (Fig. 40)

As in the epipelon, the structural variation in epipsammic diatom communities is mainly related to **sediment characteristics** and **salinity**: together these explain 27.4 % of the total variation in the epipsammic data set (Table 33). **Elevation** explains a relatively larger part of the variation than in the epipelic data set, but again this amount is negligible when the effect of the sediment variables and salinity is partialled out. Indeed, the sediment composition of most transects changed along the intertidal gradient, except at the Platen van Hulst and at Rammekenshoek. In both transects, community structure was very similar along the intertidal gradient, which confirms that the relationship with elevation is largely spurious. However, all taxa decreased in abundance with elevation (cf. below). In contrast to the epipelon, both the temporal and climatic variables only explain a very small and barely significant part of the

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* Note that for practical reasons it might still be useful to use sediment type as an approximate predictor for e.g. benthic diatom biomass or general community structure. However, it is not helpful in a more detailed analysis of the spatial and temporal analysis of these communities.

variation in the epipsammic data set. However, a relatively larger part (23.2 %) than in the epipelic data set is spatially structured. Moreover, even after the environmentally structured spatial variation has been accounted for, about **8.5 % of the spatially structured variation** remains **unaccounted for**. In total, about 40 % of the variation in the epipsammic data set can be related to the introduced explanatory variables; 60 % remains unexplained. (Fig. 40)

It thus appears that in both data sets considerable amounts of the variation in the species data remain unaccounted for (57.5 % in the epipelic data set, 69.5 % in the epipsammic data set): note however that within this unexplained fraction we can still distinguish between a part which is spatially structured (4.2 % of the total variation in the epipelon, 8.4 % in the epipsammon) but cannot be related to the measured environmental variables, and a part which is not. The significance of this fraction will be discussed below.

Low percentages of explained variance are typical of large, noisy data sets containing many zero values (cf. Cumming *et al.* 1992, Pan & Stevenson 1996). Published values for similar data sets (of protist communities) are lower or comparable to ours: e.g. 18 % (in 4 axes, Romo & Van Tongeren 1995), 23.3 % (in 3 axes, Widerman 1987), 26.1 % (all axes, Douglas & Smol 1995), 56.3 % (all axes, Pinel-Alloul *et al.* 1995). However, even when the TVE is low, the ordination can still be informative (ter Braak 1994): various measures which can be inferred from the ordination output allow to check the quality of the ordination analysis and its display (cf. ter Braak 1994). Amongst others, the cumulative fit for species indicates whether the most important taxa are well represented by the ordination. As this was the case in the separate analyses on both the epipelic and epipsammic data sets, we can conclude that the explanatory variables included are important in structuring these communities. However, note that the ordination model obtained for the free-living fraction is a better representation of the data than the one for the attached fraction, as can be inferred from the cumulative fit per taxon. The most abundant taxa in the free-living fraction have a better fit (more than 50 % in three axes for 8 taxa) than those in the attached fraction (more than 50 % in four axes for only one species).

6.4.3. The epipelon

As the ordination biplots revealed, an intricate relationship exists between both epipelic cell numbers and community structure and the amount of **silt** in the sediment. De Jonge & van Beusekom (1995) showed that in the Ems-Dollard estuary the resuspension of mud (≅ clay + silt) is mainly caused by wind-induced waves at high tide, while the redistribution of mud within the estuary is a tide-induced process. They also found that microphytobenthos (measured as chlorophyll *a*) and mud are suspended simultaneously and that both processes are a direct (linear) function of the effective windspeed (i.e. the mean wind speed during the 3 periods of high water preceding sampling) for windspeeds > 3 m/s and < 13 m/s. The strong relation found between silt and both epipelic cell abundance and community structure in the present study is in close agreement with their findings: the relationship with silt is strongest for the tychoplanktonic taxa such as *Cymatosira belgica*, *Delphineis minutissima, Paralia sulcata, Thalassiosira decipiens, Navicula* cf. *perminuta* (cf. also de Jonge 1985, as *N. diserta*?) and *Rhaphoneis amphiceros*, while motile epipelic forms are less strongly correlated (cf. Figs 34 and 41). It thus looks as if tychoplanktonic taxa actually behave as clay and silt particles and are subject to the same processes of resuspension and deposition. The co-occurrence of *Cymatosira belgica*, *Delphineis minutissima* and to a lesser extent also *Thalassiosira proschkinae* is a very characteristic feature of silt-rich sediments throughout North-West Europe [e.g. de Jonge 1985, Gätje 1992, Juggins 1992 (species group 9), Underwood 1994].

The distribution of many species belonging to the other epipelic life-forms [mainly larger (> 10 µm) motile diatoms], such as many *Navicula* species (*N. arenaria* var. *rostellata*, *N. gregaria*, *N. phyllepta* and *N. flanatica*), *Nitzschia* and *Cylindrotheca* spp., is also closely related to the amount of silt in the sediments (and hence less dynamic environments) but this relationship is not as strong as with the tychoplanktonic taxa, and unlike the tychoplankton (whose fit in the ordination is almost solely related to the silt gradient, cf. Table 28), other environmental factors influence their distribution (cf. Fig. 41). Motile forms are more or less 'attached' to sediment particles via the secretion of mucus threads; moreover, they are able to withdraw into the sediments (upper mm's) prior to tidal inundation (e.g. Pinckney *et al.* 1994 and references therein). This way they are less prone to be suspended into the water column than the tychoplanktonic taxa. However, resuspension remains an important factor in the spatial (but also temporal) dynamics of these communities. The general absence of tychoplanktonic and also larger motile taxa from sediments with low silt content confirms the importance of resuspension in structuring the benthic diatom communities.

Only a few specialized large (> 20 µm) motile taxa are adapted to life in more dynamic (and thus less silty) sediments. The results of the ordination analyses clearly show that some epipelic species such as *Navicula meniscus* are typical of these apparently hostile environments for motile, free-living diatoms. Other typical components of this specialized flora include amongst others members of the genera *Hantzschia*, certain *Amphora* spp. (e.g. *Amphora pulchella*) and *Pinnularia stauntonii*. Similar (or the same) representatives of these genera can be found in coarse-grained sediments worldwide (e.g. Peragallo & Peragallo 1897-1908, Colijn & Dijkema 1981, Garcia-Baptista 1993). Note however that most of these taxa were only recorded in low numbers and were therefore not included in the ordination analyses. The general lack of studies on this habitat is illustrated by the presence of two characteristic species from medium sandy sediments of the Westerschelde, viz. *Navicula margino-nodularis* and *N. accedens*, which are here reported for the first time (since the 1950's) outside the type locality.

Apart from this strong relationship with resuspension, the structure of the epipelic diatom communities also shows an unequivocal relationship with **salinity**. The distribution of a considerable number of epipelic taxa is largely restricted to the brackish (mesohaline) reaches of the estuary (e.g. *Navicula gregaria*, *N. phyllepta*, *N. flanatica*, *Parlibellus* sp. 2, *Cyclotella atomus*, *Cyclotella choctawhatcheeana*, *Luticola mutica*, *Thalassiosira proschkinae* and others - see Fig. 34 and Table 39) while others are predominantly found in the poly- and euhaline reaches (e.g. *Brockmaniella brockmannii*, *Plagiogrammopsis vanheurckii* and others). However, it is clear that a sharp turnover in species composition at the mesohaline-poly/euhaline transition, as can be observed for many organisms of higher trophic levels (cf. Hamerlynck *et al.* 1993), is not present in the benthic diatom communities. As already mentioned, the main discontinuity in diatom species composition which can be attributed to salinity occurs at about 2-5 ‰, which is outside the sampled salinity range. Preliminary studies of the benthic diatom communities of upper and freshwater tidal reaches of the estuary (Van Nieuwerburgh 1996) confirm the presence of a similar discontinuity in the Schelde estuary.

Epipelic cell abundance is negatively correlated to salinity. However, as already mentioned in chapter 5.2.1.2. this relationship is most probably spurious as salinity itself is correlated to various sediment characteristics including silt and medium sand.

As already mentioned, **elevation** does not have an important structuring influence on the epipelic diatom communities, at least not within the intertidal elevation range sampled during this study. Hendey (1964) already noted that the distribution of diatoms in the intertidal zone is more a mosaic than a series of more or less clearly defined parallel zones. This is in accordance with our observations: sediment composition can vary considerably along the intertidal gradient, and this factor is clearly more important than elevation.

However, there does appear to be a relationship with cell abundance but this relationship does not appear from our analyses on all 360 samples as the absolute differences in cell abundance between stations can be considerable, which obscures trends in cell abundance within transects. However, within transects with little variation in sediments composition between stations (e.g. Rammekenshoek, Platen van Hulst, Appelzak) there is a decrease in epipelic cell numbers towards the lower intertidal zone in stations with a higher silt content (e.g. Appelzak). However, in more sandy sediments (e.g. platen van Hulst), no such relationship exists. The decrease of benthic diatom biomass with decreasing elevation in silty sediments in the Westerschelde estuary is in accordance with the biomass trends based on chlorophyll *a* data (De Jong & De Jonge 1995). As in our study, this relationship did not exist in less silty sediments, possibly because of more pronounced desiccation effects in the upper intertidal zone in sandier sediments (cf. also Riznyk & Phinney 1972). In the lower intertidal zone, light might be limiting diatom growth (cf. also Asmus & Bauerfeind 1994).

Motile epipelic communities in the Schelde estuary are characterized by a typical spring bloom, comparable to the one known from periphytic and planktonic communities in temperate areas (cf. Snoeijs 1994, Reynolds 1996): cell numbers increase in late winter-early spring (February-March) and reach maximum values in late spring-early summer (May-June). In summer, the populations collapse, followed by a slight increase in autumn. Similar patterns are, within tolerances, known from epipelic diatom communities in other northern temperate areas (Round 1960, Admiraal & Peletier 1980, Admiraal *et al.* 1982, Oppenheim 1991, Asmus & Bauerfeind 1994, Underwood 1994, Cariou-Le Gall & Blanchard 1995, Peletier 1996).

However, significant differences exist between the seasonal patterns in cell abundance and community structure of motile epipelic and tychoplanktonic taxa. Motile epipelic species are characterized by a relatively stronger increase in cell numbers than tychoplanktonic ones (cf. Figs 16 and 29). Moreover, a distinct succession of different species occurs during the spring bloom (cf. chapter 5.3.3.3.). An example of a typical spring bloom of motile epipelic species is shown in Fig. 43 (BH1) which shows considerable changes in relative composition within the motile epipelic community. The relative composition within the tychoplanktonic component of the epipelon is much more stable: the seasonal changes in relative cell numbers in a tychoplankton-dominated community are shown in Fig. 43 (SN2).

The onset of the spring bloom of motile epipelic taxa coincides with both increasing **temperature and irradiance**. However, from published data it appears that the sharp increase in growth rates is mainly triggered by increasing irradiance (cf. Admiraal & Peletier 1980, Sabbe 1993) and not by increasing temperature.

The crash of the motile epipelic diatom populations in summer has been attributed to a number of factors including grazing, nutrient limitation and inhibitory effects of temperature, irradiance or oxygen, and wind-induced resuspension (Admiraal 1984, De Jonge 1992). As already mentioned, the effect of **grazing** on benthic diatoms is not well known. Literature reports are often contradictory, which can at least be partly explained by the fact that trophic interactions appear to be almost as diverse and specific as the communities involved (Vyverman *et al.* 1996); one therefore has to be careful to apply results from one situation to another without detailed knowledge of the organisms involved. A major distinction can be made between grazing by meio- and macrobenthic organisms.

Blanchard (1990) and Pinckney & Sandulli (1990) observed positive spatial associations amongst meiofauna and microphytobenthos. However, the quantitative impact of meiobenthos on benthic diatom assemblages is largely unknown (cf. Moens & Vincx 1996), as is the impact of microbenthos. Although we frequently observed nematodes and ciliates who had ingested large numbers of motile epipelic diatoms, it remains an open question whether these organisms are capable of regulating epipelic biomass and diatom biomass in general (cf. Admiraal et al. 1983). Blanchard (1990) noted that the spatial association between meiobenthos and microphytobenthos did not hold for diatom cells smaller than 40 µm. Whether the observed shift in size from larger (> 20 µm) motile to smaller motile diatoms (cf. Fig. 29, type 4) from June onwards is related to a shift in the composition of the diatom-grazing community is hard to assess as we have no data on the meiobenthic communities at our stations.

The impact of macrobenthos on benthic diatom communities appears to be more important. An interesting observation on the importance of macrobenthic grazing on epipelic diatoms is presented by Peletier (1996) who found that the recovery of dense macrobenthos populations (predominantly *Nereis diversicolor* and *Corophium volutator*) in the Ems-Dollard estuary from severe organic pollution in the seventies and eighties coincided with a shift in the seasonal pattern of the diatom communities: instead of high biomass values during a large part of the year, a bimodal seasonal biomass curve was observed. Increasing benthic macrofauna density in spring and summer probably contributed to a declining benthic diatom stock in summer. This observation suggests that grazing by macrobenthos can efficiently control the temporal dynamics of benthic diatom populations. This may also be the case in the Westerschelde estuary, where e.g. *Corophium volutator* is often present in high numbers (cf. de Jong & de Jonge 1995 and references therein).

The importance of **wind-induced resuspension** in regulating epipelic diatom biomass and community structure is well-documented (e.g. Baillie & Welsh 1980, De Jonge 1992, De Jonge & van Beusekom 1995, Schreiber & Pennock 1995). Periods of relatively high wind speeds are often correlated with strong reductions in microphytobenthos biomass and can have an important structuring effect on the benthic diatom communities present (De Jonge 1985). This in in accordance with our findings which indicate that even despite the absence of strong winds during the sampling period there still is a significant negative relationship between wind speed (WIWE) and motile epipelic diatom cell abundance. Note however that such a relationship does not exist with the tychoplanktonic fraction, which may indicate that this fraction is not lost from the sediment but settles again so that no significant decrease in cell numbers takes place. The fact that tychoplanktonic taxa [such as *Cymatosira belgica*, *Delphineis minutissima* (cf. Sabbe 1993, Denys 1995) and (?) *Thalassiosira proschkinae*, cf. Muylaert & Sabbe 1996a and references therein) are usually associated with sediment aggregates might cause them to sink more rapidly from the water column after resuspension.

Given the fact that no strong winds occurred during the summer, it is unlikely that the decline of the motile epipelic standing stocks is due to resuspension events. Grazing seems to be the most likely cause of the observed decrease.

6.4.4. The epipsammon

Epipsammic diatoms are numerically dominant in many stations in the Westerschelde estuary: maximal cell numbers are in the same order of magnitude as those of the epipelon. This is in accordance with numerous other studies on intertidal and subtidal benthic diatom communities (e.g. Amspoker 1977, Sundbäck 1983, Vos 1986, Sabbe & Vyverman 1991, Sabbe 1993); Cadée & Hegeman (1974) found that primary production by the epipsammon was more important than that of the epipelon on tidal flats in the Western Dutch Wadden Sea. A similar observation was made by

Hickman & Round (1970) on epipsammic communities in a freshwater environment.

However, despite their numerical importance and widespread occurrence, processes regulating the spatial and temporal dynamics in epipsammic species composition and abundance are far less understood than the ones governing the distribution of free-living taxa. From almost all our statistical and multivariate analyses it appears that the relationship between the epipsammon and the measured environmental variables is less pronounced: simple correlations between the epipsammon and many selected environmental parameters are lower and/or less significant (e.g. Tables 13 and 14), the overall cumulative fit in the ordination analyses with the epipsammic data set is lower than for the epipelic one (Table 29), the overall amount of unexplained variation is higher (Table 33), the species-environment correlation is lower (chapter 5.3.3.4.), etc. However, some distinct patterns emerge from the analyses.

A striking result of this study is that while epipsammic cell abundance is correlated to the amount of very fine sand and especially fine sand in the sediments, it is not correlated to silt content: epipsammic cell numbers can be as high in silty as in sandy sediments. However, epipsammic diatom communities will only develop in the presence of silt when a suitable substrate for growth is present. The presence of a high amount of very fine sand particles in the silt-rich station NB 1 (cf. Table 3) allows the development of dense epipsammic populations, while station SN 2, which also has a (comparably) high silt content but much less very fine sand supports almost no epipsammic communities. This intricate relationship between the presence of a suitable substrate (i.e. large enough sediment particles) also appears from the trend surfaces for very fine sand and fine sand on the one hand (Fig. 42), and epipsammic cell numbers on the other (Fig. 20c): the two peaks in epipsammic cell numbers coincide with the peaks in very fine sand and fine sand content of the sediments. However, while cell numbers may be in the same order of magnitude on very fine and fine sand, the physiognomy of the communities is very different (see below).

Indeed, the structure of epipsammic communities is predominantly related to the specific grain size composition of the sediments in which they occur, which itself is an indicator of the **degree of exposure** of the sediments. It is important to emphasize that the structural (both taxonomic and physiognomic) differences between epipsammic communities are not caused by the actual grain size of the sediment but by the local physical disturbance of the sediment, mainly by hydrodynamic forces. Different epipsammic communities are found on very fine sand, fine sand and medium sand (cf. chapter 5.3.3.4.). However, the ordination analyses did not allow to distinguish between this gradient in particle size and the salinity gradient of the estuary (cf. above) because sandy sediments (especially those dominated by medium sand) are more common in the lower and middle reaches of the estuary, while silty sandy and silty sediments are mainly found in the inner reaches. We therefore analyzed the distribution of selected taxa along the salinity gradient. This revealed that certain common epipsammic taxa (e.g. *Achnanthidium delicatulum*, *Catenula adhaerens*, *Opephora guenter-grassii* and others) are present (in numbers of the same order of magnitude) along the whole salinity gradient of the Westerschelde estuary. The relationship with salinity as indicated by the ordination diagram thus appeared to be spurious, at least for these taxa. This is also in accordance with literature reports of these taxa, which indicate that they can thrive both in marine and brackish environments (cf. references in chapter 4.2.). Another strong indication that grain size and not salinity is the structurally most important factor lies in the fact that epipsammic communities on fine and medium sand in nearby stations (e.g. PS 1 and RA 1 or 2 respectively) are very different.

Not only does the taxonomic composition change with grain size, but there also appears to be a striking relationship with the phsyiognomy of the communities. As expected, stalked forms (e.g. *Fragilaria* cf. *atomus*, *Opephora guenter-grassii* and *O. mutabilis*) are more abundant in fine sandy and very fine sandy sediments (cf. Fig. 41), which are less exposed and hence less dynamic than medium sandy sediments. In the latter sediment type, almost no stalked forms are present. A remarkable feature of the occurrence of stalked forms (but to a lesser degree also of some adnate forms such as *Achnanthidium delicatulum*, *Biremis lucens* and *Catenula adhaerens*) is that their occurrence appears to be independent of the amount of silt in the sediment (cf. above and Fig. 41). It is precisely the presence of these forms which is responsible for the above-mentioned high epipsammic cell abundance in sediments dominated by very fine sand. The predominance of stalked forms in less dynamic sediments was also noted by Sundbäck (1983) and is closely related to the nature of this growth form: stalked forms are rare in dynamic, coarsely grained sediments because they are more prone to abrasion when the sediments become too dynamic (cf. also Miller *et al.* 1987). In less dynamic circumstances, they can develop dense communities consisting of ribbon-like or radiating colonies emanating from the substrate surface. During certain periods of calm weather, these colonies can probably form 'mats' which lie on the sediment surface and thus display a behaviour which is more closely related to the epipelon than to the epipsammon.

Another striking feature of the distribution of epipsammic life-forms is that small (< 10 µm) motile forms (such as e.g. *Navicula* sp. 2, *N.* sp. 4 and most *Fallacia* spp.) are most abundant in medium sandy sediments (cf. Fig. 41). The presence of motile forms in these highly dynamic sediments appears contradictory at first, as it would increase their chances on resuspension. However, their motility might actually be a good adaptation to life on these larger sand grains. Their motility enables them to go for shelter (in crevices) when circumstances are most dynamic (e.g. at high tide), while in calmer periods (low tide, or on the longer term: prolonged periods of better weather conditions), they can migrate across the sand grain surface to avoid crowding or in search of optimal light conditions and/or aggregates of organic material or bacteria, where nutrients are more abundant. Note also that unlike the stalked and many adnate forms, the small motile forms do avoid silty sediments; possibly silt accretion on sand grain surfaces interferes with their motility.

It thus appears that the habitat available to colonization by epipsammic diatoms is much more heterogeneous than commonly assumed (see also Meadows & Anderson 1968, Krejci & Lowe 1986) and allows for the development of structurally different communities: not only do several niches (crevices, plateau's) exist within one sand grain but different grain sizes (which of course reflect different degrees of exposure to tidal and wind-induced wave action) also promote the development of different communities with different physiognomies.

The multivariate analyses were unable to detect any significant **temporal patterns** in the epipsammic data set. This absence of a distinct seasonal signal in epipsammic diatom communities has been frequently observed (e.g. Cadée & Hegeman 1974, Taasen & Høisæter 1981 and references therein, Sundbäck 1983, Sabbe 1993, Asmus & Bauerfeind 1994), while it appears that the absence of clear seasonal variation in some microphytobenthos biomass and/or production studies can be attributed to the fact that these studies concern sandy sediments which are probably dominated by epipsammic diatoms (e.g. Baird & Steele 1968, Varela & Penas 1985, Brotas *et al.* 1995). However, it has to be emphasized that the absence of seasonal trends does not imply that no temporal trends are present in the epipsammic diatom communities. Indeed, we did observe a distinct temporal trend in epipsammic cell numbers during the sampling period, characterized by a steady increase in cell numbers in most epipsammic communities (as examplified in Fig. 29, types 1 and 2) and the absence of a significant decrease in cell numbers, except in the four stations belonging to seasonal type 1 (cf. Fig. 29). This signal, however, was not picked up by the multivariate analyses. There are two possible explanations for this phenomenon. First, PCA (and RDA) analyses will be dominated by the taxa with the highest variance, i.e. those that display the highest rate of change: indeed, the *relative* increase in epipsammic cell numbers is much lower than in the (motile) epipelic fraction. Second, the relative composition of the epipsammic communities remains remarkably stable throughout the sampling period (cf. Fig. 43, see also below).

What is the cause of this weak temporal signal in epipsammic diatom communities? A possible explanation was put forward by Van den Hoek *et al.* (1979) who argued that the constant reworking of sandy sediments would mask biomass fluctuations. The presence of a large standing stock of epipsammic diatoms in the deeper sediment layers would obscure strongly localized increases in epipsammic cell numbers in the upper mm's of the sediment. However, there could also be a second factor contributing to the generally slow increase in overall epipsammic cell numbers in sandy sediments, viz. competition for space. Indeed, very fine and fine sandy sediments often support extremely dense epipsammic communities. It is therefore not unconceivable that during prolonged periods of favourable weather conditions the sand grains in the upper layers soon become too crowded and growth is limited. This would also be in accordance with the fact that in the more exposed medium sandy sediments, which support less dense epipsammic communities, the overall increase in cell numbers is relatively larger than in more fineley grained sediments (compare Fig. 29, type 1 and 2).

Another characteristic of the weak temporal signal in the epipsammic diatom communities of the Westerschelde estuary in the period 1991-1992 is the absence of sharp decreases in cell numbers. There are several possible explanations for this phenomenon. First, it might indicate that epipsammic diatoms can survive a long time under adverse conditions. Indeed, epipsammic diatoms appear to be very well adapted to life in a harsh environment: apart from morphological adaptations to their habitat, they possess certain physiological adaptations which not only allows them to fully exploit their environment (e.g. shade adaptation, heterotrophy, low metabolism) but also enables them to survive long periods in complete darkness and/or anoxia (Moss 1977, Nilsson 1995, Sundbäck *et al.* 1996). This would also enable them to survive cover by epipelic mats in coexisting populations; it is therefore not surprising that they can also survive and even thrive in more silty sediments with well-developed epipelic populations, provided a substrate for growth is present.

Second, the absence of severe storms during the sampling period might be responsible for the persistence of dense epipsammic diatoms communities in the very fine and fine sandy sediments. Apparently, the mechanical disturbance of the sediment has to surpass a certain treshold before significant loss of epipsammic cells occurs. This tresshold seems to be lower in medium sandy sediments, which already are more dynamic than more finely grained ones. Indeed, we did observe a significant decrease in epipsammic cell numbers in medium sandy sediments (cf. Fig. 29, type 1); cells which were able to grow on less sheltered parts of the sand grains are quickly lost when the environment becomes more dynamic.

Third, there are good reasons to believe that grazing on epipsammic communities is less important than in epipelic communities. There are very few literature data on this phenomenon. According to Miller *et al.* (1987) there is little grazing on adnate epipsammic species in freshwater environments. Sundbäck & Persson (1981) on the other hand reported that the amphipod *Bathyporeia pilosa* is capable of grazing on epipsammic populations (consisting of *Cocconeis* and *Achnanthidium* spp.), but this is the only reference we could find on this specific subject. We never observed ciliates or nematodes with ingested epipsammic diatoms. In our opinion, it is not unlikely that grazing is not important in epipsammic communities.

6.4.5. Diversity

Benthic diatom communities are characterized by an overall high diversity; N_1 is on average about twice as high in the observed benthic communities as in the phytoplankton of the Schelde estuary (Muylaert & Sabbe, subm.). The co-occurrence of a large number of species in any one habitat was also observed for intertidal estuarine nematode communities (cf. Soetaert *et al.* 1995). This high diversity in benthic diatom communities might be caused by the constant **physical disturbance*** of the sediments, which promotes species diversity by keeping the number of organisms of each species low and thus reducing the intensity and importance of direct interspecific competition for resources (cf. Begon *et al.* 1990). The intermediate disturbance hypothesis has already been put forward to explain the plankton paradox (e.g. Sommer 1995) and there are strong indications that it also plays an important role in benthic freshwater (Steinman 1996 and references therein) and estuarine alagal communities (e.g. Underwood 1994).

Different sources of disturbance can be identified. The most important disturbing factors for benthic diatom communities in intertidal sediments are the wind- and tide-induced sediment disturbance, and grazing.

The importance of the physical disturbance of the sediment in promoting species diversity appears from the fact that significant differences in diversity exist between different sediment types: diversity is significantly lower in more silty sediments (cf. chapter 5.2.2., Fig. 25). Fig. 44 shows that diversity (both N_1 and $N_{+\infty}$) decreases with decreasing median grain size, which is a good indicator of the degree of exposure of the sediment.

The lower diversity in more silty sediments can largely be attributed to the fact that these communities are often dominated by motile epipelon and tychoplankton, which only occur in more silty sediments (roughly SC 3-4). Primary production by motile epipelic diatoms mainly takes place at low tide, when they are concentrated in dense mats in the upper layers of the sediment. In these mats local nutrient depletion and inhibitory effects can occur, and competetion can become an important phenomenon (de Jong & Admiraal 1984). The occurrence of distinct seasonal succession patterns in motile epipelic communities might be an indication that competitive interactions are an important phenomenon (cf. Fig. 43). Remarkably, relative cell abundance is also very stable in the tychoplanktonic fraction (Fig. 43), which could mean that within this specialized community interspecific competition is of minor importance. The low diversity in these communities might be due to the fact that only few species have adopted this specialized life-strategy.

Epipsammic communities (which dominate the stations belonging to SC 1-2) are usually characterized by high diversity and low dominance (cf. Amspoker 1977). Miller *et al.* (1986) postulated that the constant physical disturbance of the sediments keeps freswhater epipsammic communities in a non-equilibrium pioneer state. Due to the constant physical disturbance, no strong organizing processes can occur. Epipsammic communities are thus largely free of interspecific constraints, and species only respond to their own physico-chemical requirements. The possible occurrence of competition for space in these communities (cf. above) only seems to affect overall community growth but has no strong structuring influence. The importance of disturbance in maintaining high species diversity also appears from the fact that when the sediments become less dynamic (and thus have a higher silt content, cf. SC 3-4), epipsammic diversity also decreases, possibly due to the predominance of only a few species (cf. NB 1).

Diversity appears to be maximal at median grain sizes between 150-200 µm, but is still high at higher median grain sizes. Although there appears to be a slight decrease in average diversity towards higher median grain sizes, the low number of observations from these sediments does not allow an unequivocal assessment of this phenomenon. If this trend can be confirmed by additional observations it would be in accordance with the Intermediate Disturbance Hypothesis as above a certain level of physical disturbance the diversity of diatom communities decreases.

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* Disturbance = any process or condition external to the natural physiology of living organisms that results in sudden mortality of biomass in a community on a time scale significantly shorter (e.g. several orders of magnitude faster) than that of accumulation of biomass (Huston 1994).

The significant, positive relationship between all diversity indices and **salinity** (cf. Table 14) might also reflect the degree of disturbance of the sediments. Notwithstanding the fact that it is a general rule that species diversity goes through a minimum in the brackish zone of estuaries (mainly around 5-8 ‰, cf. McLusky 1989 and references therein, cf. also Muylaert & Sabbe (subm.) for the Schelde phytoplankton), it is not unlikely that the relationship with salinity is at least partly caused by the predominance of more coarsely-grained sediments in the middle and lower reaches.

The effect of grazing on diversity is difficult to assess and depends on the specific impact of the diatom-grazing community on the diatom communities. For example, grazing of the competitive dominants prevents competitive exclusion and tends to increase overall diversity (cf. Hunter & Russell-Hunter 1983). However, when grazing does not exclusively affect the dominant species, overall diversity can decrease. However, there does seems to be a general consensus regarding the impact of intense grazing, which always reduces diversity (Steinman 1996). As we have no information on the impact of grazing on the diatom communities from the Westerschelde estuary, it is impossible to assess whether grazing might be an additional cause for the observed low diversity in epipelic communities.

Apart from the disturbance hypothesis, there might be another factor which could promote the co-occurrence of a high number of epipsammic species at any one station, namely **microhabitat heterogeneity**. The existence of distinct micro-spatial distribution patterns within single sand grains (cf. Meadows & Anderson 1968, Krejci & Lowe 1986) indicates that microhabitat heterogeneity is important in structuring epipsammic diatom communities: the number of distinct habitats available for colonization by specialized taxa is higher than generally assumed.

The **seasonal trend** in diversity, which is especially pronounced in more silty sediments (cf. Fig. 26, diversity is lowest in late spring, early summer), is probably caused by the fact that epipelic cell abundance is highest in this period, and interspecific constraints (with a negative effect on diversity) are most pronounced. However, the distinct peak in tychoplankton abundance (mainly caused by a sharp increase in the species *Thalassiosira proschkinae*) in most fine-grained sediments (cf. Fig. 29) might also have a negative effect on the diversity indices. Note that in the predominantly epipsammic communities from SC 1 no significant trends in diversity are present.

6.5. Conclusion

The macrotidal Westerschelde estuary is characterized by extensive intertidal areas. These apparently bare surfaces support dense benthic diatom communities in their upper layers. In the Westerschelde estuary, these communities can be dominated by both epipsammic and epipelic species. Epipsammic diatoms are either strongly attached to the sand grain surface (sometimes by means of short mucilage stalks), or are capable of movement, mainly within the sphere of inidvidual sand grains. Epipsammic diatoms thus live in close association with individual sediment particles. Epipelic diatoms can roughly be divided in two groups: motile species, which are capable of vertical migration through the upper mm's of the sediment, and tychoplanktonic species, whose exact life-strategy is not well-known. The occurrence of different life-forms both within the epipsammon and epipelon is an important phenomenon which has considerable implications for their ecology and their function and fate within the estuarine ecosystem as a whole.

Benthic diatom communities are not uniformly distributed within the estuary; their spatial distribution is regulated by various environmental factors which determine their taxonomic structure, physiogniomy and biomass. In addition, temporal fluctuations in environmental factors create more or less distinct seasonal patterns. However, these temporal variation patterns are distinctly subordinate to spatial ones.

The primary structuring factor in intertidal benthic diatom communities is the physical disturbance of the sediment caused by tidal currents, wind-induced waves and bioturbation. The interplay of these factors at locally varying frequencies and intensities creates a mosaic of sediment types, ranging from exposed, coarse to medium sandy flats to extremely silty mudflats. In addition, extreme weather conditions such as storms or antropogenic activities can have a sudden impact of the nature of a sediment, while different groups of organisms (including diatoms) can have a stabilizing effect on sediment stability through the secretion of extracellular substances.

Dense epipelic communities can only develop in relatively sheltered places, which are characterized by finer average grain size and silt accumulation; especially silt content is a good indicator of the degree of exposure of a sediment and can be used as a predictor for the presence of epipelic populations.

Motile epipelic forms are capable of active migration through the upper mm's of the sediment. At low tide, when light conditions are most favourable, they aggregate near the sediment surface and form dense mats. This life strategy has some important ecological implications, which largely determine the temporal but also the spatial dynamics of these diatoms. Apart from the obvious advantages of active motility, which enables these species to take maximal advantage of increases in e.g. irradiance, the formation of dense mats also has negative implications. First, periods of high primary production (with high oxygen concentrations and high pH values) can cause nutrients (mainly inorganic C) to become locally limiting. Second, the dense accumulation of cells increases the occurrence of competitive interactions, which could cause the distinct seasonal succession events in these communities. Third, the concentration of cells in narrow vertical layers makes them more susceptible for grazing, especially by deposit feeders, some of which (e.g. *Corophium volutator*) are very abundant in the intertidal Westerschelde sediments. Finally, the concentration of cells in the upper mm's of the sediments makes them more sensitive to resuspension events.

Motile epipelic forms display distinct seasonal patterns, characterized by a spring bloom with a clear succession of species, and a sharp decrease in cell numbers in summer, possibly caused by grazing.

Another group of diatoms which becomes increasingly important with decreasing physical disturbance are tychoplanktonic taxa. Little is known about the actual life strategies of this life-form. Their occurrence is very closely related to the amount of silt in the sediments, even more so than in motile epipelic communities. This suggests that they actually behave as silt particles and are subject to the same processes of resuspension and deposition. Remarkably, their temporal dynamics are rather obscure: no strong changes in relative species composition occur in this fraction, and increases in cell numbers are not as pronounced as in the motile epipelic fraction.

Salinity appears to have an important influence on the taxonomic structure of motile epipelic communities: although some species can be found throughout the whole Westerschelde estuary, some are typical of the mesohaline reaches and are rare in the more marine part of the estuary.

The occurrence of epipsammic communities is mainly determined by the presence of a suitable substrate for growth, i.e. sufficiently large sand grains. In this respect, the relationship between the *occurrence* of epipsammic communities and physical sediment disturbance does not primarily concern the stability of the sediment (as for the epipelon) but the availability of a substrate. However, the *density, taxonomic structure and physiognomy* of an epipsammic community is closely related to the degree of exposure of a sediment.

In the most exposed sediments, the diatom flora is composed of tightly adhering epipsammic taxa, which mainly colonize the sheltered crevices of the sand grains. Numbers are generally very low as the constant disturbance of the sediment prevents colonization of the more exposed parts of the sand grains. Small motile diatom taxa (< 10 µm) appear to be well-adapted to this environment, possibly because their motility enables them to actively migrate to the most favourable locations (regarding light climate, nutrient availability) on the sand grains, while they can go for shelter when circumstances turn less favourable. In periods of calm weather and optimal light and temperature conditions, epipsammic cell numbers can considerably increase and the diatoms can colonize more exposed surfaces. Increasing disturbance causes cell loss from these exposed surfaces.

In the less dynamic fine sandy sediments, epipsammic diatoms can colonize larger surfaces of the sand grains. Populations are still mainly composed of adnate and small to slightly larger (10-20 µm) motile species. However, stalked growth forms can also be present. Populations become much denser and it is not unlikely that space is a limiting factor during favourable weather conditions. In the relatively sheltered very fine sandy sediments, the epipsammic community becomes more and more dominated by stalked forms, while especially the smaller motile forms decrease in number. Very fine sand appears to form the lower size limit for epipsammic growth.

Epipsammic diatoms are well adapted to life in dynamic environments. Various studies have shown that they can survive long periods in darkness and even anoxia, are capable of uptake of dissolved organic compounds and are probably shade-adapted. The same adaptations which allow them to survive burial in deeper sediment layers probably also allows them to co-oexist with dense epipelic populations in silty sediments. Analysis of the temporal fluctuations in sympatric epipsammic and epipelic populations showed that they fluctuate independently from one another (Sabbe 1993). They live apart together in the most literal sense of the word.

In contrast to the motile epipelon, temporal fluctuations in the epipsammon are less pronounced. The absence of pronounced biomass fluctuations is probably mainly caused by the constant reworking of the sediment, although it is not unlikely that space mighht be a limiting factor for population growth in dense epipsammic communities. Epipsammic biomass gradually increases and appears to be largely unaffected by grazing. Strong disturbances (caused by storms) are probably the only important cause of cell loss. The episodic, often non-seasonal occurrence of the latter events is probably responsible for the absence of distinct seasonal patterns in epipsammic diatom communities.

A considerable part of the observed variation in epipelic and epipsammic diatom communities (42.5 % and 30.5 % respectively) can be related to changes in the above-mentioned environmental factors, viz. sediment composition, salinity and climatic factors. However, variation partitioning indicates that especially in the epipsammon there still is a considerable part of the variation (8.4 %) which is spatially structured but can not be related to the measured environmental variables. In other words, a considerable part of the spatial structure of epipsammic diatom communities can not be related to sediment characteristics, salinity or elevation. This purely spatial variation could be caused by overlooked environmental variables, but also by other, mainly biotic processes such as grazing and interspecific competition. However, as already mentioned, it is unlikely that these phenomena are important in epipsammic communities. A more likely structuring agent are contagious biological processes such as clonal population expansion or infections by e.g. chytrids, which can locally wipe out entire populations. Little is known about dispersion capacities of epipsammic diatoms, and it is not unlikely that clonal growth and local hydrodynamic patterns are responsible for spatial autocorrelation effects. In this respect it would be very useful to perform small-scale studies of temporal fluctuations in patchiness in epipsammic communities.

In addition, it is not unlikely that historic processes have an important influence on the spatial structure of epipsammic communities. As already mentioned, epipsammic diatoms can survive long periods of adverse conditions, and it is therefore not unlikely that certain components of epipsammic communities are 'ghosts of conditions past'. This could explain the occurrence of e.g. dissimilar assemblages in stations with a similar sediment composition (e.g. in the 3 Terneuzen stations).

The development of spatial and temporal variation patterns in epipsammic and epipelic community structure is a complex process, and especially in estuaries it is hard to assess the influence of single environmental variables or variable sets; correlations between observed patterns and the environment have to be interpreted with care as many factors are multicollinear.

The results of this study suggest that in intertidal estuarine environments, physical disturbance of the sediment (and various factors related to this process) and salinity (which influences taxonomic community structure) play a key role in structuring benthic diatom communities. In addition, there are indications that at least for some components of these communities (i.c. the motile epipelon), allogenic biological processes such as grazing can have a profound impact on their occurrence and dynamics.

The results of this study also show that different life-forms display different spatial and temporal patterns. The fact that this is also the case in co-existing populations belonging to various life-forms strongly suggests that these different life-forms have different life strategies. These are not only responsible for differences in responses to changing environmental conditions, but also affect autogenic biological processes which may play an important role in the spatial and temporal dynamics of the diatom communities. For instance, the physiognomy of a community largely determines its resistance and resilience against physical disturbance (cf. Peterson 1996), while other processes such as interspecific competition and sediment stabilization through production of extracellular substances are also strongly dependent on the presence of certain life-forms and/or taxa. By analogy with these physiognomic differences, taxonomic differences in community structure also affect community ecology.

However, to date, little is known about the life strategies of diatom species in estuarine and marine sediments; information on growth rates, dispersal capacities, dormancy, etc. is lacking even for the most common species. As it is not unlikely that the regularly observed large differences in spatial and temporal distribution patterns of benthic diatom communities between different areas can be related to structural differences between these communities, it is obvious that our understanding of the impact of environmental changes on benthic diatom communities (which is of paramount importance for the proper functioning of ecological models) might be strongly aided by a better knowledge of the life strategies of these organisms.

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TABLES

Table 1. Classification and terminology of the different estuarine salinity zones (after McLusky 1993). In the last column, the location of the Westerschelde transects in this classification is shown. For abbreviations of the transect names and more details on the stations, see chapter 3.

DIVISION	SALINITY (‰)	VENICE SYSTEM	WESTERSCHELDE STATIONS
River	< 0.5	limnetic	-
Tidal fresh	< 0.5	limnetic	-
Upper	0.5-5	oligohaline	-
Inner	5-18	mesohaline	BH-KS-NB-AZ
Middle	18-25	polyhaline	PH-MP-BH
Lower	25-30	polyhaline	RA-HP-SN-PS-TE
Mouth	> 30	euhaline	RA-HP

Table 2. Some commonly used abbreviations.

EC	elevation class
FS	forward selection
ISW	interstitial water
LM	light microscopy/-ic
MGS	median grain size
MTL	mean tidal level
PCA	Principal Components Analysis
RDA	Redundancy Analysis
SC	sediment class
SDW	sediment dry weight
SEM	scanning electron microscopy/-ic
ST	seasonal type
VP	variation partitioning
WC	water column

Table 3. List of the sampling stations and their main morphological, physical and chemical characteristics. Labels are used in statistical and multivariate analyses. Number: station number. Coordinates: UTM coordinates (x 10^{-3}). N°: number of measurements. Elevation is given in relation to Mean Tidal Level. Elevation class affiliation: see chapter 3.2.6. ISW =interstitial water. Water content: sediment weight percentage.

STATION	LABEL	NUMBER	X-COORDINATE	Y-COORDINATE	N°	ELEVATION (M)	ELEVATION CLASS	SALINITY ISW (‰)	WATER CONTENT
Rammmekenshoek 1	RA 1	1	34.120	385.818	12	0.66	1	30.16 ± 2.65	19.1 ± 1.7
Rammekenshoek 2	RA 2	2	34.156	385.805	12	0.50	1	30.46 ± 2.49	20.0 ± 0.1
Hooge Platen 1	HP 1	3	33.589	379.044	11	-0.70	4	30.41 ± 1.18	37.5 ± 9.3
Hooge Platen 2	HP 2	4	33.703	379.429	11	1.50	1	29.91 ± 1.84	27.3 ± 1.8
Hooge Platen 3	HP 3	5	33.992	380.398	10	1.50	1	30.15 ± 1.84	27.2 ± 3.4
Hooge Platen 4	HP 4	6	34.036	380.545	10	-0.70	4	30.40 ± 1.70	27.7 ± 3.2
Staartse Nol 1	SN 1	7	42.926	381.253	12	0.13	2	27.96 ± 1.36	53.0 ± 10.3
Staartse Nol 2	SN 2	8	42.837	381.189	12	-0.36	3	28.08 ± 1.16	54.9 ± 8.0
Paulinaschor 1	PS 1	9	39.611	374.743	12	1.13	1	27.58 ± 1.72	25.5 ± 3.5
Paulinaschor 2	PS 2	10	39.612	374.893	12	0.33	2	27.87 ± 1.42	48.0 ± 4.0
Paulinaschor 3	PS 3	11	39.612	374.994	12	-0.33	3	27.96 ± 1.50	43.8 ± 4.6
Terneuzense Pas 1	TE 1	12	49.026	373.097	11	0.01	2	25.23 ± 2.08	36.9 ± 3.4
Terneuzense Pas 2	TE 2	13	48.976	373.184	12	-0.32	3	25.87 ± 1.77	27.6 ± 3.3
Terneuzense Pas 3	TE 3	14	48.926	373.271	12	-1.20	4	25.21 ± 1.73	31.4 ± 2.7
Platen van Hulst 1	PH 1	15	54.283	376.249	12	-0.19	3	23.79 ± 1.99	27.2 ± 0.8
Platen van Hulst 2	PH 2	16	54.211	376.341	12	-0.81	4	23.83 ± 2.11	26.9 ± 1.6
Platen van Hulst 3	PH 3	17	54.130	376.443	12	-1.19	4	23.96 ± 1.91	25.8 ± 1.6
Molenplaat 1	MP 1	18	54.994	384.000	11	0.22	2	24.55 ± 1.59	27.9 ± 2.2
Molenplaat 2	MP 2	19	54.907	384.123	11	0.28	2	24.04 ± 1.65	26.2 ± 3.3
Molenplaat 3	MP 3	20	54.732	384.366	11	-0.20	3	24.45 ± 1.86	23.4 ± 1.6
Molenplaat 4	MP 4	21	54.656	384.472	11	-0.55	4	24.27 ± 2.00	22.6 ± 1.9
Molenplaat 5	MP 5	22	55.398	384.461	11	0.03	2	23.00 ± 1.90	35.4 ± 5.5
Molenplaat 6	MP 6	23	55.744	384.709	11	0.14	2	22.64 ± 1.52	27.5 ± 3.4
Baalhoek 1	BH 1	24	61.895	376.325	11	0.64	1	18.32 ± 1.94	41.7 ± 7.7
Baalhoek 2	BH 2	25	61.945	376.435	11	0.67	1	18.82 ± 1.65	30.6 ± 1.8
Baalhoek 3	BH 3	26	61.975	376.510	11	0.50	1	19.05 ± 1.60	25.8 ± 1.6
Konijnenschor 1	KS 1	27	67.350	375.755	8	1.93	1	16.50 ± 2.39	35.0 ± 3.3
Konijnenschor 2	KS 2	28	67.348	375.897	8	2.22	1	16.81 ± 2.40	31.6 ± 3.9
Nauw van Bath 1	NB 1	29	72.357	380.262	12	1.24	1	13.62 ± 2.77	38.9 ± 5.0
Nauw van Bath 3	NB 3	30	72.220	379.886	12	-0.80	4	13.79 ± 2.56	28.5 ± 5.6
Appelzak 1	AZ 1	31	75.195	377.812	12	1.01	1	12.25 ± 3.30	42.3 ± 11.3
Appelzak 3	AZ 3	32	75.016	377.810	12	-0.49	3	12.54 ± 2.97	35.1 ± 5.0

Table 3 (cont.). List of the sampling stations and their main morphological, physical and chemical characteristics (continued). For each variable its mean ± standard deviation are given. Labels are used in statistical and multivariate analyses. Number: station number. N°: number of measurements. Sediment class affiliation: see chapter 3.2.6. Clay, silt, very fine sand, fine and medium sand: sediment volume percentage. Org. C and Org. N: weight percentage.

STATION	LABEL	NUMBER	N°	SEDIMENT CLASS	MEDIAN (µM)	CLAY (%)	SILT (%)	VERY FINE SAND (%)	FINE SAND (%)	MEDIUM SAND (%)	ORG. C (%)	ORG. N (%)
Rammmekenshoek 1	RA 1	1	6	1	304.4 ± 13.8	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.3	26.6 ± 4.7	66.4 ± 4.7	0.04 ± 0.02	0.00 ± 0.00
Rammekenshoek 2	RA 2	2	6	1	306.6 ± 33.6	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.4	29.4 ± 9.1	59.0 ± 5.7	0.03 ± 0.01	0.00 ± 0.00
Hooge Platen 1	HP 1	3	6	2	105.7 ± 29.4	3.1 ± 1.6	22.8 ± 13.4	30.8 ± 1.8	32.8 ± 15.2	9.1 ± 3.9	0.58 ± 0.43	0.04 ± 0.05
Hooge Platen 2	HP 2	4	6	2	127.8 ± 19.1	2.2 ± 0.5	12.3 ± 5.6	34.0 ± 7.4	45.9 ± 12.1	5.0 ± 1.7	0.22 ± 0.05	0.03 ± 0.06
Hooge Platen 3	HP 3	5	6	2	156.1 ± 18.1	1.7 ± 0.3	10.1 ± 3.4	22.0 ± 6.8	53.5 ± 7.9	11.6 ± 2.8	0.22 ± 0.08	0.01 ± 0.01
Hooge Platen 4	HP 4	6	6	2	159.13 ± 16.4	1.7 ± 0.4	9.9 ± 3.3	20.7 ± 5.5	53.1 ± 6.3	13.4 ± 2.8	0.23 ± 0.08	0.00 ± 0.01
Staartse Nol 1	SN 1	7	6	3	125.9 ± 43.8	5.0 ± 2.7	23.8 ± 11.6	20.2 ± 4.1	29.4 ± 7.7	18.9 ± 6.4	1.37 ± 0.38	0.12 ± 0.04
Staartse Nol 2	SN 2	8	6	4	63.5 ± 41.5	11.5 ± 9.3	42.5 ± 15.7	18.3 ± 7.6	15.8 ± 10.0	10.8 ± 7.2	1.78 ± 0.59	0.13 ± 0.05
Paulinaschor 1	PS 1	9	6	1	205.4 ± 14.6	1.8 ± 1.2	8.0 ± 5.8	4.6 ± 2.5	60.2 ± 4.4	25.4 ± 6.2	0.21 ± 0.10	0.01 ± 0.01
Paulinaschor 2	PS 2	10	6	4	88.5 ± 12.3	5.7 ± 2.3	30.8 ± 3.7	26.8 ± 3.0	20.8 ± 3.1	14.7 ± 4.1	1.32 ± 0.29	0.10 ± 0.04
Paulinaschor 3	PS 3	11	6	4	94.2 ± 10.5	4.3 ± 0.9	26.9 ± 3.8	33.9 ± 3.2	23.9 ± 4.8	9.8 ± 1.0	0.95 ± 0.22	0.07 ± 0.02
Terneuzense Pas 1	TE 1	12	6	2	156.0 ± 9.5	3.0 ± 0.9	13.6 ± 3.9	16.3 ± 2.3	56.2 ± 5.6	11.1 ± 2.6	0.49 ± 0.09	0.03 ± 0.02
Terneuzense Pas 2	TE 2	13	6	2	191.2 ± 13.3	2.6 ± 1.1	10.4 ± 4.7	5.8 ± 2.1	61.8 ± 3.7	19.2 ± 4.4	0.30 ± 0.11	0.01 ± 0.02
Terneuzense Pas 3	TE 3	14	6	2	162.7 ± 6.0	3.3 ± 0.5	14.5 ± 1.7	13.5 ± 2.5	56.2 ± 5.1	12.2 ± 2.4	0.40 ± 0.13	0.01 ± 0.01
Platen van Hulst 1	PH 1	15	6	1	162.5 ± 7.2	1.0 ± 0.1	2.8 ± 0.6	17.5 ± 3.2	69.7 ± 2.6	8.9 ± 2.8	0.15 ± 0.02	0.00 ± 0.00
Platen van Hulst 2	PH 2	16	6	1	172.1 ± 9.7	1.1 ± 0.1	3.2 ± 0.7	13.8 ± 3.8	68.2 ± 2.1	13.4 ± 3.6	0.15 ± 0.03	0.00 ± 0.00
Platen van Hulst 3	PH 3	17	6	1	171.0 ± 10.1	0.9 ± 0.2	2.5 ± 0.4	14.6 ± 4.0	69.2 ± 1.8	12.6 ± 3.5	0.13 ± 0.03	0.00 ± 0.00
Molenplaat 1	MP 1	18	6	3	120.9 ± 17.9	3.7 ± 0.8	18.1 ± 3.7	30.8 ± 6.6	39.2 ± 7.9	7.7 ± 2.6	0.44 ± 0.10	0.03 ± 0.02
Molenplaat 2	MP 2	19	6	2	143.7 ± 19.3	2.9 ± 1.3	11.1 ± 3.2	25.0 ± 7.4	50.4 ± 7.0	10.1 ± 5.0	0.26 ± 0.06	0.00 ± 0.01
Molenplaat 3	MP 3	20	6	1	186.4 ± 12.1	0.7 ± 0.1	2.1 ± 0.3	10.3 ± 2.6	66.1 ± 3.9	20.1 ± 5.4	0.10 ± 0.03	0.00 ± 0.00
Molenplaat 4	MP 4	21	6	1	183.0 ± 13.7	0.3 ± 0.3	1.1 ± 1.2	10.5 ± 3.8	72.8 ± 4.6	15.4 ± 6.6	0.09 ± 0.02	0.00 ± 0.00
Molenplaat 5	MP 5	22	6	3	99.2 ± 8.5	4.1 ± 0.9	24.1 ± 4.9	35.4 ± 4.3	28.1 ± 4.4	7.5 ± 3.3	0.75 ± 0.24	0.04 ± 0.02
Molenplaat 6	MP 6	23	6	2	160.6 ± 25.8	2.4 ± 0.6	11.4 ± 4.4	18.6 ± 8.3	51.6 ± 10.0	15.3 ± 5.3	0.36 ± 0.15	0.01 ± 0.01
Baalhoek 1	BH 1	24	5	4	86.8 ± 8.0	5.9 ± 1.1	31.7 ± 3.7	30.7 ± 3.5	23.2 ± 2.4	6.3 ± 3.2	1.24 ± 0.39	0.07 ± 0.05
Baalhoek 2	BH 2	25	5	2	119.8 ± 2.4	2.6 ± 0.6	10.4 ± 3.7	42.5 ± 2.6	41.4 ± 3.4	2.7 ± 1.9	0.35 ± 0.15	0.01 ± 0.01
Baalhoek 3	BH 3	26	5	1	143.0 ± 4.3	1.2 ± 0.2	4.3 ± 1.1	27.6 ± 3.0	65.4 ± 4.4	1.4 ± 0.5	0.16 ± 0.02	0.00 ± 0.00
Konijnenschor 1	KS 1	27	4	3	95.7 ± 12.5	3.9 ± 1.4	23.7 ± 5.4	42.2 ± 3.2	26.8 ± 6.7	2.4 ± 1.4	0.62 ± 0.28	0.04 ± 0.01
Konijnenschor 2	KS 2	28	4	4	116.1 ± 32.4	3.6 ± 1.9	20.5 ± 10.5	27.7 ± 8.6	41.9 ± 20.8	5.4 ± 1.3	0.60 ± 0.35	0.02 ± 0.03
Nauw van Bath 1	NB 1	29	6	4	84.1 ± 7.4	3.9 ± 1.2	28.5 ± 7.5	43.4 ± 9.4	16.8 ± 1.4	5.6 ± 2.9	1.07 ± 0.53	0.06 ± 0.04
Nauw van Bath 3	NB 3	30	6	1	158.4 ± 21.9	1.9 ± 1.0	11.0 ± 9.3	18.8 ± 3.6	54.7 ± 10.3	14.3 ± 5.1	0.57 ± 0.53	0.00 ± 0.01
Appelzak 1	AZ 1	31	6	3	121.6 ± 48.8	3.5 ± 1.8	26.5 ± 15.6	19.2 ± 5.6	40.3 ± 20.2	9.6 ± 3.0	1.07 ± 1.06	0.06 ± 0.09
Appelzak 3	AZ 3	32	6	3	106.2 ± 11.6	3.2 ± 0.8	18.8 ± 5.1	41.6 ± 7.6	30.4 ± 6.2	4.5 ± 6.9	0.65 ± 0.34	0.03 ± 0.01

Table 4. List of monthly sampling periods and the transects that could not be sampled due to adverse weather or unfavourable tides.

MONTH	PERIOD	TRANSECTS NOT SAMPLED
October (1991)	2/10-31/10	Baalhoek, Konijnenschor
November	25/11-29/11	
January (1992)	7/1-13/1	
February	7/2-13/2	Konijnenschor
March	6/3-12/3	
April	6/4-10/4	Konijnenschor
May	5/5-8/5	Konijnenschor
June	2/6-9/6	
July	2/7-8/7	
August	29/7-3/8	Hooge Platen
September	14/9-18/9	
October	14/10-20/10	Molenplaat

Table 5. Wenthworth grade scale for sediment size classes (cf. Buchanan & Kain 1971)

SEDIMENT FRACTION	GRAIN SIZE (μM)
Clay	< 4
Silt	4-63
Very fine sand	63-125
Fine sand	125-250
Medium sand	250-500
Coarse sand	500-1000

Table 6. Sediment (SC) and elevation class (EC) affiliation of the 32 sampling stations. MTL = Mean Tidal Level. The percentages of the sediment classes refer to the sum of the clay and silt percentages. For more details, see chapter 3.2.6. For abbreviations of sampling stations, see Table 3.

	SC 1 (< 10 %)	SC 2 (10-20 %)	SC 3 (20-30 %)	SC 4 (> 30 %)
EC 1 (> +0.5 MTL)	RA 1-2 PS 1 BH 3	HP 2-3 BH 2	KS 1 AZ 1	BH 1 KS 2 NB 1
EC 2 (+0.5 - 0 MTL)		TE 1 MP 2, 6	SN 1 MP 1, 5	PS 2
EC 3 (0 - -0.5 MTL)	PH 1 MP 3	TE 2	AZ 3	SN 2 PS 3
EC 4 (< -0.5 MTL)	PH 2-3 MP 4 NB 3	HP 1, 4 TE 3		

Table 7. Summary table of explanatory environmental variables. N: number of measurements; Distribution: frequency distribution type was visually checked by plotting the frequency distribution histograms of each variable. Transformations were used in the correlation and multivariate analysis. For more details, see text.

PARAMETER	LABEL	N	UNIT	DISTRIBUTION	TRANSFORMATION	REMARKS
Climatic						
Air temperature	TCMO	360	°C	uniform	none	average month preceding sampling
	TCWE	360	°C	± normal	none	average week preceding sampling
Irradiance	RAMO	360	J/cm²	trimodal	none	total month preceding sampling
	RAWE	360	J/cm²	uniform	none	total week preceding sampling
Wind speed	WIWE	360	m/s	± normal	none	average week preceding sampling
	WIMA	360	m/s	± normal	none	maximum week preceding sampling
Precipitation	PREC	360	mm	± normal	none	total month preceding sampling
Water column						
Temperature	TCWC	360	°C	trimodal	none	
Salinity	SAWC	360	‰	slightly skewed	log (x+1)	
Transparency	DOZI	360	dm	slightly skewed	log (x+1)	
Sediment-physical						
median grain size	MEDI	185	µm	slightly skewed	log (x+1)	
clay	CLAY	185	sediment volume percentage	higly skewed	log (x+1)	
silt	SILT	185	"	highly skewed	log (x+1)	
very fine sand	VFSA	185	"	slightly skewed	log (x+1)	
fine sand	FSAN	185	"	± bimodal	none	
medium sand	MSAN	185	"	highly skewed	log (x+1)	
coarse sand	CSAN	185	"	highly skewed	log (x+1)	
water content	WACO	360	weight percentage	slightly skewed	log (x+1)	
Sediment-chemical						
Interstitial water salinity	SAIS	360	‰	slightly skewed	log (x+1)	
Organic carbon	ORGC	185	weight percentage	highly skewed	log (x+1)	
Organic nitrogen	ORGN	185	"	highly skewed	log (x+1)	
Morphology						
Elevation	ELCO	360	m	± normal	none	Height is given in relation to Mean Tidal Level

Table 8. Summary information on the different species data sets used in the statistical and multivariate analyses. See chapter 5.3.1. for more information. RA = relative abundance.

DATA SET (DS)	N° TAXA	N° SAMPLES	REMARKS
DS 0	293	360	original data matrix
DS 1	293	185	reduction n° samples
DS 2	193	185	elimination spp. < 3 occ. + plankton
DS 3	89	185	elimination spp. that do not reach RA > 2 % in at least one sample + some tychoplankton
DS 4	45	185	only epipelon
DS 5	44	185	only epipsammon

Table 9. Different sets of explanatory variables used in the variation partitioning analyses (see chapter 3.6.4.2.). a→c refers to the subsets that were used in some approaches to assess their contribution to explaining the variation in the species data and the amount of covariation between them.

1.	**Physical-chemical**	a	Sediment characteristics (grain size fractions; water content; organic C and N)
		b	Salinity (ISW + WC); Transparancy (WC)
		c	Elevation
2.	**Climatic**		Different measures of irradiance, temperature (air + WC) and wind; precipitation
3.	**Temporal**		Sampling month (dummy variable)
4.	**Spatial**		Terms from cubic trend surface regression

Table 10. List of temporal (dummy) and spatial variables used in the multivariate analyses. See chapter 3.6.4.2. for more details.

VARIABLE		LABEL
Temporal		
	October 1991	OAMO
	January 1992	JAMO
	March 1992	MRMO
	May 1992	MAMO
	July 1992	JLMO
	September 1992	SEMO
Spatial		
	x	SP01
	y	SP02
	x^2	SP03
	xy	SP04
	y^2	SP05
	x^3	SP06
	x^2y	SP07
	xy^2	SP08
	y^3	SP09

Table 12. Range in total cell numbers and cell numbers of epipelon, epipsammon and the different life forms (1-7, cf. chapter 3.4.3.) during the sampling period (October 1991 - October 1992).

LIFE FORM	CELL NUMBER RANGE (CELLS X 10^6 CELLS/G SDW)
Total	0.70 - 120.00
Epipsammon	0.30 - 67.70
Epipelon	0.10 - 100.50
Adnate	0.07 - 31.40
Stalked	0.03 - 37.31
Motile < 10 µm	0.00 - 8.10
Motile 10-20 µm	0.00 - 16.83
Motile > 20 µm	0.00 - 23.39
Tychoplankton	0.02 - 91.02
Interstitial	0.00 - 0.44

Table 11. Pearson correlation matrix of environmental variables (n = 360, Medi→OrgN: n = 185; *** = p ≤ 0.001, ** = p ≤ 0.01, * = p ≤ 0.05). For abbreviations of environmental variables, see Table 7.

	Elev	Sawc	Sais	Tewc	Dozl	Waco	Ramo	Rawe	Tcmo	Tcwe	Wiwe	Wima	Prec	Medi	Clay	Silt	Vfsa	Fsan	Msan	Csan	OrgC	OrgN
Elev	1.00																					
Sawc	-0.12*	1.00																				
Sais	-0.14**	0.93***	1.00																			
Tewc	0.01	0.00	0.00	1.00																		
Dozi	-0.07	0.43***	0.42***	0.61***	1.00																	
Waco	0.04	-0.06	-0.12*	-0.04	-0.06	1.00																
Ramo	0.00	0.01	0.01	0.89***	0.61***	-0.03	1.00															
Rawe	0.00	-0.02	-0.03	0.74***	0.50***	0.02	0.90***	1.00														
Tcmo	0.00	0.12*	0.11*	0.98***	0.66***	-0.05	0.84***	0.68***	1.00													
Tcwe	-0.01	0.06	0.06	0.93***	0.61***	-0.03	0.93***	0.80***	0.91***	1.00												
Wiwe	0.01	-0.07	-0.09	-0.44***	-0.22***	-0.04	-0.53***	-0.52***	-0.42***	-0.42***	1.00											
Wima	0.00	-0.13*	-0.13*	-0.10*	-0.12*	-0.04	0.02	0.15**	-0.17**	0.01	0.39***	1.00										
Prec	0.01	0.05	-0.01	0.41***	0.35***	0.00	0.30***	0.22***	0.46***	0.38***	-0.14**	-0.36***	1.00									
Medi	-0.09	0.19**	0.22**	-0.08	0.05	-0.80***	-0.07	-0.08	-0.05	-0.06	0.11	0.04	-0.01	1.00								
Clay	0.10	-0.09	-0.16*	0.15*	0.05	0.81***	0.12	0.10	0.13	0.12	-0.12	-0.10	0.09	-0.87***	1.00							
Silt	0.14	-0.17*	-0.22**	0.09	-0.02	0.79***	0.05	0.05	0.07	0.06	-0.09	-0.10	0.03	-0.82***	0.95***	1.00						
Vfsa	0.04	-0.35***	-0.35***	0.05	-0.16*	0.48***	0.01	0.02	0.01	0.00	-0.04	-0.07	0.01	-0.66***	0.63***	0.73***	1.00					
Fsan	-0.33***	0.01	0.05	-0.06	0.02	-0.66***	-0.04	-0.07	-0.04	-0.05	0.09	0.06	0.01	0.60***	-0.58***	-0.56***	-0.19*	1.00				
Msan	-0.13	0.45***	0.46***	-0.10	0.19*	-0.27***	-0.07	-0.08	-0.04	-0.06	0.03	-0.05	-0.05	0.66***	-0.52***	-0.53***	-0.78***	0.14	1.00			
Csan	0.18*	0.04	0.05	0.00	-0.04	0.14	-0.01	0.00	-0.01	0.01	-0.03	0.03	-0.03	0.08	-0.11	-0.12	-0.34***	-0.58***	0.37***	1.00		
OrgC	0.10	-0.12	-0.19**	0.06	-0.02	0.94***	0.06	0.07	0.04	0.04	-0.09	-0.03	0.00	-0.80***	0.83***	0.80***	0.44***	-0.71***	-0.26***	0.18*	1.00	
OrgN	0.12	0.02	-0.04	0.10	0.14	0.86***	0.16*	0.21**	0.07	0.09	-0.13	-0.02	0.03	-0.71***	0.71***	0.64***	0.27***	-0.65***	-0.16*	0.18*	0.88***	1.00

Table 13. Pearson product-moment correlation matrix between cell numbers [all log(x+1) transformed]/Hill diversity indices and sediment characteristics [all log(x+1) transformed except fine sand](n=185, *** = $p \leq 0.001$, ** = $p \leq 0.01$, $p \leq 0.05$). For abbreviations of environmental variables, see Table 7. Total: total cell numbers; Epipsa: epipsammic cell numbers; Epipel: epipelic cell numbers; the next 7 abbreviations refer to life-forms 1-7 (see chapter 3.4.3.).

	MEDI	CLAY	SILT	VFSA	FSAN	MSAN	CSAN	ORGC	ORGN
Total	-.625***	.716***	.711***	.594***	-.245***	-.464***	-.279***	.632***	.511***
Epipsa	-.053	.080	.049	.161*	.254***	-.225**	-.334***	.007	-.035
Epipel	-.735***	.883***	.910***	.659***	-.471***	-.466***	-.136	.775***	.621***
Adnate	.013	-.004	-.049	.090	.299***	-.169*	-.316***	-.056	-.103
Stalked	-.247***	.326***	.322***	.338***	.078	-.368***	-.340***	.210**	.135
Mot<10	.140	-.156*	-.191**	-.049	.286***	-.037	-.146*	-.217**	-.195**
Mot10-20	-.141	.144*	.189**	.231**	-.050	-.255***	-.066	.123	.074
Mot>20	-.580***	.652***	.707***	.671***	-.169*	-.529***	-.303***	.520***	.381***
Tychopl	-.738***	.894***	.932***	.700***	-.443***	-.482***	-.177*	.756***	.596***
Interstit	.322***	-.373***	-.408***	-.257***	.284***	.144*	-.014	-.366***	-.269***
N_0	.143	-.107	-.083	.093	.410***	-.074	-.366***	-.323***	-.306***
N_1	.478***	-.473***	-.490***	-.319***	.523***	.207**	-.207**	-.552***	-.451***
N_2	.513***	-.517***	-.542***	-.392***	.508***	.259***	-.148*	-.541***	-.433***
$N_{+\infty}$	.434***	-.427***	-.448***	-.323***	.434***	.231**	-.117	-.434***	-.343***

Table 14. Pearson product-moment correlation matrix between cell numbers [all log(x+1) transformed]/Hill diversity indices and environmental variables [Elev, Sawc, Sais, Tran and Waco log(x+1) transformed](n=360, *** = $p \leq 0.001$, ** = $p \leq 0.01$, $p \leq 0.05$). For abbreviations of environmental variables, see Table 7; for other abbreviations, see Table 13.

	ELEV	SAWC	SAIS	TCWC	TRAN	WACO	RAMO	RAWE	TCMO	TCWE	WIWE	WIMA	PREC
Total	.008	-.232***	-.341***	.237***	.089	.626***	.244***	.219***	.197***	.230***	-.114*	.012	.040
Epipsa	.019	-.153**	-.305***	.187***	.050	.014	.147**	.138**	.172***	.178***	-.022	.025	.058
Epipel	.082	-.219***	-.265***	.174**	.062	.747***	.196***	.179***	.132*	.165**	-.133*	-.016	.022
Adnate	-.032	-.158**	-.296***	.162**	.014	-.056	.134*	.123*	.148**	.162**	-.045	.019	.039
Stalked	.089	-.168***	-.346***	.170***	.038	.232***	.114*	.103*	.153**	.148**	.020	.018	.067
Mot<10	-.043	-.015	-.056	.071	.048	-.213***	.045	.051	.072	.075	.010	.044	.055
Mot10-20	.213***	-.299***	-.374***	.308***	.132**	.149**	.348***	.342***	.246***	.312***	-.127*	.123*	.089
Mot>20	.086	-.326***	-.350***	.074	-.042	.521***	.141**	.178***	.022	.087	-.155**	.050	-.071
Tychopl	.049	-.195***	-.229***	.127*	.035	.742***	.133*	.110*	.094	.117*	-.099	-.045	.035
Interstit	-.049	.108*	.108*	.131*	.127*	-.372***	.128*	.127*	.145**	.131*	-.069	-.031	.091
N_0	.023	.108*	.164**	-.118*	.059	-.356***	-.085	-.061	-.093	-.109*	-.019	-.047	.038
N_1	.031	.270***	.292***	-.224***	.060	-.509***	-.178***	-.083	-.178***	-.191***	.025	-.003	-.046*
N_2	.017	.302***	.297***	-.239***	.063	-.479***	-.190***	-.093	-.191***	-.203	.042	.013	-.073
$N_{+\infty}$	.015	.308***	.284***	-.232***	.063	-.350***	-.195***	-.091	-.187***	-.204***	.043	.006	-.052

Table 15. Pearson product-moment correlation matrix between cell numbers [different measures, all log(x+1) transformed]/Hill diversity indices (n=360, *** = $p \leq 0.001$, ** = $p \leq 0.01$, $p \leq 0.05$). For abbreviations, see Table 13.

	N_0	N_1	N_2	$N_{+\infty}$	TOTAL	EPIPSA	EPIPEL	ADNATE	STALKD	MOT<10	MOT10-20	MOT>20	TYCHOP
N_1	.700***												
N_2	.514***	.953***											
$N_{+\infty}$	.388***	.802***	.914***										
Total	-.149**	-.383***	-.366***	-.300***									
Epipsa	.114*	.173***	.206***	.166**	.615***								
Epipel	-.118*	-.494***	-.526***	-.426***	.852***	.170***							
Adnate	.122*	.198***	.231***	.183***	.537***	.969***	.081						
Stalked	.027	-.000	.035	.041	.753***	.908***	.417***	.809***					
Mot<10	.239***	.320***	.325***	.286***	.132*	.514***	-.137**	.478***	.380***				
Mot10-20	.037	-.040	-.048	-.055	.551***	.474***	.419***	.430***	.492***	.204***			
Mot>20	.070	-.268***	-.323***	-.273***	.709***	.241***	.783***	.170***	.408***	-.033	.406***		
Tychopl	-.071	-.487***	-.534***	-.430***	.809***	.123*	.982***	.035	.379***	-.159**	.319***	.768***	
Interstit	.270***	.401***	.380***	.299***	-.221***	.133*	-.368***	.174***	-.032	.232***	.030	-.277***	-.395***

Table 16. Seasonal type affiliation of the 32 sampling stations. Seasonal type refers to the type of temporal trend in the species data of the 32 sampling stations. For more details, see chapter 5.2.3.

TRANSECT	SEASONAL TYPE 1	SEASONAL TYPE 2	SEASONAL TYPE 3	SEASONAL TYPE 4
Rammekenshoek	RA 1-2			
Hooge Platen		HP 2		HP 1,3-4
Staartse Nol				SN 1-2
Paulinaschor		PS 1		PS 2-3
Terneuzense Pas		TE 1	TE 2	TE 3
Platen van Hulst		PH 1-3		
Molemplaat	MP 3-4		MP 6	MP 1-2, 5
Baalhoek		BH 2-3		BH 1
Konijnenschor		KS 1	KS 2	
Nauw van Bath		NB 1, 3		
Appelzak				AZ 1, 3

Table 17. Summary table of means of selected environmental variables (median grain size (MGS), silt and water content (WACO) of the sediment) for the 4 seasonal types (S.T.)[s.d. = standard deviation; N_a = number of samples for median grain size and silt; N_b = number of samples for water content). For more details, see chapter 5.2.3. For more information on the environmental variables, see Table 7.

S.T.	N_A	M.G.S (µM)		SILT (%)		N_B	WACO (%)	
		mean	s.d.	mean	s.d.		mean	s.d.
1	24	245.1	64.6	0.8	1.1	46	21.2	2.3
2	62	146.7	36.0	10.7	9.3	124	29.7	5.5
3	16	161.0	37.3	13.3	7.4	31	28.6	3.8
4	84	117.8	37.6	21.9	11.9	159	38.4	11.2

Table 18. Checklist and classification of the diatom taxa from the Westerschelde estuary observed in the period Oct. 1991-Oct. 1992. The first column gives the 1st ecological category (1: epipelon; 2: epipsammon; nr: not relevant), the second column the 2nd ecological category (9 life-forms: 1: adnate; 2: stalked; 3: motile < 10 µm; 4: motile 10-20 µm; 5: motile > 20 µm; 6: tychoplanktonic; 7: interstitial; 8: euplanktonic; 9: epiphytic). The third column refers to the different data sets a taxon belongs to (1: data set 1; 2: data sets 1 and 2; 3: data sets 1, 2 and 3. For more information on the data sets, see chapter 5.3.1. and Table 8). The fourth column gives the taxon labels; taxa without label were not observed during the cell counts and therefore do not occur in the ecological analyses. Taxa indicated with an asterisk are not treated in the systematical part (chapter 4.2.). (?) = the exact classification of this taxon is as yet unknown.

DIVISIO BACILLARIOPHYTA

Class COSCINODISCOPHYCEAE

Subcl. **THALASSIOSIROPHYCIDAE**

Ordo *THALASSIOSIRALES* Glezer & Makarova

Fam. **Thalassiosiraceae** Lebour

Thalassiosira angulata	2	6	2	THAL ANGU
Thalassiosira bramaputrae	2	6	2	THAL BRAM
Thalassiosira curviseriata	2	6	2	THAL CURV
Thalassiosira decipiens	2	6	3	THAL DECI
Thalassiosira eccentrica	2	8	2	THAL ECCE
Thalassiosira leptopa	2	8	2	THAL LEPT
Thalassiosira nordenskioeldii	2	8	1	THAL NORD
Thalassiosira proschkinae	2	6	2	THAL PROS
Thalassiosira cf. *simplex*	2	6	1	THAL CFSI
Thalassiosira tenera	2	6	2	THAL TENE

Fam. **Skeletonemataceae** Lebour

Skeletonema spp.*	2	8	1	SKEL SPEC

Fam. **Stephanodiscaceae** Glezer & Makarova

Cyclotella atomus	2	6	2	CYCL ATOM
Cyclotella cf. *caspia*	2	6	2	CYCL CFCA
Cyclotella choctawhatcheeana	2	6	2	CYCL CHOC
Cyclotella meneghiniana	2	6	2	CYCL MENE
Cyclotella radiosa	2	8	1	CYCL RADI
Cyclotella scaldensis	2	6	3	CYCL MENE
Cyclotella striata	2	6	2	CYCL STRI
Cyclotella sp. 1	2	6	2	CYCL SP01
Cyclotella sp. 2	2	6	2	CYCL SP02
Cyclotella sp. 3*	2	6	2	CYCL SP03
Cyclotella sp. 4*	2	6	1	CYCL SP04
Cyclostephanos dubius (Fricke) Round*	2	8	1	CYST DUBI
Stephanodiscus hantzschii Grunow*	2	8	1	STEP HANT
Stephanodiscus medius Håkansson*	2	8	1	STEP MEDI
Stephanodiscus parvus Grunow*	2	8	1	STEP PARV
(?) *Thalassiocyclus lucens*	2	6	1	STEP LUCE

Subcl. **COSCINODISCOPHYCIDAE**
Ordo *MELOSIRALES* Crawford
Fam. **Melosiraceae** Kützing

Melosira nummuloides	2	6	1	MELO NUMM

Fam. **Hyalodiscaceae** Crawford

Podosira stelliger	2	6	2	PODO STEL

Ordo. *PARALIALES* Crawford
Fam. **Paraliaceae** Crawford

Paralia sulcata	2	6	3	PARA SULC
(?) *Pseudopodosira westii*	2	6	2	PSEU WEST

Ordo *AULACOSEIRALES* Crawford
Fam. **Aulacoseiraceae** Crawford

Aulacoseira ambigua	2	8	1	AULA AMBI
Aulacoseira granulata	2	8	1	AULA GRAN

Ordo *COSCINODISCALES* Round & Crawford
Fam. **Coscinodiscaceae** Kützing

Coscinodiscus denarius A. Schmidt*	2	8	1	COSC DENA
Coscinodiscus jonesianus (Greville) Ostenfeld*	2	8	1	COSC JONE
Coscinodiscus marginatus Ehrenberg*	2	8	1	COSC MARG

Fam. **Aulacodiscaceae** (Schütt) Lemmermann

Aulacodiscus argus	2	6	1	AULA ARGU

Fam. **Hemidiscaceae** Hendey emend. Simonsen

Actinocyclus normanii f. *normanii*	2	8	1	ACTI NONO
Actinocyclus normanii f. *subsalsus*	2	8	1	ACTI NOSU
Actinocyclus octonarius	2	6	1	ACTI OCTO

Fam. **Heliopeltaceae** H. L. Smith

Actinoptychus senarius	2	6	2	ACTP SENA
Actinoptychus splendens	2	6	1	ACTP SPLE

Subcl. **BIDDULPHIOPHYCIDAE**
Ordo *TRICERATIALES* Round & Crawford
Fam. **Triceratiaceae** (Schütt) Lemmermann

Auliscus sculptus	2	6	1	AULI SCUL
Cerataulus radiatus	2	6	2	CERA RADI
Odontella aurita	2	6	3	ODON AURI
Odontella rhombus	2	6	2	ODON RHOM
Odontella rostrata	2	6	2	ODON ROST
Triceratium favus	2	6	1	TRIC FAVU

Fam. **Plagiogrammaceae** De Toni

Dimeregramma minor	1	2	3	DIME MINO
Plagiogramma staurophorum	1	2	3	PLAG STAU

Ordo *BIDDULPHIALES* Krieger
Fam. **Biddulphiaceae** Kützing

Biddulphia alternans	2	6	2	BIDD ALTE

Ordo *ANAULALES* Round & Crawford
Fam. **Anaulaceae** (Schütt) Lemmermann

Anaulus uniseptatus	2	7	2	ANAU UNIS
Eunotogramma dubium	1	2	3	EUNO DUBI

Subcl. **LITHODESMIOPHYCIDAE**
Ordo *LITHODESMIALES* Round & Crawford
Fam. **Lithodesmiaceae** Round

Lithodesmium undulatum	2	8	1	LITH UNDU

Subcl. **CYMATOSIROPHYCIDAE**
Ordo *CYMATOSIRALES* Round & Crawford
Fam. **Cymatosiraceae** Hasle, von Stosch & Syvertsen

Brockmaniella brockmannii	2	6	3	BROC BROC
Campylosira cymbelliformis	2	6	2	CAMP CYMB
Cymatosira belgica	2	6	3	CYMA BELG
Cymatosira sp. 1	2	7	3	CYMA SP01
Leyanella arenaria	2	7	3	CYMA SP01
Plagiogrammopsis minimum	2	7	3	PLAG MINI
Plagiogrammopsis sigmoideum	2	6	3	PLAG SIGM
Plagiogrammopsis vanheurckii	2	6	3	PLAG VANH
Plagiogrammopsis sp. 1*	2	6	3	PLAG SP01
Incertae sedis sp. 1	2	6	3	BROC SP01

Class FRAGILARIOPHYCEAE

Subcl. **FRAGILARIOPHYCIDAE**
Ordo *FRAGILARIALES* Silva
Fam. **Fragilariaceae** Greville

Ctenophora pulchella	nr	9	1	CTEN PULC
Fragilaria cf. *atomus*	1	2	3	FRAG CFAT
Fragilaria capensis	1	2	3	FRAG CAPE
Fragilaria capucina	2	6	2	FRAG CAPU
Fragilaria cassubica Witkowski*				(No Label)
Fragilaria eichornii	1	2	2	OPEP SPEA
Fragilaria cf. *gedanensis*	1	2	3	FRAG CFAT
Fragilaria schulzii	1	2	3	FRAG SCHU
Fragilaria cf. *subsalina*	1	2	3	FRAG CFAT
Fragilaria sp. 1	2	6	3	FRAG SP01

Fragilaria sp .2				(No Label)
Fragilariforma virescens	nr	9	1	FRAG VIRE
Martyana martyii	1	2	3	MART MART
Meridion circulare	nr	9	1	MERI CIRC
Opephora guenter-grassii	1	2	3	OPEP GUEN
Opephora marina	1	2	1	OPEP MARI
Opephora mutabilis	1	2	3	OPEP MUTA
Opephora naveana	1	2	3	OPEP MUTA
Opephora pacifica	1	2	2	OPEP PACI
Opephora sp. 1	1	2	3	OPEP SP01
Pseudostaurosira brevistriata	nr	9	2	PSEU BREV
Pseudostaurosira perminuta	1	2	3	PSEU PERM
Staurosira construens	2	6	2	STAU CONS
Staurosira construens var. *binodis* (Ehrenberg) Grunow*				(No Label)
Staurosira construens f. *triundulata*	2	6	1	STAU COTR
Synedra acus	nr	9	1	SYNE ACUS
Synedra ulna	nr	9	1	SYNE ULNA
Tabularia fasciculata	nr	9	2	SYNE FASC

Ordo *RHAPHONEIDALES* Round
Fam. **Rhaphoneidaceae** Forti

Delphineis minutissima	2	6	3	DELP MINU
Delphineis surirella	2	6	3	DELP SURI
Delphineis surirella var. *australis*	2	6	2	DELP SUAU
Rhaphoneis amphiceros	2	6	3	RHAP AMPH

Ordo *THALASSIONEMATALES* Round
Fam. **Thalassionemataceae** Round

Thalassionema nitzschioides	2	6	2	THAL NITZ

Class BACILLARIOPHYCEAE
Subcl. **BACILLARIOPHYCIDAE**
Ordo *LYRELLALES* Mann
Fam. **Lyrellaceae** Mann

Lyrella atlantica (A. Schmidt) Mann*	2	5	1	LYRE CATL
Petroneis humerosa	2	5	1	PETR HUME

Ordo *MASTOGLOIALES* Mann
Fam. **Mastogloiaceae** Mereschkowsky

Mastogloia pumila (Cleve & Möller) Cleve*	2	5	1	MAST PUMI

Ordo *CYMBELLALES* Mann
Fam. **Rhoicospheniaceae** Chen & Zhu

Rhoicosphenia abbreviata (Agardh) Lange-Bertalot*	nr	9	1	RHOI ABBR

Fam. **Anomoeoneidaceae** Mann

(?) *Dickieia subinflata*	2	5	2	DICK SUBI
(?) *Dickieia* sp. 1	2	5	2	DICK SP01

Staurophora salina	2	5	3	STAU SALI

Fam. **Cymbellaceae** Greville

Cymbella spp.*	nr	9	1	CYMB SPEC
Placoneis clementis	2	5	2	PLAC CLEM
Placoneis elginensis (Gregory) Cox*	2	5	1	PLAC ELGI

Fam. **Gomphonemataceae** Kützing

Gomphonema spp.*	nr	9	2	GOMP ANPA

Ordo *ACHNANTHALES* Silva

Fam. **Achnanthaceae** Kützing

Achnanthes amoena	1	1	3	ACHN AMOE
Achnanthes bahusiensis	1	3	2	ACHN CFBA
Achnanthes cf. *bremereyi*	1	3	2	ACHN CFBA
Achnanthes brevipes	1	2	1	ACHN BREV
Achnanthes lemmermannii var. obtusa	1	3	2	ACHN CFBA
Achnanthes parvula	1	2	1	ACHN PARV
Achnanthes submarina	1	1	1	ACHN SUBM
Achnanthes sp. 1	1	2	2	ACHA SP01

Fam. **Cocconeidaceae** Kützing

Anorthoneis cf. *pulex*	1	1	3	ANOR SPEC
Anorthoneis cf. *tenuis*	1	1	3	ANOR SPEC
Anorthoneis vortex	1	1	3	ANOR SPEC
Cocconeis disculus (Schumann) Cleve*	1	1	1	COCC DISC
Cocconeis pediculus Ehrenberg*				(No Label)
Cocconeis peltoides	1	1	3	COCC PELT
Cocconeis pinnata Gregory*				(No Label)
Cocconeis cf. *placentula*	1	1	3	COCC CFPL
Cocconeis placentula var. *euglypta*	1	1	3	COCC PLEU
Cocconeis scutellum Ehrenberg*	1	9	2	COCC SCUT
Cocconeis scutellum var. *parva* (Grunow) Cleve*				(No Label)
Cocconeis stauroneiformis	1	9	1	COCC STAU
Cocconeis sp. 1	1	1	3	COCC SP01
Cocconeis sp. 2	1	1	3	COCC SP02
Cocconeis sp. 3	1	1	2	COCC SP03
Cocconeis sp. 4	1	1	2	COCC SP04
Cocconeis sp. 5	1	1	2	COCC SP05
Cocconeis sp. 6*	1	1	1	COCC SP06

Fam. **Achnanthidiaceae** Mann

Achnanthidium delicatulum	1	1	3	ACHN DELI
Achnanthidium lanceolatum	1	1	2	ACHN LANC
Achnanthidium minutissimum Kützing*	nr	9	2	ACHN MINU
Achnanthidium sp. 1	1	1	3	ACHN SP01
Achnanthidium sp. 2	1	1	3	ACHN SP02
Achnanthidium sp. 3	1	1	3	ACHN SP03
Achnanthidium sp. 4	1	1	3	ACHN SP04

Ordo *NAVICULALES* Bessey

Subordo NEIDIINEAE Mann

Fam. **Berkeleyaceae** Mann

Berkeleya rutilans	2	5	3	BERK RUTI
Lunella sp. 1	1	3	3	NADI SP05
Parlibellus berkeleyi (Kützing) Cox*	2	5	1	PARL BERK
Parlibellus plicatus				(No Label)
Parlibellus sp. 1	2	5	3	PARL SP01
Parlibellus sp. 2	2	5	3	PARL SP02

Fam. **Diadesmidaceae** Mann

Luticola cohnii	2	4	2	LUTI MUTI
Luticola mutica	2	4	2	LUTI MUTI

Fam. **Scoliotropidaceae** Mereschkowsky

Biremis ambigua	2	5	2	BIRE AMBI
Biremis lucens	1	1	3	BIRE LUCE
Biremis sp. 1	2	3	2	BIRE SP01

Subordo SELLAPHORINEAE Mann

Fam. **Sellaphoraceae** Mereschkowsky

Fallacia aequorea	1	1	3	FALL AEQU
Fallacia amphipleuroides				(No Label)
Fallacia cryptolyra	1	1	3	FALL CRYP
Fallacia florinae	1	1	1	FALL FLOR
Fallacia forcipata	2	5	2	FALL FORC
Fallacia pygmea				(No Label)
Fallacia tenera	2	3	3	FALL TENE
Fallacia sp. 1	1	1	2	FALL SP01
Fallacia sp. 2	1	1	3	FALL SP02
Fallacia sp. 3	1	1	3	FALL SP03
Fallacia sp. 4	1	1	2	FALL SP04
Sellaphora pupula	2	5	1	SELL PUPU

Fam. **Pinnulariaceae** Mann

Caloneis amphisbaena f. *subsalina*	2	5	2	CALO AMSU
Caloneis africana/*C. crassa*	2	5	2	CALO CRAS
Pinnularia cruciformis	2	5	1	PINN CRUC
Pinnularia krookiformis	2	5	1	PINN KROO
Pinnularia stauntonii	2	5	1	PINN CSTA

Subordo DIPLONEIDINEAE Mann

Fam. **Diploneidaceae** Mann

Diploneis aestuarii	2	4	2	DIPL AEST
Diploneis didyma	2	5	2	DIPL DIDY
Diploneis interrupta	2	5	2	DIPL INTE
Diploneis litoralis	2	5	2	DIPL LITT
Diploneis oblongella	2	5	1	DIPL OBLO
Diploneis ovalis	2	5	1	DIPL OVAL
Diploneis papula	2	5	2	DIPL PAPU

Diploneis smithii var. *dilatata*	2	5	1	DIPL SMDI
Diploneis smithii var. *pumila*	2	5	1	DIPL SMPU

Subordo NAVICULINEAE Hendey

Fam. **Naviculaceae** Kützing

Cymatoneis sp. 1	2	4	1	CYMT SPEC
Navicula abscondita	2	5	2	NAVI ABSC
Navicula accedens				(No Label)
Navicula arenaria var. *rostellata*	2	5	3	NAVI ARRO
Navicula bipustulata	2	5	3	NAVI BIPU
Navicula cf. *bipustulata*	2	5	3	NAVI CBIP
Navicula bremereyi Hustedt*	2	4	1	NAVI BREM
Navicula cancellata Donkin*	2	5	2	NAVI CANC
Navicula cincta (Ehrenberg) Ralfs in Pritchard*	2	5	2	NAVI CINC
Navicula clamans Hustedt*	2	4	1	NAVI CLAM
Navicula complanata (Grunow) Grunow*	2	5	1	NAVI COMP
Navicula digitoradiata	2	5	2	NAVI DIGI
Navicula diserta	1	3	3	NAVI DISE
Navicula distans (W. Smith) Ralfs in Pritchard*	2	5	1	NAVI DIST
Navicula duerrenbergiana	2	5	1	NAVI PAVI
Navicula finmarchica var. *acuta*	2	4	2	NAVI FIAC
Navicula flanatica	2	5	3	NAVI FLAN
Navicula gregaria	2	5	3	NAVI GREG
Navicula gregaria form 1	2	4	3	NAVI GRF1
Navicula margino-nodularis	2	4	1	NAVI MARG
Navicula meniscus	2	5	3	NAVI MENI
Navicula microdigitoradiata	2	5	3	NAVI MICR
Navicula cf. *minima* Grunow*	1	3	2	NAVI CFMI
Navicula cf. *mollis*	2	4	3	NAVI CFMO
Navicula orthoneoides	2	4	2	NAVI ORTH
Navicula palpebralis	2	5	3	NAVI PALP
Navicula cf. *perminuta*	2	6	3	NAVI PERM
Navicula phyllepta	2	4	3	NAVI PHYL
Navicula salinarum Grunow in Cleve & Grunow*	2	5	2	NAVI SALA
Navicula salinicola	1	3	3	NAVI SALI
Navicula starmachioides	2	4	3	NAVI STAR
Navicula trivialis Lange-Bertalot*	2	5	1	NAVI CCAR
	2	5	1	NAVI TRIV
Navicula sp. 1	1	3	3	NAVI SP01
Navicula sp. 2	1	4	3	NAVI SP02
Navicula sp. 3	1	3	3	NAVI SP03
Navicula sp. 4	1	3	3	NAVI SP04
Navicula sp. 5	2	4	2	NAVI SP05
Navicula sp. 6	2	4	2	NAVI SP06
Navicula sp. 7	1	4	3	NAVI SP07
Navicula sp. 8	2	5	2	NAVI SP08
Navicula sp. 9	1	4	2	NAVI SP09
Navicula sp. 10	2	5	3	NAVI SP10
Navicula sp. 11	2	4	2	NAVI SP11
Navicula sp. 12	2	4	2	NAVI SP12
Navicula sp. 13	2	4	3	NAVI CSAL
Navicula sp. 14	2	4	2	NAVI SP14
Navicula sp. 15	2	4	3	NAVI CFFL
Navicula sp. 16*	2	5	1	NAVI SP16
Trachyneis aspera	2	5	2	TRAC ASPE

Fam. **Pleurosigmataceae** Mereschkowsky

Gyrosigma acuminatum	2	5	1	GYRO ACUM
	2	5	1	GYRO SPEN
Gyrosigma fasciola	2	5	2	GYRO FASC
Pleurosigma aestuarii	2	5	1	PLEU AEST

Fam. **Stauroneidaceae** Mann

Craticula cuspidata	2	5	2	CRAT CUSP
Stauroneis phoenicenteron (Nitzsch) Ehrenberg*	2	5	1	STAU PHOE

Ordo *THALASSIOPHYSALES*

Fam. **Catenulaceae** Mereschkowsky

Amphora coffeaeformis	2	5	3	AMPH COFF
Amphora coffeaeformis var. *aponina*	2	4	1	AMPH COAP
Amphora copulata	2	5	2	AMPH COPU
Amphora cf. *copulata*	2	5	2	AMPH CFCO
Amphora cymbamphora	2	4	3	AMPH CYMB
Amphora cf. *delicatissima*	1	4	3	AMPH CFDE
	1	4	2	AMPH 2624
Amphora cf. *exigua*	2	5	3	AMPH CFEX
Amphora graeffeana	2	5	1	AMPH GRAE
Amphora cf. *helenensis*	2	4	2	AMPH CFHE
Amphora hybrida	2	5	2	AMPH HYBR
Amphora laevis var. *laevissima*	2	5	1	AMPH LAEV
Amphora laevis var. *perminuta*	1	4	3	AMPH LAPE
Amphora lineolata	2	5	1	AMPH LINE
Amphora cf. *longa*	2	5	1	AMPH LONG
Amphora margaritifera	2	4	1	AMPH MARG
Amphora montana				(No Label)
Amphora ostrearia var. *belgica*	2	5	1	AMPH OSTR
Amphora ovalis				(No Label)
Amphora cf. *pediculus*	1	3	3	AMPH CFPE
Amphora pulchella	2	5	2	AMPH PULC
Amphora cf. *subacutiuscula*	1	4	3	AMPH CFTE
Amphora cf. *sublaevis*				(No Label)
Amphora tenerrima	1	4	3	AMPH TENE
Amphora wisei	2	4	2	AMPH WISE
Amphora sp. 1*	2	4	2	AMPH SP01
Amphora sp. 2	1	4	3	AMPH SP02
Amphora sp. 3	1	3	2	AMPH SP03
Amphora sp. 4	1	3	2	AMPH SP04
Amphora sp. 5	2	4	3	AMPH SP05
Amphora sp. 6	2	4	3	AMPH SP06
Catenula adhaerens	1	1	3	CATE ADHA

Ordo *BACILLARIALES*

Fam. **Bacillariaceae** Ehrenberg

Bacillaria paxillifer	2	5	1	BACI PARA
Cylindrotheca spp.*				(No label)
Denticula subtilis	2	4	2	DENT TENU
Denticula tenuis	2	4	2	DENT TENU

Hantzschia cf. *distinctepunctata*	2	5	1	HANT DIST
Hantzschia marina	2	5	2	HANT MARI
Hantzschia virgata var. *virgata*	2	5	1	HANT VIRG
Hantzschia/Nitzschia sp. 1	2	4	1	HANI SP01
Hantzschia/Nitzschia sp. 2	2	4	2	HANI SP02
Hantzschia/Nitzschia sp. 3	2	5	1	HANI SP03
Nitzschia cf. *aequorea*	2	5	1	NITZ CFAE
Nitzschia bergii Cleve-Euler*				(No label)
Nitzschia brevissima	2	5	1	NITZ BREV
Nitzschia commutata	2	5	1	NITZ COMM
Nitzschia cf. *dissipata*	2	5	2	NITZ CFDI
Nitzschia dubia	2	5	1	NITZ DUBI
Nitzschia cf. *frustulum*	1	3	3	NITZ FRUS
	1	3	2	NITZ CFFR
Nitzschia hybrida	2	5	1	NITZ HYBR
Nitzschia minutula (*lanceola* var.?)	2	4	1	NITZ MINU
Nitzschia nana	2	5	1	NITZ NANA
Nitzschia palea (Kützing 1844) W. Smith 1856*	2	5	1	NITZ CFPA
Nitzschia pellucida	2	5	1	NITZ PELL
Nitzschia cf. *rosenstockii*	2	4	3	NITZ CFRO
Nitzschia sigma	2	5	1	NITZ SIGM
Nitzschia valdestriata	1	3	1	NITZ VALD
Nitzschia sp. 1	2	5	3	NITZ SP01
Nitzschia sp. 2	2	5	3	NITZ SP02
Nitzschia sp. 3	2	4	2	NITZ SP03
Nitzschia sp. 4	2	5	2	NITZ SP04
	2	5	1	NITZ CCAP
Psammodictyon panduriforme var. *delicatulum*	2	4	2	PSAM PADE
Tryblionella acuminata W. Smith 1853*				(No label)
Tryblionella apiculata	2	5	2	TRYB APIC
Tryblionella coarctata	2	5	2	TRYB COAR
Tryblionella debilis	2	5	1	TRYB DEBI
Tryblionella granulata	2	4	1	TRYB GRAN
Tryblionella hungarica				(No label)
Tryblionella levidensis var. *levidensis*	2	4	1	TRYB LELE
Tryblionella levidensis var. *salinarum*	2	4	1	TRYB LESA
Tryblionella litoralis (Grunow) Mann*				(No label)
Tryblionella marginulata	2	5	1	TRYB MARG
Tryblionella navicularis	2	5	2	TRYB NAVI
Tryblionella parvula	2	5	2	TRYB PARV
Tryblionella punctata	2	5	2	TRYB COMP

Ordo *RHOPALODIALES* Mann

Fam. **Rhopalodiaceae** (Karsten) Topachevs'kyj & Oksiyuk

Epithemia adnata (Kützing) Brébisson*	nr	9	1	EPIT ADNA
Epithemia sorex Kützing*	nr	9	1	EPIT SORE
Rhopalodia musculus (Kützing) O. Müller*	2	5	1	RHOP MUSC

Ordo *SURIRELLALES* Mann

Fam. **Entomoneidaceae** Reimer

Entomoneis sp. 1*	2	6	2	ENTO SPE1
Entomoneis sp. 2*	2	6	1	ENTO SPE2

Fam. **Surirellaceae** Kützing

Petrodictyon gemma	2	5	2	PETR GEMM
Surirella brébissonii	2	5	2	SURI BREB
Surirella minuta	2	4	1	SURI MINU
Surirella ovalis	2	5	1	SURI OVAL

Table 19. Main features of taxa belonging to the family Cymatosiraceae.

	CYMATOSIRA	*Cymatosira* sp. 1	*PLAGIOGRAMMOPSIS*	*Plagiogrammopsis minimum*	*Plagiogrammopsis* sp. 1	*BROCKMANNIELLA*	*INCERTAE SEDIS* sp. 1
Description	Hasle *et al.* (1983)	this study	Hasle *et al.* (1983), Gardner & Crawford (1994)	Salah (1955), this study	this study	Hasle *et al.* (1983)	this study
Fascia	-	-	+	+		+	-
Pseudoseptum	-	?	+/-	+		-	-
Pili	-	?	Incomplete	?		-	-
Spines	Linking spines, colonies inseparable	+ (?)	Long spines, colonies separable	Long spines, separable colonies?		Long spines, colonies separable	Short linking spines
Ocelluli	Two, opening only slightly laterally	Two, opening only slightly laterally	Two, opening laterally	Two, opening laterally		Two, offset, opening laterally	Two, offset, opening laterally
Process	One rimoportula / cell, central, submarginal	?	One rimoportula / cell, central, submarginal	One rimoportula (/ cell ?), central, submarginal		One rimoportula / cell, central, submarginal	No portulae!
Specialized end valves	+	?	-	?		-	- (?)
Occlusion type	External cribrum with spinules	External, rather simple cribrum	External cribrum with spinules	External cribrum with spinules	External cribrum, no spines	External cribrum; no spinules (?)	Simple poroids, no occlusions visible/present?
Cingulum	4-7 open, porous bands	?	5-8 split, ligulate, porous copulae	?	Numerous porous copulae	10-15?, ligulate, porous copulae	numerous porous copulae
Other			Spindle-shaped foramen between cells				

Table 20. Main features of the genera belonging to the family Fragilariaceae (VC = valvocopula)

	Fragilaria s.s.	*Synedra*	*'F. capensis'* group	*Stauroforma*	*Staurosira*	*Staurosirella*	*Pseudostaurosira*	*Punctastriata*	*Martyana*	*Opephora*
references	Round *et al.* 1990	Round *et al.* 1990	this study, Witkowski *et al.* 1995/1996	Flower *et al.* 1996	Round *et al.* 1990	Round *et al.* 1990	Round *et al.* 1990, Sabbe & Vyverman 1995	Round *et al.* 1990	Round *et al.* 1990,	Round *et al.* 1990, Sabbe & Vyverman 1995
habit	ribbon-like colonies, benthic, planktonic	usually solitary or in radiate colonies, epiphytic	solitary, epipsammic	solitary or colonies, epilithic/benthic	solitary or colonies, attached or freeliving	solitary or colonies, often epipsammic	ribbon-like colonies	ribbon-like or branching colonies	solitary, epipsammic	solitary or ribbon-like colonies, epipsammic, epiphytic
habitat	freshwater	freshwater	marine-brackish	oligotrophic freshwater	freshwater	freshwater	freshwater, brackish to marine?	freshwater	freshwater	marine-brackish
rimoportula	present, one	present, two	absent	absent	absent	absent	absent	absent	absent	absent
spines	present	absent	absent	present/absent	present, on virgae	present, on virgae	present, in striae	present	absent	sometimes present
striae/areolae	uniseriate, areolae simple, occluded by cribra/rotae?	uniseriate, simple areolae, velum structure unknown	uniseriate, simple areolae, occluded by hymenes?	uniseriate, opposite, simple areolae with vela?	uniseriate, velum structure unknown	uniseriate; slit-like areolae with small outgrowths	uniseriate, areolae sparse, marginal, with complex vela	multiseriate	uniseriate, slit-like areolae, no occlusions	uniseriate, areolae with complex vela
pore fields	two	two, often ocellulimbi	two, circular	two or none	two	two	two	one	one, foot pole	two
cingulum	several (usually 4), punctate, split?	several, narrow, complete	2 (?), punctate (only VC? - 2 to3 rows of areolae), not curved	4-6, split, curved at apices, ligulate, VC wide	6-8 or more, split, curved, ligulate, VC wide	8-10, split, curved, VC wide	several (up to 10), split, curved, VC wide	several, split, VC wide	up to 5, split, curved, VC wide	about 4-6, split, curved, VC wide
other	mantle plaques		'mantle plaques'	somtimes mantle plaques sternum narrow to absent	sometimes small mantle plaques, sternum expanded	often mantle plaques	mantle plaques	'step', sometimes mantle plaques	'step' , no mantle plaques	

Table 21. Comparison between some genera of the old taxon *Navicula* s.l. for plastid and frustule structure (C: central; P: polar)

	Navicula **s.s.**	***Dickieia***	***Staurophora***	***Parlibellus***	***Lunella***	***Fallacia***	***Sellaphora***	***Biremis***
groups/taxa acc. Hustedt (1927-66)	Lineolatae	Microstigmaticae p.p.	*Stauroneis* p.p.	Microstigmaticae p.p.	-	Lyratae p.p.	Bacillares p.p. and others?	*Pinnularia*, *Amphora*, ...
typus generis	*N. tripunctata*	*D. ulvacea*	*S. amphioxys*	*P. delognei*	*L. bisecta*	*F. pygmea*	*S. pupula*	*B. ambigua*
plastids	two, girdle-appressed	one, girdle-appressed, complex (two K-shaped plates, extending under the valve)	one, girdle-appressed, complex (two K-shaped plates, extending under the valve)	two, girdle-appressed, butterfly-shaped	?	one, H-shaped, with two girdle-appressed lobes connected via an isthmus	one, H-shaped, with two girdle-appressed lobes connected via an isthmus, extending onto hypovalve	two, fore and aft in the cell; each consists of two girdle-appressed lobes connected via a bridge
striae	uniseriate (rarely biseriate)	uniseriate, more widely spaced in centre	unseriate	uniseriate, more widely spaced in centre	uniseriate	uniseriate (rarely partly biseriate)	uniseriate	uniseriate
areolae	apically elongate linear poroids with internal hymenes	circular poroids with internal hymenes	circular poroids with internal hymenes	circular poroids with internal hymenes	circular poroids, occlusion type unknown (absent?)	circular poroids with internal hymenes	circular poroids with internal hymenes	peculiar stria structure with internal chambers and external foramina
raphe	sternum thickened (esp. on primary side), usually with accessory rib, elaborate internal structure	simple, sternum unthickened, no accessory ribs	simple, sternum internally thickened (?), no accessory ribs	simple, sternum internally thickened, no accessory ribs	sternum internally thickened, no accessory rib	simple, sternum unthickened, no accessory ribs	simple, sternum unthickened, no accessory ribs	simple, sternum wide, no accessory rib
cingulum	several, open, plain copulae	several narrow, porous (1 or 2) copulae	several open, porous (2) copulae	many open, porous copulae	3-4 open, porous copulae	a few plain, open copulae	a few, open, usually non-porous copulae	numerous open, porous copulae
other			stauros! central raphe endings!	sometimes presence of cuniculi in central area	catenuloid cell construction!	hyaline lyre! conopeum!	sometimes conopeum	
references	Cox 1979	Cox 1985, Mann 1994	Mann in Round *et al.* 1990	Cox 1988a	Snoeijs 1996	Stickle & Mann in Round *et al.* 1990	Mann 1989	Mann in Round *et al.* 1990, Sabbe *et al.* 1995, Vyverman *et al.*, in press

Table 22. Main features of genera belonging to the Ordo Achnanthales.

	Achnanthes Bory 1822	*Achnanthidium* Kützing 1844	*Cocconeis* Ehrenberg 1837	*Anorthoneis* Grunow 1868
plastids	2 or many	1, girdle-appressed, with lobes under valves	1, C-shaped, simple or lobed	1, C-shaped
striae	uni-, bi- or triseriate	uni- to multiseriate	mostly uniseriate to multiseriate or loculate	uniseriate
occlusion type areola	vola	hymen	hymen	hymen (often supported by 1-4 pegs)
R-valve	usually with fascia or stauros		often submarginal silica ring	raphe-sternum eccentric
P-valve	no fascia or stauros	central sternum often wider or different shape than raphe-sternum	central sternum often wider than on R-valve	central sternum eccentric, often wider than raphe-sternum
raphe				
central raphe endings	(E) straight (I) coaxial	(E) straight (I) non-coaxial	(E) straight (I) non-coaxial	(E) straight (I) non-coaxial
terminal raphe endings		no terminal fissures	no terminal fissures	no terminal fissures
cingulum	3-7 open, porous copulae	shallow, open, non-porous copulae	shallow, non-porous copulae. Valvocopula often closed and with projections, other copulae open.	(?) non-porous bands as in *Cocconeis*

(E) = externally, (I) = internally

Table 23. Main characteristics of *Anorthoneis* spp. based on own observations and

	A. cf. *pulex* Sterrenburg 1988	*A. pulex* Sterrenburg 1988	*C. tenuis* Hustedt 1939	*A.* cf. *tenuis* Hustedt 1955	*A. tenuis* Hustedt 1955	*A. vortex* Sterrenburg 1988	*A. dulcis* Hein
Refs.	This study, Vos (1986), Cooper (1995)	Sterrenburg (1988), Hein (1992)	Hustedt 1939	This study, Cooper (1995)	Hustedt (1955), Simonsen (1987)	Sterrenburg (1988), Hein (1991)	Hein (1991)
Length (µm)	8.5-18.5	9-13	10-18	(12.5)13.1-15.7(-16.9)(*)	12	15-22	14-17
Width (µm)	5.6-14.1	6-7.5	6.5-14	(6.1-)9-11.2(-12.5)(*)	9	12-19	10-13
Stria density	(R) 23-29.5; (P) 16-25	(R) 24; (P) 18-22	(R) ?; (P) 14-22	(R) 14.5-21 (s), 22-26.5 (m); (P) 12-16 (s), 21-22(-23)(*)(m)	(R) ?; (P) 18-20 (s), 20-22 (m)	(R/P) (18?-)20-24(-26?)	(R/P) 19-21
P-valve	More or less large central hyaline area, none or only a few short striae at margin. Rarely 'faint striae' up to central sternum.	More or less large central hyaline area, few short striae at margin	Large elliptical hyaline (axial and central) area, few short striae at margin. 'Faint striae' up to central sternum ?.	Small or absent central hyaline area, often 'faint striae' up to sternum. Different stria pattern in marginal zone.	More or less large, asymmetrical central hyaline area	'Small' asymmetric central area, only very few short striae	'Small' asymmetric central area
R-valve	Axial area very narrow, central area small, roundish, few short striae	?	?	Axial area narrow, central area small, roundish. Short and long striae.	?	'Small' asymmetric central area, only very few short striae	'Small' asymmetric central area
Marginal areolae	(R) biseriate, internal costate virgae; (P) uniseriate	No split marginal areolae on P-valve (only one SEM-picture!)	?	(R) biseriate, internal costate virgae; (P) 'biseriate'(**)	?	(R) biseriate, internal costate virgae; (P)	Split marginal areolae on R-valve, split or C-, L- or U-shaped on P-valve
Mantle areolae (R-valve)	Yes. Small, elliptical, single	No? (Sterrenburg, pers. comm. in Hein 1991)	?	?	?	Yes. Small, roundish, single	Yes. Slit-like.
P- and R-valves	Strongly dissimilar	?	?	Strongly dissimilar	?	Sometimes (rarely) different	Similar
Habitat	Marine-estuarine	Marine	Marine	Marine-estuarine	Marine	Marine	Freshwater
Locality	Westerschelde and Oosterschelde (Nl), Chesapeake Bay (USA)	North Sea coast (Nl)	Wadden Sea (Nl)	Westerschelde (Nl), Chesapeake bay (USA)	Beaufort (USA)	Westerschelde (Nl), North Sea coast (Nl), Australia, Western Samoa	Florida (USA)

(*) The numbers between brackets refer to Salah's material from Blakeney Point (England); (**) The marginal striae are not really biseriate as in the R-valve. See the detailed description of this taxon.
(s): refers to the stria density measured along the central (P-valve) or raphe-sternum (R-valve); (m) refers to the stria density measured along the valve margin

Table 24. Summary table of some ordination characteristics of different ordination analyses on different data sets. n(e) = number of constraining environmental variables (a: all variables; b: after forward selection and exclusion of all multicollinear variables); TVE = total variance explained by all constraining variables (as percentage of total variance in species data) in RDA; VE(1-4) = TVE by the constraining variables in the first 4 axes (RDA) and total variance in species data accounted for by first 4 axes (PCA); VE1→4 = cf. VE(1-4) but by 1st → 4th axis separately. Information on data sets, see chapter 5.3.1.

ORDINATION TYPE	DATA SET	N(E)	TVE	VE(1-4)	VE1	VE2	VE3	VE4
PCA	2	-	-	37.5	19.6	8.6	5.8	3.5
PCA	3	-	-	41.6	20.3	10.4	6.6	4.3
RDA(a)	3	28	40.0	29.4	15.5	6.7	4.7	2.4
RDA(b)	3	13	34.9	28.4	15.4	6.4	4.3	2.2
RDA(a)	4	28	45.3	36.4	23.8	6.5	3.6	2.5
RDA(b)	4	14	41.2	35.5	23.6	6.4	3.3	2.2
RDA(a)	5	28	35.2	26.6	13.0	7.4	3.6	2.4
RDA(b)	5	12	29.4	24.8	12.1	7.0	3.3	2.3

Table 25. Canonical coefficients (can) for environmental variables (included by forward selection, $p \leq 0.05$, and after elimination of multicollinear variables): contribution of the environmental variables to axes 1-4 of redundancy analyses on the different data sets (DS 3 = 89 taxa, DS 4 = 45 epipelic taxa, DS 5 = 44 epipsammic taxa). For each axis its eigenvalue is given. Note that the t-values (t) are approximate; (absolute) values greater than 2.1 (shown in italics) are significant ($p < 0.05$: ter Braak 1990). For abbreviations see Table 7.

	Data set 3								Data set 4								Data set 5							
	Axis 1		Axis 2		Axis 3		Axis 4		Axis 1		Axis 2		Axis 3		Axis 4		Axis 1		Axis 2		Axis 3		Axis 4	
	0.154		0.064		0.043		0.022		0.236		0.064		0.033		0.022		0.121		0.070		0.033		0.023	
	can	t	can	t	can	t	can	t	can	t	can	t	can	t	can	t	can	t	can	t	can	t	can	t
medi	*-0.32*	*-3.0*	0.01	0.1	-0.03	-0.2	0.12	0.7	*-0.20*	*-3.1*	-0.11	-1.2	*-0.29*	*-2.40*	*-0.36*	*-2.6*	0.33	1.5	*-0.46*	*-3.2*	-0.28	-1.3	*-0.86*	*-4.7*
silt	*-0.95*	*-10.7*	-0.13	-0.9	-0.12	-0.9	*0.71*	*4.9*	*-1.00*	*-13.7*	0.04	0.4	-0.03	-0.20	0.28	1.8	*0.48*	*2.6*	*-0.56*	*-4.8*	0.15	0.9	*-0.98*	*-6.4*
vfsa	0.05	0.6	-0.12	-0.9	-0.20	-1.7	-0.24	-1.8	-0.02	-0.4	0.00	0.0	-0.19	-1.80	*0.26*	*2.2*	-0.15	-0.9	0.12	1.1	-0.25	-1.6	*0.59*	*4.3*
fsan	*0.19*	*3.2*	*-0.59*	*-6.0*	*-0.70*	*-7.7*	0.02	0.2	0.01	-0.1	-0.14	-1.9	0.16	1.80	*0.51*	*4.9*	*-0.82*	*-6.5*	*-0.19*	*-2.4*	-0.20	-1.7	-0.05	-0.5
msan	0.05	0.6	0.23	1.6	0.18	1.3	-0.19	-1.3									0.10	0.5	*0.41*	*3.6*	0.31	1.8	*0.96*	*6.4*
sawc	*0.39*	*3.5*	*-1.29*	*-7.3*	*-0.78*	*-4.8*	0.08	0.5	*0.21*	*2.2*	0.11	0.8	-0.11	-0.70	*0.82*	*4.3*	*-1.36*	*-6.0*	*-0.88*	*-6.2*	-0.06	-0.3	*-0.45*	*-2.5*
sais	*-0.41*	*-3.8*	*1.74*	*9.9*	-0.06	-0.4	*0.43*	*2.4*	*-0.28*	*-3.1*	*-0.89*	*-6.8*	-0.01	0.00	*-0.44*	*-2.4*	*1.36*	*6.0*	*1.32*	*9.3*	*-0.52*	*-2.5*	*-0.39*	*-2.1*
dozi									-0.04	-0.7	*-0.22*	*-3.1*	-0.06	-0.70	*0.27*	*2.7*								
waco	*-0.26*	*-2.9*	-0.02	-0.1	*-0.41*	*-3.0*	*-0.56*	*-3.9*	*-0.22*	*-3.1*	*-0.38*	*-4.1*	-0.12	-0.80	*-0.60*	*-4.5*	0.07	0.4	*-0.46*	*-3.9*	*-0.77*	*-4.4*	-0.04	0.2
ramo									-0.04	-0.4	0.01	0.1	0.08	0.40	0.05	0.2								
tcmo	0.08	1.5	-0.07	-0.8	0.11	1.3	*0.25*	*2.9*	0.12	1.6	*0.24*	*2.3*	*-0.93*	*-7.10*	-0.28	-1.8								
tcwe																	-0.17	-1.8	*-0.14*	*-2.3*	0.18	2.0	*-0.28*	*-3.5*
wiwe	0.08	1.6	-0.14	-1.8	-0.06	-0.8	-0.12	-1.5	0.08	1.4	0.03	0.4	*-0.63*	*-6.10*	*-0.26*	*-2.2*								
oamo	*0.11*	*2.5*	*-0.17*	*-2.4*	0.10	1.6	*-0.60*	*-8.4*	*0.14*	*2.5*	0.02	0.3	*-0.40*	*-4.00*	*-0.40*	*-3.7*	-0.10	-1.1	*-0.22*	*-3.9*	0.06	0.7	*0.49*	*6.8*
jamo																	-0.17	-1.6	*-0.16*	*-2.6*	0.03	0.3	-0.12	-1.5
jlmo	0.02	0.4	*-0.26*	*-3.1*	0.02	0.3	*0.19*	*2.3*	0.04	0.7	*0.25*	*3.5*	*-0.27*	*-3.10*	*0.22*	*2.3*								
elco	0.03	0.6	-0.14	-2.0	*0.21*	*3.3*	*0.38*	*5.5*	0.01	0.3	*0.17*	*3.3*	0.06	0.90	*0.35*	*4.8*	-0.04	-0.4	-0.06	-1.0	*0.58*	*6.9*	*-0.23*	*-3.1*

Table 26. Intra-set correlations for environmental variables (included by forward selection, p≤ 0.05, and after elimination of all multicollinear variables): contribution of the environmental variables to axes 1-4 of redundancy analyses on the different data sets (cf. Table 25). Correlation coefficients ≥ 0.50 are shown in italics. For abbreviations see Table 7.

	Data set 3				Data set 4				Data set 5			
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4
medi	*0.76*	0.17	0.03	0.08	*0.76*	-0.14	0.01	0.04	-0.40	*0.57*	0.27	-0.03
silt	*-0.96*	-0.22	-0.07	0.01	*-0.97*	0.13	-0.11	-0.01	0.48	*-0.73*	-0.25	-0.19
vfsa	*-0.62*	-0.44	-0.16	-0.09	*-0.68*	0.25	-0.01	0.16	0.18	*-0.64*	-0.30	0.02
fsan	*0.67*	-0.31	-0.41	0.00	*0.55*	-0.09	0.10	0.38	*-0.83*	0.28	-0.08	0.04
msan	0.39	*0.55*	-0.01	-0.05					0.06	*0.60*	0.08	0.17
sawc	0.16	0.47	*-0.63*	0.26	0.12	*-0.82*	-0.31	0.22	-0.04	0.48	-0.40	-0.43
sais	0.16	*0.66*	*-0.58*	0.27	0.14	*-0.87*	-0.27	0.17	0.10	*0.66*	-0.41	-0.38
dozi					-0.03	-0.39	-0.47	*0.53*				
waco	*-0.84*	0.00	-0.11	-0.24	*-0.82*	-0.08	-0.04	-0.29	*0.55*	*-0.58*	-0.43	0.18
ramo					-0.05	0.24	-0.42	0.43				
tcmo	0.03	-0.17	0.03	0.48	0.01	0.18	*-0.78*	0.24				
tcwe									-0.09	-0.06	0.15	-0.41
wiwe	0.08	-0.07	-0.02	-0.25	0.09	-0.01	0.07	-0.22				
oamo	0.00	0.15	-0.07	-0.43	0.04	-0.23	-0.32	-0.42	0.09	0.01	-0.13	0.36
jamo									-0.02	0.01	0.02	0.10
jlmo	0.00	-0.17	0.09	*0.56*	-0.01	0.24	-0.47	0.43				
elco	-0.15	-0.07	0.49	0.43	-0.10	0.34	0.05	0.22	0.24	-0.14	*0.70*	-0.30

Table 27. Cumulative fit per taxon for the first 4 RDA axes for **data set 3** as fraction of the variance of taxa and the total variance per taxon [VAR(Y)]. Only those taxa which have at least 30 % of their variance accounted for by the first 4 axes are listed. For taxon abbreviations, see Table 18.

NAME	AX1	AX2	AX3	AX4	VAR(Y)	% EXPL
DELP MINU	0.7153	0.7753	0.8591	0.8591	1.00	88.58
CYMA BELG	0.6931	0.7632	0.8434	0.8438	0.96	86.74
PARA SULC	0.5990	0.6018	0.6499	0.6502	1.26	66.60
THAL DECI	0.6359	0.6445	0.6468	0.6498	1.40	67.09
RHAP AMPH	0.6079	0.6190	0.6192	0.6192	1.23	63.75
FRAG SP01	0.5128	0.5365	0.5470	0.5596	1.22	57.96
NAVI GREG	0.1299	0.3430	0.5326	0.5370	1.81	58.48
OPEP GUEN	0.0227	0.4880	0.5109	0.5110	1.30	54.82
NAVI ARRO	0.3693	0.3876	0.4456	0.4511	1.79	50.31
PLAG VANH	0.4212	0.4235	0.4489	0.4491	1.31	47.30
DELP SURI	0.3687	0.3798	0.4471	0.4471	1.41	49.51
NAVI FLAN	0.3754	0.4040	0.4228	0.4236	1.73	54.63
NAVI PERM	0.2912	0.2913	0.4117	0.4120	0.61	43.97
FRAG CFAT	0.0200	0.4039	0.4102	0.4110	1.87	43.47
PARL SP02	0.0462	0.0831	0.3600	0.4092	0.96	46.79
ACHN DELI	0.0056	0.3860	0.3869	0.3926	0.82	42.25
BROC BROC	0.2798	0.3284	0.3910	0.3911	1.26	42.64
NAVI PHYL	0.2769	0.3027	0.3866	0.3866	1.75	40.32
ODON AURI	0.2454	0.2815	0.3707	0.3707	1.19	39.24
PLAG SIGM	0.2868	0.3265	0.3567	0.3654	1.16	39.18
NAVI DISE	0.2043	0.2338	0.3042	0.3638	1.16	40.82
NAVI SP02	0.2731	0.3405	0.3414	0.3489	0.81	40.47
NAVI SP01	0.2625	0.3321	0.3326	0.3349	1.54	36.40
AMPH SP02	0.0492	0.2325	0.3185	0.3348	0.21	37.77
NAVI SP04	0.2957	0.2996	0.3300	0.3346	1.17	40.61
FALL CRYP	0.1924	0.2555	0.2679	0.3267	0.91	42.71
AMPH CFTE	0.1461	0.2880	0.2941	0.3231	1.41	35.23
ACHN SP02	0.2337	0.2355	0.2761	0.3141	1.19	34.71
OPEP MUTA	0.0035	0.2659	0.2718	0.3106	1.36	36.06
ANOR SPEC	0.0855	0.2061	0.2938	0.3016	0.65	35.76

Table 28. Cumulative fit per taxon for the first four RDA axes for **data set 4** (epipelon) as fraction of the variance of taxa and the total variance per taxon [VAR(Y)]. Only those taxa which have at least 30 % of their variance accounted for by the first 4 axes are listed. For taxon abbreviations, see Table 18.

NAME	AX1	AX2	AX3	AX4	VAR(Y)	% EXPL
DELP MINU	0.8152	0.8154	0.8200	0.8272	1.06	88.47
CYMA BELG	0.7953	0.7953	0.8002	0.8104	1.02	86.85
THAL DECI	0.6280	0.6298	0.6411	0.6594	1.47	66.72
PARA SULC	0.6416	0.6535	0.6536	0.6540	1.33	66.98
RHAP AMPH	0.6106	0.6186	0.6188	0.6230	1.30	64.44
NAVI GREG	0.1136	0.5734	0.5853	0.5879	1.91	60.61
FRAG SP01	0.5488	0.5524	0.5650	0.5695	1.29	58.18
NAVI FLAN	0.3694	0.4311	0.5320	0.5322	1.82	55.00
NAVI ARRO	0.3914	0.4638	0.4738	0.4817	1.89	51.93
PLAG VANH	0.4507	0.4556	0.4594	0.4612	1.38	47.06
DELP SURI	0.3823	0.4378	0.4514	0.4543	1.48	50.00
NAVI SP10	0.0437	0.0944	0.4359	0.4492	1.23	48.26
PARL SP02	0.0253	0.3025	0.3762	0.4487	1.01	46.91
NAVI PERM	0.3321	0.3966	0.3966	0.3972	0.65	43.51
BROC BROC	0.2837	0.3764	0.3859	0.3879	1.33	42.80
ODON AURI	0.2592	0.3807	0.3807	0.3818	1.25	39.93
NAVI PHYL	0.2491	0.3601	0.3602	0.3710	1.85	40.74
PLAG SIGM	0.2879	0.3503	0.3587	0.3588	1.22	41.75

Table 29. Cumulative fit per taxon for the first four RDA axes for **data set 5** (epipsammon) as fraction of the variance of taxa and the total variance per taxon [VAR(Y)]. Only those taxa which have at least 30 % of their variance accounted for by the first 4 axes are listed. For taxon abbreviations, see Table 18.

NAME	AX1	AX2	AX3	AX4	VAR(Y)	% EXPL
OPEP GUEN	0.1467	0.5205	0.5208	0.5293	1.24	55.84
FRAG CFAT	0.2478	0.3977	0.4023	0.4037	1.78	42.13
NAVI SP02	0.0500	0.3689	0.3821	0.3893	0.76	40.12
NAVI SP04	0.1680	0.3534	0.3541	0.3885	1.11	40.56
ACHN DELI	0.2018	0.3674	0.3756	0.3860	0.78	40.60
NAVI DISE	0.2732	0.3180	0.3187	0.3781	1.10	41.03
NAVI SP01	0.2909	0.3072	0.3508	0.3559	1.46	36.48
FALL CRYP	0.0136	0.2206	0.3194	0.3245	0.86	41.45
OPEP MUTA	0.1529	0.3037	0.3042	0.3193	1.30	35.66
ACHN SP02	0.1877	0.2824	0.2837	0.3154	1.13	34.05
AMPH CFTE	0.2741	0.2747	0.2955	0.3140	1.34	35.81
ANOR SPEC	0.0150	0.1812	0.3014	0.3059	0.62	35.20
AMPH CFPE	0.0983	0.2532	0.2931	0.3006	1.38	34.11
AMPH SP02	0.0503	0.2271	0.3005	0.3005	0.20	37.13

Table 30. Tests of significance of environmental variables in different data sets (cf. Table 8). VE = percentage variation explained = eigenvalue of a constrained axis (RDA) with each environmental variable in turn as the only constraining variable. p = significance probability of constrained axis in a Monte Carlo permutation test (H_0 = influence of the variable on the diatoms not significantly different from zero). N.S. = not significant. Variables included by forward selection ($p \leq 0.05$) in bold italics (note that the number of selected variables included is higher than in Tables 25 and 26, where all multicollinear variables have been excluded). TVE (sign) = total variation explained by significant variables; TVE (all) = total variation explained by all variables. The approximate increase of the variation explained by subsequent inclusion of the variables is given in brackets. For abbreviations see Table 7.

	Data set 3			Data set 4			Data set 5		
	VE		p	VE		p	VE		p
medi	***9.3***	(1)	≤ 0.01	***13.6***	(1)	≤ 0.01	***5.6***	(1)	≤ 0.01
clay	***12.8***	(1)	≤ 0.01	***19.4***	(1)	≤ 0.01	***7.1***	(1)	≤ 0.01
silt	***14.4***	(14)	≤ 0.01	***21.6***	(22)	≤ 0.01	***8.2***	(5)	≤ 0.01
vfsa	***7.6***	(1)	≤ 0.01	***11.5***	(1)	≤ 0.01	***4.2***	(1)	≤ 0.01
fsan	***8.4***	(4)	≤ 0.01	***7.6***	(1)	≤ 0.01	***9.1***	(9)	≤ 0.01
msan	***4.6***	(1)	≤ 0.01	6.1		≤ 0.01	***3.3***	(1)	≤ 0.01
csan	3.1		≤ 0.01	1.3		≤ 0.01	4.7		≤ 0.01
sawc	***3.9***	(2)	≤ 0.01	***5.2***	(1)	≤ 0.01	***2.8***	(3)	≤ 0.01
sais	***5.0***	(5)	≤ 0.01	***5.8***	(6)	≤ 0.01	***4.2***	(4)	≤ 0.01
tcwc	1.8		≤ 0.01	2.7		≤ 0.01	1.0		N.S.
dozi	2.2		≤ 0.01	***2.6***	(1)	≤ 0.01	1.9		≤ 0.01
waco	***11.2***	(1)	≤ 0.01	***15.8***	(1)	≤ 0.01	***7.3***	(1)	≤ 0.01
orgC	11.2		≤ 0.01	15.4		≤ 0.01	7.5		≤ 0.01
orgN	7.6		≤ 0.01	10.1		≤ 0.01	5.4		≤ 0.01
ramo	1.6		≤ 0.01	2.0		≤ 0.01	1.2		≤ 0.04
rawe	1.4		≤ 0.01	***1.7***	(1)	≤ 0.01	1.1		≤ 0.04
tcmo	***1.7***	(2)	≤ 0.01	***2.6***	(3)	≤ 0.01	0.9		N.S.
tcwe	1.8		≤ 0.01	2.7		≤ 0.01	***1.1***	(1)	≤ 0.05
wiwe	***0.7***	(1)	N.S.	***0.9***	(2)	N.S.	0.6		N.S.
wima	1.1		≤ 0.03	1.7		≤ 0.01	0.5		N.S.
prec	2.0		≤ 0.01	2.9		≤ 0.01	1.2		N.S.
oamo	***1.5***	(1)	≤ 0.01	***1.9***	(2)	≤ 0.01	***1.1***	(1)	≤ 0.05
jamo	0.6		N.S.	***0.7***	(1)	N.S.	***0.5***	(1)	N.S.
mrmo	1.2		≤ 0.01	2.0		≤ 0.01	0.4		N.S.
mamo	0.9		N.S.	***1.3***	(1)	≤ 0.02	0.6		N.S.
jlmo	***1.4***	(1)	≤ 0.02	***1.9***	(1)	≤ 0.01	0.9		N.S.
semo	0.9		≤ 0.04	1.3		≤ 0.02	0.6		N.S.
elco	***2.2***	(2)	≤ 0.01	***1.6***	(1)	≤ 0.01	***2.8***	(2)	≤ 0.01
TVE (sign)	35.7			42.5			30.5		
TVE (all)	40.0			45.3			35.2		

Table 31. Global approach (a): variables selected by forward selection on the full set of explanatory variables without the spatial variables* for *data sets 3-5*. **Additive approach** (b): variables selected by forward selection on the variables selected in the independent approaches on all explanatory variable sets (including the spatial ones) for *data sets 3-5* (cf. Table 32). Unless explicitly listed, all p-values are ≤ 0.01.

Variable set	Variable	D.S. 3 (a)	p	D.S. 3 (b)	p	D.S. 4 (a)	p	D.S. 4 (b)	p	D.S. 5 (a)	p	D.S. 5 (b)	p
Physical-chemical	medi	x	0.02			x	0.03			x			
	clay	x				x	0.02			x	0.04		
	silt	x		x		x		x		x		x	
	vfsa	x	0.02	x		x		x		x		x	
	fsan	x		x		x		x		x		x	
	msan	x								x			
	csan												
	waco	x		x	0.02	x		x		x		x	
	orgC												
	orgN												
	sawc	x		x		x		x		x		x	
	sais	x				x				x		x	
	dozi					x	0.03					x	0.05
	elev	x		x		x		x		x		x	
Climatic	ramo			x		x	0.04	x	0.02			x	
	rawe					x		x	0.02				
	tcmo	x				x		x					
	tcwe									x			
	tcwc												
	wiwe	x				x		x					
	wima												
	prec			x		x		x					
Temporal	oamo	x		x		x		x		x			
	jamo							x		x	0.03		
	mrmo							x					
	mamo							x					
	jlmo	x	0.02	x		x							
	semo												
Spatial	x			x				x	0.02			x	
	y			x				x				x	
	x^2							x				x	
	xy			x									
	y^2			x				x				x	
	x^3			x				x				x	
	x^2y			x								x	
	xy^2							x				x	
	y^3												

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[*] As we did not eliminate multicollinear variables (cf. also Table 30) the number of variables selected in this approach is higher than the number selected in the RDA analysis in chapter 5.3.3. See also Tables 25, 26.

Table 32. **Independent approach**: variables (and their p-values) which significantly contribute to explaining the variation in the 3 different species data sets (*D.S. 3: complete species data set; D.S. 4: epipelic species data set; D.S. 5: epipsammic species data set*) in 4 sets of explanatory variables (cf. Table 8). Unless explicitly listed, all p-values are ≤ 0.01. Variables shown in italics never give a significant contribution to the variation explained by the different sets of explanatory variables.

Variable set	Variable	D.S. 3	p	D.S. 4	p	D.S. 5	p
Physical-chemical	medi	x	0.02	x	0.02	x	0.02
	clay	x	0.02	x		x	
	silt	x		x		x	
	vfsa	x	0.03	x	0.04	x	0.02
	fsan	x		x		x	
	msan	x				x	
	csan						
	waco	x		x		x	
	orgC						
	orgN						
	sawc	x		x	0.02	x	
	sais	x		x		x	
	dozi	x		x		x	
	elev	x		x		x	
Climatic	ramo	x		x		x	0.03
	rawe	x	0.03	x			
	tcmo	x		x	0.02		
	tcwe						
	tcwc	x	0.03	x			
	wiwe			x			
	wima						
	prec	x		x			
Temporal	oamo	x		x		x	0.05
	jamo	x	0.03	x			
	mrmo			x			
	mamo			x			
	jlmo	x	0.02				
	semo	x	0.02				
Spatial	x	x		x		x	
	y	x		x		x	
	x^2			x		x	
	xy	x				x	
	y^2	x		x		x	
	x^3	x		x		x	
	x^2y	x					
	xy^2			x	0.02		
	y^3						

Table 33. Spatial component of variation in benthic diatom data sets: variation partitioning of the three different species data sets (cf. Table 8) by different (sub)sets of explanatory variables (E = environmental, E+S = environmental + spatial, S = spatial, cf. Table 9) according to the independent, global and additive approaches. The best models are indicated in bold face (see chapter 5.3.4.6.)(FS = forward selection; TVE = total variance explained (%), * = 0.01<p<0.05).

Variable set	Variable	D.S. 3				D.S. 4				D.S. 5			
		E	E+S	S	TVE	E	E+S	S	TVE	E	E+S	S	TVE
Independent	Spat	-	-	21.0	21.0	-	-	17.6	17.6	-	-	23.2	23.2
	P-C	19.1	12.8	8.2	40.1	22.9	12.2	5.4	40.5	15.9	12.7	10.5	**39.1**
	Sediment	16.4	9.9	11.1	37.4	19.0	10.8	6.8	36.6	12.7	8.6	14.6	35.9
	Salinity	3.4	4.9	16.1	24.4	2.8	4.6	13.0	20.4	3.4	5.1	18.1	26.6
	Elevation	1.8	0.4	20.6	22.8	1.6	0.0	17.6	19.2	1.5	1.4	21.8	24.7
	Clim	4.8	3.8	17.2	25.8	7.7	4.0	13.6	25.3	1.2*	0.0	23.2	24.4
	Temp	4.8	0.0	21.0	25.8	6.3	0.2	17.4	23.9	1.2*	0.0	23.2	24.4
Global	All	22.0	13.7	7.3	43.0	29.1	13.4	4.2	**46.7**	17.1	13.4	8.4	**38.9**
Additive with FS	All	20.0	9.8	11.2	41.0	27.7	12.4	5.2	45.3	13.2	12.6	10.6	36.4
Additive without FS	All	23.7	14.0	6.0	**43.7**	29.1	13.8	3.8	**46.7**	15.8	14.5	8.7	**39.0**

Table 34. Differential approach: variation partitioning of data set 3 (all taxa) by different (sub)sets [or combinations of (sub)sets] of environmental variables. n(U) and n(T): number of variables selected by FS on the (sub)sets of environmental variables U and T; VE is the percentage of variance explained by the selected variables of U or by the selected variables of the two sets (U and T) together; δVE is the effect on VE of adding the second set of variables T [thus by partialling out the selected variables of U in a RDA (with FS) on T]. The p-value of this addition is calculated by a Monte Carlo permutation test (99 unrestricted permutations). ** = $p=0.01$; * = $p \leq 0.05$; ^{ns} = not significant.

U	T	n(U)	n(T)	VE (%)	δVE (%)	p-value 1st axis	p-value trace
(U constraining variables)							
sediment		9		26.3		0.01**	0.01**
salinity		3		8.3		0.01**	0.01**
elevation		1		2.2		0.01**	-
climatic		5		8.6		0.01**	0.01**
temporal		4		4.8		0.01**	0.01**
sediment, salinity		10		30.9		0.01**	0.01**
sediment, climatic		14		32.4		0.01**	0.01**
sediment, temporal		12		30.1		0.01**	0.01**
temporal, climatic		7		9.5		0.01**	0.01**
temporal, salinity		7		12.9		0.01**	0.01**
sediment, temporal, climatic, elevation, salinity[*]		14		35.7		0.01**	0.01**
(U covariables)	(T constraining variables)						
sediment	salinity	9	3	31.9	5.6	0.01**	0.01**
sediment	elevation	9	1	27.2	0.9	0.01**	0.01**
salinity	elevation	3	1	10.2	1.9	0.01**	0.01**
sediment	climatic	9	5	32.1	5.8	0.01**	0.01**
sediment	temporal	9	4	30.7	4.4	0.01**	0.01**
sediment, climatic	temporal	14	4	33.8	1.4	0.03*	0.01**
sediment, temporal	climatic	12	5	33.1	3.0	0.01**	0.01**
sediment, salinity	climatic	14	5	35.4	4.5	0.01**	0.01**
temporal	climatic	4	5	10.4	5.6	0.01**	0.01**
climatic	temporal	5	4	10.4	1.8	0.04*	0.02*
climatic	salinity	5	3	11.8	5.1	0.01**	0.01**
temporal, salinity	climatic	7	5	15.3	2.4	0.06^{ns}	0.02*

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[*] = global approach (all explanatory variables except spatial variables)

Table 35. Differential approach: variation partitioning of data set 4 (epipelon) by different (sub)sets [or combinations of (sub)sets] of environmental variables (excl. spatial and temporal variables). n(U) and n(T): number of variables selected by FS on the (sub)sets of environmental variables U and T; VE is the percentage of variance explained by the selected variables of U or by the selected variables of the two sets (U and T) together; δVE is the effect on VE of adding the second set of variables T [thus by partialling out the selected variables of U in a RDA (with FS) on T]. The p-value of this addition is calculated by a Monte Carlo permutation test (99 unrestricted permutations). ** = p=0.01; * = $p \leq 0.05$; ^{ns} = not significant.

U	T	n(U)	n(T)	VE (%)	δVE (%)	p-value 1st axis	p-value trace
(U constraining variables)							
sediment		7		29.8		0.01**	0.01**
salinity		2		7.4		0.01**	0.01**
elevation		1		1.6		0.01**	-
climatic		6		11.7		0.01**	0.01**
sediment, salinity		9		34.4		0.01**	0.01**
sediment, climatic		14		39.5		0.01**	0.01**
sediment, elevation, salinity		10		35.1		0.01**	0.01**
(U covariables)	(T constraining variables)						
sediment	salinity	7	2	33.8	4.0	0.01**	0.01**
sediment	elevation	7	1	30.4	0.6	0.01**	-
salinity	elevation	2	1	8.5	1.1	0.03*	-
sediment	climatic	7	6	38.8	9.0	0.01**	0.01**
sediment, salinity	climatic	9	6	41.0	6.6	0.01**	0.01**
salinity	climatic	2	6	14.7	7.3	0.01**	0.02*
climatic	salinity	6	2	14.7	3.0	0.03*	0.01**
sediment, elevation, salinity	climatic	10	6	41.7	6.6	0.01**	0.01**

Table 36. Differential approach - temporal component of the variation in data set 4 (epipelon): variation partitioning by different (sub)sets [or combinations of (sub)sets] of environmental variables (excl. spatial) and the temporal dummy variable set (for VE by other subsets than temporal, see Table 35). n(U) and n(T): number of variables selected by FS on the (sub)sets of environmental variables U and T; VE is the percentage of variance explained by the selected variables of U or by the selected variables of the two sets (U and T) together; δVE is the effect on VE of adding the second set of variables T [thus by partialling out the selected variables of U in a RDA (with FS) on T]. The p-value of this addition is calculated by a Monte Carlo permutation test (99 unrestricted permutations). ** = p=0.01; * = p≤0.05; ^{ns} = not significant.

U	T	n(U)	n(T)	VE (%)	δVE (%)	p-value 1st axis	p-value trace
(U constraining variables)							
temporal		4		6.5		0.01**	0.01**
sediment, temporal		11		36.2		0.01**	0.01**
temporal, climatic		6		12.3		0.01**	0.01**
temporal, salinity		7		14.3		0.01**	0.01**
sediment, temporal, climatic, elevation, salinity (=pelga1)		16		42.5		0.01**	0.01**
(U covariables)	(T constraining variables)						
sediment	temporal	7	4	35.8	6.0	0.01**	0.01**
sediment, climatic	temporal	14	4	40.6	1.1	0.01**	0.01**
sediment, temporal	climatic	11	6	40.0	3.8	0.01**	0.01**
temporal	climatic	4	6	13.6	7.1	0.01**	0.01**
climatic	temporal	6	4	13.6	1.9	0.09^{ns}	0.05*
temporal, salinity	climatic	7	6	16.9	2.6	0.34^{ns}	0.14^{ns}
sediment, elevation, salinity	temporal	10	4	40.9	5.8	0.01**	0.01**

Table 37. Differential approach: variation partitioning of data set 5 (epipsammon) by different (sub)sets [or combinations of (sub)sets] of environmental variables (excl. spatial and temporal variables). n(U) and n(T): number of variables selected by FS on the (sub)sets of environmental variables U and T; VE is the percentage of variance explained by the selected variables of U or by the selected variables of the two sets (U and T) together; δVE is the effect on VE of adding the second set of variables T [thus by partialling out the selected variables of U in a RDA (with FS) on T]. The p-value of this addition is calculated by a Monte Carlo permutation test (99 unrestricted permutations). ** = p=0.01; * = p≤0.05; ^{ns} = not significant.

U	T	n(U)	n(T)	VE (%)	δVE (%)	p-value 1st axis	p-value trace
(U constraining variables)							
sediment		8		21.3		0.01**	0.01**
salinity		3		8.5		0.01**	0.01**
elevation		1		2.9		0.01**	-
climatic		1		1.2		0.04*	-
sediment, salinity		10		27.4		0.01**	0.01**
sediment, climatic		11		24.4[*]		0.01**	0.01**
sediment, elevation, salinity		11		28.6		0.01**	0.01**
(U covariables)	(T constraining variables)						
sediment	salinity	8	3	27.9	6.6	0.01**	0.01**
sediment	elevation	8	1	22.5	1.2	0.01**	0.01**
salinity	elevation	3	1	11.2	2.7	0.01**	0.01**
sediment	climatic	8	1	22.4	1.1	0.03*	-
sediment, salinity	climatic	10	1	28.0	0.6	0.15^{ns}	-
salinity	climatic	3	1	9.1	0.6	0.31^{ns}	-
climatic	salinity	1	3	9.1	7.9	0.01**	0.01**
sediment, elevation, salinity	climatic	11	1	29.2	0.6	0.14^{ns}	-

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[*] Note that the TVE by the sediment and climatic variables together is higher than the sum of their individual contributions. This is mainly due to the fact that in the forward selection procedure a larger number of less significant (i.e. 0.05≥p≥0.01) have been included.

Table 38. Differential approach - temporal component of the variation in data set 5 (epipsammon): variation partitioning by different (sub)sets [or combinations of (sub)sets] of environmental variables (excl. spatial) and the temporal dummy variable set (for VE by other subsets than temporal, see Table 37). n(U) and n(T): number of variables selected by FS on the (sub)sets of environmental variables U and T; VE is the percentage of variance explained by the selected variables of U or by the selected variables of the two sets (U and T) together; δVE is the effect on VE of adding the second set of variables T [thus by partialling out the selected variables of U in a RDA (with FS) on T]. The p-value of this addition is calculated by a Monte Carlo permutation test (99 unrestricted permutations). ** = $p=0.01$; * = $p \leq 0.05$; $^{\mathrm{ns}}$ = not significant.

U	T	n(U)	n(T)	VE (%)	δVE (%)	p-value 1st axis	p-value trace
(U constraining variables)							
temporal		1		1.2		0.03*	-
sediment, temporal		9		22.4		0.01**	0.01**
temporal, climatic		1		1.2		0.04*	-
temporal, salinity		4		9.7		0.01**	0.01**
sediment, temporal, climatic, elevation, salinity (=psaga1)		13		30.5		0.01**	0.01**
(U covariables)	(T constraining variables)						
sediment	temporal	8	1	22.4	1.1	0.01**	-
sediment, climatic	temporal	11	1	25.2	0.8	0.05*	-
sediment, temporal	climatic	11	1	23.2	0.8	0.06^{ns}	-
temporal	climatic	1	1	2.1	0.9	0.09^{ns}	-
climatic	temporal	1	1	2.0[*]	0.8	0.11^{ns}	-
temporal, salinity	climatic	4	1	10.3	0.6	0.41^{ns}	-
sediment, elevation, salinity	temporal	11	1	29.7	1.1	0.01**	-

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[*] This value should be identical to the previous one (=2.1). The slight difference is most probably due to successive approximations during the calculations (cf. Borcard *et al.* 1992).

Table 39. Number of occurrences (OCC), minimum (Min), maximum (Max) and mean (Mean) abundance [log(x+1) transformed values, excluding zero values], optima and tolerances for selected taxa and environmental variables, based on weighted averaging regression (WACALIB 2.1, Line & Birks 1990) on 185 sediment samples from the Westerschelde estuary (The Netherlands). For abbreviations of environmental variables, see Table 7. For species labels, see Table 18.

					MEDI		SILT		FSAN		MSAN		SAIS		RAMO		TCMO		ELCO	
	OCC	Min	Max	Mean	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol
ACHN AMOE	53	0.939	3.408	1.846	150	34	12.2	9.5	53	17	11.4	6.5	23.5	4.4	32608	18211	11.71	4.52	1.318	0.768
ACHN CFBA	45	0.683	2.497	1.404	170	56	10.0	7.7	52	16	16.7	17.0	24.0	6.4	33589	17894	11.78	4.55	1.390	0.850
ACHN DELI	181	0.716	4.129	2.789	145	51	14.6	12.1	46	19	13.0	11.9	23.1	5.8	31386	18456	11.02	4.56	1.371	0.847
ACHN MINU	12	1.063	2.527	1.762	121	38	22.5	12.9	39	18	9.0	3.6	17.7	6.5	29154	24304	10.88	5.22	1.720	0.798
ACHN SP01	92	0.685	3.179	1.985	153	45	11.4	9.9	52	18	12.9	11.3	23.8	5.1	30152	18427	11.00	4.54	1.132	0.827
ACHN SP02	159	0.989	3.644	2.405	157	56	11.9	10.8	49	18	15.2	15.0	24.4	5.0	31375	18432	11.15	4.59	1.345	0.818
ACHN SP03	92	0.701	3.000	1.907	167	56	9.5	9.7	51	18	17.6	15.7	25.8	4.3	30772	18247	10.97	4.54	1.217	0.770
ACHN SP04	36	0.683	2.726	1.604	179	55	5.6	8.5	58	18	19.2	17.2	24.4	4.0	34054	18503	11.47	4.70	0.855	0.615
ACTP SENA	62	1.073	2.665	1.841	113	42	23.6	12.8	34	16	10.2	6.5	23.9	6.0	31544	18127	11.35	4.48	1.508	0.813
AMPH CFCO	34	0.716	2.703	1.565	138	41	14.9	11.3	46	19	10.5	6.8	21.4	6.5	31347	17924	11.07	4.75	1.470	1.056
AMPH CFDE	56	0.753	3.182	1.762	153	56	13.4	10.7	46	18	14.8	15.2	25.0	5.2	37755	19556	11.98	4.80	1.535	0.915
AMPH CFEX	34	0.716	3.019	1.850	137	36	14.9	8.7	46	15	9.7	8.0	23.6	5.0	41635	16814	14.60	3.56	1.601	1.011
AMPH CFPE	128	1.063	3.331	2.136	160	55	11.1	10.4	50	18	15.7	15.3	25.2	4.5	32274	17891	11.17	4.47	1.226	0.795
AMPH CFTE	101	0.942	3.532	1.969	156	53	11.2	11.3	51	18	13.5	14.1	23.3	5.6	34104	19068	11.80	4.68	1.398	0.888
AMPH COFF	56	0.785	3.059	1.766	135	45	16.7	13.2	45	19	10.9	7.4	24.2	6.0	35124	19539	12.23	4.15	1.469	0.912
AMPH CYMB	26	0.989	2.869	1.789	137	32	14.2	8.3	47	13	9.0	5.5	26.8	3.9	42191	19453	13.77	4.15	1.600	0.828
AMPH HYBR	12	0.737	1.975	1.524	152	42	12.3	8.0	49	16	13.3	12.9	19.2	5.9	42448	19716	13.37	4.47	0.861	0.916
AMPH LAPE	29	0.716	2.608	1.764	139	45	15.8	9.7	44	15	11.0	10.6	26.3	4.2	42950	16735	12.93	4.46	1.691	0.993
AMPH PULC	10	0.937	2.173	1.464	137	57	17.0	11.3	38	17	12.6	15.3	23.2	6.1	28894	13409	10.11	4.51	1.534	0.855
AMPH SPEC	35	0.785	2.791	1.765	129	42	18.3	13.6	44	18	10.0	6.0	24.3	7.0	35161	19392	12.62	4.19	1.346	0.850
AMPH TENE	53	0.701	2.773	1.772	159	52	10.2	10.8	53	19	13.5	14.1	21.6	5.0	36923	18086	11.55	4.77	1.285	0.994
AMPH SP02	18	0.701	1.908	1.337	224	89	7.2	8.9	35	11	38.3	26.2	27.9	4.6	32055	18556	10.35	4.31	1.651	0.429
AMPH SP05	63	0.805	3.678	1.869	141	39	14.6	11.2	48	17	10.5	7.4	23.0	5.4	39550	20049	13.11	4.66	1.441	0.851
AMPH SP06	34	0.709	3.016	1.838	128	41	16.2	11.4	43	20	8.5	8.7	20.0	5.7	31084	19439	10.97	4.97	1.821	1.075
ANOR SPEC	39	1.014	2.424	1.727	193	82	9.6	10.6	42	19	27.7	24.1	26.1	5.4	27691	16012	10.57	4.35	1.712	0.842
BERK RUTI	13	1.332	3.004	2.282	96	23	25.5	9.1	26	13	5.6	3.3	16.0	3.4	29019	16377	10.16	4.69	2.332	0.944

					MEDI		SILT		FSAN		MSAN		SAIS		RAMO		TCMO		ELCO	
	OCC	Min	Max	Mean	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol
BIRE AMBI	21	0.683	2.076	1.402	157	36	8.4	6.0	53	14	13.5	11.0	23.0	5.5	33115	14638	10.28	3.74	1.272	0.786
BIRE LUCE	142	0.771	3.749	2.339	155	51	12.0	10.8	50	18	13.8	13.1	23.1	5.4	30916	18736	10.96	4.63	1.311	0.820
BIRE SP01	10	0.683	2.160	1.553	160	69	12.4	9.7	40	19	18.7	19.2	20.4	7.0	35153	18064	9.50	3.87	1.723	0.666
BROC BROC	93	0.798	2.982	1.891	122	43	21.1	13.3	38	17	11.3	6.9	25.4	5.3	31487	18705	11.00	4.47	1.272	0.771
BROC SP01	59	0.688	2.749	1.680	174	62	9.7	9.8	50	18	20.1	18.7	25.9	4.8	34586	17173	11.86	4.38	1.492	0.797
CALO CRAS	10	0.753	1.871	1.255	158	20	4.8	3.4	62	11	9.8	5.7	23.5	3.4	15264	9643	5.98	1.08	1.200	0.792
CAMP CYMB	62	0.750	2.511	1.834	121	38	20.9	12.2	37	16	10.9	5.6	24.8	5.9	33441	17876	11.31	4.12	1.287	0.674
CATE ADHA	148	0.688	3.919	2.376	147	48	13.4	11.5	48	19	12.9	11.4	23.1	5.4	31626	18416	11.17	4.57	1.333	0.859
COCC CFPL	107	0.939	3.217	2.096	151	58	13.6	13.2	48	20	14.6	14.5	23.7	5.4	30885	18452	11.24	4.62	1.365	0.936
COCC PELT	103	0.939	3.304	2.181	151	51	12.4	12.1	50	19	13.1	11.7	23.5	5.2	29958	18056	11.01	4.59	1.365	0.880
COCC PLEU	28	1.033	2.581	1.768	135	56	18.5	11.8	39	18	15.1	14.0	25.1	6.1	25446	15995	10.06	4.23	1.245	0.611
COCC SP01	65	1.248	3.115	2.149	159	31	8.3	7.7	58	15	12.8	7.1	23.6	4.1	30445	19001	10.73	4.60	1.056	0.680
COCC SP02	81	0.973	3.074	2.134	129	45	17.3	12.8	43	20	9.9	7.6	23.0	5.8	30015	17120	11.01	4.41	1.373	0.920
CYCL ATOM	113	1.033	3.870	2.329	121	42	20.9	12.3	38	18	10.1	6.5	21.2	6.3	28945	18021	10.00	4.36	1.447	0.847
CYCL CFCA	103	0.771	2.757	1.936	127	41	19.6	12.2	40	17	11.1	6.3	24.8	5.4	32345	18137	11.85	4.38	1.292	0.742
CYCL CHOC	84	0.785	2.778	1.891	122	41	20.5	12.5	39	17	9.9	6.1	23.0	5.2	34433	18793	11.35	4.56	1.306	0.788
CYCL MENE	82	0.884	3.015	1.998	119	39	21.1	11.9	37	17	9.3	6.1	20.6	6.4	30793	17192	10.38	4.40	1.476	0.859
CYCL SP01	19	0.771	2.476	1.835	110	45	25.7	14.8	34	18	9.6	5.2	24.6	4.6	34729	13566	13.27	4.41	1.225	0.899
CYCL SP03	13	1.068	1.908	1.518	130	36	18.0	8.1	39	14	12.1	5.4	28.2	3.0	25028	17528	11.41	3.83	1.356	0.593
CYMA BELG	176	0.685	3.813	2.805	132	43	17.5	12.2	43	18	11.2	7.7	23.7	5.9	31145	18282	10.98	4.52	1.371	0.832
CYMA SP01	56	0.840	2.431	1.722	174	59	8.4	8.6	52	17	18.3	17.4	24.2	5.6	37141	16478	12.37	4.17	1.282	0.719
DELP MINU	176	0.709	3.888	2.874	132	43	17.6	12.3	43	18	11.2	7.7	23.7	5.9	30990	18240	10.96	4.53	1.371	0.834
DELP SURI	114	0.785	2.920	2.059	125	39	19.6	11.3	39	17	11.0	5.7	24.8	5.5	30942	17695	11.11	4.40	1.332	0.779
DICK SP01	20	0.903	2.539	1.732	140	56	17.1	13.9	44	19	13.2	11.6	25.2	5.8	39089	18195	12.80	4.06	1.763	0.972
DICK SUBI	13	0.753	2.440	1.630	159	28	8.3	7.7	60	14	11.3	5.3	22.2	5.1	30568	20436	11.03	4.72	1.175	1.108
DIME MINO	105	0.688	2.859	1.913	141	49	16.0	13.0	46	19	12.8	9.5	25.8	4.2	32525	17714	11.44	4.32	1.063	0.708
DIPL AEST	64	0.683	2.402	1.749	125	38	20.1	10.1	38	15	11.9	7.1	24.1	5.8	27444	16171	10.19	4.29	1.292	0.699
DIPL DIDY	27	1.290	2.233	1.737	152	24	10.0	5.7	55	12	10.7	6.6	23.3	4.0	32553	16471	12.05	4.14	0.992	0.713
EUNO DUBI	22	0.771	2.511	1.723	114	38	22.6	12.2	35	16	9.2	5.1	23.5	4.8	36535	17786	11.31	4.63	1.077	0.626
FALL AEQU	136	0.884	3.408	2.100	156	55	12.1	11.6	50	18	14.8	14.4	24.8	4.8	29837	18015	10.76	4.57	1.259	0.801
FALL CRYP	53	1.014	2.710	1.815	194	72	8.1	10.8	49	18	25.9	21.3	26.9	4.0	34593	17478	12.34	4.26	1.550	0.676
FALL FORC	29	0.683	2.236	1.407	161	40	10.8	6.6	53	14	14.6	11.8	25.2	4.8	33288	18929	10.93	4.50	1.410	1.016
FALL TENE	97	0.683	2.856	1.817	145	49	13.2	11.2	47	19	12.3	12.0	22.5	6.1	28475	18406	10.22	4.49	1.390	0.882
FALL SP01	18	0.685	2.206	1.326	162	51	10.0	7.0	50	15	15.7	15.3	24.4	4.8	30091	17895	10.96	4.23	1.318	0.634

					MEDI		SILT		FSAN		MSAN		SAIS		RAMO		TCMO		ELCO	
	OCC	Min	Max	Mean	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol
FALL SP02	37	0.709	2.603	1.460	190	79	8.0	12.8	48	20	24.2	23.7	26.8	4.4	30084	18012	11.07	4.67	1.273	0.836
FALL SP03	41	0.683	2.206	1.388	183	73	9.9	10.3	46	18	24.1	21.0	26.1	4.8	33556	16888	11.30	4.31	1.381	0.632
FALL SP04	10	0.709	1.937	1.293	212	85	9.2	10.4	38	11	33.7	25.4	26.9	5.1	36128	13247	11.38	4.21	1.463	0.805
FRAG CAPE	64	0.720	3.069	1.757	153	49	11.4	9.4	51	18	13.0	12.0	24.8	5.5	26126	17596	10.49	4.43	1.383	0.826
FRAG CFAT	127	0.683	3.611	2.310	144	43	13.5	10.8	49	19	11.1	9.4	22.3	5.9	31747	18636	11.14	4.65	1.401	0.946
FRAG SCHU	24	0.685	2.903	1.796	159	51	11.0	12.9	54	17	13.4	12.8	24.9	5.6	32187	18921	9.58	4.39	1.811	0.913
FRAG SP01	153	0.971	3.355	2.285	128	42	18.8	12.3	41	18	10.6	7.1	23.6	6.0	31778	18323	11.17	4.56	1.403	0.819
GOMP ANPA	20	0.884	2.098	1.787	132	39	17.4	10.4	41	17	12.0	7.2	22.1	5.8	25975	19113	9.58	4.65	1.068	0.762
LUTI MUTI	15	0.750	2.281	1.741	119	42	21.4	15.2	41	19	8.1	4.7	18.1	6.1	23034	16746	8.52	3.96	1.680	0.867
MART MART	48	0.937	2.856	1.949	149	47	12.6	9.8	48	17	12.7	12.1	20.8	7.0	27190	16913	10.27	4.18	1.331	0.834
NADI SP05	23	0.941	2.344	1.794	173	54	7.9	8.6	55	17	16.7	16.6	23.5	4.4	36790	13279	12.58	4.29	1.569	0.980
NAVI ABSC	38	0.716	2.495	1.749	132	45	17.9	10.8	41	17	12.2	9.0	25.7	5.2	35238	16020	13.18	3.78	1.367	0.773
NAVI ARRO	120	0.840	3.615	2.275	126	42	19.5	12.0	40	18	11.1	6.6	24.7	5.3	30348	18196	10.42	4.32	1.391	0.786
NAVI BIPU	33	0.709	2.236	1.551	152	42	9.5	8.7	54	16	11.8	12.0	23.6	4.9	25820	14037	8.28	2.92	1.344	0.931
NAVI CFMO	19	0.720	2.022	1.304	213	97	9.7	11.8	32	12	36.9	26.0	29.1	4.4	32131	15371	12.05	3.82	1.486	0.552
NAVI DIGI	19	0.973	2.212	1.448	151	28	11.9	7.9	53	13	12.0	4.6	28.0	3.9	32257	19075	11.28	4.35	1.360	1.032
NAVI DISE	156	1.436	3.435	2.360	157	54	11.8	10.3	49	18	14.9	14.5	24.3	5.5	31491	18471	11.08	4.65	1.330	0.830
NAVI FIAC	26	0.966	2.212	1.642	134	28	15.0	7.1	44	14	10.0	6.4	22.0	6.1	36904	17783	12.29	4.23	1.206	0.853
NAVI FLAN	134	0.683	4.177	2.231	124	43	19.6	12.6	40	19	10.2	7.2	22.2	6.1	31040	18022	10.31	4.51	1.464	0.836
NAVI GREG	94	0.753	3.749	2.229	123	39	19.4	11.1	40	18	8.8	6.1	20.0	5.8	35411	18966	11.97	4.67	1.547	0.903
NAVI GRF1	126	0.716	3.433	2.049	159	62	12.2	12.2	48	19	16.1	16.6	23.6	5.8	32175	18585	10.98	4.62	1.419	0.824
NAVI MENI	41	0.771	2.770	1.848	153	47	11.3	12.7	53	20	13.1	10.1	23.9	4.3	23070	15143	7.75	2.97	1.028	0.688
NAVI MICR	61	0.805	3.756	2.003	121	45	21.9	12.2	37	17	10.9	7.5	23.3	5.6	38814	16425	11.46	4.27	1.516	0.808
NAVI PALP	44	0.750	2.411	1.627	142	33	11.4	9.0	51	17	9.9	6.8	22.9	5.3	27289	17992	9.46	4.31	1.486	0.821
NAVI PERM	179	0.963	3.728	2.587	141	53	16.3	12.4	43	19	13.3	12.2	24.1	5.8	30759	17995	10.88	4.50	1.340	0.811
NAVI PHYL	99	0.688	4.056	2.150	120	43	21.3	12.2	37	17	9.8	7.1	21.8	6.9	32740	18072	11.21	4.51	1.550	0.835
NAVI SALI	31	1.063	2.782	1.970	130	41	19.7	10.3	41	17	10.7	6.8	21.7	6.7	34912	18432	12.82	4.44	1.779	1.076
NAVI STAR	91	0.683	3.580	1.868	146	47	13.2	10.1	47	18	12.3	12.0	22.9	5.6	32934	19288	10.96	4.79	1.672	0.938
NAVI SP01	132	0.771	3.343	2.224	161	54	10.8	10.3	51	18	15.6	14.8	23.5	5.5	31903	18542	11.17	4.58	1.345	0.804
NAVI SP02	62	0.716	2.731	1.628	188	60	6.1	6.4	54	17	21.9	19.3	26.0	3.7	30761	18435	10.49	4.50	1.282	0.779
NAVI SP03	79	0.683	3.517	1.865	149	54	14.3	10.4	45	17	13.7	14.4	23.6	6.2	35927	20363	12.05	4.97	1.775	0.899
NAVI SP04	75	0.701	2.879	1.854	176	48	6.5	6.1	57	14	17.5	15.6	25.1	4.4	29731	17903	10.63	4.43	1.153	0.792
NAVI SP05	10	0.798	1.929	1.530	168	39	7.2	4.9	59	13	14.3	14.3	23.4	4.8	12512	9084	5.78	0.94	1.638	1.011
NAVI SP07	33	0.688	3.545	1.852	166	50	9.8	8.6	52	15	16.5	13.5	20.9	6.5	32579	18279	11.18	4.55	1.347	0.792

					MEDI		SILT		FSAN		MSAN		SAIS		RAMO		TCMO		ELCO	
	OCC	Min	Max	Mean	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol
NAVI SP08	26	0.716	2.484	1.532	143	52	15.5	11.0	43	18	13.6	13.4	22.4	6.3	33575	15789	11.54	4.63	1.678	0.948
NAVI SP10	54	0.720	3.160	1.997	141	47	15.8	12.3	46	19	12.7	9.3	24.1	4.4	22468	13528	7.28	2.66	1.394	0.854
NAVI SP12	56	0.737	2.406	1.557	137	47	16.2	13.1	44	19	12.7	8.7	25.8	4.6	29733	17375	11.94	4.47	1.352	0.751
NAVI CSAL	23	0.785	2.660	1.727	138	45	13.6	9.0	45	16	10.5	12.4	23.3	6.7	30058	19984	10.58	4.55	1.972	1.057
NAVI CFFL	16	1.227	3.467	2.131	109	35	25.2	9.8	32	12	9.6	4.4	21.7	5.6	42671	10734	11.23	3.53	1.595	0.924
NITZ CFFR	26	0.805	2.665	1.743	124	44	19.8	11.0	37	17	11.9	8.9	23.8	6.8	28772	19507	8.96	4.20	1.478	0.814
NITZ FRUS	137	0.683	3.096	2.004	144	51	14.4	13.0	47	20	13.1	11.4	24.5	4.9	30959	18375	10.90	4.55	1.182	0.759
NITZ SP01	17	0.707	2.036	1.404	166	51	9.9	7.1	52	15	15.6	14.0	25.0	5.5	33102	13674	12.04	4.17	1.183	0.891
NITZ SP02	33	0.750	2.858	1.999	125	45	19.2	13.6	40	17	10.0	7.2	23.2	5.5	41300	19178	12.91	4.80	1.589	0.781
NITZ SP04	32	0.716	3.016	2.054	114	40	22.2	11.6	35	17	8.9	7.2	20.2	6.2	35933	18070	12.13	4.82	1.829	0.996
ODON AURI	76	0.753	3.012	1.887	125	40	20.6	11.8	39	16	11.9	6.0	25.5	4.7	30130	17549	10.52	4.32	1.252	0.679
ODON ROST	84	0.716	2.687	1.854	118	42	22.0	12.9	36	17	10.6	6.8	24.1	6.4	28928	18678	10.50	4.42	1.382	0.785
OPEP GUEN	172	0.683	4.324	2.619	139	45	15.6	12.2	46	19	11.6	9.0	23.0	5.9	31988	18421	11.26	4.56	1.403	0.885
OPEP MUTA	136	0.683	3.375	2.085	144	43	13.9	11.0	48	18	12.0	9.3	22.5	6.1	30207	17699	10.81	4.45	1.361	0.832
OPEP SP01	58	0.701	2.771	1.714	162	66	12.6	11.9	46	18	17.5	18.0	25.9	6.1	20749	15665	9.51	4.36	1.563	0.856
OPEP SPEA	33	0.683	2.475	1.654	154	46	12.4	10.3	51	19	14.1	10.5	24.3	4.5	30447	16849	10.75	4.29	1.668	0.894
PARA SULC	158	0.683	3.473	2.394	129	43	18.6	12.2	41	18	11.2	7.3	23.9	5.9	30644	18029	10.86	4.49	1.383	0.824
PARL SP01	18	0.716	2.165	1.601	147	31	10.1	5.1	50	9	10.3	10.1	22.8	5.7	34442	15236	10.91	4.53	1.583	0.687
PARL SP02	54	0.683	2.935	1.794	129	53	18.6	11.9	38	18	11.1	11.9	18.6	6.8	27519	17583	9.51	4.27	1.615	0.833
PLAG MINI	70	0.750	2.665	1.666	168	71	12.2	11.8	45	18	20.5	19.4	27.1	4.5	30374	18042	11.47	4.35	1.267	0.729
PLAG SIGM	85	0.884	2.839	1.833	123	46	21.7	13.1	37	18	11.7	7.2	25.3	5.6	31305	18666	11.16	4.61	1.380	0.817
PLAG SP01	81	0.683	2.922	1.901	124	43	20.0	12.9	40	18	10.2	6.8	23.6	5.4	34255	17854	11.08	4.79	1.277	0.748
PLAG STAU	40	0.785	2.860	1.932	158	32	9.2	8.2	58	16	12.3	8.0	24.5	3.3	30430	18472	11.27	4.61	0.796	0.688
PLAG VANH	131	0.753	2.973	2.064	125	40	19.6	12.3	40	18	10.5	6.0	23.7	5.9	30939	18255	10.70	4.49	1.402	0.835
PLEU AEST	16	0.989	2.612	1.692	127	45	19.4	14.1	40	17	11.9	6.1	29.1	3.2	33867	17789	12.29	4.19	1.504	0.824
PODO STEL	10	1.068	2.009	1.602	111	33	25.0	8.2	34	16	9.1	3.2	26.1	5.4	28985	19841	10.01	4.93	0.980	0.681
PSAM PADE	40	0.771	2.608	1.755	121	39	21.0	12.2	37	16	11.6	6.5	25.4	5.5	32128	20023	10.84	4.76	1.246	0.643
PSEU PERM	169	0.978	3.729	2.368	146	53	14.6	12.2	46	19	13.4	12.5	23.9	5.6	31476	18543	10.89	4.60	1.348	0.809
PSEU WEST	19	0.840	2.206	1.670	118	38	22.2	10.4	35	17	11.1	4.2	25.6	6.3	23635	15793	10.02	3.98	1.300	0.791
RHAP AMPH	147	0.750	3.234	2.187	126	40	19.3	11.6	40	18	10.5	6.3	23.3	6.1	30944	18248	10.85	4.48	1.435	0.849
STAU CONS	14	0.701	1.908	1.431	150	42	12.5	9.3	50	15	12.0	10.7	24.2	5.8	34774	18302	12.30	4.64	1.528	1.063
STAU SALI	29	0.750	3.455	1.847	120	43	20.9	14.0	39	18	8.8	6.0	19.4	6.7	38578	17366	11.80	4.47	1.492	0.722
THAL ANGU	101	0.716	2.958	1.915	123	41	21.2	12.2	38	17	11.4	5.9	24.4	5.8	29695	17298	10.50	4.29	1.279	0.726
THAL CURV	69	0.750	3.163	2.017	116	40	23.1	12.3	35	16	10.3	5.5	24.1	5.3	36323	17692	11.10	4.49	1.241	0.724

					MEDI		SILT		FSAN		MSAN		SAIS		RAMO		TCMO		ELCO	
	OCC	Min	Max	Mean	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol	Opt	Tol
THAL DECI	144	0.683	3.288	2.263	125	42	20.0	12.2	39	18	10.5	7.1	23.5	6.2	31010	18231	11.02	4.46	1.399	0.830
THAL NITZ	106	0.683	3.164	1.971	123	44	21.1	12.5	38	17	11.0	7.4	23.8	6.1	31941	18287	11.03	4.51	1.429	0.818
THAL PROS	175	0.971	4.499	3.102	131	43	17.8	12.3	42	19	11.0	7.6	23.2	6.0	31682	18402	11.07	4.54	1.373	0.834
THAL TENE	12	1.227	2.061	1.725	112	51	24.3	17.2	35	20	10.2	5.9	24.4	4.2	38016	17855	11.40	4.49	1.116	0.594
THAL TENE	13	1.173	2.371	1.797	104	30	26.4	10.0	30	11	11.0	5.3	22.3	6.0	22161	11712	9.90	3.18	1.231	0.631
TRYB APIC	26	1.173	2.856	2.060	103	36	27.0	12.6	31	15	7.6	4.9	18.4	6.1	36967	17488	12.05	4.24	1.829	0.868

Table 40. Preliminary checklist of Cyanobacteria and Protista (excl. Bacillariophyta) observed in samples from the Westerschelde estuary collected in summer 1992. Classification according to Margulis *et al.* (1990) and van den Hoek *et al.* (1993). Identification was mainly based on Kaas *et al.* (1985), Larsen & Patterson (1990) and Larsen (1987).

REGNUM PROKARYOTA Phylum CYANOBACTERIA Class *CYANOPHYCEAE*	
	Merismopedia glauca (Ehrenberg) Nägeli *Microcoleus chthonoplastes* Gomont *Microcrocis sabulicola* (Lagerheim) Geitler *Lyngbya* cf. *fragilis* (Gomont) Compère *Oscillatoria* cf. *brevis* (Kützing) Gomont *Spirulina major* Kützing ex Gomont
REGNUM EUKARYOTA Phylum CRYPTOPHYTA Class *CRYPTOPHYCEAE*	
	Chroomonas sp. *Cryptomonas* spp. *Platychilomonas psammobia* Larsen & Patterson
Phylum ZOOMASTIGINA Class *KINETOPLASTIDA*	
	Bodo spp. *Rhynchomonas* sp.
Phylym EUGLENIDA Class *EUGLENOPHYCEAE*	
	Euglena deses Ehrenberg *Heteronema* sp.
Phylym DINOFLAGELLATA Class *DINOPHYCEAE*	
	Amphidinium britannicum (Herdman) Lebour *Amphidinium* cf. *herdmanii* Kofoid & Swezy *Amphidinium operculatum* Claparède & Lachmann *Amphidinium semilunatum* Herdman *Amphidinium* spp. *Gymnodinium* sp. *Katodinium* sp. *Prorocentrum* sp. *Protaspis* sp.
Phylum CHRYSOPHYTA Class *PEDINELLOPHYCEAE*	
	Pteridomonas danica Patterson & Fenchel
Phylum CHLOROPHYTA Class *CHLOROPHYCEAE*	
	Chlamydomonas spp.

Table 41. List of the dominant epipelic and epipsammic taxa in the 32 sampling stations in the Westerschelde estuary during the sampling period. See text for more details.

EPIPELON	EPIPSAMMON
Amphora sp. 5	*Achnanthes amoena*
A. sp. 6	*Achnanthidium delicatulum*
Cymatosira belgica	*A.* sp. 2
Delphineis minutissima	*Amphora* cf. *pediculus*
D. surirella	*A.* cf. *subacutiuscula*
Fragilaria sp. 1	*Anorthoneis* spp.
Navicula arenaria var. *rostellata*	*Biremis lucens*
N. flanatica	*Catenula adhaerens*
N. gregaria	*Cocconeis peltoides*
N. gregaria f. 1	*C.* cf. *placentula*
N. meniscus	*C.* sp. 1
N. microdigitoradiata	*C.* sp. 2
N. cf. *perminuta*	*Fallacia cryptolyra*
N. phyllepta	*Fragilaria* cf. *atomus*
N. starmachioides	*Navicula diserta*
N. sp. 10	*N.* sp. 1
Paralia sulcata	*N.* sp. 7
Parlibellus sp. 2	*Nitzschia* cf. *frustulum*
Rhaphoneis amphiceros	*Opephora guenter-grassii*
Staurophora salina	*O. mutabilis*
Thalassiosira decipiens	*Pseudostaurosira perminuta*
T. proschkinae	

FIGURES

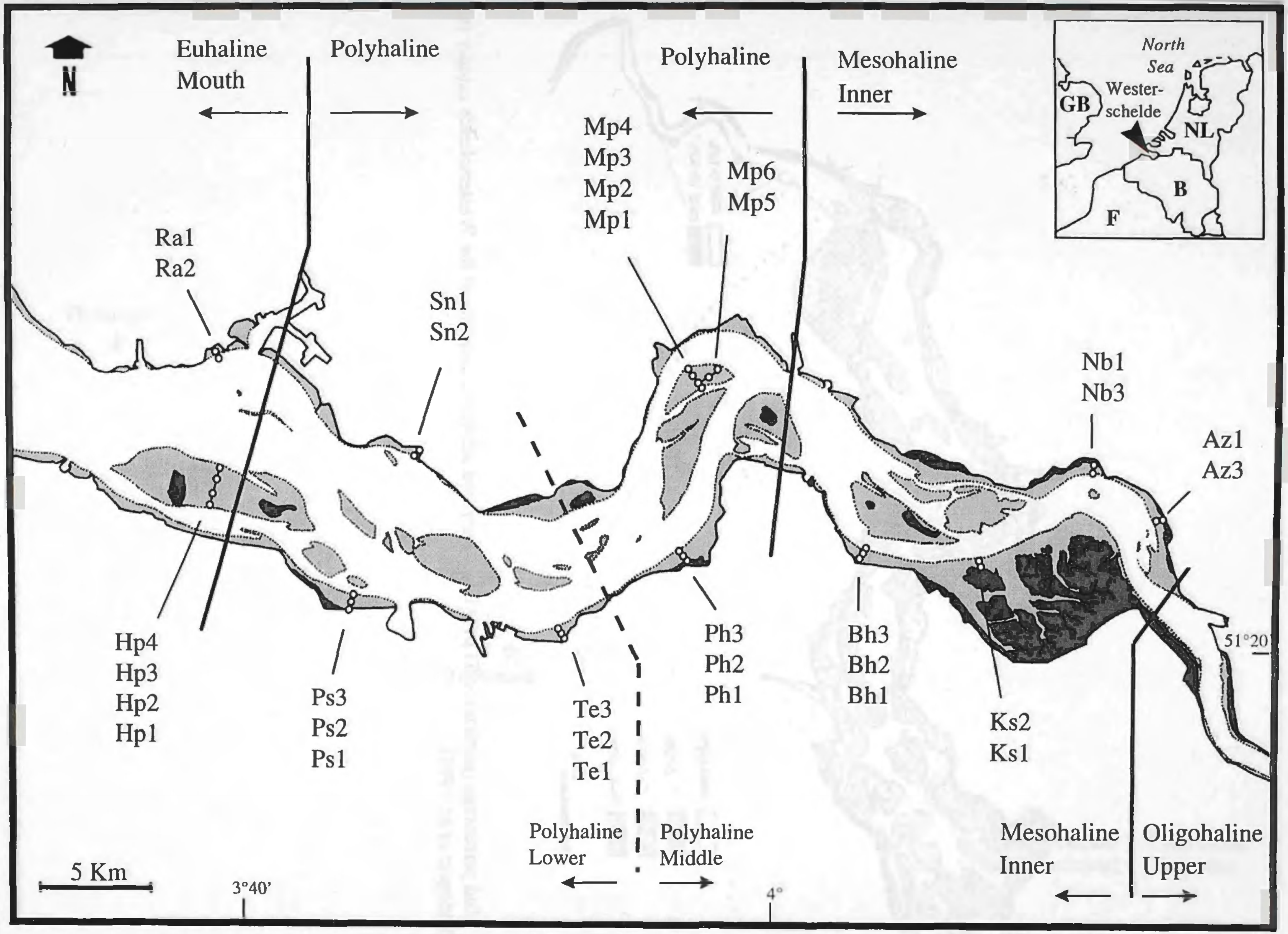


Fig. 1. Map of the Westerschelde estuary showing the position of the salinity zones (cf. McLusky 1993)(average value for period October 1991-October 1992) and the location of the sampling stations (see also Fig. 2). Intertidal areas below mean high water are shown in light grey, intertidal and supra-tidal areas above mean high water (predominantly saltmarshes) in dark grey.

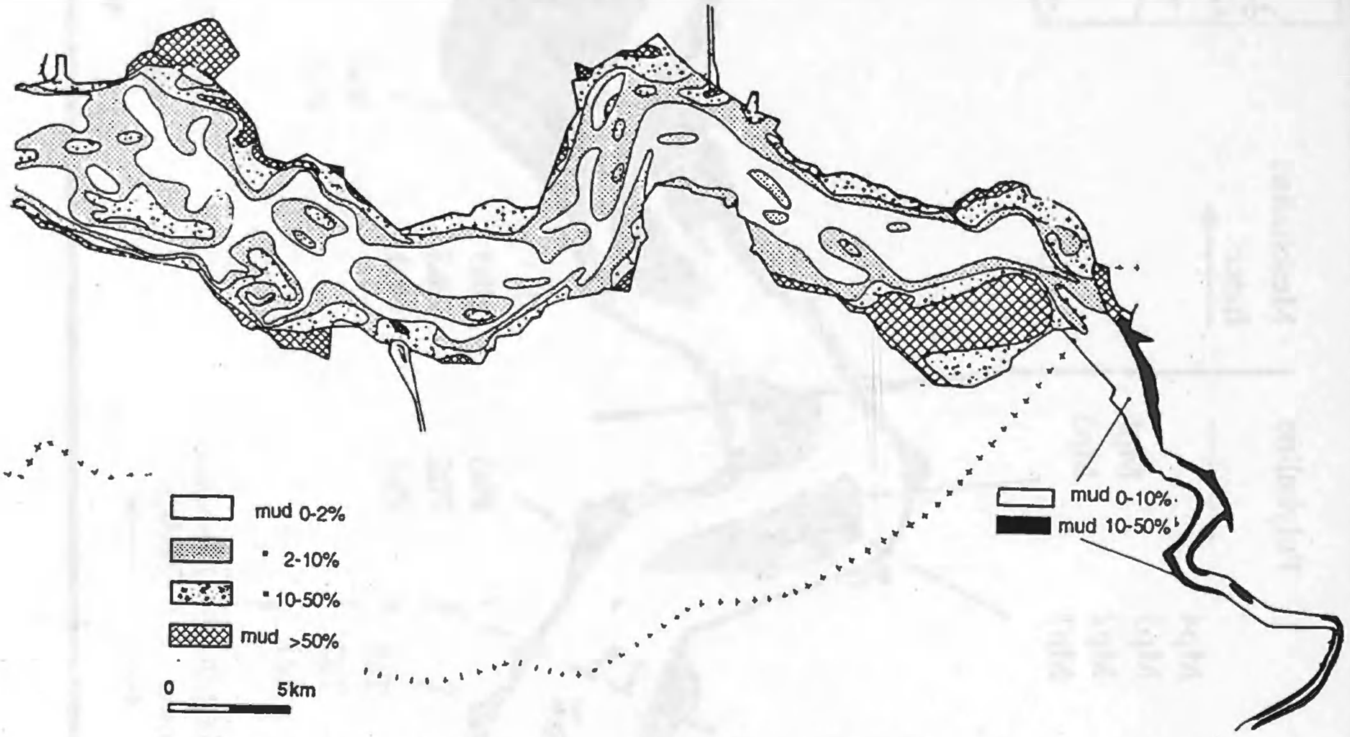


Fig. 2. Mud percentage (particles < 63 μm) in the inter-and subtidal sediments of the Westerschelde estuary (after Van Maldegem *et al.* 1993).

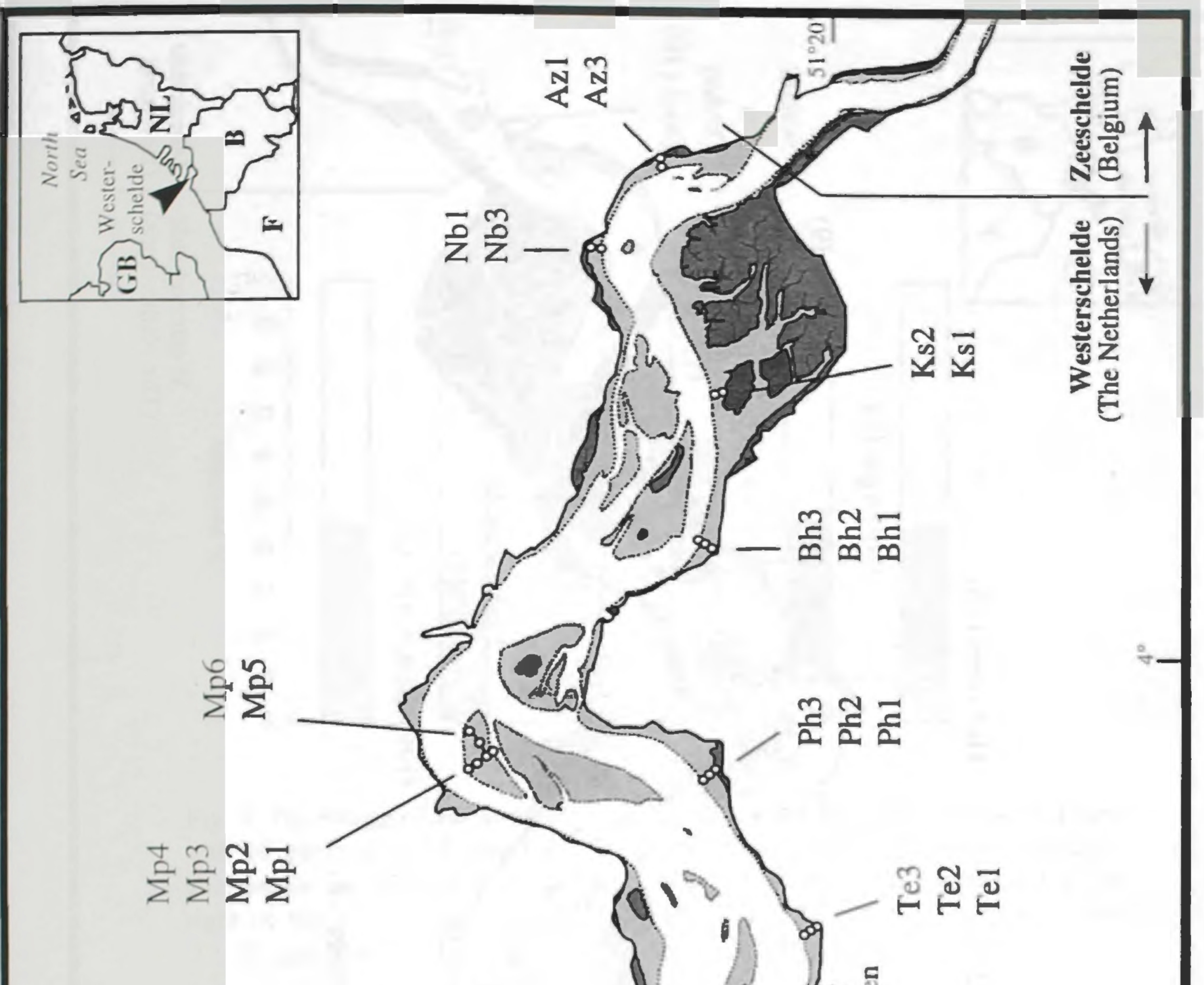


Fig. 3. Map of the Westerschelde estuary showing the location of the 11 intertidal transects with the 32 sampling stations. Intertid areas below mean high water are shown in light grey, intertidal and supra-tidal areas above mean high water (predominantl saltmarshes) in dark grey.

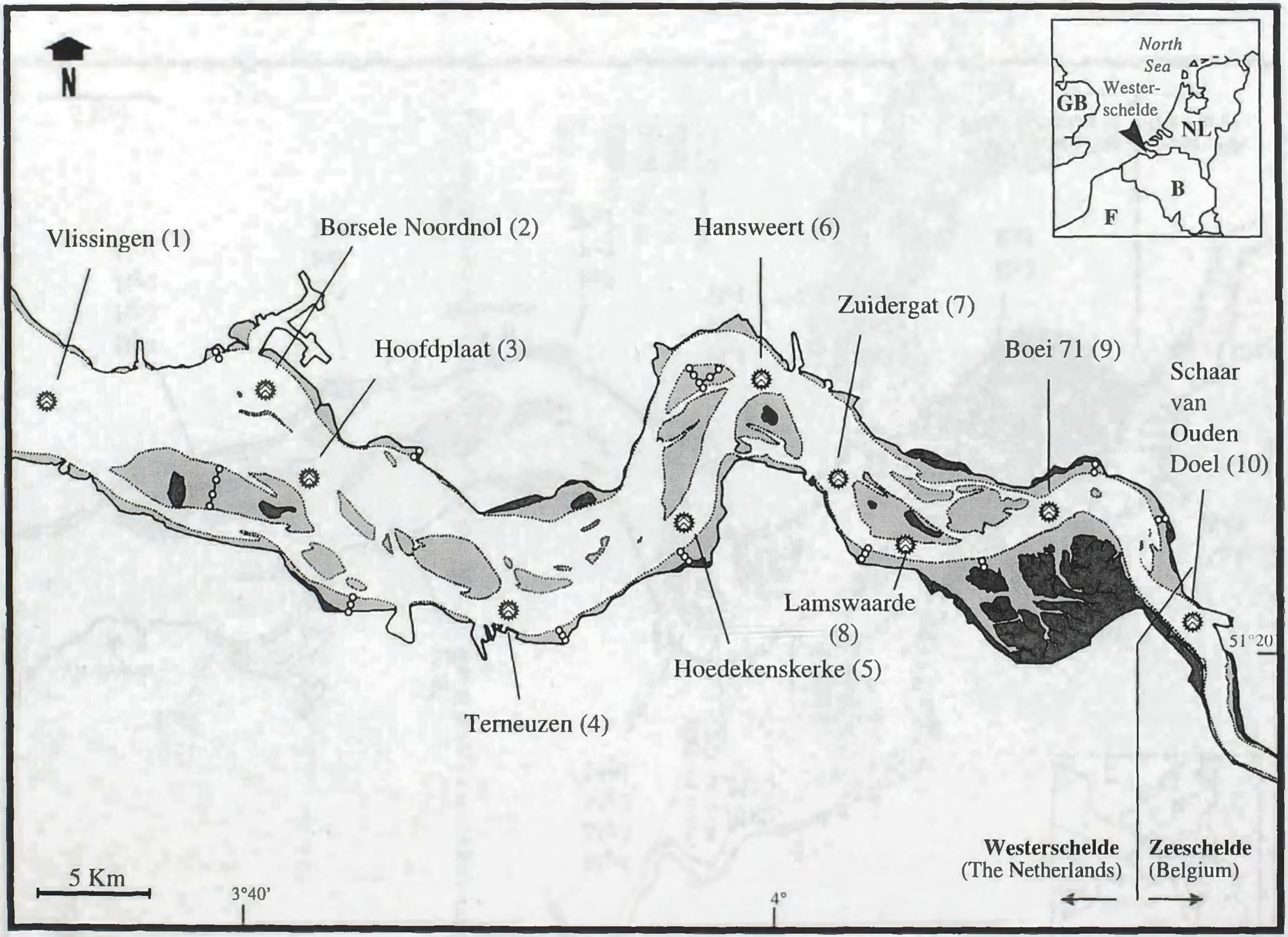


Fig. 4. Map of Westerschelde estuary showing the position of 10 pelagic stations.

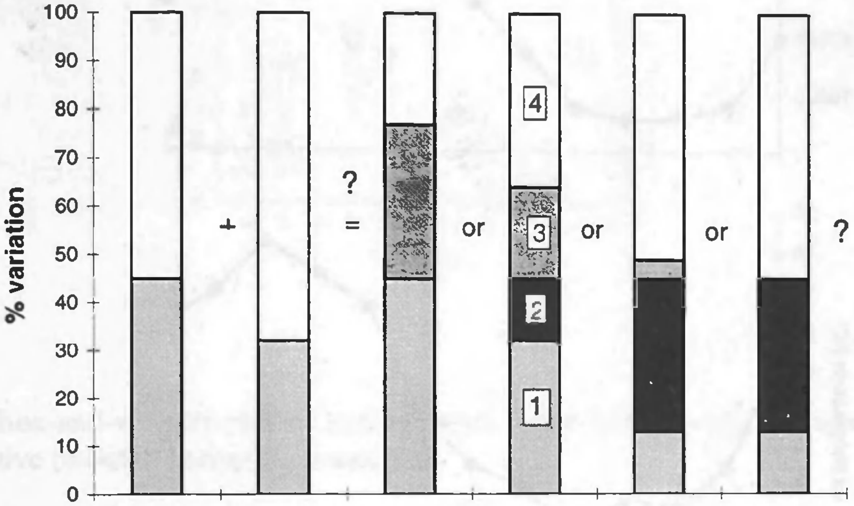


Fig. 5. Percentage of variation of a species data matrix explained by two different sets of environmental variables, U and T (two left-hand columns). Separate analyses do not allow discrimination between the 4 situations represented at the right of the equals sign. 1 = U/T; 2 = $U \cap T$; 3 = T/U; 1-3 = $U \cup T$; 4 = 100-($U \cup T$)(unexplained variation)(after Borcard *et al.* 1992).

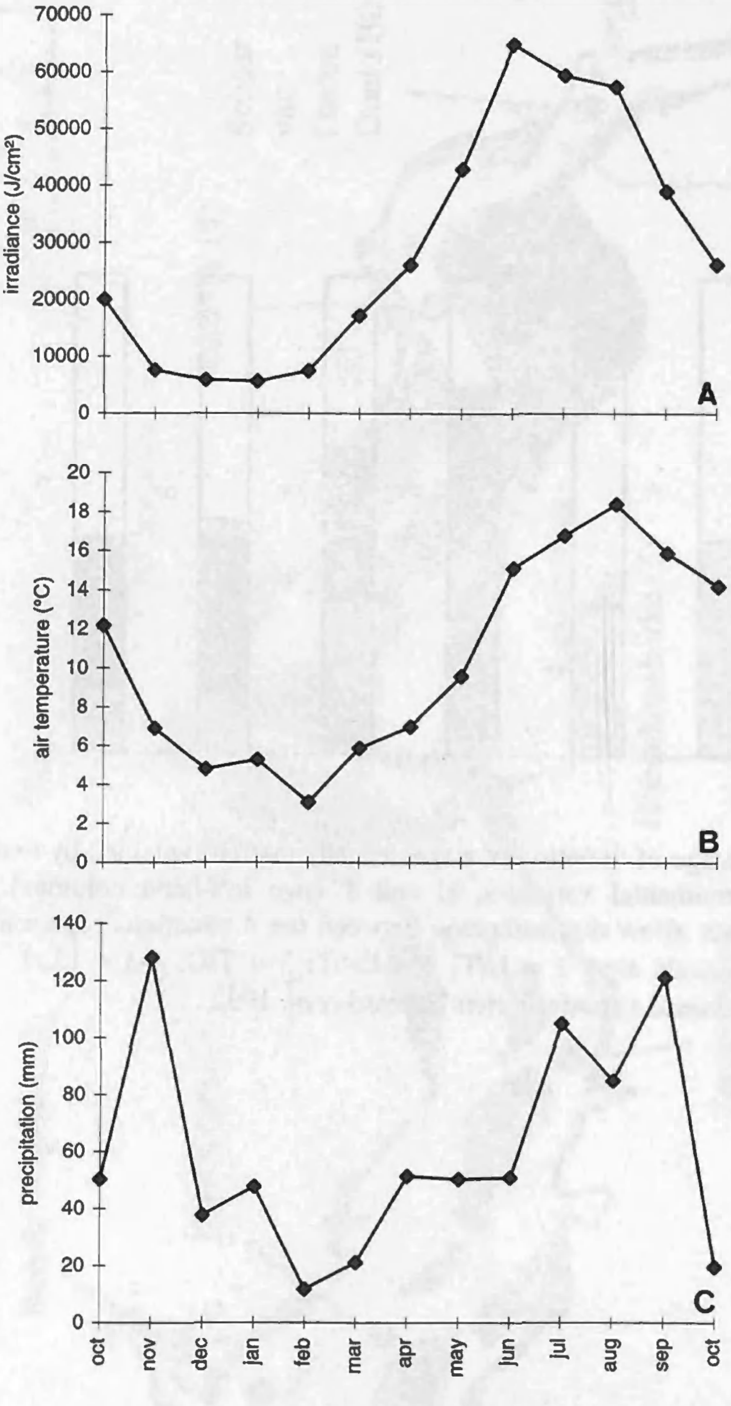


Fig. 6. a: total irradiance; b: average air temperature; c: precipitation during the sampling period (October 1991-October 1992).

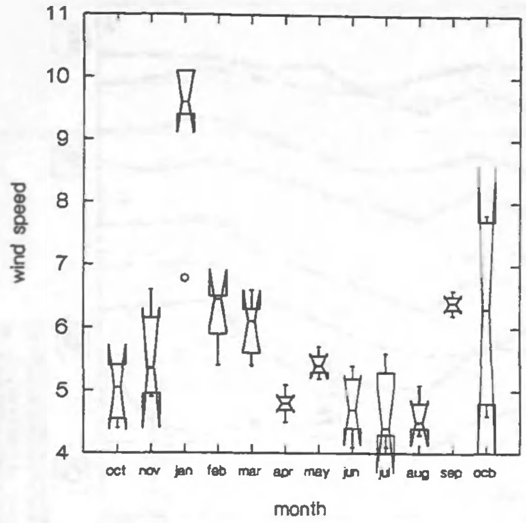


Fig. 7. Box-and-whisker plot of average wind speed (m/s) during the week preceding the consecutive (monthly) sampling occasions.

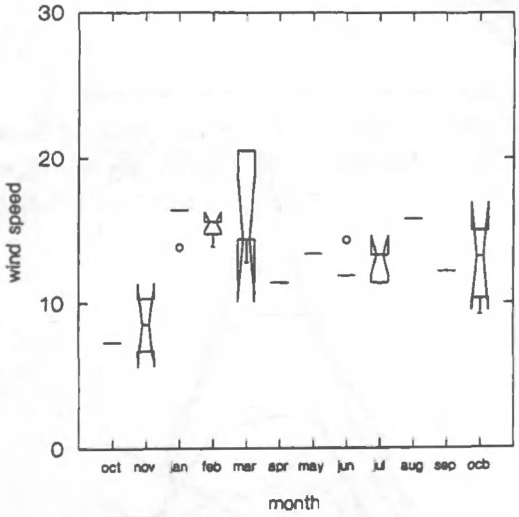


Fig. 8. Box-and-whisker plot of maximal wind speed (m/s) recorded during the week preceding the consecutive (monthly) sampling occasions.

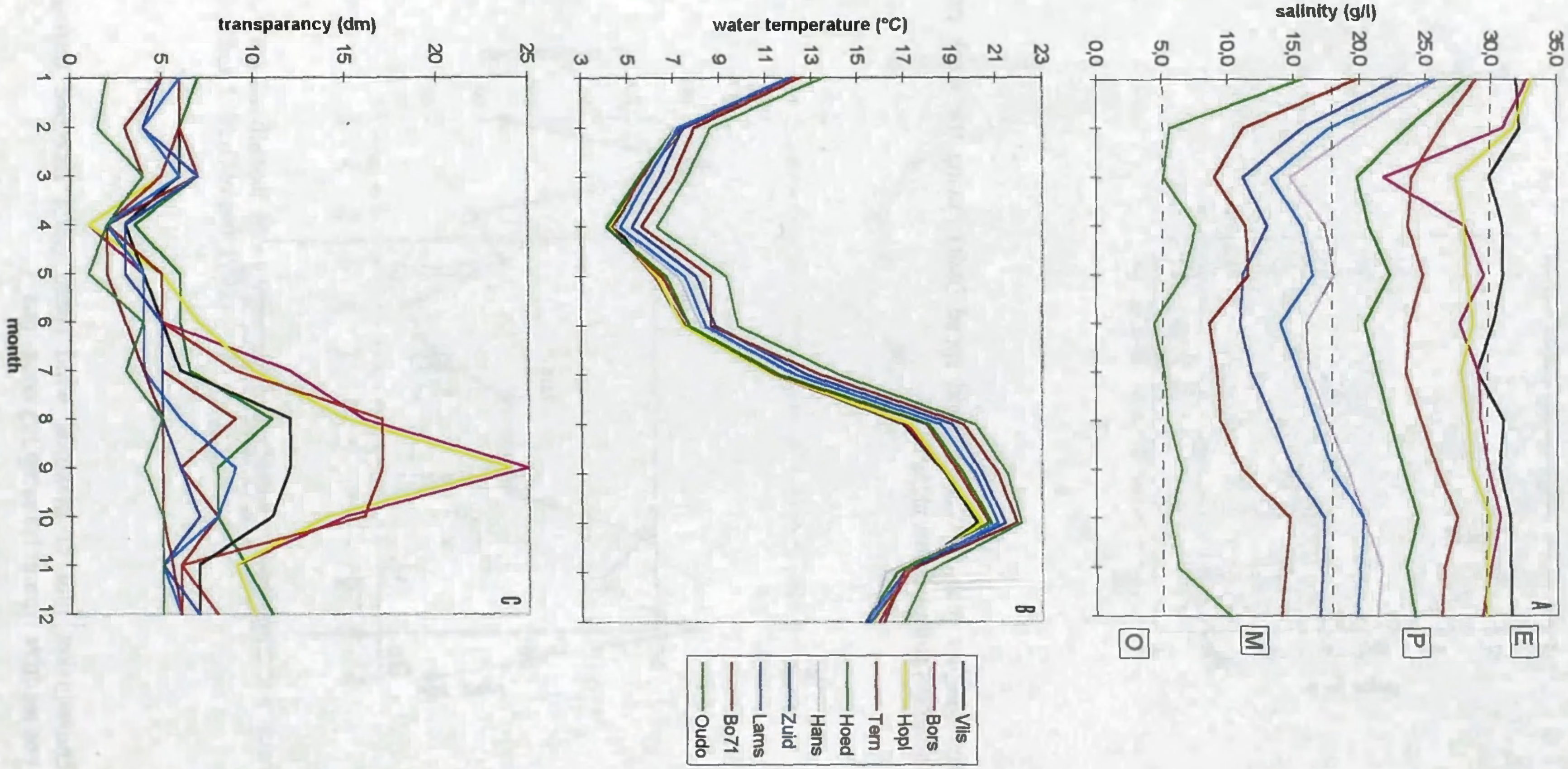


Fig. 9. Seasonal fluctuations in water column salinity (‰)(A), water column temperature (B) and transparancy (C) in 10 pelagic stations (cf. Fig. 4) in the Westerschelde estuary during the period October 1991-October 1992. E: euhaline; P: polyhaline; M: mesohaline; O: oligohaline to freshwater. 1: Oct. 1991; 2: Nov. 1991; 3: Jan. 1992 etc. until 12: Oct. 1992. Vlis: Vlissingen, Bors: Borsele Noordnol, Hopl: Hoofdplaat, Tern: Terneuzen, Hoed: Hoedekenskerke, Hans: Hansweert, Zuid: Zuidergat, Bo71: Boei 71, Oudo: Schaar van Ouden Doel.

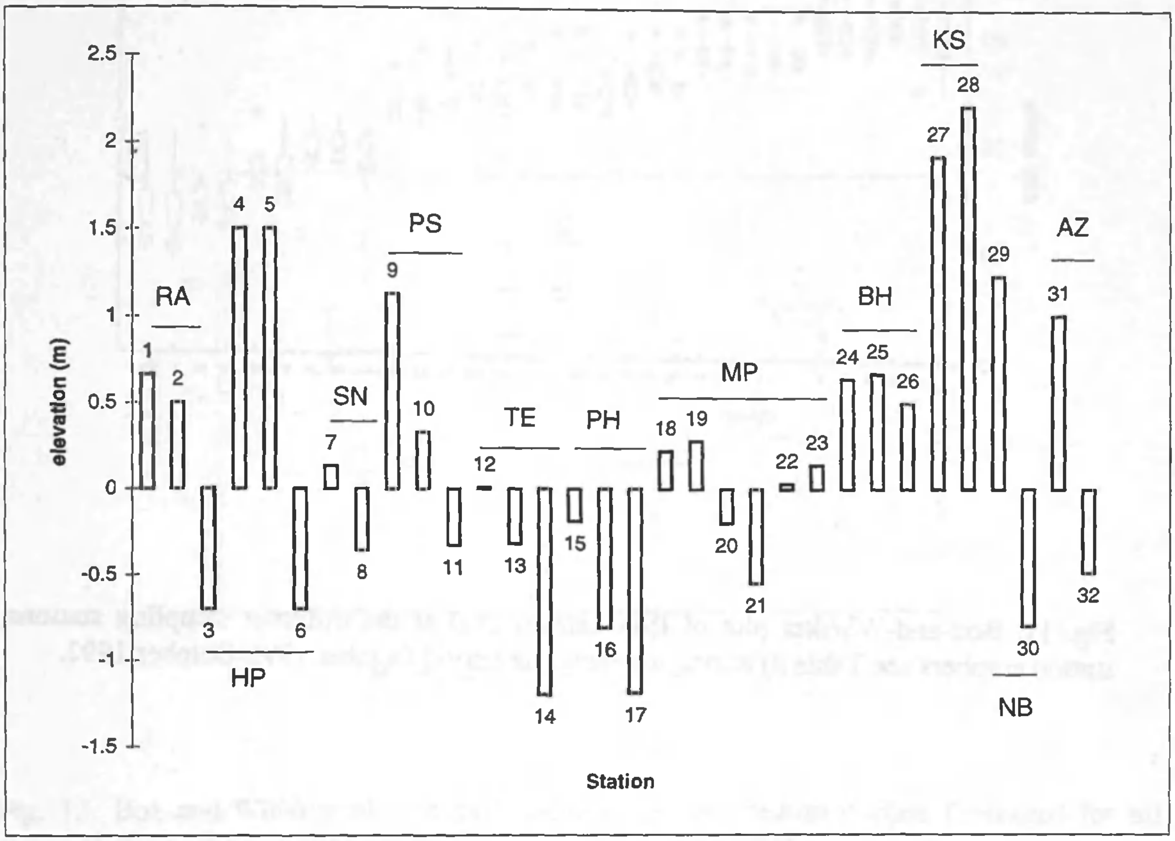


Fig. 10. Elevation of 32 sampling stations along the longitudinal estuarine gradient. Elevation is given as the height of the station (in meter) in relation to Mean Tidal Level. For transect abbreviations and station numbers, see Table 3.

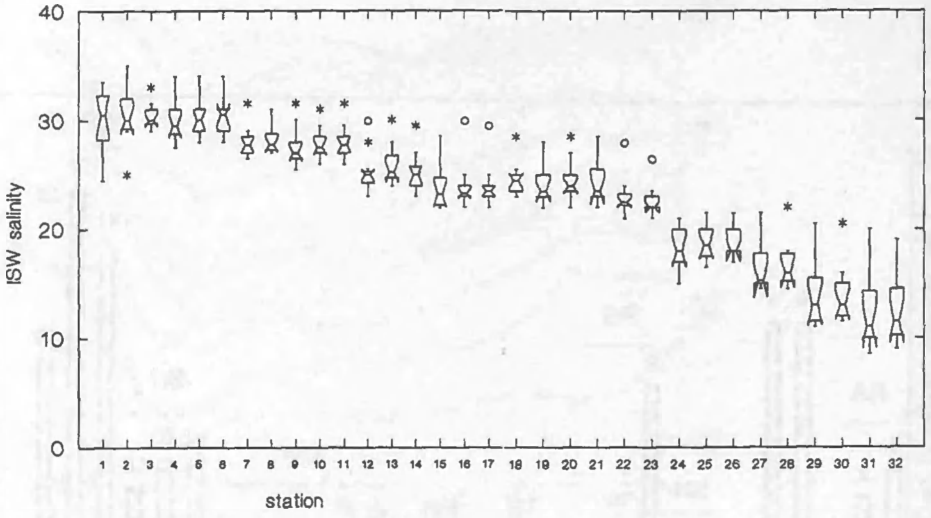


Fig. 11. Box-and-Whisker plot of ISW salinity (‰) at the different sampling stations (for station numbers see Table 3) during the sampling period October 1991-October 1992.

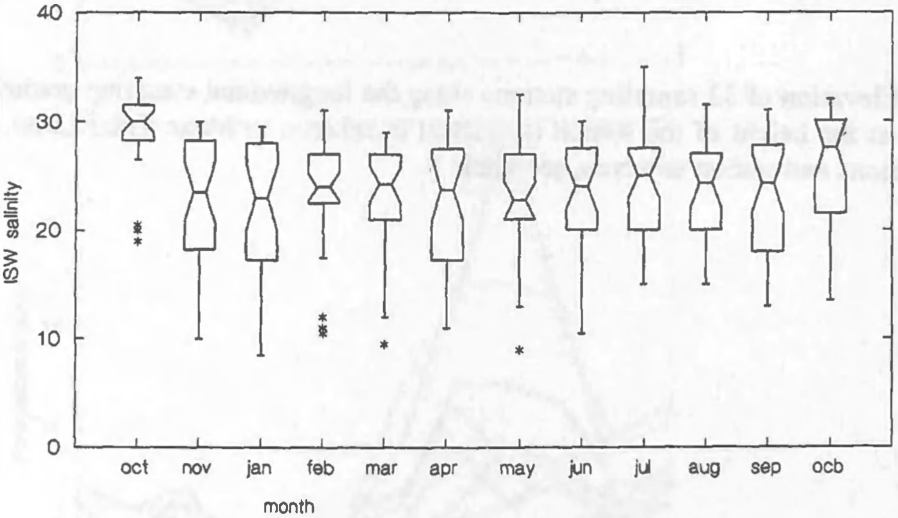


Fig. 12. Box-and-Whisker plot of ISW salinity (‰) per month (averaged for all stations) during the sampling period October 1991 (Oct) - October 1992 (Ocb).

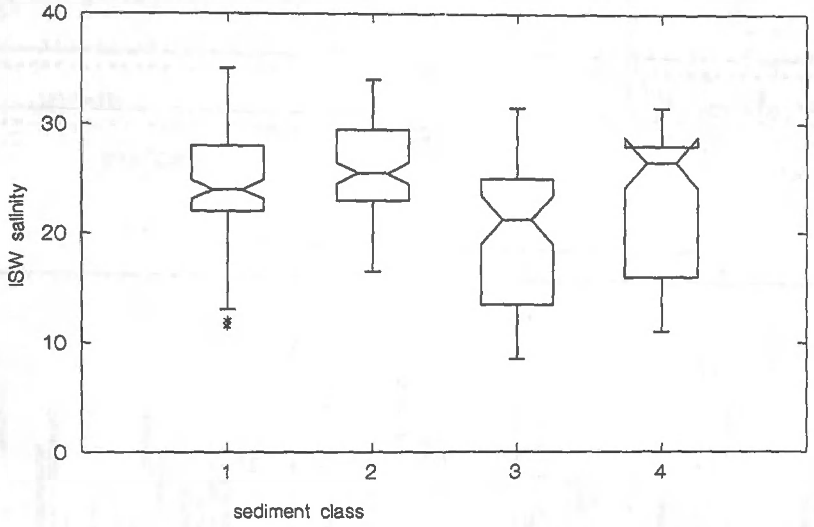


Fig. 13. Box-and-Whisker plot of ISW salinity (‰) per sediment class (averaged for all stations) during the sampling period October 1991-October 1992.

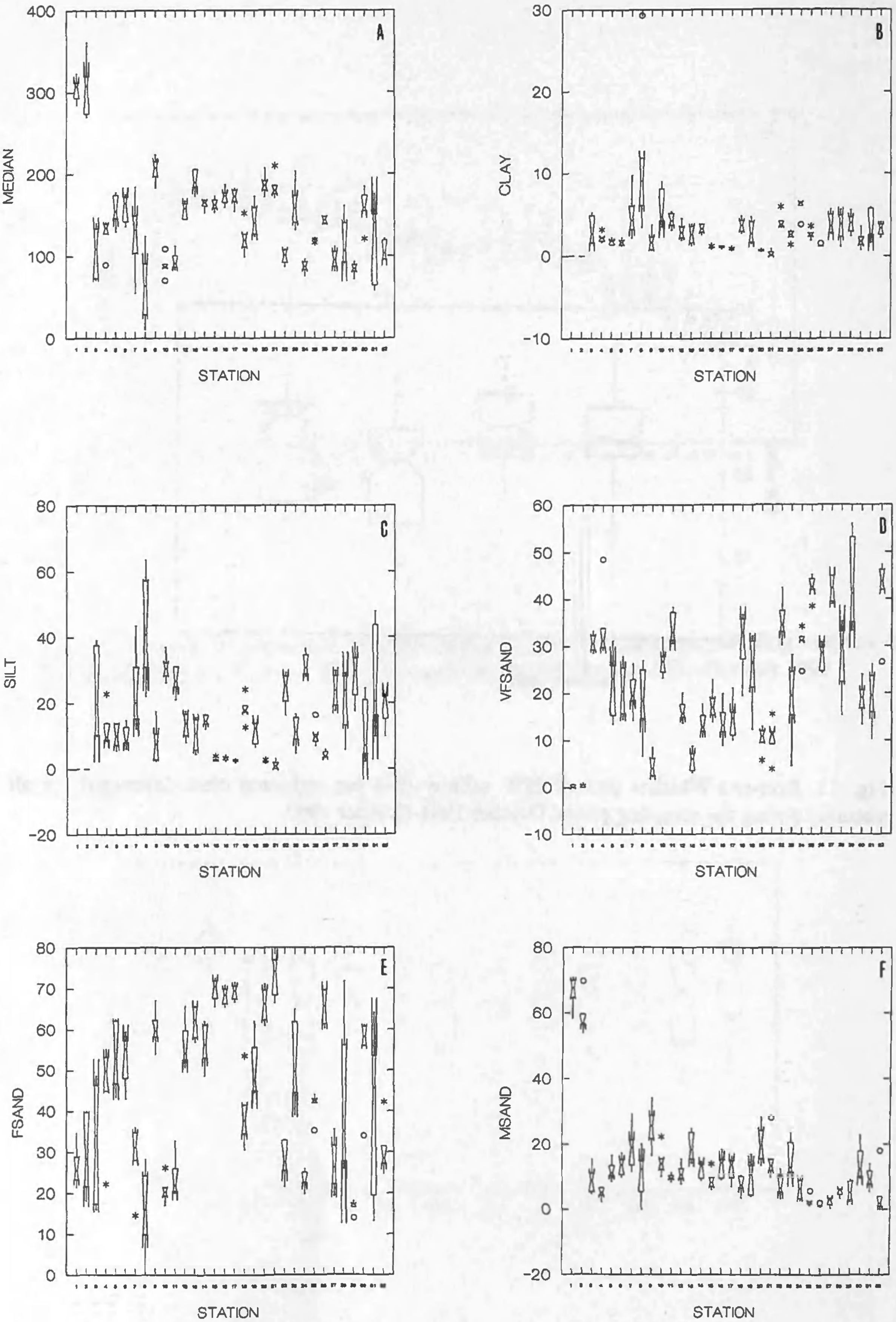


Fig. 14 (a-f). Box-and-Whisker plots of physical and chemical sediment characteristics per station during the sampling period October 1991-October 1992. For variable labels and units, see Table 7; for station numbers, see Table 3.

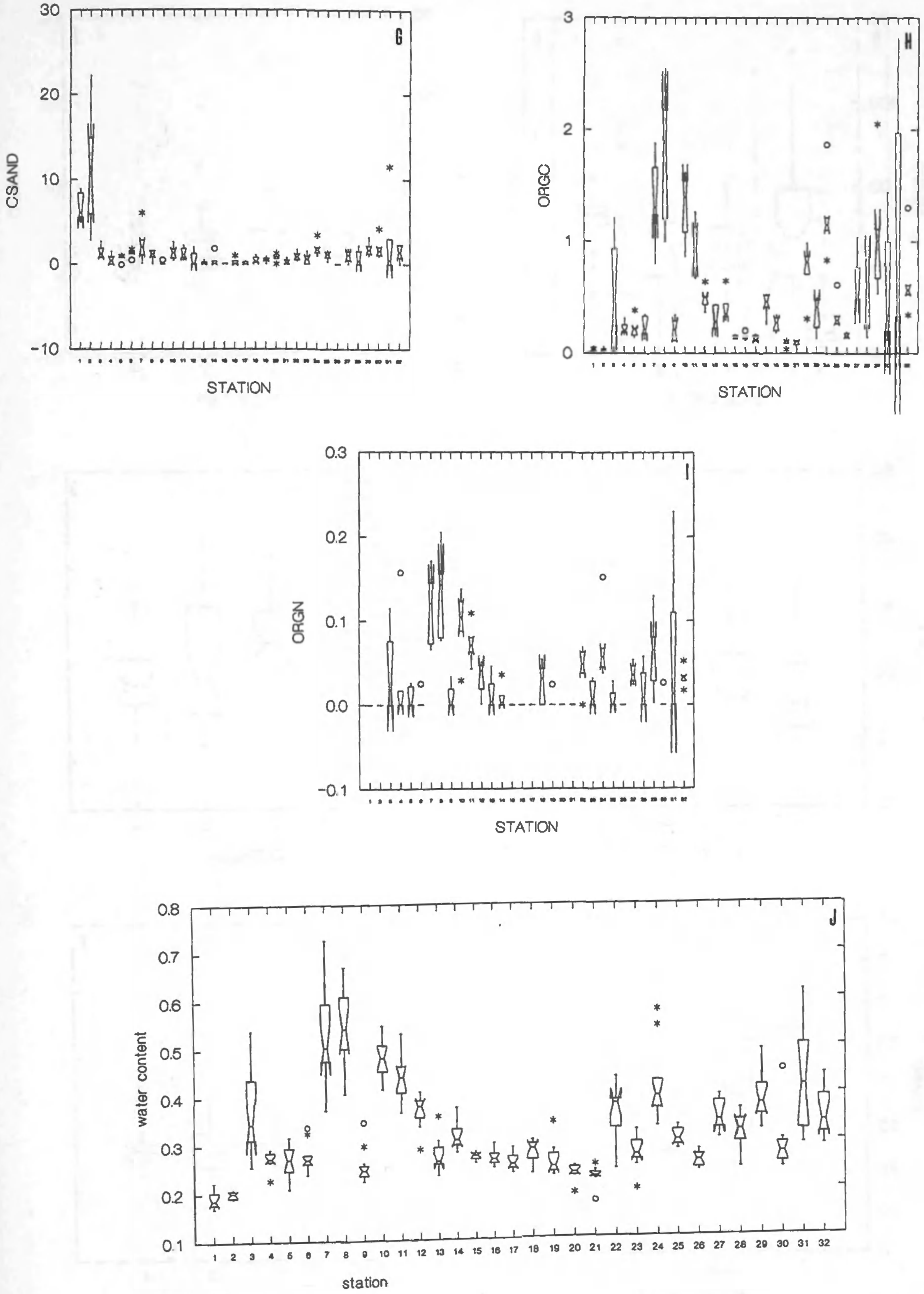


Fig. 14 (g-j). Box-and-Whisker plots of physical and chemical sediment characteristics per station during the sampling period October 1991-October 1992. For variable labels and units, see Table 7; for station numbers, see Table 3. Note that for water content the unit is weight % x 10^{-2}.

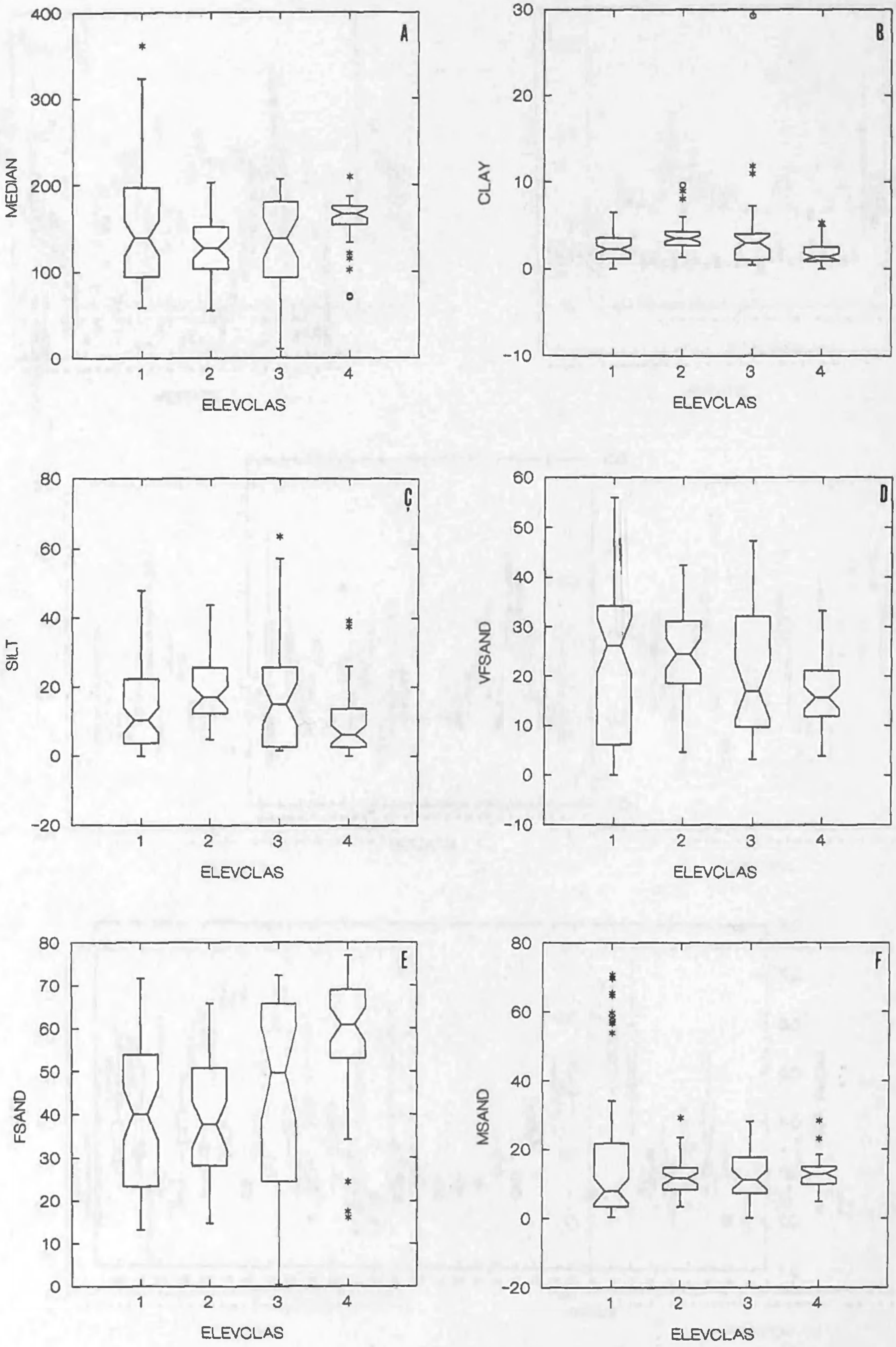


Fig. 15 (a-f). Box-and-Whisker plots of physical and chemical sediment characteristics per elevati class during the sampling period October 1991-October 1992. For variable labels and units, s Table 7; for station numbers, see Table 3.

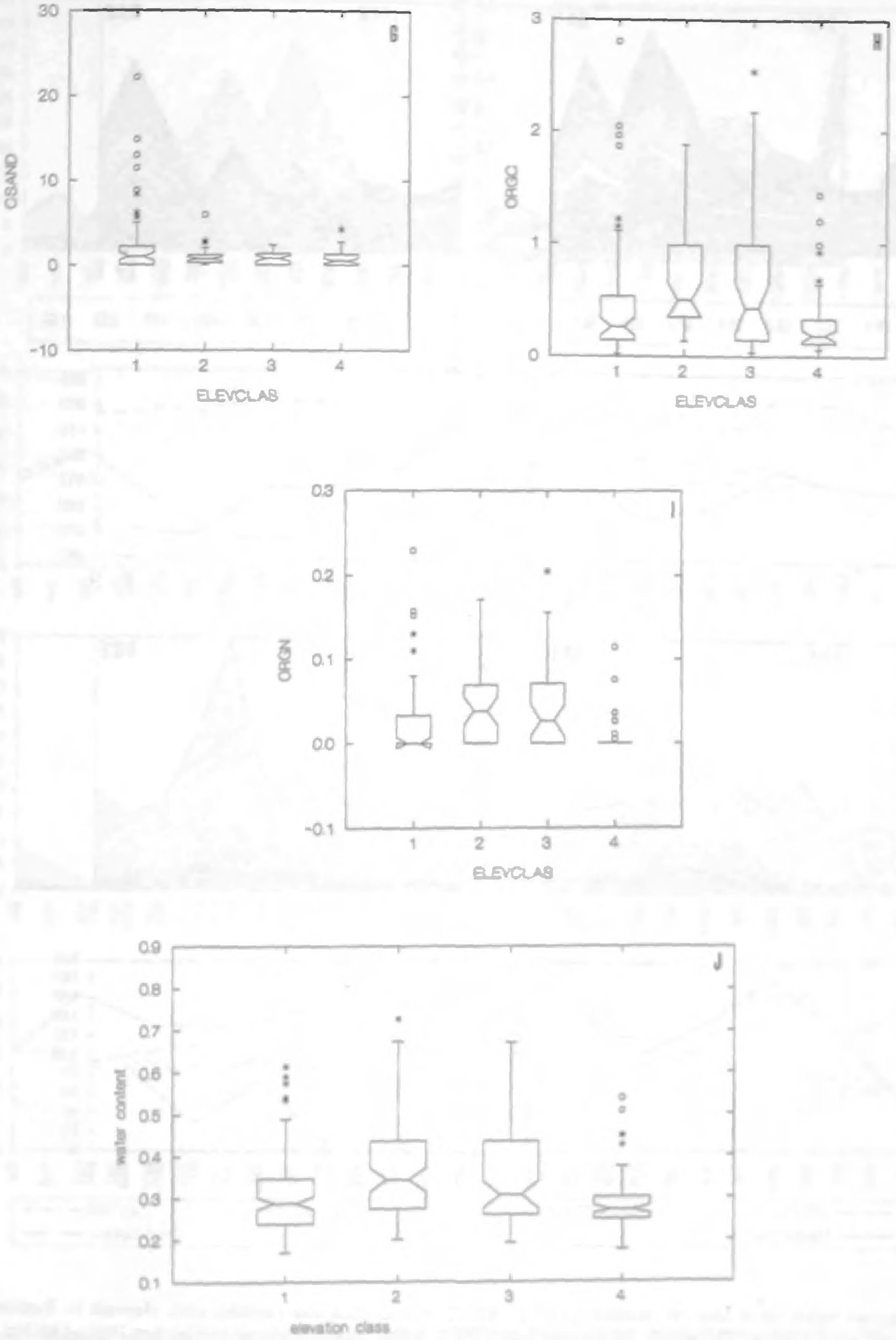


Fig. 15 (g-j). Box-and-Whisker plots of physical and chemical sediment characteristics per elevation class during the sampling period October 1991-October 1992. For variable labels and units, see Table 7; for station numbers, see Table 3. Note that for water content the unit is weight % x 10^{-2}.

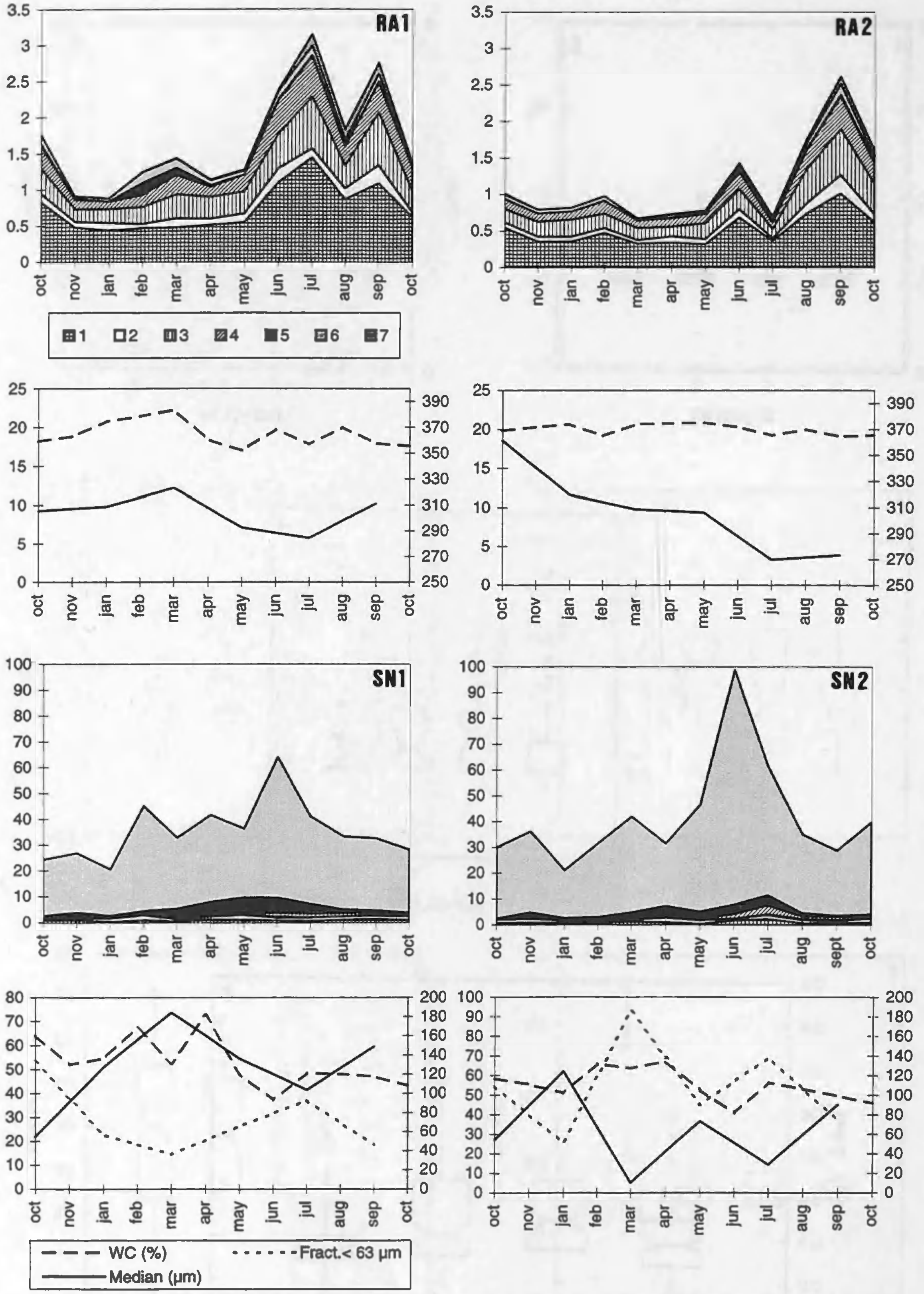


Fig. 16. Seasonal variations in total cell numbers (x10^6 g^{-1} SDW), median grain size (median, µm), clay+silt (= fraction < 63 volume %) and water content (WC, weight %) for RA1-2 and SN1-2 during the sampling period (October 1991 - October 1992). numbers are shown for 7 different life-forms (1: adnate, 2: stalked; 3: motile < 10 µm, 4: motile 10-20 µm, 5: motile > 20 µm tychoplankton, 7: interstitial. Plankton (8) and epiphyton (9), whose numbers were negligible anyway, are not shown). For station lab see Table 3.

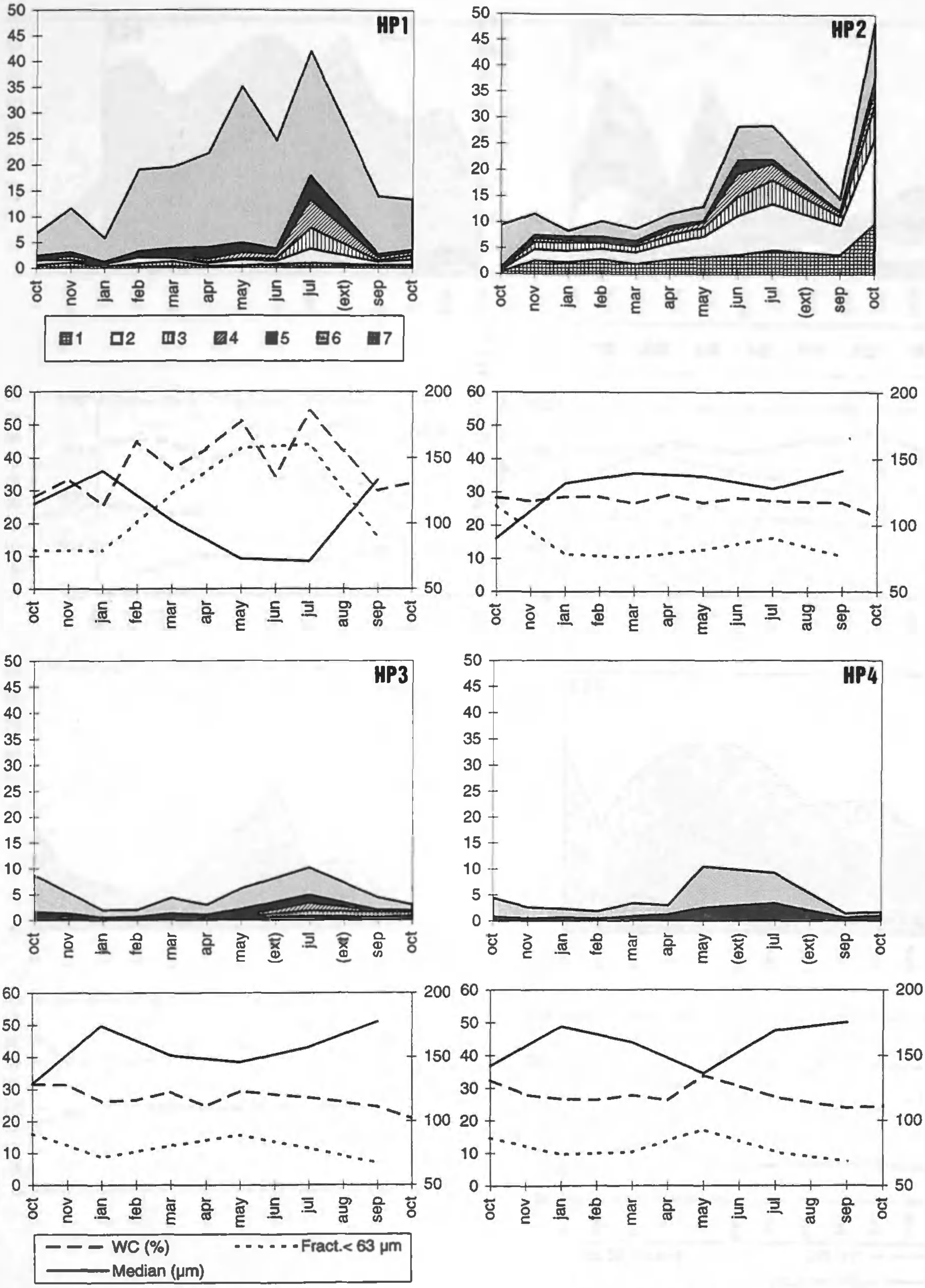


Fig. 16 (cont.). Seasonal variations in total cell numbers ($x10^6$ g^{-1} SDW), median grain size (median, µm), clay+silt (= fraction < 63 µm volume %) and water content (WC, weight %) for HP1-4 during the sampling period (October 1991 - October 1992). Cell numbers ar shown for 7 different life-forms (1: adnate, 2: stalked; 3: motile < 10 µm, 4: motile 10-20 µm, 5: motile > 20 µm, 6: tychoplankton, 7 interstitial. Plankton (8) and epiphyton (9), whose numbers were negligible anyway, are not shown). For station labels, see Table 3.

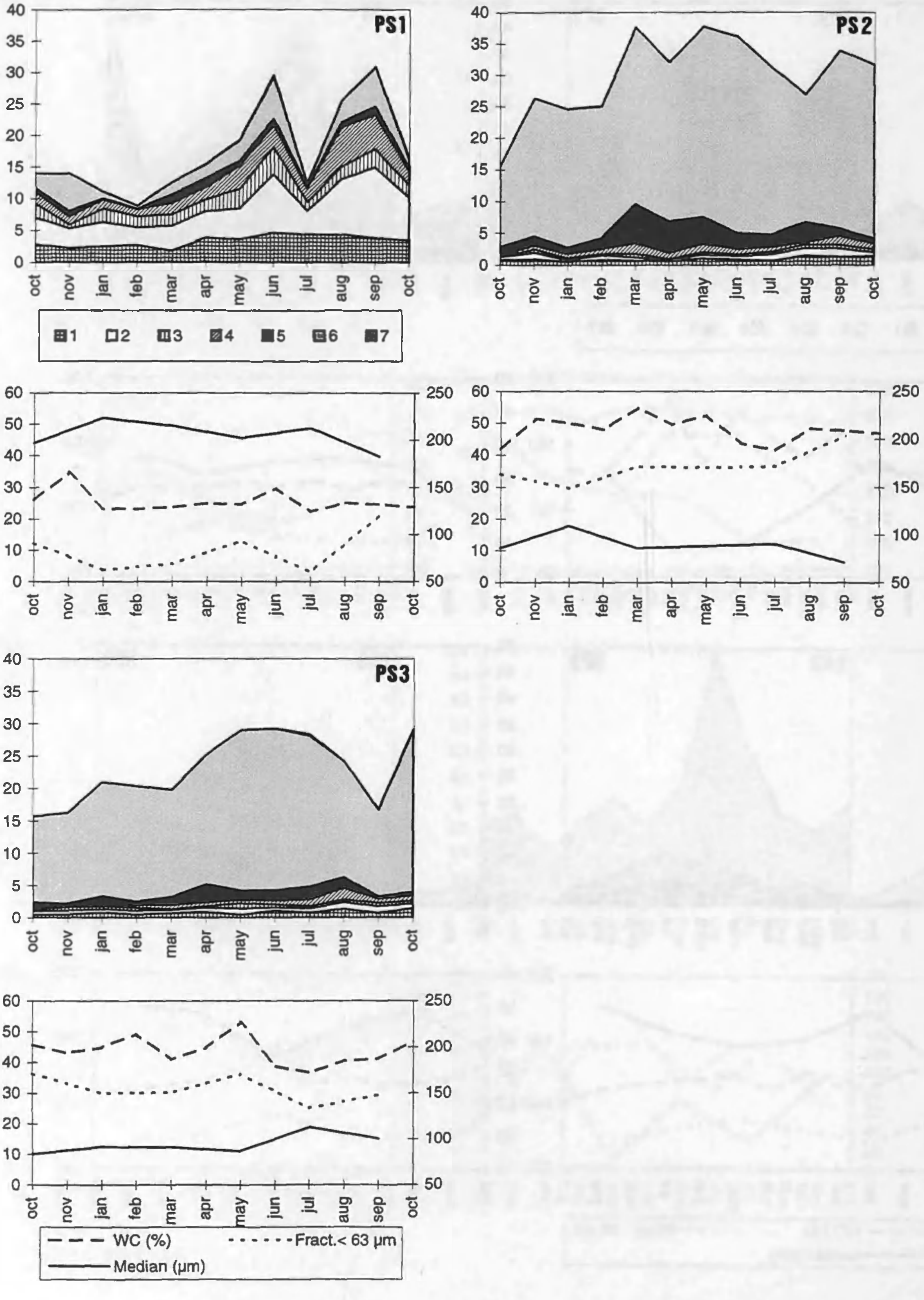


Fig. 16 (cont.). Seasonal variations in total cell numbers (x10^6 g^{-1} SDW), median grain size (median, µm), clay+silt (= fraction < 63 µm volume %) and water content (WC, weight %) for PS1-3 during the sampling period (October 1991 - October 1992). Cell numbers ar shown for 7 different life-forms (1: adnate, 2: stalked; 3: motile < 10 µm, 4: motile 10-20 µm, 5: motile > 20 µm, 6: tychoplankton, 7 interstitial. Plankton (8) and epiphyton (9), whose numbers were negligible anyway, are not shown). For station labels, see Table 3.

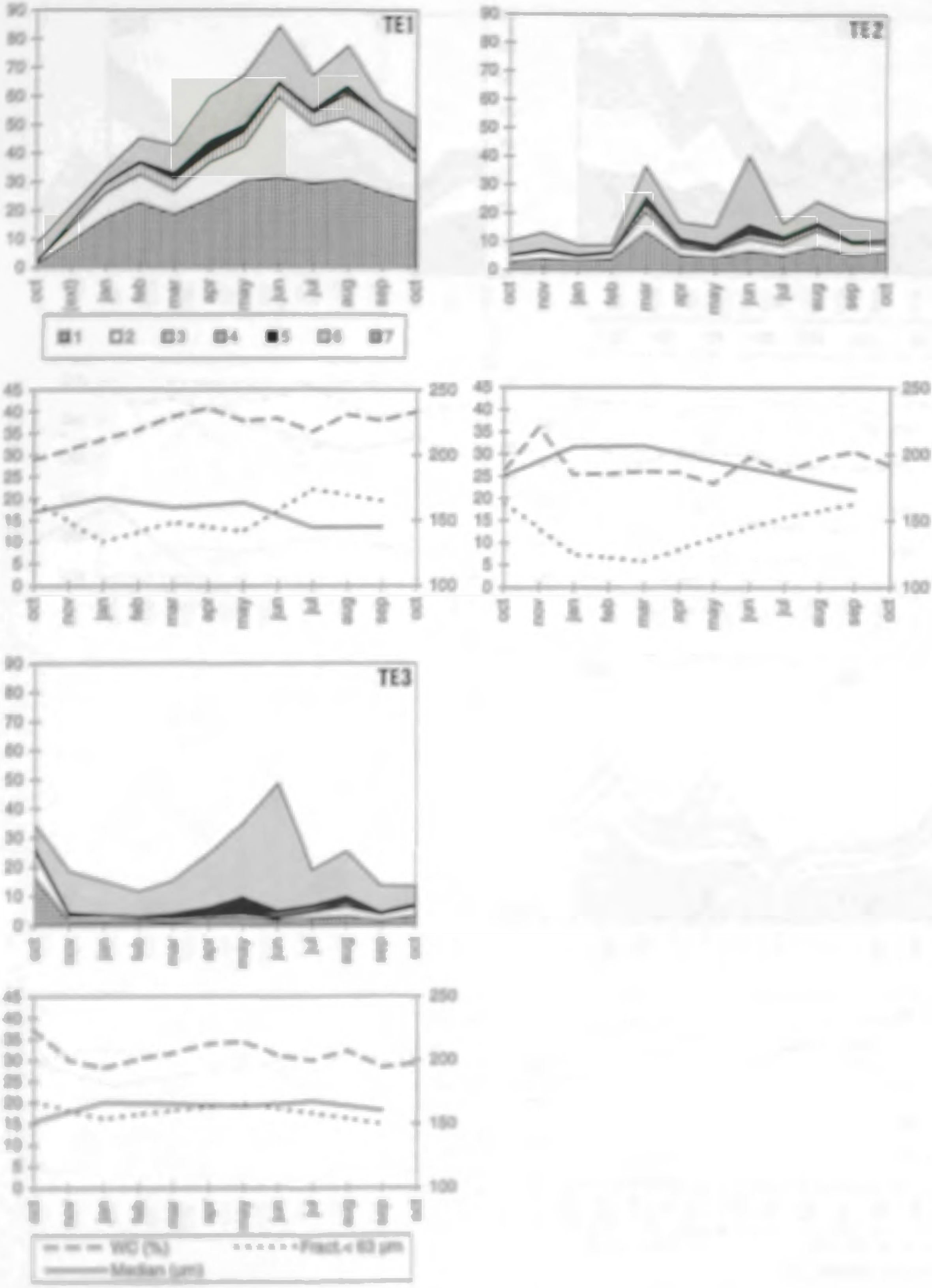


Fig. 16 (cont.). Seasonal variations in total cell numbers (x10^6 g^{-1} SDW), median grain size (median, µm), clay+silt (= fraction < 63 µ
volume %) and water content (WC, weight %) for TE1-3 during the sampling period (October 1991 - October 1992). Cell numbers a
shown for 7 different life-forms (1: adnate, 2: stalked; 3: motile < 10 µm, 4: motile 10-20 µm, 5: motile > 20 µm, 6: tychoplankton,
interstitial. Plankton (8) and epiphyton (9), whose numbers were negligible anyway, are not shown). For station labels, see Table 3.

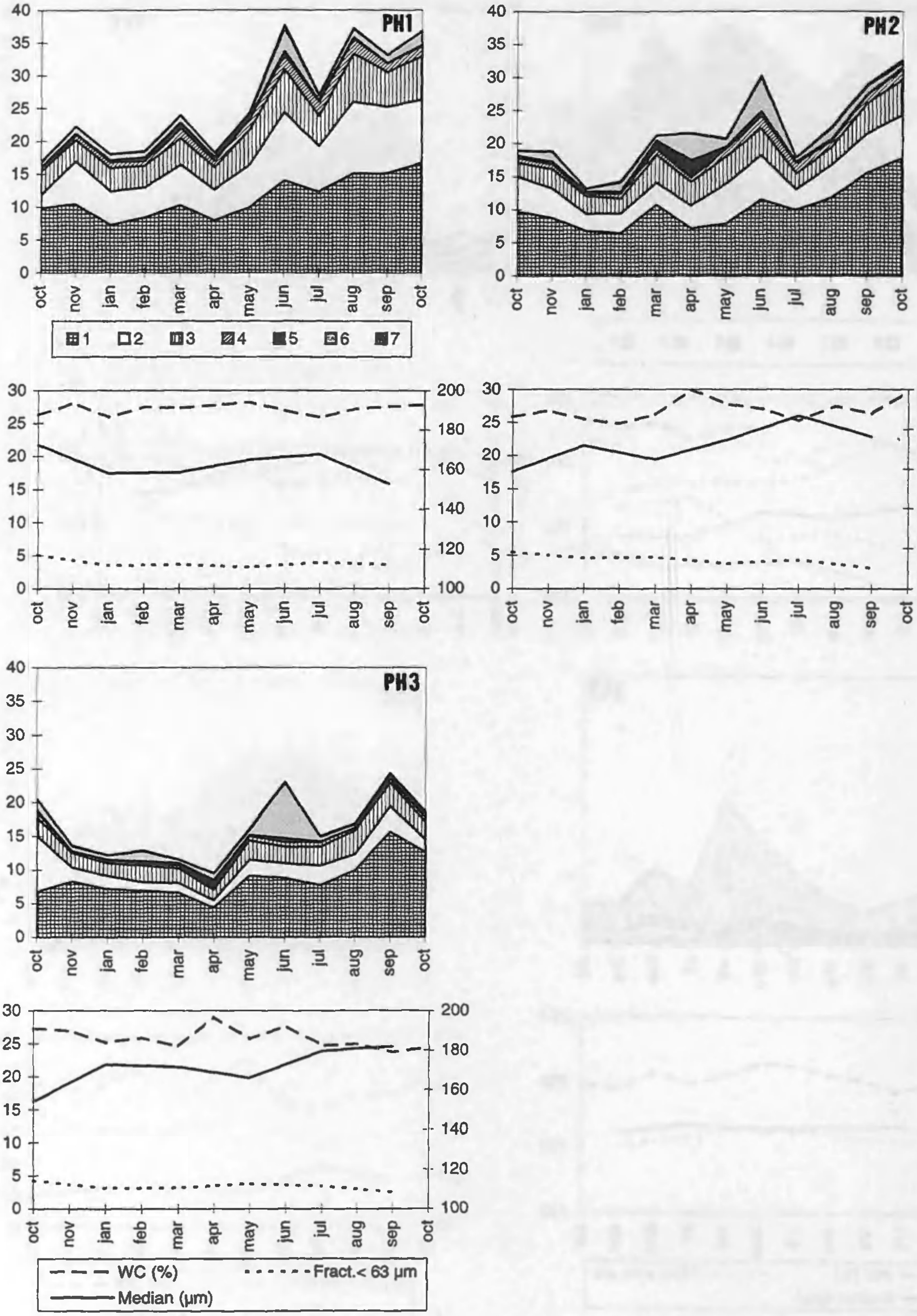
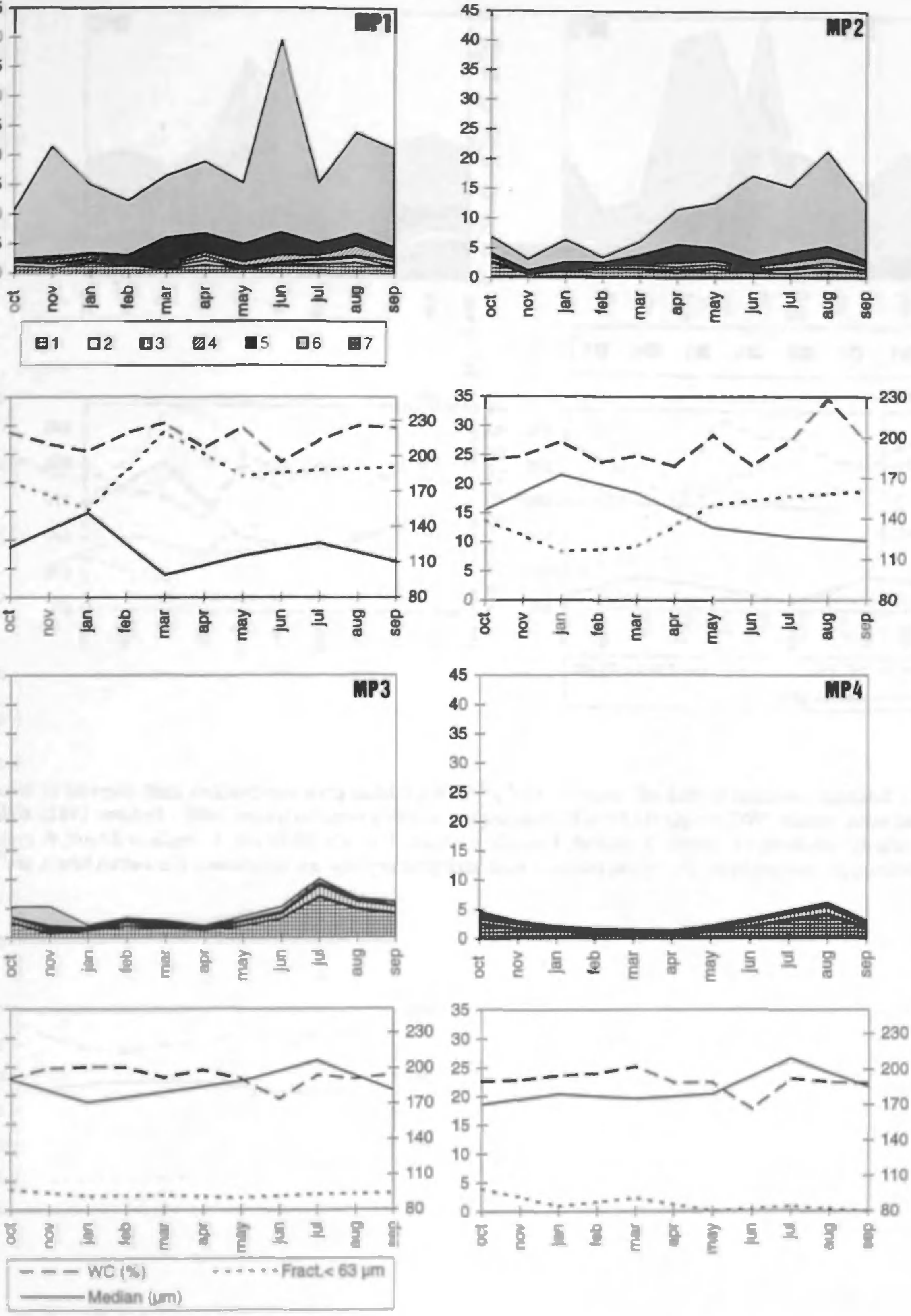


Fig. 16 (cont.). Seasonal variations in total cell numbers ($x10^6$ g^{-1} SDW), median grain size (median, µm), clay+silt (= fraction < 63 µm volume %) and water content (WC, weight %) for PH1-3 during the sampling period (October 1991 - October 1992). Cell numbers are shown for 7 different life-forms (1: adnate, 2: stalked; 3: motile < 10 µm, 4: motile 10-20 µm, 5: motile > 20 µm, 6: tychoplankton, 7: interstitial. Plankton (8) and epiphyton (9), whose numbers were negligible anyway, are not shown). For station labels, see Table 3.


MP1
MP2
MP3
MP4
45
40
35
30
25
20
15
10
5
0
oct
nov
jan
feb
mar
apr
may
jun
jul
aug
sep
1
2
3
4
5
6
7
230
200
170
140
110
80
WC (%)
Fract.< 63 µm
Median (µm)

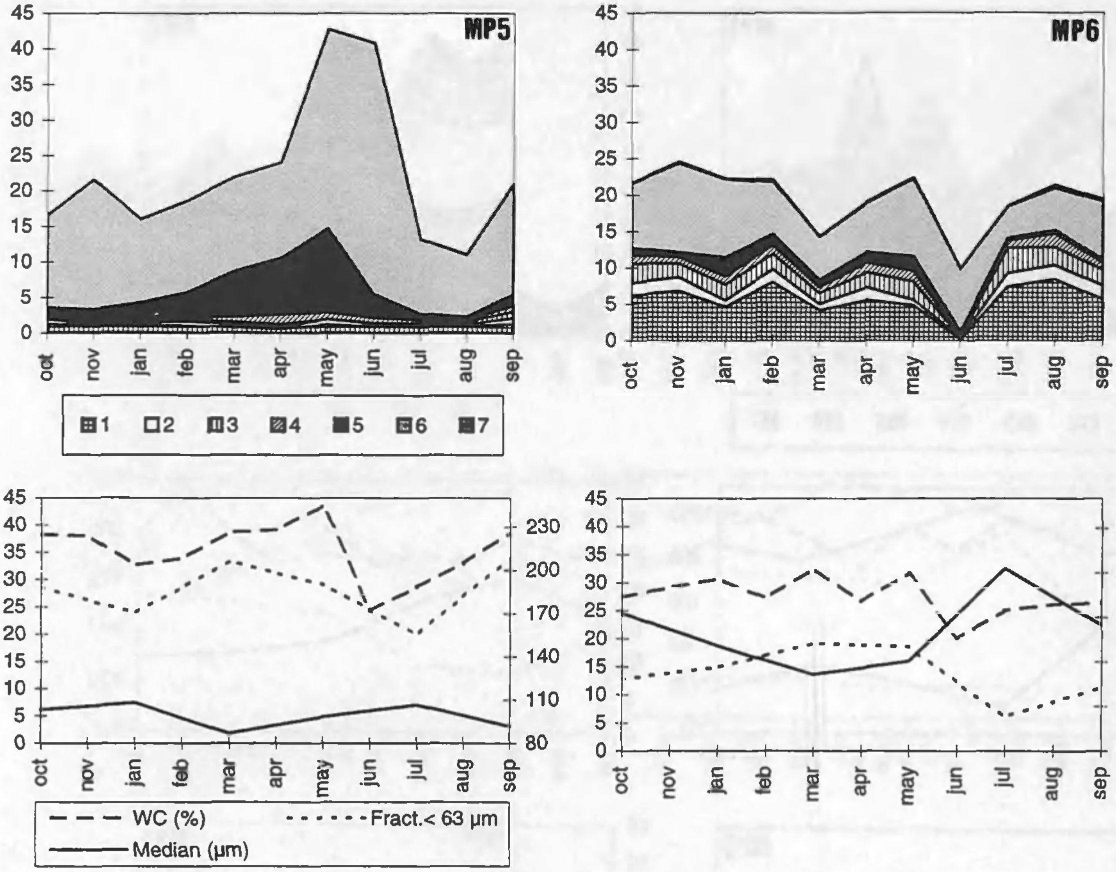


Fig. 16 (cont.). Seasonal variations in total cell numbers (x10^6 g^{-1} SDW), median grain size (median, µm), clay+silt (= fraction < 63 µ volume %) and water content (WC, weight %) for MP1-6 during the sampling period (October 1991 - October 1992). Cell numbers ar shown for 7 different life-forms (1: adnate, 2: stalked; 3: motile < 10 µm, 4: motile 10-20 µm, 5: motile > 20 µm, 6: tychoplankton, interstitial. Plankton (8) and epiphyton (9), whose numbers were negligible anyway, are not shown). For station labels, see Table 3.

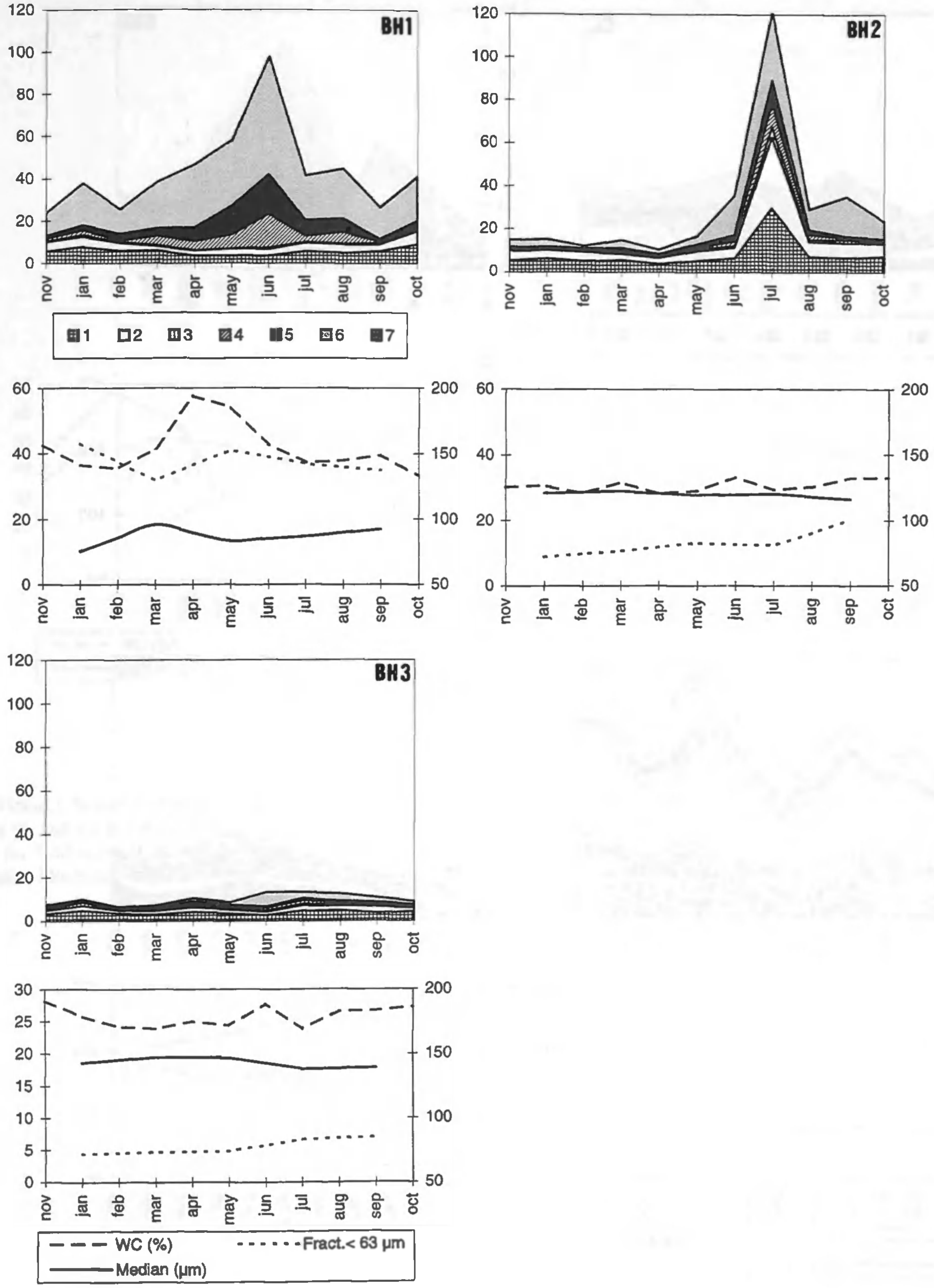


Fig. 16 (cont.). Seasonal variations in total cell numbers (x10^6 g^{-1} SDW), median grain size (median, µm), clay+silt (= fraction < 63 µm, volume %) and water content (WC, weight %) for BH1-3 during the sampling period (October 1991 - October 1992). Cell numbers are shown for 7 different life-forms (1: adnate, 2: stalked; 3: motile < 10 µm, 4: motile 10-20 µm, 5: motile > 20 µm, 6: tychoplankton, 7: interstitial. Plankton (8) and epiphyton (9), whose numbers were negligible anyway, are not shown). For station labels, see Table 3.

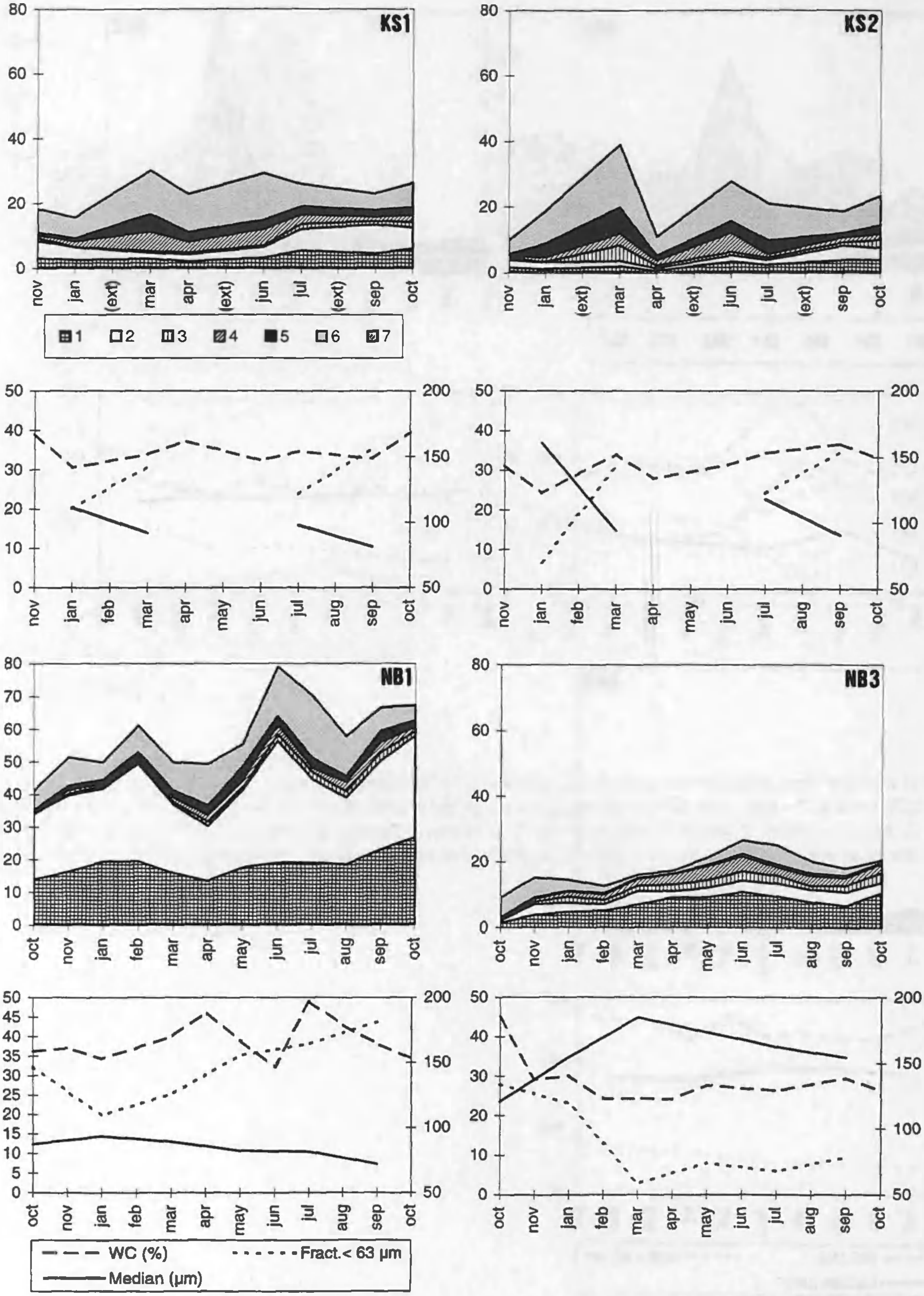


Fig. 16 (cont.). Seasonal variations in total cell numbers (x10^6 g^{-1} SDW), median grain size (median, µm), clay+silt (= fraction < 63 µm, volume %) and water content (WC, weight %) for KS1-2 and NB1, 3 during the sampling period (October 1991 - October 1992). Cell numbers are shown for 7 different life-forms (1: adnate, 2: stalked; 3: motile < 10 µm, 4: motile 10-20 µm, 5: motile > 20 µm, 6: tychoplankton, 7: interstitial. Plankton (8) and epiphyton (9), whose numbers were negligible anyway, are not shown). For station labels, see Table 3.

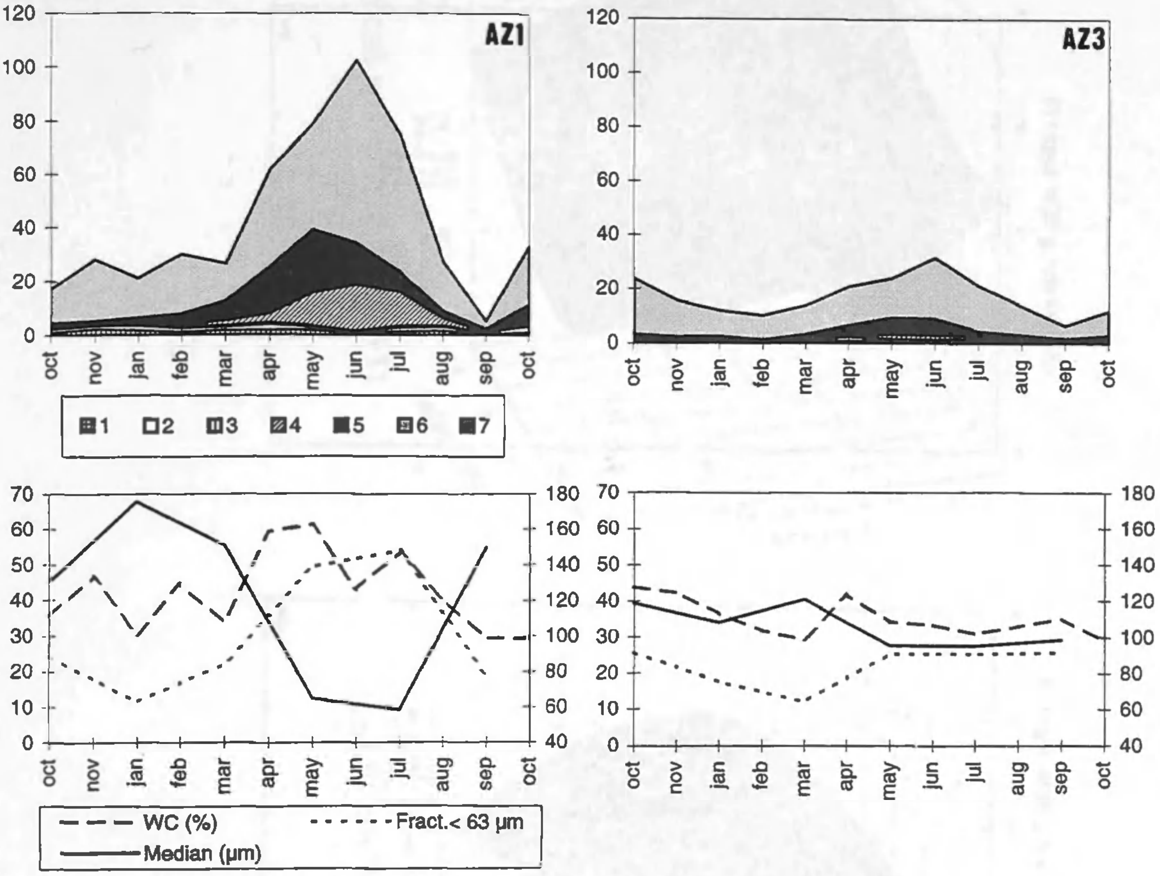


Fig. 16 (cont.). Seasonal variations in total cell numbers ($x10^6$ g^{-1} SDW), median grain size (median, µm), clay+silt (= fraction < 63 µm, volume %) and water content (WC, weight %) for AZ1, 3 during the sampling period (October 1991 - October 1992). Cell numbers are shown for 7 different life-forms (1: adnate, 2: stalked; 3: motile < 10 µm, 4: motile 10-20 µm, 5: motile > 20 µm, 6: tychoplankton, 7: interstitial. Plankton (8) and epiphyton (9), whose numbers were negligible anyway, are not shown). For station labels, see Table 3.

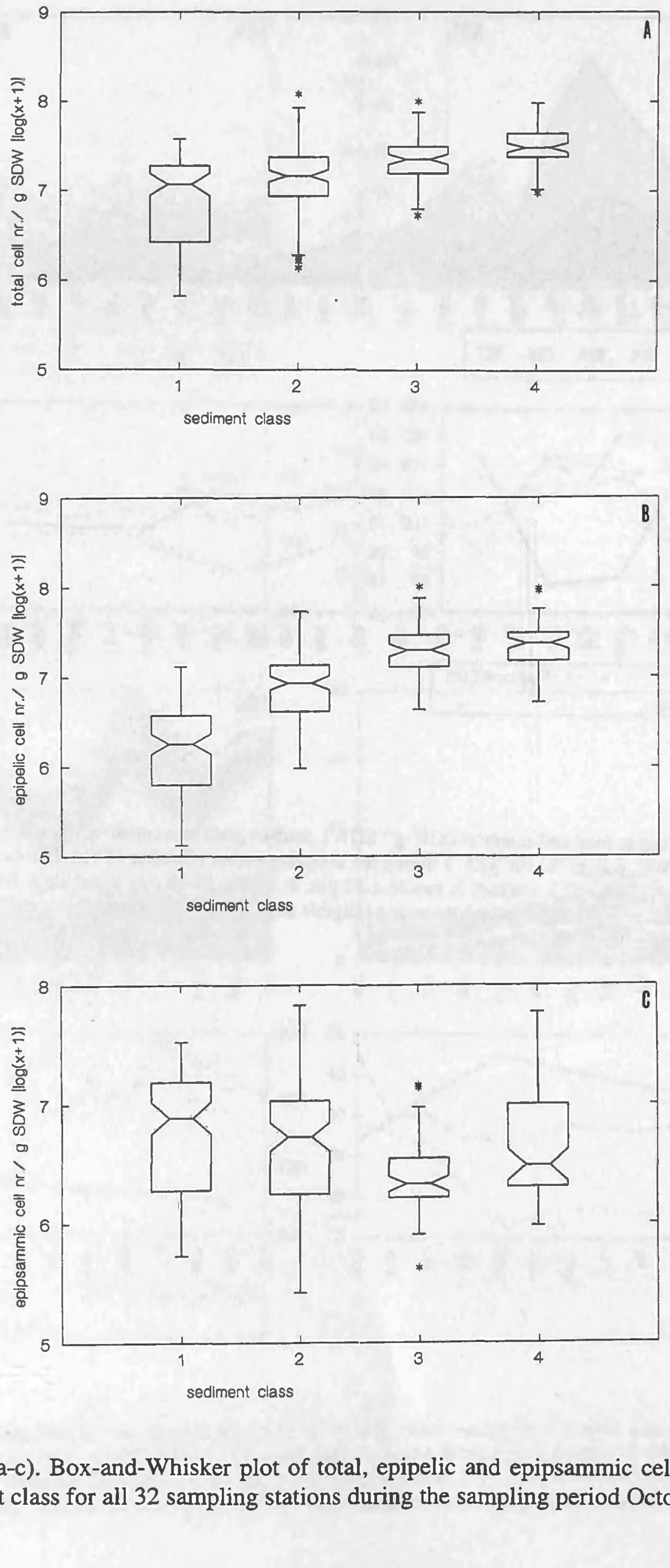


Fig. 17(a-c). Box-and-Whisker plot of total, epipelic and epipsammic cell numbers [log(x+1)] per sediment class for all 32 sampling stations during the sampling period October 1991-October 1992.

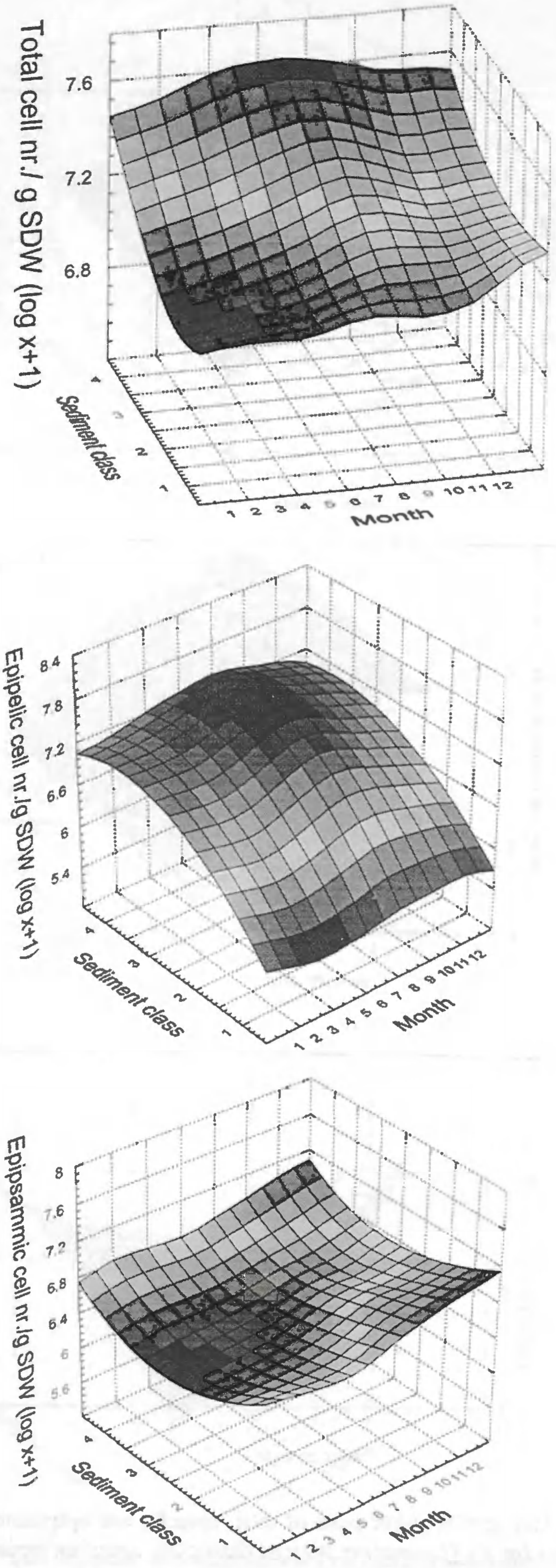


Fig. 18(a-c). Temporal patterns in total, epipelic and epipsammic cell numbers decomposed into sediment class. For sediment class delimitation and station affiliation, see chapter 3.2.6. and Table 6. Months: 1 = Oct. 1991; 2 = Nov. 1991; 3 = Jan. 1992 etc. until 12 = Oct. 1992.

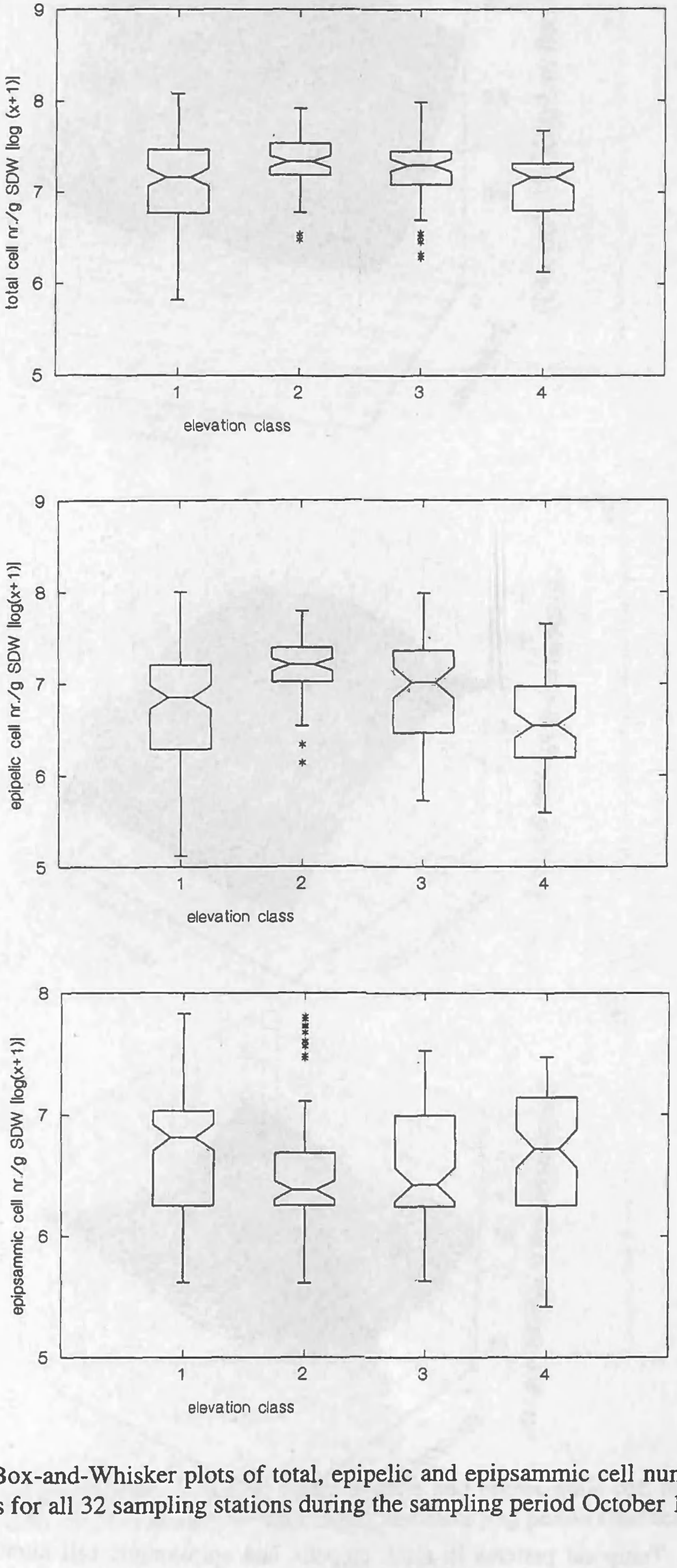


Fig. 19(a-c). Box-and-Whisker plots of total, epipelic and epipsammic cell numbers [log(x+1)] per elevation class for all 32 sampling stations during the sampling period October 1991-October 1992.

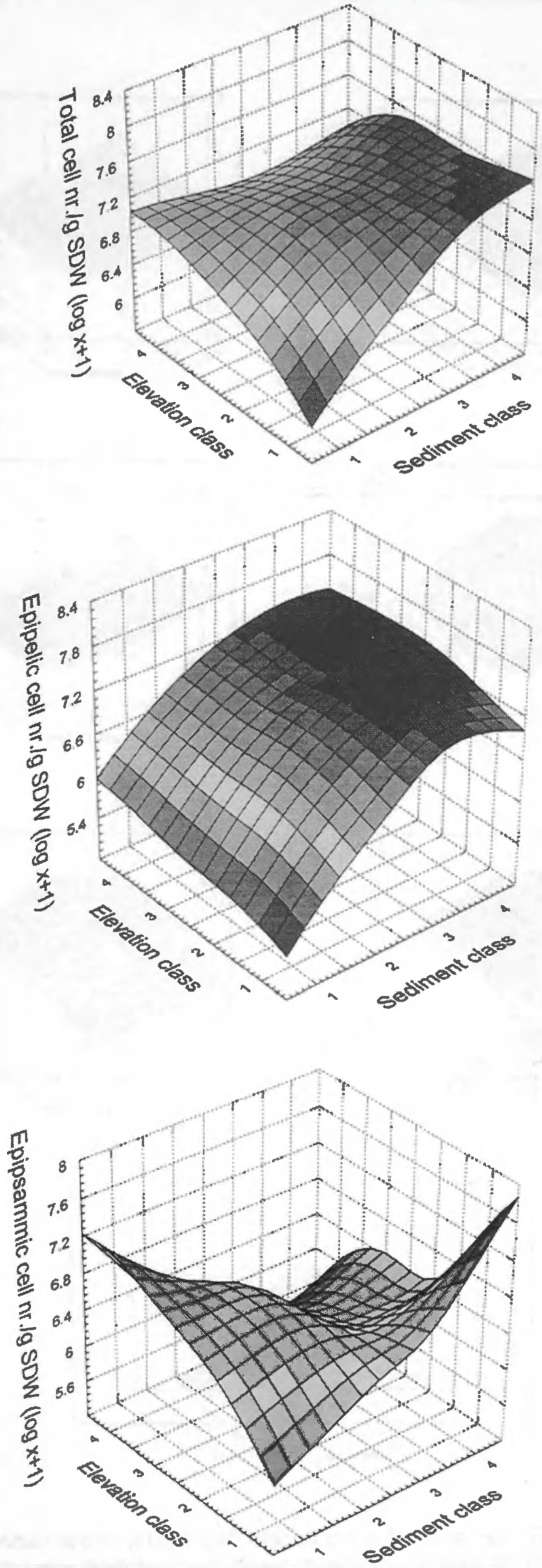


Fig. 20(a-c). Patterns in total, epipelic and epipsammic cell number decomposed into sediment and elevation class. For sediment and elevation class delimitation and station affiliation, see chapter 3.2.6. and Table 6.

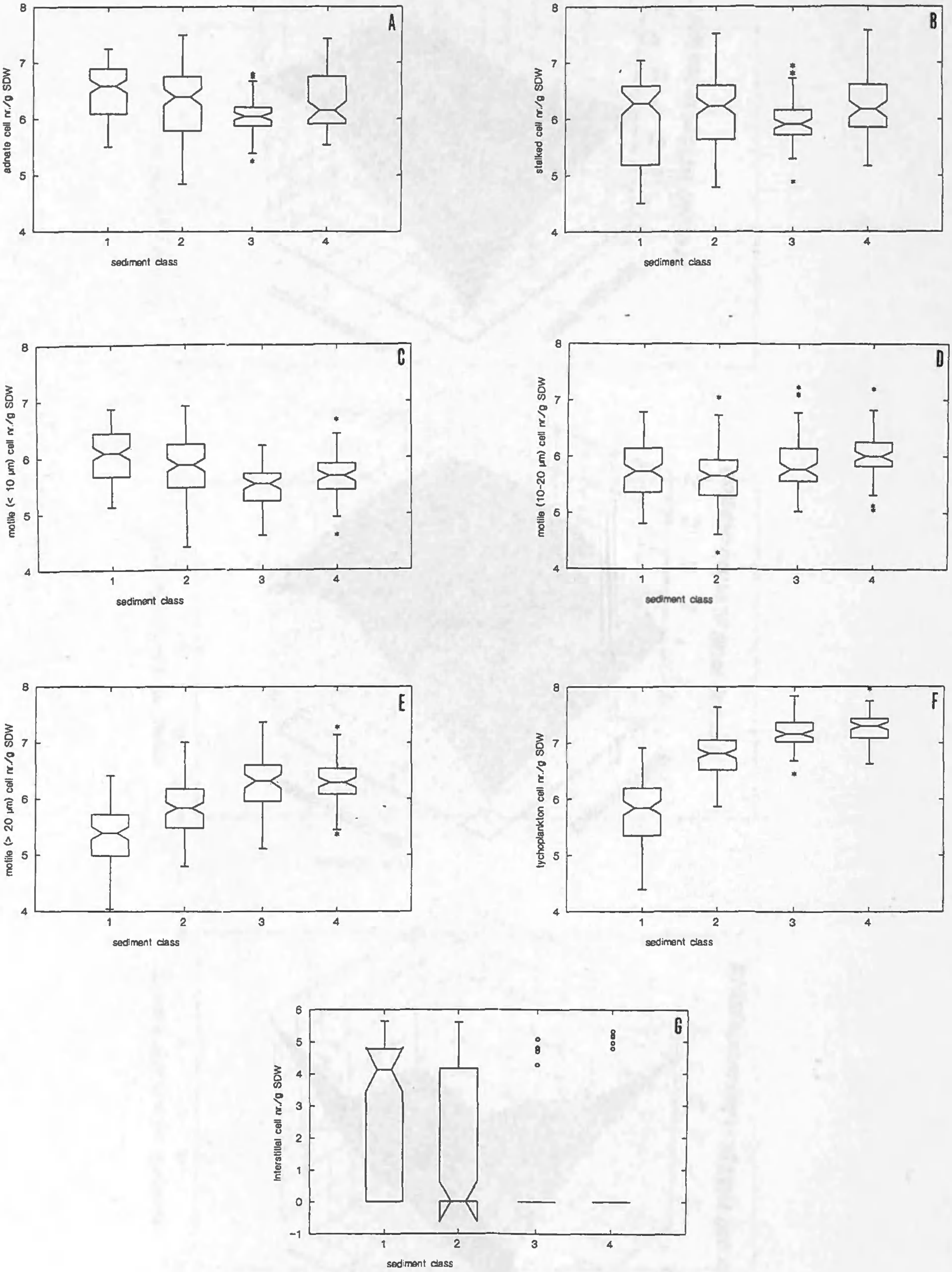


Fig. 21(a-g). Box-and-Whisker plots of cell numbers [log (x+1)] of the various life-form categories per sediment class for all 32 sampling stations during the sampling period October 1991-October 1992.

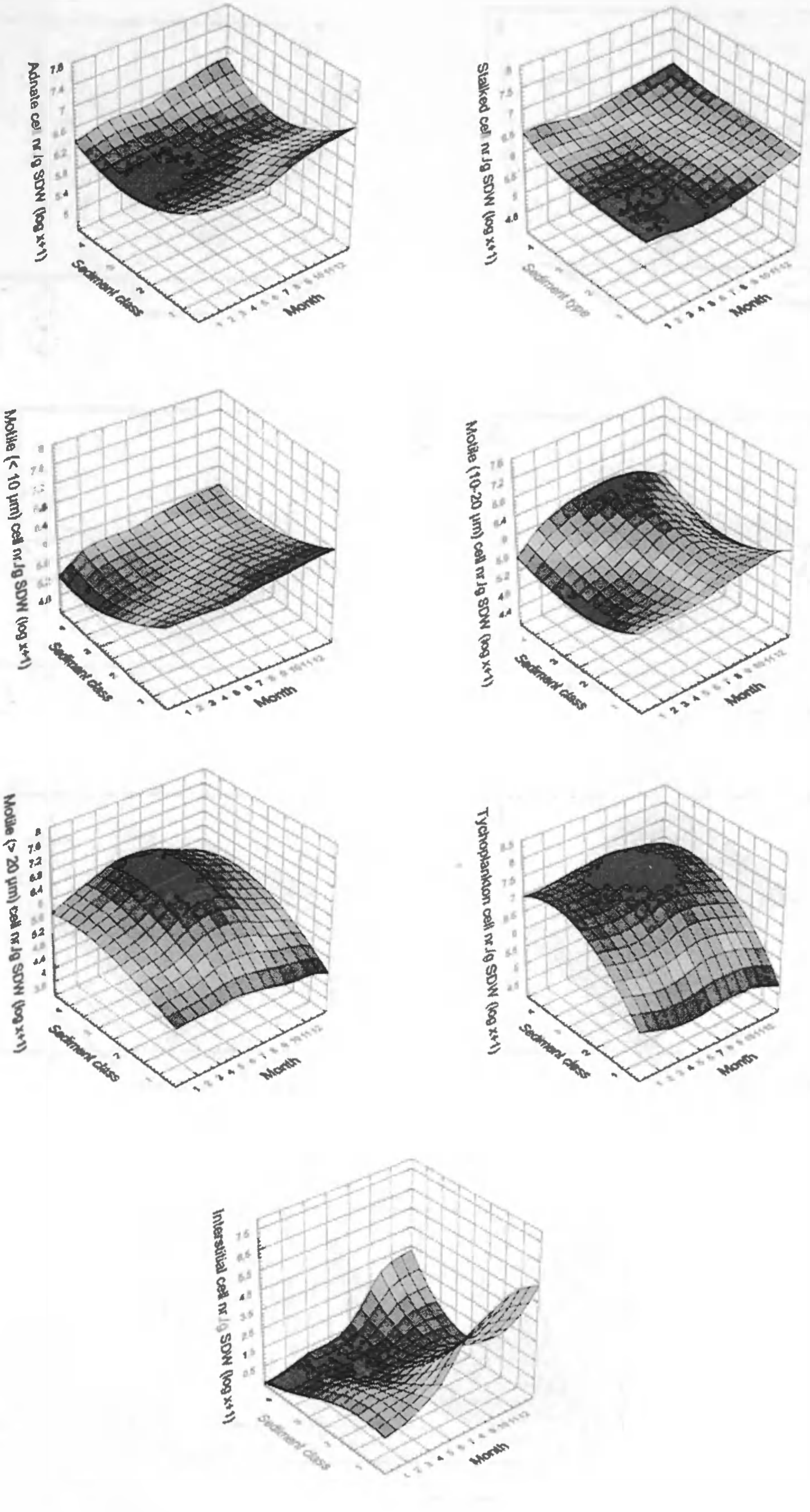


Fig. 22(a-g). Temporal patterns in cell numbers of the various life-form categories decomposed into sediment class. For sediment class delimitation and station affiliation, see chapter 3.2.6. and Table 6. Months: 1 = Oct. 1991; 2 = Nov. 1991; 3 = Jan. 1992 etc. until 12 = Oct. 1992.

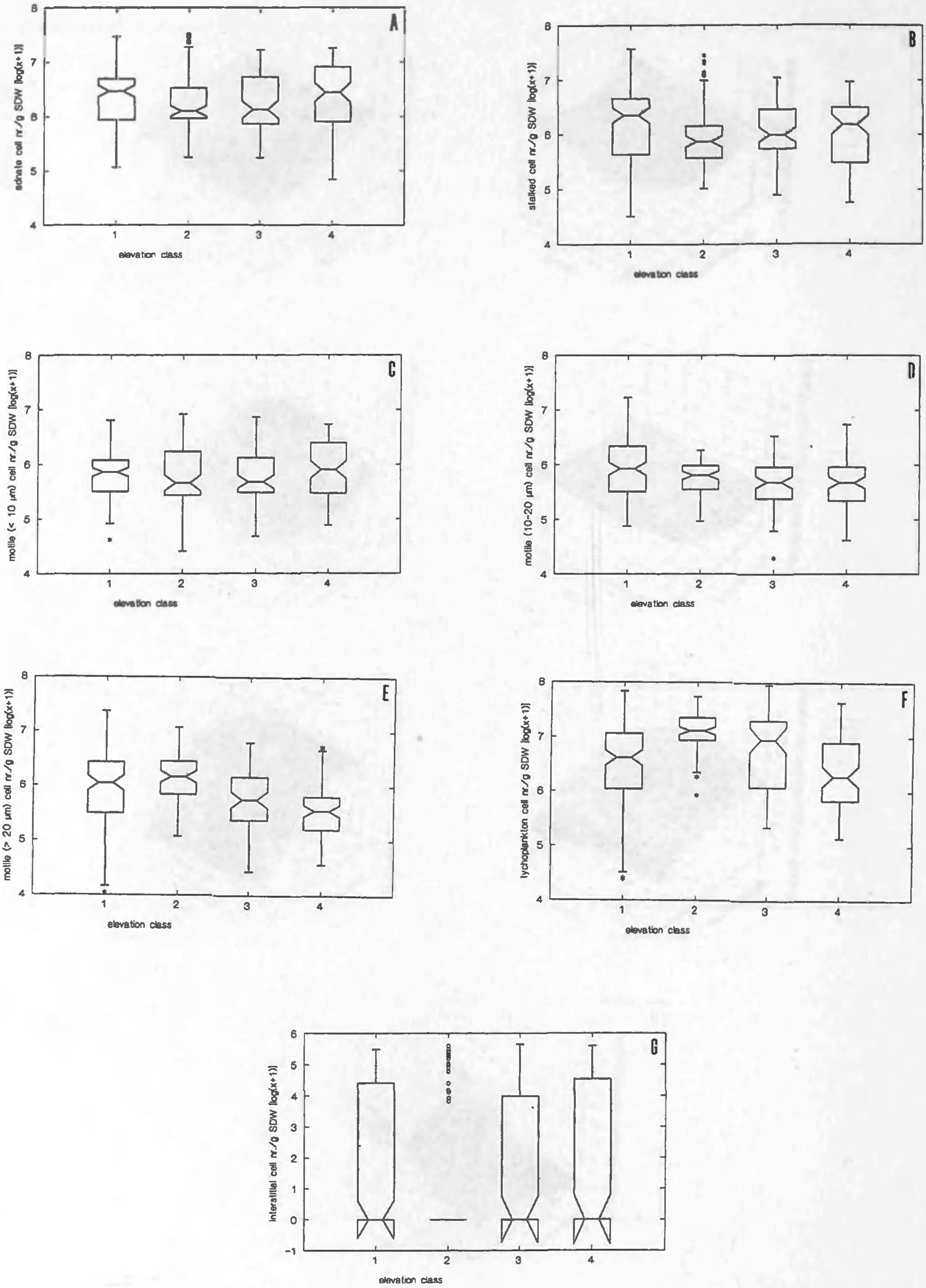


Fig. 23(a-g). Box-and-Whisker plots of the cell numbers of the various life-form categories per elevation class for all 32 sampling stations during the sampling period October 1991-October 1992.

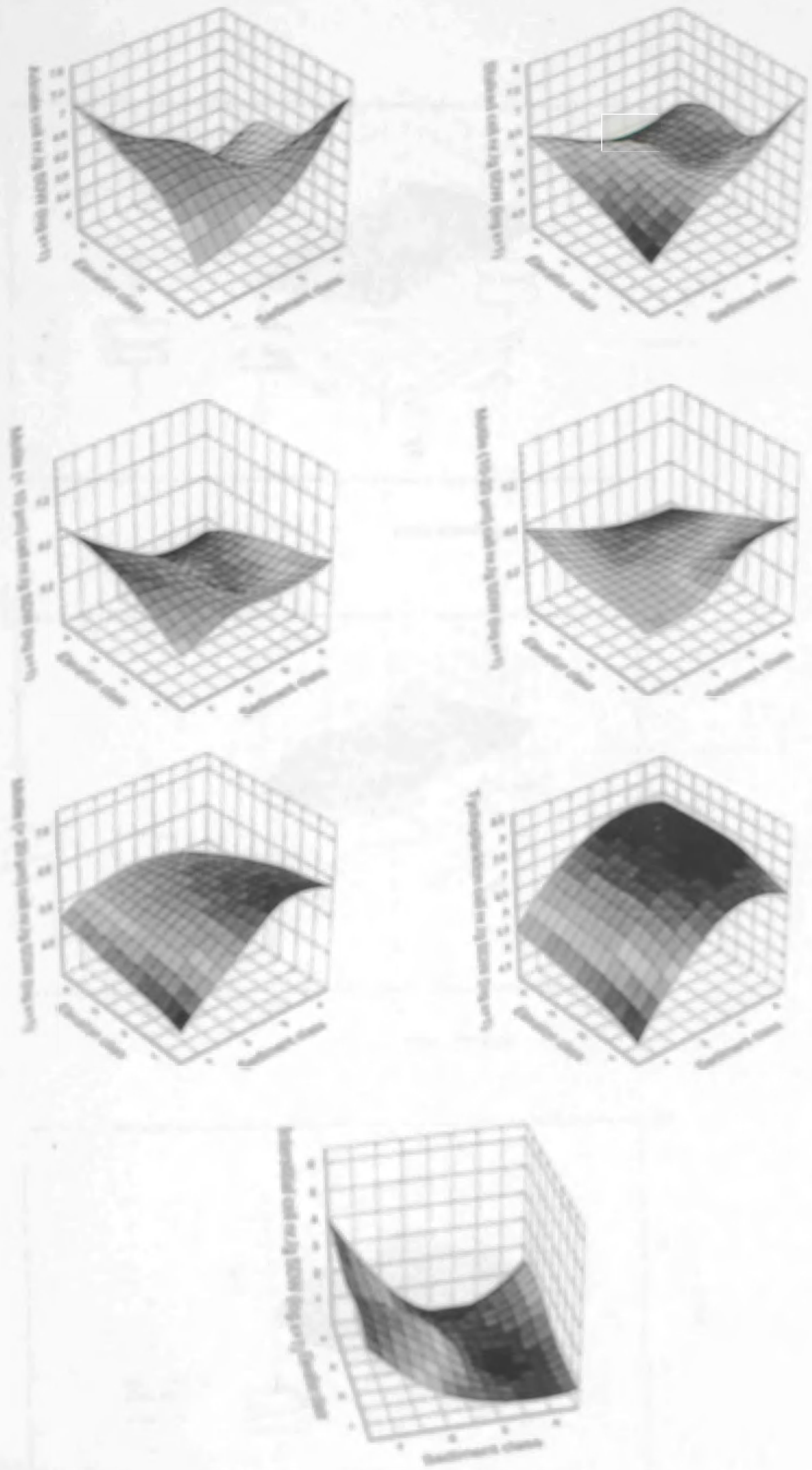


Fig. 24(a-g). Patterns in cell numbers of the various life-form categories decomposed into sediment and elevation class. For sediment and elevation class delimitation and station affiliation, see chapter 3.2.6. and Table 6.

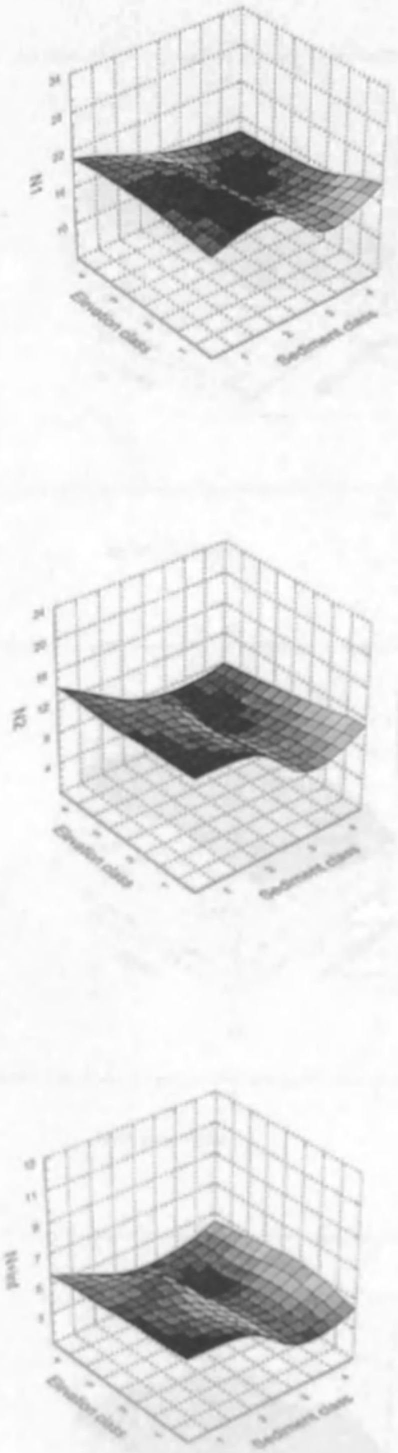


Fig. 27(a-c). Patterns in diversity $(N_1 \rightarrow N_{+\infty})$ decomposed into sediment and elevation class. For sediment and elevation class delimitation and station affiliation, see chapter 3.2.6. and Table 6.

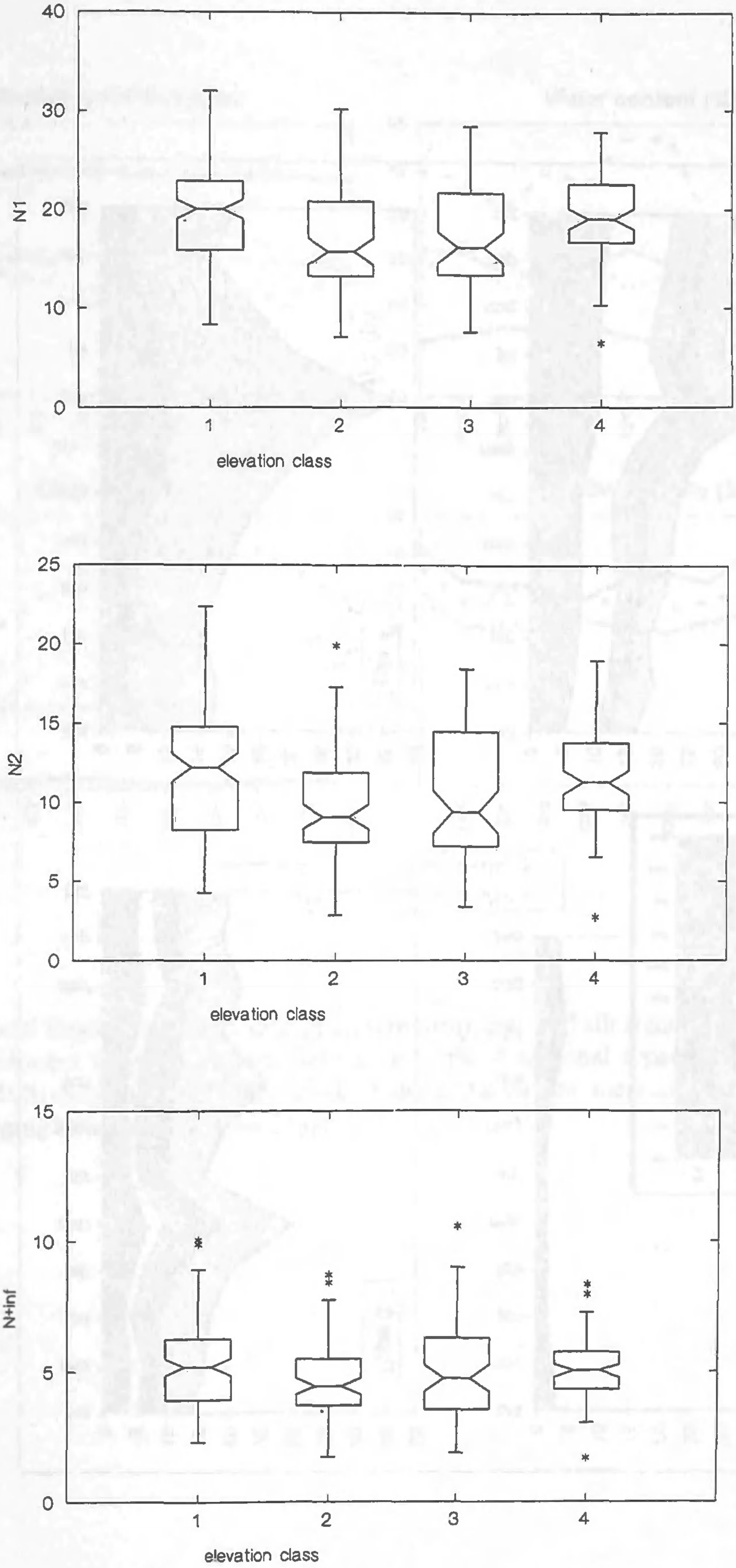


Fig. 28(a-c). Box-and-Whisker plots of diversity indices ($N_1 \rightarrow N_{+\infty}$) per elevation class for all 32 sampling stations during the sampling period October 1991-October 1992.

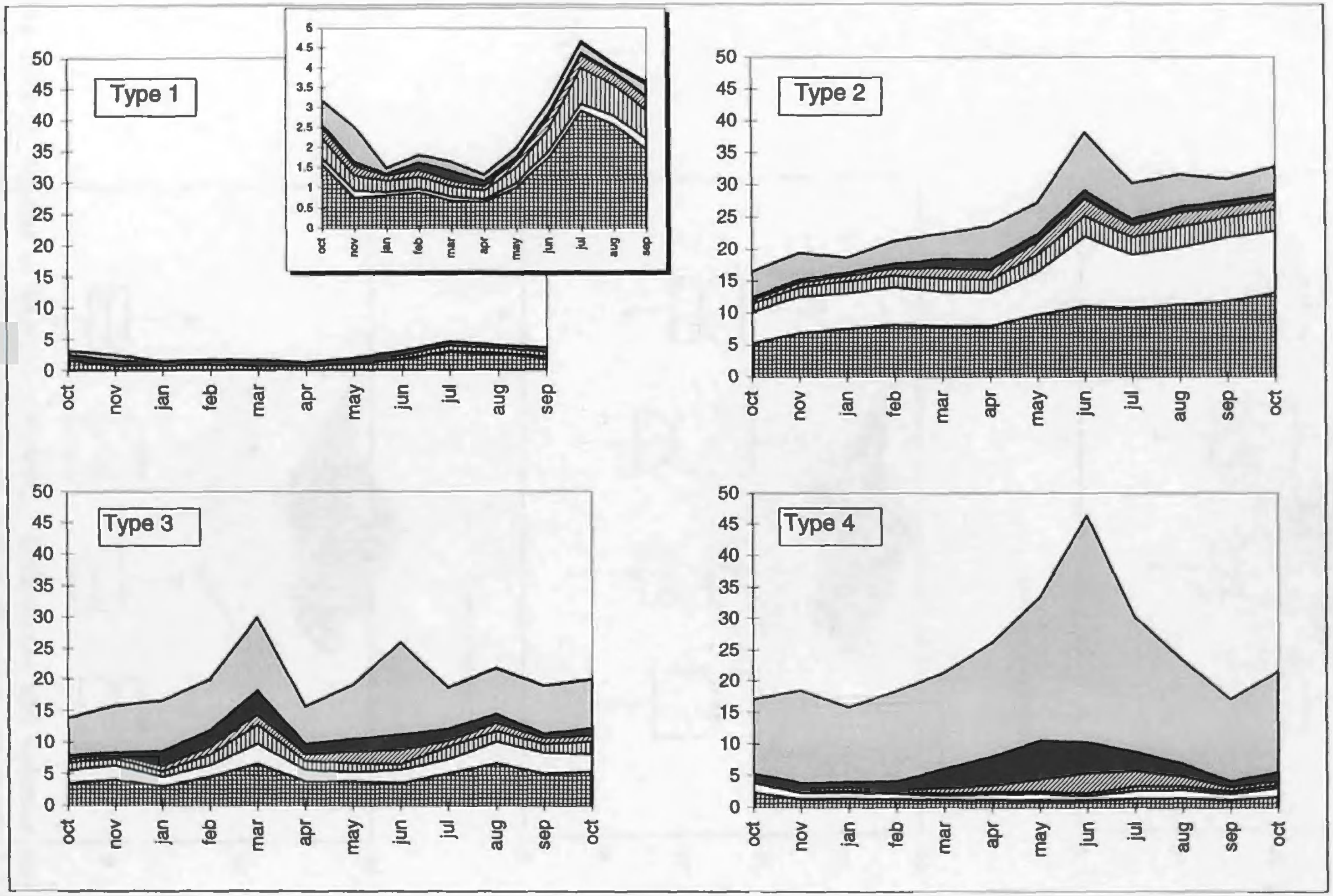


Fig. 29. Four types of seasonal patterns observed in the 32 sampling stations during the period Oct. 1991-October 1992. Cell abundance values shown are mean values per month for all stations belonging to a certain seasonal type (cf. Table 16). For more details, see chapter 5.2.3.

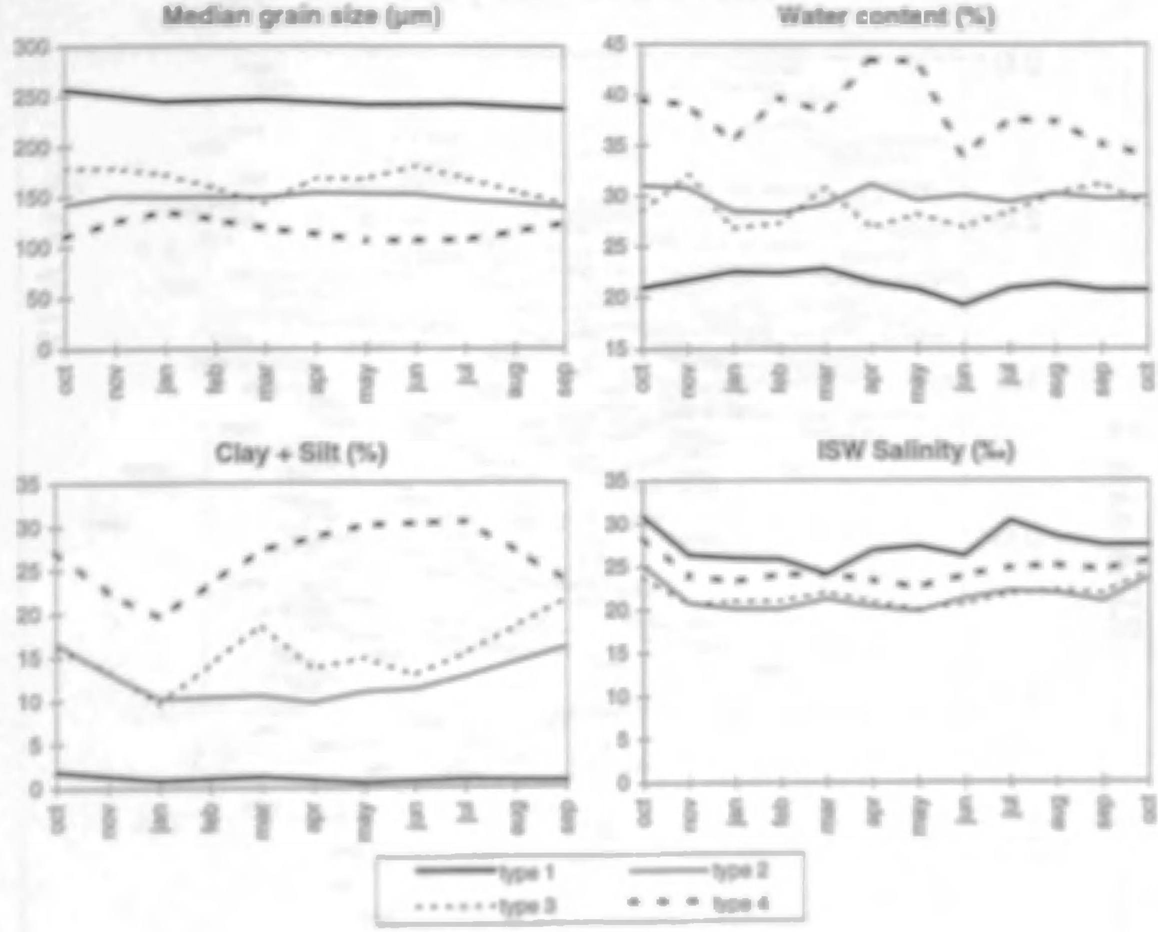


Fig. 30. Seasonal fluctuations in median grain size (µm), clay and silt fraction (%) and water content (%) of the sediment between stations belonging to the 4 seasonal types (cf. Fig. 43) during the period Oct. 1991-September/October 1992. Values shown are mean values per month for all stations belonging to a certain seasonal type.

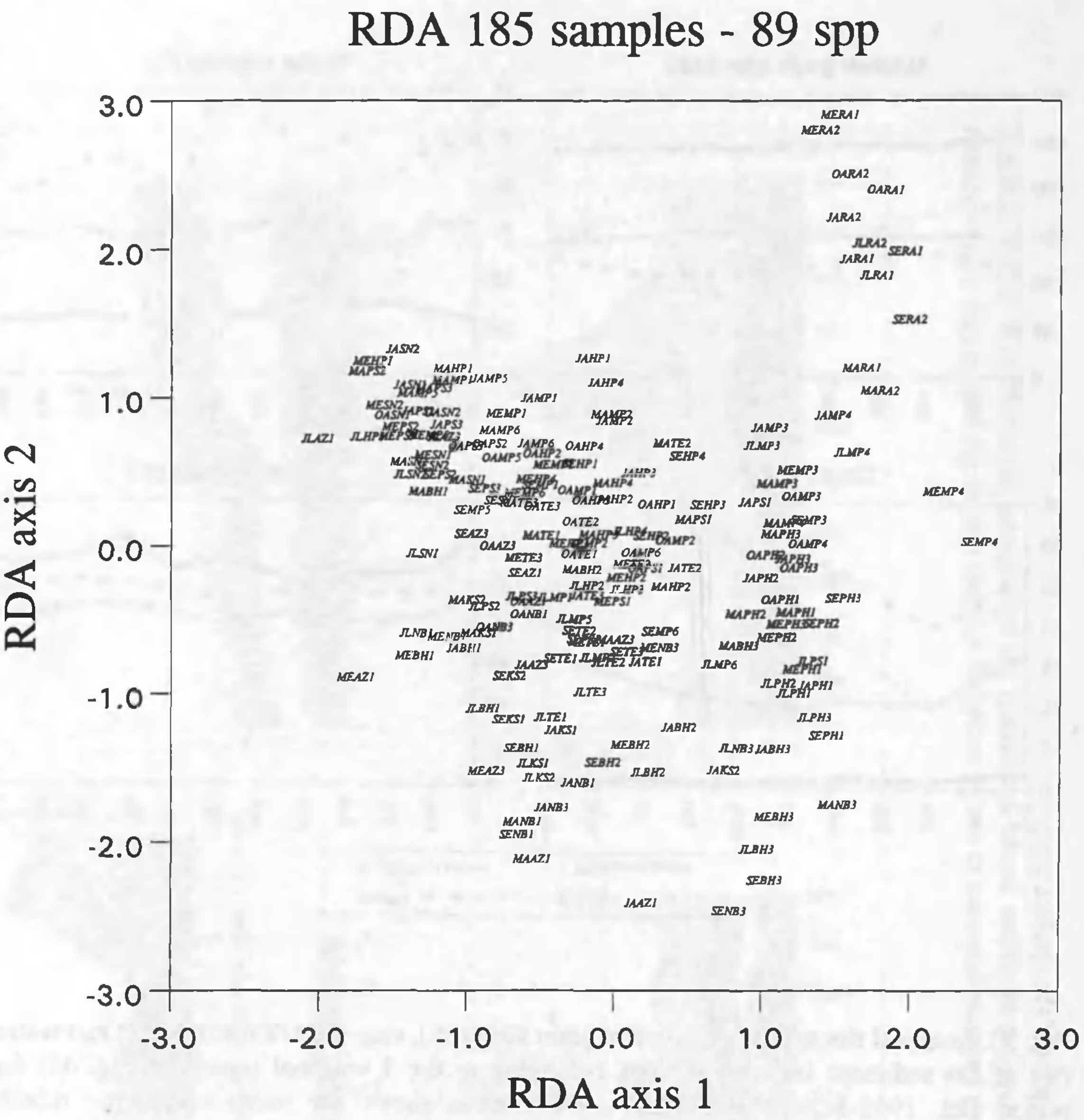
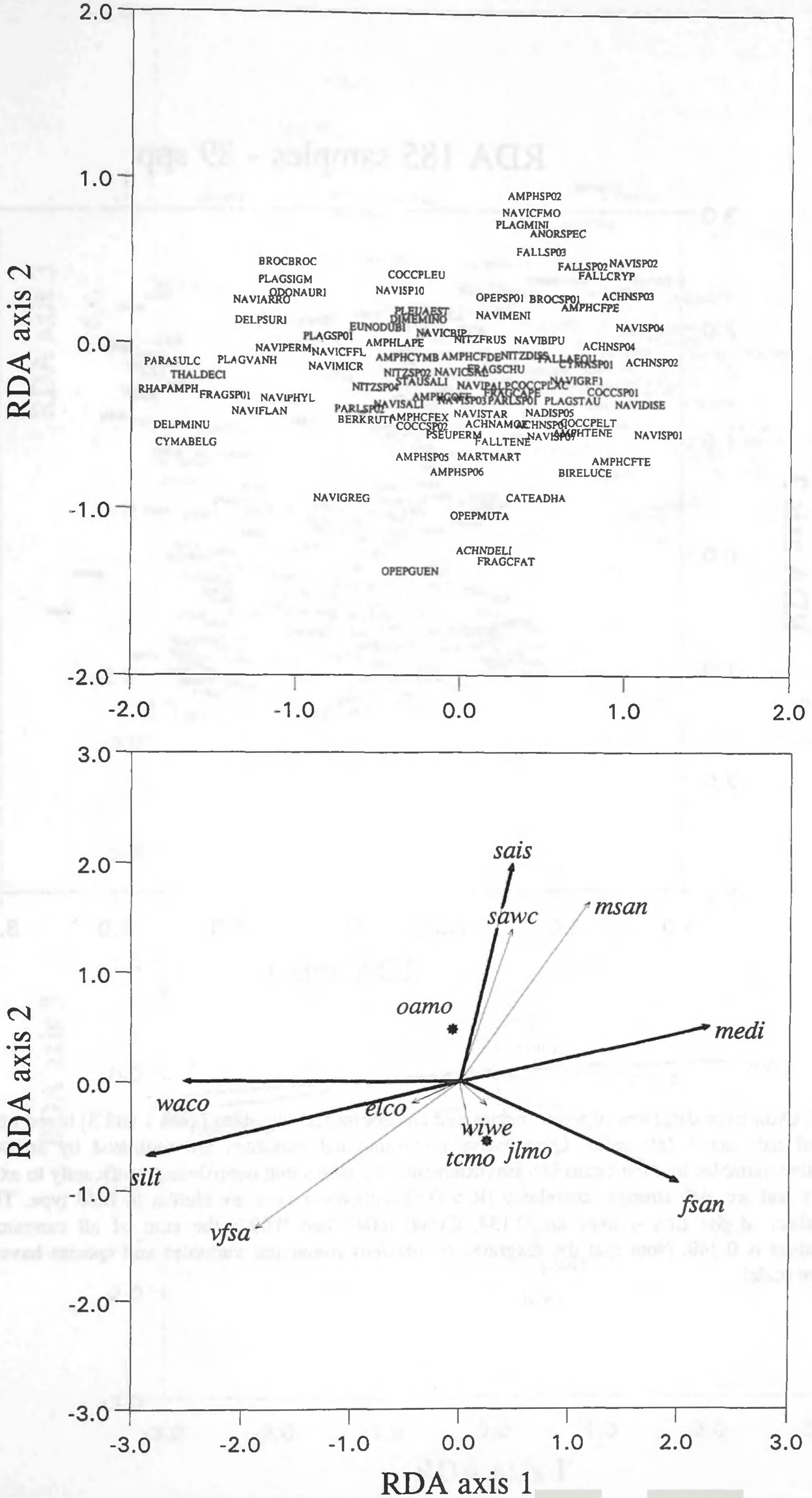


Fig. 31. Ordination diagrams of sites, species and environmental variables (axes 1 and 2) based on a RDA of data set 3 (89 taxa). Quantitative environmental variables are indicated by arrows, qualitative variables by their centroids. Environmental variables that contribute significantly to axes 1 and 2 and are also strongly correlated (R > 0.5) with these axes are shown in bold type. The eigenvalues of the first 4 axes are 0.154, 0.064, 0.043 and 0.022; the sum of all canonical eigenvalues is 0.349. Note that the diagrams of sites/environmental variables and species have a different scale!



2.0
1.0
0.0
-1.0
-2.0
RDA axis 2
AMPHSP02
NAVICFMO
PLAGMINI
ANORSPEC
FALLSP03
BROCBROC
FALLSP02
NAVISP02
FALLCRYP
PLAGSIGM
COCCPLEU
ODONAURI
NAVIARRO
NAVISP10
OPEPSP01
BROCSP01
ACHNSP03
AMPHCFPE
PLEUAEST
DIMEMINO
NAVIMENI
DELPSURI
EUNODUBI
NAVISP04
NAVICBIP
PLAGSP01
NITZFRUS
NAVIBIPU
AMPHLAPE
ACHNSP04
NAVIPERM
NAVICFFL
AMPHCYMB
AMPHCFDE
NITZDISS
FALLAEQU
PARASULC
PLAGVANH
CYMASP01
ACHNSP02
NAVIMICR
FRAGSCHU
THALDECI
NITZSP02
NAVICSAL
NAVIGRF1
STAUSALI
NAVIPALP
COCCPLAC
RHAPAMPH
NITZSP04
FRAGCAPE
COCCSP01
FRAGSP01
NAVIPHYL
AMPHCOFF
NAVISP03
PARLSP01
PLAGSTAU
NAVIDISE
NAVISALI
NAVIFLAN
PARLSP02
BERKRUTI
AMPHCFEX
NAVISTAR
NADISP05
DELPMINU
COCCSP02
ACHNAMOE
ACHNSP01
COCCPELT
PSEUPERM
NAVISP07
AMPHTENE
NAVISP01
CYMABELG
FALLTENE
AMPHSP05
MARTMART
AMPHCFTE
AMPHSP06
BIRELUCE
NAVIGREG
CATEADHA
OPEPMUTA
ACHNDELI
FRAGCFAT
OPEPGUEN
-2.0
-1.0
0.0
1.0
2.0
3.0
2.0
1.0
0.0
-1.0
-2.0
-3.0
RDA axis 2
sais
sawc
msan
oamo
medi
waco
elco
wiwe
jlmo
tcmo
silt
fsan
vfsa
-3.0
-2.0
-1.0
0.0
1.0
2.0
3.0
RDA axis 1

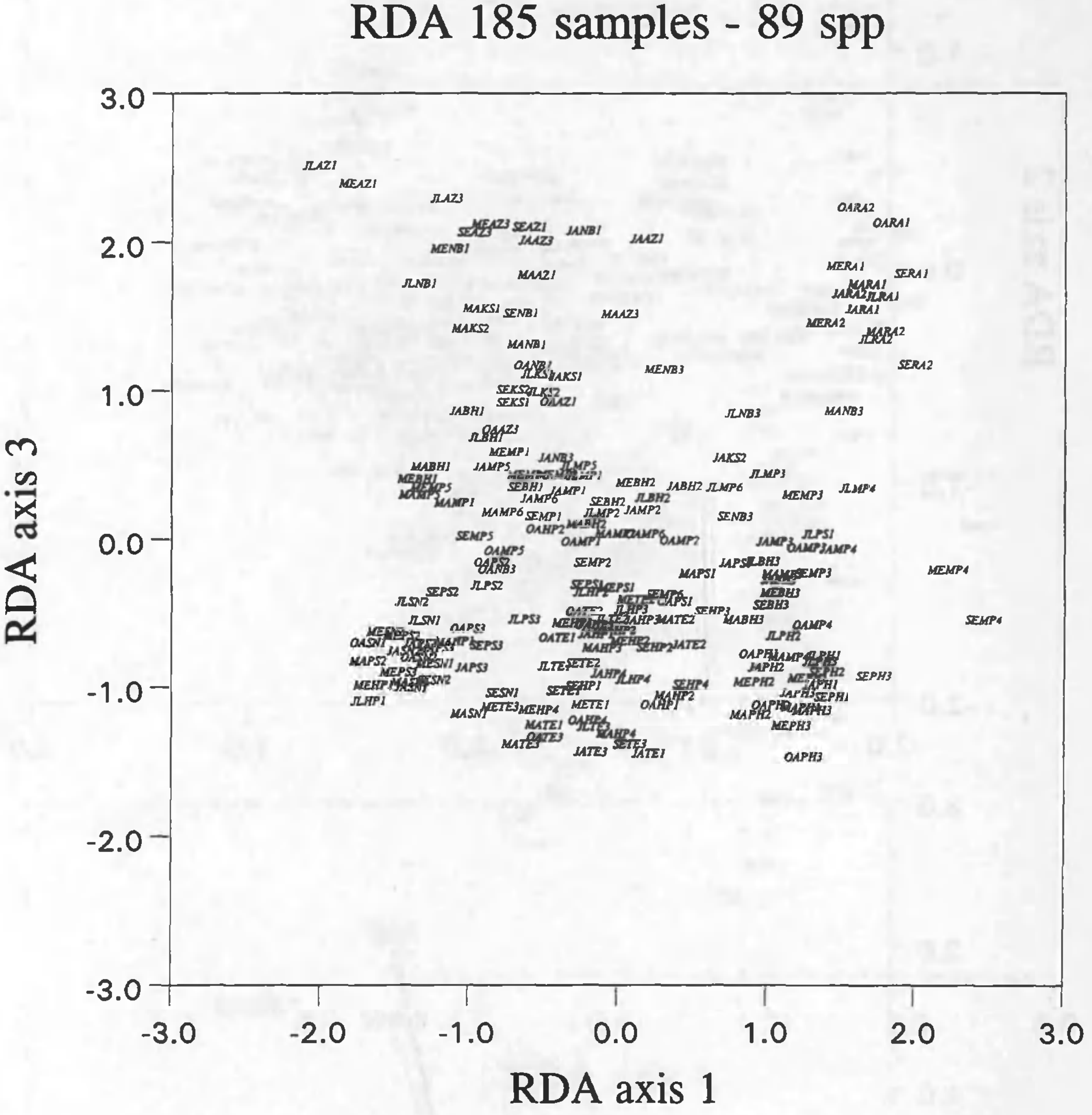
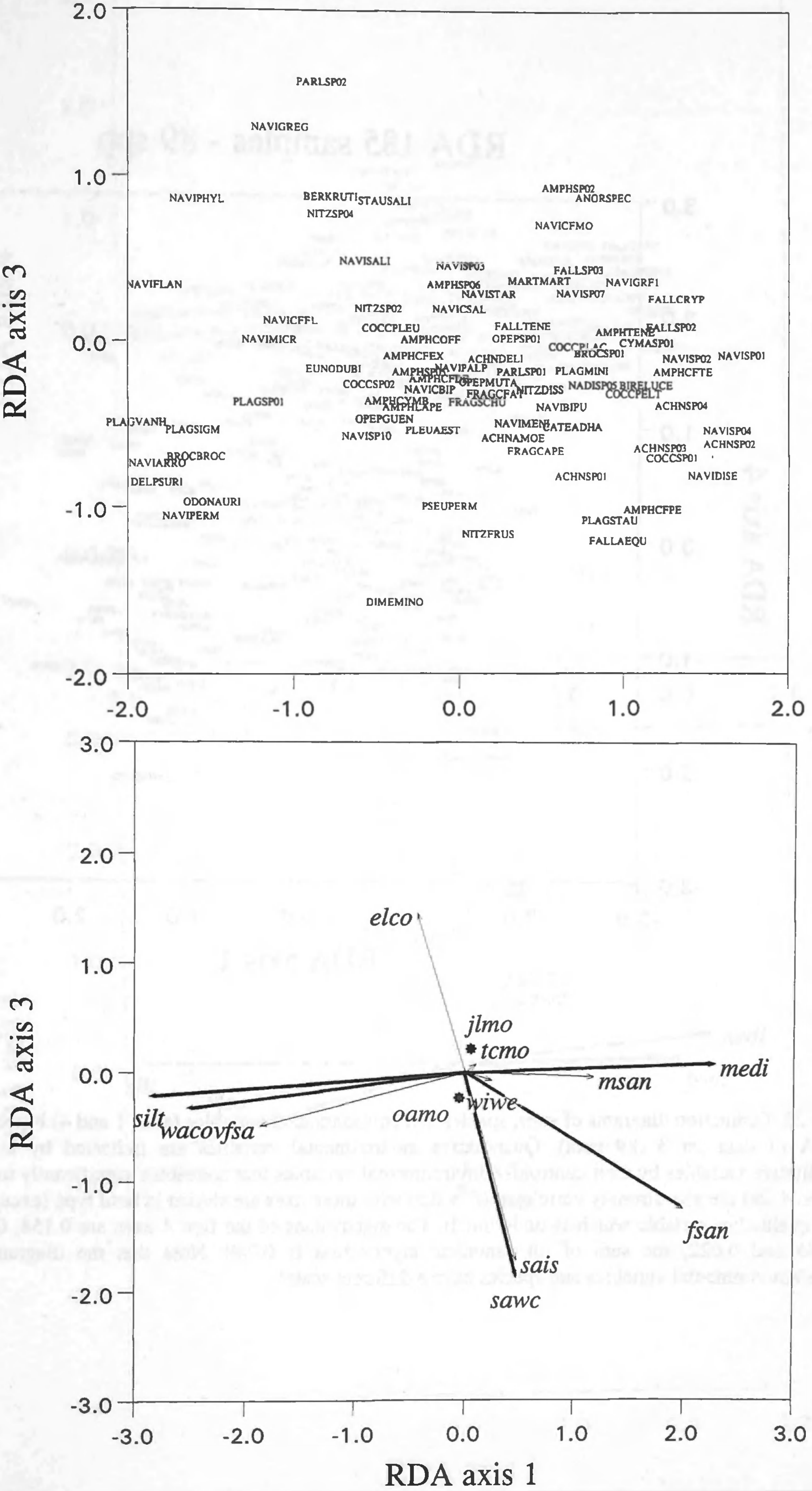


Fig. 32. Ordination diagrams of sites, species and environmental variables (axes 1 and 3) based on a RDA of data set 3 (89 taxa). Quantitative environmental variables are indicated by arrows, qualitative variables by their centroids. Environmental variables that contribute significantly to axes 1 and 3 and are also strongly correlated (R > 0.5) with these axes are shown in bold type. The eigenvalues of the first 4 axes are 0.154, 0.064, 0.043 and 0.022; the sum of all canonical eigenvalues is 0.349. Note that the diagrams of sites/environmental variables and species have a different scale!


RDA axis 3
2.0
1.0
0.0
-1.0
-2.0
-2.0
-1.0
0.0
1.0
2.0
PARLSP02
NAVIGREG
NAVIPHYL
BERKRUTI
STAUSALI
NITZSP04
AMPHSP02
ANORSPEC
NAVICFMO
NAVISALI
NAVISP03
FALLSP03
NAVIFLAN
AMPHSP06
MARTMART
NAVIGRF1
NAVISTAR
NAVISP07
FALLCRYP
NITZSP02
NAVICSAL
NAVICFFL
COCCPLEU
FALLTENE
AMPHTENE
FALLSP02
NAVIMICR
AMPHCOFF
OPEPSP01
CYMASP01
COCCPLAC
BROCSP01
AMPHCFEX
ACHNDELI
NAVISP02
NAVISP01
EUNODUBI
AMPHSP05
NAVIPALP
PARLSP01
PLAGMINI
AMPHCFTE
AMPHCFDE
OPEPMUTA
COCCSP02
NAVICBIP
FRAGCFAT
NITZDISS
NADISP05
BIRELUCE
COCCPELT
PLAGSP01
AMPHCYMB
AMPHLAPE
FRAGSCHU
NAVIBIPU
ACHNSP04
OPEPGUEN
PLAGVANH
PLAGSIGM
NAVIMENI
CATEADHA
NAVISP04
PLEUAEST
NAVISP10
ACHNAMOE
ACHNSP02
FRAGCAPE
ACHNSP03
BROCBROC
NAVIARRO
COCCSP01
DELPSURI
ACHNSP01
NAVIDISE
ODONAURI
PSEUPERM
AMPHCFPE
NAVIPERM
PLAGSTAU
NITZFRUS
FALLAEQU
DIMEMINO
RDA axis 3
3.0
2.0
1.0
0.0
-1.0
-2.0
-3.0
-3.0
-2.0
-1.0
0.0
1.0
2.0
3.0
RDA axis 1
elco
jlmo
tcmo
medi
msan
silt
wiwe
oamo
wacovfsa
fsan
sais
sawc

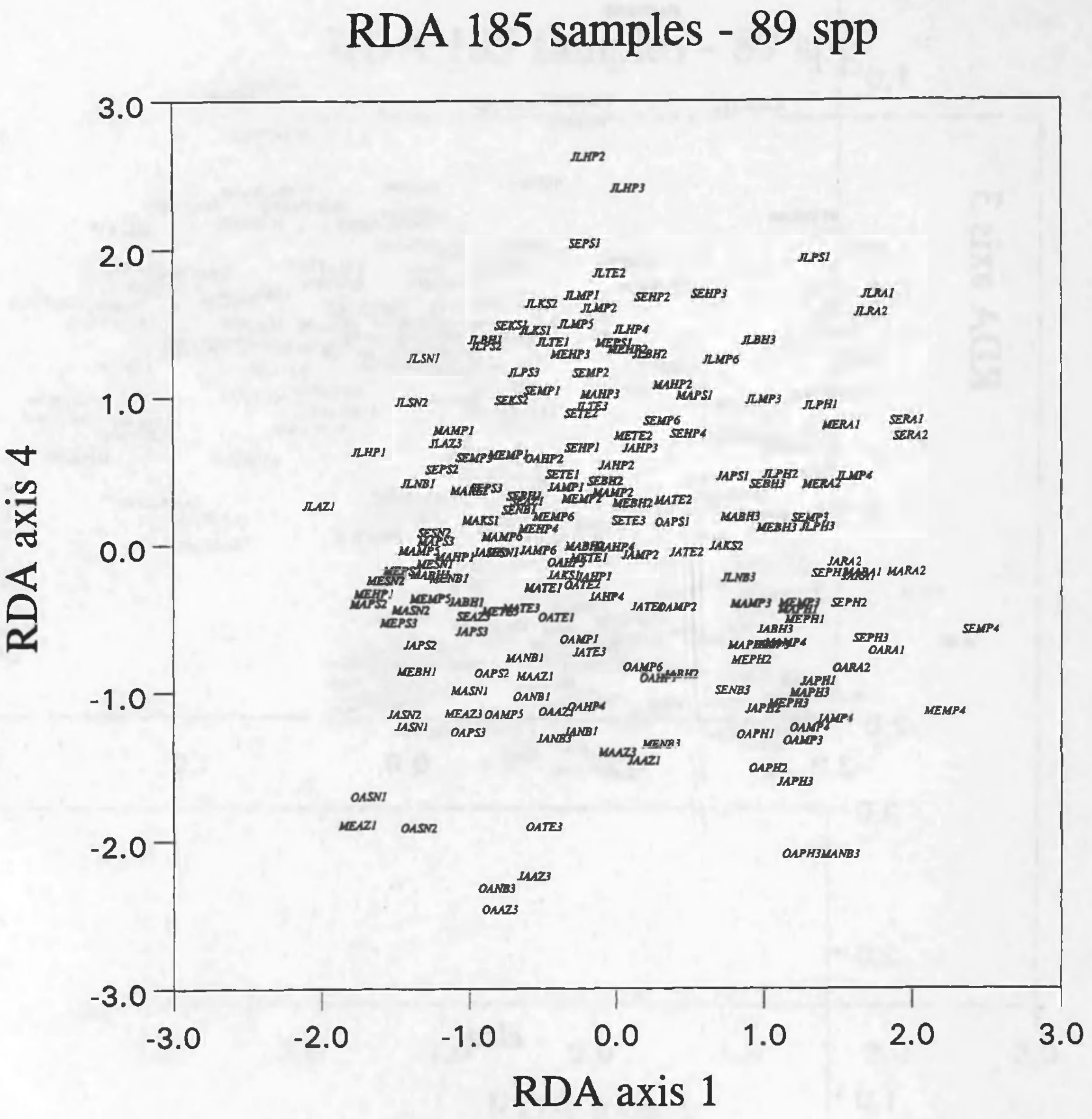
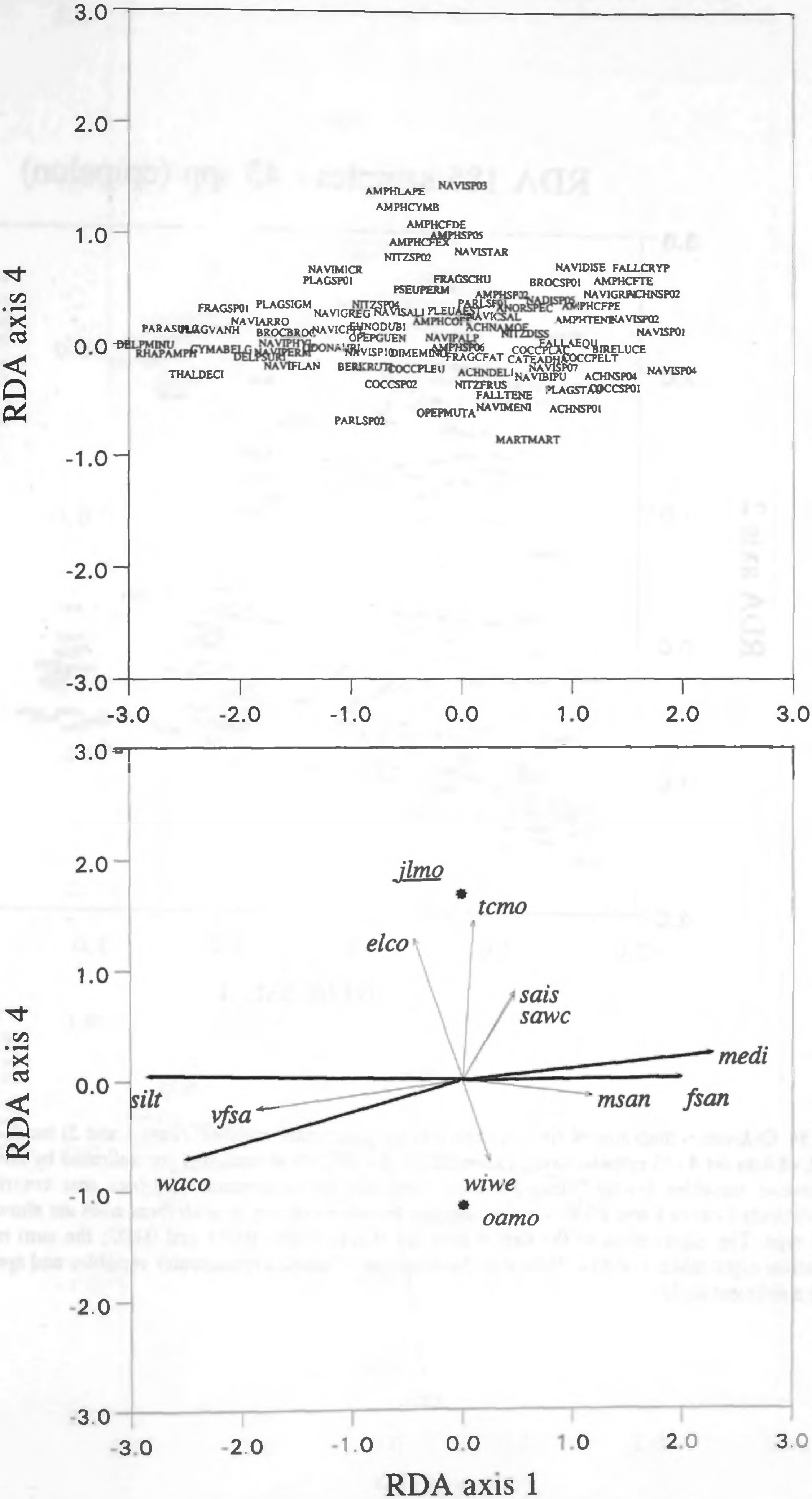


Fig. 33. Ordination diagrams of sites, species and environmental variables (axes 1 and 4) based on a RDA of data set 3 (89 taxa). Quantitative environmental variables are indicated by arrows, qualitative variables by their centroids. Environmental variables that contribute significantly to axes 1 and 4 and are also strongly correlated (R > 0.5) with these axes are shown in bold type (except for the qualitative variable which is underlined). The eigenvalues of the first 4 axes are 0.154, 0.064, 0.043 and 0.022; the sum of all canonical eigenvalues is 0.349. Note that the diagrams of sites/environmental variables and species have a different scale!


RDA axis 4
3.0
2.0
1.0
0.0
-1.0
-2.0
-3.0
NAVISP03
AMPHLAPE
AMPHCYMB
AMPHCFDE
AMPHSP05
AMPHCFEX
NAVISTAR
NITZSP02
NAVIMICR
PLAGSP01
NAVIDISE
FALLCRYP
FRAGSCHU
BROCSP01
AMPHCFTE
PSEUPERM
AMPHSP02
NAVIGRI
ACHNSP02
PARLSP01
NADISP05
FRAGSP01
PLAGSIGM
NITZSP04
ANORSPEC
AMPHCFPE
NAVIGREG
NAVISALI
PLEUAEST
NAVICSAL
NAVIARRO
AMPHCOFF
AMPHTENE
NAVISP02
PARASULC
PLAGVANH
BROCBROC
NAVICFTT
EUNODUBI
ACHNAMOE
NITZDISS
NAVISP01
OPEPGUEN
NAVIPALP
DELPMINU
NAVIPHYL
FALLAEQU
RHAPAMPH
CYMABELG
NAVIPERM
ODONAURI
NAVISP10
DIMEMINO
AMPHSP06
COCCPLAC
BIRELUCE
DELPSURI
FRAGCFAT
CATEADHA
COCCPELT
NAVIFLAN
BERKRUTI
COCCPLEU
ACHNDELI
NAVISP07
THALDECI
NAVIBIPU
ACHNSP04
NAVISP04
COCCSP02
NITZFRUS
PLAGSTAU
COCCSP01
FALLTENE
NAVIMENI
ACHNSP01
OPEPMUTA
PARLSP02
MARTMART
-3.0
-2.0
-1.0
0.0
1.0
2.0
3.0
RDA axis 4
3.0
2.0
1.0
0.0
-1.0
-2.0
-3.0
jlmo
tcmo
elco
sais
sawc
medi
silt
msan
fsan
vfsa
waco
wiwe
oamo
-3.0
-2.0
-1.0
0.0
1.0
2.0
3.0
RDA axis 1

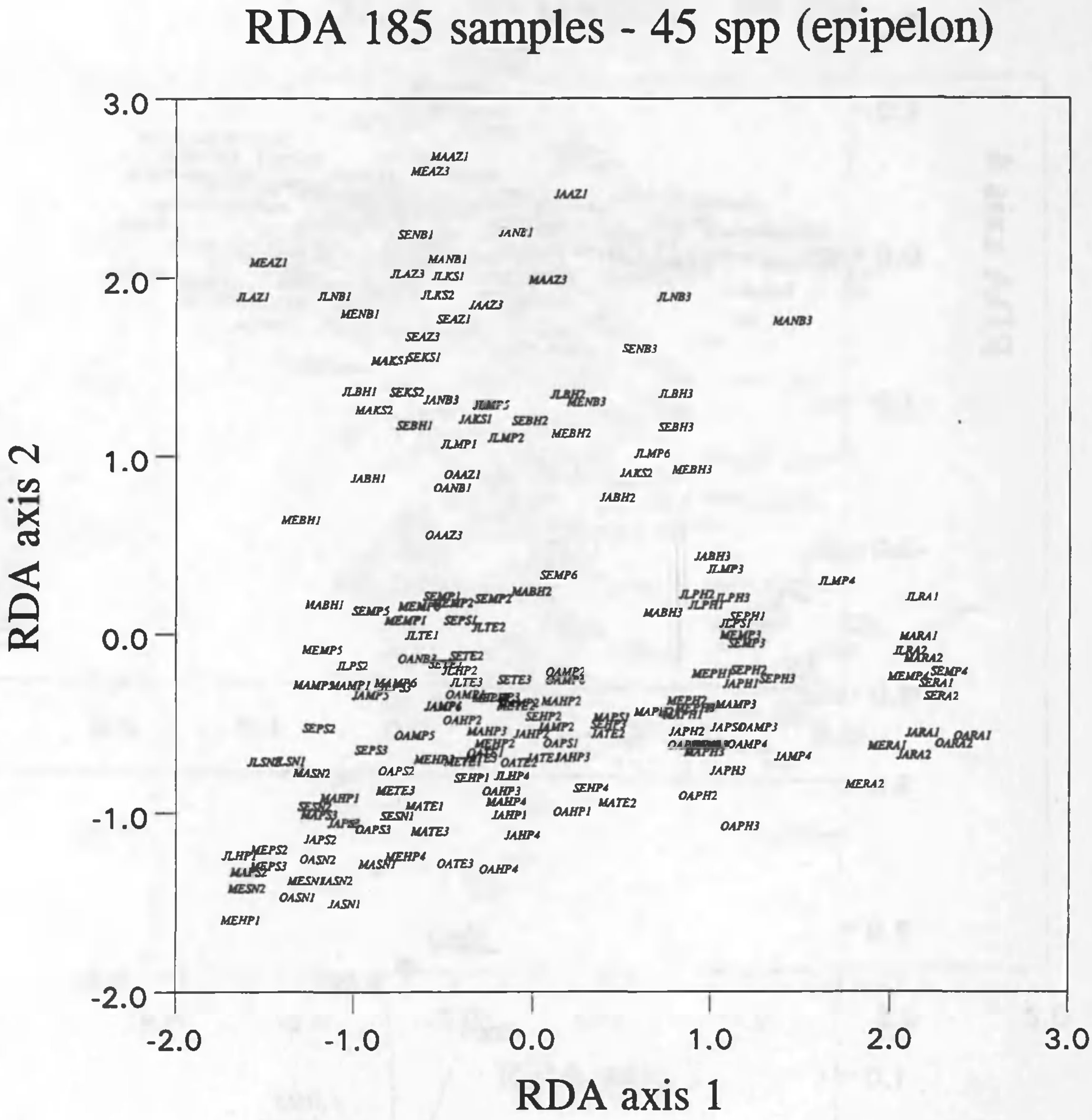
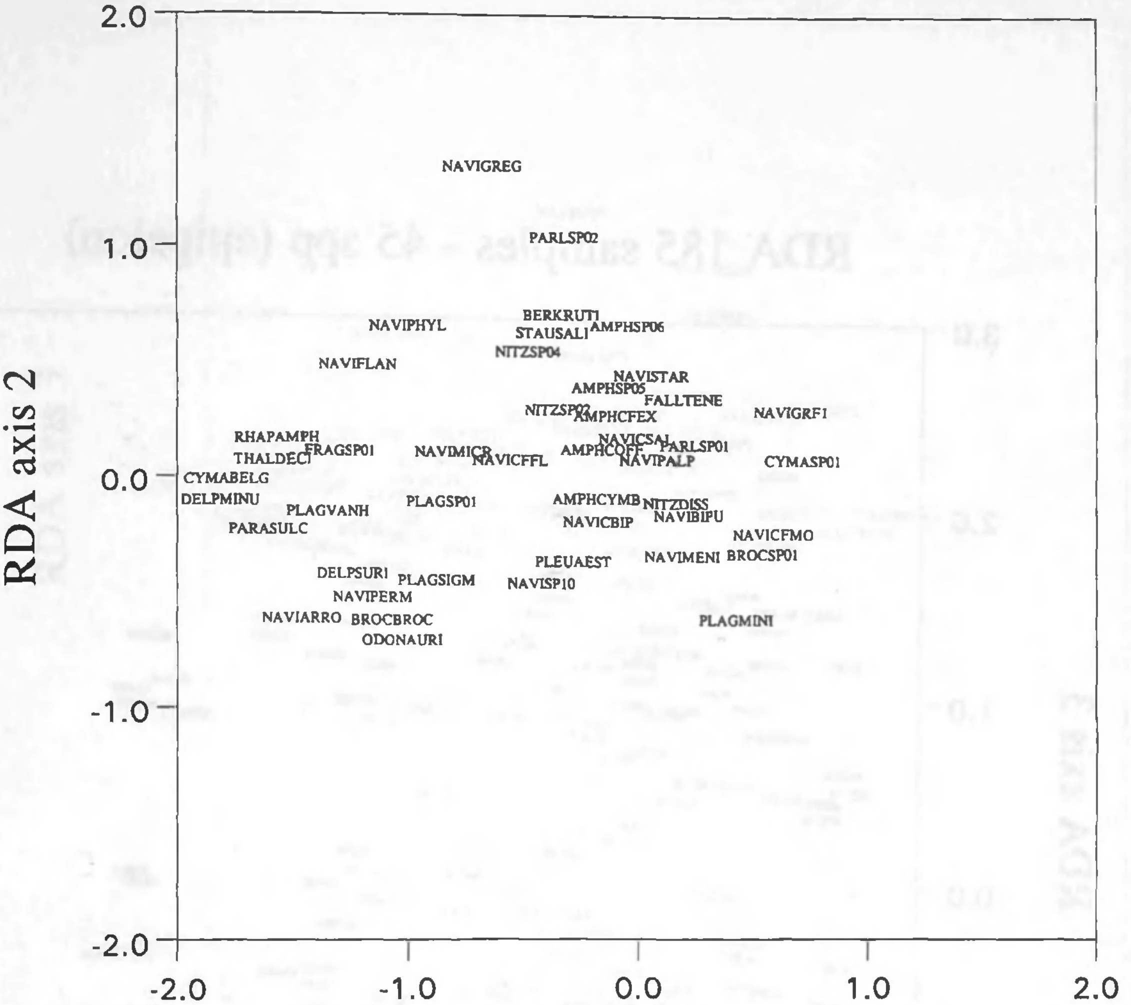
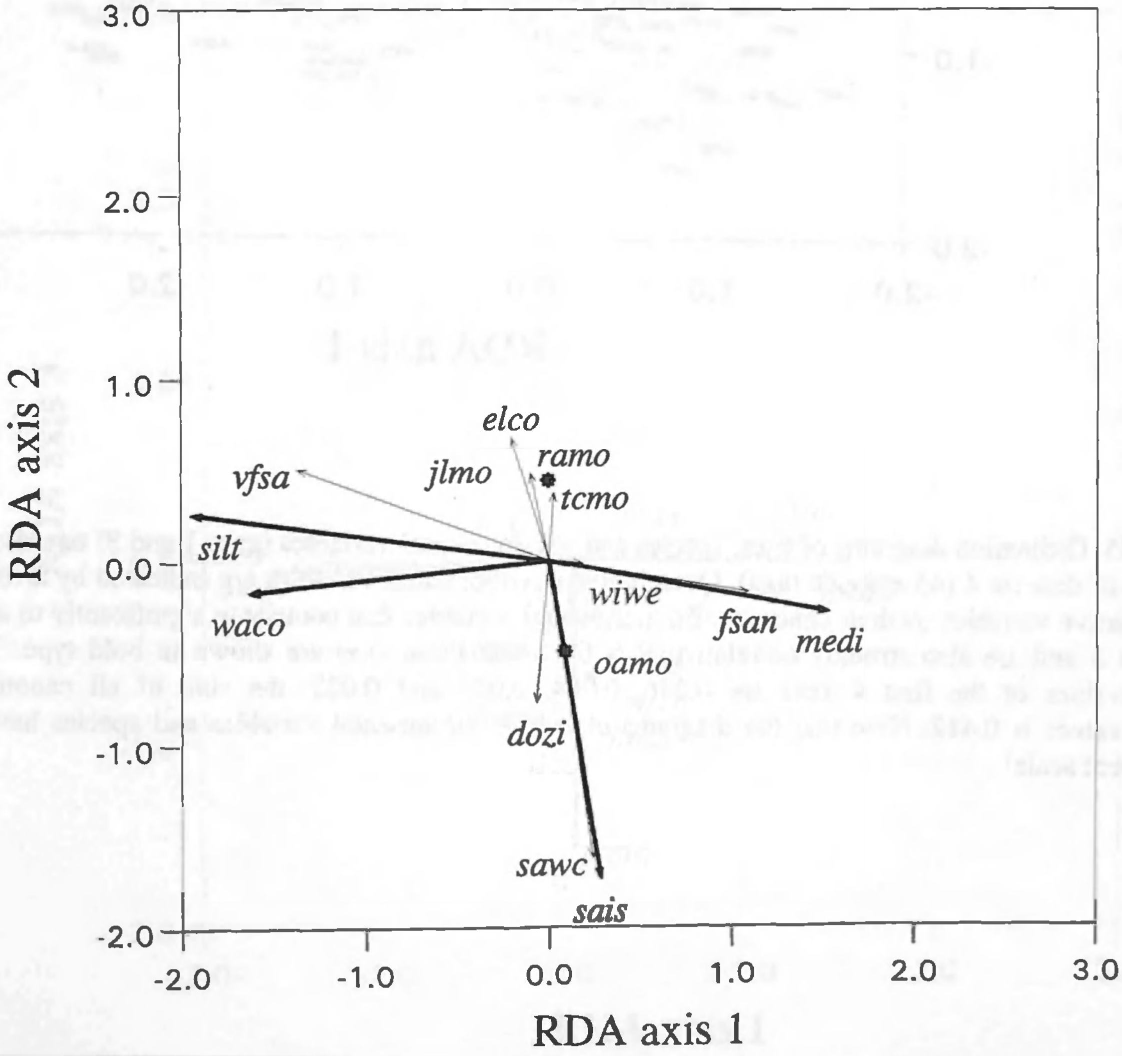


Fig. 34. Ordination diagrams of sites, species and environmental variables (axes 1 and 2) based on a RDA of data set 4 (45 epipelic taxa). Quantitative environmental variables are indicated by arrows, qualitative variables (oamo, jlmo) by their centroids. Environmental variables that contribute significantly to axes 1 and 2 and are also strongly correlated (R > 0.5) with these axes are shown in bold type. The eigenvalues of the first 4 axes are 0.236, 0.064, 0.033 and 0.022; the sum of all canonical eigenvalues is 0.412. Note that the diagrams of sites/environmental variables and species have a different scale!


2.0
1.0
0.0
-1.0
-2.0
-2.0
-1.0
0.0
1.0
2.0
RDA axis 2
NAVIGREG
PARLSP02
BERKRUT1
NAVIPHYL
STAUSAL1
AMPHSP06
NITZSP04
NAVIFLAN
NAVISTAR
AMPHSP05
FALLTENE
NITZSP02
AMPHCFEX
NAVIGRF1
RHAPAMPH
FRAGSP01
THALDECI
NAVIMICR
NAVICFFL
NAVICSAL
AMPHCOFF
PARLSP01
NAVIPALP
CYMASP01
CYMABELG
DELPMINU
PLAGVANH
PLAGSP01
AMPHCYMB
NITZDISS
NAVIBIPU
NAVICBIP
PARASULC
NAVICFMO
PLEUAEST
NAVIMENI
BROCSP01
DELPSURI
PLAGSIGM
NAVISP10
NAVIPERM
NAVIARRO
BROCBROC
PLAGMINI
ODONAURI


3.0
2.0
1.0
0.0
-1.0
-2.0
-2.0
-1.0
0.0
1.0
2.0
3.0
RDA axis 2
RDA axis 1
elco
ramo
jlmo
vfsa
tcmo
silt
wiwe
waco
fsan
medi
oamo
dozi
sawc
sais

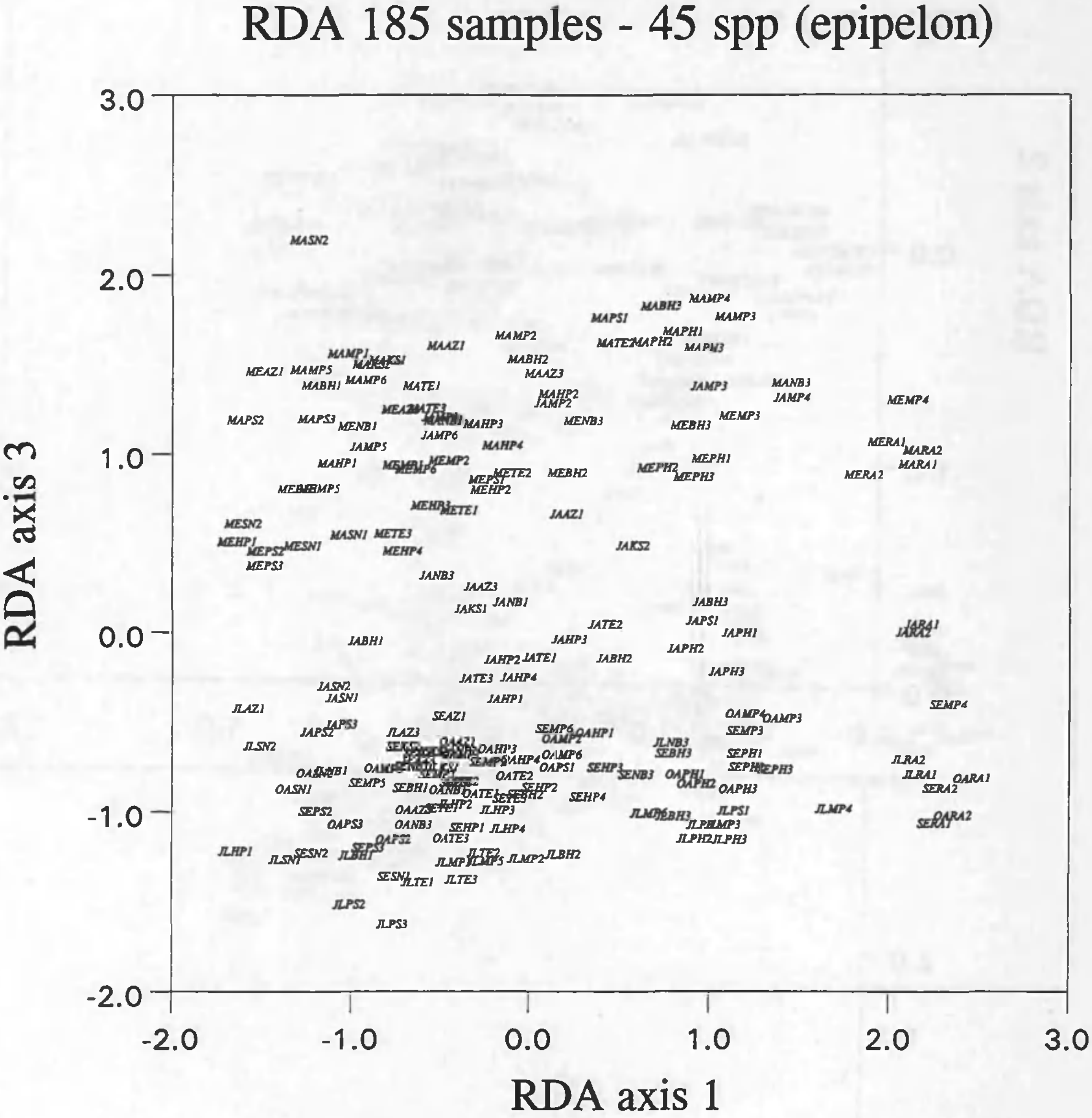
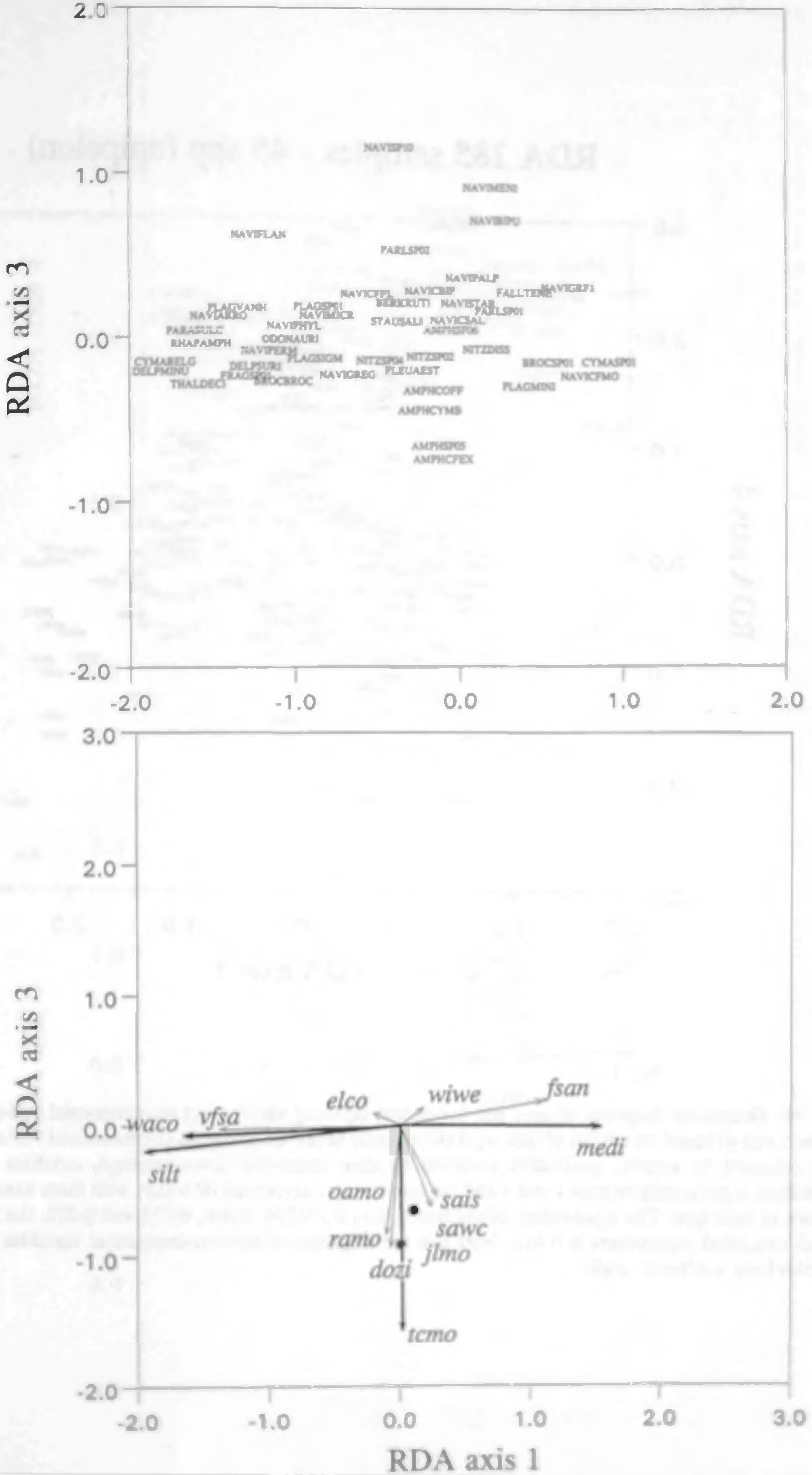


Fig. 35. Ordination diagrams of sites, species and environmental variables (axes 1 and 3) based on a RDA of data set 4 (45 epipelic taxa). Quantitative environmental variables are indicated by arrows, qualitative variables by their centroids. Environmental variables that contribute significantly to axes 1 and 3 and are also strongly correlated (R > 0.5) with these axes are shown in bold type. The eigenvalues of the first 4 axes are 0.236, 0.064, 0.033 and 0.022; the sum of all canonical eigenvalues is 0.412. Note that the diagrams of sites/environmental variables and species have a different scale!


2.0
1.0
0.0
-1.0
-2.0
RDA axis 3
-2.0
-1.0
0.0
1.0
2.0
NAVISP10
NAVIMENI
NAVIBIPU
NAVIFLAN
PARLSP02
NAVIPALP
NAVICFPL
NAVICRIP
FALLTENE
NAVIGRF1
PLAGVANH
PLAGSP01
BERKRUTI
NAVISTAR
NAVIARRO
NAVIMICR
PARLSP01
STAUSALI
NAVICSAL
PARASULC
NAVIPHYL
AMPHSP06
RHAPAMPH
ODONAURI
NAVIPERM
NITZDISS
CYMABELG
PLAGSIGM
NITZSP04
NITZSP02
BROCSP01
CYMASP01
DELPMINU
DELPSURI
FRAGSP01
NAVIGREG
PLEUAEST
NAVICFMO
THALDECI
BROCBROC
AMPHCOFF
PLAGMINI
AMPHCYMB
AMPHSP05
AMPHCFEX
3.0
2.0
1.0
0.0
-1.0
-2.0
RDA axis 3
fsan
elco
wiwe
waco
vfsa
medi
silt
oamo
sais
sawc
ramo
jlmo
dozi
tcmo
-2.0
-1.0
0.0
1.0
2.0
3.0
RDA axis 1

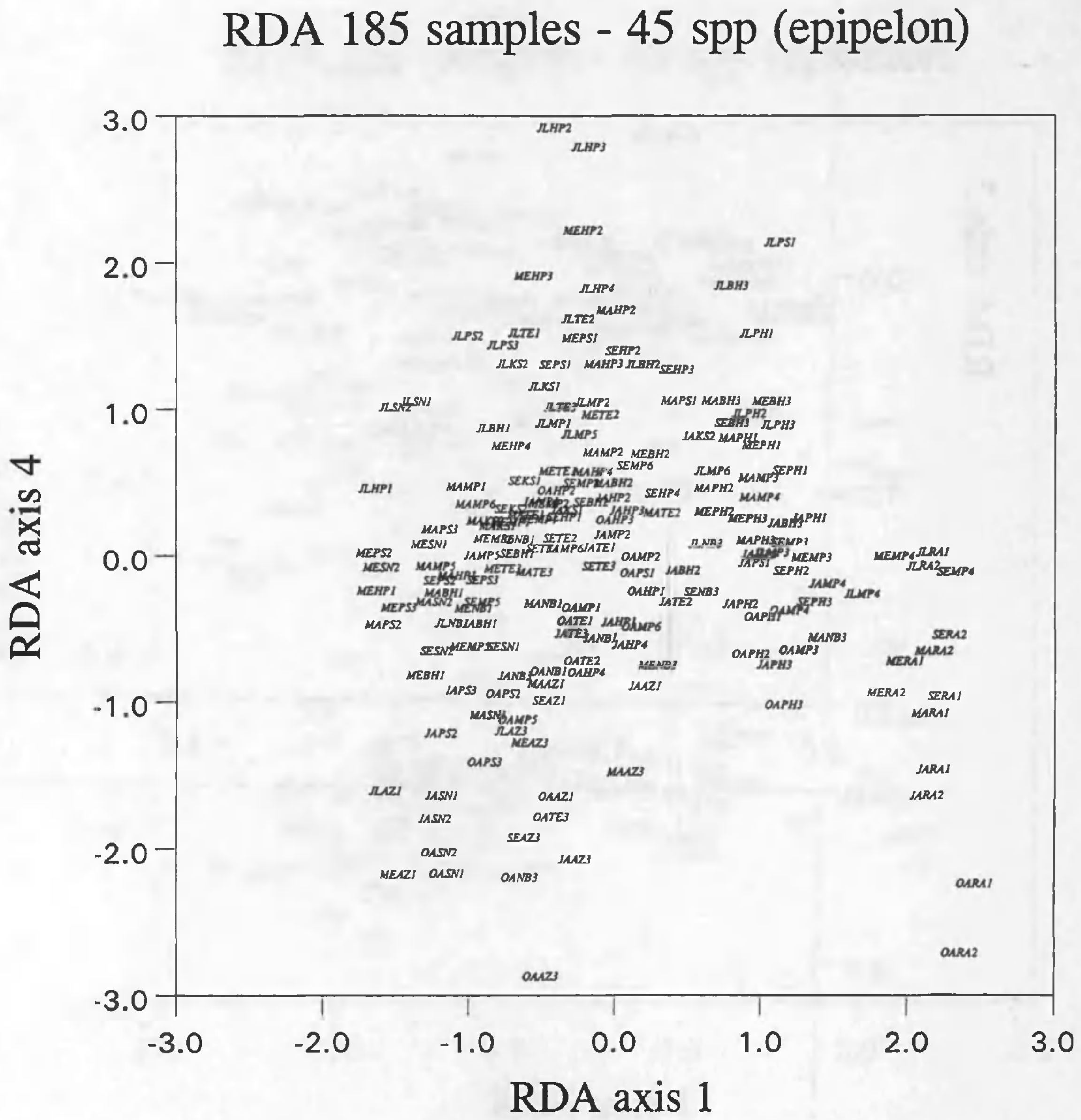
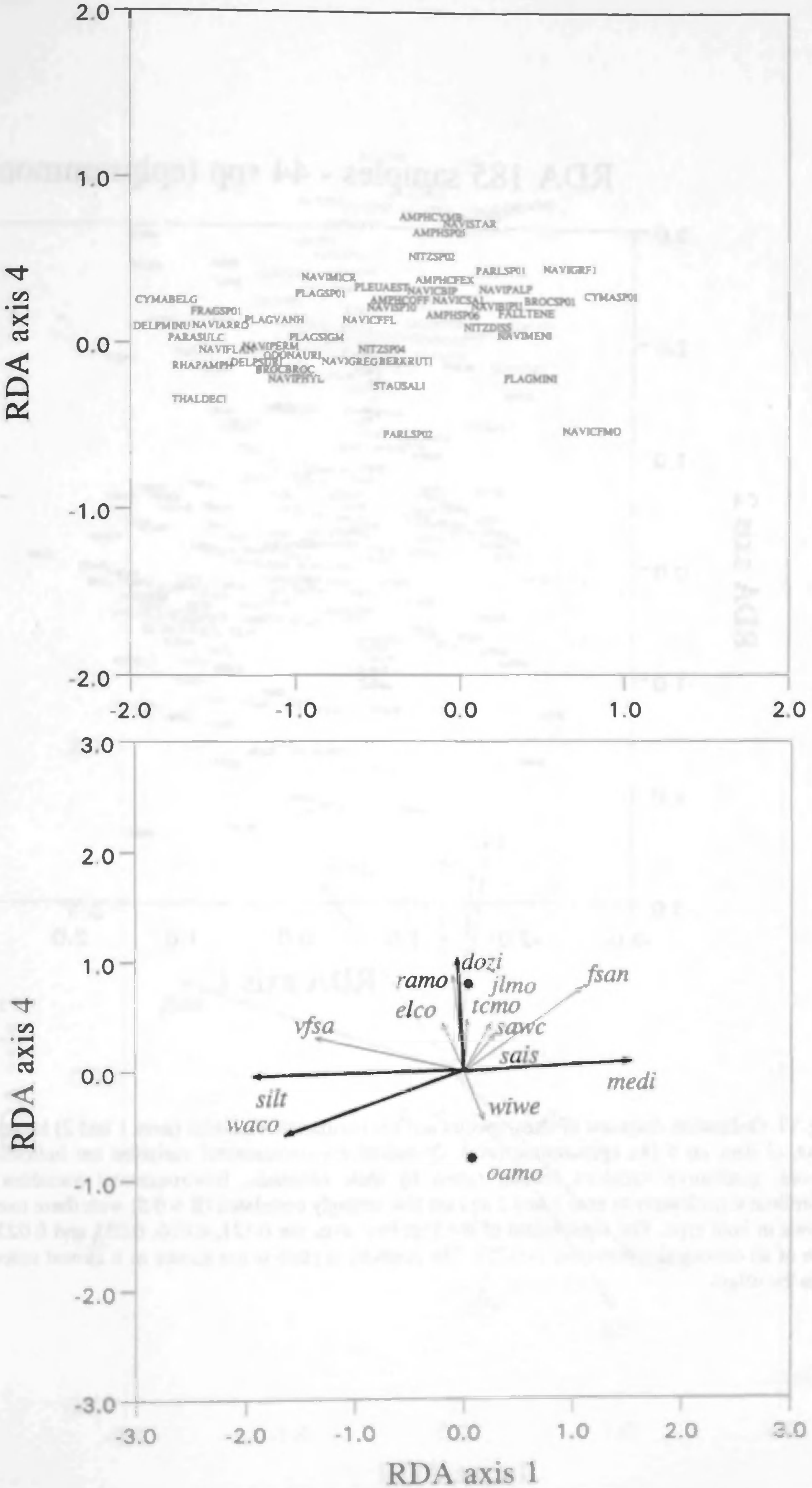


Fig. 36. Ordination diagrams of sites and correlation biplot of species and environmental variables (axes 1 and 4) based on a RDA of data set 4 (45 epipelic taxa). Quantitative environmental variables are indicated by arrows, qualitative variables by their centroids. Environmental variables that contribute significantly to axes 1 and 4 and are also strongly correlated (R > 0.5) with these axes are shown in bold type. The eigenvalues of the first 4 axes are 0.236, 0.064, 0.033 and 0.022; the sum of all canonical eigenvalues is 0.412. Note that the diagrams of sites/environmental variables and species have a different scale!


RDA axis 4
2.0
1.0
0.0
-1.0
-2.0
-2.0
-1.0
0.0
1.0
2.0
AMPHCYMB
NAVISTAR
AMPHSP05
NITZSP02
PARLSP01
NAVIGRF1
NAVIMICR
AMPHCFEX
PLEUAEST
NAVICBIP
NAVIPALP
PLAGSP01
CYMABELG
AMPHCOFF
NAVICSAL
NAVIBIPU
BROCSP01
CYMASP01
NAVISP10
FRAGSP01
AMPHSP06
FALLTENE
PLAGVANH
NAVICFFL
DELPMINU
NAVIARRO
NITZDISS
NAVIMENI
PARASULC
PLAGSIGM
NAVIFLAN
NAVIPERM
NITZSP04
ODONAURI
RHAPAMPH
DELPSURI
NAVIGREG
BERKRUTI
BROCBROC
NAVIPHYL
STAUSALI
PLAGMINI
THALDECI
PARLSP02
NAVICFMO
RDA axis 4
3.0
2.0
1.0
0.0
-1.0
-2.0
-3.0
-3.0
-2.0
-1.0
0.0
1.0
2.0
3.0
dozi
ramo
jlmo
fsan
elco
tcmo
vfsa
sawc
sais
medi
silt
wiwe
waco
oamo
RDA axis 1

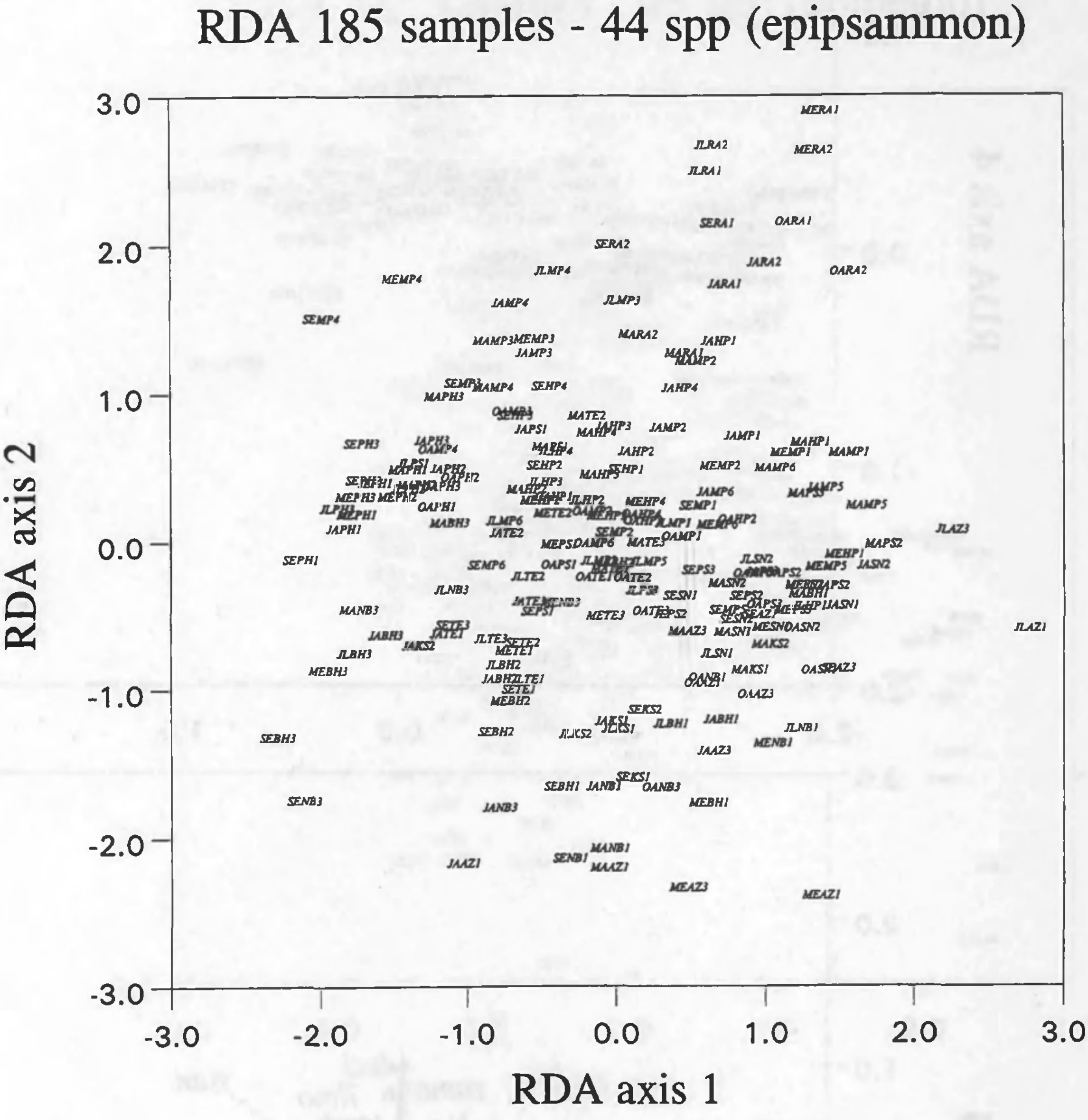
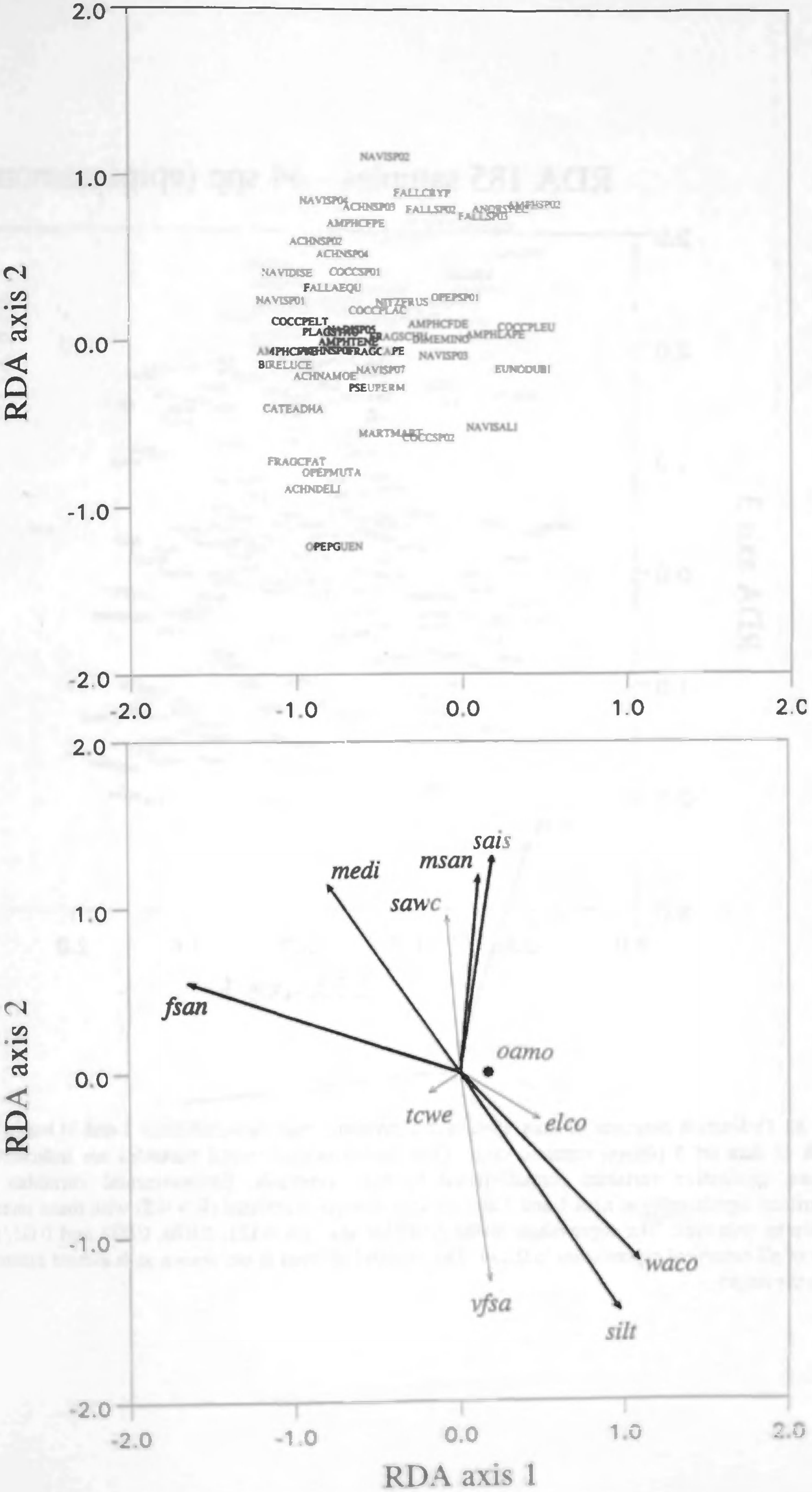


Fig. 37. Ordination diagrams of sites, species and environmental variables (axes 1 and 2) based on a RDA of data set 5 (44 epipsammic taxa). Quantitative environmental variables are indicated by arrows, qualitative variables (oamo, jamo) by their centroids. Environmental variables that contribute significantly to axes 1 and 2 and are also strongly correlated (R > 0.5) with these axes are shown in bold type. The eigenvalues of the first four axes are 0.121, 0.070, 0.033 and 0.023; the sum of all canonical eigenvalues is 0.294. The centroid of jamo is not shown as it almost coincides with the origin.


RDA axis 2
2.0
1.0
0.0
-1.0
-2.0
-2.0
-1.0
0.0
1.0
2.0
NAVISP02
FALLCRYP
NAVISP04
ACHNSP03
FALLSP02
FALLSP03
AMPHSP02
AMPHCFPE
ACHNSP02
ACHNSP04
NAVIDISE
COCCSP01
FALLAEQU
NAVISP01
NITZFRUS
OPEPSP01
COCCPLAC
COCCPELT
AMPHCFDE
COCCPLEU
AMPHTENE
FRAGSCHU
DIMEMINO
AMPHLAPE
FRAGCAPE
NAVISP03
BIRELUCE
NAVISP07
EUNODUBI
ACHNAMOE
PSEUPERM
CATEADHA
NAVISALI
MARTMART
COCCSP02
FRAGCFAT
OPEPMUTA
ACHNDELI
OPEPGUEN
RDA axis 2
2.0
1.0
0.0
-1.0
-2.0
sais
msan
medi
sawc
fsan
oamo
tcwe
elco
waco
vfsa
silt
-2.0
-1.0
0.0
1.0
2.0
RDA axis 1

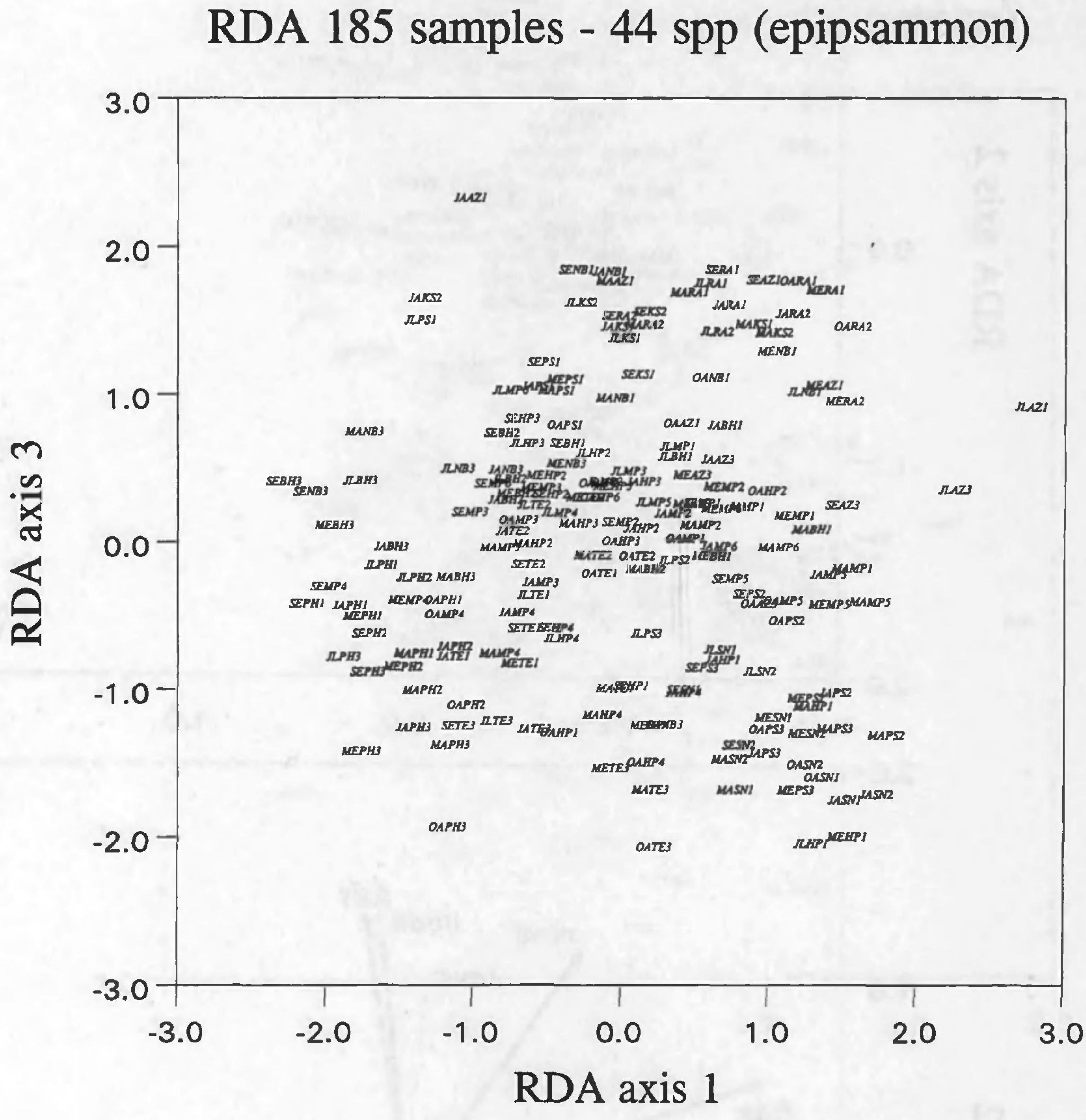
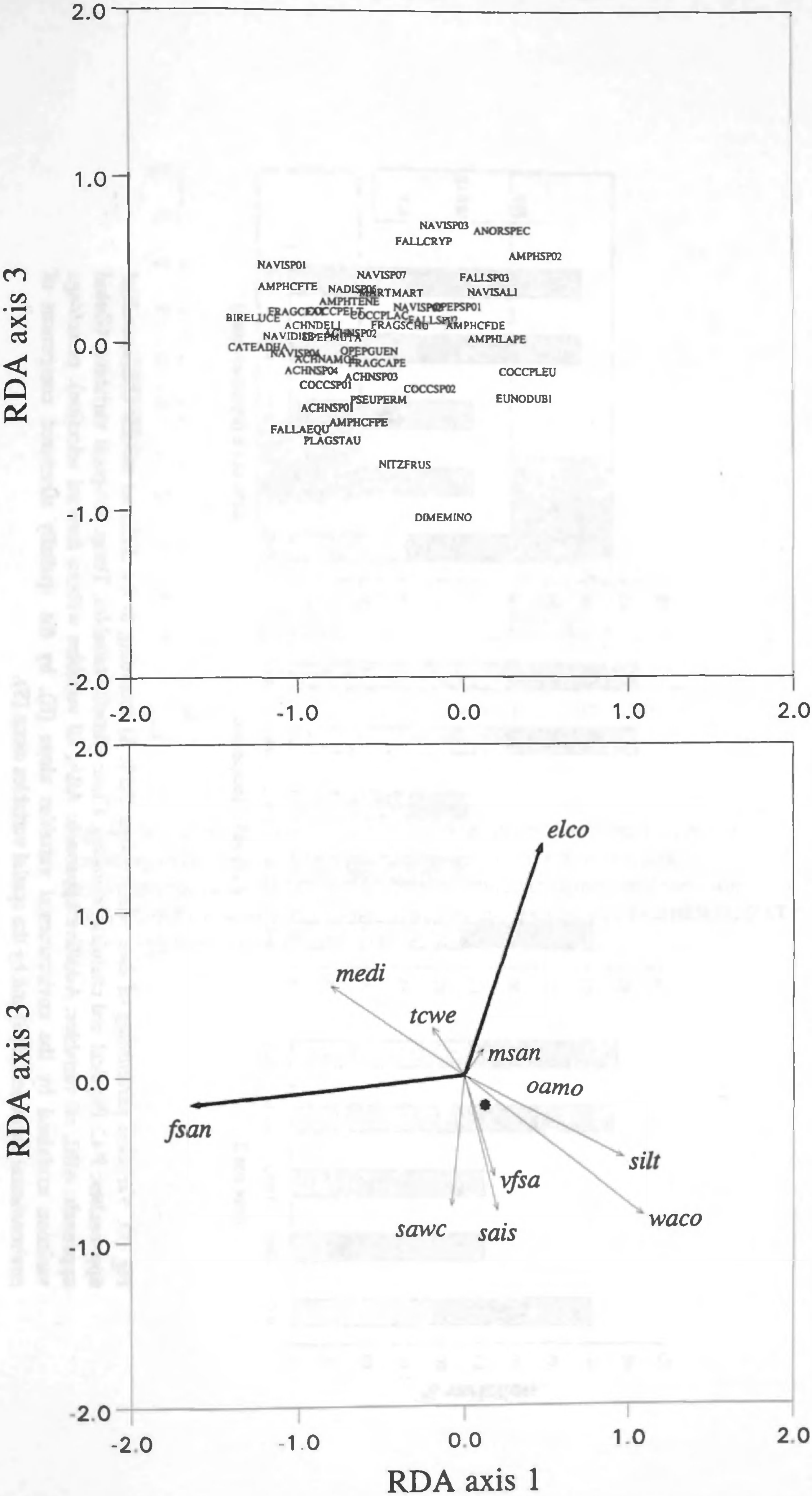


Fig. 38. Ordination diagrams of sites, species and environmental variables (axes 1 and 3) based on a RDA of data set 5 (44 epipsammic taxa). Quantitative environmental variables are indicated by arrows, qualitative variables (oamo, jamo) by their centroids. Environmental variables that contribute significantly to axes 1 and 3 and are also strongly correlated (R > 0.5) with these axes are shown in bold type. The eigenvalues of the first four axes are 0.121, 0.070, 0.033 and 0.023; the sum of all canonical eigenvalues is 0.294. The centroid of jamo is not shown as it almost coincides with the origin.


RDA axis 3
2.0
1.0
0.0
-1.0
-2.0
-2.0
-1.0
0.0
1.0
2.0
NAVISP03
ANORSPEC
FALLCRYP
AMPHSP02
NAVISP01
NAVISP07
FALLSP03
AMPHCFTE
NADISP05
MARTMART
NAVISALI
AMPHTENE
NAVISP02
OPEPSP01
BIRELUCE
FRAGCEXI
COCCPELT
COCCPLAC
FALLSP02
ACHNDELI
FRAGSCHU
AMPHCFDE
NAVIDISP
ACHNSP02
OPEPMUTA
AMPHLAPE
CATEADHA
NAVISP04
OPEPGUEN
ACHNAMOE
FRAGCAPE
ACHNSP04
ACHNSP03
COCCPLEU
COCCSP01
COCCSP02
PSEUPERM
EUNODUBI
ACHNSP01
AMPHCFPE
FALLAEQU
PLAGSTAU
NITZFRUS
DIMEMINO
RDA axis 3
2.0
1.0
0.0
-1.0
-2.0
-2.0
-1.0
0.0
1.0
2.0
elco
medi
tcwe
msan
oamo
fsan
silt
vfsa
waco
sawc
sais
RDA axis 1

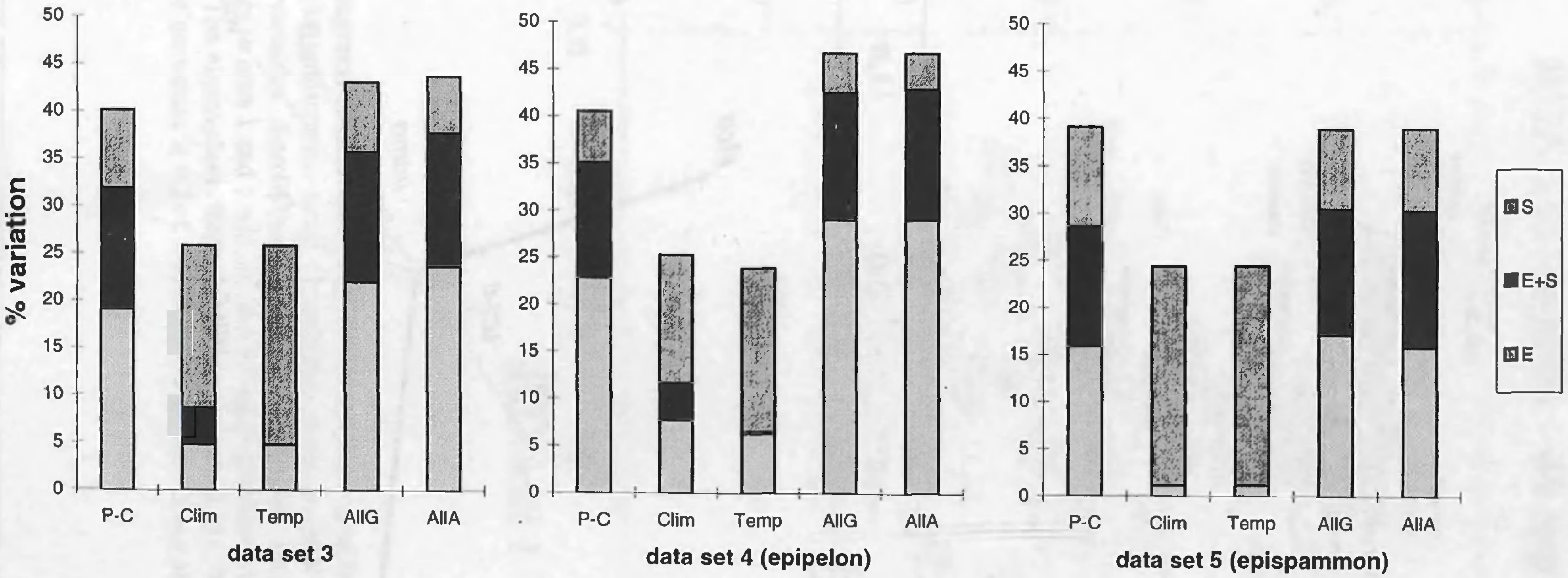


Fig. 39. Variation partitioning of data sets 3-5 (see Table 8) according to the different models (**Independent approaches**: P-C: Physical and chemical variables; Clim: climatic variables, Temp: temporal variables. **Global approach**: AllG, all variables; **Additive approach**: AllA, all variables without forward selection): percentage variation explained by the environmental variables alone (E), by the spatially structured component of environmental variables (E+S) and by the spatial variables alone (S).

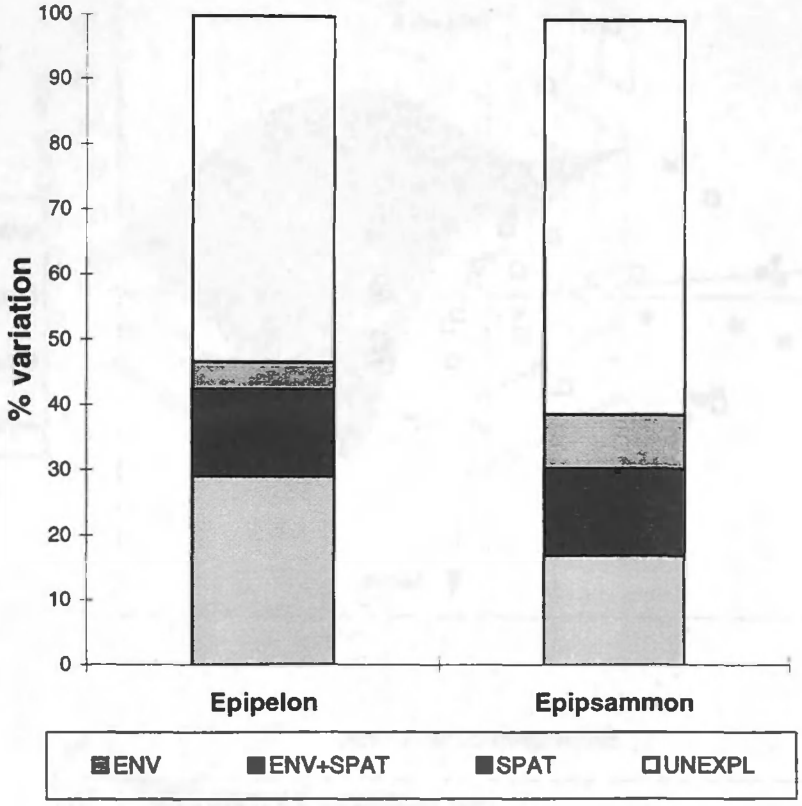
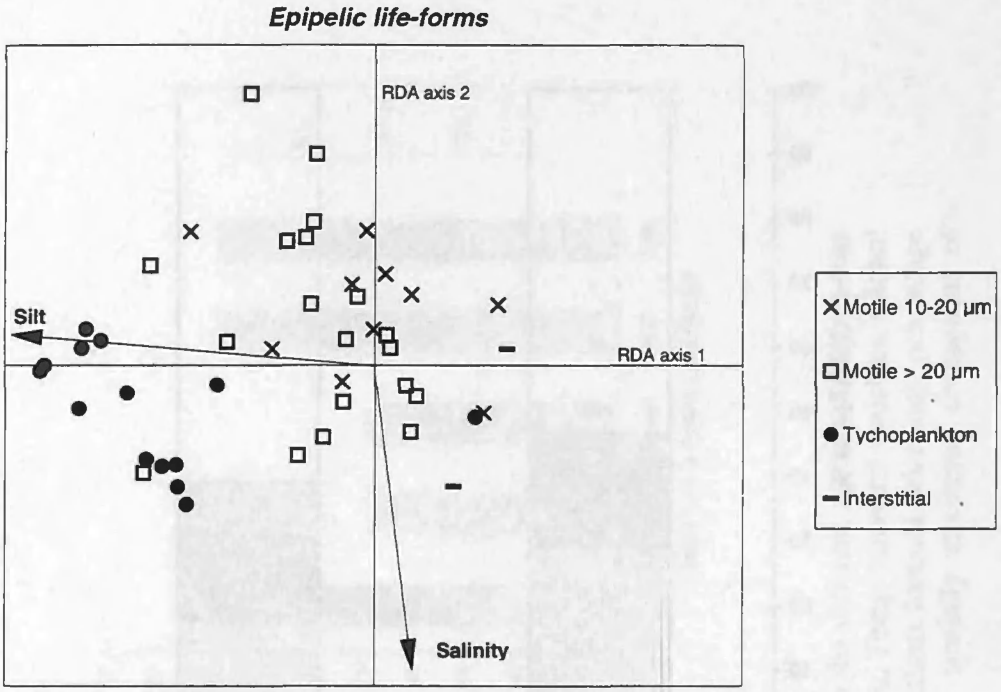


Fig. 40. Variation partitioning of data sets 4 (epipelon) and 5 (epipsammon) according to the best model (i.e. the global approach) into non-spatial environmental variation (ENV), spatially structured environmental variation (ENV+SPAT), spatial variation not shared by the environmental variables (SPAT) and unexplained variation (UNEXPL).



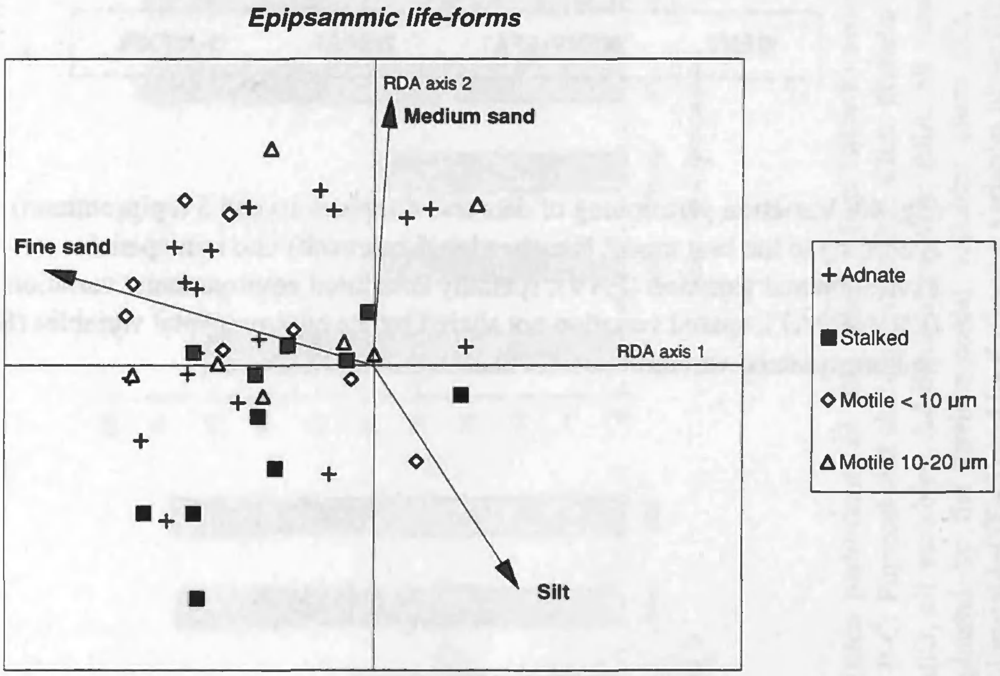


Fig. 41. The distribution of epipelic and epipsammic life-forms in relation to the most important environmental variables. These figures are identical to the ordination diagrams shown in Figs 34 and 37 respectively.

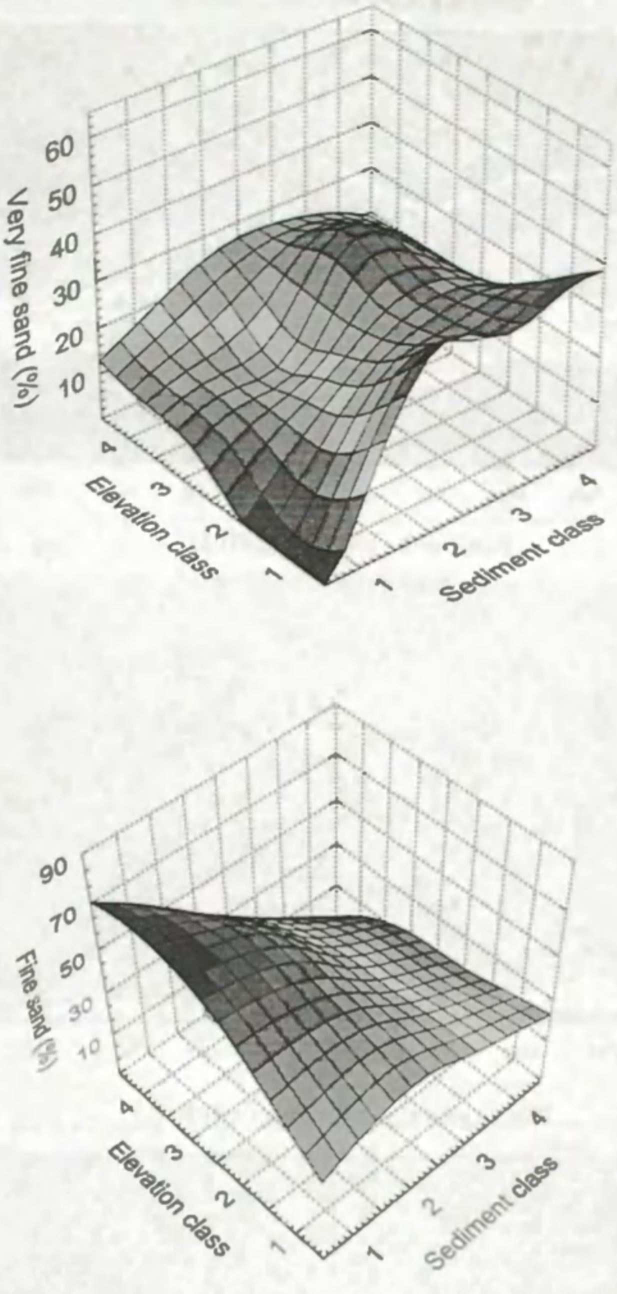


Fig. 42. Patterns in very fine sand and fine sand content of the sediment decomposed into sediment and elevation class. For sediment and elevation class affiliation, see chapter 3.2.6. and Table 6.

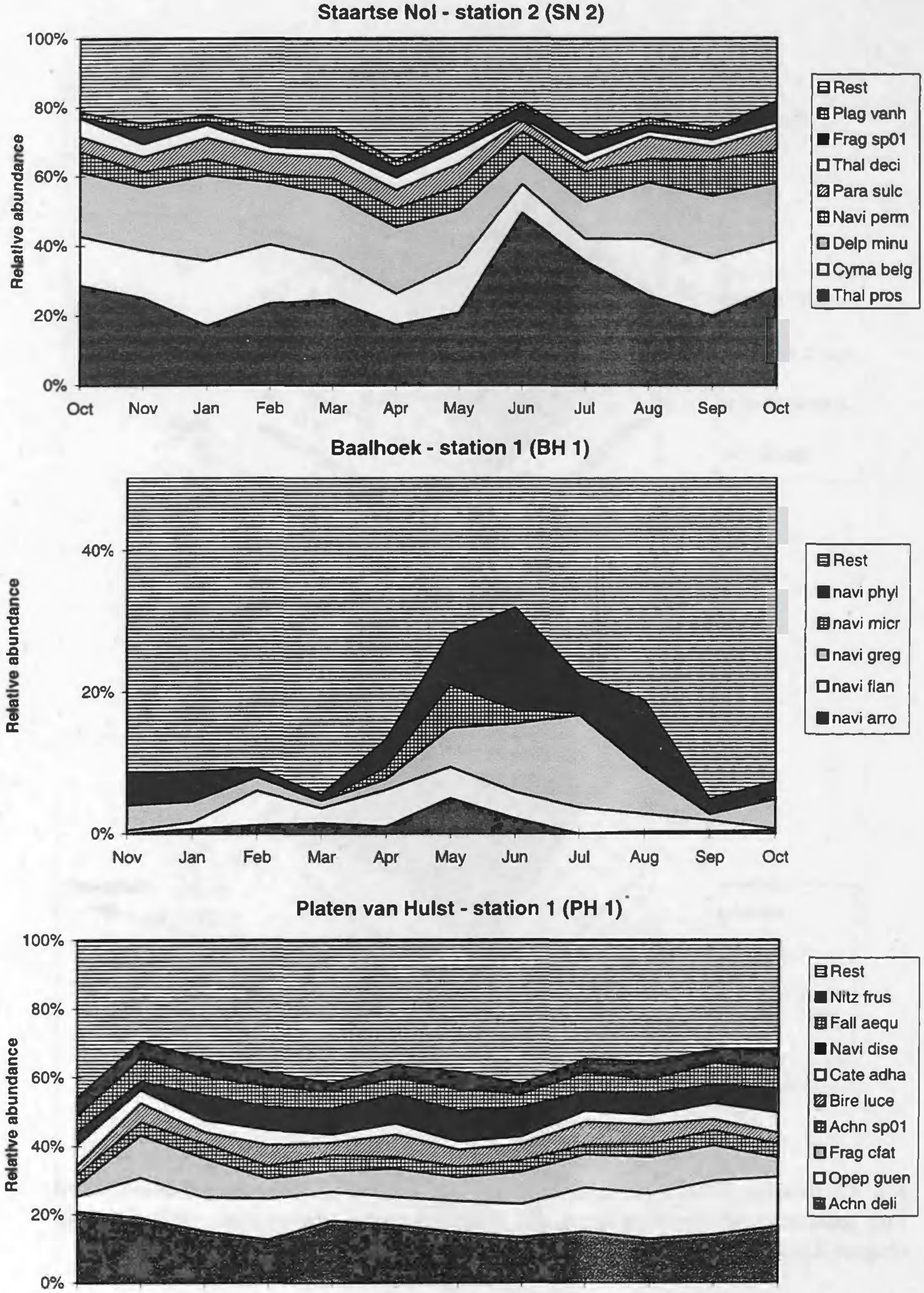


Fig. 43. Three examples of seasonal changes in relative cell numbers during the sampling period in diatom communities dominated by tychoplanktonic taxa (SN 2), motile epipelic taxa (BH 1) and epipsammic taxa (PH 1) respectively. Note that only the relative abundance of the relevant taxa has been shown; the remainder of taxa has been lumped together. For taxon abbreviations, see Table 18.

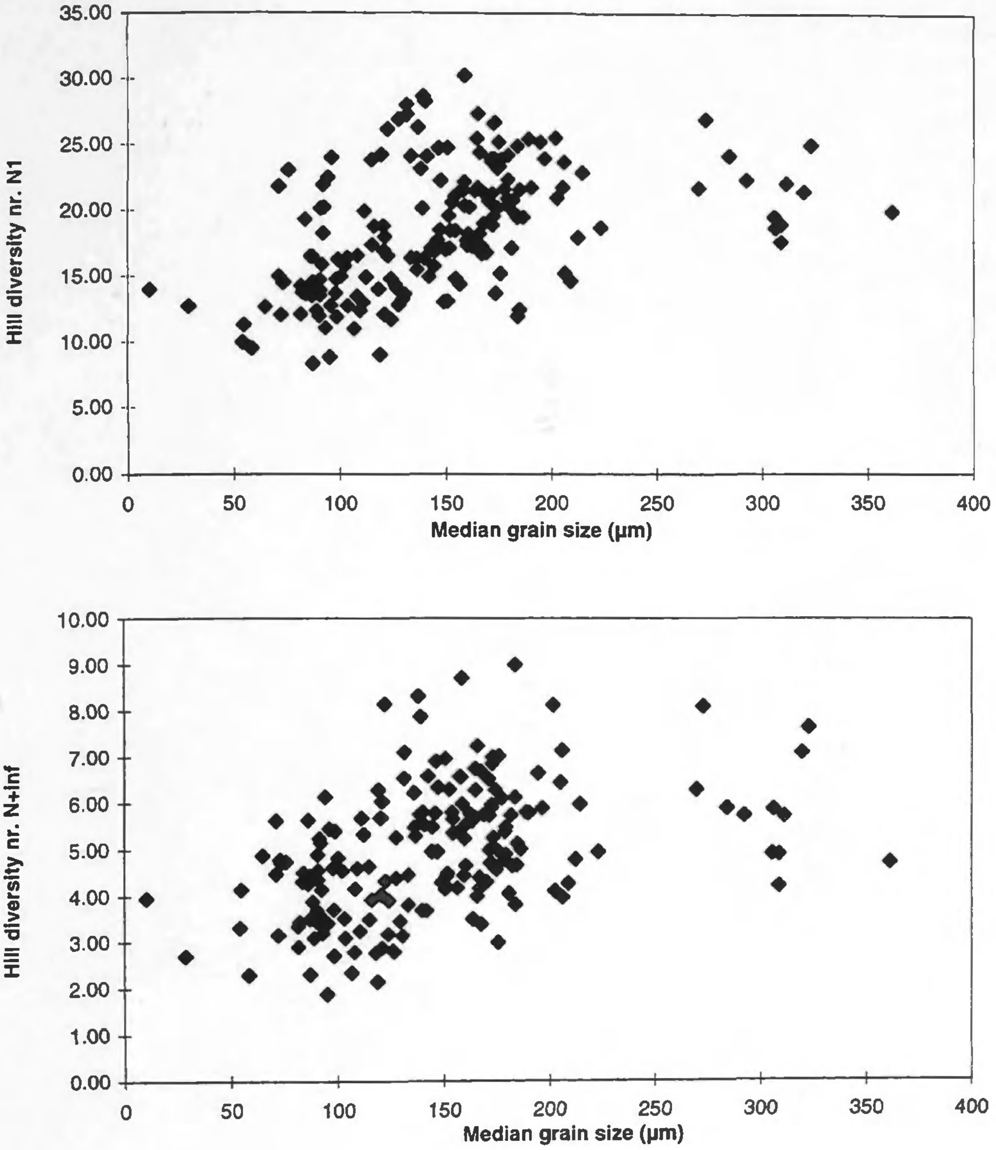


Fig. 44. Relationship between median grain size (µm) and diversity (Hill diversity numbers N1 and N+inf).