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Intertidal benthic diatoms of the Tagus estuary: Taxonomic composition and spatial-temporal variation

(Volume 1)

Lourenço Luís Cardoso Soares Ribeiro

DOUTORAMENTO EM BIOLOGIA
Especialidade Biodiversidade
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Tese orientada por:
Prof. Doutora Vanda Brotas e Prof. Doutor Yves Rincé

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à Laura e ao Luís Alberto

O apanhador de nabos

aponta o caminho

com um nabo

Issa Kobayashi, séc. XVIII-XIX.

versão de Jorge Sousa Braga,

in “Primeira Neve”, Ed. Assírio & Alvim

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Acknowledgements

First and foremost, I wish to thank my two supervisors, Prof. Vanda Brotas and Prof. Yves Rincé for their support and advice. I am deeply grateful to Prof. Vanda Brotas for introducing me to microphytobenthos ecology and for always foster my interest in diatom taxonomy. To Prof. Yves Rincé, many thanks for kindly receiving me in his laboratory and home and for his promptness in responding to my solicitations, even when I was not in France. To both of them, I acknowledge their trust, patience and graciousness in dealing with a sometimes stubborn and single-minded student.

Some of the fondest memories of this period are from my stays at the Laboratoire de Biologie Marine in Nantes. For welcoming me as part of the family, I would like to thank the staff of the "ISOMER". So, to Bruno, Christophe, Jean-Bernard, Laurent, Philippe, Pierre, Priscilla, Richard, Sindy, Vona et tous les autres: un grand merci!

I am very grateful to my colleagues of the Instituto of Oceanografia and, in particular, to the botany group. It will be hard to name everyone who works or worked there without, regretfully, forgetting someone. So, to all of you: thank you for your steady and generous support, companionship and example. In spite of all the difficulties and complaints you kept showing up, every morning, with an undying passion for the science you do! Special thanks to Bruno Jesus, Paulo Cartaxana and Rafael Mendes for all the hard work during the HIMOM project. Their enormous contribution to this work was absolutely essential.

Most of the electron microscopy presented in this work was made by Prof. Dr. Dr. h.c. Horst Lange-Bertalot, Manfred Ruppel (J.-W. Goethe University) and Prof. Dr. hab. Andrzej Witkowski (University of Szczecin). For kindly accepting to explore the Tagus estuary material, but also for the fruitful and lasting discussions on the taxonomy and beauty of marine benthic diatoms, my sincere and deepest gratitude.

I would also like to express my gratefulness to the fellow diatomists who provided their PhD. thesis or research papers and gave me great insights and knowledge on the difficult subject of marine benthic diatom taxonomy. I have particularly appreciated the "arguments" given by Frithjof Sterrenburg; the discussions on *Amphora* with Eugenia Sar and

the suggestions given by Koen Sabbe, whose own work on the ecology and systematics of the benthic diatoms of the Westerschelde estuary greatly influenced this thesis.

The diatom plates in Volume 2 were made possible by the expertise and know-how of my cousins Bárbara and Tiago Soares Ribeiro (Zazádesign – Dá saúde e faz crescer). I will be forever grateful for their wonderful work and, mostly, for their lifelong friendship.

I am very thankful to all my friends and family for all their love and support during all these years. It would have been impossible without their belief in me and their help in putting things into perspective. In particular, I would like to thank my father for putting on the lab coat and helping me with the preparation of the diatom slides. It was great fun! Muito obrigado a todos!

Finally, I specially thank Susanne, my partner in all of this and in much more. I cannot imagine pulling trough this thesis without your constant support, love and understanding. Merci viu mau für aues!

This work was funded by FCT - Fundação para a Ciência e Tecnologia with a PhD research grant from SFRM/BD-10426-02.

Summary

The taxonomic composition of intertidal benthic diatom communities of many estuarine and coastal areas worldwide is still fairly unknown. In order to increase knowledge on the biodiversity and community structure of the intertidal benthic diatoms of the Tagus estuary, a two-year survey was carried out in 6 stations with distinct sediment structure. The main output of the study is the Identification Guide which is supplemented by 1019 micrographs (volume 2). This detailed systematic account of 185 diatom taxa observed includes: morphological descriptions and comparisons to similar species, as well as information on biogeography and autoecology. Moreover, the structure of the diatom communities was characterized by its diversity and other features related to community physiognomy, such as size-class or life-form distribution. Temporal patterns were clearly subordinate to spatial ones; mud content was found to be the environmental variable most correlated to the multivariate patterns of the biotic data. The level of physical disturbance of the sediment was found to be responsible for the structure of the diatom communities as it controls the interplay between two different functional groups composing the diatom assemblages: the epipelon and the epipsammon. The epipelon, a less diverse community, mainly composed of medium-sized species, shows a certain degree of seasonal variation. This community dominates sheltered areas and its occurrence can be predicted by the mud content of the sediment, a good indicator of the level of sediment exposure. The epipsammon, a very diverse community composed by minute species, does not show temporal patterns. Its occurrence is conditioned by the presence of the substrate (*i.e.* sand-grains) that is colonized by several types of life-forms. Alternatives to species-level identification were examined in order to bridge the gap between functional and structural ecological studies. The major multivariate patterns were mostly replicated but with unequal success. Species presence/absence and genus-level abundance data generated the best results. However, the temporal patterns were clouded by the decrease in taxonomical resolution or the loss of abundance data. The great intrinsic value of biodiversity assessment, even of microscopic organisms, is recognized and well established nowadays. Floristic studies made in conjunction with ecological-oriented research on microphytobenthos enhance our understanding of the structure and function of this important community and provide much needed data on the biogeography and autoecology of these microorganisms. Key words: *diatoms, ecology, taxonomy, microphytobenthos, spatial-temporal distribution, diversity, epipelon, epipsammon, life-form, community, intertidal flat, estuary.*

Resumo

As diatomáceas bênticas são o componente principal das comunidades de algas microscópicas que colonizam as zonas de sedimentos intertidais na maioria dos estuários e áreas costeiras da costa atlântica europeia, formando extensos biofilmes à superfície desse sedimentos. Essas comunidades são também conhecidas como microfitobentos (MPB) e são responsáveis pela elevada produção primária nos espraiados de maré, que pode corresponder a 50% do total da produção primária estuarina (Underwood & Kromkamp 1999). As diatomáceas presentes nessas comunidades têm sido tradicionalmente classificadas como epipsâmicas, quando vivem agarradas a partículas de areia, e epipélicas, quando vivem em sedimentos vasosos. No entanto estas definições foram consideradas demasiado simplistas por alguns autores (Sabbe 1997), tendo sido mesmo rejeitada por outros (de Jonge 1985).

Grande parte da investigação científica sobre o microfitobentos tem sido focada em diversos aspectos da sua ecologia funcional como, por exemplo, os padrões espácio-temporais de biomassa e/ou de produção primária, o seu papel na circulação de nutrientes ou em detalhes ligados à sua ecofisiologia (*e.g.* ritmos migratórios endógenos dos biofilmes microfitobênticos). Apesar ter sublinhado o papel fundamental que o microfitobentos tem para o funcionamento dos ecossistemas estuarinos, este género de investigação tende a considerar os biofilmes de microfitobentos como um todo (uma “caixa-negra”) ou então a limitar o estudo da estrutura das comunidades microfitobênticas à análise pigmentar, recorrendo cromatografia líquida de alta precisão (HPLC). A análise pigmentar, no entanto, apenas permite estabelecer a identidade e a contribuição de cada grupo de microalgas que constituem esse biofilmes (*e.g.* diatomáceas, euglenófitas e cianobactérias), mas não fornece mais informação sobre a estrutura taxonómica contida em cada uma dessas fracções. Por outro lado, os estudos florísticos que se debruçam sobre a estrutura dessas comunidades e/ou a taxonomia das espécies que as constituem são comparativamente

mais raros que os estudos funcionais, havendo igualmente um divórcio cada vez mais claro entre estas duas vertentes (Underwood 2005, Underwood & Barnett 2006). As dificuldades associadas aos estudos florísticos das comunidades de diatomáceas bênticas estuarinas são inúmeras e encontram-se resumidas na introdução desta tese (**capítulo 1**). Como resultado, pouco se sabe da auto-ecologia e da taxonomia de muitas das espécies diatomáceas bênticas intertidais. Além disso, a biodiversidade e a estrutura das comunidades praticamente desconhecida em muitas áreas costeiras e estuários, entre os quais o estuário do Tejo.

Esta tese tem como principais objectivos: (1) identificar, descrever e ilustrar as espécies que compõem as comunidades de diatomáceas bênticas dos substratos móveis intertidais do estuário do Tejo; (2) determinar os diferentes tipos de comunidades de diatomáceas bênticas, descrever a suas variações espácio-temporais e relacioná-las com as variáveis ambientais; (3) avaliar e comparar o desempenho de alternativas à identificação ao nível das espécies, na detecção de padrões espácio-temporais nas comunidades de diatomáceas bênticas estuarinas. De forma a aumentar o conhecimento sobre a composição taxonómica e estrutura das comunidades de diatomáceas bênticas intertidais do estuário do Tejo, um programa de amostragem foi conduzido durante 2 anos (2003-2004) em 6 estações de amostragem com estrutura sedimentar distinta e organizadas em 2 transectos, tendo um sedimento mais vasoso e outro sedimento mais arenoso. A área de estudo, bem como o estuário do Tejo, são descritos no **capítulo 2**.

Na primeira parte desta tese é descrita a estrutura e a variação espácio-temporal das comunidades de diatomáceas bênticas encontradas nas 6 estações de amostragem durante o período de estudo. A estrutura das comunidades de diatomáceas foi caracterizada não só em termos da sua composição taxonómica e diversidade, mas também através da sua fisiognomia. Neste estudo, o termo “fisiognomia das comunidades” foi utilizado no sentido botânico clássico do termo, isto é, referindo-se a aspectos podem ser ligados à aparência e tipo de “formação vegetal” como, por exemplo, a distribuição dos indivíduos encontrados em classes de tamanho ou descriminando as diferentes “formas de vida” presentes. Todos estes termos encontram-se definidos no capítulo dedicado ao material e métodos (**capítulo 3**). A dinâmica dos padrões espácio-temporais na estrutura das comunidades de diatomáceas foi determinada utilizando métodos estatísticos não-paramétricos de análise multivariada, baseados em similaridades Bray-Curtis, e que derivam de uma matriz de abundâncias de espécies (Clarke & Warwick 2001). Adicionalmente, essa matriz biótica foi correlacionada, também através de métodos estatístico não-paramétricos (BIO-ENV), com a matriz das variáveis ambientais. Os resultados deste trabalho são apresentados no **capítulo 4** e discutidos em detalhe no **capítulo 5**.

Os padrões temporais foram claramente subordinados aos padrões espaciais, de acordo com a análise de similaridades (ANOSIM). Em termos espaciais, parece haver uma separação clara das amostras por estação de amostragem, ao passo que, em termos temporais, apenas nas estações de sedimento vasoso houve uma separação significativa entre amostras colhidas no Inverno/Primavera e as amostras colhidas no Verão/Outono. As amostras das estações arenosas e as amostras provenientes das estações de sedimento vasoso mostraram ter o menor grau de similaridade. Embora menos evidente, houve também uma distinção entre amostras provenientes de estações arenosas com texturas sedimentares diferentes. A análise da composição e da fisiognomia comunidades demonstrou que as diferenças entre povoamentos das estações de amostragem eram taxonómicas, sendo também dependentes das abundâncias das espécies presentes. Por outro lado, essas diferenças puderam ser replicadas pelas diferenças entre as proporções relativas dos dois grupos funcionais (*i.e.* o epipsammon e o epipelon) ou na distribuição das formas de vida que estão incluídas em cada desses grupos funcionais.

Os povoamentos encontrados em sedimentos muito vasosos tinham uma diversidade baixa, sendo dominadas apenas por algumas espécies de diatomáceas birafídeas e móveis como *Navicula spartinetensis, Navicula gregaria, Gyrosigma fasciola* e *Cylindrotheca signata.* As amostras provenientes das estações mais vasosas tiveram as similaridades intra-estação mais baixas. Estas comunidades mostraram, ainda, um certo grau de sazonalidade, causado pela alternância temporal das espécies que foram dominando sucessivamente os povoamentos durante o período de estudo. Em relação à fisiognomia das comunidades encontradas nas estações mais vasosas, houve uma quase total dominância de formas epipélicas móveis, embora também seja de registar a presença um pequeno grupo de formas diminutas e imóveis (*e.g. Cymatosira belgica*). Estas formas comportam-se, aparentemente, como partículas de silte, usando a ressuspensão dos sedimentos como forma de dispersão (*viz.* Sabbe 1997). Em termos da distribuição das classes de tamanho, estes povoamentos foram dominados por diatomáceas de tamanho médio (*i.e.* 250-1000 μm^3), um grupo composto maioritariamente por espécies de *Navicula*. Houve também grupo menos abundantes de espécies grandes (*i.e.* >1000 μm^3) e de espécies pequenas (*i.e.* 100-250 μm^3). As espécies muito pequenas (*i.e.* <100 μm^3) estiveram praticamente ausentes nas estações vasosas.

Os povoamentos de diatomáceas presentes nas estações arenosas apresentaram diversidades bastante mais elevadas que os presentes nas estações vasosas e não mostraram nenhum padrão sazonal, mantendo-se a estrutura das comunidades constante ao longo de todo o período de estudo. Estas comunidades eram tipicamente formadas por diatomáceas pequenas ou muito pequenas (*i.e.* com um biovolume <250 μm^3), sendo compostas por variadas formas de vida epipsâmicas. Uma das formas de vida mais importantes nas estações arenosas foi o grupo formado por pequenas espécies móveis pertencentes aos géneros *Navicula* (*e.g. N. viminoides*, *N.* aff. *aleksandrae*; *N. germanopolonica*), *Fallacia*, *Nitzschia* ou *Cocconeiopsis*. Outra forma de vida bastante comum nessas estações foi a das espécies prostradas, que vivem mais firmemente agarradas aos grãos de areia. Estas espécies podem ser birafídeas (*e.g. Biremis lucens, Catenula adhaerens, Catenula* sp.1) ou monorafídeas como *Planothidium delicatulum* e espécies do género *Cocconeis* (*e.g. C. hauniensis*, *C. peltoides* e *C. pelta*). As espécies arafídeas, que se encontram ligadas à superfície dos grãos de areia por um pedúnculo de mucilagem, correspondem a uma terceira forma de vida epipsâmica. Estas espécies pedunculadas pertenciam essencialmente aos géneros *Opephora* e *Fragilaria* (*e.g. O. guenter-grassii*, *Opephora* sp.1) e ocorreram quase exclusivamente na estação mais elevada do transecto arenoso. Esta estação distinguia-se também por ser composta por sedimento arenoso de calibre médio e fino. As restantes estações arenosas eram compostas principalmente por areias de calibre médio e grosseiro, tendo também uma maior fracção de sedimento vasoso. Este último facto parece ter contribuído para distinção entre os povoamentos encontrados na primeira estação dos das outras estações arenosas, pois com o aumento do conteúdo em vasa aumentou também a importância relativa das diatomáceas epipélicas, enquanto a abundância relativa das pequenas espécies epipsâmicas móveis (*e.g. Navicula germanopolonica*; *N. bozenae*) diminuiu drasticamente.

De facto, este estudo confirmou a importância fundamental que o tipo de sedimento tem na estrutura das comunidades estuarinas de diatomáceas bênticas encontradas em substratos móveis intertidais. De acordo com a rotina BIO-ENV, que relaciona as variáveis ambientais à matriz de abundância das espécies, o conteúdo em vasa (*i.e.* siltes e argilas) mostrou ter maior correlação significativa com a matriz biótica, apresentando uma correlação elevada (ρ = 0.863, p <0.1 %). O teor em vasa é um excelente indicador do grau de exposição do sedimento. A perturbação física do sedimento, causada pelas correntes de maré, ondas ou pela bioturbação, parece ser o factor determinante para estrutura das comunidades de diatomáceas bênticas em substratos móveis intertidais. Assim, nas zonas menos hidrodinâmicas, a vasa deposita-se e os espraiados entre-marés são dominados por espécies epipélicas (móveis ou não), sendo que a ausência de grãos de areia não permite a colonização dessas áreas por espécies epipsâmicas. A diversidade desses povoamentos é baixa, provavelmente devido a fenómenos de competição inter-específica que causam a dominância de apenas algumas espécies e, em parte, a alternância sazonal destas. Nas zonas mais hidrodinâmicas, há acumulação de grão de areias mas o siltes e argilas não se conseguem depositar. Nessas áreas instala-se uma comunidade epipsâmica que é muito diversa não só devido ao tamanho reduzido das espécies, mas também devido à maior variedade de formas de vida que exploram diferentemente os microhabitats existentes em cada grão de areia. Além disso, a constante perturbação mecânica a que esses sedimentos estão sujeitos promove a diversidade e impede a dominância, ao manter o número de indivíduos de cada espécie relativamente baixo, bem como forçando a estabilidade sazonal na estrutura dessas comunidades. Ambas as comunidades podem, no entanto, co-existir desde que as condições locais possibilitem a deposição de partículas de vasa e a sobrevivência das espécies epipélicas, sendo dinâmicas o suficiente para não permitir que o substrato das espécies epipsâmicas (*i.e.* os grão de areia) fique completamente soterrado. Mesmo nestes casos, os padrões temporais das duas comunidades permanecem independentes, como já tinha sido demonstrado anteriormente por Sabbe (1993).

Tendo descrito a estrutura das comunidades de diatomáceas bênticas com o máximo de resolução taxonómica possível, bem como a dinâmica dos padrões espácio-temporais dessas comunidades, foi realizado um exercício de comparação de alternativas à identificação ao nível da espécie que possam fornecer alguma dessa mesma informação (**capítulo 6**). O objectivo desta análise comparativa foi avaliar o desempenho de alternativas como a utilização de dados qualitativos (*i.e.* presença-ausência), da identificação taxonómica apenas até ao nível do género, a conversão dos dados de abundância relativa em biovolume relativo, a utilização substitutos taxonómicos (*i.e.* classes de tamanho ou formas de vida) e, finalmente, o efeito de exclusão de espécies muito raras. Este sexto capítulo é, de certa forma, independente dos três capítulos anteriores, embora utilize o mesmo conjunto de dados e partilhe muitos métodos estatísticos multivariados. Como se insere numa problemática diferente, possui uma introdução, métodos, resultados e discussão

próprias. Apesar de este género de exercício ser comum em estudos sobre diatomáceas bênticas de água doce (*e.g.* Lavoie *et al.* 2008) ou sobre a meiofauna estuarina (*e.g.* Warwick 1988), nunca foi realizado em diatomáceas bênticas estuarinas. Neste contexto, é pertinente avaliar se existem alternativas válidas à identificação até à espécie que sejam mais acessíveis à maioria dos investigadores trabalhando em ecologia do microfitobentos, mas que consigam descrever satisfatoriamente a estrutura das comunidades de diatomáceas bênticas estuarinas.

Os resultados mostram que a exclusão das espécies muito raras teve um efeito muito reduzido mas, de certa forma, positivo pois aumentou ligeiramente a nitidez dos padrões multivariados observados e a correlação com os dados ambientais. A matriz de presença-ausência de espécies (*i.e.* elevada resolução mas sem abundâncias) e a matriz de géneros (*i.e.* resolução mais baixa mas com abundâncias) parecer ser as alternativas que melhor replicam os padrões multivariados obtidos pela matriz de abundância de espécies. No entanto, e apesar de terem ambas tido correlações elevadas com a matriz das espécies ($\rho \geq 0.95$), não conseguiram detectar quaisquer variações sazonais nas estações de sedimento vasoso que são dominadas por espécies epipélicas. Por essa razão, o uso destas duas alternativas deve ser aconselhado somente para trabalhos que apenas requeiram uma distinção espacial. De realçar que todas as outras alternativas falharam na detecção de diferenças espaciais mais subtis, como a ligeira distinção entre povoamentos nas estações arenosas, para além de não detectarem diferenças sazonais nas comunidades epipélicas.

A principal contribuição deste trabalho é, sem dúvida, o Guia de Identificação de Diatomáceas (**capítulo 7**) que é suplementado com 1019 fotografias em microscopia óptica e electrónica de varrimento, organizadas em 59 estampas (**volume 2**). Este guia representa, provavelmente, a mais detalhada descrição florística das comunidades de diatomáceas bênticas das zonas estuarinas intertidais feita até ao momento em Portugal. O guia inclui a seguinte informação: (1) dados morfométricos que resultaram de mais de 7000 medições biométricas (*e.g.* intervalos de tamanhos das valvas, densidade de estrias ou biovolume); (2) informação importante sobre a biogeografia e ecologia das espécies encontradas; (3) discussão da literatura relevante para cada taxon; (4) comparação com outras espécies que sejam morfologicamente semelhantes e facilmente confundíveis.

No total, 185 taxa de diatomáceas foram observados e descritos até ao nível do género, espécies ou infra-específico (secção 7.3). Desses, 108 foram identificados até ao nível da

espécie (ou infra-específico), não tendo sido possível determinar a identidade de 77 taxa (42% do total de taxa). Neste segundo grupo, 45 taxa (24% do total) foram atribuídos provisoriamente a uma espécie conhecida, o que é indicado pelas abreviações “cf.” ou “aff.” no binomial. Neste grupo encontram-se taxa que são semelhante a espécies cuja identidade taxonómica ou auto-ecológica se encontra ainda aberta a debate. Os restantes 32 taxa (27 % do total) não puderam ser inequivocamente identificados para além do género a que se julga pertencerem. Neste último grupo incluem-se espécies mas também géneros que poderão ser novos para a ciência (*e.g. Haslea* sp.1, *Catenula* sp.1 e *Catenula* sp.2). A descrição formal de um novo género e uma espécie nova, *Pierrecomperia catenuloides*, encontra-se a aguardar publicação (Sabbe *et al.* submitted).

A flora descrita neste trabalho é bastante semelhante às encontradas noutras áreas intertidais das costas atlânticas do Norte da Europa (*e.g.* Hustedt 1939, Sabbe 1997) e, em particular, na costa ocidental francesa (*e.g.* Méléder *et al.* 2007). Tendo em conta que apenas foi estudada uma zona bastante restrita do estuário, o número total de espécies de diatomáceas bênticas existentes no estuário do Estuário do Tejo é provavelmente bastante mais elevado. Uma estimativa conservadora apontaria para um número superior aos 300 taxa, em consonância com os valores obtidos para os estuários do Tamisa (Juggins 1992) e do Escalda Ocidental (Sabbe 1997).

Num contexto de uma crescente percepção do importante papel que a biodiversidade tem nos ecossistemas marinhos mas também do contributo que a correcta identificação taxonómica pode ter em trabalhos de ecologia, espera-se que este trabalho, ainda que de forma incompleta, possa contribuir preencher uma lacuna existente nos estudos do microfitobentos do estuário de Tejo e ajude, futuramente, na melhor compreensão dessa importante comunidade de microrganismos.

Chapter 1

Introduction

1. Introduction

Diatoms (Bacillariophyta) are an extremely diverse group of microalgae with an estimated number of species between 10^4–10^5, depending on the species concept (Stoermer & Smol 1999). Mann & Droop (1996) suggested that the total species number could be as high as two hundred thousand. They have a worldwide distribution and constitute a major component of planktonic and benthic algal communities, from oceanic oligotrophic waters to polar ice caps; from moist soils to freshwater alkaline lakes or eutrophic estuaries (*e.g.* Round *et al.* 1990). Diatoms have a global significance, as they may to be responsible for one-fifth of the total of the Earth's photosynthesis (Mann 1999). Their contribution to total global primary production is bigger than all of the rainforests put together (Nelson *et al.* 1995, Field *et al.* 1998, Mann 2010) with the important difference that their organic carbon is rapidly consumed and made available to the foodwebs. The diatoms are a fairly recent group of heterokontic eukaryotes (*i.e.* Stramenopiles; Patterson 1999, Adl *et al.* 2005). They rose to prominence in the early Cretaceous oceans (*e.g.* Medlin *et al.* 1993, Sims *et al.* 2006) and effectively changed the global silicon and carbon cycle, lowering the Earth's atmospheric carbon concentration to modern levels about 50 million years ago (Armbrust 2009). Apart from their distinctive siliceous cell wall (*i.e.* frustule), diatoms have a range of animal-like attributes that separates them from other primary producers and help to explain their undeniable success. For example, diatoms have a complete urea cycle (Armbrust *et al.* 2004) and are able to heterotrophically metabolize organic substrates (*e.g.* Tuchman *et al.* 2006). They also combine the animal-like ability to generate chemical energy from the breakdown of fat with a plant-like ability to generate metabolic intermediates from the same breakdown, a combination of features that probably allows diatoms to survive long periods of darkness and then resume to photosynthesis when re-exposed to light (Armbrust 2009 and references herein).

In estuarine and shallow coastal benthic environments, diatoms are often the most important and dominant component of the benthic microalgal assemblages (Round 1971, McIntire & Moore 1977, Admiraal 1984, Sullivan 1999). The terminology chosen to describe these communities may differ, depending on the author or their habitat, but it always refers to biofilms composed of a mix of microscopic algae, bacteria and fungi that cover the different available subtracts. Periphyton and microphytobenthos (MPB) are two of the most commonly used terms. Periphyton is usually applied to describe any biofilm covering hard substrata (*i.e.* rocks, plants, debris) in freshwaters but also in intertidal and subtidal areas (Trobajo 2007). Microphytobenthos mainly refers to the specific transient microalgal biofilms that colonize the illuminated subtidal and intertidal sediments (*e.g.* MacIntyre *et al.* 1996), although non-European authors still prefer to use other terms, such as edaphic microalgae (*e.g.* Sullivan & Currin 2002) or, simply, benthic microalgae (Cahoon 1999). In addition to diatoms, the microphytobenthic biofilms can be composed by a diverse array of microalgal groups, such as cyanobacteria, euglenids, dinoflagellates and chrysophytes (*e.g.* Cariou-Le Gall & Blanchard 1995, Brotas & Plante-Cuny 2003). However, in most cases, pennate diatoms are ubiquitous and the dominant group in terms of biomass (*e.g.* McIntire & Moore 1977, Admiraal 1984, Consalvey *et al.* 2004, Underwood & Barnett 2006).

Microphytobenthos are the main primary producer in the intertidal flats, which are characterized by high biological productivity (*e.g.* Heip & Herman 1995, Heip *et al.* 2005). In the turbid estuarine and coastal waters the primary production of the MPB can be very high (Brotas & Catarino 1995, MacIntyre *et al.* 1996, Cahoon 1999, Cahoon 2006) and may contribute with more than 50% of the total estuarine primary production (Underwood & Kromkamp 1999). The MPB primary production is of such importance that Guarini *et al.* (2008) suggested its global production may well correspond to the “missing carbon sink” from the global budget, estimated at *ca.* 1.8 ± 0.5 (Pg C) y^{-1} by Schindler (1999). These diatom-dominated biofilms are also important mediators in several biogeochemical processes (*e.g.* nitrogen, phosphorus and silicon cycles), namely in nutrient transformation and exchange in the intertidal sediments surface (*e.g.* Cabrita & Brotas 2000, Dong *et al.* 2000, Sundbäck & Miles 2002, Rysgaard-Petersen 2003) and, therefore, contribute to the attenuation of the elevated water-column nutrient concentration, brought by high nutrient loads in coastal areas. Another important property of these biofilms is the production of vast amounts of mucilage, also known as extracellular polymeric substances (EPS), that plays a central role in the stability of the sediments, increasing the erosion-threshold of the tidal platforms (*e.g.* Paterson 1989, Black *et al.* 2002, Underwood & Paterson 2003). The EPS seems to be mainly produced by pennate motile diatoms, exuded when diatoms migrate through the sediment (*e.g.* Smith & Underwood 1998). Additionally, EPS production can act as an photo-protective overflow mechanism in photosynthesis (*e.g.* Staats *et al.* 2000a). Given its massive production, EPS is essential in the construction of the biofilm matrix that binds the particles together and augments the cohesiveness of the sediments (*e.g.* Decho 2000, Stal & de Brouwer 2003). The organic matter produced by the MPB is transferred very rapidly and efficiently to the bacteria and into the benthic food chains (*e.g.* Sullivan & Moncreiff 1990, Miller *et al.* 1996, Herman *et al.* 2000, Middleburg *et al.* 2000, Cook *et al.* 2004), which makes MPB a very important resource for a wide array of benthic grazers and deposit feeders (*e.g.* McLusky & Elliott 2004). Also, due to sediment resuspension and benthic-pelagic coupling (*e.g.* Marcus & Boero 1998, Lucas *et al.* 2000, Lucas *et al.* 2001), coastal and estuarine benthic diatoms are an important resource to pelagic food-webs and to suspension feeders (*e.g.* Cognie *et al.* 2001, Decottignies *et al.* 2007).

Benthic diatom communities of intertidal flats have traditionally been divided in two main groups, with regard of their structure: the epipelon and the epipsammon (*e.g.* Round 1965, Round 1971, Admiraal 1984). The epipelon consists of free-living diatoms and dominates the mudflat assemblages, whereas the epipsammon is mainly composed by diatoms attached to sand-grains and, therefore, more common in sandflats. The epipelic diatoms are usually larger and motile species, while the epipsammic diatoms are frequently small, sessile or slow-moving. As it equally refers to the type of sediment colonized and the way the diatoms attach (or not) to the sediment particles, this practical distinction is not always clear-cut in natural assemblages (McIntire & Moore 1977). On tidal flats with mixed sandy and muddy sediments the diatom assemblages consist of both epipsammic and epipelic taxa (Hamels *et al.* 1998). Partly as a result of the continuous effect of resuspension and re-deposition of sediment particles and diatom cells in estuarine areas, some authors defend the existence of a continuum from species easily suspended from the sediment to those firmly attached to sand grains (van den Hoek *et al.* 1979, de Jonge 1985, Delgado *et al.* 1991b, de Jonge & van Beusekom 1995). Nonetheless, this division remains very useful and with slight modifications to the long-established definitions it can still provide meaningful ecological insights (Sabbe 1997, but see below section 3.5). Namely, this distinction clear reflects the fundamental influence that the physical and chemical properties of the sediments themselves have over the taxonomical structure of sediment-associated estuarine diatom assemblages (*e.g.* Hustedt 1939, Riznyk & Phinney 1972, Amspoker & McIntire 1978, Whiting & McIntire 1985, Sabbe 1993, Hamels *et al.* 1998, Sahan *et al.* 2007). Given that the epipelic diatoms are larger, motile and easily resuspended, they require simpler sampling techniques, such as the lens-tissue method (Eaton & Moss 1966), that selectively but easily collects these diatoms from the sediments. As a consequence, the epipelon has been more thoroughly studied than the difficult to sample epipsammon (*e.g.* Sabbe 1997, Paterson & Hagerthey 2001). Therefore, the importance of the epipsammic diatoms has been considerably overlooked (*e.g.* Sabbe 1993, Méléder *et al.* 2007) even though they may dominate, both in abundance and biomass, many costal and estuarine diatom communities (*e.g.* Riznyk 1973, Sundbäck 1983, Sabbe & Vyverman 1991, Witkowski 1991, Asmus & Bauerfeind 1994).

Numerous studies have dealt with the spatial and seasonal distribution of sediment-associated benthic diatom assemblages in coastal and estuarine intertidal areas worldwide, albeit they were mainly concentrated in Northern European and North American estuaries (Round 1971, McIntire & Moore 1977) and, as mentioned above, usually restricted to the epipelic fraction (*e.g.* Riaux 1983, Oppenheim 1991, Underwood 1994, Haubois *et al.* 2005, Ohtsuka 2005). When considering the entire tidal profile, it is well established that saltmarsh diatom assemblages are floristically distinct from the tidal flat assemblages (*e.g.* Oppenheim 1988, Zong & Horton 1998, Sullivan & Currin 2002). In the sheltered tidal platforms the distribution of diatom assemblages has been long recognized as patchy (*e.g.* Hustedt 1939, Brockmann 1950, Hendey 1964) although in certain environments, like wave-exposed beaches, the diatom spatial distribution is more homogenous (Amspoker 1977). This spatial patchiness has been perceived over different scales (*i.e.* cm to km) and it has also been detected in terms of biomass (*e.g.* Jesus *et al.* 2005). Sediment properties, like texture and granulometry or cohesiveness, were signalled by early researchers (Hustedt 1939, Brockmann 1950) as a major environmental variable responsible for the taxonomic structure of the tidal flat diatom assemblages. This perception was later confirmed with the introduction of multivariate analyses in spatial distribution studies (*e.g.* Amspoker & McIntire 1978, Whiting & McIntire 1985, Saburova *et al.* 1995). Seasonal shifts in sediment texture may also explain the replacement of epipsammon-dominated assemblages by epipelon dominated ones, during calm, less hydrodynamic periods (Wulff *et al.* 1997, Méléder *et al.* 2007). Other variables were also found to be important in epipelon-oriented studies, where the spatial distribution patterns of the epipelic species have been related to salinity and nutrient gradients (*e.g.* Peletier 1996, Underwood *et al.* 1998, Underwood 2005) or to tidal elevation (Sullivan 1982, Oppenheim 1988). Seasonality of the epipelic species has been attributed to variations in climatic factors such as temperature and light regimes (*e.g.* Sabbe 1993, Underwood 1994) or to grazing pressures (*e.g.* Hagerthey *et al.* 2002). On the other hand, still little is known about the epipsammic communities, except that are mainly influenced by changes in sediment granulometry and local hydrological conditions (Sundbäck 1983, Delgado *et al.* 1991a). In addition, epipsammic species do not show any apparent seasonality (*e.g.* Whiting & McIntire 1985, Sabbe 1997).

Community structure and distributional studies rely heavily on sound taxonomic identification of the encountered species. However, when compared to freshwater and oceanic environments, the taxonomy of many estuarine diatoms, both benthic and planktonic, is poorly known. The autoecology of individual species is also poorly understood, with the ecological optima and life-forms of many species still undetermined or confusing. The identification of resident benthic diatoms species in any intertidal area has traditionally been a difficult and complex task (Sullivan & Currin 2002). Several of difficulties are associated with the diatom analysis, taxonomy and systematics of intertidal benthic diatoms. These reasons are manifold but are mainly related to:

1. Separation of diatoms from sediment samples and slide preparation is technically difficult when compared to plankton and periphyton. As referred above, the main problem is to find a method that does not selectively favours the epipsammon or the epipelon fraction, while discarding most of silt and clay particles. In addition, the possible contamination from deposits of epilithic, epiphytic and planktonic diatoms and the problem of separating living and dead cells should also be considered (McIntire & Moore 1977). The destruction of the frustule of fragile forms during strong-acid cleaning, particularly in the epipelon, can also create important biases, during cell counts, causing an over-representation of diatoms with sturdier frustules (Sabbe 1997).
2. Shortage of specialized literature. Floras like the “Süsswasserflora von Mitteleuropa” (Krammer & Lange-Bertalot 1986, 1988, 1991a, 1991b) or identification guides of marine planktonic diatoms (*e.g.* Hasle & Syversten 1996) have been instrumental in the recent worldwide progress in freshwater and marine diatom studies. The lack of a similar counterpart for brackish waters has long hampered research in coastal benthic environments. Diatomists have to make do with older

works (*e.g.* Peragallo & Peragallo 1897-1908, Hendey 1964) and with numerous and scattered literature. There are also very few monographic works on marine taxa (Sullivan 1999, Sullivan & Currin 2002), which reflects the basic lack of experts in diatom taxonomy and a consequence of the continuous, decades-long, disinvestment in taxonomy of science budgets worldwide (Kociolek & Stoermer 2001, Sterrenburg 2005). Further difficulties are brought by various nomenclatural and taxonomic problems, such as a high level of synonymy in benthic diatom taxonomy (Underwood & Barnett 2006), which were further exacerbated by the recent developments in diatom systematics (Sabbe 1997). Finally, in many published ecological and even floristic studies, the available taxonomical information is limited to a taxa list, often only to the genus level, thus not allowing any comparative analysis of the literature (Underwood 1994, Sterrenburg 2005).

3. Considerable morphological variability of widely distributed taxa (Cox 1986) is particularly common in estuarine species, which exhibit high morphological plasticity along the salinity gradient (Underwood & Provot 2000, Trobajo 2007). This leads to problems related to the interpretation of morphological variation patterns (Tropper 1975, Sabbe *et al.* 1995, Trobajo *et al.* 2004). Furthermore, this variability can be related to cryptodiversity phenomena in benthic diatoms, where the occurrence of slightly different morphotypes can be related to ecological differences but may also have a genetic basis (Sarno & Kooistra 2005, Créach *et al.* 2006, Vanelslander *et al.* 2009a).
4. Force-fitting of taxa into existing freshwater and marine species (Sabbe 1997, Kociolek & Stoermer 2001, Flower 2005). The force-fitting or “shoe-horning” of taxa aggravates even further the problems associated with the identification of coastal and estuarine benthic diatoms, as it inevitably leads to the overestimation of the range of morphological variability of the diatom species. In addition, it artificially increases the biogeographical range attributed to many species (Morales *et al.* 2001, Vanormelingen *et al.* 2008). Therefore, the reliability of published ecological and biogeographical information is jeopardized.

Regardless of these difficulties, several relevant works on marine benthic diatoms have been produced over the last 20 years. Several PhD theses (*e.g.* Kuylenstierna 1989-1990, Rincé 1993, Sabbe 1997), regional studies (*e.g.* Cardinal *et al.* 1984, Poulin *et al.* 1984a, b, c, Bérard-Therriault *et al.* 1986, Cardinal *et al.* 1986, Witkowski 1994a, Pienitz *et al.*

2003) and one major flora (Witkowski *et al.* 2000) became valid alternatives to the widely use of freshwater floras. These works also provide other invaluable insights to ecologists and taxonomist alike, such as morphometry data, biogeographical, autoecological and bibliographical information on a great number of diatom species. One example is the series of 5 identification guides that resulted of the species intercalibration programme by the Baltic Marine Biologists (Snoeijs 1993, Snoeijs & Vilbaste 1994, Snoeijs & Potopova 1995, Snoeijs & Kasperoviciene 1996, Snoeijs & Balashova 1998). By bringing together illustrations, literature listings and other relevant information published in a simple and succinct fashion (Kociolek 2005) this intercalibration programme was in the basis of an important and ever growing number of publications on coastal benthic diatom ecology and distribution in the Baltic Sea and elsewhere (*e.g.* Vilbaste *et al.* 2000, Busse & Snoeijs 2002, Snoeijs *et al.* 2002, Busse & Snoeijs 2003a, Ulanova & Snoeijs 2006). It has, therefore, become less complicated to correctly identify marine benthic diatoms. In spite of this, many of the worldwide intertidal flat areas lack basic floristic data on the diatom communities (Sterrenburg 2005). Even in the relatively well studied European Atlantic coast a survey of the floristic, distributional and taxonomical literature on tidal flat diatoms reveals that most of published studies are from the North Sea, British and French Atlantic coasts. The intertidal diatom flora of the Iberian Atlantic coasts remains conspicuously unexplored.

Functional studies form the bulk of the benthic diatom ecological studies in most coastal and estuarine areas since the 1970’s, when research became dominated by studies focused on ecological processes and mechanisms (McIntire & Moore 1977, Admiraal 1984). Most of these studies ignore species composition and focus on the MPB biofilm (*i.e.* a “black box” approach; Kociolek & Stoermer 2001, Underwood 2005) used, for example, in energy flow studies. Ideally, as McIntyre and Moore (l977) wrote, ‘both the structural and functional attributes of diatom assemblages should be investigated simultaneously, although there are very few examples of such studies in the literature’. Furthermore, it has become clear that species composition influences the MPB biofilm function (Underwood *et al.* 2005, Underwood & Barnett 2006) and the role of biodiversity of benthic diatom assemblages on ecosystem-function has began to be explored (*e.g.* Forster *et al.* 2006, Vanelslander *et al.* 2009b). However, in the last decades, a widening gap has grown between MPB functional studies on biofilms and intertidal benthic diatom species distribution studies. These floristic or structural studies usually have a very descriptive approach and may disregard the intrinsic changeable nature of the intertidal environment (Underwood 2005). This partly results from the traditional separation between the disciplines of *Ecology* and *Taxonomy* in diatom studies brought by different approaches to taxonomy and the limited number of formally trained diatom taxonomists that could work in collaboration with ecologists (Kociolek & Stoermer 2001, Kociolek 2005). Many research groups in MPB ecology lack a diatom flora of their main study area and/or have limited training in diatom identification finding it hard to produce "consistent taxonomy" (*viz.* Kociolek & Stoermer 2001, Kociolek 2005). They are, therefore, constrained to more functional-oriented research and to a pigment analysis of the communities (Cariou-Le Gall & Blanchard 1995, Brotas & Plante-Cuny 2003), with taxonomic resolution limited to the major MPB algal groups.

Several alternatives have been suggested to address this problem. Ideally, taxonomists and ecologists should increase their collaborations and a maximum of taxonomic information (*e.g.* micrographs, nomenclatural synonymies or ecological data) should be made easily available online, in an effort involving museums and collections but also ongoing research projects (*e.g.* Sterrenburg 2002, Flower 2005, Kociolek 2006, Mann *et al.* 2006). Another alternative to circumvent this "Taxonomic Impediment" (Taylor 1983) is the use of higher taxonomical resolution or other surrogates to species-level identification in routine community ecology or environmental monitoring studies (*e.g.* Hill *et al.* 2001, Passy 2007, Lavoie *et al.* 2008). Albeit not consensual and much less ambitious than the latter alternatives it has obvious practical advantages to many ecologists with reduced diatom identification skills and could help bridge the gap between functional and structural ecological studies in MPB research.

The MPB research in the Tagus estuary certainly reflects this divide between functional and structural studies. Microphytobenthos ecology has been continuously studied over the past 25 years, with an handful of PhD and MSc thesis and extensive and relevant published research, covering a wide range of subjects, such as spatial-temporal patterns of variability of MPB biomass (*e.g.* Brotas *et al.* 1995, Jesus *et al.* 2009), MPB primary production (*e.g.* Brotas & Catarino 1995, Serôdio & Catarino 1999, Perkins *et al.* 2001), nitrogen cycling (Cabrita & Brotas 2000), endogenous epipelic migratory rhythms (*e.g.* Serôdio *et al.* 1997, Tolhurst *et al.* 2003, Jesus *et al.* 2006a), remote sensing and photophysiolgy (*e.g.* Serôdio *et al.* 2001, Jesus *et al.* 2006a, Jesus *et al.* 2006c, Jesus *et al.*

2008) or pigment analysis (Brotas & Plante-Cuny 1998, Cartaxana *et al.* 2006). In spite of this large and significant scientific production, only one published research paper has directly addressed the taxonomic composition of the Tagus epipelic diatom assemblages (Ribeiro *et al.* 2003) and two others provided micrographs of the most important diatom taxa (Brotas & Plante-Cuny 1998, Jesus *et al.* 2009). This general lack of illustrated published reports of coastal diatoms is extendable to other estuarine and intertidal areas of the Portuguese coast (Moita & Vilarinho 1998). One illustrative example of this situation is the 128-taxa list corresponding to slide nº 50 of the second edition of the Tempére & Peragallo diatom collection (1907-1915) and made from material of a Sado estuary mudflat. Given it was almost fully illustrated in the "Diatomées Marines de France" (Peragallo & Peragallo 1897-1908) it still remains as one of the most complete floristic accounts of intertidal benthic diatoms of the Portuguese coast.

The present study tries to address the paucity of data on taxonomical composition of the benthic diatom flora of the Tagus estuary. The main objectives of this work were:

1. **Determine and describe the spatial-temporal distribution of diatom communities and its relationship with measured environmental variables**

An ecological study of the structure and distribution of the benthic diatom communities of six stations on the Tagus estuary over a two-year period was the one of the main outputs of this thesis (**chapters 3, 4 and 5**). The structure of the diatom communities was characterized in terms of their taxonomic composition and diversity but also by other features related to community physiognomy, such as size-class or life-form distribution in each assemblage. Spatial-temporal distributional patterns of the assemblages were described and considered in relation to the measured environmental patterns using non-parametric multivariate analysis.

2. **Evaluate and compare the performance of alternatives to species-level identification in the detection of spatial-temporal distribution patterns of intertidal benthic diatom communities**

Although species-level identification cannot be entirely replaced in community structure ecological studies, MPB ecologists would probably welcome a valid alternative that could approximately but correctly describe the diatom community structure and replicate the spatial-temporal patterns given by species abundances datasets. Having described these patterns, as well as the structure of the intertidal benthic diatom communities with the highest resolution possible, the third and final objective of this work was to assess the possibility of using surrogates to species-level identification in intertidal benthic diatom community structure studies (**chapter 6**). The effect of excluding rare diatom taxa and abundance data, reducing the taxonomic resolution to genus-level and using taxonomic surrogates (*i.e.* size-classes, life-forms) on multivariate analysis was tested and compared.

3. Identify, describe and illustrate the taxa composing the benthic diatom communities present in the Tagus estuary

A detailed systematic account of the observed diatom flora represents the largest part of this study (**chapter 7**). Information on each taxon includes, light microscopy (LM) and, often, scanning electron microscopy (SEM); morphometric data (*e.g.* size ranges, striae density, biovolume); biogeography and also detailed autoecological information (*e.g.* seasonal dynamics, preferred substrate and life-form). In many cases a detailed morphological description is also given. This chapter is organized as an identification guide that can be useful to ecologists and taxonomists alike. The procedure and rationale behind the identification of each taxon is explained in detail and includes discussions on relevant literature and on morphologically similar species.

Chapter 2

Study area

2. Study area

2.1. Tagus estuary

The river Tagus is the longest river in the Iberian Peninsula, extending over 1038 kilometres. It has the second largest in drainage basin of the Peninsula, after the Douro basin, with a total area of about 80629 km². The Tagus estuary (38º44'N, 9º08 W) is located near Lisbon and is one of the largest wetlands in Western Europe, with a total area of circa 320 km^2. The morphology of the estuary fits better into the category of tidal lagoons, as defined by Dronkers and Zimmerman (1982), and can be divided in four sections (Silva 1987):

1. The freshwater tidal reach, between Muge and the upstream limit of saline intrusion in Vila Franca de Xira, 80 km and 50 km from the river mouth, respectively.
2. An upper section, delimited between Vila Franca de Xira and a line linking Alcochete (south margin) and Sacavém (north margin). It characteristically has a deltoid formation in the northern area and comprises the majority of the intertidal flats of the estuary. The average depth is of 2 m. This area includes the Tagus Estuary Nature Reserve, with 14660 ha and a Ramsar site.
3. An intermediate section, with an average depth of 7 m, where most of the intertidal flats are located in the convoluted southern shore. Most of the heavy industry and densely populated areas are located in this part of the estuary. Together with the upper section, it forms a large inner basin (over 25 km long and 15 km wide).
4. A lower section, mainly composed by a straight channel, about 15 km long and 2 km wide, linking the vast inner basin to river mouth and the sea. The inlet is very deep, attaining a maximal depth of 46 m.

The Tagus estuary is a mesotidal estuary with semidiurnal tides. Tidal range, *i.e.* surface level difference between consecutive high and low water in a tidal cycle, varies from 0.8 m during neap tides to 4.0 m in spring tides (Fortunato *et al.* 1999). The average volume of water entering and leaving the estuary, during each tidal cycle, is about 7.5 x 10^8 m^3 which is about 40 % of total subtidal volume of the estuary (*i.e.* 19 x 10^8 m^3, Vale & Sündby 1987). According to Vale (1986), the tidal currents attain a maximal velocity of 1.2 m s^{-1} and a minimum of 0.2 m s^{-1} near the bottom and during neap tides.

The Tagus River is the main source of freshwater into the estuary. The freshwater discharge in the estuary shows large seasonal fluctuations, with an average monthly value varying from 120 m^3 s^{-1} in summer to 653 m^3 s^{-1} during winter (Gameiro & Brotas 2010). This means that, in each tidal cycle, the freshwater influx to the estuary is usually comparatively small to the water already in the estuary and that the influx is concentrated in the winter months. In addition, the winter inflow can also show great inter-annual variation (Gameiro *et al.* 2007). The estimated water residence times ranges from 6 to <65 days, for winter and summer average river discharges, respectively (Martins *et al.* 1984). One consequence of the typical seasonal variation in freshwater discharge is fluctuation of salinity in the central basin, with the polyhaline and mesohaline zones moving downstream during the winter and upstream during the summer (*e.g.* Costa & Salgado 1999). Most nutrient concentrations in the water column seem also to follow a seasonal pattern and are negatively correlated to salinity. Dissolved inorganic nitrogen (DIN) and silicate maximal concentrations occur in winter−spring, indicating a freshwater origin, while dissolved inorganic phosphorus (DIP) does not show any evident seasonal pattern (Gameiro & Brotas 2010). The total annual nitrogen loading to the estuary was estimated, for 1997, in 26 000 tones by Cabeçadas *et al.* (2000) and the average DIN concentrations in the water column range from 5.4 to 42.3µmol l^{-1} (Ferreira 2000, Gameiro *et al.* 2004).

As a result of its relative shallowness, strong tidal currents and low river input, the Tagus estuary as been classified as partially mixed during neap tides and well mixed during spring tides (Vale & Sündby 1987). The water column is usually highly turbid even in neap tides (Gameiro *et al.* 2007). According to Vale (1986), the turbidity of the water is mainly controlled by the amplitude of the tide and maximal sediment resuspension is achieved during spring tides. The action of the wind in water turbidity is only of secondary importance, namely in the intermediate section of the estuary (Gameiro 2009). Water circulation is, therefore, mainly driven by the tides, which redistribute the resuspended sediments and make the southern margin the main deposition area (Freitas *et al.* 1999).

The Tagus estuary has extensive intertidal areas (circa 126 Km^2) that correspond to 22% and 38% of the estuary total area in neap and spring tides, respectively (Brotas & Catarino 1995). These areas are mainly composed of salt marshes, mud and sandflats and ancient oyster beds, but also by sandy estuarine beaches and artificial margins and cliffs. Brotas (1995) estimated that the intertidal flats have a total area of about 100 km^2.

Most of the intertidal sediments are muddy, being composed in more than 96% by silt and clays (Calvário 1982). Sandflats are comparatively rare and most of the sandy sediments are associated with the estuarine beaches, mainly found along the southern margin, from Alcochete to Alfeite (Taborda *et al.* 2009). These sandy beaches are protected from the ocean waves but are still subject to a low energy wave climate, related to locally generated wind waves. The dominant wind directions are N and NW and have a maximum fetch of 13 km (Freire & Andrade 1999, Freire *et al.* 2007). The locally generated waves, with heights from 0.3 to 1.3 m (in extreme conditions), can cause bottom-sand resuspension in the shallow intertidal flats at 1 to 2 m water depth (Freire & Andrade 1999).

The intertidal flats of the Tagus estuary are known to support important and diverse benthic invertebrate communities (Calvário 1982, Rodrigues *et al.* 2006, Silva *et al.* 2006) which, in turn, are preyed upon large populations of waders and other resident and migratory shorebirds (Granadeiro *et al.* 2007, Rosa *et al.* 2008), as well as nekton and fish assemblages (Salgado *et al.* 2004, França *et al.* 2008).

The microphytobenthic communities are the main primary producers in the soft-bottom intertidal flats of the Tagus estuary. The mean annual MPB primary production (PP) for the intertidal areas of the Tagus estuary has been estimated in 113 g C m^{-2} $year^{-1}$ (Brotas & Catarino 1995) and 156 g C m^{-2} $year^{-1}$ (Serôdio & Catarino 2000), which are similar to values estimated for the MPB in other temperate estuarine areas (MacIntyre *et al.* 1996, Underwood & Kromkamp 1999), and well above the PP average value estimated for the phytoplankton of the Tagus estuary (*i.e.* 85 g C m^{-2} $year^{-1}$) by Gameiro (2009). Microphytobenthos biomass proxies, like chlorophyll *a* concentration, have been estimated within 10 – 240 mg m^{-2} (Brotas *et al.* 1995), also within the range reported for other estuarine areas (MacIntyre *et al.* 1996). The bulk of MPB biomass is concentrated in the top millimetre, just beneath the surface, although in sandy sediments it is distributed further down (Brotas & Serôdio 1995, Cartaxana *et al.* 2006, Jesus *et al.* 2006a). Spatial patterns of biomass distribution seem to be quite variable and mainly dependent on tidal height and sediment type (Brotas *et al.* 1995, Mendes 2005, Jesus *et al.* 2009). Biomass was found to be positively correlated to elevation, which is also in agreement with the higher rates of primary productivity observed for areas with longer emersion times (Serôdio & Catarino 2000). There are also clear indications that MPB biomass does not show any clear temporal patterns in mudflats (Brotas *et al.* 1995, Cabrita & Brotas 2000, Jesus *et al.* 2009), although seasonal variations in biomass may be present in sandflats (Jesus *et al.* 2009). Microphytobenthos seem also to be important mediators of the nutrient fluxes between sediment and the water column and may act as relevant sinks of nitrogen in the Tagus estuary (Cabrita & Brotas 2000). Recurrent studies in sediment pigment analysis by HPLC have given valuable information on the overall structure of the microphytobenthic communities found in the Tagus intertidal flats, as well as their seasonal and spatial variation. Diatoms completely dominate most of these assemblages, particularly in mudflats. Occasionally, euglenids and cyanobacteria may be also important components of these communities, especially during summer (*e.g.* Brotas & Plante-Cuny 1998, Brotas & Plante-Cuny 2003, Mendes 2005, Cartaxana *et al.* 2006, Jesus *et al.* 2009).

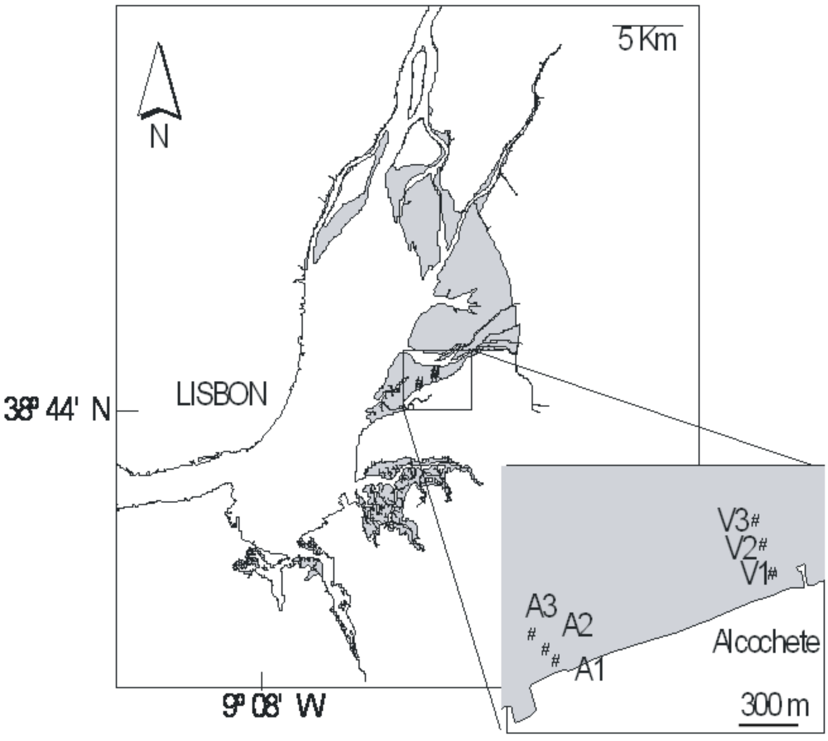

Figure 1 – Study area. Sampling stations identified by the letters in the box, grey areas represent intertidal areas. Adapted from Jesus (2006).

2.2. Alcochete intertidal flats

This study is a continuation of research work developed under the European project HI-MOM (contract EVK3-2001-00043) that took place from 2002 to 2004, in the Alcochete intertidal flats site and that has been previously published (Cartaxana *et al.* 2006, Jesus 2006, Jesus *et al.* 2006a, Jesus *et al.* 2009). This resulted in a very complete description of the microphytobenthos and of the environmental conditions of that area of the Tagus estuary. Therefore, only a summarized account of the main environmental parameters and of the spatial and temporal variation of MPB community, that was found to be relevant to this study on benthic diatoms, is given. For further details, including sampling and analysis methods, the above mentioned works must be consulted.

The sampling area (Figure 1) was located on the eastern shore of the Tagus Estuary in the estuarine beach, south of the town of Alcochete. This beach typical of a mesotidal estuary, given that the tidal range is higher than the normal wave height (Freire *et al.* 2006). These estuarine beaches are divided in two geomorphological units: a beach face, characterized by a steep slope, and a broad low-tide terrace, where dissipative conditions prevail. At the Tagus estuary, this lower unit can also be considered as a tidal flat, since it is not always connected to a beach face and is locally dominated by fine-grained sediments, suggesting that wind-induced waves are not the prevailing sediment reworking processes of this unit (Freire *et al.* 2007).

The sampling consisted of two transects, 1 km apart, running perpendicular to the shore and crossing the tidal flat. Each transect was 270 m long and was composed of 3 sampling sites. The two transects were chosen because of their very contrasting sediment structure. Transect V (stations V1, V2 and V3) was muddier and crossed a mud flat that bordered an ancient oyster reef. The site nearest to the shore (V1) was located at a zone were the mudflat became sandier, due to the influence of the neighbouring sandy beach. Transect A (stations A1, A2 and A3) crossed a sandflat. The tidal heights (relative to the hydrographical zero) were: 2.17, 1.16 and 1.02 m at A1, A2 and A3, respectively, and 1.4, 0.98 and 1.06 m at V1, V2 and V3, respectively. Since the station were located in the medium intertidal zone, their low tide exposure period was of about 1h30-2h30.

Sampling was carried out in two consecutive days and always at spring low tide. The study area was sampled every two months, in a total of 12 field campaigns, from September 2002 to July 2004. Diatom sampling was carried out simultaneously but, since it only started in January 2003, it was prolonged until November 2004 in order to complete also 12 field campaigns (see below section 3.1.1.).

2.2.1. Sediment characterisation and environmental parameters

Multidimensional scaling ordination (MDS) based on sediment grain size distribution (Figure 2), clearly separated samples accordingly to the sediment type found in each station (Figure 3). The sediment type changed little throughout the two years in most sites and their samples always clustered together.

Figure 2 – Multidimensional scaling ordination (MDS) of sediment samples collected at the studied sites. MDS was performed based standardized sediment grain size fractions and Euclidean distance similarity. The two dimensional ordination has a stress value of 0.01

The sites V2 and V3 were very distinct from the other 4 sites. They were composed of well to moderately well sorted muddy sediments. Although both sites had little temporal variation, V2 had a small but increasing contribution of the sand fraction. Site A1 was the sandiest, being composed essentially by fine and medium sand. The sediment was moderately sorted and had some temporal variation, seen by the point dispersion in Figure 2. Sites A2 and A3 were very similar and the most stable throughout the sampling period. They had poorly sorted, slightly muddy sands, mainly composed by medium and coarse sands, with a small but significant contribution of mud. Site V1 had the highest average mud content found in the sandy sites and it was the site that showed the biggest temporal variation (Jesus *et al.* 2006a). It had an important mud fraction in January and March 2003 (35 and 25% of sediment below 63 µm, respectively) but, after those initial months, it became progressively sandier. In this station, the sediment was poorly sorted, with the medium sands being the biggest individual contributor; coarse and fine sands had similar average contributions. The analysis of the < 63 µm fraction in all stations showed that this sediment fraction was composed by an average 66% of silt to 34 % of argyles. Thus the sands and muddy sands can be described as slightly silty and the muddy sediments as clayey silts accordingly to the sediment classification by Flemming (2000).

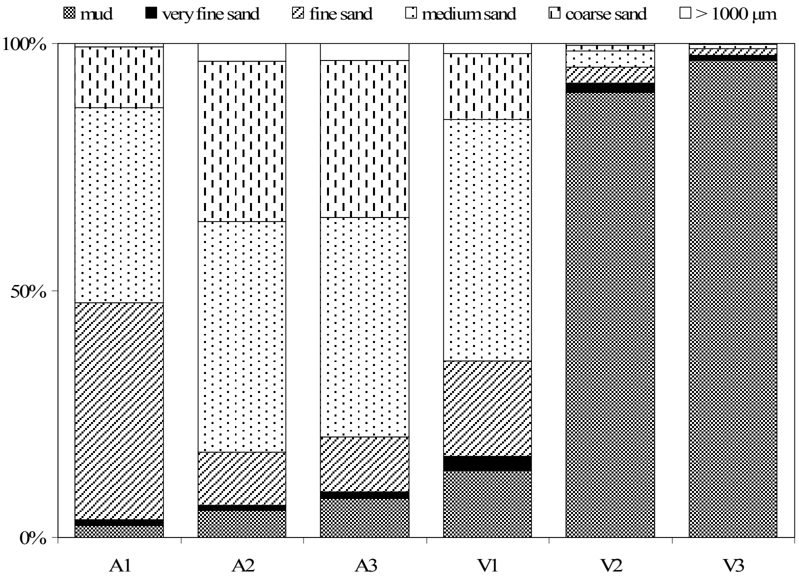

Figure 3 – Average grain size distribution in the studied sites. Grain size fractions expressed in percentage and consist of mud (<63 µm), very fine sand (63-125µm), fine sand (125-250 µm), medium sand 250-500 µm), coarse sand (500-1000 µm) and gravel (>1000 µm).

The sediment water and organic contents were very different in muddy and sandy stations (Figure 4A and 4B). Stations V2 and V3 had much higher water content and ash-free dry weight (AFDW). Conversely, the station V1 had a value range for those variables that were still closer to the values found for the stations of the sandy transect.

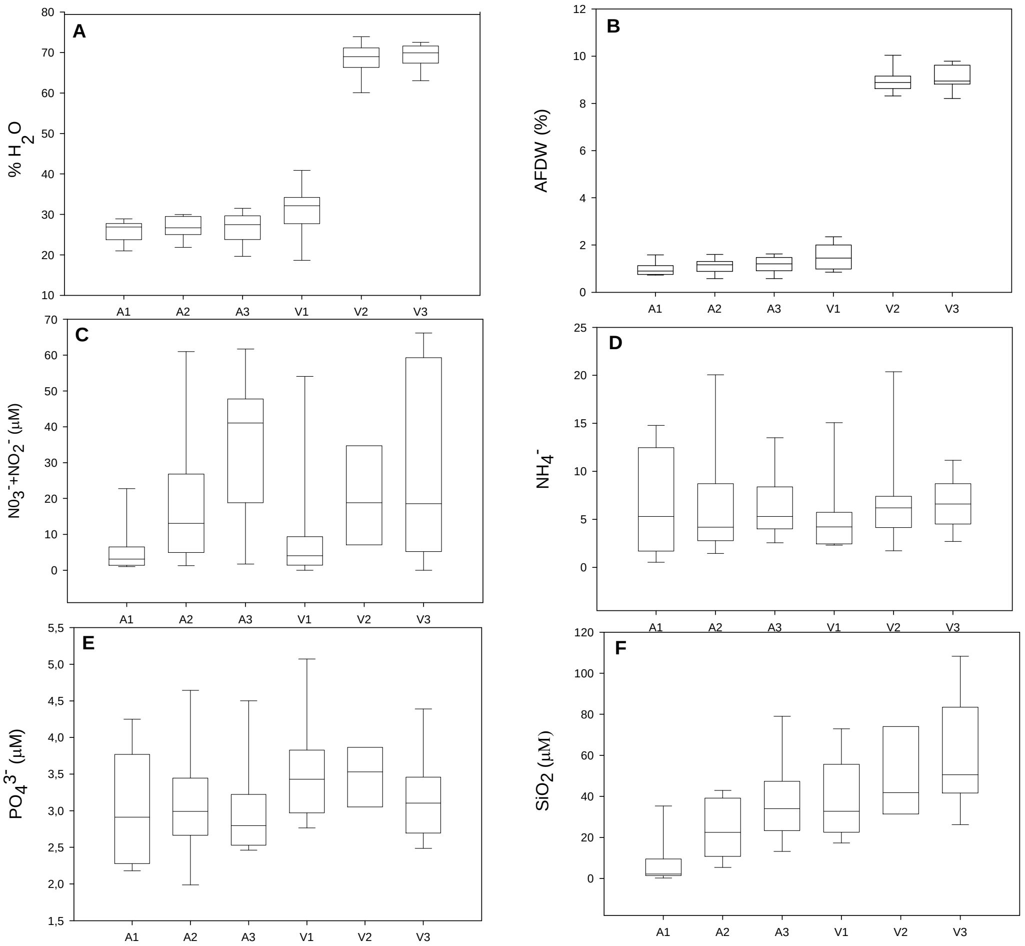

Figure 4 – Physical and Chemical characteristics of the sampled sites. Water content and Ash-free dry weight (AFDW) expressed in percentage; nutrients in μM.

The concentrations of the nutrients found in the sediment interstitial water varied considerable over time in all sites, but usually within the same range (Figs. 4C-4F). The seasonal variations are explained in detail in Jesus (2006). The NO_3^-+NO_2^- concentration had a wide variation. The upper shore sites (A1 and V1) had, on average, lower values than the lower shore sites (A3 and V3) (Figure 4C). According to Jesus (2006) there was a seasonal peak in winter. The SiO_2 concentration also showed an average increase from upper shore sites to lower shore sites (Figure 4F). However, the values were, on average, much lower in the sandy sites (A1-A3). In the latter sites, it also exhibited a seasonal pattern, similar to the one found in the NO_3^-+NO_2^- concentrations. This pattern was not evident in sites V2 and V3. The NH_4^+ concentrations ranged from 0.3 to 22 µM and did not show any kind of spatial or seasonal pattern (Figure 4D). The PO_4^{3-} did not show a spatial pattern, as well, but the values had a much smaller variation in range (Figure 4E).

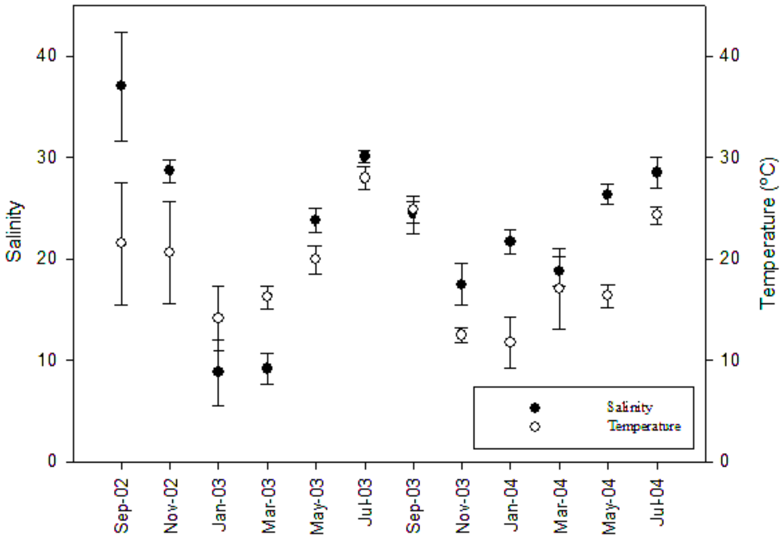

Figure 5 – Temporal variation of Salinity and Temperature (average of all sites) during the sampling period. Includes data from two previous sampling campaigns (September and November 2002).

Interstitial water salinity also showed a wide variation during the sampling period (Figure 5). The salinity did not show any significant differences between stations (ANOSIM test for site differences not rejected: R = -0.08, p = 99.5%). There was, however, a clear seasonal trend: salinity rose to around 30, in the warmer summer months, while in the colder and rainier autumn and winter months it was much lower (*viz.* around 10 in 2003 and 20 in 2004). This means that this area shifts between two salinity classifications changing, according to the Venice system (Anonymous, 1958), from mesohaline in the winter to polyhaline during the summer. It should also be noted that in January and March 2003 the salinity was lower than in the rest of the studied period.

2.2.2. MPB biomass, MPB pigment and microalgal composition

Microphytobenthic biomass on the sediment surface (Figure 6, *cf.* Jesus 2006) was estimated by different proxies: Spectral reflectance (NDVI), Fluorescence measurements

(F_0^{15}) and Chlorophyll *a* content (chl*a*) (*viz.* Jesus 2006, Jesus *et al.* 2009). Chlorophyll *a* concentrations of the sediment's top 2 mm varied from a maximum of 155 ± 11 $mg.m^{-2}$ in A1, to a minimum of 21±2 $mg.m^{-2}$ in A3. In the sandy transect, the concentrations decreased from the upper shore to the lower shore whereas, in the muddy transect, the opposite happened: V1 had lower chl*a* concentrations than V3. The same pattern occurred with the other biomass proxies, NDVI and F_o^{15} (Figure 6). Tidal exposure and, to some extent, SiO_2 concentration were more important structuring biomass distribution than sediment type (Jesus *et al.* 2009). Regarding the biomass temporal patterns (Figure 7, *cf.* Jesus *et al.* 2009), only in A2 and A3 an obvious late winter/spring peak was recorded. In the other stations a clear pattern was not perceived, with the exception of a common decrease in biomass in November 2003.

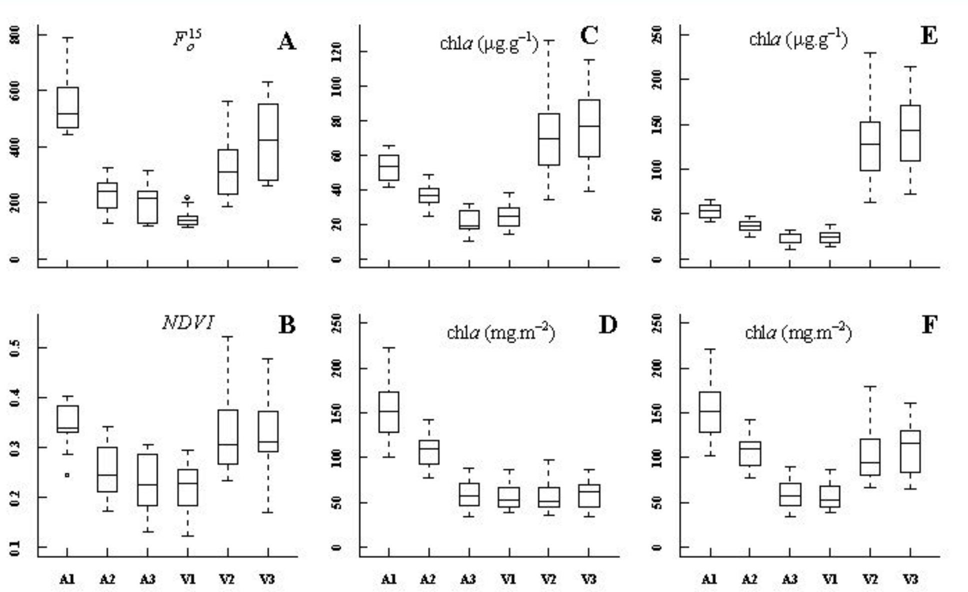

Figure 6 – Microphytobenthos biomass proxy parameters. A, F_0^{15}; B; NDVI; C, chlorophyll *a* content; D, chlorophyll *a* concentration; E, chlorophyll *a* content corrected for depth distribution; F, chlorophyll *a* concentration corrected for depth distribution. Adapted from Jesus (2006).

Chlorophyll *a* depth profile concentrations differed with sediment type. In muddy sediments, chl*a* typically had high concentrations on the first 500 µm whereas, in the sandy sediments, chl*a* was fairly constant throughout the sediment profile (Cartaxana *et al.* 2006).

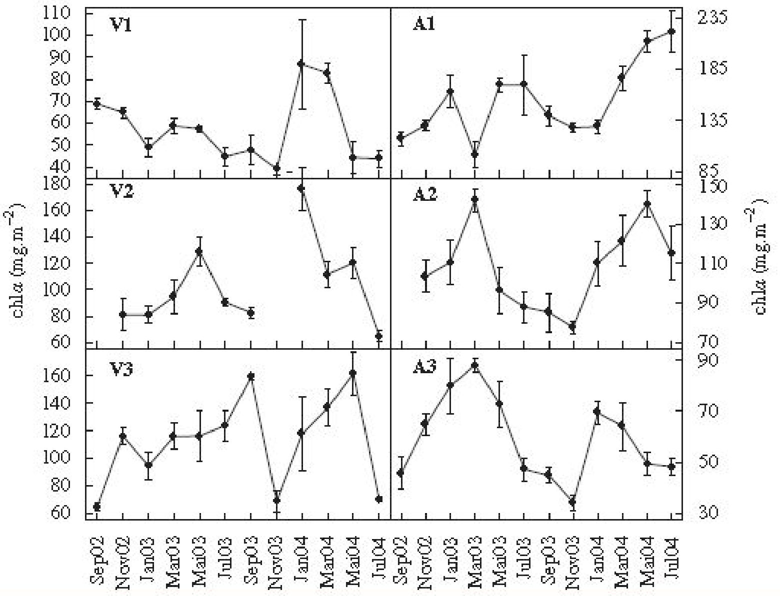

Figure 7 – Biomass variation at the 6 sampling stations over the course of the sampling period. Only chlorophyll *a* concentration corrected for depth distribution is presented. y-axis is different for each station. Adapted from Jesus *et al.* (2009).

Microalgal group counts established that diatoms were the most dominant group in all stations. Cyanobacteria were absent at site V2 but were present, in a small proportion, at the other sites. Euglenids only appeared in A1. These results confirmed the pigment analysis. Chlorophyll *a* correlated highly with pigments present in diatoms, like fucoxanthin and chl*c*, but to a lesser extent to zeaxantin (typical of cyanobacteria) and not with chl*b* (present in euglenids) at the muddy transect (Cartaxana *et al.* 2006, Jesus *et al.* 2009). The source of chl*b* at these stations was probably detritus material either from macroalgae or from vascular plants. Conversely, in the sandy transect zeaxantin and chl*b* correlated with cyanobacteria and euglenid counts, respectively (Jesus *et al.* 2009). Therefore, sandier sites were more diverse, in terms of MPB taxonomic groups, than the muddy sites, which were composed almost exclusively by diatoms

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Chapter 3

Material and methods

3. Material and methods

3.1. Sampling and slide preparation

3.1.1. Diatom sampling, extraction, and preservation

Samples for diatom community analysis were collected by scraping the surface of the exposed sediment (upper 2 mm) with a scalpel. An approximate 3 mL of sediment was collected and placed in disposable 5 mL polypropylene tubes, to which was added approximately 1 mL of a 2.5 % glutaraldehyde solution in filtered estuarine water, thus reaching a final and constant volume of 4 mL. Three samples per station were collected and stored at 6 ºC for later processing.

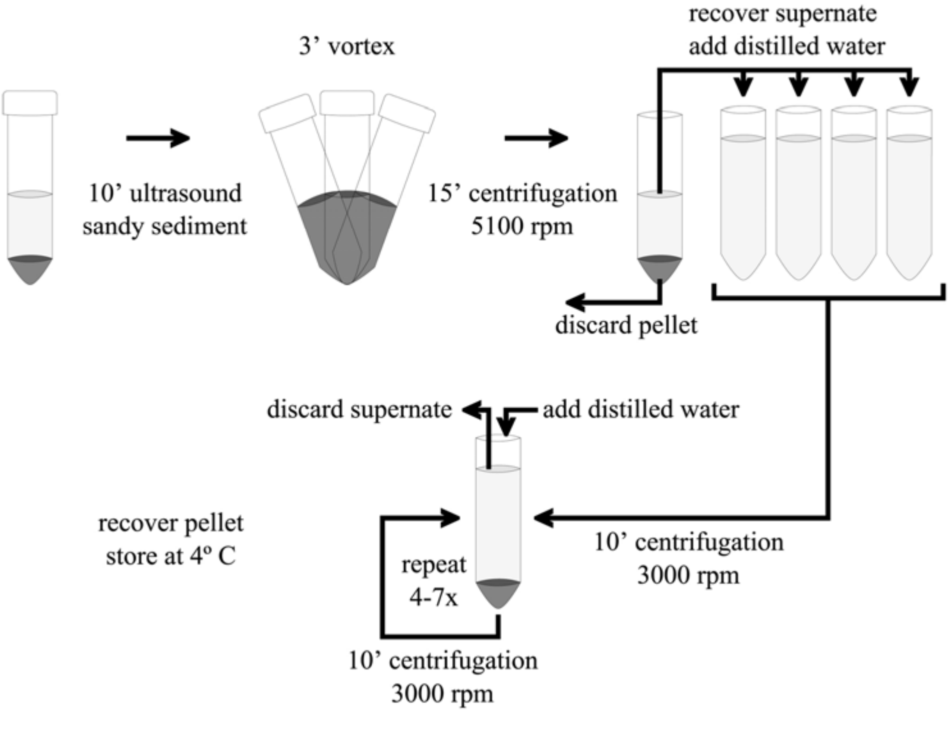

Figure 8 – Microphytobenthos extraction method.

The method chosen to extract the MPB communities from the sediment was an isopycnic separation technique using the silica sol Ludox® (HS-40) which is schematically described in Figure 8. This technique was first applied to diatoms of intertidal sediments by de Jonge (1979). The protocol followed was adapted from Blanchard *et al.* (1988), Burgess (2001) and Méléder *et al.* (2007), in order to minimize the effect of sediment granulometry on the extraction efficiency and selectiveness. Density gradient centrifugation was unnecessary due to the very different densities of the two main fractions of the sediment: the mineral fraction and the organic fraction (*i.e.* biofilms and meiofauna).

The sediment samples were homogenized in a vortex mixer and transferred to 50 mL polypropylene centrifuge tubes, to which was added full concentrated Ludox, with a density of 1.31 g cm^{-3}. Sensitivity to divalent cations in seawater may cause gelling of the Ludox but it seldom occurred (two samples lost), given the reduced quantity of sample pore water, in most samples, and the fact that it usually had a lower salinity than seawater. The risk of losing cells by pre-washing the sediment in distilled water, prior to adding Ludox, was considered higher. Approximate 25 mL of Ludox were added to the centrifuge tube, resulting in a final sample volume of 30 mL. Circa 20 mL of air were left in the tube to allow the sample to be thoroughly mixed. Samples composed of sandy sediment were ultrasonicated for 10 minutes, permitting the separation of the epipsammic diatoms attached to the sand grains. After this step, all samples were mixed during 30 seconds at maximum speed in the vortex mixer. The centripetal acceleration was then slowly reduced to half, permitting the sediment/Ludox mélange to continue in a fluid state. The samples were left in the vortex mixer for 3 minutes, in order to allow a greater interaction of the sediment particles with the silica sol. During this step no excessive damage to the cells was noticed and even large cyanobacterial colonies (*e.g. Merismopedia*) were preserved. The samples were then centrifuged at 5100 rpm, during 15 minutes in a Rotinna 35 R Hettich centrifuge (*i.e.* 3720 *g*). This centrifugation accelerates the sedimentation of the mineral fraction of the sediment (including the fine silts and clay) and pellets it firmly to the bottom of the tube. Most organic material and the silica sol did not deposit at this *g* force. The supernate was then poured evenly in 4 centrifuge tubes (50 mL tubes) which were filled with ultra pure distilled water. This step was necessary to rinse the excess Ludox, thus separating the organics from the silica sol. A relatively mild centrifugation (at 1300 rpm) was used to accelerate the deposition of the MPB and organic material. The supernate (*i.e.* silica sol) was discarded and the tubes filled again with distilled water. This step was repeated 4-7 times to ensure a complete elimination of Ludox vestiges. Finally, the rinsed pellets (extracts) were transferred to a single 1.5 mL eppendorf microcentrifuge tube filled with distilled water and a few drops of 2.5 % glutaraldehyde. The extracts were stored at 6 ºC for microalgae group counts and diatom analysis.

3.1.2. Diatom cleaning procedures and slide preparation

Microscopic observations of the extracts, prior to diatom cleaning, revealed high abundances of very fragile and barely silicified diatoms, in particular *Cylindrotheca closterium* and *C. signata,* in several samples. These species are usually destroyed when the traditional oxidation cleaning methods are used (*e.g.* Sabbe 1997).In order to avoid the underestimating of at least these two very important elements of the assemblages, two complementary cleaning methods were used and, as a result, two permanent slides were made for each sample. The two methods were the following:

Oxidation method: The method chosen was essentially adapted from Batterbee (1986). It is a relative aggressive chemical procedure that cleaned thoroughly the frustules by oxidation but destroyed the *Cylindrotheca* frustules. A subsample of 750 µl of extract was oxidized with 5-7 mL of hydrogen peroxide (30 %) at 90 ºC for at least 4 hours. When the reaction was over, 2 mL of hydrochloric acid (6M) were added for the elimination of carbonates. Subsequently the oxidized extract was washed 4 times with ultrapure distilled water and a few drops of ammonia, for extra clay removal. The cleaned extract (diatom valves) was deposited in previously cleaned coverglasses and, after drying in a dust-free environment, mounted in Naphrax™ (refractive index, 1.73).

Incineration method: The method chosen was adapted from Méléder *et al.* (2007). It is a gentler method that consumes the organic matter by incineration, leaving all frustules intact. However, it also hinders the identification of very small diatoms as it may also leave mineral material (*e.g.* carbonates) that may hide important fine structure details of the frustules. A 15 µl subsample of extract and 400 µl of ultrapure distilled water were placed on previously cleaned 20 mm coverglasses. The resulting water meniscus was homogenized with a Pasteur's pipette to ensure an evenly distribution of the frustules and it was left to settle and dry in a dust free environment for 24-48 hours. The coverglasses were placed in a Muffle oven during 2h at 450 ºC, and mounted in Naphrax™.

3.1.3. Diatom identification and cell counting

Cell counting and the observation and identification of diatom valves was made in a Zeiss Axioskop 50 optical microscope, equipped with Bright field, Phase and DIC optical microscopy (MO), was used to count and identify diatoms valves. Observations and counts were made using the Plan-NEOFLUAR oil immersion objective 100 coupled with a 1.6x optovar. Digital microphotographs were made using a Nikon DS-5M digital camera. Scanning electron microscopy (SEM) was carried out, using a Hitachi S 4500, at the Botanical Institute of J.-W. Goethe University, Frankfurt am Main (Germany). The stubs were deposited in Coll. LANGE-BERTALOT.

Diatom identification, mainly followed: Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b); Lange-Bertalot (2001); Sabbe (1997); Simonsen (1987); Snoeijs (1993); Snoeijs and Vilbaste (1994); Snoeijs and Potapova (1995); Snoeijs and Kasperoviciene (1996); Snoeijs and Balashova (1998); Witkowski *et al.* (2000). The complete literature used in the identification of each taxon is given in chapter 7.

As explained above, the significant presence of fragile *Cylindrotheca* spp. required the diatom cell counting on two types of slides per sample. For each sample, the relative percentage of *C. signata* and *C. closterium* determined first, from the counts of 300-500 frustules in the slide of the incinerated material. Secondly, 300-500 valves of all the other diatom taxa were scored in the slide of the oxidised material. The percentage abundance of each taxon was calculated in relation to the previously established relative percentage of *Cylindrotheca*. For example, in a sample where the *Cylindrotheca* specimens accounted for 55 % of the total scores in the “incinerated” slide (V3, September 2003), the relative abundances of the other species were recalculated for the remaining 45 %. It was thus assumed that the distribution of all other species was equal in both types of slides of a given sample.

A random field counting method is preferable to a transect method, since it allows to counter the common margin effect, caused by non random valve/frustule deposition in cover glasses, when counting transects in permanent slides (Alverson *et al.* 2003). In order to produce random fields, the Cartesian coordinate range that delimits the coverglass perimeter in the permanent slides was determined, using the Vernier scale of the microscope platinum stage. The coordinates of 100 random fields per slide were then generated, using the RAND function in Microsoft Excell^{TM} 2003. All complete valves/frustules in each field were counted until the above mentioned 300-500 scores were reached and a minimum of 50 random fields were covered. Only pennate diatoms with at least one pole and the central area were considered complete. In the case of centric diatoms, more than 50 % of the valve surface, including the central area, was necessary.

The contamination effect of dead frustules in the diatom counts was considered negligible, since the Ludox method effectively separated them from the "live" diatoms when extracting organic matter from the sediment. This was confirmed during the microalgal group counts, when the almost complete absence of empty, "dead" frustules was noticed. A similar result was obtained by Vilbaste *et al.* (2000), for Baltic Sea benthic diatoms preserved in glutaraldehyde. Previous comparisons showed also that the ratio between live and dead cells in epipsammic and epipelic communities is quite stable (Sundbäck & Snoeijs 1991, Sabbe 1993) and, therefore, does not seriously affect the counts.

3.2. Data screening: species datasets

The species abundance-by-sample matrix that resulted from cell counts consisted of 181 taxa and 68 samples. The term "species" is used throughout this work to denote different taxa. Not only species but other taxa, such as varieties, morphotypes and merged species (see chapter 7). This initial matrix is henceforth named as SPECIES DATASET 1 (DS1) and it was already standardized, due to the counting procedure (see above, section 3.1.3). It was used for calculating diversity indexes (section 3.3) and in describing graphically the diatom size-classes, functional groups and life-forms (section 3.5)

The abundance data matrix (DS1) was reduced, both in number of taxa and in number of samples, prior to multivariate analysis (section 3.4). All species with less than two occurrences and/or that never surpassed, at least in one sample, 1% of abundance were discarded. After this screening the abundance matrix was standardized again. The species abundance matrix is referred as SPECIES DATASET 2 (DS2). This dataset consisted of 68 samples and 94 species (see Diatom taxa list, section 7.3).

The deletion of species from the data matrix is not absolutely necessary for non-parametric multivariate analysis and it can be often an arbitrary process (Clarke & Warwick 2001). However, it was considered best to eliminate the species with very low and erratic sparse counts. These species were extremely rare and many of were probably allochtonous (see chapter 7). The effect of this data screening was studied in detail and it was confirmed that it did not caused important loss of information in the several multivariate routines used (see below, chapter 6).

Finally, the linkage of the biotic, species abundance dataset and the environmental variables dataset mandates a complete correspondence in sample label and number (see section 3.4.6). Consequently, the SPECIES DATASET 2 (DS2) had to be reduced to the same number of samples present in the environmental dataset, thus creating a SPECIES DATASET 3 (DS3) with 52 samples but with the same 94 species of DS2.

3.3. Diversity

Diatom assemblage diversity was measured using univariate statistics, such as diversity indexes, but also by construction of graphical/distributional plots, such as the *k*-dominance curves. Both type of routines were made using the software package PRIMER© version 6.1.9. (Plymouth Marine Laboratory, U.K.) and accordingly to methods described in Clarke & Warwick (2001) and Clarke & Gorley (2006).

Besides the Species richness (S), expressed as number of species per sample, the calculated species indexes included the Shannon's (H and H'), Margalef's (d) and Hill's numbers, (N_1, N_2 and N_∞) Diversity indexes; the Pielou's (J') and Simpson's (λ) Dominance and indexes and, finally, the Inverted Simpson's ($1-\lambda$) Evenness indexes. The formulae are listed in table below (Table 1):

Table 1 – Formulae of the Diversity, Dominance and Evenness indexes. S = number of species per sample; $p_i = n_i/N$, with n_i as the number of cells of species *i* and N total number of cells per sample.

Index	**Formula**
$H\ (\log_2)$	$H = -\sum_{i=1}^{S} p_i \log_2 p_i$
$H'\ (\log_e)$	$H' = -\sum_{i=1}^{S} p_i \log_e p_i$
d	$(S\text{-}1)/\log N$
N_1	$e^{H'}$
N_2	$1 / \Sigma p_i^2$
N_∞	$1 / \max p_i$
J'	$H / \log_e S$
$1\text{-}\lambda$	$1 - (\Sigma p_i^2)$
λ	Σp_i^2

The information obtained from the indices was supplemented with diversity profiles that resulted from plotting *k*-dominance curves (Lambshead *et al.* 1983). They are similar to ranked species abundance curves (or Dominance curves), where the species, ranked in a log scale (*x*-axis), in decreasing order of their importance in terms of abundance, are plotted against their actual values of abundance percentage (*i.e.* % of dominance). In the case of *k*-dominance curves, the log species rank (*x*-axis) is plotted against the cumulative ranked abundances (*y*-axis). This has an effect of smoothing the curves. In both cases logging the *x* (rank) axis enables the distribution of the commoner species to be better visualized (Clarke & Warwick 2001). However, in *k*-dominance plots, the most elevated curves have the lowest diversity. Given that the diversity cannot be assessed unambiguously in a plot with 68 curves (*i.e.* the total number of samples in DS1), it was decided to average the species abundance per site before plotting the curves.

3.4. Multivariate data analysis

Community structure studies such as this one typically generate species abundance per sample datasets. These data matrixes have extremely high dimensionality, with scores or even hundreds of species as variables (rows) and the samples in columns. The prevalence of “zero values” also makes the distribution of the individual species counts depart from normality. It is then advisable to use non-parametric multivariate methods that are robust and need to make very few assumptions on the normality of the original data set (Clarke 1993). Therefore, diatom community structure was analyzed using non-parametric multivariate tools, found in PRIMER software package, accordingly to methods described in detail in Clarke & Warwick (2001) and Clarke & Gorley (2006) and, in a summarized fashion, in the following sections.

3.4.1. Similarity measurement: Bray-Curtis Similarity

Most of the multivariate methods (*e.g.* clustering, ordination and discriminating tests) used in this study are based on the similarity of the assemblages found between any pair of samples. The similarity coefficient chosen to build the similarity triangular (sample-by-sample) resemblance matrix was the non-correlation based Bray-Curtis coefficient (S_{jk}), which varies from 0 (total dissimilarity) to 100 (total similarity):

$$S_{jk} = 100\left\{1 - \frac{\sum_{i=1}^{p}\left|y_{ij} - y_{ik}\right|}{\sum_{i=1}^{p}\left(y_{ij} + y_{ik}\right)}\right\}$$

where y_{ij} represents the abundance of the i^{th} species in the j^{th} sample (p; $j = 1, 2, \ldots, n$), and y_{ik} stands for the count of the same species (i^{th}) on the k^{th} sample. Samples with more species in common, as well as similar species abundance will have higher similarity, making this index ecologically relevant (Clarke & Warwick 2001). In order to avoid an over-domination of few very abundant species, it is advisable to pre-transform the original data matrix. Root-root transformation was used to down-weight the contribution of the most abundant species, allowing the mid-range as well as the rarer species to exert influence on the calculation of similarity (Clarke & Green 1988). This kind of transformation is recommended by several authors (*e.g.* Thorne *et al.* 1999), as it lets abundance retain a certain role, albeit reduced. The final result is a triangular matrix that compares similarity of all samples with each other.

3.4.2. Classification: CLUSTER

The PRIMER's classification routine CLUSTER uses Hierarchical Agglomerative Clustering of the samples and it was performed on the triangular similarity matrix (see section 3.4.1), using group-average linking. This kind of link clustering joins two groups of samples together at the average level of similarity, that is, at the average distance of any member of the first group to any member of the second group of samples (Field *et al.* 1982). The statistical significance of the cluster groups created was tested by a "similarity profile" routine (SIMPROF), during the construction of the dendrogram. Calculated for every node, SIMPROF is a permutation test of the null hypothesis that a set of samples below a node does not show any multivariate structure (Clarke & Gorley 2006).

A similarity profile is a plot of the ordered similarities of a given group of samples against their rank of resemblances. Very similar samples have the highest rank and very dissimilar samples, the lowest. The departure of this real similarity curve from the shape of the "expected" shape under the null hypothesis is the basis of the test. The mean null hypothesis profile is obtained from averaging 1000 random similarity profiles derived from permuting the species entries in that subset of samples, separately for each species, thus randomly creating rearranged samples with no group structure. The summed absolute distances between the real similarity profile and this simulated mean profile is the test statistic (π). This process is repeated another 999 times in order to produce a null hypothesis distribution of a 1000 π statistics, a range of likely null π values. If the real π is larger than any of the simulated values, then there is evidence of group structure at a significance level of $p < 0.1$ %. The level of significance can be chosen. In the SIMPROF test performed, a p-level of 1 % was picked so that at each successive node of the dendrogram, this process was repeated until a non-significant group was detected.

3.4.3. Ordination: MDS

In order to better visualise the structure of Bray-Curtis similarity matrix in a two dimensional plot, a non-metric Multi-Dimensional Scaling (MDS) ordination was performed. This non-parametric unconstrained ordination, constructs a configuration “map” of samples, which attempts to satisfy all the conditions imposed by the underlying similarity matrix (Clarke 1993, Clarke & Warwick 2001). The distances between pairs of samples in the plot reflect their relative dissimilarity in species composition and abundance. This is achieved by rank-ordering the similarities of all the samples (points in the map) in relation to each one of them, by an iterative analytical process. The most similar samples have a lower rank order and are closely placed on the plot; whereas the most dissimilar have a higher rank order and are more distant. The stress value indicates the degree to which the two-dimensional plot successfully reflects the multidimensional sample relationships. Consequently, good two-dimensional representations have the lowest stress values (*e.g.* Clarke 1993). The MDS was chosen above other ordination methods because it is a good method to use when data are not normally distributed (Clarke & Warwick 2001, Quinn & Keough 2002) but also because it relieves the "zero-truncation problem" (Beals 1984), which affects all other ordination methods (*e.g.* PCA, CCA, DCA) of heterogeneous data sets (McCune & Grace 2002).

3.4.4. Hypothesis testing for differences between groups of samples: ANOSIM

The analysis of similarities routine, or ANOSIM, allows determining if there are any statistically significant differences between groups of samples defined *a priori*, such as replicates or samples from a number of different sites and/or collected in different dates (Clarke & Warwick, 2001).

It is a Mantel-type permutation procedure that does not make any distributional assumptions, since it depends only on sample rank similarities. It is analogous to the univariate ANOVA test (Clarke & Warwick 2001), but compares the difference between rank similarities between and within groups of samples defined *a priori* (*e.g.* sites, times) using a randomisation test of significance. The test statistic R, varies from 0 (null hypothesis accepted) to 1 (null hypothesis rejected) at a significance level that depends of the times the true value of R is compared with the permuted values (usually 999 for a $p < 0.1$ %, Clarke & Warwick 2001). The permuted values are obtained in a similar fashion as in the SIMPROF test.

Since there were no replicates (one sample per each date at each site) the ANOSIM two-way crossed (with no replicates) layout was chosen to test the spatial and temporal differences, as it also allows a pairwise removal of missing data (*i.e.* missing samples). The routine rationale and method is explained in detail in Clarke & Warwick (1994). The two null hypotheses tested were: H_{01}, “there are no site-to-site differences”; H_{02}, “there are no temporal differences”, in this case, no difference between sampling dates. The two-way ANOSIM removes the effects of one factor (*e.g.* time) when considering the significance of the other factor (*e.g.* site). If one of the two null hypotheses is not rejected (*e.g.* time), then a one-way ANOSIM test can be performed the other factor (*i.e.* site). In that case, the samples collected throughout the study period are considered as *site* replicates. Pairwise ANOSIM tests comparing sites can, consequently, be computed.

3.4.5. Species similarities percentage analysis: SIMPER

Analysis of similarity percentages (SIMPER) was used to identify diatom species primarily responsible for differences between sites. This routine, based on root-root transformed data matrix, examines the actual contribution of individual species to the measures of Bray-Curtis similarities/dissimilarities between groups of samples in what is called Similarity Breakdown (Clarke & Warwick 2001). This approach is much more informative than the simple ranking of each species’ average abundance.

A given species (*i*) *typifies* a group if it is consistently abundant throughout the samples of that group, *i.e.* it has to have a high average contribution ($\overline{S_i}$) to the overall similarity ($\overline{S}$) and its standard deviation SD (S_i) is low.

Since the calculation of the Dissimilarity between two samples *j* and *k* (δ_{jk}) derives from equation:

$$\delta_{jk} = 100 - S_{jk}$$

a similar reasoning can be followed: a species (*i*) is considered as a *good discriminating species* if it has a high average contribution ($\overline{\delta_i}$) to the overall dissimilarity ($\overline{\delta}$) and a low standard deviation SD (δ_i), when all pairs of inter-group samples are being compared.

The most influential species to the assemblage structure, *i.e.* the ones that better typify a particular group of samples or help to discriminate two groups of samples are not necessarily the most abundant ones.

3.4.6. Linking multivariate community structure to environmental variables: BIOENV

The relationship between the multivariate diatom community structure and certain environmental variables at the same set of samples were examined using the biological environmental gradients procedure (BIO-ENV). The premise of this method is that pairs of samples that are similar in terms of physico-chemical variables should be expected to have similar species composition, provided that the environmental parameters relevant in structuring the communities were included in the analysis (Clarke & Ainsworth 1993). If that is the case, it is expected that an ordination based on the abiotic information would group samples in the same way as for the biotic information (Clarke & Warwick 2001). If not, the omission of key environmental variables may deteriorate the matching of the plots, which can also be worsened by the inclusion of variables irrelevant to the community structure.

The BIO-ENV routine tries to find the combination of environmental variables that produce the best match between the biotic and abiotic datasets. This *best fitting* environmental combination is, therefore, the one that is most responsible for the community multivariate patterns. To measure the agreement between the two datasets, the BIO-ENV routine computes a rank correlation coefficient of all the elements of the two triangular similarity matrices underlying the ordinations of environmental variables and biota. Even though the two matrices may have different similarity measures (Euclidean for abiotic and Bray-Curtis for biotic matrices), the ordering of the samples (rank-order) within each matrix can always be compared. The coefficient used was the Spearman's coefficient (ρ_s), defined has:

$$\rho_s = 1 - \frac{6}{N(N^2 - 1)} \sum_{i=1}^{N} (r_i - s_i)^2$$

where r_i (i = 1, …, N) are the ranks of all sample similarities calculated using the biotic data, s_i (i = 1, …, N} are the ranks of sample similarities calculated using the abiotic data and N = n(n-1)/2, with n as the number of samples. The coefficient ρ_s varies between -1 and 1. Values around zero correspond to the absence of any match and around 1 to a complete agreement of the two sets of ranks.

The two datasets are matched in the following way: using always the same species abundance matrix, combinations of the n environment variables are considered at steadily increasing levels of complexity, *i.e.*, k variables at a time (k = 1, 2, 3…v). The best matches of the biotic and the created abiotic similarity matrices for each k, as measured by ρ_s, are sequentially retained. The process ends when all combinations were tried, and the combination with the highest correlation with the biotic matrix is the one that best explains the community patterns.

A global match permutation test was performed during the BIO-ENV procedure. The null hypothesis of "no agreement in the multivariate pattern" between two resemblances matrices can be measured by the rank correlation coefficient ρ, and corresponds to ρ = 0. By randomly permuting one set of sample labels relative to the other, and then running through the full BIO-ENV procedure a best match ρ is generated. This process can be repeated again and again (in this case, 999 times), thus generating 999 ρ values that represent the null hypothesis case. The real ρ is compared with these and if it is larger than any of them, the null hypothesis is rejected at p<0.1%.

Regarding the studied datasets, several remarks must be made. The environmental variables chosen were: Tidal height, Temperature, Light, Salinity, >1000, 1000-500, 500-250, 250-125, 125-63 and <63 µm sediment size-fractions and the pore-water concentrations of NH_4^+, NO_2^-, total-N, PO_3^{+4} and SiO_2. As the mud fraction, the sediment water content and organic matter content showed very high Pearson's correlations (>0.95), only the mud content was included in the consequent analysis. The nutrient concentrations were log-transformed prior to the construction of a normalised Euclidean distance triangular matrix. The matching of the matrices during the BIO-ENV routine *implies* the same number (and labels) of samples in the biotic and the abiotic matrices. There the biotic dataset (*i.e.* DS2) had to be reduced to the same number of samples of the abiotic dataset (see section 3.2).

3.5. Terminology of functional-groups, life-forms and size-classes

The purpose of this section is to define unambiguously a series of ecological terms that are recurrently employed throughout this study.

Diatom **community** – this term is used here in the most general sense. It is also considered as a synonym of diatom **assemblage**, following the definition, advanced by Round (1971), of an assemblage as "a collection of populations of different species, within a defined area or volume". Round (1971) also mentioned that the term "assemblage" could just refer to any collection diatom frustules, such as fossil deposits or samples with live and dead cells. However, since the diatom slides seemed to consist mainly of live diatoms (see section 3.1.3) the correspondence between community and assemblage was thought to be valid.

Community physiognomy – this term is used in the classical botanical sense. It can be defined as way of "describing vegetation by means of broad-scale morphological characters, abstracting from specific species identities" (Jax 2009). It is, therefore a "combination of the external appearance of vegetation, its architecture or biomass structure and the growth forms of its dominant taxa (Barbour *et al.* 1987). In diatom studies this term has been applied mostly to community structure description using life-forms (*e.g.* Hudon & Legendre 1987, Pringle 1990).

Functional group – The terms epipsammon and epipelon were not considered as life-forms (*viz.* Round 1971) but as “functional groups” (*viz.* Forster *et al.* 2006), each one of with several possible types of life-form. One common synonym of “functional group” in community ecology is the term **guild**, which is defined as a “group species that exploit the same class of environmental resources in a similar way” (Root 1967). This has been mainly use in animal ecology (*e.g.* Simberloff & Dayan 1991) but it was recently employed to diatom studies to designate the epipelon, the epipsammon and the epiphyton (Passy 2007). The definitions of epipelon and epipsammon proposed by Sabbe (1997) were adopted:

Epipelon – groups “**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**” (Sabbe 1997). Therefore, the term epipelon is to be used *sensu* the original definition by Round (1956), which considers epipelic diatoms as “diatoms that live freely on and in sediments” and not only to “pennate motile diatoms” (Admiraal, 1984) or to the widely used “diatoms growing in mud”. This means that, diatom epipelic species can co-habit with the epipsammic community in sandy sediments, moving on and between sand grains (*viz.* Moss & Round 1967, Round *et al.* 1990), thus including large motile diatoms living in sandy sediments. According to the broader definition of Sabbe (1997), the tychoplanktonic taxa, that accumulates in muddy sediments (*e.g. Cyclotella* or *Thalassiosira* spp.), as well as the species living interstitial space between sand grains should also be considered as part of the epipelon (see below, life-form categories).

Epipsammon – includes “**those taxa that live in close association (either attached or free-living) with individual sediment particles**” (Sabbe 1997). Since it includes small motile diatoms, capable of exploring the micro-environment and topography of a single sand-grain, the term epipsammon is to be used in a slightly different sense than in Round *et al.* (1990) or Admiraal (1984), *i.e.*, “attached or almost immobile diatoms growing in sand grains”.

Life-form – this term was used here as an equivalent of growth-form, found in classical Plant Ecology, thus referring both to the architecture of the organism and to its auto-ecology. In the physiognomic classification proposed here, life-forms are to be considered as categories of the function-groups. The life-form of each taxon was determined by microscopical examination and by literature research (mainly Round *et al.* 1990, Sabbe 1997, Witkowski *et al.* 2000). Following the definitions proposed by Sabbe (1997) and Sundbäck (1983), ten categories were established:

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* species) or by their girdle (*e.g.* colony forming biraphid diatoms *Catenula adhaerens* or *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. **Epipsammic motile < 20 µm (Mo<20sm):** small, mostly biraphid taxa (mainly *Navicula, Amphora* and *Fallacia*) which live in close association with sand grains.

4. **Epipelic motile < 20 µm (Mo<20pl)**: group small diatoms including representatives of the genera *Navicula* and *Nitzschia*. It roughly corresponds to size-class B in mudflats.

5. **Motile > 20 µm (Mo>20)**: this group mainly comprises the larger taxa belonging to genera *Amphora*, *Diploneis*, *Gyrosigma*, *Navicula* and *Nitzschia*. This group roughly corresponds to size-class C and D in mudflats but also includes a few large motile species that live in sandflats (*e.g. Petroneis*).

6. **Tychoplankton**: this life-form (as applied here) refers to non-motile species, mainly found in muddy benthic environments, which are easily resuspended to the water column. It includes centric diatoms belonging to the Cymatosiraceae but also genera like *Cyclotella* or *Thalassiosira*). A few araphid taxa (*e.g. Rhaphoneis* and *Neodelphineis*) are also included in this group.

7. **Interstitial**: this group is composed by free-living non-motile species that occur in interstitial spaces between particles in sandy sediments. It only includes a small number of little-known taxa (*e.g. Leyanella*, *Pierrecomperia*).

8. **Plankton:** includes truly planktonic species (*e.g. Coscinodiscus* spp.), which are allochtonous to the benthic environment.

9. **Epiphyton:** comprises taxa which live attached to macro-algae and higher plants. In our material it mainly concerns taxa that have been washed in from vegetated areas (*e.g. Cocconeis scutellum*) and are allochtonous to the tidal flats.

10. **Undefined**: includes taxa which have an unknown or undetermined life-form but also the ones which cannot be included in the 9 life-form categories defined above (*e.g.* tube-dwelling diatoms) and that were represented by only a few species.

More detailed autoecological information can be found in the systematic part (chapter 7) and the exact life-form of each taxon is given in the Appendix (section 7.1.3.). **Life-form categories 1 to 3 were assigned to the Epipsammon and life-forms 4 to 7 to the Epipelon**. The few tube-dwelling species found in this study were also assigned to the epipelon, since they were always biraphid motile species.

Size-classes – in the present study, the size classes were defined in terms of cell biovolume, *i.e.* in μm^3. For each species, an average biovolume was determined following the geometrical calculations proposed by Hillebrand *et al.* (1999) and Olenina *et al.* (2006). Diatom length, width or cell diameters were determined from micrographs of valve views. Pervalvar axes were obtained from girdle views but, in several cases, they had to be estimated from SEM micrographs and from literature. Snoeijs *et al.* (2002) presented a very extensive list of coastal diatom biovolumes (515 taxa) and that work was used for confirmation of the calculations. The established four size classes (Table 2) were adapted from Sundbäck (1983) and Snoeijs *et al.* (2002) but with some important differences: Snoeijs *et al.* (2002) established just two groups (smaller or bigger than 1000 µm3), whereas Sundbäck (1983) subdivided the diatoms smaller than 250 μm^3 in 3 groups. The separation, proposed by Sundbäck (1983), of diatoms with volumes smaller than 50 μm^3 and smaller than 100 μm^3 seemed unrealistic and far too dependent of a correct (and extremely difficult) measurement of the pervalvar axis.

The contribution of each function-group, life-form and size-class in each sample was calculated by simple aggregation of the relative abundances of the taxa allocated to each group and then averaged per station. Relative abundances of each species in each sample were also weighted by each species median biovolume (see section 7.1.3.). Then, the ensuing standardized matrix was reorganized accordingly, thus giving the relative contribution of each species to the total biovolume of each sample.

Table 2 – Biovolume size-classes and the length range (and median value) of the pennate diatom allocated to each class. Diameters of cylindrical centric diatoms were not considered in the length range.

Size-Class	**Biovolume (µm^3)**	**Length range (µm)**
A – Very small	< 100	4 - (9) - 16
B – Small	100 – 250	8- (13) - 30
C – Medium-sized	250 – 1000	11 - (20) - 126
D – Large and very large	> 1000	20 - (57) -170

Chapter 4

Results

4. Results

4.1. Diversity

Most of the diversity indexes used in marine communities studies are presented in Table 3. Species richness (*S*) and diversity (H, H', d, N_1, N_2 and N_∞) was higher, in average, in the sandier sites (A1, A2, A3 and V1). The assemblages in the muddier sites, V2 and V3, had in average a much higher dominance (λ) and lower evenness (J', $1-\lambda$). Site A1 had a slighter lower diversity, when compared with the other sandy sites. The muddy sediment sites were typically colonized by a small number of species that dominated the assemblages.

Table 3 – Main diversity, evenness and dominance indexes averaged per site. Diversity: Species richness (*S*), Mergalef's index (*d*), Shannon's indexes (*H* and *H'*) and Hill's numbers, (N_1, N_2 and N_∞). Evenness: Pielou's index (J') and inverted Simpson's index ($1-\lambda$). Dominance: Simpson's index (λ).

Index	A1	A2	A3	V1	V2	V3
S	48 ± 5	58 ± 7	63 ± 6	52 ± 9	30 ± 6	19 ± 4
d	10.1 ± 1.2	12.4 ± 1.5	13.4 ± 1.3	11.0 ± 2.1	6.5 ± 1.3	3.8 ± 0.9
H	4.35 ± 0.33	4.96 ± 0.18	4.96 ± 0.40	4.44 ± 0.82	2.94 ± 0.44	2.51 ± 0.30
H'	3.01 ± 0.23	3.43 ± 0.13	3.44 ± 0.27	3.08 ± 0.57	2.03 ± 0.31	1.74 ± 0.21
N_1	20.8 ± 5.4	31.3 ± 4.0	32.2 ± 7.9	24.3 ± 9.8	7.9 ± 2.1	5.8 ± 1.2
N_2	12.9 ± 4.5	20.9 ± 4.1	19.7 ± 7.6	14.9 ± 7.5	4.9 ± 1.5	4.3 ± 1.1
N_∞	6.0 ± 2.2	8.6 ± 1.9	7.2 ± 2.7	6.1 ± 2.8	2.9 ± 0.8	2.8 ± 0.8
J'	0.78 ± 0.04	0.85 ± 0.02	0.83 ± 0.05	0.78 ± 0.12	0.59 ± 0.08	0.60 ± 0.07
$1-\lambda$	0.92 ± 0.02	0.95 ± 0.01	0.94 ± 0.03	0.89 ± 0.12	0.77 ± 0.09	0.75 ± 0.07
λ	0.08 ± 0.02	0.05 ± 0.01	0.06 ± 0.03	0.11 ± 0.12	0.23 ± 0.09	0.25 ± 0.07

This spatial pattern can be seen more clearly when plotting the averaged ranked species-abundance dominance curves (Figure 9). The *k*-dominance curves of sites V2 and V3 have distinct logarithmic profile that contrasts with the almost semi-sinusoidal profile of the curves of the other sites. The logarithmic profile is an indication of *lower* diversity, given that a cumulative dominance of circa 80% is attained with only 5 species, in the muddy sites. The site A1 has the less semi-sinusoidal curve of the sandier sites.

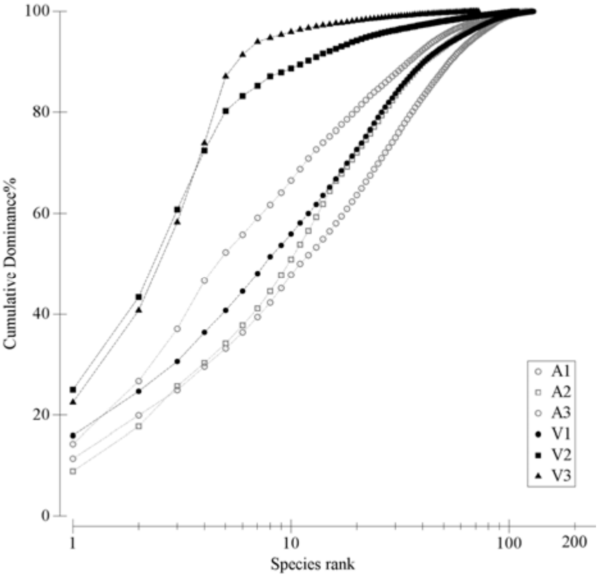

Figure 9 – *k*-Dominance curves. Diatom abundance samples averaged per site.

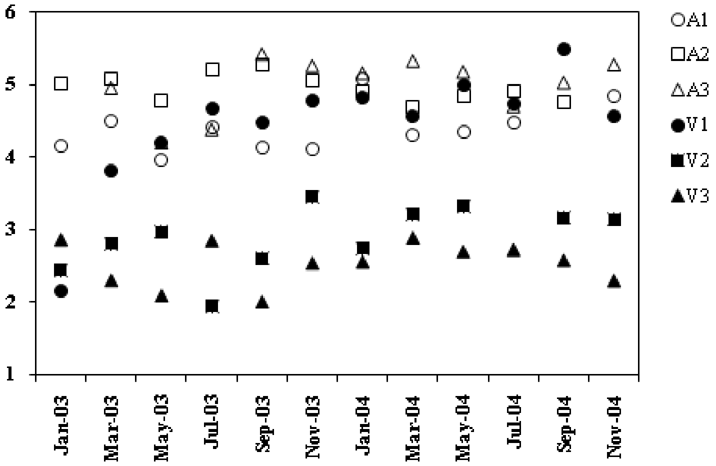

Figure 10 – Shannon's diversity index values (*H'*) during the study period in each of the six sampling stations.

There was no evident seasonal pattern in the variation of Shannon (*H'*) diversity index during the two-year sampling period (Figure 10). Sites A1, A2 and A3 ranged between 3.96 and 5.49, whereas sites V2 and V3 varied between 1.95 and 3.45 but there was no consistent increase or decrease in *H'* values in summer or winter samples in any of the sites. The only noteworthy evidence of a temporal shift was seen in the station V1, where after two months of lower values (January and March 2003), the diversity increased to values similar to the ones observed in the sandy transect sites. This shift mirrored the changes observed in mud content and salinity at site V1.

4.2. Diatom community structure: biotic and environmental multivariate patterns (ANOSIM, MDS, CLUSTER, BIOENV)

The two-way crossed ANOSIM (with no replicates) test revealed that differences in the structure of the diatom assemblages among sites were very important (R = 0.932, in an $R_{\max}$=1) and significant ($p < 0.01$ %); whereas the magnitude of the differences between sampling dates was much lower (R = 0.308) but still statistically significant ($p < 0.01$ %). This meant that both null hypotheses, *i.e.* "no site-to-site differences" (H_{01}) and "no sampling dates differences" (H_{02}), could be rejected and that a one-way ANOSIM test on *site* differences could not be performed. However, such a low value of the global test on the *time* effects implies that a global separation of the samples throughout the sampling period existed but was relatively weak.

Given the extremely high value of the R statistic obtained for the "no site differences" test, even if not precluding the "time differences", the SIMPER routine was performed to calculate the average similarity ($\overline{S}$) of the samples of each site, but also the average dissimilarity ($\overline{\delta}$) of all pairs of inter-site samples (Table 4). The average similarity percentages were above 70% in the three stations of the sandy transect, while the lowest intra-site similarity occurred in mudflat site V2 (58.6%). The stations A2 and A3 had the lowest inter-site dissimilarity (28%), followed by the pairs A1*vs.*A2 and A3*vs.*V1. The two mudflat sites (V2*vs.*V3) had intermediate inter-site dissimilarities (43%), which was also the case of the pairs V1*vs.*A1, V1*vs.*A2 and A1*vs.*A3. The highest dissimilarities were between the sandy stations (A1, A2, A3 and V1) and the muddy sites (V2 and V3).

Table 4 - SIMPER analysis. Values on the diagonal (light grey) are average similarity of diatom samples within each site $\overline{S}$ (%) and values below the diagonal (dark grey) are the average dissimilarity of sample between two sites $\overline{\delta}$ (%).

	A1	**A2**	**A3**	**V1**	**V2**	**V3**
A1	**70.5 %**					
A2	36%	**77.4 %**				
A3	43 %	28 %	**73.0 %**			
V1	52 %	43 %	37 %	**63.3 %**		
V2	80 %	77 %	66 %	58 %	**58.6 %**	
V3	89 %	86 %	76 %	67 %	43 %	**62.3 %**

Non-metric Multi-Dimensional scaling (MDS) ordination (Figure 11) and the hierarchical clustering dendrogram (Figure 12), based on root-root transformed densities and Bray-Curtis similarities for 94 diatom species (DS2), produced the same general multivariate pattern of the diatom samples from the six studied sites. Two very dissimilar groups can de distinguished: one grouping the 4 sandier sites (A1, A2, A3 and V1) and another grouping by the two muddy sites (V2 and V3). According to the SIMPER analysis, these two groups had an average intra-sample similarity of 62.4 % (sandy sites) and 58.7 % (muddy sites) and an average inter-group dissimilarity of 74.8 %, in an indication of the clear differences between two groups.

The stress value of the MDS ordination two-dimension plot (Figure 11) was 0.09, which corresponds to a good representation with no real prospect of misleading interpretation (Clarke and Warwick, 2001). Presenting an homogenous cluster in the left, the samples of site A1 are positioned closely to a more loose cluster composed by the samples of the sites A2, A3 and, finally, by samples of V1. Opposite to this main group, the other cluster aggregates the samples of the site V2 and, more to the right, site V3. The samples of these two muddy sites are more scattered about than the samples from the sandier sires, an evidence of lower intra-sample similarity. Positioned between these two main groups, there are two isolated samples of V1, corresponding to the assemblages of January (right) and March (left) 2003.

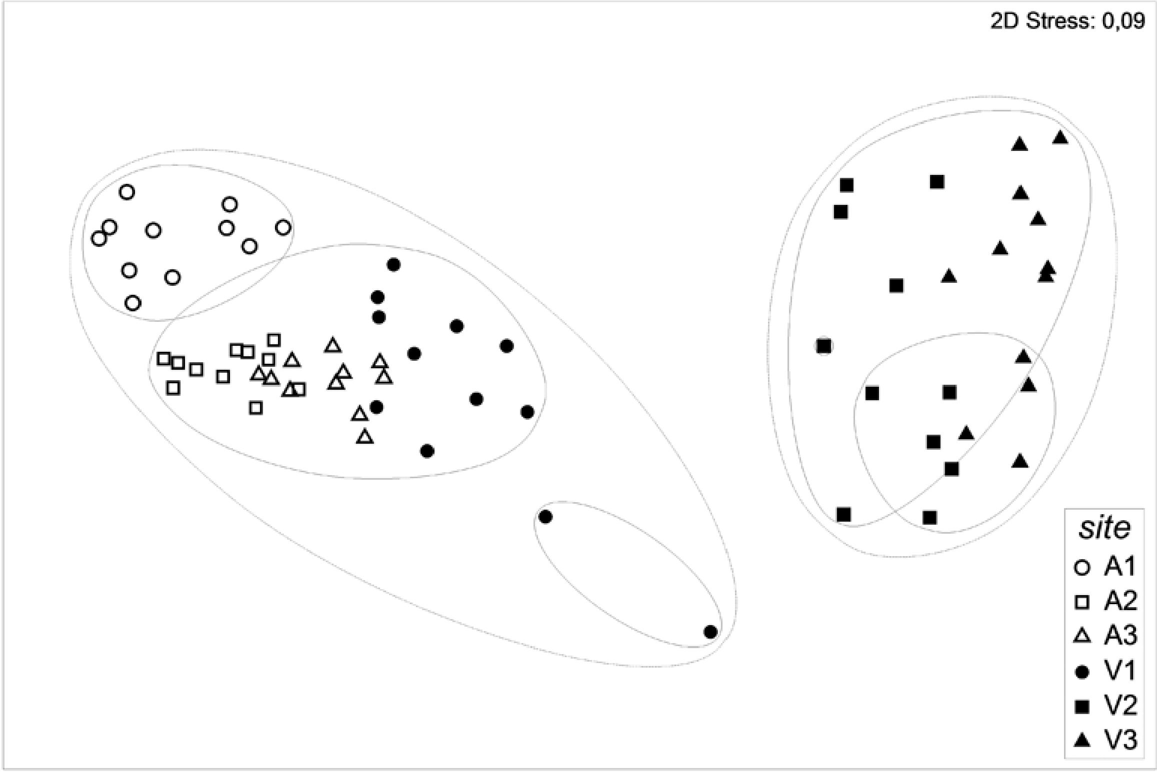

Figure 11 – Multidimensional scaling ordination (MDS) of the diatom assemblages from the six sampling sites. It was performed on standardized and root-root transformed abundance data. The two dimensional ordination has a stress value of 0.09. The two overlay lines aggregate clusters at the 28 % (inside lines) and 58 % (outside lines) Bray–Curtis similarity levels.

The SIMPROF test, associated to CLUSTER analysis (Figure 12), allows an objective selection of the groups and sub-groups of dendrogram, where each subdivision marked by dashed lines indicates a group of samples without further significant multivariate structure, thus establishing the boundary of permissible interpretation of the complex structure of the dendrogram. According to this analysis, there was evidence of further multivariate structure beyond the simple separation of the diatom samples per station, with the establishment of 9 groups of samples, 2 pairs and a singleton, at a SIMPROF test significance level of p<1%.The samples of the muddy sites (V2 and V3) split form the others at a very low similarity level. This separation had a very high test statistic ($\pi = 13.8$) at a very low significance level (p<0.1 %). A pair of isolated samples of V1, already singled out in the

MDS ordination (*i.e.* January and March 2003; Figure 11), also detached early from the samples of the sandy sites ($\pi = 5.1$, p<0.1%).

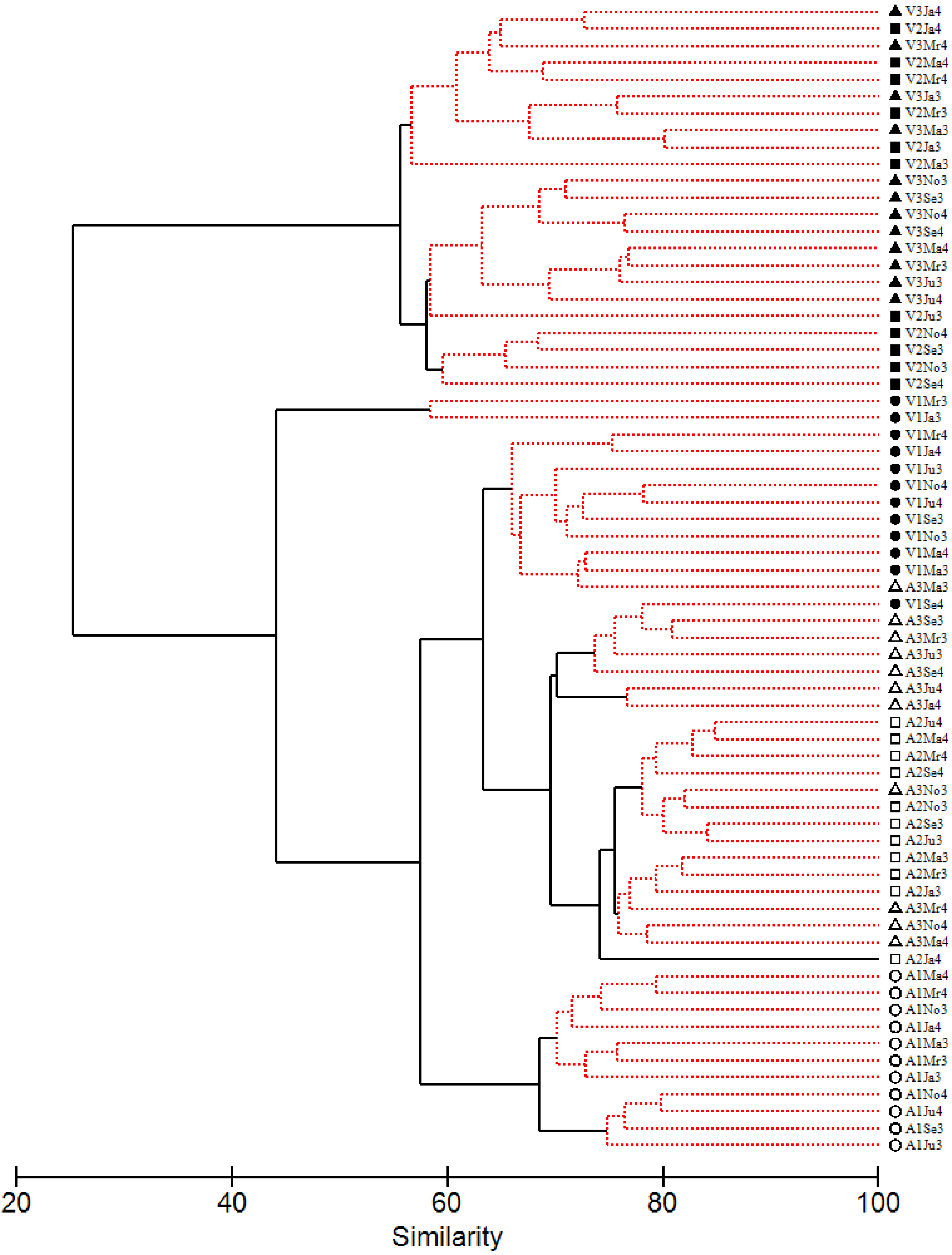

Figure 12 –Dendrogram for hierarchical clustering of diatom abundance samples of the studied sites using group average linking of Bray–Curtis similarities. Data previously standardized and root-root transformed. Grey dotted indicate non-significant clustering (SIMPROF test; significance level: p < 1%); the π-values of several nodes are referred in the text. Sampling stations: A1 (○); A2 (□); A3 (Δ); V1 (●); V2 (■); V3 (▲).

Around the 57% similarity level the Station A1 formed a separate group form the other sandy stations (π = 4.1, p<0.1%) but still further showed evidence of structure (π = 1.1, p<0.6%). Most of the samples from V1 split, later, from the samples from A2 and A3 (π = 3.0 p<0.1%) without further evidence of multivariate structure. On the contrary, the samples of the sites A2 and A3 (and one from V1) subdivided in more groups with still a significant multivariate structure (always with p<1% significance level) which composed of samples from different sites.

Regarding the assemblages of V2 and V3, the significant groupings were established at similarity levels around 58 % (π = 1.04, p < 0.6 %) and 55% (π = 1.55, p < 0.6 %) and were composed of samples from both sites. One group corresponded to the smaller smoothed convex hull in the MDS ordination (Figure 11, lower right) and comprised samples from January, March and May of both years, with the exception of two samples of V3. The other two groups mostly aggregated samples from July, September and November (the smallest one, only including 4 samples from V2). This evidence of a separation of mudflat diatom assemblages in winter-early spring and summer-autumn assemblages is not perceived in multivariate structuring of the samples from the sandy sites.

The results of a BIOENV analysis showed that sediment grain size composition can be considered as the main factor explaining the structure of the diatom assemblages found in this study (Table 5). The best fit between the diatom community patterns and a single environmental variable was achieved with the sediment's fraction of silt and clay, which had a very high correlation (ρ = 0.863, p < 0.1 %). Actually, the mud content alone was also the best "set" of variables and the only one present in all the 10 selections of variables with the highest correlations. Its importance can clearly be perceived when the samples' mud content is superimposed over the MDS ordination obtained from the diatom abundance data (Figure 13). Other high correlation sets of variables included several sediment fractions (*e.g.* medium sand and coarse sand), sometimes associated with tidal height. Most of the sediment fractions and the tidal height had much higher individual correlations than any of the other environmental variables, such as nutrients concentration or salinity (Table 6).

Table 5 – Correlations (ρ) of the ten best environmental variable selections with the diatom abundance data matrix, using the BIOENV routine. Global match permutation test significance level $p < 0.01\%$ (999 random permutations).

Nº of variables	**ρ**	**Selections of variables**
1	**0.863**	Mud
4	**0.847**	Tidal height; Coarse sand; Medium sand; Mud
3	**0.842**	Tidal height; Medium sand; Mud
4	**0.836**	Coarse sand; Medium sand; Fine sand; Mud
3	**0.830**	Medium sand; Medium sand; Mud
5	**0.809**	Tidal height; Temperature; Coarse sand ; Medium sand; Mud
5	**0.806**	Temperature; Coarse sand; Medium sand; Fine sand; Mud
5	**0.803**	Tidal height ; Salinity; Coarse sand; Medium sand; Mud
5	**0.803**	Tidal height; Light; Coarse sand; Medium sand; Mud
5	**0.801**	Light ; Coarse sand; Medium sand; Fine sand; Mud

Table 6 – BIOENV routine correlations of individual environmental variables with the diatom abundance matrix. Global match permutation test significance level $p < 0.01\%$ (999 random permutations).

Variable	**ρ**	**Variable**	**ρ**	**Variable**	**ρ**
Mud	0.863	Very coarse sand	0.191	Very fine sand	-0.001
Medium sand	0.723	SiO_2	0.188	Salinity	-0.003
Coarse sand	0.451	Total N	0.053	Temperature	-0.011
Fine sands	0.435	NO_2^-	0.049	Light	-0,024
Tidal height	0.293	NH_4^+	0.025	PO_3^{+4}	-0.042

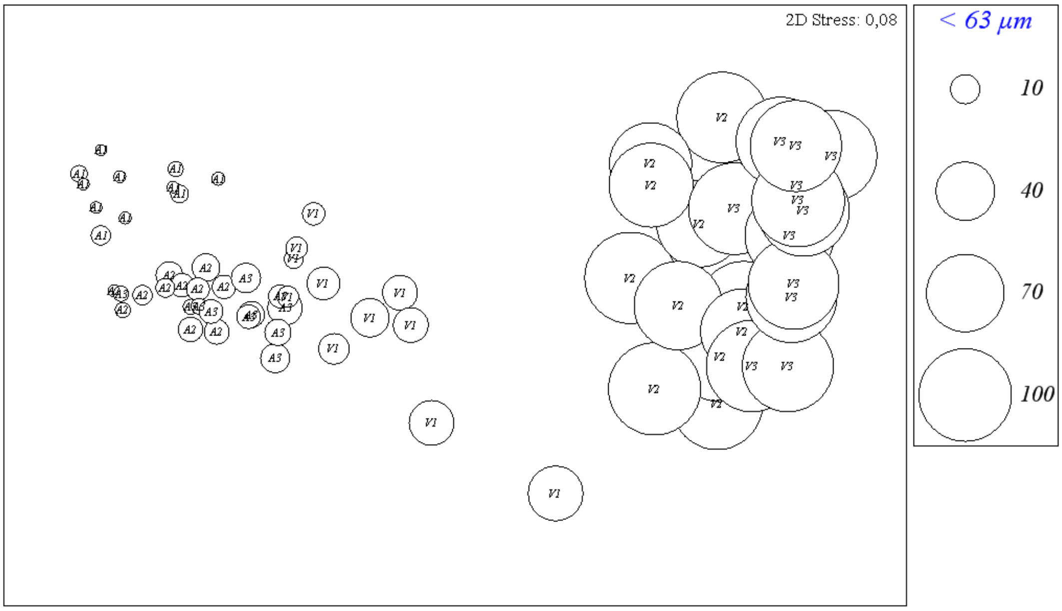

Figure 13 – Bubble plot. Sediment mud content superimposing the MDS ordination of the diatom assemblages (see Figure 8). Larger circles represent a larger percentage of the mud fraction

4.3. Diatom community structure: taxonomic composition of the assemblages (SIMPER)

The examination of the individual contributions of each species to average sample similarity in each of the 6 sites (Table 7), but also to all 15 inter-site dissimilarities (Table 8), allowed to highlight the diatom taxa most responsible for the multivariate patterns and assemblage structure. The following remarks can be made:

1. The sites A1, A2, A3 (and to some extent, V1) had many epipsammic species in common. A typically diverse group of small-sized *Navicula* (*e.g. N. viminoides*; *N. aleksandrae*; *N. germanopolonica*; *N. bozenae; Navicula* sp.2) was accompanied by other biraphid species like *Nitzschia frustulum*, *Biremis lucens*, *Amphora* cf. *tenuissima*, *Cocconeiopsis breviata*, *Fallacia* spp. (*e.g. F. florinae*, *F.*cf. *teneroides*) and finally, *Catenula adhaerens* and *Catenula* sp. 1. Monoraphid taxa like *Planothidium* (*e.g.* different morphotypes of *P. delicatulum*) and *Cocconeis* (*e.g. C. hauniensis*, *C. peltoides* and *C. pelta*) were also important.

2. In the sandy transect, the assemblages of A1 diverged from the assemblages of A2 and A3 for three main reasons. The first was the much more relevant presence of araphid species, especially from the genus *Opephora* (*e.g. O. guenter-grassii*, *Opephora* sp.1) in the site A1. Secondly, to differences in the spatial distribution of several common species, such as some small motile epipsammic species (*e.g. N. germanopolonica*; *N. bozenae*) that had particular higher contributions to the average intra-site similarity in A1 samples, or *Navicula* sp.2 and *N.* cf. *aleksandrae* in the samples from A2 and A3. Thirdly, the existence of several epipelic species in A2 and A3 was also noteworthy. Although not as important to the overall assemblage structure as the epipsammic taxa, the co-occurrence of motile epipelic species like *Navicula* cf. *phyllepta*, *N. gregaria* m.1, *Cylindrotheca closterium*, *Dickieia sp.1* and *Gyrosigma fasciola* further contributed to the distinction of the assemblages of A2 and A3 from the diatom assemblages found in A1 samples (Table 8) . Minor differences in the abundance of epipelic species were the main cause of the dissimilarities between the two down shore sites (Table 8, A2*vs.*A3).
3. The assemblages in site V1 were similar to ones encountered in A2 and A3. Composed mostly by the same taxa, the assemblages of these 3 sites differed in the relative contributions of each species. But in fact, the muddy sandy sediments of station V1 were actually dominated numerically by epipelic species (Figure 16). The constant presence of epipsammic species was responsible for augmenting intra-site average similarity in V1 (Table 7) and separating those assemblages from the ones found in V2 and V3 (Table 8).
4. The assemblages of the muddy sites V2 and V3 were completely dominated by motile epipelic species of the genus *Navicula* (*e.g. N. spartinetensis*, *N. gregaria*, *N.* cf. *phyllepta*), *Cylindrotheca* (*C. closterium* and *C.* cf. *gracilis*) and *Gyrosigma* (*e.g. G. acuminatum* and G. *fasciola*). *Nitzschia* cf. *aequorea*, *N.* cf. *parvula*, *Plagiotropis vanheurckii* apiculata were also important but had much lower percentages of contribution to intra-site average similarity (*i.e.* below 5%, Table 7). Apart from the motile taxa, tychoplanktonic species like

A1				A2				A3			
N. viminoides	4.1	9.1	5.7	*N. aleksandrae*	3.1	10.4	4.0	*B. lucens*	2.9	11.9	3.9
N. frustulum	4.0	9.2	5.6	*N. viminoides*	2.9	12.4	3.8	*N.. aleksandrae*	2.4	11.6	3.3
N. bozenae	3.8	10.6	5.3	*B. lucens*	2.9	9.3	3.8	*N. gregaria* m.1	2.3	2.8	3.2
N. germanopolonica	3.4	6.5	4.8	*A.* cf. *tenuissima*	2.6	10.8	3.3	*A.* cf. *tenuissima*	2.1	8.2	2.9
P. delicatulum m. 2	3.1	6.5	4.5	*P. delicatulum* m.2	2.5	13.8	3.2	*C. breviata*	2.1	8.0	2.8
P. delicatulum m. 1	2.8	8.9	4.0	*C. hauniensis*	2.4	9.9	3.2	*N. viminoides*	2.1	14.0	2.8
B. lucens	2.5	9.0	3.6	*N. frustulum*	2.4	12.6	3.2	*F.* cf. *teneroides*	2.0	9.9	2.8
A. cf. *tenuissima*	2.5	5.0	3.5	*P. delicatulum* m.1	2.3	6.2	3.0	*N. frustulum*	2.0	8.0	2.7
F. florinae	2.5	8.2	3.5	*F.* cf. *teneroides*	2.3	8.5	3.0	*N.* cf. *phyllepta*	1.9	4.7	2.6
O. guenter-grassii	2.4	5.9	3.5	*N.* cf. *aleksandrae*	2.3	7.9	3.9	*N.* cf. *aleksandrae*	1.8	13.1	2.5
V1				V2				V3			
N. cf. *phyllepta*	3.6	4.6	5.7	*N. spartinetensis*	7.2	6.2	12.3	*N. spartinetensis*	10.0	7.7	16.1
B. lucens	2.9	7.9	4.6	*N.* cf. *phyllepta*	6.6	5.9	11.2	*G. fasciola*	9.6	7.5	15.3
N. gregaria m. 1	2.9	3.4	4.5	*G. fasciola*	6.5	6.2	11.1	*C. signata*	9.2	3.7	14.8
N. spartinetensis	2.6	4.9	4.1	*N. gregaria* m. 1	5.7	4.1	9.6	*N.* cf. *phyllepta*	8.4	6.3	13.5
G. fasciola	2.5	2.9	4.0	*C. signata*	4.0	1.8	6.8	*N. gregaria* m. 1	7.4	4.0	11.9
A. cf. *tenuissima*	2.5	8.9	3.9	*C. closterium*	3.4	1.9	5.8	*C. closterium*	3.1	1.0	5.0
C. breviata	2.1	5.1	3.3	*N.* cf. *aequorea*	2.8	1.9	4.8	*Navicula* sp.3	2.7	1.0	4.3
P. delicatulum m.1	2.1	6.5	3.3	*P. minima*	2.5	2.0	4.3	*G. acuminatum*	2.4	1.1	3.9
P. delicatulum m.2	2.0	5.8	3.2	*N.* cf. *parvula*	2.4	1.3	4.1	*P. vanheurckii*	1.9	0.8	3.0
C. hauniensis	2.0	6.5	3.2	*T. pseudonana*	2.3	2.0	4.0	*T. pseudonana*	1.5	0.9	2.4
Species	$\bar{S}_i$	$\bar{S}_i$/SD	%	*Species*	$\bar{S}_i$	$\bar{S}_i$/SD	%	*Species*	$\bar{S}_i$	$\bar{S}_i$/SD	%

Table 7 - SIMPER analysis. The most contributing species of intra-site similarities are reported with their average similarity, *Si*, ratio values, *Si* / SD(*Si*), and percentage of contribution to the average intra-group similarity (%).

A1 & A2				A1 & A3				A2 & A3				A1 & V1				A2 & V1			
O. guenter-grassii	1.1	2.7	3.1	*O. guenter-grassii*	1.2	3.6	2.8	*C. closterium*	0.8	1.4	2.8	*N.* cf. *phyllepta*	1.6	1.7	3.1	*N.* cf. *phyllepta*	1.2	1.5	2.9
Navicula sp.2	1.0	2.9	2.7	*N. gregaria* m.1	1.0	1.5	2.3	*N. gregaria* m.1	0.8	1.4	2.7	*N. bozenae*	1.6	3.5	3.1	*G. fasciola*	1.0	1.7	2.3
N. cf. aleksandrae	0.9	1.9	2.6	*C. closterium*	1.0	1.5	2.2	*N.* cf. *phyllepta*	0.6	1.3	2.2	*N. germanopolonica*	1.6	2.6	3.0	*N. bozenae*	1.0	2.4	2.3
N. diserta	0.9	1.9	2.5	*Dickieia* sp.1	1.0	1.7	2.2	*G. fasciola*	0.6	1.4	2.1	*G. fasciola*	1.4	2.4	2.7	*N. viminoides*	0.9	1.5	2.2
Dickieia sp.1	0.8	1.5	2.2	*Cavinula* sp.1	0.9	2.7	2.2	*Dickieia* sp.1	0.6	1.4	2.1	*N. viminoides*	1.3	1.8	2.5	*N. diserta*	0.9	1.7	2.2
Opephora sp.1	0.8	1.8	2.2	*N.* cf. *phyllepta*	0.9	1.8	2.1	*N. spartinetensis*	0.6	1.4	2.0	*O. guenter-grassii*	1.3	2.8	2.4	*N. spartinetensis*	0.9	1.8	2.1
N. germanopolonica	0.8	1.7	2.1	*N. bozenae*	0.8	3.1	2.0	*N. gregaria* m.2	0.6	1.3	2.0	*N. spartinetensis*	1.3	2.7	2.4	*P. vanheurckii*	0.9	1.6	2.1
H. caotica	0.8	3.0	2.1	*H. caotica*	0.8	2.3	2.0	*N. arenaria*	0.6	1.3	2.0	*N. frustulum*	1.0	1.8	2.0	*C.* cf. *hauniensis*	0.8	3.5	2.1
A. cf. *fogedii*	0.8	2.0	2.1	*N. spartinetensis*	0.8	2.1	1.9	*P. vanheurckii*	0.6	1.5	2.0	*C. closterium*	1.0	1.6	1.9	*C. closterium*	0.9	1.5	2.0
P. cf. *perminuta*	0.8	2.0	2.0	*G. fasciola*	0.8	1.7	1.9	*S. salina*	0.5	1.0	1.9	*N. gregaria* m.1	1.0	1.5	1.9	*F.* cf. *scaldensis*	0.8	2.7	1.9
A3 & V1				**A1 & V2**				**A2 & V2**				**A3 & V2**				**V1 & V2**			
H. caotica	0.8	2.5	2.1	*N. spartinetensis*	2.7	3.5	3.4	*N. spartinetensis*	2.1	2.7	2.8	*B. lucens*	1.9	4.7	2.9	*B. lucens*	1.9	3.7	3.3
Dickieia sp.1	0.7	1.3	2.0	*G. fasciola*	2.5	3.8	3.2	*B. lucens*	1.9	4.3	2.5	*N. aleksandrae*	1.4	3.3	2.2	*A. cf. tenuissima*	1.5	3.5	2.6
N. flagellifera	0.7	1.3	2.0	*N. viminoides*	2.5	4.0	3.1	*N. viminoides*	1.9	3.6	2.5	*A. cf. tenuissima*	1.4	3.7	2.2	*C. hauniensis*	1.3	2.9	2.3
N. germanopolonica	0.7	1.9	1.9	*N. germanopolonica*	2.4	5.4	3.0	*G. fasciola*	1.9	2.5	2.5	*N. viminoides*	1.3	3.0	2.0	*P. delicatulum* m.1	1.2	2.3	2.1
N. diserta	0.7	1.5	1.8	*N. bozenae*	2.3	4.9	2.9	*N. aleksandrae*	1.8	4.1	2.4	*N. spartinetensis*	1.3	2.3	2.0	*P. delicatulum* m.2	1.2	2.4	2.1
P. vanheurckii	0.7	1.5	1.8	*N.* cf. *phyllepta*	2.2	2.0	2.7	*C. signata*	1.7	2.2	2.2	*F.* cf. *teneroides*	1.3	3.1	2.0	*C.* cf. *placentula*	1.2	1.9	2.1
N. cf. *phyllepta*	0.7	1.2	1.8	*N. frustulum*	1.9	2.9	2.4	*A.* cf. *tenuissima*	1.7	4.1	2.2	*C. breviata*	1.3	2.3	1.9	*Catenula* sp.1	1.2	2.4	2.1
S. salina	0.7	1.2	1.8	*P. delicatulum* m.2	1.9	3.4	2.3	*N.* cf. *phyllepta*	1.6	1.8	2.1	*Cavinula* sp.1	1.3	3.6	1.9	*C. breviata*	1.2	2.0	2.1
N. cf. *parvula*	0.6	1.1	1.8	*C. signata*	1.9	2.2	2.3	*C. hauniensis*	1.6	4.1	2.1	*Catenula* sp.1	1.2	3.9	1.9	*C. signata*	1.2	1.5	2.0
N. arenaria	0.6	1.3	1.8	*O. guenter-grassii*	1.8	4.9	2.2	*C. adhaerens*	1.6	5.4	2.0	*G. fasciola*	1.2	1.5	1.9	*N. flagellifera*	1.1	1.1	1.9
A1 & V3				**A2 & V3**				**A3 & V3**				**V1 & V3**				**V2 & V3**			
C. signata	3.0	3.4	3.4	*C. signata*	2.7	3.4	3.1	*B. lucens*	2.2	6.4	2.9	*B. lucens*	2.2	4.7	3.3	*C. signata*	1.8	1.1	4.1
N. viminoides	2.9	5.9	3.3	*N. viminoides*	2.3	5.3	2.6	*C. signata*	2.1	2.0	2.3	*C. signata*	2.0	1.9	2.9	*N.* cf. *parvula*	1.6	1.3	3.6
G. fasciola	2.9	4.4	3.3	*B. lucens*	2.2	5.8	2.6	*C. breviata*	1.7	4.5	2.2	*A.* cf. *tenuissima*	1.7	3.8	2.5	*Navicula* sp.3	1.5	1.3	3.5
N. frustulum	2.8	6.2	3.2	*N. spartinetensis*	2.2	3.1	2.5	*F.* cf. *teneroides*	1.7	8.0	2.2	*P. delicatulum* m.1	1.7	5.5	2.5	*C. closterium*	1.5	1.4	3.5
N. spartinetensis	2.8	4.4	3.2	*G. fasciola*	2.2	2.8	2.5	*N. viminoides*	1.6	5.3	2.1	*C. breviata*	1.7	3.8	2.5	*N.* cf. *aequorea*	1.5	1.5	3.5
N. bozenae	2.8	9.6	3.1	*N. aleksandrae*	2.0	3.1	2.3	*A.* cf. *tenuissima*	1.6	4.0	2.1	*P. delicatulum* m.2	1.7	5.7	2.5	*G. acuminatum*	1.3	1.4	3.0
N. germanopolonica	2.7	5.4	3.0	*C. hauniensis*	1.9	9.1	2.2	*N. aleksandrae*	1.6	2.6	2.1	*C. hauniensis*	1.6	6.1	2.5	*P. minima*	1.3	1.5	2.9
P. delicatulum m.2	2.4	6.3	2.7	*A.* cf. *tenuissima*	1.9	4.5	2.2	*N. frustulum*	1.5	4.6	2.0	*Catenula* sp.1	1.4	2.8	2.1	*S. lucens*	1.2	1.2	2.9
N. cf. *phyllepta*	2.2	2.0	2.5	*P. delicatulum* m.2	1.9	10.8	2.2	*N.*cf. *aleksandrae*	1.5	8.4	2.0	*N. frustulum*	1.4	2.6	2.0	*T. apiculata*	1.2	1.4	2.7
P. delicatulum m.1	2.1	7.5	2.4	*F.* cf. *teneroides*	1.9	7.5	2.1	*Cavinula* sp.1	1.5	5.7	1.9	*C.* cf. *placentula*	1.3	1.8	2.0	*N. gregaria* m.1	1.1	1.4	2.6
Species	$\overline{\delta}_i$	$\overline{\delta}_i$/SD	%	Species	$\overline{\delta}_i$	$\overline{\delta}_i$/SD	%	Species	$\overline{\delta}_i$	$\overline{\delta}_i$/SD	%	Species	$\overline{\delta}_i$	$\overline{\delta}_i$/SD	%	Species	$\overline{\delta}_i$	$\overline{\delta}_i$/SD	%

Table 8 - SIMPER analysis. The most contributing species for inter-site dissimilarities are reported with their average dissimilarity ($\overline{\delta}_i$), $\overline{\delta}_i$ /SD ratio values and percentage of contribution to the average intra-group dissimilarity.

Thalassiocyclus lucens and several *Thalassiosira* spp. also had relevant contributions to intra-site similarity in the mudflat stations. Only 10 taxa contributed for the most part of the intra-site similarity (74 % in V2; 91 % in V3) and most of the epipsammic taxa were absent in these assemblages or had extremely low abundances. The slight differences between V2 and V3 assemblages were caused by differences in the relative contributions of a restricted number of species. For example, *Cylindrotheca* cf. *gracilis* was more abundant in V3 than in V2, whereas the opposite happened to *Nitzschia* cf. *parvula*.

4.4. Diatom community physiognomy: spatial distribution of size-classes, functional-groups and life-forms

4.4.1. Size-classes

With an average cell volume of only 22 µm^3, *Lunella* cf. *garyae* was the smallest diatom encountered. The largest one was *Gyrosigma balticum*, with an average biovolume 244295 µm^3 (see section 7.1.3.). When the relative abundances of each species (averaged per site) were allocated to one of the four size classes, clear differences could be seen between assemblages of the sandier sites and of the muddy sites (Figure 14).

In the sandy transect, the assemblages were mainly composed of small-sized diatoms (classes A and C), but with an increase of medium and large species in sites A2 an A3. This caused by a greater contribution of medium sized and larger motile epipelic species (*e.g. N. gregaria*, *S. salina*). This left-skewed size distribution reflected the importance, in the sandy sediments, of the small-sized species of the genus *Navicula*, *Fallacia*, *Planothidium* and *Amphora*. A completely different diatom size distribution was present in the assemblages of the muddy sites (V2 and V3). The size-class A (*i.e.* < 100 µm^3) was almost inexistent and the most important contribution was given by species of size-classes B (*i.e.*100 – 250 µm^3), C (*i.e.* 250 – 1000 µm^3) and D (*i.e.* > 1000 µm^3).

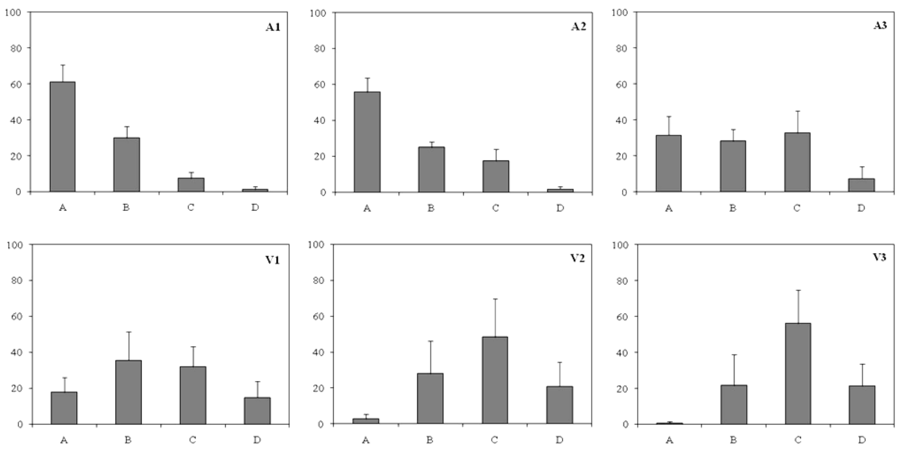

Figure 14 - Size-class distribution in the six studied sites. Average relative abundance of 4 size-classes: A (< 100 µm^3); B (100 – 250 µm^3); C (250 – 1000 µm^3) and D (> 1000 µm^3).

In these sites, these classes were mainly represented by small and medium sized species of the genus *Navicula*, *Cylindrotheca* and the large species of *Gyrosigma*, *Plagiotropis* and *Surirella*. Site V1 had an intermediate size-class distribution and somewhat similar to site A3. In both sites, the small epipsammic species co-occurred with the medium-sized and large motile epipelic species. Finally, regarding size-classes B and C, there was a taxonomic shift from the sandy sites to the muddy sites. *Navicula* cf. *phyllepta* and *Cylindrotheca closterium* dominated size class B in the mudflat sites but also in V1 and A3. In sites A1 and A2, *N. germanopolonica*, *P. delicatulum* m.1 were the most important species of size-class B. Considering the medium sized diatoms (*i.e.* size-class C), *Biremis lucens* was very important in the sandy sites, but disappeared in sites V2 and V3, which were dominated by *Cylindrotheca signata*, *Navicula gregaria* and *Navicula spartinetensis*.

The species diversity was not constant across the size-spectrum in most sites (Figure 15). The fractions of the diatom assemblages corresponding to the very small and small diatoms (size-classes A and B) were more diverse than the fractions of the other size-classes. This was particularly evident the sandy stations and less so in the mudflat stations (*i.e.* V2 and V3), where the smaller diatoms became less diverse and abundant. Even though the differences were less obvious, the diversity of size-classes C (*i.e.*250 – 1000 µm^3) and D (*i.e.* > 1000 µm^3) were slightly higher, in average, in the sandy sites.

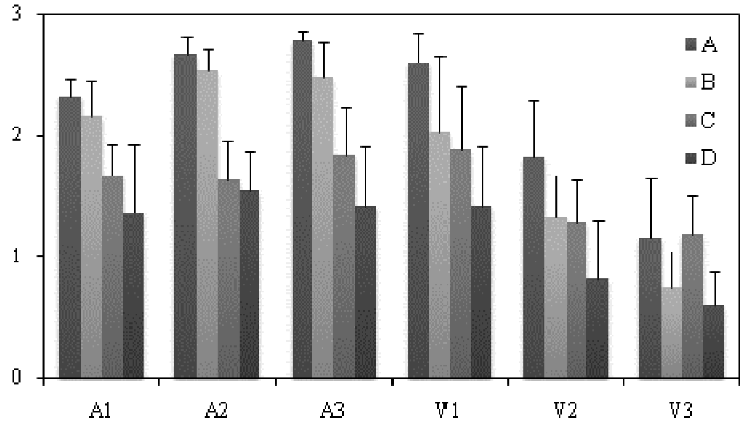

Figure 15 – Shannon's diversity index values (*H'*) of 4 size-class fractions in each sampling station during the study period. Biovolume range of each class: A (< 100 μm^3); B (100 – 250 μm^3); C (250 – 1000 μm^3) and D (> 1000 μm^3).

4.4.2. Functional groups and Life-forms

The differences between muddy and sandy sites were also very clear when the ecology of each diatom species was considered. Figure 16 (top) displays the relative proportions of the cumulative abundances of the epipsammic and epipelic species along the 6 studied sites. These two function-groups represented, in average, 97.5 to 99.5 % of the total number of diatoms present in each station. The sandy stations A3 and V1 contrasted with the other two sandy stations by having a much larger epipelic fraction, which even dominated the diatom assemblages in V1. The stations A3 and V1 had higher average mud content than the other sandy stations (7.7 and 13.5 %, respectively). The larger size of these species greatly accentuated the relative contribution of epipelic fraction to total biovolume at each site (Figure 16, bottom). The cumulative biovolume of the epipelon was almost equal to the epipsammon in A2 and completely dominant in site A3, even if the epipelic diatoms were much less abundant than the epipsammic taxa in those sites.

The differences between muddy and sandy stations were also very evident when the relative abundance of each life-form was considered (Figure 17). In the mudflat stations (V2 and V3), the assemblages were almost completely composed by medium and large motile species. In both sites, the group Mo<20pl roughly corresponds taxonomically to size class B and group Mo>20 to the sum of size-classes C and D (see above, Figure 14).

The diatom assemblages of the sandy sites showed a wider variety of life-forms and, in addition, had different distributions of those life-forms in each station. Station A1, for example, was dominated by small motile diatoms (*e.g. Navicula germanopolonica*) and it had a small contribution of staked species (*e.g. Opephora guenter-grassii*), a lifeform that was almost absent in the other stations. The minute epipelic fraction in stations A1 and A2 was almost entirely composed of large motile biraphid diatoms (*e.g. Dickieia* sp.1). In stations A3 and V1, the lower abundances of small motile epipsammic diatoms were replaced by a larger presence of large motile epipelic taxa. The adnate life-form was the only one which had relatively constant abundance in all 4 sandy stations.

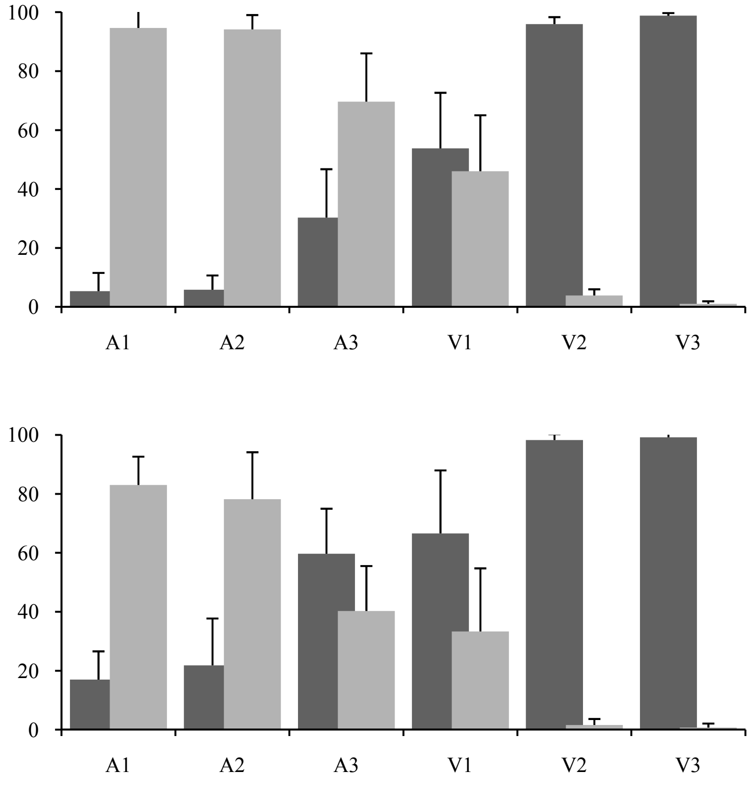

Figure 16 – Average relative abundances (top) and average contributions to total biovolume (bottom) of the epipelic (dark grey) and epipsammic (light grey) fractions of the diatom assemblages in the six studied sites.

All the other life forms had very low average abundances. For example, epiphytic or tube-dwelling taxa (*e.g. Parlibellus, Berkeleya*) appeared mainly in sites A2 and A3 but never surpassed the 0.8 % of total average abundance. Most of the counts scored refer to tychoplanktonic diatoms (*e.g. Thalassiocyclus lucens, Cymatosira belgica*). The presence of planktonic and tychoplanktonic was mainly recorded in the muddy transect, reflecting the higher deposition conditions of those sites but the truly planktonic species were extremely rare.

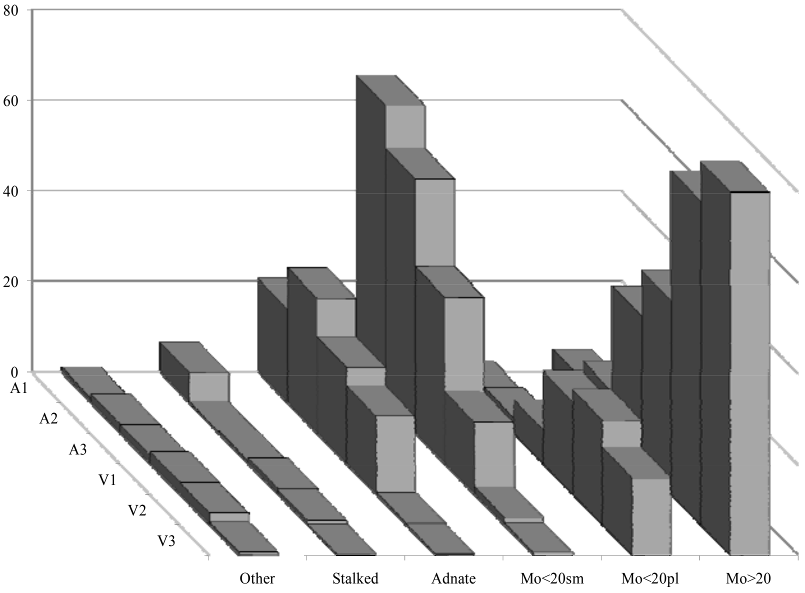

Figure 17 – Average relative abundances of Diatom life-forms in the six studied sites. Motile pennate diatoms were divided in 3 length classes: Epipsammic with less than 20 µm (Mo<20sm); Epipelic with less than 20 µm (Mo<20pl) and Epipelic with more than 20 µm (Mo>20). Stalked and adnate diatoms are also represented, whereas the abundances of plankton, tychoplankton and other life-forms were merged in a single column (Other). Standard deviation is not shown for visual clarity.

4.5. Temporal variation of diatom assemblages and individual species

The multivariate analysis detected some temporal variation of the diatom assemblages underpinning the much more obvious spatial variation (see section 4.2).The examination of the changes in relative abundance of some of the most important species found in each

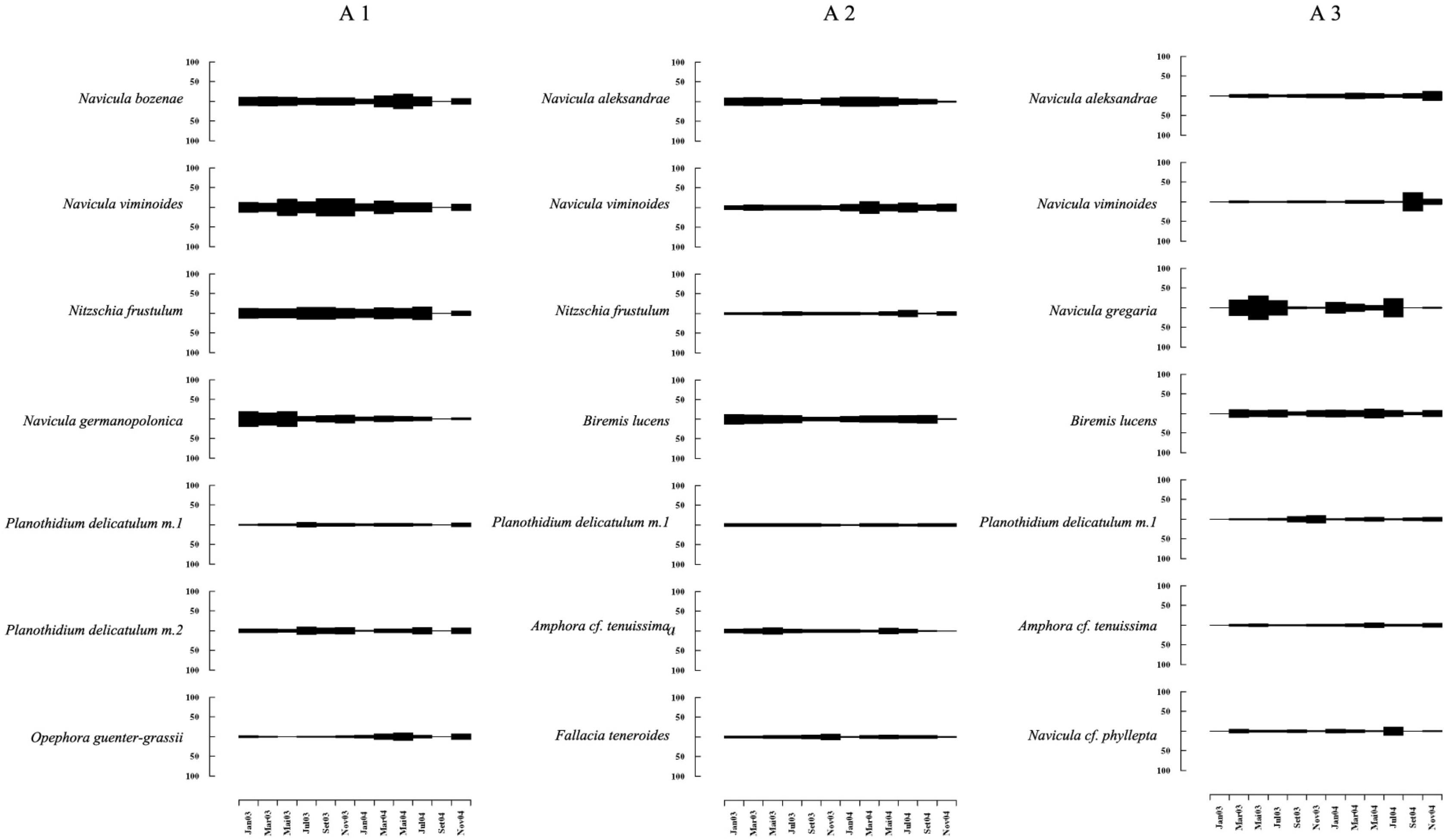

Figure 18 – Temporal variation of dominant diatom species of at sites A1, A2 and A3. Values represent percentages values relative to the entire assemblage.

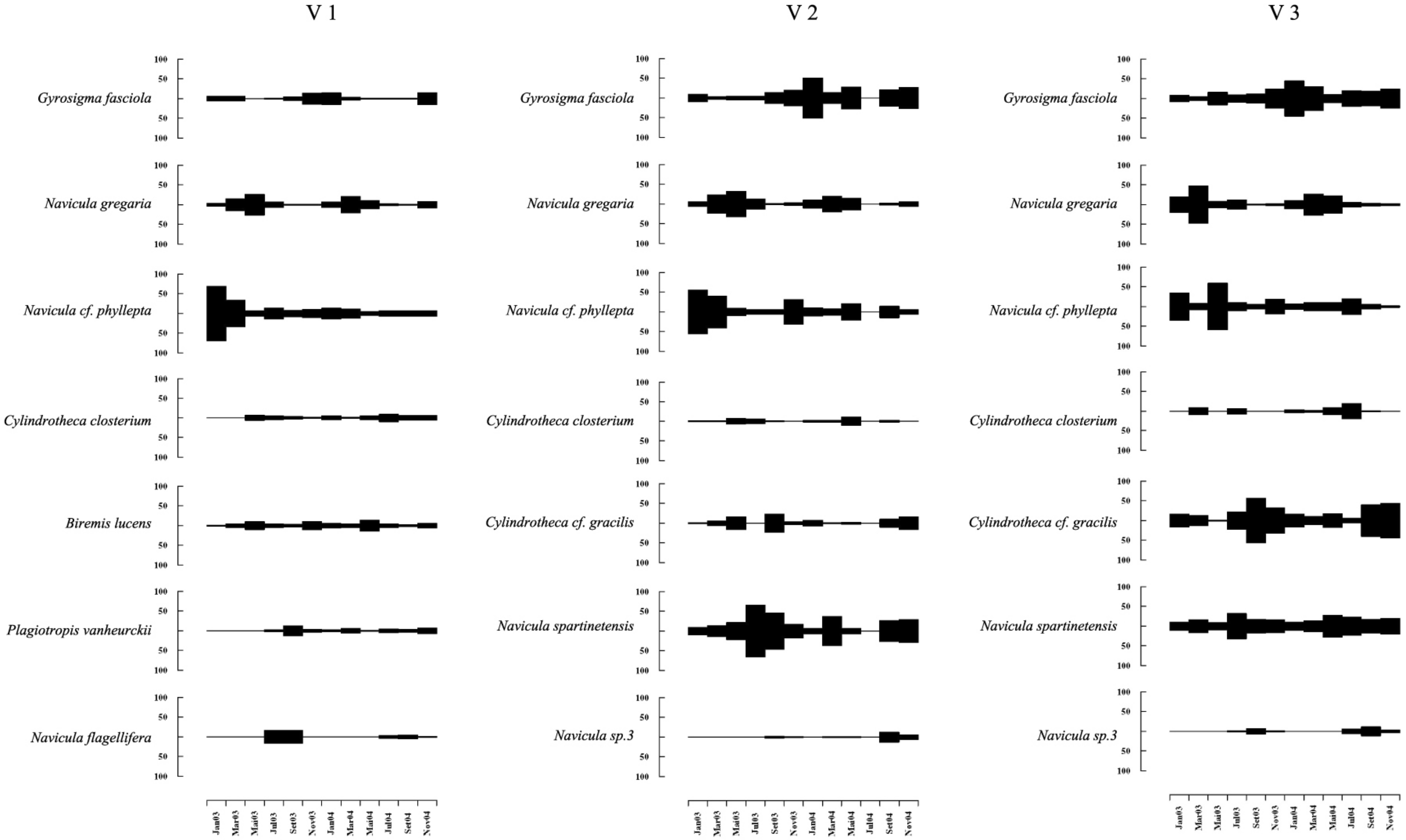

Figure 19 – Temporal variation of dominant diatom species of at sites V1, V2 and V3. Values represent percentages values relative to the entire assemblage

site, during the two years of sampling (Figures 18 and 19) demonstrated that the taxa belonging to the epipelon exhibit clear temporal (and seasonal) patterns, in sharp contrast to the much more slight variation in abundances of the epipsammic diatoms.

The epipsammic species persisted throughout the seasons in more stable numbers. Species like *B. lucens*, *N. viminoides*, *N. frustulum* or *P. delicatulum* (Figure 18) showed minimal changes in their relative abundance, during the studied period. This also reflected the multivariate analysis results. Higher intra-site similarity and lower point dispersion in the MDS plot (Figure 11) are consequences of this lack of seasonal patterns in the sandy sites assemblages. In fact, CLUSTER analysis of the samples of the sandy site, that included only epipsammic taxa, failed to find any significant multivariate structure (SIMPROF test: $\pi= 4.3$, sig. level: $p < 0.1$ %), beside the separation between A1 samples and the ones from other two sites (Figure 20, but compare also to Figure 12). The epipelic species, regardless if they were found muddy or sandy sediments exhibited much more perceptible temporal patterns. *Navicula gregaria* m.1 and *C. closterium* were two examples, showing obvious seasonal patterns, with regular synchronous blooms in spring/early summer, either it the sandy sites A3 and V1 or in the muddy transect sites V2 and V3). The other abundant epipelic taxa present in site V1 (muddy sand), even if they did not dominated the assemblage, also had smaller but punctuated seasonal peaks (Figure 19).

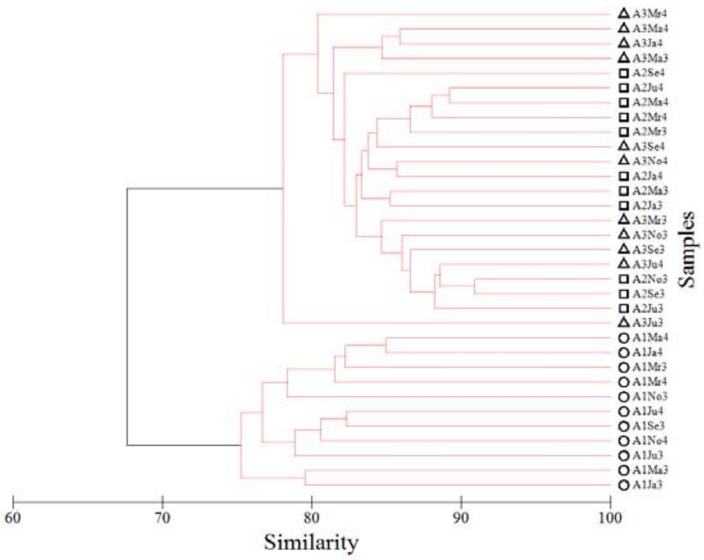

Figure 20 – Dendrogram for hierarchical clustering of epipsammic diatoms abundance samples of the sandy transect sites using group average linking of Bray–Curtis similarity. Data previously standardized and root-root transformed. Dotted grey lines indicate non-significant clustering (SIMPROF test; sig. level: $p < 0.1$ %). Sampling stations: A1 (○); A2 (□); A3 (Δ);

During the two year survey there was a perceptible and parallel succession of epipelic species replacing themselves in the dominance of the assemblages, in the mudflats sites V2 and V3 (Figure 19). In 2003, an initial dominance of *N.* cf. *phyllepta* was replaced, gradually, by a mixed assemblage of *N. gregaria* m.1, *C. closterium* and *N. spartinetensis*. Towards the end of the year, *C.* cf. *gracilis* and *G. fasciola* became increasingly important. In 2004, *N.* cf. *phyllepta* was much less abundant than in the preceding year and the winter assemblage was composed mainly by *G. fasciola*. This dominance was again replaced by *N. gregaria*, *N. spartinetensis* and *C. closterium* during spring/summer and *C.* cf. *gracilis* and *G. fasciola* reappeared in great numbers, later in the year. These abrupt shifts in the relative abundances of the epipelic species may explain the higher point dispersion of the mudflat assemblage samples in the multivariate space, suggested by the CLUSTER, MDS and SIMPER analysis (section 4.2.). The clustering in winter/spring *vs.* summer/autumn assemblages reflected the succession described above. The domination of *N.* cf. *phyllepta* in the first months of sampling was the main cause of the low diversity values registered in V2, V3 and especially in V1. Its decline in 2004, together with the relative increase of *G. fasciola*, seems to indicate that there was also inter-annual variation.

Chapter 5

Discussion

5. Discussion

In this study, multivariate analysis was used to investigate the spatial and temporal patterns of the intertidal benthic diatom communities but also to relate those patterns to the measured abiotic environment. In addition, the assemblages were compared in terms of diversity but also by using useful descriptors of the physiognomy of the diatom communities, such as size-class and life-form distribution.

Three main results could be gathered from the multivariate analysis used on our data. The first was the fact that the temporal patterns appeared to be clearly subordinate to spatial ones (ANOSIM). The second was the selection of sediment texture as the main responsible for diatom distributional patterns, according to the BIO-ENV routine. Mud content, in particular, had a very high correlation with the biotic matrix. Finally, the third major result was the clear distinction between the diatom assemblages of the mudflat and sandflat stations and, to a lower but still significant degree, between sandy sites with different sand textures (MDS, CLUSTER and SIMPER). The outcome is believed to be a thorough and detailed description of the structure of benthic diatom communities of the surveyed area. Spatial and temporal patterns, as well as community physiognomy and diversity are discussed separately.

5.1. Spatial variation and the role of sediment texture

The multivariate results obtained in this work underline the paramount role of sediment composition in structuring benthic diatom communities, particularly when considering the mesoscale (*i.e.* up to 1 km^2), in spatial-temporal studies of estuarine tidal areas. In our study, sediment texture had such an overriding effect that was hard to discern the contributions of other abiotic variables to the structure and spatial patterns of the diatom assemblages. As sampling was limited to a small area of the estuary, many environmental variables had similar values in the sampled sites (*e.g.* salinity). Other variables were intimately linked to sediment grain size distribution (*e.g.* ASFDW and sediment water content). Moreover, a possible effect of gradients in nutrient concentrations (*e.g.* SiO_2 in the sandy transect) or of tidal height was hidden or confused by the abrupt changes of sediment type along the vertical profile on both transects. The difficulty of separating the effects of concurring or opposing gradients in diatom communities on tidal shores and estuaries has already been pointed out by Round (1960) and Underwood (Underwood 2005). The distribution of diatoms in the intertidal zone is more a mosaic than a series of more or less clearly defined parallel zones (Hendey 1964). This perception agrees with our observations, as sediment composition varied considerably along the intertidal gradient (Figure 3), and this factor was clearly more important than elevation. In any case, mud content alone had an extremely high and significant correlation with the diatom abundances matrix (ρ=0.863) and was the abiotic variable most responsible for the structure of the diatom communities in the surveyed area.

The grain size composition of the sediment determines its porosity and other important factors, such as water and organic matter content. The sediment may also have a direct influence on benthic diatom communities, as sand grains act as a substratum for epipsammic diatoms and influence community composition and microscale distribution patterns through their microtopography (*e.g.* Sabbe 1997). However, the most relevant feature to the structure and spatial distribution benthic diatom communities is that sediment texture directly reflects the degree of exposure to wave action and currents. Since the distribution of different sediment types along estuarine intertidal areas is mainly related to local hydrodynamic conditions (Flemming 2000), so would be the case of the benthic diatom communities.

Exposure to wave action is a major environmental factor affecting the structure diatom epiphytic communities of the Baltic Sea (Busse & Snoeijs 2002, Snoeijs *et al.* 2002, Busse & Snoeijs 2003a, Ulanova & Snoeijs 2006) but also of epipsammic assemblages in subtidal sandy sediments (Sundbäck 1983). Several works in European (*e.g.* Brockmann 1950, Colijn & Nienhuis 1978, Sabbe & Vyverman 1991) and North American (Riznyk 1973, Amspoker & McIntire 1978) estuarine tidal flats documented floristic discontinuities which were attributed to differences in sediment type. Saburova *et al.* (1995) studied the structure of an intertidal diatom-dominated MPB community in different spatial scales (cm^2 to 10 km^2), and concluded that spatial distribution of MPB on the mesoscale depends mostly on the granulometry of sediments and on factors influenced by particle size and density (*i.e.* water or organic content). Other works, however, found less obvious differences and described more gradual transitions in intertidal flats (*e.g.* Admiraal &

Peletier 1980, Colijn & Dijkema 1981, Whiting & McIntire 1985, Asmus & Bauerfeind 1994, Méléder *et al.* 2007) or in subtidal sandy sediments (Sundbäck 1983, Vilbaste *et al.* 2000). Finally, more comprehensive studies, which included large sets of sediment samples covering whole estuaries, established that there is a general absence of sharp discontinuities, both in space and time and a gradual turnover in species composition, along various environmental gradients, is to be expected in large scale studies (*e.g.* Juggins 1992, Sabbe 1997). These two latter works also concluded that the structure of diatom communities is strongly related to spatial gradients in sediment composition, followed by salinity and, to a lesser degree, elevation.

In our study, the multivariate spatial patterns of the diatom abundance taxa (CLUSTER and MDS) point to a patchy distribution. In a relatively small area (transect points only distancing about 100m) several discrete assemblages were found for muddy samples (V2 & V3), sandy muddy (V1, January and March 2003), medium to fine sands (A1) and medium to coarser muddy sands (V1, A2 and A3). However, it should be noted that only six stations were sampled and a wide but not continuous range of sediment types was sampled (Figs. 2 and 3). For example, none of sampling stations had sandy muddy sediment (50-75% of mud content; Flemming 2000). In spite of the obvious taxonomical differences between mudflat and sandflat assemblages (Table 8), that were greatly responsible for inter-site dissimilarities (Table 4), there was also some overlap in the distribution of individual taxa along both transects. This was particularly noticeable in sites of comparable sediment composition (*e.g.* A2/A3 and V2/V3), where the assemblage structure was much more similar (Table 4) and the differences encountered had also to be partially attributed to quantitative rather than qualitative variations (Tables 7 and 8). Nevertheless, the diatom assemblages maintained their site-specificity, as the ANOSIM test demonstrated (section 4.2.).

This dichotomy of a continuous *vs.* patchy spatial distribution of benthic diatom in estuarine areas seems, therefore, to be partly related to the scale of the surveyed area (*i.e.* mesoscale or macroscale) and to the chosen sampling strategy. A more continuous and gradual spatial distribution is attainable when a considerable number of sites, including all sediment types, are sampled in large areas (*cf.* Juggins 1992, Sabbe 1997). Alternatively, gradual distribution patterns could also be found when a restricted number of sites are sampled along less extreme variations in sediment composition and exposure gradients (Vilbaste *et al.* 2000) or when the sampling method (*e.g.* lens-tissue; Eaton & Moss

1966) selectively collects only the motile epipelic diatoms (*e.g.* Colijn & Dijkema 1981, Oppenheim 1988, 1991, Ribeiro *et al.* 2003).

To further understand the spatial patterns, it seemed useful to study the diatom abundance data in function of the diatom community physiognomy. As it is shown in Figure 16, the shift from sandflat diatom assemblages to mudflat diatom assemblages can be clearer assessed as a shift between epipsammic dominated assemblages and epipelon dominated ones. As a proxy for hydrodynamic physical disturbance, sediment texture affects the interplay between these two diatom functional groups found in intertidal flats. In less dynamic areas silt accumulates and a cycle of resuspension-deposition is established (de Jonge & van Beusekom 1995). These conditions are most favourable to the epipelic diatoms; either motile or easy resuspended (*i.e.* tychoplankton). In areas of higher hydrodynamism, only sand grains are deposited. Even though they are being constantly reworked, they provide a series of microhabitats that can be explored and occupied by epipsammic diatoms. Different levels of dynamism select different sizes of sand grains and favour different epipsammic taxa. In certain hydrological conditions mixed sediment can be deposited and both diatom communities can co-exist: the sand grains provide habitats for the epipsammon and the silt accretion, a signal of frequent periods of low hydrodynamism, allows the establishment of the epipelon. The discussion of the distribution and physiognomy of the two functional groups is pursued in detail in the next section.

5.2. Two main types of communities

The similarity distances of the diatom abundance samples in the MDS ordination (Figure 11) corresponded also to differences or resemblances in terms physiognomy of the diatom community. Two main types of diatom communities could be described; one dominated by the epipsammon and the other by the epipelon. These two were found to differ in size-class distributions life-forms types and were addressed and discussed separately.

5.2.1. Epipsammon-dominated community

5.2.1.1. Size-class distribution

In site A1 and A2, the left-skewed biovolume distribution (Figure 14) was in agreement with the size-class abundance distributions found in epipsammon-dominated sandflats (Asmus & Bauerfeind 1994, Sabbe 1997, Hamels *et al.* 1998, Woelfel *et al.* 2007) or shallow brackish water sand bottoms (*e.g.* Sundbäck 1983, Sundbäck & Snoeijs 1991, Vilbaste *et al.* 2000) or tropical marine sands (Plante-Cuny 1973). The dominance of small sized diatoms is a well known characteristic of the epipsammon in freshwater and marine habitats (Round 1971). Small diatoms have obvious advantages when living highly dynamic sandy sediments. Their smaller size protects them from abrasive forces and also lets them to colonize the sheltered small valleys and crevices of sand grains (Miller *et al.* 1987). A higher surface-to-volume (S/V) ratio is another advantage of smaller cells for it allows higher light absorption and nutrient assimilation (Hudon & Legendre 1987). The sandy site A1 had the lowest concentrations of SiO_2 and NO_3^--NO_2^- but, conversely, also had the highest Chl*a* content (Jesus *et al.* 2009).

5.2.1.2. Life-forms

Small motile epipsammic forms (Mo<20sm): Small motile diatoms were the dominant epipsammic life-form in the sandy transect and were also very common in site V1. This group was also the most diverse of the epipsammic life-forms (37 taxa), which was quite elucidative of this life-form importance and of the quantity of niches it encloses. Such a high diversity is partly explained by the uneven distribution of these species across the sandy sites. Some species were more abundant in site A1, namely *N. frustulum*, *N. boz-enae* or *N. germanopolonica*, while others (*e.g. N. aleksandrae*) were more abundant in the coarser sands of A2 and A3 (Table 7 and 8).

The importance of this characteristic life-form was already remarked by Sundbäck (1983) for subtidal sediments in the Baltic Sea and also by Sabbe (1993, 1997) and Hamels *et al.* (1998), for intertidal flats of the Westerschelde estuary. In that North Sea estuary, these forms were most abundant in medium sandy sediments and seemed to avoid muddier sediments (Sabbe & Vyverman 1991, Sabbe 1997). This was confirmed by our own observations as all sandy sites had an important medium sand fraction (Figure 3). There was also a sharp decrease in sites A3 and V1, when compared with site A2, of similar tidal height, and site A1. This decrease in the relative abundance of this life-form seems likely to be linked to the increase of mud content (Figure 17), as these diatoms were probably more affected by the presence of silts and clays than by the larger fine sand fraction or longer emersion time characteristic of site A1. Exactly the same pattern was, again, noticed by Sabbe (1997), who further suggested that silt accretion on sand grain surfaces may impair the motility of small forms, thus contributing for a less successful colonization by this life-form of the silty sandflats in the Westerschelde estuary.

Small motile diatoms are more fragile and prone to resuspension than their adnate or stalked counterparts (de Jonge & van den Bergs 1987), so their obvious aptitude to dominate diatom assemblages in dynamic sandy environments could come as a surprise. However, the adequacy of small *Navicula* to flourish in constantly moving sands was already tested in a study by Delgado *et al.* (1991a) where, after seven days of steady moving inoculated sands, a natural multispecific epipelic assemblage (namely species from *Navicula*, *Nitzschia*, *Pleurosigma*) became dominated by small *Navicula*. As Sabbe (1997) explained, there are actually several advantages in possessing motility when living in coarse-grained sands. Firstly, as discussed above, small diatoms have a lower probability of being smashed by colliding sand grains. Secondly, their motility allows them to fully explore the micro-topography of a sand grain. In more dynamic conditions, they can actively seek for protection from abrasion in crevices and depressions, while in calmer periods they can avoid the over-crowded sheltered areas and occupy regions with better light conditions or less nutrient-depleted (*cf.* Hudon & Legendre 1987). In these conditions, a more dispersed distribution would stimulate cell division (Hudon & Bourget 1981) and the fact that these forms are easily resuspended, allows them to quickly occupy bare sand grains recently brought back to the surface (*cf.* Patrick 1967). Small *Navicula* are known to have very fast doubling times (Williams 1964b). So, it is likely that these species can compensate losses suffered during high energy-events more quickly than the more resistant adnate and stalked forms. In conclusion, although more fragile than other epipsammic life-forms, the flexibility and opportunistic traits of small motile diatoms make them extremely well adapted and successful in a continuously disturbed environment.

Adnate forms: The adnate forms were the second most common life-form in the sandy sites but were less diverse (26 species) and less abundant than small motile epipsammic diatoms. It was the only epipsammic life-form that did not show any kind of preference for a particular sandy sediment composition and was equally numerous in all sandy sites. This feature was already noticed by Asmus and Bauerfeind (1994), Whiting & McIntire (1985) and by Sabbe (1997). Differences in species-level distribution patterns were observed, but it was evident that many adnate species colonized the sites of the sandy transect regardless variations in sediment silt content (*e.g. B. lucens*), or to differences in sand fractions (*e.g. C. adhaerens*) or to both (*e.g. P. delicatulum* species group).

Tightly appressed to the substrate, adnate diatoms are probably the growth form most resistant to scouring. Living below the boundary lawyer adjacent to wet sand grain surfaces, they are subjected to much smaller drag forces (Silvester & Sleigh 1985) and have strong adherence as they attach along their raphe-bearing valve(s). Albeit their low motility, adnate diatoms tend to concentrate in crevices and hollowed areas of sand grains (*e.g.* Miller *et al.* 1987, Mudryk & Podgórska 2006) which gives them extra protection from abrasion. All these features make adnate forms extremely resilient to any kind of sediment reworking (Sundbäck 1983, Sundbäck & Snoeijs 1991) and, concomitantly, mean that their distribution is most likely less affected by sediment grain size or sorting coefficient. The distribution of individual species and genera is to likely to be more dependent on sand grain crevice size (Bergey 1999, Bergey & Weaver 2004) and roughness (Nickels *et al.* 1981, Murdock & Dodds 2007); nutrient uptake (Burkholder *et al.* 1990) or grazing (McCormick 1991, Hagerthey *et al.* 2002).

To conclude, it should be noted that adnate and small motile diatoms are probably part of the same continuum of small prostrate diatoms that trade high adherence and lower dispersion rates (low-risk strategy) for higher motility but also higher resuspension/dispersal rates (high-risk strategy). In one end of this spectrum there are adnate species like *Catenula adhaerens* or *Cymbellonitzschia diluviana*, which have very strong adherence and low motility (Sundbäck & Medlin 1986) and are probably slow growing (Jewson & Lowry 1993). Extremely resistant, they form flat ribbon-like colonies and may have to endure local nutrient depletions, poor light conditions and accumulation of excretory products (Hudon & Legendre 1987). On the other end of the spectrum, are the small motile *Navicula* (*i.e.* Mo<20sm). They are more affected by resuspension and abrasion during high energy events but can out-compete and out-grow adnate forms in calmer periods. This said, it should be noted that is difficult to place in this spectrum species like the monoraphid diatom *Planothidium delicatulum*, that seems to be easily resuspended (de Jonge 1985) or many *Fallacia* species, considered by some authors (Sabbe *et al.* 1999) as adnate forms. The exact motility capabilities of these species are still to be explored. More studies on the auto-ecology of adnate and small motile diatoms in intertidal marine sediments are needed.

Stalked species: The presence of stalked diatoms was almost exclusive to site A1. Species like *Opephora guenter-grassii* and *Opephora* sp.1, although not dominant, were among the taxa that most separated samples of A1 from other epipsammic dominated assemblages.

Epipsammic assemblages where stalked, protruding diatoms co-dominate with prostrate species are usually associated with non-cohesive sediments under calmer hydrodynamic conditions (Paterson & Hagerthey 2001). Sundbäck (1983) studied the diatom assemblages of two Baltic Sea sub-tidal sites with similar fine sand sediments. In her study, the most exposed site was only colonized by prostrate, *i.e.*, adnate and small motile diatoms, while an assemblage composed by prostrate and stalked species colonized the site less exposed to water movements. Sabbe and Vyverman (1995) noticed that species like *Opephora guenter-grassii* or *O. mutabilis* were actually indifferent to sediment silt content or salinity in the Westerschelde tidal flats and that they were absent in medium sandy sediments. Sabbe (1997) also reported that the correlation between very fine and fine sands and the epipsammon was solely due to stalked diatoms, in the same estuary.

It is extremely difficult to separate the effects of wave energy and particle size on biological communities (McLachlan 1996). Although the exclusive occurrences of chain-forming stalked species such as *O. mutabilis* (Sundbäck 1987, Sabbe & Vyverman 1995) or species like *O. guenter-grassii* (Witkowski 1994a, Witak & Jankowska 2005), indicate lower sediment disturbance in site A1, the absence of stalked species in the coarser sandy sediments of A2 and A3 cannot be attributed with absolute certainty to stronger wave action. Conditions in those sites were sufficiently calm to allow mud particles to settle and the presence of an epipelic community throughout the studied period. However, it is plausible that calm periods of higher silt accretion in those lower shore stations are interrupted by intervals of higher dynamism that are deleterious to both epipelic (Delgado *et al.* 1989) and stalked diatoms (Weise & Rheinheimer 1978), but facilitates the accumulation of coarse sand grains in sites A2 and A3. As these intervals are followed by calmer conditions, the deposition of silt resumes and the fast re-colonisation by epipelic diatoms is favoured (see below 5.2.2).

Apart from the hydrodynamic conditions the actual grain size composition could also be playing major roles in the selective distribution of the stalked species recorded in the sandy transect during this study. Stalked species like *Martyana martyi*, for example, possess a flexible but strong mucilage stalk that make these forms extremely well adapted to endure life in exposed areas of sand grains (Witkowski *et al.* 1995b) being, concurrently, less prone to be resuspended by water currents than even adnate species, such as *P. delicatulum* or *C. adhaerens* (de Jonge & van den Bergs 1987). They also have a characteristic cell division, dispersion and ecology that are explained in detail, for *M. martyi*, by Jewson *et al.* (2007). After division, the two daughter cells remain linked by their apical pore fields, in a hinged position. When in contact to an adjacent sand grain, the second cell is able to swing, bridge out and attach its free apex to its surface by developing a stalk. Only then separation occurs. This peculiar process enables an easy dispersion for these non-motile species that, actually, is favoured by the continuous rearrangement of sand grains. As stalked diatoms are able to colonize bare substrata (Miller *et al.* 1987, and references herein), they are excellent pioneers of exposed areas of sand grains. A random distribution on the micro-topography of sand-grains (Jewson *et al.* 2007) or, even, a predisposition to occupy the exposed surfaces of sand grains may enable, consequently, the diatoms with this life-forms to avoid competition for space and co-exist with the prostrate diatoms in the same sand grain.

The most common stalked species found in our study are likely to have a similar dispersion method. As fine grained sands are more densely packed and have much more contact points between grains, the dispersion of these species is greatly facilitated. Higher division rates and easier dispersion can, therefore, compensate for the continuous burial and dislodging processes typical of these dynamic benthic environments. In coarser sands, scouring is stronger and dispersion between larger grains is likely to be much harder. It is probable that the compensation point will not be attained making impossible, for a species like *O. guenter-grassii* to colonize successfully the sediments of sites A2 and A3. The larger fraction of fine sands of site A1 may have given these stalked species a favourable subtract and higher dispersion opportunities to maintain a small but continuous presence in that diatom community.

5.2.2. Epipelon-dominated community

5.2.2.1. Size-class distribution

Only a few works (*i.e.* Riaux 1983, Baillie 1987, Snoeijs *et al.* 2002, Haubois *et al.* 2005) explored the size distribution of the epipelic diatoms and, as different methods were used to establish size-classes, a certain care was necessary when comparing those results to the ones obtained in this study. Using length measurements, Baille (1987) found a bimodal size distribution in the epipelic assemblages with a more abundant group of small-sized diatoms and a second, less important, fraction of larger cells. This distinction was already noticed by Riaux (1983) when she divided the epipelic diatoms into nanophytobenthos (< 30 µm in length) and microphytobenthos (> 30 µm in length). These two length classes roughly correspond to the two biovolume classes (in µm^3) proposed by Snoeijs *et al.* (2002) for epiphytic diatom communities of the Baltic Sea (see section 3.5). Recently, Haubois *et al.* (2005) used these biovolume classes to follow seasonal changes of inter-tidal epipelic diatom assemblages of the Marennes-Oléron bay (West French coast), where the domination of small species (*i.e.* < 1000 µm^3, mostly *Navicula* spp.) was sometimes interrupted by the dominance of larger cells (*i.e.* > 1000 µm^3, mostly *Gyrosigma* spp.) when considering their relative contribution to total biovolume per sample, but not in regard to relative abundances of each sample.

In our study, the size-class distribution in the epipelon dominated muddy sites was right-skewed, with an abundance peak in the 250-1000 µm^3 size-group (class C, Figure 14). If the size classes A, B and C were to be fused in one < 1000 µm^3 "small diatoms" groups, then our results would be very similar to any of the works cited above. The division of the "small diatoms" fraction in three size-classes provided further information that was not available in the former works. The taxonomical analysis revealed that the diatom species colonising the mudflat stations (*i.e.* V2 and V3) could be allocated into a small-size group (Class B, *i.e.* 100-250 µm^3), mainly composed by *C. closterium* and *N.* cf. *phyllepta*); a medium-size group (Class C, *i.e.* 250-1000 µm^3), essentially composed by *N. spartinetensis*, *N. gregaria* and *C.* cf. *gracilis*) and finally a large-size group, (Class D, *i.e.* > 1000 µm^3), mainly corresponding to the *Gyrosigma* spp.. The trimodal distribution of cell length-classes described for site V2 by Jesus *et al.* (2009) is a reflection of this pattern, although the cells of *Cylindrotheca* were not counted in that study. This said, the commonly attributed dominance of smaller diatoms in European mudflats (*e.g.* Riaux 1983, Admiraal *et al.* 1984, Haubois *et al.* 2005, Sahan *et al.* 2007) should, in fact, be attributed to a medium-sized group (*i.e.* 250 – 1000 μm^3) which is mainly composed of several *Navicula* species.

The micro-scale bio-physical conditions such as sediment viscosity, grain-size and a compact, dense, EPS matrix (*e.g.* Paterson 1989, Decho 2000, Herlory *et al.* 2004) probably does not allow for biraphid diatoms with less than 15 μm in length (and <100 μm^3 in biovolume) to move efficiently and be competitive in this environment (Sabbe 1997). These species were limited to more sandy sites where they lived in association to sand grains (see above, section 5.2.1). Size-class A (*i.e.* <100 μm^3) was almost absent in the muddy sites, being mainly composed by small non-motile tychoplanktonic species.

The stable, less hydrodynamic conditions, clearly favour larger diatoms which can cover larger distances at higher speeds (Hay *et al.* 1993), migrate vertically and horizontally at the surface and sub-surface of cohesive sediments (*e.g.* Saburova *et al.* 1995, Herlory *et al.* 2004, Jesus *et al.* 2006b) and exhibit the typical endogenous rhythms observed in intertidal mudflats (*e.g.* Serôdio *et al.* 1997, Consalvey *et al.* 2004). High superficial biomass and small particle size produce severe vertical gradients (Paterson *et al.* 1998), which result in a very restricted spatial biotope demarcation (Paterson & Hagerthey 2001). However, the distribution of the epipelic diatoms in three different size-classes could be used to indicate putative temporal differentiations in the way this same habitat is explored during one tidal cycle. Temporal changes in surface species composition in intertidal mudflats, during an emersion period have been frequently reported (*e.g.* Round 1981, Paterson *et al.* 1998). Brotas *et al.* (2003) described the sequential replacement of smaller diatoms (<25 μm in length), that dominated the first emersion hours, by medium and larger diatoms towards the end of an emersion period in a Tagus estuary mudflat. Similar patterns were also found in other Tagus (Tolhurst *et al.* 2003) and U.K. tidal mudflats (*e.g.* Paterson 1986, Consalvey 2002, Underwood *et al.* 2005). Species-specific photo-physiological adaptations and behaviour responses to light conditions seem to be responsible (Sauer *et al.* 2002, Underwood *et al.* 2005) for the complex micro-migrations observed within biofilms (*e.g.* Kromkamp *et al.* 1998). Diatom size could be a crude reflection of those species-specific differences but could also be playing, per se, a major role in biofilm cell micro-cycling and stratification potentiating niche differentiation in MPB biofilms.

The three size-classes may also have differences in cell doubling times and nutrient uptake rates. Small *Navicula* spp. and *C. closterium* may have more than 2 cell divisions per day (Williams 1964b), while the doubling time of larger *Gyrosigma* and *Pleurosigma* spp. vary between 2 to 5 days (Williams 1964b, Smith *et al.* 1996) depending on light, salinity and temperature. Small cells, with their higher S/V ratios and lower silica needs, as well as their higher division rates, do certainly have an advantage in the densely packed, potentially nutrient-deficient, biofilms. In our study, an overall dominance of medium sized diatoms was, at times, replaced by the smaller diatoms group (*i.e.* the *N.* cf. *phyllepta* bloom in the beginning of 2003) or, in the winter 2003/04, by the large diatoms fraction (*i.e.* the *G. fasciola* bloom). Evidence of a seasonal succession of different size-groups in epipelic biofilms was also reported by Haubois *et al.* (2005) and could be linked to seasonal variations in nutrient concentrations in the intertidal sediments. The seasonal variations of the N:P and Si:P ratios for the studied sites, given in Jesus (2006), show that these ratios were below the Redfield ratios (Redfield *et al.* 1963) with the exception to the 2003/04 winter period. This period corresponds to a bloom of larger diatoms (mostly *G. fasciola*) but, in the precedent winter, when the ratios were below the Redfield ratios this bloom did not occur. This period had also the lowest observed salinities, which may have given a competitive advantage to the small sized *N.* cf. *phyllepta* (see below, section 5.3.). An occasional nutrient-deficiency in the biofilms could, therefore, be limiting the growth of larger species in some periods of the year. However, nutrient concentrations alone are not the only cause of epipelic species successions and many other factors are certainly evolved (see below, section 5.3). In the particular case of *G. fasciola*, an inherent higher capacity of Non-photochemical quenching (NPQ) seems to protect this species from high irradiances at lower temperatures, giving this species a competitive advantage in the winter months (Serôdio *et al.* 2005). It remains, however, difficult to discern the separate effects of irradiance, temperature, salinity and nutrient concentrations that fluctuate seasonally. Nevertheless, it still remains reasonable to assume that the observed suboptimal nutrient concentrations could explain the recurrent numerical dominance of the small and medium sized diatoms in the epipelic assemblages. Sporadically, the rarer, slow-dividing larger species may, for several reasons, out-compete them but only if the nutrient requirements are met.

Finally, grazing could also have played a part in the observed size-class distribution. Especially mudflat meiofauna is known for being particularly selective, as is the case of benthic ciliates (Fenchel 1968, Epstein *et al.* 1992, Hamels *et al.* 2005), nematodes (Admiraal *et al.* 1983), harpaticoids (Azovsky *et al.* 2005, De Troch *et al.* 2006a, De Troch *et al.* 2006b). This grazer selectivity to particular diatom sizes could have an impact in the community structure and size-class distribution (Admiraal 1984 and references herein). However, this effect may be limited to the meiofauna as the macrofaunal consumers, such as polychaethes, gastropods or amphipods (Smith *et al.* 1996, Hagerthey *et al.* 2002) and the mugilid fish *Liza ramada* (Almeida *et al.* 1993, Laffaille *et al.* 2002) are much less selective. Macrofaunal impact on the benthic diatom communities appears to be more important, when considering MPB biomass variations (Peletier 1996, Trites *et al.* 2005). Nevertheless, the above mentioned seasonal shift in size-class dominance could also be related to changes in diatom-grazing community but this could not be assessed as the meiobenhic community was not studied at the sampled sites.

5.2.2.2. Life-forms

Small and large motile forms: motile pennate diatoms completely dominated the assemblages inhabiting mudflat sites (V2 and V3). Extensive reviews explain the reasons for the success of epipelic diatoms in intertidal cohesive sediments, where they can have very high biomass and productivity (MacIntyre *et al.* 1996, Underwood & Kromkamp 1999). Motility is one of the main reasons, as it offers them great advantage in an environment where superficial cells are constantly buried (Admiraal 1984, Consalvey *et al.* 2004) but also allows them to counter resuspension by withdrawing into deeper layers of the sediment, prior to inundation (*e.g.* Pinckney *et al.* 1994, Kingston 1999). Finally, micro-migrations (or microcycling) could allow motile epipelic to adjust to local conditions (in a µm level), thus avoiding overexposure to high irradiances, high temperatures, to grazing or escape nutrient and CO_2 limitation (*e.g.* Perkins *et al.* 2001, Consalvey *et al.* 2004, Underwood *et al.* 2005 and references herein).

Dominating the assemblages in the muddy sites, motile epipelic diatoms also were an important component of the diatom assemblage in sites with relatively low mud content. Stations A2, A3 and V1 had an average mud content of 5, 8 and 14 %, respectively, had epipelic fractions that represented 12, 40 and 63 % of the total average cell counts (respectively). The difficulty of these diatoms to withstand great physical disturbances in sandy sediments is well-known (Delgado *et al.* 1991a), so it could be hypothesized that the epipelic diatoms counted were deposited there and were not a viable, active part of the sandflat diatom community. However, microscopic observations of the MPB extracts during microalgal group counts showed that the majority of the epipelic diatoms were in good condition, unbroken and with plastids. Therefore, the aptitude of viable epipelic fractions to survive throughout the two-year study period, in exposed sandy sites was unquestionable. Diatoms like *Navicula gregaria* and the fragile *Cylindrotheca closterium* had similar average relative abundances in A3, V1, V2 and V3 (around 4 and 11%, respectively), some were less common in the sandier sites (*e.g. Navicula spartinetensis*, *Gyrosigma fasciola* and *Cylindrotheca* cf. *gracilis*) while others more abundant in these sites than in the mudflat ones (*e.g. Staurophora salina*, *Plagiotropis vanheurckii* and *Pleurosigma angulatum*).

Mixed epipelon/epipsammic assemblages have been frequently found in other estuarine sandflats (Sabbe 1993, Hamels *et al.* 1998, Méléder *et al.* 2007). They occur when physical disturbances decrease sufficiently to allow the resettling of silts and clay particles and of resuspended epipelic diatoms and their survival (Paterson & Hagerthey 2001). If fine particle accretion proceeds, it can lead to the establishment of an assemblage dominated by the epipelon (Wulff *et al.* 1997). The high mobility of the epipelic diatoms, in this situation, is a selective advantage over the epipsammon.

Studies in the Ems and Shelde estuaries demonstrated that epipelic diatoms are easily resuspended, along silt and clay, by wind-induced waves during high tide (Delgado *et al.* 1991b, de Jonge & van Beusekom 1995). They are subsequently redistributed in the tidal channels in low tide and, during the next high tides. Re-sedimentation can take place in the channels and in submerged tidal flats, under calmer weather conditions (de Jonge & van Beusekom 1992). It is likely that, following a similar cycle, the muddy coarse sands of sites V1 and A3 were able to maintain a recurrent but important fraction of epipelic diatoms. Station V1 was very close to the muddy sites (circa 100 m) and A3 was the lowest and the most offshore site of the sandy transect, making these sites privileged areas for the resettling of suspended sediment particles and epipelic diatoms. Physicochemical conditions were suitable enough to permit their maintenance there and it should also be noted that nutrient concentration ranges in those sites were similar to the muddy sites (Figure 4). These conditions were probably not met in site A2, although it had similar sediment texture to A3, for the epipelic presence was much less important. As for site A1, even though wave exposure was probably less important (see above, section 5.2.1) the elevation impeded the resettling of mud and epipelic diatoms in that higher shore station.

In the present study, a small group of large motile diatoms was found exclusively in sandy sediments. Large biraphid diatoms with heavy, sturdy frustules are frequently referred as part of the diatom assemblages living in unstable, wave-exposed, sandflats (*e.g.* Brockmann 1950, Colijn & Dijkema 1981). They are, by definition, part of the epipelon but their distributions is limited to the sandflats and are adapted to a very different environment of other large species found exclusively in mudflats. They certainly seem to cope better the collisions with sand grains but are also able to migrate down and avoid the wave-disturbed sediment surface during high tide (Admiraal 1984 and references herein, Kingston 1999) or to escape high irradiance conditions (Mitbavkar & Anil 2004). Only *Dickieia* sp.1, *Navicula flagellifera* and *Navicula* cf. *mollis* appeared consistently in the sandy sites, but always in low abundances. Some species, like *Petroneis humerosa*, were so rare that had less than 1% abundance in one sample and never plus than 2 occurrences. As a consequence, were not used in the multivariate analysis. In spite of this, optical microscopy screening of the sand samples at low magnification showed that the presence of *P. humerosa* was not negligible. Moreover, the relative contribution of these large species to total biovolume was important in the sandy stations (Figure 16). The fixed number of around 400 valves scored per slide, during diatom counts, caused the underestimation of this group. In future studies, separate counts of small and large diatoms, as suggested by Snoeijs (2002), should perhaps be applied in sandflat areas in order to explore the ecological role in Tagus estuary sandflat diatom communities of this apparently well defined growth form.

Tychoplankton: this life-form was never common in the sampled sites, never surpassing 5 % in relative abundance and occurred mainly in high deposition areas, *i.e.* mudflat sites and/or low shore sandy stations. In certain conditions tychoplankton can be the dominant epipelic life-form, with species like *Paralia sulcata*, *Brockmanniella brockmanni* or *Cymatosira belgica* representing more than 50% of total cell counts in certain mudflats and coastal areas (*e.g.* Vos & de Wolf 1988, Sabbe & Vyverman 1991, Trites *et al.* 2005) but that was not the case in our study area.

It should be stressed that the chosen definition of tychoplankton is more restricted than the more classical definition of "non-adapted (benthic) organisms present in the water mainly by chance" (*cf.* Reynolds 2006). In estuarine areas subject to strong tidal flushing and to wind-induced wave action (de Jonge & van Beusekom 1992), this broader definition should include also many motile species (*e.g. Cylindrotheca*, *Navicula*, *Surirella*) that seem to be, nonetheless, primarily adapted to live on the benthic environment but are found recurrently in plankton samples. By restricting to non-motile centric or araphid diatoms that live more or less freely between sediment particles, Sabbe (1997) attempted to circumscribe tychoplankton as a growth-form that "behaves" like silt particles, using resuspension as a way of facilitating dispersion. Many species were very small (*i.e.* < 100 μm^3) and were placed the size-class A, replacing the very small motile diatoms in the muddy sites (Figure 17). They are probably very well-adapted to benthic silty environments, with physiological mechanisms to cope burial periods and low-light/low oxygen episodes (*cf.* Jewson *et al.* 2007) but, unfortunately, sill little is known about the autoecology of these species.

5.3. Temporal variation in both types of communities

During the two year period of this study temporal variations of the diatom assemblages were much less evident the sediment-driven spatial patterns the spatial ones. Nevertheless, as the multivariate analysis detected, temporal variations did exist but were mostly limited to mudflat assemblages. Part of the temporal variation must be attributed to changes in sediment composition in each site, with the best example being the transformation observed in site V1 in the first months of the study (*i.e.* January to march 2003). Seasonal variations in sediment texture, caused by cyclic changes in hydrological conditions (and consequently sediment texture), are known to add a temporal effect in MPB spatial community structure (*e.g.* Méléder *et al.* 2007). However, in the other sampling stations of the muddy transect (*i.e.* V2 and V3) , the sediment composition (particularly the mud content) remained more or less constant throughout the studied period (Figure 2), thus reducing its overall temporal effect.

Climate-related environmental variables such as sediment temperature, light, interstitial water salinity had seasonal variations that were similar in all studied sites (Figure 5). Regarding nutrient concentrations clear seasonal patterns were not always visible (Jesus

2006). Nevertheless there was a clear distinction in temporal patterns observed in mudflat and sandflat diatom communities, a phenomenon already reported in short-term (Sabbe 1993) or long-term (Sabbe 1997, Hamels *et al.* 1998) spatial-temporal estuarine diatom studies. This contrasting seasonality is, therefore another contributing factor, adding to distinct size-class distributions or diverse life-forms, to elucidate the basic differences between the epipsammic and epipelic communities. The temporal variation of both functional groups will be discussed separately.

5.3.1. Epipsammon

Considering the variation of biomass and Fucoxanthin/Chl*a* ratios during the study period, the epipsammic diatoms in the sandy transect showed a certain seasonal periodicity, with peaks on late spring/early summer (Jesus *et al.* 2009). However, the epipsammic community structure, in the same sites, remained constant and no seasonal patterns were observed. High intra-site average similarity (Table 4) and the non-significant clustering (SIMPROF test, Fig 19) of the epipsammon-dominated assemblages of the sandy transect stations indicate that there was no distinct temporal succession of taxa and that epipsammic species relative abundances remained fairly stable throughout the two-year study period.

In station A1, in particular, variations in MPB biomass and summer peaks of cyanobacteria and euglenids (Jesus *et al.* 2009) were not reflected in discernible changes of the taxonomical structure of the diatom communities, throughout the studied period. In September 2003, that station was dominated by euglenids, a bloom that was detected by cell counts, pigment analysis (Jesus 2006, Jesus *et al.* 2009). However, in the station with the highest intra-site average similarities, the diatom assemblages of that month had Bray-Curtis similarities with the immediate preceding and following samples above 70 %. Seemingly, the epipsammic diatom community structure was not greatly affected by fluctuations in biomass or by increasing interactions with other microalgae. Hamels *et al.* (1998) draw a similar conclusion when studying both the pigmented and non-pigmented microbenthic communities on intertidal estuarine flats of the Westerschelde

The absence of clear seasonal trends in the estuarine an coastal epipsammic flora has been frequently reported (*e.g.* Riznyk 1973, Sundbäck 1983, Sabbe 1993, Asmus & Bauerfeind 1994, Sabbe 1997, Hamels *et al.* 1998, Vilbaste *et al.* 2000, Woelfel *et al.* 2007), even when biomass/cell numbers estimations detect spring peaks (Taasen & Høisæter 1981, Asmus & Bauerfeind 1994) or steady increases during short-term study periods (Sabbe 1993).

With the exception of extreme storm events that destroy and remove biomass and the MPB community (Miller 1989, de Jonge & van Beusekom 1992), the constant reworking of the upper layers of sandy sediments, is actually capable of promoting a unvarying and predictable environment for species well adapted to this kind of physical stress. Punctuated storm events, with extreme high-energy wave conditions, probably affect the epipsammic community as a whole and do not selectively favour certain epipsammic species over the others. Highly resilient to physical disturbance, epipsammic diatoms are also capable of withstanding other adverse conditions. Several species are capable of surviving extended periods of anoxia and darkness (Moss 1977, Sundbäck *et al.* 1996) and recover astonishingly quickly when brought to the upper layers (Jewson *et al.* 2007). This means that large standing stocks of living diatoms on the deeper layers are being continuously brought to the surface by the constant sediment reworking and that this endlessly trade-off of specimen burial and resurfacing stabilizes the assemblage structure (Amspoker 1977). Their small size and higher surface-to-volume (S/V) ratio also makes them less susceptible to seasonal drops in nutrient availability (Hillebrand *et al.* 2000) and also allows them to escape grazing (Admiraal 1984).

Grazing seems to have a lesser impact on epipsammic communities than on epipelic ones including in their temporal patterns (Sahan *et al.* 2007). Ciliates, for example, prefer feeding on free-living diatoms to epipsammic taxa (Hamels *et al.* 1998). When comparing the dynamics of ciliate communities in sandy and muddy sediments for a 1-year period, Hamels *et al.* (2005) concluded that the food webs in sandy sediments are more complex and their structure remains stable over time. Harpaticoids also prefer to graze on medium-sized epipelic diatoms, even when living in silty fine-grained sands (Azovsky *et al.* 2005). Nonetheless, epipsammon can be potentially grazed by more generalist sediment surface consumers; such has the amphipod *Bathyporeia pilosa* (Sundbäck & Persson 1981).

In conclusion, a continuous cycle of abrasion/removal and re-colonization of barren areas, as well as, burial and resurfacing of sand grains creates a “fluctuating but predictable environment” for epipsammic diatoms (Kingston *et al.* 1983). Seasonal variations in light, temperature, salinity and nutrients, affect the community as a whole and are responsible for biomass peaks and crashes or the occurrence of other algal groups. However, these seasonal environmental changes do not seem alter the basic taxonomic structure of the intertidal diatom epipsammic community.

5.3.2. Epipelon

The epipelic diatom dominated mudflat MPB communities did not exhibited evident seasonal patterns in terms of biomass (Jesus *et al.* 2009) but, contrary to the epipsammic fraction, the epipelon showed a clear temporal succession of dominant species throughout the studied period (Figure 19). A bi-modal annual biomass (or cell numbers) pattern, with peaks in spring and late summer, is frequently recorded for European intertidal epipelic diatoms estuarine communities (Riaux 1983, Hamels *et al.* 1998, Sahan *et al.* 2007) although it does not always occur (Oppenheim 1991, Wolfstein *et al.* 2000). A lack of seasonal MPB biomass patterns in other Tagus estuary mudflats had also been recorded by Brotas *et al.* (1995), who further suggested that a lower position, in the tidal profile, partially, be responsible for this lack of a clear seasonal pattern. This seems also to be the case in stations V2 and V3 (Jesus *et al.* 2009). Lower shore mudflats have shorter light exposure periods annually and are subjected to a minor degree of seasonal variation in environmental conditions than higher shore mudflats (Underwood 1994). For example, lower shore sites are subjected to less pronounced effects of desiccation (Riznyk & Phinney 1972). Bi-monthly sampling also reduced the perception of an epipelon biomass temporal pattern, although it did not completely hidden changes in epipelon community structure.

Even though percentage abundance does not necessarily reproduce the abundance in absolute cell numbers, as diatom population density varies over time (Peletier 1996), the seasonal patterns of replacement and species alternation in the assemblage dominance can still be clearly reflected (Figure 19). This typical temporal succession of epipelic diatom species have been recorded in many works (Aleem 1950, Round 1960, Hendey 1964, Underwood 1994, Sabbe 1997, Witkowski *et al.* 2004b, Haubois *et al.* 2005) and contrasts with the apparent seasonal stability of the structure of the epipsammic assemblage (see above 5.3.1). This discrepancy was particularly clear in the mixed epipelon/epipsammon assemblages of sites A3 and V1 (Figure 18 and 19) and has already been observed in other studies (Sabbe 1993, 1997, Hamels *et al.* 1998). These works concluded that both fractions fluctuated independently from one another. In a short-term study (Sabbe 1993), where sediment samples were collected every two days during a month, temporal variations of the epipsammon were reduced and remained unaccounted for, while the rapid expansion of the epipelic diatom fraction was attributed (in part) to the increase of irradiance and organic matter. Epipelic diatoms may be more affected by temporal changes in environmental conditions (such as irradiance or resuspension) but also are capable of responding more rapidly than the epipsammon. This translates in a more pronounced fluctuation in biomass and/or assemblage structure and is in agreement with the findings of our study.

There was a distinction between Winter/Spring and Summer/Autumn epipelic assemblages in mudflat stations V2 and V3. This temporal separation was stronger than the spatial differences, as both clusters include samples from the two mudflat stations (Figure 11 and 12). A similar pattern was found in the mudflats in the German Bight (Witkowski *et al.* 2004b) and in the Westerschelde estuary (Sahan *et al.* 2007). Haubois *et al.* (2005) found a Spring/Summer and Autumn/Winter distinction but it had a different dominant species set. In the above mentioned studies and our own work, the separation into two-season groups was observed and it was always due to periodical sharp shifts in abundance of a few dominant species, most of them occurring throughout the year.

The sequential replacement of the dominant diatom species in intertidal mudflats throughout the seasons has long been attributed to species-specific differences in the responses to environmental conditions (Hendey 1964) and to the great impact that interspecific competition has on the taxa composition of densely populated biofilms. In a series of algal culture competition experiments, de Jong & Admiraal (1984) demonstrated that different combinations of temperature, salinity and inorganic carbon favoured different epipelic diatom species and determined the outcome of the competition experiments. Temperature and light (Admiraal & Peletier 1980), salinity (*e.g.* Williams 1964a) and/or nitrate and ammonium concentrations have a profound effect on epipelic diatom division rates (Underwood & Provot 2000). Brackish water benthic diatoms possess somewhat wide niches and are very euryhaline and eurythermal (Snoeijs 1999) but they do have specific growth optima (but see Underwood 2005). Therefore, spatial concomitant changes in salinity, nutrients or irradiance have been related to spatial distribution of estuarine mudflat (*i.e.* epipelic) diatoms (Juggins 1992, Underwood *et al.* 1998, Cabrita & Brotas 2000, Underwood 2002).

By the same reasoning, temporal changes of the structure of estuarine epipelic assemblages can be attributed to fluctuations in these environmental conditions. In epipelic biofilms, the dense accumulation of cells promotes interspecific competition and the dominance of just a few species (Paterson & Hagerthey 2001). Seasonal changes in temperature and other variables will sequentially enhance or impair the growth and competitive ability of the different dominant species causing the community structure to continuously shift. Admiraal *et al.* (1984), were able to replicate seasonal pattern of two dominant Ems-Dollar diatoms in culture competition experiments by controlling the temperature, light and desiccation periods. Oppenheim (1991) showed that variations of salinity, organic matter, pH and moisture content were instrumental on the seasonal changes detected in the structure of the epipelic diatom assemblages and Peletier (1996) attributed the long-term shift in species composition detected for the Ems-Dollar estuary epipelic assemblages to the reduction in organic waste input (notably ammonium concentration). These fluctuations in assemblage structure are usually more pronounced in early spring in brackish sites with the concomitant changes in salinity, temperature, day-length and light (Sabbe 1993, Sahan *et al.* 2007). Finally, the seasonal succession of the ciliates and other meiofaunal communities (*e.g.* Hamels *et al.* 1998) may also influence the taxonomical temporal sequence of the estuarine epipelon.

It is extremely difficult to explain the temporal pattern of each dominant species because of the rareness of autoecological data for estuarine benthic diatoms (Sullivan 1999). However, comparisons can be made between the seasonal patterns of the most abundant epipelic diatoms found in this study and the patterns described for them in the literature (Table 9). Being one of the south-most European tidal flat areas, the similarity of the seasonal patterns of Tagus estuary diatoms with the ones of their counterparts of the North Sea was very striking. The environmental conditions seem to have been sufficiently similar to allow the occurrence of many of the same taxa and their temporal variations were parallel enough to produce the same temporal patterns.

Table 9 - Reported seasonality of the dominant epipelic species in other European estuaries.

Taxon	Season	Location	Reference
C. closterium	Late Spring/early Summer	Tagus estuary	this study
	Late Spring/early Summer	Severn estuary	Underwood 1994
	Spring	Whitstable coast	Aleem 1949
	Spring	Severn estuary	Oppenheim 1991
	Spring	Westerschelde estuary	Sabbe 1993
C. cf. *gracilis*	Late Summer/Autumn	Tagus estuary	this study
	Summer (as *C. signata*?)	Severn estuary	Underwood 1994
G. fasciola	Winter	Tagus estuary	this study
	Winter	Dee estuary	Round 1960
	Winter	Ems-Dollar estuary	Admiral *et al.* 1984; Peletier 1996
N. gregaria	Spring	Tagus estuary	this study
	Spring/Summer	Nord-Finistère coast	Riaux 1983
	Late Spring / Summer	Westerschelde estuary	Sabbe 1997
	Late Spring / Summer	Elbe estuary	Gätje 1992
	Common throughout the year	Severn estuary	Oppenheim 1991
N. spartinetensis	Summer (common throughout year)	Tagus estuary	this study
	Summer	German Bight	Witkowski *et al.* 2004
	Spring/ Summer	Bourgneuf Bay	Méléder 2007
N. cf. *phyllepta*	Winter/early Spring 2003	Tagus Estuary	this study
	Winter (as *N. phylleptosoma?)*	German Bight	Witkowski *et al.* 2004
	Brackish (lower salinities)	Westerschelde Estuary	Sabbe *et al.* 2004; Créach *et al.* 2006

Beside the seasonal differences, there were also slight distinctions between the two years of the study, namely between the two winters surveyed. If the 2004 bloom of *G. fasciola* could be attributed, in part, to higher nutrient concentrations (see above, 4.2.2.1), the almost complete dominance of *N.* cf. *phyllepta* in the first months of 2003 in the muddy transect was most likely related to the lower salinity observed during this period (Figure 5). *N.* cf. *phyllepta* seems to be a semi-cryptic species included in the *N. phyllepta* species group but with a different genome from *N. phyllepta* s.s. and very slight morphological differences (Sabbe *et al.* 2004b, Vanelslander *et al.* 2009a). It has been described recently for the oligohaline reaches of the Westerschelde estuary (*viz.* Créach *et al.* 2006). Since our study area is situated in the fluctuating poly-oligohaline boundary, the exceptional drop in salinity that occurred in the beginning 2003 seems to have triggered the over-dominance of this otherwise uncommon species.

5.4. Diversity

Differences in assemblage diversity mirrored the spatial variation, revealed by the multivariate analysis and by the physiognomic description of those assemblages (*i.e.* size-class and life-form distribution), whilst not showing any discernible seasonal pattern in any of the six sampling stations (Figure 10). There was a clear distinction between assemblages living in cohesive sediments (low diversities) and non-cohesive sediments (high diversities) with the assemblages occurring in sites with mixed sediment types (*i.e.* muddy sands) being the most diverse. This pattern was also registered by several other authors in coastal and estuarine intertidal flats (*e.g.* Juggins 1992, Sabbe 1997, Méléder *et al.* 2007).

Low diversity and high dominance have long been attributed to epipelic communities that populate intertidal mudflats (*e.g.* Round 1971, Admiraal & Peletier 1980, Underwood 1994, Witkowski *et al.* 2004b), where the assemblages may even form almost monospecific mats (Peletier *et al.* 1996, Agatz *et al.* 1999). This low diversity is a direct consequence of the habitat characteristics but also of the physiognomy of the epipelic assemblages. During low tide, MPB primary production and biomass is concentrated in a very narrow superficial layer (about 200 µm) in cohesive intertidal sediments (*e.g.* Jesus *et al.* 2006a, Tolhurst *et al.* 2007). The biological activity of the biofilms and the nature of the sediment (*e.g.* porosity and permeability) are the main factors behind the formation of steep vertical gradients of nutrients, light or oxygen (*e.g.* Paterson *et al.* 1998, Stal & de Brouwer 2003). This implies that there is a very restricted spatial zonation and that, in these densely packed mats, local nutrient depletion and inhibitory effects are bound to be established. Competitive interactions can also become an important factor (de Jong & Admiraal 1984) in lowering diversity but also in triggering the seasonal succession of dominant epipelic species (Admiraal *et al.* 1984). The biofilm, being a narrow band of diatoms and bacteria embedded within a matrix of extracellular polymeric secretions (EPS) which closely surround sediment particles, seems only to allow the establishment of two specialized diatom life-forms (*i.e.* motile pennate diatoms and tychoplankton). This lack of variety in life-form types, derived from low niche availability, is likely to be partly responsible for the lower diversities observed in mudflat diatom assemblages, which are more susceptible to inter-specific competition and grazing (Hamels *et al.* 2005). These two factors seem to be driving forces in the seasonal shift in the species composition (de Jong & Admiraal 1984, Sahan *et al.* 2007), while keeping the epipelon diversity low.

The sandy sites diversity values were characteristically high and very similar to the ones reported in other works (*e.g.* Amspoker 1977, Sundbäck 1983, Vilbaste *et al.* 2000). The physiognomy of the sandflats diatom assemblages seems to be instrumental for their high diversity and low dominance: First, the different micro-habitats provided by the topography of individual sand grains allows the establishment of various epipsammic life forms in a fashion that does not occur in cohesive sediments. In addition to high niche differentiation, the constant physical disturbance keeps the cell numbers of each species low and maintains the epipsammic communities in non-equilibrium pioneer state (Miller *et al.* 1987). Consequently, direct interspecific competition for resources appears to be reduced to the occasional competition for space (*e.g.* in sand grain crevices) and does not have the same structuring effect to the community as in epipelon. Finally, the minuteness of the majority of the epipsammic diatoms seemed also to influence the final diversity of the sandflat assemblages. As figure 15 shows, the two size-classes where smaller species were allocated (*i.e.* <250 μm^3) were much more diverse than the others, contributing positively to the higher diversity observed in the sandy sites.

The highest diversities were found in sites with mixed muddy sandy sediments (*i.e.* A2, A3 and V1), where epipelic and epipsammic species coexisted and, therefore, in the sediments which provided the highest niche differentiation. The slightly lower diversity found in the almost mud-less site A1, where the epipelic forms were almost absent, seems to confirm this supposition. However, the higher variety of life-forms present in the sandy stations cannot explain, alone, the small diversity differences found in the sandy transect. Actually, the higher diversity values in A2 and A3 are maintained even if the epipelic species are excluded from the calculation of the indexes. Furthermore, site A1 was less diverse than A2 in spite of having a similar epipelon/epipsammon ratio plus the exclusive contribution of stalked diatoms (Figure 17). By examining the k-dominance profiles (Figure 6) and the SIMPER analysis (Table 7), it becomes clear that site A1 differs from the other sandier sites thanks to a slightly higher predominance of a small group of epipsammic species (*viz. N. viminoides*, *N. frustulum*, *N. bozenae* and *N. germanopolonica*) that decreased the overall diversity. Therefore, factors other than niche differentiation seem to be involved in shaping diversity in the sandy sites.

Paterson and Hagerthey (2001) explained in great detail the main physical constraints that regulate the composition of the MPB assemblages in cohesive and non-cohesive intertidal sediments. In that review, the authors proposed a conceptual model where the stability of intertidal sediments is a function of both hydrodynamics and biology. Along the continuum from non-cohesive to cohesive sediment the maximum of diversity is attained in mixed sediments where, thanks to the presence of mud and sand-grains, the epipelic and epipsammic fractions may co-exist. If there is a reduction in disturbance episodes, the EPS production by the epipelic diatoms will favour the deposition of silt, making the sediment even more cohesive. The epipsammic diatoms may then disappear if their substratum (*i.e.* sand-grains) is covered permanently in fine mud. Furthermore, the diversity in the epipelic fraction will decrease due to competition (*e.g.* Admiraal & Peletier 1980) and/or herbivory (*e.g.* Hagerthey *et al.* 2002, Trites *et al.* 2005). In the non-cohesive end of the continuum, high hydro-dynamism does not allow the settling accumulation of mud particles and the epipelic diatoms are unable to survive in such harsh conditions (*e.g.* Delgado *et al.* 1991a). In the most extreme cases, only coarse sand is selected and just a few epipsammic species can thrive there, thus diminishing the diversity. This conceptual model was inspired in the Intermediate Disturbance Hypothesis (IDH), which predicts that diversity will be highest in communities with intermediate levels of disturbance (Connell 1978, Collins & Glenn 1997).

From this perspective, the diversity patterns found in our study seem to basically confirm the conceptual model proposed by Paterson and Hagerthey (2001). Even the diversity found in station A1, with a particular sediment texture (fine sands with low mud content) can still be explained within the empirical framework of their model, although it was not explicitly investigated in their study. As discussed above (section 5.2.2.1) the presence of stalked diatoms in A1, the higher MPB biomass (Figure 6), as well as a larger fraction of fine sands (Figure 3), seem to support the notion than the diatom assemblages of that station endured less dynamic conditions than that other assemblages of the same transect. Conversely, the coarser sands found in the muddy sandy sites (*i.e.* A2, A3 and V1) may indicate intermittence of strong hydrodynamic episodes with calmer periods when silt accretion is favoured. Therefore, the lower diversity of diatom assemblages of the station A1 could be a reflection of lower wave exposure, a likely result of tidal elevation (McLachlan 1996). This hypothesis is also supported by the observations made by Sabbe (1997) in Westerschelde Estuary, where he found out that diversity tended to be maximal at median grain sizes and that epipsammic diversity decreased when sediments became less dynamic and the predominance of fewer species become established.

Chapter 6

Assessing alternative approaches

6. Assessing alternative approaches to species abundance-by-sample community structure description in intertidal benthic diatom studies

6.1. Introduction

Environmental monitoring and community ecology studies are dependent on the correct taxonomic identification and sound multivariate analysis. These two factors are decisive for an accurate description of the community structure patterns and a meaningful linkage between these patterns and the measured environmental variables (Olsgard *et al.* 1998). However, structural studies have often been criticised for being time-consuming, expensive and laborious, both in field sampling and laboratory analysis. In order to have sound species-level identification the services of a trained taxonomist is also mandatory. Depending on the biological group studied, this expertise can be difficult to find. For example, in the case of the present work, the diatom analysis required lengthy sample processing and the scoring of 300 to 600 valves per slide (see chapter 3). In a total 68 samples, 52398 diatoms were counted and identified.

Less time-consuming and less effort demanding approaches have been consistently explored by community ecologists, particularly after the application of novel non-parametric multivariate analysis in community studies (*e.g.* Warwick 1988, Somerfield & Clarke 1995) and the great increase in water-quality bioassessment studies in freshwater and marine environments (*e.g.* Olsgard *et al.* 1997, Schmidt-Kloiber & Nijboer 2004). The discussion has been centred on benthic invertebrate communities, although there are some examples of diatom studies (*e.g.* Hill *et al.* 2001, Kociolek 2005, Lavoie *et al.* 2008). It has been mainly focused on the subject of taxonomic sufficiency (TS), which proposes the reduction of taxonomic resolution or the use of functional surrogates in water-quality and bioassessment programs. Related methodological arguments have also been thoroughly discussed. Two significant examples have been the effect of rare species exclusion (*e.g.* Cao & Williams 1999, Marchant 1999) and the consequences of different transformations of abundances-by-sample data in multivariate analysis (*e.g.* Thorne *et al.* 1999, Heino 2008).

Taxonomic sufficiency (TS) is the minimum taxonomic resolution needed to meet the study objective (Ellis 1985) and can be seen as the best compromise between scientifically sound community description and logistical limitations caused by the lack of available expertise, time and money. The defenders of TS emphasize that there is great structural redundancy in the natural communities, in the way that only a small set of species (*e.g.* Clarke & Warwick 1998) or higher taxonomical levels (*e.g.* Olsgard *et al.* 1997) may be required to fully describe the community patterns and its response to natural or anthropogenic disturbances. The accuracy of higher taxa identification by non-experts is also more easily assured. Therefore, providing it maintains strong correlations with species-level analysis (*e.g.* Chainho *et al.* 2007, Mendes *et al.* 2007), the advantages in time- and cost-savings in large scale or long-term monitoring programs are obvious (Dauvin *et al.* 2003).

Another way to circumvent what has been coined as taxonomic impediment (Taylor 1983) in community ecology is to use functional surrogates as the “fundamental building blocks” of the community instead of the taxonomical units (Simberloff & Dayan 1991). This functional surrogacy has usually been based in growth forms or ecological guilds in diatom studies (*e.g.* Passy 2007). Size-class frequency distribution has also been regarded, if not as an alternative, at least as a complementary approach to taxonomic description of phytoplankton community structure (Quintana *et al.* 2006, Kamenir *et al.* 2010). In benthic diatom communities of the Baltic Sea, the small and large diatom species seemed to respond differently to the environmental gradients (Busse & Snoeijs 2002, Snoeijs *et al.* 2002, Busse & Snoeijs 2003a, Ulanova & Snoeijs 2006), so the size of the diatom taxa may also have a structuring effect on the community. Other studies also demonstrated that ecological information can still be preserved when excluding rare species (*e.g.* Marchant 1999 and references herein) or, even, when restricting to qualitative, presence/absence, species datasets (*e.g.* Carballo & Naranjo 2002).

However, as several authors argue, there is no biological justification for excluding rare species (Cao *et al.* 2001). Taxonomic surrogacy and the use of higher rank taxa also lacks justification and it is founded on misconceptions about the properties of Linnaean classification (Bertrand *et al.* 2006). Maurer (2000) criticized the use of TS and the exclusion of rare species from benthos monitoring studies because it may lead to unacceptable losses of ecological information and promotes even further disinvestment in taxonomy and systematics training, thus exacerbating the taxonomic illiteracy in the context of increasing biodiversity concerns.

Most of these relevant questions have not yet been addressed in the context of the microphytobenthos studies and intertidal benthic diatom communities. The description of the community structure of the MPB has often been limited to the account of the major microalgal groups revealed, for example, by HPLC pigment analysis (*e.g.* Cariou-Le Gall & Blanchard 1995, Brotas & Plante-Cuny 2003). This method lacks sufficient taxonomic resolution and gives no insight on the structure contained within each microalgal fraction, particularly in the diatom-dominated biofilms found in the temperate estuaries (MacIntyre *et al.* 1996, Underwood & Kromkamp 1999). Although a species-level survey provides information on diatom community structure which cannot be obtained otherwise (*e.g.* Juggins 1992, Sabbe 1997), MPB ecologists would probably welcome a valid alternative that retains much of the communities structural information, without having to invest the huge effort and time required for taxonomic identification. The existence of such an alternative could help narrowing the gap between functional studies, that view the MPB “biofilm” as a black box and ignore species composition, and the more descriptive studies mainly based on species distribution (Underwood 2005).

The preceding chapter described in great detail the taxonomical structure of the diatom communities in contrasting intertidal flats, with additional information on life-form and size-class distribution. Having as a starting point this very complete species abundance dataset, the present study provides an excellent opportunity to test several of the alternative approaches to species-level studies referred above. Only by comparing the performance of the different approaches, deriving from the same dataset, it is possible to objectively evaluate the usefulness of each alternative and to determine exactly what kind of information is lost in each simplification.

6.2. Methods

6.2.1. Matrix selection and data transformation

Several different approaches were tested in this study. Some discarded or transformed the abundance data, while maintaining a high taxonomic resolution. Others reduced the taxonomic resolution or used a different classification but kept the abundance data. The tested matrices either derived from the original 181-species abundances matrix, *i.e.* SPECIES DATASET 1 (DS1), or from 94-taxa SPECIES DATASET 2 (DS2), which excluded all extremely rare taxa and was used in the multivariate analysis presented above, in chapter 4. Both datasets were also compared to each other, in an exercise that allowed testing if the criteria chosen to eliminate extremely rare species were sound (see section 3.2). For this test the species abundance matrix DS1 was root-root transformed (*cf.* in DS2).

The matrices selected were:

1. Presence/absence (species-level): The original species abundances matrix (DS1) was chosen because in a real situation, where this approach was to be applied, the deletion of extremely rare species would not have been possible, as a result of the lack of abundance data. The DS1 matrix was transformed in a presence/absence matrix which gives the same weight to all species present in each sample. Therefore, it shifts the emphasis of the multivariate description of the communities from the dominant and intermediate species to the rarer taxa and to changes in the taxonomic composition only (Clarke & Warwick 2001). This approach discarded the abundance data, whilst maintaining the highest taxonomic resolution available.
2. Biovolume: A matrix based on the relative contribution of each taxon to the total biovolume present in each sample was constructed (*cf.* Haubois *et al.* 2005). This matrix was derived from the standardised SPECIES DATASET 2 (DS2). For each sample, the weighted relative biovolume of each taxon derived from its relative abundance and from its previously calculated median biovolume (see Diatom taxa list; section 7.3.). This approach should be considered as a severe data transformation that counters the over-estimation of the abundant small diatoms, during cell counts, whilst still retaining a high taxonomical resolution (Snoeijs *et al.* 2002).

3. Genus level: the genera abundances-per-sample matrix was obtained from DS2 by simple aggregation of the species abundance to the genus level. The resulting species abundances matrix was root transformed.
4. Presence/absence (genus level): as in the case of the species presence/absence matrix, original DS1 was chosen and root transformed.
5. Size-classes: the size-class abundances-per-sample matrix was obtained from DS2 by simple aggregation of species abundance in one of the 4 size-classes defined in section 3.2. The resulting abundances matrix was root transformed.
6. Life-forms: the life-form abundances-per-sample matrix was obtained from DS2 by simple aggregation of the species abundance to each of the 10 life-form categories. Life-form types were defined in section 3.2. The resulting abundances matrix was root transformed.

In summary, matrices with abundance data (*i.e.* biovolume, genus, size-class, life-forms and function-groups matrices) derived from DS2, whilst the presence/absence matrices (species and genus) derived from the initial species abundances matrix (DS1). Finally, a species abundance matrix that included only species from the genus *Navicula* present in DS2 was also selected and tested. All the above mentioned matrices were composed by 68 samples collected in the six sampling stations during the study period (see sections 2.2 and 3.2).

6.2.2. Matrix comparison and multivariate analyses

Sample similarities of all matrices were calculated with the Bray-Curtis coefficient (see section 3.4.1). The resulting similarity matrices, also known as resemblance matrices, were compared with each other in two different ways:

1. RELATE test and Second-stage MDS

The RELATE routine allows to measure how closely related two sets of multivariate data are. For a matching set of samples, it calculates the rank correlation coefficient (Spearman's ρ) between all the elements of their respective similarity matrices (Clarke & Gorley

2006). Very similar to the BIO-ENV routine, it is also a Mantel type test (*i.e.* with element-by-element correlations of two similarity matrices). As all resemblance matrices tested derived from the initial DS1, the permutations tests are not independent. Therefore, the concordance between two matrices was not evaluated by the significance of the test but only by the strength of their rank correlation (ρ). Not only correlations with DS2 were calculated, but all inter-matrix rank correlations were also determined. This allowed a construction of a "second-stage" non-metric MDS (Somerfield & Clarke 1995), which permits simultaneous comparisons of all different datasets. This second-stage ordination uses rank correlations calculated between pairs of similarity matrices, derived from the different datasets, which become elements of a second similarity matrix, which then is used as the input resemblance matrix of the MDS. In this ordination each point represents a similarity matrix derived from each dataset (defined in section 6.2.1.) and the distances between them (and particularly to DS2) can be evaluated.

2. ANOSIM test, diatom assemblage multivariate patterns (MDS, SIMPER) and linkage to abiotic matrix (BIOENV)

In chapter 4, the spatial and temporal patterns of the intertidal benthic diatom communities, as well as their relation to the measured abiotic environment, were investigated using several multivariate analyses. Another way of comparing the performance of the different approaches (as defined in 6.2.1.) and determine their validity and usefulness, is to apply to them the same multivariate routines used with the species abundance dataset (*i.e.* DS2). The multivariate routines used were:

a) The ANOSIM hypothesis test for differences between groups of samples (see section 3.4.4). The two-way crossed (with no replicates) layout was chosen to test the spatial and temporal differences (Clarke & Warwick 1994). The two null hypotheses tested were: H_{01}, no spatial differences and H_{02}, no temporal differences. The significance level of sample statistic was 0.1% (*i.e.* 999 permutations). When one of the null hypotheses was not rejected a one-layout was carried out.
b) MDS ordinations were performed to better visualise the different similarity matrices (see section 3.4.3). CLUSTER analyses with the associated SIMPROF test (see section 3.4.2) were also carried out, in some of the

similarity matrices (*e.g.* DS1 species abundance and presence/absence sets). The significance level of the tests was 5%.

c) The linkages of the different biotic matrices to the environmental matrix were made with the BIOENV routine (see section 3.4.6). The associated global match permutation tests had a significance level of 0.1%, above which there was no agreement in the multivariate pattern of the biotic and abiotic matrix. The biotic matrices had the same number of samples as the abiotic matrix (*i.e.* 52 samples).

6.3. Results

The root-root transformed Bray-Curtis similarity matrices of the two species abundances datasets (DS1 and DS2) scored the highest correlation (Table 10; ρ = 0.996) and there was a superposition of both points in the second-stage MDS ordination (Figure 21). The match between the two resemblance matrices was almost perfect and this was a strong indication that the removal of more than 100 extremely rare species caused only small differences between the two species datasets. The other multivariate routines applied to DS1 bore similar results to DS2, as can be seen in the MDS ordination (Figure 22). In both cases, the two-way ANOSIM test rejected the null hypotheses (Table 11). However, with the DS1 species abundance data, the SIMPROF test associated with the CLUSTER analysis failed to find significant separation between winter/spring and summer/autumn samples in the mudflat stations V2 and V3, even at a 5% p-level (Figure 23; π= 0.58, p=14.1%). The linkage of DS1 to the environmental data (BIOENV) was significant (match test p=0.1%) and there was a high correlation between matrices (ρ= 0.860); also very similar to the one obtained with DS2 abundance matrix (Table 11). On the whole, these results confirm that there was no significant loss of information with the screening of data chosen in section 3.2, and that the multivariate routines gained in clarity with the species matrix reduction and simplification. For these reasons, the comparisons between the alternative approaches to species-level analysis were made in relation to DS2 species abundance matrix, which was used to study the multivariate patterns of the benthic diatom assemblages of the studied area (see sections 3.4, 4.2 and 5.1). The multivariate results for the different approaches are presented separately.

Table 10 – Pairwise Spearman's rank correlation between similarity matrices. All species abundance matrices (DS1, DS2 and *Navicula*) were previously root-root transformed. Genera abundance matrix, life-form and size-class matrices were previously root-transformed. The relative biovolume dataset was not transformed. All correlations significantly different from zero by a permutation test (RELATE) at p < 0.1 % (999 permutations).

	Species DS2	**Species DS1**	**Species 0-1**	**Biovolume**	**Genera**	**Gen. 0-1**	***Navicula***	**Size-class**
Species DS1	0.996							
Species 0-1	0.971	0.979						
Biovolume	0.617	0.605	0.506					
Genera	0.950	0.946	0.901	0.629				
Genera 0-1	0.890	0.898	0.935	0.455	0.844			
Navicula	0.849	0.841	0.763	0.713	0.787	0.644		
Size-class	0.796	0.793	0.726	0.612	0.780	0.648	0.760	
Life-forms	0.831	0.827	0.738	0.672	0.829	0.656	0.833	0.912

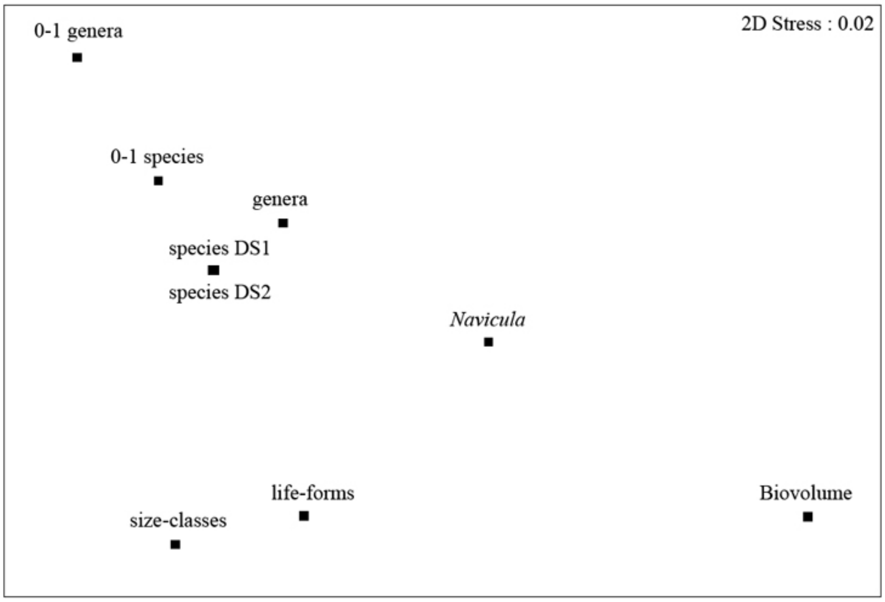

Figure 21 – Second-stage ordination by MDS of ranked inter-matrix pairwise Spearman rank correlations. Resemblance matrices included: DS1, DS2 and *Navicula* species abundances datasets; Species relative biovolume dataset; Species and genera presence-absence datasets; Life-form and Size-class abundances datasets.

6.3.1. Higher taxonomical resolution: species presence/absence matrix

The DS1 species presence/absence similarity matrix scored an extremely high Spearmen's rank correlation with DS2 species abundance similarity matrix (ρ=0.971, Table 10). The MDS ordination was very similar to the ones obtained with species abundance data (Figure 22). Even so, it had a higher stress value (0.12) and the samples of sites V2 and V3 were more dispersed, comparatively.

Both spatial and temporal null-hypotheses were rejected (Table 11), but the global statistic for temporal differences was considerable lower (R = 0.190). Conversely, most sites were well discriminated, with a global test R statistic for spatial differences of R = 0.927 ($p < 0.01\%$). However, the SIMPROF test associated with the CLUSTER analysis failed find any significant multivariate groups within the mudflat samples, at a 5% p-level (Figure 24; π = 0.34, p = 89.3%). This indicated a higher sample superposition than with the species abundances set and, although temporal null-hypothesis in the 2-way ANOSIM test was not rejected, the R statistics was very low. Finally, in the BIO-ENV routine the mud content scored a high correlation (ρ = 0.822, $p < 0.1$ %) with the biotic, presence/absence species matrix.

6.3.2. Higher taxonomical resolution: species relative biovolume matrix

While maintaining a high taxonomical resolution, the resemblance matrix of the species relative biovolumes scored the lowest correlation with the species abundance similarity matrix (ρ = 0.617). This matrix was also relatively separated from the other matrices (Table 10 and Figure 21), including from the size-classes matrix (ρ = 0.612). The species biovolume set had also did not reject the temporal null-hypothesis (at a p-level = 0.1%) and scored the lowest global R values for the spatial null-hypothesis (R = 0.644), failing to discriminate four pairs of sites. The correlation with the environmental variable set was also low (ρ = 0.599), when compared with the other matrices. Mud content, together with coarse sand and tidal height, was selected as the best environmental variable set.

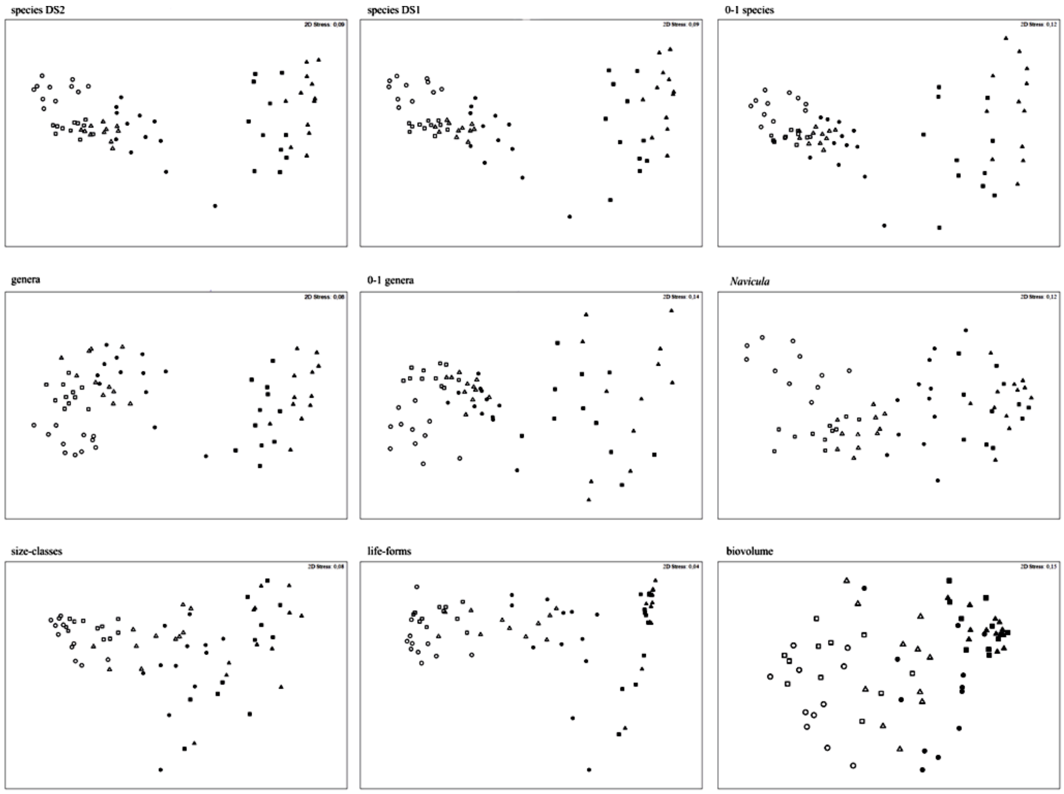

Figure 22 – MDS ordinations, based on Bray-Curtis similarity. Resemblance matrices included: DS1, DS2 and *Navicula* species abundances datasets; species relative biovolume dataset; species and genera presence-absence datasets; life-form and size-class abundances datasets. Sampling stations: A1 (○); A2 (□); A3 (Δ); V1 (●); V2 (■); V3 (▲).

6.3.3. Lower taxonomical resolution: genera matrices

The DS1 species abundance matrix was composed by 57 genera, 29 of which were represented by only one species. *Navicula*, with 29 species, was the most diverse and abundant genus; followed by *Cocconeis* (12 species) and *Fallacia* (10 species). Several genera were extremely rare and 25 of them were excluded from the DS2 species matrix because they had less the 1% in abundance and less than two occurrences. The genera abundances similarity matrix was highly correlated with the ranked similarities of the DS2 species abundances matrix (ρ = 0.95). Conversely, the genera presence/absence matrix had a much lower correlation (ρ = 0.89) and was relatively isolated from all other matrices in the second-stage MDS ordination (Figure 21).

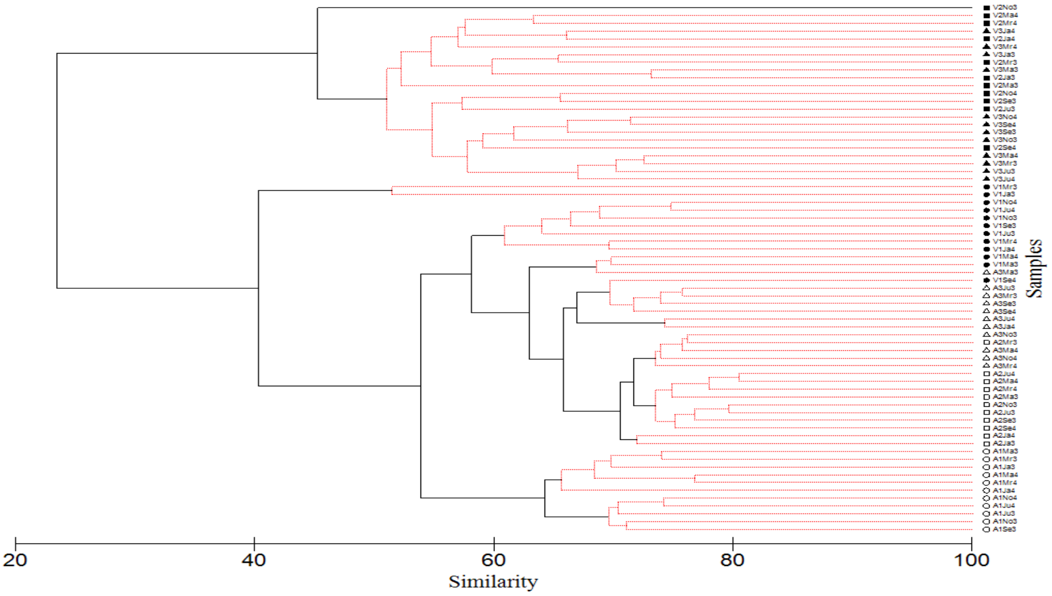

Figure 23– Dendrogram derived from DS1 species abundances matrix. Dendrogram for hierarchical clustering of diatom samples of the studied sites using group average linking of Bray–Curtis similarity. Data previously standardized and root-root transformed. Grey dotted indicate non-significant clustering (SIMPROF test; significance level: p < 5%).

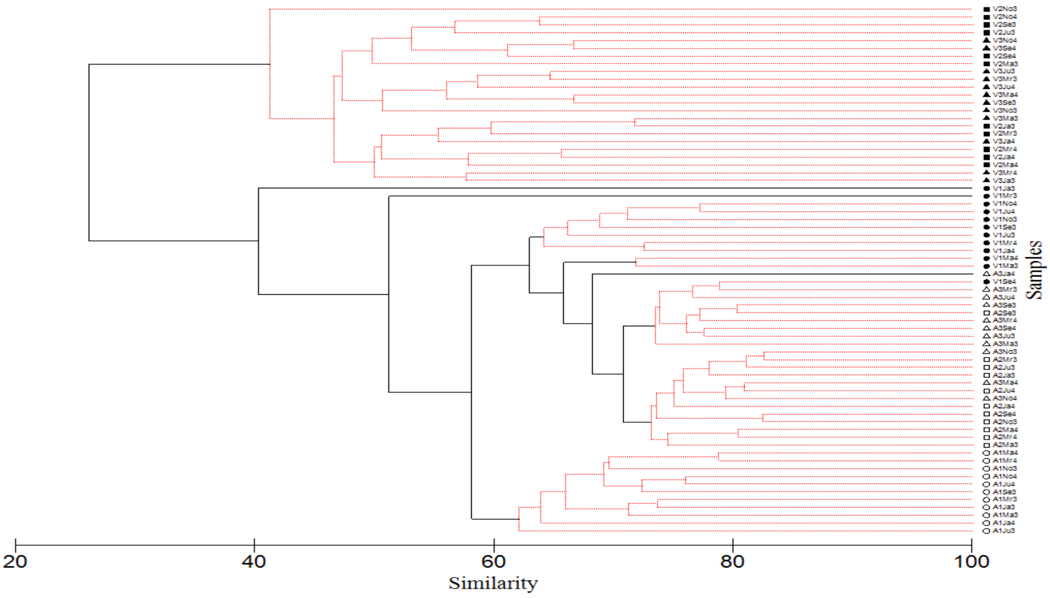

Figure 24 – Dendrogram derived from DS1 presence/absence matrix. Dendrogram for hierarchical clustering of diatom samples of the studied sites using group average linking of Bray–Curtis similarity. Grey dotted indicate non-significant clustering (SIMPROF test; significance level: p < 5%).

Table 11 – Comparison of different approaches used to study the multivariate structure of the diatom communities. The ANOSIM global test statistic (*R*) and the results of the sites' pair-wise tests (significance level $p < 0.01\%$) allow evaluating if the ability to discriminate sites is maintained. The BIOENV best environmental variable set correlation Spearman's value (ρ) measures the link between the environmental set and the different transformations of the biotic data

Similarity matrix	**2-way ANOSIM not rejected hypothesis**	**2-way ANOSIM Global *R***	**1-way ANOSIM non-significant inter-site pairwise tests ($p > 0.01\%$)**	**BIOENV (ρ)**	**Best environmental variable set**
Species - DS1		sites: 0.916 time: 0.293		0.860	Mud
Species - DS2		sites: 0.932 time: 0.308		0.863	Mud
Navicula spp.		sites: 0.688 time: 0.271		0.749	Mud, coarse sand, tidal height
Species (pres./abs.)		Sites: 0.927 Time:0.190		0.822	Mud
Species - DS2 (biovolume)	H_{02} (0.1%)	sites: 0.644 time: 0.168	A2/A3 (0.06%); A3/V1 (6.3%); V1/V2 (0.06%); V2/V3 (27.7%)	0.599	Mud, coarse sand, tidal height
Genus	H_{02} (0.03%)	sites: 0.889 time: 0.215	A3/V1 (0.2%); V2/V3 (0. 1 %)	0.859	Mud, coarse sand, medium sand, tidal height
Genus (pres./abs.)	H_{02} (11.2%)	sites: 0.840 time: 0.048	V2/V3 (1.1%)	0.767	Mud, coarse sand, medium sand
Size-classes	H_{02} (0.4%)	sites: 0.682 time: 0.131	A1/A2 (0.5%); A3/V1 (2.6%); V2/V3 (73.3 %)	0.707	Mud
Life-forms	H_{02} (3.1%)	sites: 0.806 time: 0.103	A1/A2 (0.02%); A2/A3 (0.03%); A3/V1 (0.5%); V2/V3 (25.6%)	0.773	Mud

It had a higher concordance with species presence/absence matrix than with the abundance matrices of species and genera (Table 10 and Figure 21).This lower correlation with the species matrices can be perceived in the MDS ordinations (Figure 22), where the genera presence/absence matrix has higher point dispersion, particularly the samples from station A1 and the muddy sites.

Both genera matrices did not reject the second hypothesis of the 2-way ANOSIM (*i.e.* temporal differences). In the case of the genera abundance matrix, the second hypothesis was not rejected at a slightly higher p-level (Table 11). In any way, the global R for "time differences" was low and, considering the 1-way pairwise test, the genera matrices also failed to discriminate between mudflat samples. The genera abundance matrix presented a high correlation with the environmental matrix (ρ = 0.859; Table 11). The best set of abiotic variables included mud content, coarse and medium sand fractions and tidal height. The same sediment fractions were also selected by the genus presence/absence matrix, but that set had a lower correlation (ρ = 0.795; Table 11) with the biotic data.

According to the SIMPER analysis of the genera abundances data, the genus *Navicula*, albeit being the biggest contributor to each intra-site similarity, it seldom had an impact in inter-site dissimilarities. As the most abundant and diverse genus, the 29-species *Navicula* abundance matrix had a relatively high correlation with DS2 abundance matrix (ρ = 0.849; Table 10), while maintaining both spatial and temporal signals (*i.e.* both 2-way ANOSIM hypothesis rejected, Table 11) and a relatively high correlation with abiotic matrix (ρ = 0.749; Table 11).

6.3.4. Alternative classifications: size-classes and life-forms matrices

The resemblance matrix, derived from the 4 size-classes abundance matrix, scored the second lowest Spearman's rank correlations with the DS2 species abundance set (ρ = 0.796; Table 10) as well as with the environmental set (ρ = 0.707; Table 11). Additionally, it was unable to reject the temporal null-hypothesis in the 2-way ANOSIM test. Furthermore, it had low global *R* values, in comparison with the other matrices. In the 1-way ANOSIM test, it failed to discriminate three pairs of sites (A1/A2, A3/V1 and V2/V3; Table 11), a pattern easily perceived in the MDS ordination (Figure 22).

The similarity matrix of the different life-forms abundances had a correlation of $\rho = 0.831$ with the species abundances set. It scored the highest correlation with the size-class abundances set ($\rho = 0.912$; Table 10). Both similarity matrices were separated for the others in the second-stage MDS (Figure 21). The life-form abundance matrix also failed to reject the temporal null-hypothesis, in the 2-way ANOSIM test. In the one-way ANOSIM test for spatial differences it was unable to discriminate the A3/V1 and V2/V3 pairs of sites (Table 11). The linkage to the environmental matrix was significant but it only attained a Spearman's rank correlation of $\rho = 0.773$, selecting only mud content as the best variable set.

6.4.Discussion

6.4.1. Rare species exclusion

The simplification of the diatom abundances matrix from the 181 taxa DS1 to the 94 taxa DS2 had a minor influence in the overall results. Contrary to PCA and DCA ordinations, the construction of Bray-Curtis resemblance matrices or MDS ordinations does not require the exclusion of rare species (Clarke & Warwick 2001). Rare taxa exclusion can be somewhat arbitrary and may have a great impact in the overall results of several multivariate approaches (Cao *et al.* 1997, 1999, Cao *et al.* 2001) but it also eliminates accidental occurrences that cloud the final multivariate outcome (Marchant 1999). In a careful study that evaluated the effect of exclusion of diatom taxa and of taxonomical resolution on multivariate analysis, Lavoie *et al.* (2008) concluded that the exclusion of taxa based on relative abundances could be confidently made until the ≥ 2 % threshold, however extra care must be taken when excluding taxa based on frequency of occurrence. The optimal combination for excluding rare species depends on the starting dataset and of the number of samples (Cao *et al.* 2001).

In our study, a very conservative cut-off line was chosen: species were not excluded if more less than two occurrences (in a total of 68 samples) and more than 1 % in relative abundance in one sample at least. The Bray-Curtis similarity matrices derived from DS1 and from DS2 were an almost perfect match with a very high correlation (Figure 21). In fact, the multivariate results gained in clarity with the exclusion of extremely rare taxa. The temporal signal in the mudflat assemblages became more obvious, as the SIMPROF tests of the CLUSTER analysis suggest. The elimination of allochtonous species (*e.g.* all phytoplanktonic taxa) reduced the point dispersion of the samples from V2 and V3 in the MDS ordination (Figure 22). These results showed that the chosen cut-off line proved to be adequate for it excluded 48% of DS1 taxa without loss of information.

6.4.2. Qualitative analysis: species presence-absence

Species composition studies only score the presence or the absence of taxa in each sample. High taxonomical resolution is maintained but there is no species abundance data. This approach is much less time-consuming since the scoring of 300-600 cells per sample is not necessary. However, most authors advise against the use of binary data in monitoring studies. Lavoie *et al.* (2008) demonstrates that ordinations based on presence/absence data are only capable of gross separations between impacted and reference sites in large-scale monitoring studies, while Thorne *et al.* (1999) showed that clustering of Bray-Curtis similarities and ANOSIM analyses on binary matrices performed poorer than any other transformation of the same data (*i.e.* original, root and root-root transformed data). Giving the same weight to all taxa may have major consequences when the community patterns are dependent on the abundance of a few dominant species.

Our results showed that the matrix based on binary data replicated well the several multivariate analyses outcomes and had high correlation with the environmental variables matrix. Conversely, it barely rejected the temporal ANOSIM null-hypothesis, and the CLUSER analysis failed to find any significant multivariate structure within the group of samples from the mudflat sites (stations V2 and V3), thus indicating that the seasonal signal of the epipelon is considerably diminished when the species abundances are discarded. This was expected since the SIMPER analysis of the DS2 demonstrated that the differences between sites were mainly taxonomic. The assemblages of the mudflat sites, however, where mainly distinguished by differences in the abundances of a restricted number of species (see above, chapter 4). The temporal variation of diatom mudflat assemblages was also mainly caused by shifts in abundance of the dominant species (Figure 19, chapter 4). In both cases, the binary data transformation resulted in important loss of information in the epipelon-dominated sites.

Taxonomical information alone seemed, nonetheless sufficient to spatially discriminate samples from different sediments. Therefore, it can be concluded that, given the particularities of the studied sites, the information taken from multivariate analysis based on binary, qualitative data was sufficient to adequately display the spatial patterns shown by the benthic diatom communities surveyed. However, this approach should not be used in seasonal variation studies of epipelon-dominated assemblages. Ultimately, special caution is advised in larger spatial surveys, as small differences present in similar sediment sites may remain undetected.

6.4.3. Species relative biovolume analysis

Diatoms, as other microalgae, possess a wide variety of shapes and a wide range of cell sizes, spanning over several orders of magnitude (Round *et al.* 1990). Relative abundance may inadequately represent diatom community structure because it does not account for volume differences among taxa (Hillebrand *et al.* 1999, Lavoie *et al.* 2006). As it can be seen in Figure 16 (chapter 4), high relative abundances of small-sized epipsammic diatoms may actually contribute to a smaller fraction of the overall community, when it is expressed in terms of biovolume. It also underestimates large diatoms, not only because of their higher cell volume, but also because of their rareness in routine counts (Snoeijs *et al.* 2002).

Even though these facts have long been recognised, relatively few studies have been carried out regarding the question of whether diatom community analysis should be based on biovolume or abundance data. They have been limited to the epiphyton of the Baltic Sea (Busse & Snoeijs 2002, Snoeijs *et al.* 2002, 2003a, Ulanova & Snoeijs 2006) and of Canadian freshwater systems (Cattaneo *et al.* 1997, Wunsam *et al.* 2002, Lavoie *et al.* 2006). Only a study by Haubois *et al.* (2005) dealt with this question in intertidal flats communities. The effect of biovolume in community multivariate analysis (*viz.* CCA and DCA ordinations) was measured but with different approaches. The Baltic Sea studies separated the diatom abundance matrix in two datasets (*viz.* small and large diatoms), whereas Haubois *et al.* (2005) and Lavoie *et al.* (2006) transformed the species relative abundances matrix in a relative biovolume one.

To our knowledge, the present study is the first to explore the merits of biovolume metrics in non-parametric, similarities-based, multivariate analysis in marine benthic diatom communities. The results showed that the species relative biovolume matrix performed rather poorly, when compared with the abundance-based and qualitative approaches. It had the lowest correlations with the species abundance matrices and with the environmental variables. In spite of the high taxonomic resolution, it failed to detect temporal changes and to discriminate between several pairs of sites. The studies by Haubois *et al.* (2005) and Lavoie *et al.* (2006) showed that both relative abundance and relative biovolume metrics obtained the same results but the explained percentage of species variance was higher with relative abundance data than with the relative biovolume metric.

Besides a lower ability in highlighting the spatial and temporal differences present in this group of samples, this approach has further problems. In addition to the lengthy taxonomical identifications, biovolume calculations add substantially time to the analysis in order to correctly apply the geometric formulas for each genus presented, for example, by Hildebrand *et al.* (1999). Cell size variations, brought by each species life cycle, make average biovolume measurements for each species throughout the year and from different sites inaccurate to use (Hillebrand *et al.* 1999). *Biremis lucens* is an excellent example of the large variations in cell-size that can be found in natural populations (Sabbe *et al.* 1995). Moreover, cytology and morphological plasticity of algal cells are affected by environmental conditions (Sicko-Goad & Ladewski 1977), which imply that a different vacuole correction would have to be applied for each species in every sample. It is, therefore, impractical to account for vacuole size in routine biovolume estimates since a single correction factor cannot be applied. Therefore, the employment of the relative biovolume approach in routine monitoring programs or seasonal studies in intertidal flats should be avoided.

6.4.4. Taxonomic sufficiency: genus-level analyses

Reduction of taxonomical resolution in analyses of multivariate patterns of benthic communities has obvious advantages. As lower taxonomical expertise is needed, labour and time spent on the surveys may be considerably reduced (Warwick 1988). The aggregation of species abundances to genus, family or even phylum level is fairly common in marine macroinvertebrate community analysis (Anderson *et al.* 2005 and references herein) seems to be very effective, at least to the family level (Bailey *et al.* 2001). In diatom studies, genus-level identification has been used in stream water-quality assessment with mixed results (*e.g.* Hill *et al.* 2001, Passy & Bode 2004). Round (1991) considered diatom generic identifications use in bioassessment highly dubious and Kociolek (2005) strongly advised against it, as it greatly affects diversity and richness values. Lavoie *et al.* (2008) found that genus-level multivariate analysis was only capable of detecting gross differences between impacted and reference sites, mirroring the effects of binary data transformation or to excessive exclusion of rare taxa. Conversely, other authors found rather high correlations between diatom species and genus richness (*e.g.* Hill *et al.* 2001, Passy & Legendre 2006) and/or assemblage structure (Heino & Soininen 2007).

Since the community analysis, in this study, was made at the species level, a simple aggregation of the species abundances data allowed testing the effect of genus-level identification. Further reduction of taxonomical resolution seemed to be premature, although Heine & Soininen (2007) tested family level analysis. Many higher taxonomical groups are paraphyletic (Round *et al.* 1990, Medlin & Kaczmarska 2004) and a more natural system of classification with monophyletic groups, determined by morphological and molecular techniques still needs to be implemented (Williams & Kociolek 2007). Even at the genus level, some problems still persist. Some genera, like *Navicula* s.s. (Cox 1995, Lange-Bertalot 2001), have been more correctly circumscribed but in others cases (*e.g.* *Nitzschia*) still much research is needed. Moreover, the high species-to-genus ratios in diatoms may result in lower correlations between species and genus matrices, when compared to the ones obtained with other groups of organisms used in monitoring programs, such as the macroinvertebrates (Heino & Soininen 2007).

On the whole, no notable differences between the analyses of species and genus abundances data were found. The genus-level dataset had an extremely high correlation with the full species dataset and both similarity matrices can be considered interchangeable. The overall pattern of community structure was retained (MDS, Figure 22), and even the correlation with the environmental variables set was very high. These were all strong indications that little information was lost by the reduction in taxonomical resolution and that change in intertidal diatom communities can still be clearly reflected at the genus-level. The massive effect of sediment composition on community structure, reflected by the high structural redundancy (at species-level), was also replicated here. Genus-level identification could, therefore, be considered as more than sufficient to detect changes in diatom community structure living in contrasting sediment types.

There are, however, some cautionary points that should be discussed. First, the seasonal changes in the mudflat assemblages were reduced to changes in the relative proportions of, essentially, three genera (*i.e. Navicula*, *Cylindrotheca* and *Gyrosigma*). The species-specific blooms (*e.g. N. gregaria* and *N. spartinetensis*) disappeared with the aggregation to genus-level. Temporal changes may, therefore, become less visible with a reduction of taxonomical resolution. Second, when sediment differences were less marked, or the assemblages were less diverse (*e.g.* mudflat assemblages) the detection of community change, at the genus-level, became much more difficult (one-way ANOSIM test, table 11). Finally, some information is bound to be lost when dealing with ubiquitous, abundant genus such as *Navicula*, which have high beta-diversity (with large variations in species from site to site). The analysis of the 29-species *Navicula* set, clearly showed the importance of this genus and of species-level community studies. It still had a high correlation with the full species set even though it failed to discriminate between muddy sites.

As in the case of the presence/absence data, some of the more subtle spatial and temporal changes may pass undetected with the genus–level approach (*viz.* Somerfield & Clarke 1995, Hill *et al.* 2001, Lavoie *et al.* 2008). Some authors (*e.g.* Bowman & Bailey 1997, Thorne *et al.* 1999) consider that preservation of abundance data is preferable to the maintenance of high taxonomic resolution in qualitative data. In our study the genus abundance matrix had lower discriminative power (ANOSIM) but a higher correlation with the abiotic data (BIOENV). Both approaches produced very similar results and the recommendations given above for the use of binary data are also applicable to genus-level analyses. On the other hand, when binary data is coupled with lower taxonomical resolution the results were considerably worse (Table 11; Figures 21 and 22), which is in agreement with several other studies (Bowman & Bailey 1997, Heino 2008).

6.4.5. Taxonomic surrogacy: size-classes and life-forms analysis

A different cost-effective approach is to avoid diatom identification altogether, using more straightforward alternative classifications that still can provide relevant ecological information on community structure. One simple way to do so is to separate the diatoms into size-classes. As discussed above, cell size has important ecological consequences but, instead of transforming the species abundances dataset into species relative bio-volumes, one can re-organize the diatom abundance data in a few, well defined size-classes. This approach was tested by Cattaneo *et al.* (1997) and Wunsam *et al.* (2002) in freshwater periphytic communities. These authors concluded that there was no complete correspondence between the set of environmental variables most responsible for the distributions of the diatom size-classes and of the diatom species. Nevertheless, the size class approach was still able to detect the effect of nutrient and trophic gradients in freshwater periphyton.

In this study, the size-class relative abundance matrix achieved average results, when compared with the other essayed approaches. The issuing resemblance matrix had lower correlations with the species matrices and with environmental dataset, but still above 0.7 and significant. It failed, however, to detect the temporal signal and to discriminate significantly the samples of 3 pairs of sites (Table 11). This seemed to be one of the greater limitations, given that it was unsuccessful in separating the assemblages from stations with distinct sediment textures (*i.e.* A1/A2 and V1/V2). Moreover, the actual ecological meaning in the intertidal context of the four predefined size-classes remains to be confirmed. For example, the fact that the small motile epipsammic and epipelic species are included in the same size-class may pose a problem. Nevertheless, this approach produced interpretable multivariate results, separating the mudflat and sandflat assemblages and linking this pattern to sediment texture. Nonetheless, the results of multivariate analysis on size-classes datasets in intertidal benthic diatom studies seem limited.

Another alternative is to aggregate biota into functional groups with consistent morphology, behaviour and/or life history strategies. The functional group approach stresses similarities among unrelated species that share critical organismal features (Steneck & Dethier 1994). Functional groups have been recurrently used in estuarine and coastal macrofaunal (*e.g.* Bonsdorff & Pearson 1999), fish (Elliott *et al.* 2007) and macroalgal (Steneck &

Dethier 1994) community ecology studies, and recently in oceanic phytoplankton (Nair *et al.* 2008). The ecological value of epiphytic algal growth forms is well established in lotic systems studies (Biggs 1996) and the advantages of integrating morphology, ecological and physiological functions in an epibenthic diatom growth form approach were already pointed out by Hudon and Legendre (1987). This approach has been successfully applied by Kutka & Richards (1996) and Passy (2007), which obtained a high congruence between diatom species distribution and diatom ecological guild distribution along nutrient and disturbance gradients in running freshwaters.

Overall, the life-form approach had a slightly better performance than the size-class approach. The basic separation between mudflat and sandflat assemblages was maintained and a fairly high and significant correlation with mud content was achieved. Nevertheless, it failed to detect any temporal signal and to discriminate sites with similar sediment. In addition, it was only capable discriminating the samples from sites A1 and A2 at a slightly higher significance level (p-level = 0.02%). These two sites had slightly different sediment texture and the stalked diatoms were almost exclusively present in A1 (Figure 17, chapter 4). The great similarity between the life-form and size-class resemblance matrices was probably due to the fact that the separation of motile biraphid diatoms in three life-forms was partially size-based (*i.e.* Mo<20sm, Mo<20pl and Mo>20pl). This classification replicated the division between diatoms with biovolumes above or below 1000 μm^3 (*viz.* sections 3.5 and 4.4). Although the life-form groups have greater ecological meaning than cruder size-class separations, there was still a relevant loss of information in comparison to the other approaches. This was probably caused by the remaining species variability, still contained within each functional group. As discussed in section 4.4., there were differences in the spatial distribution of individual species on small motile epipsammic diatom taxa, in the sandy transect, and also in the distribution of motile epipelic species in the mudflat stations. An additional caveat of this approach is the assignment of each species to the correct life-form. The autoecology of most coastal benthic species is little known (Sullivan 1999) and, as stated in section 4.4., there may be an apparent superposition between life-forms (*e.g.* the adnate-small motile epipsammic forms continuum). The functional group approach does not perform as well as the species, but may legitimately be used to detect shifts in the dominant algal form (Phillips *et al.* 1997).

6.5. Conclusion

We do not advocate replacement of species-level identification by any surrogate and we are well aware of the limitations that can brought by a lack of sufficient taxonomic resolution in community ecology studies (Kociolek & Stoermer 2001, Kociolek 2005). The impressive performance of the set composed by the 29 species of *Navicula* is a shining example of the variation that exists within each genus and the amount of useful information that is contained in species-level studies. However, taking into account that many MPB ecologists lack satisfactory diatom identification skills, we hope that this type of study can allow them to confidently choose the surrogate to species-level analysis that is more adequate to their particular kind of study.

All approaches performed quite well and replicated more or less satisfactorily the multivariate patterns given by the species-level study (described in detail in chapter 4). This overall success in detecting shifts in community structure seems to be, at least in part, a consequence of the particular set of samples chosen in this study. As discussed in chapter 4, the very contrasting sediment textures and disturbance conditions of the 6 sampling stations were clearly reflected in the differences in community structure, not only taxonomically but also in diatom size functional groups distribution. Therefore, all alternative approaches tested here were sensitive enough to detect these sharp environmental changes. There were, however, sufficient differences between the performances of the tested approaches to establish a set of guidelines to be followed:

1. **Species presence/absence and genera abundances approaches were the most promising alternative approaches to species abundance studies.** If a fast and crude spatial distinction of tidal flats with contrasting sediments is suspected, probably the most adequate choice is a genus-level abundances matrix. This approach retains some of the abundance information and does not need great identification skills.
2. **Seasonal variations can only be confidently detected with species level abundance studies.** Species-specific blooms disappear even in the presence/absence and genus-level alternatives and they are responsible for the temporal shifts in the

mudflat diatom assemblages. Hence, neither the qualitative nor the genera approaches are advised to temporal studies.

3. **Size class or life-form surrogate datasets may not detect important environmental shifts, such as slight differences in sediment texture.** However, their suitability in detecting nutrient gradients should be further explored. They also bring pertinent functional information to the ecology of the community.
4. **The relative biovolume approach should be avoided.** This method is very time-consuming and failed to detect important differences in the structure of assemblages collected in different sediments.
5. **The employment of a surrogate should always keep in mind the study objectives and the sediment characteristics of sampled areas.** Each of the surrogates can be very practical and useful depending on the objectives of the study. However, if the sampled area has only slight variations of sediment texture or the detecting the seasonal variation of epipelic communities is a main objective of the study, species abundance matrices with high taxonomic resolution are mandatory for community studies.

Chapter 7

Diatom Identification Guide

7. Diatom Identification Guide

7.1. Introduction

The classification system adopted in this guide was recently proposed by Medlin & Kaczmarska (2004). It combines molecular and morphological data in its construction and intends to replace the former three-class system established by Round *et al.* (1990). The latter system proved to be wrong, given that the ancestor of the two pennate diatoms groups (*i.e.* araphids and raphids) was not also the ancestor of the centric diatoms group; instead, the possible ancestor was a centric diatom belonging to one of several benthic centric diatom lineages (Medlin 2006, Williams & Kociolek 2007, Mann 2010). The newer classification acknowledged this fact and created two subdivisions: Coscinodiscophytina and Bacillariophytina. The first subdivision is composed by the emended class Coscinodiscophyceae and includes all radial centric diatoms. The second subdivision includes the class Mediophyceae (for the bipolar centrics and Thalassiosirales) and an emended class of Bacillariophyceae (comprising all pennate diatoms). Mann (in Adl *et al.* 2005) mostly agreed with this new system and adopted Medlin & Kaczmarska's names but noted that the subdivision Coscinodiscophytina and the class Mediophyceae might be paraphyletic. In his proposed system, the formal taxa advanced by Medlin & Kaczmarska (2004) were used only where there seemed to be good support for monophyly (*i.e.* the Bacillariophytina and Bacillariophyceae). However, both systems were heavily criticized for still producing paraphyletic groups (Williams & Kociolek 2007). This discussion on the phylogeny and systematics of diatoms falls outside the scope of the present work and, although not consensual, the new system was adopted. This new classification is thought to have a more natural arrangement than the system proposed by Round *et al.* (1990), for it better reflects the findings of the fossil record (*e.g.* Sims *et al.* 2006).

As a matter of convenience, the system proposed by Medlin & Kaczmarska (2004) was preferred over the one advanced in Adl *et al.* (2005). Following suggestions by Medlin & Kaczmarska (2004), the orders of the Bacillariophyta given in Round *et al.* (1990) were rearranged in the three classes. The taxa described in this guide were ordered alphabetically within each family and genus. Following suggestions by Medlin & Kaczmarska (2004), the orders of the Bacillariophyta given in Round *et al.* (1990) were rearranged in the three classes. For each taxon entry the following information is given (fields in bold):

- **Name** and **author**
- **Micrographs** – plate and number of LM and/or SEM micrographs
- **Synonyms** – list of the most commonly used synonyms
- **Similar species** – list of morphologically similar taxa
- **Morphometrics**
    - **Biovolume** – median cell volume in µm^3. Calculated according to Hillebrand *et al.* (1999). For further information see section 3.5.
    - **Frustule geometry** – genus cell volume geometry proposed by Hillebrand *et al.* (1999).
    - **Length** – valve length (in µm), with minimum - (median) - maximum values and number of measurements (n). For radial centrics the **diameter** is given.
    - **Width** – valve largest breadth (in µm), with minimum - (median) - maximum values and number of measurements (n).
    - **Pervalvar axis** – estimated or measured width of cells girdle view (in µm).
    - **Striae** – number of striae in 10 µm with minimum – (median) – maximum values and number of measurements (n). Separate measurements were made in heterovalvar and dorsiventral pennate frustules. For centric diatoms, the number of areolae and/or striae was noted. When of interest the number of punctae (in 10 µm) composing the striae is also given.
    - **Processes/other features** – remarks (*e.g.* number and/or arrangement) on rimoportulae and fultoportulae of centric and pennate diatoms.
- **Description** – a detailed morphological description was added in the case of taxa that were not identified to the species level. In the other cases the references given should be consulted.
- **Notes** – remarks on morphology, nomenclature and systematics. It may include plots with striae densities of closely related taxa.
- **Distribution & Ecology** – information on spatial and seasonal distribution, biogeography and ecology. In the case of common or important taxa, a table with average relative abundances and occurrences per sampling station was added. Data on ecology was obtained from the results of this study and from consulted references.
- **References** – relevant bibliography with descriptions and/or illustrations of the identified taxon.

Terminology used in the description of the cell wall, raphe structure, valve outline and other features follows the definitions gathered in Barber & Haworth (1981), Cox (1996), Krammer & Lange-Bertalot (2000b), Ross *et al.* (1979) and Round *et al.* (1990).

7.2. Diatom taxa entries

DIVISION BACILLARIOPHYTA

SUBDIVISION COSCINODISCOPHYTINA

CLASS COSCINODISCOPHYCEAE

ORDER COSCINODISCALES

Fam. Hemisdicaceae Hendey *emend*. Simonsen

Actinocyclus Ehrenberg 1837

Genus description: Round *et al.* (1990), Hasle & Syversten (1996)

Actinocyclus normanii (Gregory) Hustedt 1857

Micrographs: Pl. 1:1-2

Synonyms:
Coscinodiscus normanii Gregory *in* Greville
Coscinodiscus subsalsus Juhlin-Dannfelt

Similar species:
Thalassiosira bramaputrae (Ehrenberg) Håkansson & Locker

Morphometrics:
Biovolume (μm^3): 2788
Frustule geometry: cylinder
Diameter (µm): 11 – (17.2) – 22.6 (n=7)
Pervalvar axis (µm): 12 (estimated)
Valve areolae/striae in 10 µm: 9 – (10) – 11 (n=7, valve face)
Processes/other features: marginal rimoportulae; central annulus indistinct or missing and also a sole marginal "pseudonodulus", typical of this family (Hasle & Syversten 1996).

Notes: *Actinocyclus normanii* has two *formae* (f.), mainly differing in size: f. *normanii* and f. *subsalsus*. Our specimens are close to f. *subsalsus* which is smaller and, more abundant in lower salinities than the nominative form, occurring even in freshwaters (*e.g.* Round *et al.* 1990). However there seems to exist a large overlap both in dimensions and in salinity ranges (Sabbe 1997 and references herein).

Distribution & Ecology: only a few valves were found in our sediment samples. *Actinocyclus normanii* is a cosmopolitan, mainly brackish water, planktonic species, common in European estuaries (*e.g.* Hasle & Syversten 1996, Witkowski *et al.* 2000). It is an invasive species in North America (Kipp 2008). It blooms in late summer and autumn.

References:
Hasle & Syversten (1996) – pg. 119
Krammer & Lange-Bertalot (1991) – pg. 88, fig. 81/1-5; 82/1-7
Snoeijs & Vilbaste (1994) – # 105/106
Witkowski *et al.* (2000) – pg. 21 fig. 4/7

Fam. Heliopeltaceae H.L. Smith

Actinoptychus Ehrenberg 1843

Genus description: Round *et al.* (1990)

***Actinoptychus* senarius** (Ehrenberg) Ehrenberg 1843

Micrographs: Pl. 1: 3-4; Pl. 37: 1

Synonyms:
Actinoptychus undulatus (Bailey) Ralfs *in* Pritchard

Morphometrics:
Biovolume (µm^3): 6923
Frustule geometry: cylinder
Diameter (µm): 14.9 – (24.2) – 35.0 (n=5)
Pervalvar axis (µm): 15 (estimated)
Valve areolae/striae in 10 µm: 5 (n=2)

Notes: valves are usually divided in six sectors with one marginal rimoportula for each raised sector. The central area is hyaline in LM.

Distribution & Ecology: cosmopolitan, solitary, thycoplanktonic species. It was extremely rare, with only two occurrences in the studied samples.

References:
Bérard-Therriault *et al.* (1987) – fig. 77, 79
Hasle & Syversten (1996) – pg. 141
Hendey (1964) – pg. p. 95, fig. XXIII: 1-2
Hustedt (1930) – pg. 475, fig. 264
Snoeijs & Potapova (1995) – # 208

ORDER MELOSIRALES

Fam. Melosiraceae Kützing

Pseudopodosira Jousé *in* Proschkina-Lavrenko 1949

Genus description: Olshtynskaya (1990)

***Pseudopodosira* sp.1**

Micrographs: Pl. 1: 5-6

Similar species:
Pseudopodosira kosugii Tanimura & Sato

Morphometrics:
Biovolume (µm^3): 589
Frustule geometry: sphere
Diameter (µm): 9.2 – (10.4) – 11.5 (n=3)
Processes/other features: this genus has rimoportulae in the valve mantle but they were not observed in our specimens.

Notes: this taxon was provisionally assigned to the genus *Pseudopodosira* because it shared many common characters with *P. kosugii,* an extant coastal marine/brackish water species (García-Rodríguez & Witkowski 2003). Namely, both are subspherical heavily silicified diatoms of the same size range, with tube-like spines and granules scattered on the valve surface. However, only a few valves were found, no observations in SEM pictures were made and this taxon has almost no recognizable features in LM. Therefore, a sound and correct identification of this small diatom was impossible. It can be easily confused with the, usually larger, *Melosira* resting spores (Tanimura & Sato 1997). Ecology unknown but, most probably, it is a thycoplanktonic species.

ORDER AULACOSEIRALES

Fam. Aulacoseiraceae Crawford

Aulacoseira Thwaites 1848

Genus description: Round *et al.* (1990); Krammer & Lange-Bertalot (1991a)

Aulacoseira granulata (Ehrenberg) Simonsen 1979

Micrographs: Pl. 1: 7-8; Pl. 37: 3

Synonyms:
Melosira granulata (Ehrenberg) Ralfs *in* Pritchard (1861)

Morphometrics:
Biovolume (µm^3): 568
Frustule geometry: cylinder
Diameter (µm): 4.4 – (5.1) – 6.6. (n=10)
Pervalvar axis (µm): 24.2 – (27.8) – 33.2 (n=6)
Valve mantle areolae (in 10 µm): 11 – (12) – 13 (n=7) areolae on each row
Processes/other features: the processes were not seen in our observations but are situated in the valve mantle near the ringleiste (*i.e.* internal annular ledge, *cf.* Round *et al.* 1990).

Notes: *Aulacoseira granulata* is an easily identifiable species, within the genus of *Aulacoseira*, because it has a large pervalvar axis, coarse mantle areolae and long linking spines. However, it is most probably that *A. granulata* is a species complex with a large amount of variation in characters within populations (Edgar & Theriot 2004).

Distribution & Ecology: *Aulacoseira granulata* is a typical planktonic species of eutrophic freshwaters (Cox 1996). The few valves found in our samples (3 occurrences) were most likely brought from the freshwater inflows.

References:
Germain (1981) – pg. 24, fig. 3: 1-6
Kobayasi, Idei *et al.*(2006) – fig. 11/12
Krammer & Lange-Bertalot (1991ab) – pg. 23, fig.16: 1, 5; 17: 1-14: 19: 1-9

Aulacoseira islandica (O. Müller) Simonsen 1979

Micrographs: Pl. 1: 9-12; Pl. 37: (?) 2

Synonyms:
Melosira islandica O. Müller

Similar species:
Aulacoseira crenulata (Ehrenberg) Thwaites

Morphometrics:
Biovolume (µm^3): 362
Frustule geometry: cylinder
Diameter (µm): 4.8 – (5.7) – 7.4 (n=3)
Pervalvar axis (µm): 14 (estimated)
Valve mantle areolae (in 10 µm): 12 (n=1) areolae for each row; 11 (n=1) areolae rows
Valve face areolae (in 10 µm): 31 (n=2)
Processes/other features: ringleiste of medium depth. Rimoportulae located both close to the ringleiste and in the middle of the mantle (Usoltseva & Likhoshway 2007).

Notes: in *Aulacoseira islandica* the rows of mantle areolae are more or less parallel to the pervalvar axis, as it is the case in *A. crenulata* (Krammer & Lange-Bertalot 1991a). This latter species, however, has more robust valves and longer connection spines.

Distribution & Ecology: freshwater planktonic species, probably cosmopolitan (*e.g.* Krammer and Lange-Bertalot 1991a) found very rarely in our samples (only 3 occurrences).

References:
Babanarzarova *et al.* (1996) – figs. 37-40
Bérard-Therriault *et al.* (1999) – pg. 29, fig. 12d
Crawford & Likhoshway (2002) – figs. 23-36
Snoeijs & Vilbaste (1994) – # 113
Krammer & Lange-Bertalot (1991a) – pg. 26, fig. 22: 1-12

Aulacoseira subartica (O. Müller) Haworth 1988

Micrographs: Pl. 1: 13-16; Pl. 37: 4-5

Synonyms:
Melosira italica subsp. *subartica* O. Müller
Aulacoseira italica subsp. *subartica* (O. Müller) Simonsen

Similar species:
Aulacoseira ambigua (Grunow) Simonsen

Morphometrics:
Biovolume (µm^3): 302
Frustule geometry: cylinder
Diameter (µm): 3.4 – (6.2) – 9.1 (n=5)
Pervalvar axis (µm): 10 (estimated)
Valve mantle areolae (in 10 µm): 18 – (22) – 25 (n=3) areolae in each row

Notes: *Aulacoseira subartica* has typically acute connection spines that are formed every two areolae rows. This feature, as well as a more inward developed ringleiste, helps to distinguish this species from *A. ambigua*, which also has helicoidally mantle areola rows.

Distribution & Ecology: cosmopolitan freshwater planktonic species (Krammer & Lange-Bertalot 1991a). Extremely rare, with only one occurrence during cell counts but it was also found in the SEM analyses.

References:
Crawford & Likhoshway (2002) – figs. 17-22
Kobayasi *et al.* (2006) – figs. 19, 20
Krammer & Lange-Bertalot (1991ab) – pg. 28; figs. 2: 1; 3: 3; 23:1-11
Snoeijs & Kasperoviciene (1996) – # 321

SUBDIVISION BACILLARIOPHYTINA

CLASS MEDIOPHYCEAE

ORDER ANAULALES

Fam. Anaulaceae (Schütt) Lemmermann

Eunotogramma Weisse 1854

Genus description: Round *et al.* (1990)

Eunotogramma dubium Hustedt 1939

Micrographs: Pl. 2: 1-8

Similar species:
Eunotogramma laevis Grunow
Eunotogramma marinum (W. Smith) Peragallo

Morphometrics:
Biovolume (µm^3): 120
Frustule geometry: half-elliptic prism
Length (µm): 8.7 – (11.4) – 21.6 (n=9)
Width (µm): 2.7 – (3.7) – 4.2 (n=6)
Pervalvar axis (µm): 5.6 – (7.3) – 10.5 (n=3)
Processes/other features: one small rimoportula near the central ventral margin. Areolation on valve face is not resolvable in LM and each valve has 2-5 transverse pseudosepta.

Notes: according to Fourtanier & Kociolek (2007), the type of this genus is not correctly designated in Round *et al.* (1990) due to the use of *E. laevis* Grunow as the generitype that is "an untenable choice unless it can be demonstrated that this species is conspecific with the material considered in the original publication". This problem was also addressed by Hustedt (1939), in his original description of *E. dubium*, and it was caused by an incomplete original description and illustration by Grunow. These two species are quite similar and can be distinguished by the fact that *E. laevis* is larger and has areolation easily resolvable in the LM (Witkowski *et al.* 2000). Additionally, *E. dubium* has a less clear valve convexity in the connective view than the *E. laevis*.

Distribution & Ecology: this species was originally described by Hustedt (1939) for intertidal sandflats of the Wadden Sea. It was also reported as common in the sandy sediments of the Westerschelde estuary (Sabbe 1997) and Brazil (Garcia-Baptista 1993). This species is likely adnate or it may be living in the interstitial space between sand grains. In our samples it was rare, with only 6 occurrences and with very low abundances, mainly in stations A3 and V1 (sandy muddy sediments), and during autumn and winter months.

References:
Hustedt (1939) – fig. 8-10
Klein (2006) – figs. 4/3(?), 5; 9/2
Sabbe (1997) – fig. 3-6
Simonsen (1987) – fig. 374/1-6

ORDER CYMATOSIRALES

Fam. Cymatosiraceae Hasle, Von Stosch & Syvertsen

Cymatosira Grunow 1862

Genus description: Hasle *et al.* (1983); Round *et al.* (1990)

Cymatosira belgica Grunow *in* Van Heurck 1881

Micrographs: Pl. 2: 9-15; Pl. 37: 6-7

Synonyms:
Cymatosira elliptica Salah

Similar species:
Cymatosira lorenziana Grunow

Morphometrics:
Biovolume (µm^3): 295
Frustule geometry: prism on parallelogram
Length (µm): 7.0 – (10.4) – 18.6 (n=22)
Width (µm): 3.4 – (4.1) – 4.5 (n=15)
Pervalvar axis (µm): 4.4 (n=4)
Punctae in 10 µm: 9 – (11) – 13 (n=21)
Processes/other features: one rimoportula placed off-centre in one valve only (per frustule). Rimoportulae present on both valves in the case of end cells. Two small ocelli, one located in each apex. Non-areolated area present in the middle of the valve but not forming a real sternum.

Notes: this species, as well as the genus, is described in detail in Hasle *et al.* (1983). *Cymatosira belgica*, as it is common in many Cymatosiraceae, exhibits a wide variation in shape and size. The recorded size range was in concordance with the observations by Sabbe (1997).

Distribution & Ecology: *Cymatosira belgica* is a common, cosmopolitan species found both in plankton and in the benthos. In the latter case, it is frequently found in sandy beaches (*e.g.* Hendey 1964; Hasle *et al.* 1983) but it can also be very abundant in silty sediments (*e.g.* Underwood 1994; Sabbe 1997). This colonial, thycoplanktonic species (*e.g.* Vos & de Wolf 1993), is probably interstitial and was found recurrently in our samples of sandy muddy stations but also in one low shore mudflat station. Although it had a high number of occurrences (23) it was present always with extremely low relative abundances (lower than 1%).

References:
Hasle *et al.* (1983) – figs. 26-71
Round *et al.* (1990) – pg. 296; figs. b-g
Witkowski *et al.* (2000) – pg. 27; fig. 10/18-22

***Cymatosira* sp.1**

Micrographs: Pl. 2: 16-17

Morphometrics:
Biovolume (µm^3): 325
Frustule geometry: prism on parallelogram
Length (µm): 13 (n=1)
Width (µm): 5.3 (n=1)
Pervalvar axis (µm): 3 (estimated)
Punctae in 10 µm: 20 (n=1)

Description: valves broadly lanceolate with a row of marginal linking spines (apparently, in LM) and a sub central rimoportula near the margin. Areolae are randomly scattered along the valve face and the higher brightness observed in the valve ends in phase-contrast LM may be attributed to the presence of apical ocelli.

Notes: only one valve was found during this study, making identification and the morphological description very difficult and incomplete. All the above described features place this unidentified species in the genus *Cymatosira* (see Hasle *et al.* 1983) but this needs to be confirmed by further observations. Ecological preferences could not to be determined, although it is likely a thycoplanktonic species.

Plagiogrammopsis Hasle, von Stosch & Syvertsen 1983
Genus description: Hasle *et al.* (1983), Round *et al.* (1990), Gardner & Crawford (1994)

Plagiogrammopsis minima *(*Salah 1955) Sabbe & Witkowski comb.nov. prov.

Micrographs: Pl. 2: 18-25; Pl. 37: 8-11

Synonyms:
Plagiogramma minimum Salah

Similar species:
Plagiogrammopsis crawfordii Witkowski, Lange-Bertalot & Metzeltin
Plagiogrammopsis mediaequatus Gardner & Crawford
Plagiogrammopsis vanheurckii (Grunow *in* Van Heurck) Hasle, von Stosch & Syversten

Morphometrics:
Biovolume (µm^3): 113
Frustule geometry: elliptic prism
Length (µm): 3.5 – (7.9) – 16.5 (n=21)
Width (µm): 1.5 – (2.0) – 2.7 (n=16)
Pervalvar axis (µm): 4 – (9) – 13(n=3)
Punctae in 10 µm: 11 – (17) – 29 (n=18)
Processes/other features: one transversal pseudoseptum within a fascia in the slightly constricted centre of the valve. One rimoportula per frustule located on the side of the pseudoseptum and slightly offset. At the poles raised ocelli open laterally in the opposite directions. Areolae are not present at the central fascia and at the poles. They are rounded and occluded externally by cribrate vela, where the presence of spinules was not asserted. All copulae apparently lack poroids. Marginal spines long, thin, branching only in flattened ends.

Notes: this species must be transferred from the genus *Plagiogramma* to the genus *Plagiogrammopsis* (Sabbe *et al.* submitted) given that *Plagiogramma* is not heterovalvous and does not have processes (Hasle *et al.* 1983, Round *et al.* 1990). Conversely, the presence of pili, which is a typical feature of *Plagiogrammopsis*, was not yet confirmed. Nonetheless, the transfer seems to be justifiable as all other features correspond to the genus description of *Plagiogrammopsis* (*e.g.* plastid morphology, presence of pseudosepta; long spines, rimoportulae, apical elevations bearing ocelli and absence of sternum), and do not occur in *Plagiogramma*.
The closely related genus *Brockmanniella* does not possess pseudosepta or external cribra with spinules (*viz.* Gardner & Crawford, 1994). Moreover it has flat valves, small marginal spines and non-elevated ocelli. *Cymatosira*, conversely, lacks fascia, pseudosepta and has a different type of spines.
The pseudoseptum is not an obligatory feature of *Plagiogrammopsis*, as two species (*P. mediaequatus* and *P. crawfordii*) lack this structure. *Plagiogrammopsis crawfordii* is extremely close to *P. minima* since the only differences seem to be the absence of pseudosepta, the existence of a fascia and a higher areolae density. In fact, Sabbe *et al.* (submitted) suggest that figs. 37-39 of plate 10 in Witkowski *et al.* (2000) rather refer to *P. minima* and not to *P. crawfordii.*

Distribution & Ecology: *Plagiogrammopsis minima* forms small zigzag colonies (2-3 cells) that are attached to themselves and to sand grains by the poles (Sabbe *et al.* submitted). It has been reported for the North Sea (*e.g.* Salah 1955) but also for North America (Cooper 1995, Witkowski *et al.* 2000). Sabbe (1997) reported this species has being restricted to fine and medium sandy sediments in the poly- to euhaline reaches of the Westerschelde estuary, whit peak abundances during summer. In our study it appeared recurrently in the samples of all stations at relatively low abundances (always less than 5%), although it was more common during summer and in sandy muddy to muddy stations.

References:
Cooper (1995) – fig. 101
Sabbe (1997) – figs. 4/6-9, 36/7-8
Salah (1955) – figs. 1/15
Witkowski *et al.* (2000) – figs. 10/37-39(?)

Pierrecomperia Sabbe, Vyverman & Ribeiro gen. nov. prov.

Genus description: taken from Sabbe *et al.* (submitted)

Cells without processes, rectangular in girdle view, forming ribbon-like colonies. Valves semi-elliptical to slightly semi-arcuate; no sternum or fascia is present. One plastid per cell, lying beneath one valve. Valve face more or less flat to curved (in transapical direction); sometimes, the central part appears to be raised. Mantle shallow. Areolae very small, more or less irregularly distributed. Simple, sometimes bifurcate linking spines are present along the valve face margin. Subapical ocelluli diagonally opposite. Cingulum deep, copulae numerous, finely porous, open, slightly ligulate. Probably belongs to the interstitial or attached flora of marine sandflats.

Pierrecomperia catenuloides Sabbe, Vyverman & Ribeiro spec. nov. prov.

Micrographs: Pl. 2: 26-30; Pl. 38: 1-4

Similar species:
Brockmanniella brockmannii (Hustedt) Hasle, von Stosch & Syvertsen
Catenula adhaerens Mereschkowsky
Hyalinella lateripunctata Witkowski, Lange-Bertalot & Metzeltin
Pteroncola inane (Giffen) Round

Morphometrics:
Biovolume (μm^3): 51
Frustule geometry: elliptic prism
Length (µm): 7.6 – (8.7) – 10.8 (n=7)
Width (µm): 2.2 – (2.5) – 3.0 (n=7)
Pervalvar axis (µm): 3 (estimated)
Punctae in 10 µm: 26 – (28) – 30 (n=3)

Description: valves small, semi-elliptical to semi-arcuate, with a slight dorsiventral asymmetry and with cuneate to rostrate ends. Valve face is almost flat, sometimes curved (in transapical direction), with the central part slightly raised. Areolation is minute, barely visible in LM, and arranged more or less irregularly in the centre of the valve. No clear hyaline area, fascia or sternum present. At each pole, an ocellus is present, opening slightly laterally, in opposite directions. The subapical ocelli have about 8 porelli. The presence of a subcentral rimoportula was not confirmed and the valves are linked by a marginal ring of simple, sometimes bifurcate, small spines.

Notes: even if the presence of a subcentral rimoportulae was not established, this taxon most probably belongs to *Cymatosiraceae*. Sabbe (1997) discusses the possible appurtenance to the sub-family Exotubocelluloideae (see Hasle *et al.* 1983), given the lack of central area and the areolae ultrastructure. However, *Exotubocellulus,* the only genus of this sub-family has a considerable higher pervalvar/apical axis length ratio, *i.e.* the valves are almost circular and cingulum has many copulae.
This species was initially assigned to *Brockmanniella* because the valves may have a slightly bulged centre and the offset position of the ocelli but it differs from *B. brockmannii* by the absence of fascia. In LM, this species may be confused with small specimens of the biraphid species *Catenula adhaerens* (see below), which also occurs in the same psammic habitats and also forms ribbon-like colonies. Other hyaline araphid species like *Pteroncola inane* or *Hyalinella lateripunctata* are larger and more robust a have completely different morphological features in SEM (see Witkowski *et al.* 2000). A more complete description and other remarks are given in Sabbe *et al.* (submitted).

Distribution & Ecology: This species typically forms ribbon-like colonies and is associated to detrital particles (Sabbe *et al.* submitted). *Pierrecomperia catenuloides* was found in the fine/medium sand stations, throughout the sampling period, with very low abundances (up to 1.1%). Sabbe (1997) also recorded this species has part of the interstitial flora living in fine sandy sediments in the poly- euhaline reaches of the Westerschelde estuary. He remarked that distribution contrasted with the distribution of *C. belgica* and *B. brockmannii* which occurred in silty sediments. He also reported that *P. catenuloides* is present in Hustedt's material from the German Wadden Sea.

References:
Sabbe (1997) – pg. 71; figs. 4/16-17; 37/3-4

ORDER THALASSIOSIRALES

Fam. Thalassiosiraceae Lebour

Minidiscus Hasle 1973

Genus description: Quiroga & Chrétiennot-Dinet (2004); Round *et al.* (1990)

Minidiscus chilensis Rivera *in* Rivera & Koch 1984

Micrographs: Pl. 2:31-34; Pl. 38: 5-6

Similar species:
Minidiscus decoratus Quiroga & Chrétiennot-Dinet

Morphometrics:
Biovolume (µm^3): 75
Frustule geometry: cylinder
Diameter (µm): 3.5 – (4.6) – 7.3 (n=11)
Pervalvar axis (µm): 4 (estimated)
Valve areolae in 10 µm: 98 (n=3, marginal rows of areolae)
Processes/other features: 3 central fultoportulae around the central areola, one near the depressed area and the other two on the elevated area. The rimoportulae are located between these two elevated fultoportulae.

Notes: it is extremely difficult to correctly identify *Minidiscus* species in LM, since their very small cells can be easily overlooked. Our observations in the SEM consistently found the same taxon, *M. chilensis*, in different samples. This species differs from the other closely related taxa not only by its characteristic central process arrangement but also for having, typically, very small and dense areolae organized on radial rows that are present only near the margin of the valve.

Distribution & Ecology: coastal marine planktonic species originally described for the coast of Chile but also found the Mexican Pacific coast, in the NW Atlantic coasts (*e.g.* Gulf of St. Laurent) and in the Indian ocean (*e.g.* Kerguelen Islands coast). Common in the Antarctic ocean (Kang *et al.* 2003). More recently it has been found in the English Channel and in the French Atlantic coast (Quiroga & Chrétiennot-Dinet; 2004). This constitutes, most likely, the first description of the species for Portugal. Extremely rare in our samples, with only two occurrences during cell counts, but it was also found during the SEM studies.

References:
Bérard-Therriault *et al.* (1999) – pg. 29, fig. 2/b
Bérard-Therriault *et al.* (1987) – fig. 21
Hasle and Syvertsen (1996) – pg. 39; fig 2
Quiroga & Chrétiennot-Dinet (2004) – figs. 7, 8 and 16
Kang *et al.* (2003) – figs 2/a-f, 3/a-f

Thalassiosira Cleve 1873

Genus description: Hasle & Syversten (1996), Round *et al.* 1990

Thalassiosira angulata (Gregory) Hasle 1978

Micrographs: Pl. 2: 35-39; Pl. 39: 4

Synonyms:
Thalassiosira decipiens (Grunow) Jørgensen
non Thalassiosira decipiens (Grunow) Jørgensen *in* Hasle

Similar species:
Thalassiosira decipiens (Grunow) Jørgensen
Thalassiosira pacifica Gran & Angst

Morphometrics:
Biovolume (µm^3): 796
Frustule geometry: cylinder
Diameter (µm): 8.7 – (13.0) – 20.5 (n=35)
Pervalvar axis (µm): 6 (estimated)
Valve areolae/striae in 10 µm: 10 – (14) – 17 (n=35, valve face); 14 – (19) – 23 (n=23, valve margin)
Processes: marginal fultoportulae, 2 – (3) – 5 in 10 µm (n=28); one central fultoportula; one submarginal rimoportula, between two fultoportulae and closer to one of them.

Notes: *Thalassiosira angulata* is morphologically very similar to *T. decipiens*, with which it can be easily confused, as they can co-occur in the same estuaries and coastal zones. Hasle (*e.g.* 1978c) compared the holotype of both species and concluded that *T. angulata* has smaller areolae and a larger distance between the marginal fultoportulae (about 3 in 10 µm). The position of the marginal rimoportula is also different (close to one fultoportula in *T. angulata*, between two fultoportulae in *T. decipiens*). Other differences include the shape of the ends of the fultoportulae external tubes and the arrangement of the areolae near the mantle (but see Muylaert & Sabbe 1996b). In addition, it should be noted that the position of the submarginal rimoportulae may vary slightly with salinity in *T. decipiens* (McMillan & Johansen 1988).

Distribution & Ecology: *Thalassiosira angulata* is considered to be mainly planktonic and a typical marine species (Hasle, 1978), whereas *T. decipiens* is more common in great inland seas, estuaries, bays, shallow coastal waters and rivers influenced by the tide (Hasle 1979). These two species can co-occur but have different autoecologies. It is likely that *T. decipiens* is a thycoplanktonic and even benthic species (Muylaert & Sabbe 1996b and references herein). Extremely rare in our samples, it had only 8 occurrences, mainly in silty sediments, and always with less than 0.3 % in relative abundance.

References:
Harris *et al.* (1995) – figs. 3, 21
Hasle (1978a) – figs. 70-99
Hasle & Syversten (1996) – pg. 51
Hoppenrath *et al.* (2007) – figs. 4-5
Muylaert & Sabbe (1996) – figs. 2-6

Thalassiosira binata Fryxell 1977

Micrographs: Pl. 2: 40-41; Pl. 39: 5-6

Similar species:
Thalassiosira nordenskioeldii Cleve

Morphometrics:
Biovolume (µm^3): 99
Frustule geometry: cylinder
Diameter (µm): 6.0 – (6.5) – 7.5 (n=4)
Pervalvar axis (µm): 3 (estimated)
Valve areolae/striae in 10 µm: Irresolvable in the LM, 30-40. Areolae in radial rows.
Processes: one central fultoportula; five marginal fultoportulae, (n=4); one marginal rimoportula, near a fultoportula.

Notes: this taxon was described in detail by Hasle & Fryxell (1977) and by Takano (1978). It resembles *T. nordenskioeldii*, as both species have similar process patterns and have a sharp shift of angle of the valve at the mantle. *Thalassiosira binata* is generally smaller and has much finer areolation than *T. nordenskioeldii*. Additionally it has a shorter pervalvar axis.

Distribution & Ecology: Planktonic coastal and estuarine species occurring in temperate to warm waters (Hasle & Syversten 1996). This species only occurred twice in our study (max. abundance < 3%).

References:
Hasle (1978c) – pg. 78
Hasle & Fryxell (1977) – figs. 24-38
Licea (1990) – fig. 2
Takano (1978) – figs 1-9

Thalassiosira minima Gaarder 1951

Micrographs: Pl. 2: 42-47; Pl. 38: 7-8

Synonyms:
Thalassiosira floridana (Cooper) Hasle

Similar species:
Thalassiosira decipiens (Grunow) Jørgensen (small valves)

Morphometrics:
Biovolume (µm^3): 201
Frustule geometry: cylinder
Diameter (µm): 7.5 – (8.0) – 9 (n=4)
Pervalvar axis (µm): 4 (estimated)
Valve areolae/striae in 10 µm: 40 (n= 1, valve face), in LM areolation barely resolvable at the centre of the valve.
Processes: 4 marginal fultoportulae in 10 µm (n=2), 7-8 in total; two central fultoportulae; one marginal rimoportula, next to one strutted process.

Notes: this species has very small frustules and is one of the few *Thalassiosira* that has two central strutted processes and one ring of marginal fultoportulae.

Distribution & Ecology: planktonic, cosmopolitan with the exception of polar regions (Hasle & Syversten 1996). Extremely rare in our samples, it was found only once during cell counts and twice in the SEM mounts.

References:
Bérard-Therriault *et al.* (1999) – pg. 25, fig. 11/f-g(?)
Harris *et al.* (1995) – figs. 14, 31
Hasle & Syversten (1996) – pg. 65
Hoppenrath *et al.* (2007) – figs. 38-40
Muylaert & Sabbe 1996 – figs. 2-6

Thalassiosira cf. ***profunda*** (Hendey) Hasle 1973

Micrographs: Pl. 2: 48-49

Similar species:
Thalassiosira proschkinae Makarova *in* Makarova, Genkal & Kuzmln

Morphometrics:
Biovolume (µm^3): 35
Frustule geometry: cylinder
Diameter (µm): 3 (n=2)
Pervalvar axis (µm): 3 (estimated)
Valve areolae in 10 µm: irresolvable in LM, 40-50 (in Aké-Castillo *et al.* 1999)
Processes: four marginal fultoportulae; one central fultoportulae; two marginal rimoportulae (in Aké-Castillo *et al.* 1999).

Notes: *Thalassiosira profunda* has very small valves and almost imperceptible features in LM, making identification tentative without SEM. However, the size range and the marginal processes make this identification very plausible.

Distribution & Ecology: probably thycoplanktonic. It was recurrently found in samples of the muddy transect but with low abundances (<2%). This species is described for temperate to subtropical waters (Hasle 1973 b, Hallegraeff 1984).

References:
Aké-Castillo *et al.* (1999) – fig. 22

Thalassiosira proschkinae Makarova in Makarova, Genkal & Kuzmln 1979

Micrographs: Pl. 2: 50-51; Pl. 38: (?) 9-10

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

Similar species:
Thalassiosira perpusilla Kozlova

Thalassiosira levanderi Van Goor

Morphometrics:
Biovolume (µm^3): 88
Frustule geometry: cylinder
Diameter (µm): 4.4 – (6.1) – 8.7 (n=15)
Pervalvar axis (µm): 3 (estimated)
Valve areolae in 10 µm: 20 – (27) – 31 (n=13, valve face)
Processes: 4 – (5) – 6 marginal fultoportulae in 10 µm (n=15); one central fultoportula; one subcentral rimoportula.

Notes: this very small species is easily recognisable and can be distinguished from other small *Thalassiosira,* not only by its areolation and marginal fultoportulae pattern but, especially, by its uncommon subcentral rimoportula (*viz.* Hasle & Syversten 1996). *T. spinulata* has silicified spines covering the external valve face (seen only with SEM) that were not observed in our specimens. Both taxa have been considered conspecific (Hasle & Syversten 1996).

Distribution & Ecology: cosmopolitan, frequently found in plankton (*e.g.* Hasle and Syversten 1996, Krammer and Lange-Bertalot 1991a) and in the benthic assemblages in brackish waters worldwide (*e.g.* Bérard-Therriault *et al.* 1987; Snoeijs 1993). Muylaert and Sabbe (1996) frequently found this species in the polyhaline and mesohaline reaches of the Schelde estuary, particularly in intertidal sediments. According to these authors most of its cells are covered with sediment and detrital material, which can cause suspended cells to sink faster. They concluded that this could be an indication that it is a truly thycoplanktonic life-form and might play a role in confining *T. proschkinae* mainly to estuaries. This taxon was extremely rare in our samples, with only two occurrences (max. abundance < 0.63%).

References:
Bérard-Therriault *et al.* (1987) – fig. 57
Bérard-Therriault *et al.* (1999) – pg. 27; fig. 11/a
Hasle & Syversten (1996) – pg. 84; fig. 13/a-c
Hoppenrath *et al.* (2007) – fig. 48
Muylaert & Sabbe (1996) – fig. 24, 26
Krammer & Lange-Bertalot (1991a) – pg. 79; fig. 78/1-3
Snoeijs (1993) – #99
Witkowski (1994a) – pg. 82; fig. II/3-5, III/6-7

Thalassiosira cf. ***pseudonana*** Hasle & Heimdal 1970

Micrographs: Pl. 2: 52-53; Pl. 39: 1

Synonyms:
Cyclotella pseudonana (Hasle & Heimdal) Chang in Chang & Steinberg

Similar species:
Thalassiosira guillardii Hasle
Thalassiosira mala Takano
Thalassiosira oceanica Hasle

Morphometrics:
Biovolume (µm^3): 50
Frustule geometry: cylinder
Diameter (µm): 4.2 – (4.6) – 5.8 (n=3)
Pervalvar axis (µm): 3 (estimated)
Valve areolae/striae in 10 µm: irresolvable in LM
Processes: One central fultoportula; 8 – (10) – 12 marginal fultoportulae (n=3); one marginal rimoportula, close to one marginal fultoportula.

Notes: the very minute valves found during this study do not totally suit the descriptions and illustrations, given in the literature, for either *T. pseudonana* or *T. oceanica*. Apparently, they have one central fultoportula and a marginal rimoportulae close to a marginal fultoportula, which is in agreement with the descriptions of *T oceanica*. Additionally, the cells have the same size range and valve areolae of *T. oceanica* are also irresolvable in the LM. However, the marginal fultoportulae are not has widely spaced (they are around 8 in 10 µm, see references below). The density marginal processes is closer to the one found in *T. pseudonana*. This species, however, may have zero to three subcentral fultoportulae and marginal rimoportulae midway between two strutted processes, accordingly to Hasle and Heimdal

(1970) in their original LM and SEM observations of *T. pseudonana* (see also Hasle & Syversten 1996).
The SEM micrograph of the external valve was not conclusive (although it is most probably *T. oceanica*). For these reasons, the diatom found in our study was provisionally identified as *T.* cf. *pseudonana*. It is possible that both species were co-occurring in our samples but no distinction was made during counts.

Distribution & Ecology: *Thalassiosira pseudonana* is a cosmopolitan planktonic species, occurring both in freshwater (*e.g.* Krammer and Lange-Bertalot 1991a) and in estuarine and coastal waters (see references below). As for *T. oceanica*, this species is reported mainly for warm water coastal areas (Hasle and Syversten 1996). Frequently found in our samples, with 34 occurrences and being present in almost all muddy transect samples. Relative abundances varied from 0.2 to 4.6%, being most common during autumn/winter.

References: only for *T. pseudonana*. Please check also *T. oceanica*
Aké-Castillo *et al.* – figs. 23-25
Bérard-Therriault *et al.* (1999) – pg. 27; figs. 11/b, e
Harris *et al.* (1995) – fig. 25
Hasle & Heimdal (1970) – figs. 27-38
Hasle & Syversten (1996) – pg. 79; figs. 11/a-c
Muylaert & Sabbe (1996) – fig. 28
Krammer & Lange-Bertalot (1991) – pg. 80; fig. 60/6a-6b
Simonsen (1987) – fig.657/20-21
Snoeijs (1993) – #100

Thalassiosira* cf. *visurgis Hustedt 1957

Micrographs: Pl. 2: 54-55; Pl. 39: 2

Similar species:
Thalassiosira oestrupii (Ostenfeld) Hasle
Thalassiosira elsayedii Fryxell

Morphometrics:
Biovolume (µm^3): 333
Frustule geometry: cylinder
Diameter (µm): 8.7 – (10.3) – 12.3 (n=4)
Pervalvar axis (µm): 4 (estimated)
Valve areolae in 10 µm: 10 – (12) – 14 (n=4, valve face); 17 – (20) – 24 (n=4, valve margin)
Processes: four marginal fultoportulae in 10 µm (n=5); one central fultoportula and 2 marginal rimoportulae almost opposite to each other.

Notes: the few valves found in our study correspond well to the descriptions and photographs given by Aké-Castillo *et al.* (1999) and by Bérard-Therriault *et al.* (1987) for smaller specimens of *T. visurgis*. Namely, there was a good agreement in marginal and valve face areolae densities and the marginal fultoportulae distances. These authors followed description advanced by Hasle (1978b) but the overall areolation pattern, in these smaller specimens, seems to be different from the one observed in larger specimens taken from Hustedt's type material (*viz.* Simonsen 1987, Krammer & Lange-Bertalot 1991a). This discrepancy needs to be addressed in subsequent studies. Nevertheless, in the specimens found in our study, the presence of one central fultoportula and two marginal rimoportulae (a rare feature in this genus) was confirmed in the SEM. It was decided, therefore, to provisionally identify this taxon as *T.* cf. *visurgis*.

Distribution & Ecology: planktonic species common in fresh and brackish-waters in Europe and in both coasts of North America. Extremely rare in our samples, it had one occurrence in LM cell counts but was also found in SEM mounts.

References:
Aké-Castillo *et al.* (1999) – figs. 45, 46
Bérard-Therriault *et al.* (1987) – fig. 51, 53
Krammer & Lange-Bertalot (1991) – pg. 78; figs. 77/5a-b

Thalassiosira sp.1

Micrographs: Pl. 3: 1-3

Morphometrics:
Biovolume (µm^3): 468
Frustule geometry: cylinder
Diameter (µm): 8.4 – (12.2) – 15.4 (n=9)
Pervalvar axis (µm): 4 (estimated)
Valve areolae/striae in 10 µm: irresolvable in the LM
Processes: two to three sub-marginal fultoportulae in 10 µm (n=8); one central fultoportula and 1 marginal rimoportula, placed beside a sub-marginal fultoportula.

Description: valves weakly silicified, with the exception of the apparently operculate fultoportulae and the random deposition of silica over the indistinct areolae. One sub-central fultoportula is located the centre of the valve. The areolation pattern is unclear in LM.

Notes: only a few valves of this unknown species were found and in a single sample during our study. Since some of the useful details (*e.g.* areolae pattern and density) are invisible in LM, added to the overall the fragility of the valves, it was not possible to identify this *Thalassiosira*. It seems to bare some similarities to *T. rosulata* (Takano 1985) but in this species, the ring of strutted processes is near the margin and the labiate process is more isolated, in a sub marginal position and between two fultoportulae. The ecology is also unknown, although it is probably planktonic, given its rarity.

Fam. Stephanodiscaceae (Fricke) Round

Cyclotella (Kützing) *ex* Brébisson 1838

Genus description: Round *et al.* 1990; Håkansson (2002)

Cyclotella cf. *ambigua* Grunow in Cleve & Grunow 1880

Micrographs: Pl. 3: 7-9

Synonyms:
Cyclotella striata var. *ambigua* (Grunow) Grunow in Van Heurck

Similar species:
Cyclotella striata (Kützing) Grunow *in* Cleve & Grunow
Cyclotella baltica (Grunow) Håkansson = *Cyclotella littoralis* Lange & Syvertsen

Morphometrics:
Biovolume (µm^3): 1191
Frustule geometry: cylinder
Diameter (µm): 13.8 – (17.4) – 23 (n=3)
Pervalvar axis (µm): 5 (estimated)
Valve areolae/striae in 10 µm: irresolvable in the LM
Processes/other features: two central fultoportulae seen in one specimen; 8-9 marginal costae in 10 µm (n=3); marginal fultoportulae and rimoportula not determined.

Notes: the few specimens found in our study have valves that are divided in a clearly striated marginal ring and a strongly tangentially undulate central area, which has a colliculate structure (*i.e.* covered with small, rounded or hill-like elevations). This includes them in the *Cyclotella striata* species complex, which has been revised by Håkansson (1996). From the several species studied by this author, our specimens correspond to either *C. striata* or to *C. ambigua*, although the size range, marginal costa density and, apparently, valve fultoportulae are closer to the latter species. The position of the rimoportula and the density of the marginal fultoportulae could not be determined and these characters are fundamental for a correct and definite identification.

Distribution & Ecology: *Cyclotella striata* is a cosmopolitan planktonic, brackish-marine species common in the Northern Hemisphere (Hasle & Syversten 1996), whereas *C. ambigua* is an estuarine species that can be found further inland (Hustedt

1927-1930). This species was only present in a single sample.

References:
Hustedt (1927-1930) – pg. 347; fig. 176/d-e
Håkansson (1996) – figs. 40-44
Håkansson (2002) – pg. 104; figs. 371-372

Cyclotella atomus Hustedt 1937

Micrographs: Pl. 3:4-6

Similar species:
Cyclotella choctawhatcheeana Prasad
Cyclotella cryptica Reimann, Lewin & Guillard
Cyclotella meduane Germain
Cyclotella meneghiniana Kützing (small valves)

Morphometrics:
Biovolume (µm^3): 57
Frustule geometry: cylinder
Diameter (µm): 3.0 – (4.9) – 6.7 (n=17)
Pervalvar axis (µm): 3 (estimated)
Valve areolae/striae in 10 µm: irresolvable in LM and located in the marginal zone. The central area is structureless.
Processes/other features: 10 – (17) – 22 marginal costae in 10 µm (n=17). Every third or fourth costa is thickened. One subcentral fultoportula is visible. The marginal fultoportulae and one marginal rimoportula are located in some of the costa but this is visible only in SEM.

Notes: a very complete description of the morphology of this species (including type material) is given in Håkansson & Clarke (1997), which also includes comparisons with similar taxa. Genkal and Kiss (1993) described a new variety, named C. *atomus* var. *gracilis*, which is mainly distinguished from the nominate variety by a clear division of the marginal "closed" chambers from the hyaline central area, instead of a *meneghiniana*-like continuity between the centre and the marginal "open" chambers. This distinction is not clearly seen in the LM and, as Sabbe (1997) and Håkansson & Clarke (1997) pointed out, this feature is very variable. However, there is a clear difference in the position of the marginal fultoportulae in both varieties. Since it was not possible to do SEM studies on our material, the variety was not determined.

Distribution & Ecology: planktonic, cosmopolitan species, it has been found worldwide in freshwaters but also coastal marine areas (Hasle 1962). It is considered to be primarily an oligohaline species (Hasle 1962). With only two occurrences, it was extremely rare in our samples.

References:
Germain (1981) – figs. 8/1-7
Genkal & Kiss (1993) – figs. 1-16
Hasle (1962) – fig.III/19, IV/20-22, V/23-28, VI/32
Håkansson (2002) – pg. 106; figs. 381-388
Håkansson & Clarke (1997) – figs. 1-21
Kramer & Lange-Bertalot (1991a) – pg. 53; fig. 51/19-21
Simonsen (1987) – fig. 320/9-12
Snoeijs & Potapova (1995) – #226

Cyclotella meneghiniana Kützing 1844

Micrographs: Pl. 3: 10-12; Pl. 39:11-12

Synonyms:
Cyclotella kuetzingiana var. *meneghiniana* (Kützing) Brun

Similar species:
Cyclotella atomus Hustedt
Cyclotella caspia Grunow
Cyclotella choctawhatcheeana Prasad
Cyclotella cryptica Reimann, Lewin & Guillard
Cyclotella scaldensis Muylaert & Sabbe

Morphometrics:
Biovolume (µm^3): 957
Frustule geometry: cylinder
Diameter (µm): 4.9 – (13.2) – 27.5 (n=19)
Pervalvar axis (µm): 7 (estimated)
Valve areolae/striae in 10 µm: irresolvable in LM; in SEM 52 areolae in 10 µm (n=1, intercostae striae)

Processes/other features: central area usually undulated with one subcentral fultoportula in the elevated part. Marginal area well defined by radial costae, 6 – (8) – 11 in 10 µm (n=18). Short marginal fultoportulae (4 in 10 µm, n=1) present in almost every costae (*i.e.* 60% of costae). One marginal rimoportula located in one costa, opposite to the central fultoportula and radially oriented.

Notes: *Cyclotella meneghiniana* is one of the most problematic species in diatom studies, showing a wide range of habitat types and a large morphological variation (Håkansson & Cherpurnov 1999). Recently, the genetic variability of this species has been studied and it was found to consist of a large number of cryptic species (Beszteri *et al.* 2007). In estuarine waters and sediments it can be easily confused with several close species, in particular with *C. scaldensis.* The specimens observed in the SEM show several features that are common to both *C. scaldensis* and *C. meneghiniana*, such as a smooth central area (inside valve view) and marginal fultoportulae with 3 satellite pores (instead of the two pores existing in *C. atomus*, *C. choctawatcheeana* and *C. caspia* fultoportulae). It also has only marginal fultoportulae in 60% of the costae, which is a character frequently encountered in *C. scaldensis* (Muylaert & Sabbe 1996a). However, many other features of our specimens point to *C. meneghiniana*, namely, the open alveolar chambers and the radially oriented rimoportula. Moreover, in the external valve view, many characters typical of *C. scaldensis* are lacking, *viz.* the defined external openings of the fultoportulae, distinctly shaped external marginal spines and also a conspicuously colliculate central area (Beszteri *et al.* 2005). The presence of a fultoportula in every costate interstria may not be an obligatory character in *C. meneghiniana* (Håkansson 2002, fig. 278). This said, although the SEM micrographs unmistakably illustrate *C. meneghiniana*, it is possible that during counts both *C. scaldensis* and *C. meneghiniana* were co-occurring, and no distinction between them was made in the LM cell counts.

Distribution & Ecology: *Cyclotella meneghiniana* is a planktonic/thycoplanktonic cosmopolitan species that is known to prefer brackish waters or eutrophic waters with high conductivity (Sabbe 1997 and references herein). *C. scaldensis* was more recently described for the Schelde estuary (Muylaert and Sabbe 1996). These authors found that, in this estuary, C. *meneghiniana* was more common in the mesohaline reaches of the estuary, during colder months, whereas *C. scaldensis* was more abundant during spring and in the oligohaline and freshwater tidal reaches of the same estuary. In our study, only a few valves were found and only in our mudflat samples (3 occurrences, max abundance <0.32%).

References:
Bérard-Therriault *et al.* (1987) – figs. 7, 9-10
Beszteri *et al.* (2005) – figs. 1-26 (both *C. scaldensis* and *C. meneghiniana*)
Germain (1981) – pg. 32, figs. 7/1-6
Håkansson (2002) – pg. 79; figs. 263-268
Håkansson & Cherpurnov (1999) – figs. 1-49
Krammer & Lange-Bertalot (1991) – pg. 44, fig. 43/1-10
Snoeijs (1993) – #32

Thalassiocyclus Håkansson & Mahood 1993

Genus description: Håkansson & Mahood 1993

Thalassiocyclus lucens (Hustedt) Håkansson & Mahood 1993

Micrographs: Pl. 3: 13-15; Pl. 39: 7-10

Synonyms:
Cyclotella lucens (Hustedt) Simonsen
Stephanocostis lucens (Hustedt) Genkal & Makarova in Makarova & Genkal
Stephanodiscus lucens Hustedt

Similar species:
Thalassiocyclus pankensis Hiroyuki and Tamotsu

Morphometrics:
Biovolume (µm^3): 236
Frustule geometry: cylinder
Diameter (µm): 5.2 – (10.0) – 26.1 (n=26)
Pervalvar axis (µm): 3 (estimated)
Valve areolae/striae in 10 µm: irresolvable in LM; 65 – (87) – 112 (n=6, valve face), 87 (n=1, mantle) in SEM
Processes: one to three subcentral fultoportulae; 3 – (5) – 6 marginal fultoportulae in 10 µm (n=11); one marginal rimoportula, near one of the fultoportula. The fultoportulae appear to have 5 satellite pores.

Notes: a detailed morphological description of this species can be found in Håkansson & Mahood (1993). These authors established the genus *Thalassiocyclus* to accommodate *Stephanodiscus lucens*, a species that combines features of *Stephanodiscus* (*e.g.* marginal fultoportulae at the distal end of interfascicules), *Thalassiosira* (*e.g.* fultoportulae with four satellite pores, areolae organized in fascicules) and *Cyclotella* (*e.g.* tangentially undulate central area, external opening without tubulus). The taxonomical validity of the genus *Stephanocostis*, proposed earlier by Makarova and Genkal (1989) to accommodate the same taxon, was not attested.
Recently, Hiroyuki and Tamotsu (2008) described a new species, *Thalassiocyclus pankensis*, found in a brackish water swamp in Northern Japan and the second species to be described in this genus. However, apart from a slightly higher density of marginal fascicules (and of marginal fultoportulae), the two species are virtually indistinct in the LM. Most of the diagnosis of *T. pankensis* is based on SEM observations, where small differences were detected. As an example, in *T. pankensis* a small siliceous thickening transversely separates the fascicules in the central area and, in the larger cells, this feature also occurs in the marginal area. The authors also proposed that the number and position of valve face fultoportulae is different in the two species: 1 to 3 valve face fultoportulae in the elevated part and always one on the depressed part, in *T. pankensis* and only one valve face fultoportulae in *T. lucens.* However, our own SEM observations, as well as of Simonsen (1987), show that the number of valve face fultoportulae is highly variable. We frequently found 3 strutted processes in the elevated part of the central area and, in one case, a fultoportula in the depressed part. Other minute differences noticed by the authors, such as the variable number of satellite pores of the valve face fultoportulae, external openings of the rimoportulae and marginal fultoportulae may not be sufficient to cast away the possibility of conspecificity between these two close taxa. A more thorough analysis of both types, in order to establish the range of morphological variability, is therefore advisable.

Distribution & Ecology: Hustedt (1939) originally described this species from sediments of the Ems estuary and considered it has oligohalobous. Subsequently it has been reported for estuaries in Europe and also in San Francisco Bay (*e.g.* Krammer & Lange-Bertalot 1991a, Sabbe 1997). This species is probably interstitial and/or thycoplanktonic but, due to the very few reports available, its ecology is still unknown. It was fairly common in our samples (20 occurrences) being most abundant in sandy muddy and mudflat stations (up to 3.7 % of maximal abundance), in particularly during winter, when the salinity is lower.

References:
Ludes & Coste (1996) – figs. III/12-14 pg 172
Krammer & Lange-Bertalot (1991) – pg. 75; figs. 78/4-7
Simonsen (1987) – pg. 250; 372/1-10

ORDER TRICERATIALES

Fam. Plagiogrammaceae De Toni

Dimeregramma Ralfs *in* Pritchard 1861

Genus description: Round *et al.* 1990

Dimeregramma minor (Gregory) Ralfs *in* Pritchard 1861

Micrographs: Pl. 3: 16-21

Synonyms:
Denticula minor Gregory 1857

Morphometrics:
Biovolume (µm^3): 916
Frustule geometry: elliptic prism
Length (µm): 11.0 – (19.7) – 25.0 (n=3)
Width (µm): 7.4 (n=3)
Pervalvar axis (µm): 8 (estimated)
Striae in 10 µm: 10 – (13) – 14 (n=3)
Processes/other features: no rimoportula. Apical pore plates present.

Notes: most valves found in our study seemed to be of the nominate variety but valves of a smaller form (length: 11 µm, width, 7.6 µm) were also encountered and might correspond to the variety *Dimeregramma minor* var. *nana* (Gregory) Van Heurck 1885. However, the striae density of those smaller valves is lower (10 in 10 µm) than the one given in the description of that variety (*e.g.* 14 in 10 µm, Hustedt 1927-1930). Moreover, the larger specimens found in our study have, actually, a finer striation than what is given in the literature for the nominate variety *Dimeregramma minor* var. *minor* (*e.g.* 10 in 10 µm, Hustedt 1927-1930). This lack of correspondence to the original descriptions has been repeatedly noticed (*e.g.* Poulin *et al.* 1984c, Sabbe 1997) and Cooper (1995) combined both varieties, because she found intermediate forms in her study, as well as no direct relationship between length and striae density.

Distribution & Ecology: apparently cosmopolitan benthic species (*e.g.* Hendey 1964, Cooper 1995 and references herein) it is usually more abundant in sandy sediments of the polyhaline reaches in estuaries and bays (*e.g.* Sabbe 1997). It is a stalked species that attaches to the sand grains or other algae. It was very rarely found in our study, and only in samples from sandy sediments (4 occurrences, < 0.5 % of abundance).

References:
Cooper (1995) pg. 56; figs. 16/a-b
Round *et al.* (1990) – pg. 242; figs. a-k
Snoeijs & Potopova (1995) – #230
Tolomio *et al.* (1999) – figs. 23-24Floras:
Witkowski *et al.* (2000) – pg. 29; figs. 11/3-9

CLASS BACILLARIOPHYCEAE

ORDER FRAGILARIALES

Fam. Fragilariaceae Greville

The family Fragilariaceae is a traditionally difficult group given the problematic identification of many species and the distinction between them. This results from a relatively character-poor morphology of most taxa in LM; but it also derives from a confusing and complicated taxonomy, associated to most species.

The classification and systematics of fragilarioid diatoms have been subject to a lively debate during the past two decades. Krammer & Lange-Bertalot (1991a, 2000a) and colleagues (*e.g.* Witkowski *et al.* 1995a, Witkowski *et al.* 1995b) defended the maintenance (and even amplification) of *Fragilaria sensu lato*, mainly on the grounds that preserving a “conservative nomenclature” (*i.e.* attributing a sub-generic status to species groups within *Fragilaria s.l.*) was preferable to a over-splitting of *Fragilaria s.l.* in several monotypic genera, and thus increasing enormously the number of synonyms of already chaotic nomenclatural situation (Lange-Bertalot 1997a). With an opposite position, Williams & Round (1987) and Round *et al.* (1990 advocated the splitting of the large genus *Fragilaria s.l.* and created or re-established several genera. This separation and the breakup of *Fragilaria s.l.* relies heavily on new morphological information brought by electron microscopy, such as the presence/absence of rimoportulae; the structure of the striae; the presence/absence of marginal spines, their shape and type; or the presence and structure of the apical pore fields.

In recent years, this second classification system seems to have prevailed and it has been improved by the refining or by the enlarging of the circumscription of the recently created genera but also of the re-established ones (*e.g. Opephora*, Sabbe & Vyverman 1995). The description of even more fragilarioid genera and the consequent transfer of numerous taxa from the old *Fragilaria s.l.* has also been taking place (*e.g.* Morales 2003). Witkowski *et al.* (2000) still maintained a rather enlarged *Fragilaria s.l.* but accepted the transfer of several species and the creation of some of the new genera (*e.g. Pseudostaurosira*) proposed by Williams & Round (1987). In this study the *sensu stricto* definition of Fragilaria was adopted (see below).

Fragilaria Lyngbye 1819

Genus description: *sensu stricto*, Williams & Round (1987) Round *et al.* (1990); *sensu lato*, Krammer & Lange-Bertalot (1991a).

The *sensu stricto* definition of *Fragilaria* restricts this genus to mostly freshwater taxa that form ribbon-like colonies, have striae composed by simple rows of areolae, separated in the middle by a central longitudinal sternum, and have a single rimoportula. Given the still recent discussions on the concept of this genus (see above) the correct taxonomic position of some taxa is not yet known. Therefore, it is explicitly stated when the species assigned here do not belong to *Fragilaria sensu stricto*.

Fragilaria cf. **cassubica** Witkowski & Lange-Bertalot 1993

Micrographs: Pl. 4: 1-2

Synonyms:
Fragilaria subsalina (Grunow) Lange-Bertalot

Similar species:
Fragilaria atomus Hustedt
Fragilaria gedanensis Witkowski
Fragilaria schulzii Brockmann

Morphometrics:
Biovolume (µm^3): 81
Frustule geometry: elliptic prism
Length (µm): 10.3 – (12.8) – 14 (n=3)
Width (µm): 2.2 – (2.7) – 2.9 (n=3)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 17 – (18) – 19 (n=3)

Description: valves heteropolar, with a broadly rounded head pole and a cuneately rounded to slightly produced rostrate foot pole. Axial area absent and striae parallel throughout and opposite. Their structure is indistinct in LM and they are not present near the apices.

Notes: the specimens found in our study belong to the group of species around *F. schulzii* and *F. atomus*, which have as common feature striae running uninterrupted from margin to margin of the valve (Witkowski & Lange-Bertalot 1993). Snoeijs *et al.* (1991) considered that both species did not belong to *Fragilaria s.s.* but their proposed transfer to *Martyana*, a freshwater genus, needs further study (Witkowski & Lange-Bertalot 1993, Sabbe 1997). *Fragilaria cassubica* also belongs to this group and has similar size range and striae density to our specimens (Witkowski *et al.* 2000). However, only a few valves were found in our study and we were unable to confirm (with SEM) if the transapical striae were composed by circular areolae and also the existence of marginal spines. Therefore, we restrain to make a more definitive identification. According to Sabbe (1997) it is possible that *F. cassubica* and *F. atomus* are very closely related, but the type material of the latter was not yet studied in SEM, making it impossible to infer on their conspecificity. The differences to *O. gedanensis* are explained elsewhere (Witkowski 1993c). With no rimoportula and central sternum, neither

F. atomus nor *F. cassubica* seem to belong to *Fragilaria sensu stricto*.

Distribution & Ecology: small stalked species. *F. cassubica* is reported as an epipsammic species, widespread in the Baltic Sea littoral sandy sediments (Witkowski *et al.* 2000). In this study only a couple of valves of this taxon were found in a single sample of the upper shore station of the sandy transect.

References:
Krammer & Lange-Bertalot (2000a) – pgs. 138, 582; figs. 127/9-14 (as *F. subsalina*)
Witkowski & Lange-Bertalot (1993) – pg. 65; figs. 4/a-m
Witkowski *et al.* (2000) – pg. 49; 24/28-31

Fragilaria cf. ***sopotensis*** Witkowski & Lange-Bertalot 1993

Micrographs: 4: 3-7;

Synonyms:
(?) *Nanofrustulum shiloi* (Lee *et al.*) Round, Hallsteinsen & Paasche (syn. *Fragilaria shiloi* Lee, Reimer & McEnery; *Pseudostaurosira shiloi* (Lee *et al.*) Hallegraeff & Burford)

Similar species:
Fragilaria sopotensis Witkowski
Opephora krumbeinii Witkowski, Witak & Stachura

Morphometrics:
Biovolume (µm^3): 63
Frustule geometry: elliptic prism
Length (µm): 4.4 – (5.2) – 6.7 (n=9)
Width (µm): 4.1 – (4.4) – 4.9 (n=7)
Pervalvar axis (µm): 4 (estimated)
Striae in 10 µm: 16 – (19) – 22 (n=9)

Description: valves elliptical, almost circular. Axial area is distinct, linear to lanceolate. The striae are finely punctate in LM, parallel at the centre and slightly radiate towards the apices. A marginal ring of short spines seems to be present.

Notes: our specimens belong to the group of small and more or less circular species around *F. sopotensis*, *F. shiloi* and *O. krumbeinii*. These species have many similarities and overlapping size ranges and striae densities that were all considered as synonyms of *Nanofrustulum shiloi* by Sabbe *et al.* (2003). The authors did not, however, substantiate this transfer, even though *N. shiloi* (syn. *F. shiloi*) does show a certain degree of morphological variability (Round *et al.* 1999). The removal of, at least, *F. shiloi* from *Fragilaria s.s.* seems to be con*sensu*al but its transfer to the freshwater genus *Pseudostaurosira* does not seem justified (*e.g.* Witkowski *et al.* 2000). *Nanofrustulum*, a marine a brackish water genus, was therefore created to reallocate *F. shiloi* (Round *et al.* 1999).
Due to its rarity, we were unable to study this diatom in SEM and cannot be absolutely certain of its identity. The striae density in our specimens is slightly higher than the one given for *F. sopotensis* (13-17 in 10 µm, Witkowski *et al.* 2000). Conversely, *F. shiloi* has more distinctly punctate striae and *O. krumbeinii* has a zigzag shaped sternum and lacks the marginal ring of spines (*cf.* Witkowski *et al.* 2000).
The ultrastructural similarities of *N. shiloi* (see Round *et al.* 1999) and *F. sopotensis* (Witkowski *et al.* 2000, Trobajo 2007) are striking and a transfer of *F. sopotensis* to the genus *Pseudostaurosira* should be considered. Further studies are needed, however, to determine if both taxa are really conspecific.

Distribution & Ecology: *Fragilaria sopotensis* has been mainly reported for the Baltic Sea but also for the Mediterranean (Witkowski *et al.* 2000). *Nanofrustulum shiloi* is a cosmopolitan species that has been isolated from coastal and littoral environments across the world (*e.g.* Round *et al.* 1999, Sabbe *et al.* 2003), both in brackish and marine waters. Both species, as well as the specimens found in this study, can form small chain-like colonies attaching to substrates. In our study this diatom was extremely rare, only found in two samples from sandy stations and at a very low abundances (max. abundance < 0.28%).

References:
Bogaczewicz-Adamczak & Dziengo (2003) – figs. 11-13
Sabbe *et al.* (2003) – pg. 239; figs 16 & 17 (as *N. shiloi*)
Trobajo (2007) – fig. 3/16
Witkowski & Lange-Bertalot (1993) – pg. 67; figs. 6/a-p
Witkowski *et al.* (2000) – pg. 54; figs. 17/27-31, 28/36-39

***Fragilaria* sp.1**

Micrographs: Pl. 4: 8-9

Similar species:
Fragilaria subsalina (Grunow) Lange-Bertalot 1993

Morphometrics:
Biovolume (µm^3): 104
Frustule geometry: elliptic prism
Length (µm): 9.6 (n=1)
Width (µm): 4.6 (n=1)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 18 (n=1)

Description: valves elliptical and almost isopolar, with slightly produced, cuneately rounded apices. The axial area is more or less narrow and lanceolate. The striae are finely punctate and their structure is not resolvable in LM. They are almost parallel at the centre and slight radiate towards the apices. In addition, the striae alternate very slightly. In LM, the valve margin seems to be covered by a ring of interlocking spines.

Notes: the specimens found in our study are very reminiscent of the cosmopolitan species *Fragilaria subsalina*. However, they differ from that species by the fact that they have a lanceolate axial area and the striae are not distinctly punctate in LM and have a slightly higher density. Further studies, including SEM are necessary to identify the species and to determine if it even belongs to *Fragilaria sensu stricto*.

Distribution & Ecology: this diatom only occurred in a sample from the upper shore sandy station of the mudflat transect. It is epipsammic, probably stalked and, given the presence of spines may form ribbon-like colonies.

Opephora Petit 1888

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

Traditionally a "waste bin genus" used to accommodate many heteropolar fragilarioid diatoms, *Opephora* was circumscribed by Round *et al.* (1990) to house marine species, with no linking spines, no rimoportula, two apical pore fields and striae composed by slit-like areolae which are occluded by complex vela. Their definition was thought to be too narrow by several authors (*e.g.* Witkowski *et al.* 1995a). For example, the occurrence of a marginal ring of spines was found to be facultative. Although advocating that the genus *Opephora* should be maintained and that the alveolar ultrastructure of the striae (only visible in SEM) should be considered a generic feature, Sabbe & Vyverman (1995) proposed widening the interpretation given by Round *et al.* (1990), in order to include spine-bearing taxa. This suggestion was followed, for example, by Andrén (1997) in her study of *O. marina* (Gregory) Petit. More recently, Morales (2003) decided to follow the narrower circumscription of Round *et al.* (1990) in order to create new genera (*e.g. Pseudostaurosiropsis*, *Sarcophagodes*) to accommodate the taxa transferred from *Opephora* that do not share all the above mentioned features. However, in our study we decided to follow Sabbe & Vyverman (1995) wider definition of the genus. Further studies are still needed to clearly establish the taxonomic significance of morphological features (*e.g.* marginal ring of spines) within this group.

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

Micrographs: Pl. 4: 10-28; Pl. 40: 1-2

Synonyms:
Fragilaria guenter-grassii Witkowski & Lange-Bertalot

Similar species:
Fragilaria gedanensis Witkowski
Opephora horstiana Witkowski

Morphometrics:
Biovolume (µm^3): 62
Frustule geometry: elliptic prism
Length (µm): 5.7 – (9.6) – 19.2 (n=50)
Width (µm): 2.0 – (2.4) – 2.8 (n=34)
Pervalvar axis (µm): 2.8 – (3.4) – 4.7 (n=15)
Striae in 10 µm: 10 – (13) – 16 (n=52)

Notes: this species was described in detail, both in LM and SEM, by Witkowski (1994) and by Sabbe & Vyverman (1995). The original description by Witkowski & Lange-Bertalot (1993) was not consulted. Sabbe & Vyverman (1995), after numerous measurements, expanded the original morphometric data range (*e.g.* striae 9-12 in 10 µm *in* Witkowski 1994, striae density 12-17 in 10 µm *in* Sabbe & Vyverman 1995) and transferred this species from the genus *Fragilaria* to the genus *Opephora*. Our specimens fully correspond to the above mentioned descriptions. The valves have alternating striae, which are composed by areolae with indistinct cross lineolate in LM and which are not crossed by marginal longitudinal crossbars. The valves seem also to lack interlocking spines and rimoportulae.

The similarities of *O. guenter-grassii* to *F. gedanensis* were already discussed by Sabbe & Vyverman (1995) and it is very difficult to distinguish both species in LM, given the overlapping size and striae density ranges. The only distinctive feature visible in LM is the opposite stria (*i.e.* the striae do not alternate) whether, in SEM, the structure of the areolae of both species seems to be different (*e.g.* Witkowski 1993c, Witkowski 1994a). It is, therefore, possible that *F. gedanensis* is present in our samples but it was scored together with *O. guenter-grassii*, as both species are known to co-occur (Witkowski 1994, Sabbe 1997).

Opephora horstiana is another very closely related species, also with overlapping size and striae density ranges and alternating striae pattern. The main differences to *O. guenter-grassii* are the existence of marginal longitudinal crossbars from which minute interlocking spines are developed externally (Witkowski 1994). These features are not easily seen in LM. Given the fact that, in the incinerated slides, some *O. guenter-grassii*-like frustules formed chain like colonies, instead of the usual short radiating colonies (see below), it is possible that *O. horstiana* was also co-occurring in the samples studied. These possible co-occurrences may only be confirmed with further SEM observations of the collected Tagus estuary material.

Recently Morales (2002) suggested the transfer of *O. guenter-grassii* to the freshwater genus *Staurosirella* (Williams & Round 1987) on the grounds that it could not be maintained in *Opephora sensu stricto*. He did not elaborated on this decision but, given the lack of interlocking spines in *O. guenter-grassii*, it is probably related to the structure of the areolae. He also considered that the closely related *O. horstiana* and *O mutabilis* should be taken out of *Opephora*, although he did not clarify if they should be transferred to *Staurosirella*. It should be noted that, according to Williams & Round (1987), the species of *Staurosirella* have marginal spines.

Distribution & Ecology: this species has been commonly reported for sandy sediments in brackish water to marine sediments in the Baltic Sea and the North Sea coasts (Witkowski *et al.* 2000). This small epipsammic species has a stalked life-form. In the incinerated slides, the frustules were found solitary, in couples linked by the poles in a hinged position or in short radiating colonies. This confirms the observations made by Sabbe & Vyverman (1995) although, small chain-like colonies were also found (but see discussion above on *O. horstiana*). This taxon was mainly found in the upper shore fine sandy station of the sandy transect (17 occurrences), being the most common *Opephora* species found in this study (max. abundance <9.13%).

References:
Sabbe (1997) – pg. 86; figs. 5/27-35, 39/3-4
Sabbe & Vyverman (1995) – pg. 241; figs. 29-42, 66-71
Witkowski (1994) – pg. 127; figs. 5/27-31, 8/1-5
Witkowski *et al.* (2000) – pg. 70; figs. 24/40-44

Opephora mutabilis (Grunow) Sabbe & Vyverman 1995

Micrographs: Pl. 4: 29-35

Synonyms:
Opephora olsenii M. Møller
Opephora parva (Grunow *in* Van Heurck) Krasske
Sceptroneis mutabilis Grunow (*marina* var?) *in* Cleve & Möller

Similar species:
Opephora guenter-grassii (Witkowski & Lange-Bertalot) Sabbe & Vyverman
Opephora horstiana Witkowski
Opephora naveana Le Cohu (syn. *Pseudostaurosira naveana* (Le Cohu) Morales & Edlund)

Morphometrics:
Biovolume (μm^3): 167
Frustules geometry: elliptic prism
Length (µm): 5.6 – (13.6) – 23.0 (n=18)
Width (µm): 2.7 – (3.9) – 5.9 (n=11)
Pervalvar axis (µm): 3.7 – (3.95) – 4.1 (n=5)
Striae in 10 µm: 8 – (9) – 11 (n=17)
Lineolatae in 10 µm: 25 (n=1)

Notes: a detailed LM and SEM description of this species (as *O. olsenii*) was given by Sundbäck (1987). Sabbe & Vyverman (1995) described and explained the intricate nomenclatural history of this taxon. According to the latter authors, this species is closely related to *O. horstiana* and *O. guenter-grassii*. In LM, the main differences to those species are the usually very narrow sternum, the clearly cross-lineolae areolae composing the striae and, especially, the distinct longitudinal ring of spines along the valve margin. The striae alternate and are interrupted by a longitudinal crossbar. The specimens found in the Tagus estuary have a lower striae density than the specimens observed by Sabbe & Vyverman (1995) but conform well to the observations made by Sundbäck (1987).

Distribution & Ecology: this species is cosmopolitan and widespread in brackish waters, being abundant in the Baltic Sea and the North Sea (*e.g.* Witkowski *et al.* 2000). It is a small, epipsammic stalked species. It typically forms short ribbon-like colonies, which are attached to sand grains by a mucilage stalk (Sundbäck 1987). According to Sabbe & Vyverman (1995) it seems indifferent to the silt content in the sandy sediments. In our study it was much rarer than *O. guenter-grassii* (max. abundance <1.65 %) and it was found exclusively in the upper shore station of the sandy transect, which has low mud content and finer sands.

References:
Krammer & Lange-Bertalot (1991a) – pg. 166; fig. 134/9-20 (as *O. olsenii*)
Sabbe (1997) – pg. 89; figs. 5/18-25, 39/7
Sabbe & Vyverman (1995) – pg. 241; figs. 13-28, 61-63
Snoeijs (1993) – # 79
Sundbäck (1987) – pg. 142; figs. 1-39 (as *O. olsenii*)
Witkowski (1994) – pg. 174; figs. 11/4-6, 12/14-17 (as *O. olsenii*)
Witkowski *et al.* (2000) – pg. 72, figs. 25/10-17

Opephora pacifica (Grunow) Petit 1888

Micrographs: Pl. 4: 36-39

Synonyms:
Fragilaria pacifica Grunow
Grunoviella pacifica (Grunow) F.W. Mills
Sceptroneis pacifica (Grunow) Elmore

Similar species:
Opephora mutabilis (Grunow) Sabbe & Vyverman

Morphometrics:
Biovolume (µm^3): 443
Frustule geometry: elliptic prism
Length (µm): 14.6 – (21.5) – 26.0 (n=5)
Width (µm): 7.0 – (7.5) – 8.4 (n=4)
Pervalvar axis (µm): 3.5 (estimated)
Striae in 10 µm: 6 – (7) – 7 (n=5)

Notes: detailed descriptions of this well-known species were given, for example, by Poulin *et al.* (1984c, 1991a) or by Sabbe & Vyverman (1995), who studied the isotype material. The specimens found in this study conform to those descriptions even though they were only observed in LM. This taxon shows similarities to *O. mutabilis* (= *O. olsenii*) and *O. naveana*, having a certain overlap in size and striae density ranges, but it can be distinguished by the type of areolar occlusions, the absence of marginal crossbar and spines (Sabbe & Vyverman 1995).

Distribution & Ecology: stalked, epipsammic and cosmopolitan species, reported for sandy intertidal sediments and as an epiphytic species in European and in the Pacific coasts (*e.g.* Sabbe & Vyverman 1995; Witkowski *et al.* 2000). According to Sabbe & Vyverman (1995) it occurs in solitary cells. In our study, it was very rare with only two occurrences, although one of those samples had a relative abundance of 2.12 %. It was only found in the upper shore station of the sandy transect.

References:
Krammer & Lange-Bertalot (1991a) – pg.160 figs. 134/32-33
Round *et al.* (1990) –pg. 392; figs. d-j
Sabbe & Vyverman (1995) – pg. 244; figs. 45-53, 72
Witkowski (1994) – pg. 174;
Witkowski *et al.* (2000) – pg. 72, figs. 25/18-26

***Opephora* sp.1**

Micrographs: Pl. 4: 40-44; Pl. 40: 3-(?) 4

Morphometrics:
Biovolume (µm^3): 137
Frustule geometry: elliptic prism
Length (µm): 5.9 – (12.4) – 17.8 (n=12)
Width (µm): 3.9 – (4.7) – 6.2 (n=12)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 13 – (14) – 15 (n=12)
Punctae in 10 µm: 43-44 (n=2)

Description: valves are elliptical, heteropolar to almost isopolar, with broadly rounded to cuneate apices. The valve face is flat, merging gradually to a shallow mantle. The axial area is very narrow and linear. The striae are parallel at the centre and slightly radiate at the poles. In LM they are not distinctly punctate and alternate slightly throughout the valve. In SEM, the striae are composed by apically elongate areolae, which are internally occluded by vela. Interlocking spines are visible externally, along the narrow marginal crossbar. These were seldom seen in LM. Typical to this species were the minute siliceous granules on the vimines, between the areolae. On both apices there are apical pore fields. In the larger pole, these pores seem to be organized apically, whereas in the more cuneate pole they are randomly placed.

Notes: this taxon seems to correspond to the unidentified *Opephora* sp.1 described by Sabbe (1995) for the Westerschelde estuary. Both SEM and LM observations, as well as the morphometric data conform well to his observations. Sabbe (1997) also discusses the similarities and differences between his *Opephora* sp.1 and *O. mutabilis*, to which our taxon seems also to be close, namely the identical areolar occlusions and apical pore fields. Valve outline and the “small spines” found in the vimines allow the separation of both taxa. Sabbe (1995) further discusses the similarities to *Fragilaria flavovirens* Takano (1986) but this could not be assessed in the present study.

Distribution & Ecology: Sabbe (1997) reported this taxon as a common species in fine and medium sands in the lower reaches of the Westerschelde estuary and also found in Salah’s material from Blakeney Point (England, U.K.). It is a stalked, epipsammic species, forming small ribbon-like colonies. In our study this taxon was mainly found in the upper station of the sandy transect (10 out of 13 occurrences) where it also reached its higher abundances (max. abundance < 2.93%).

References:
Sabbe (1997) – pg. 93; figs. 5/36-40, 39/9-10, 40/2

Pseudostaurosira Williams & Round 1987

Genus description: Williams & Round (1987); Round *et al.* (1990); Sabbe & Vyverman (1995)

This genus was split from *Fragilaria* by Williams and Round (1987) to include a group of small species that usually form ribbon-like colonies and that are characterised by a broad sternum and by marginal areolae with branched areolar occlusions. The marginal ring of spines is obligatorily present, with each spine located between each pair of striae. Rimoportulae are absent and apical pore fields are sometimes present. Sabbe & Vyverman (1995*)* slightly emended the original description of the genus, in order to include taxa with more than two marginal areolae and variable sternum shape.

Pseudostaurosira cf. ***perminuta*** (Grunow) Sabbe & Vyverman 1995

Micrographs: Pl. 4: 45-46; Pl. 40: 5

Synonyms:
Fragilaria neoelliptica Witkowski
Opephora marina var. *perminuta* (Grunow *in* Van Heurck) Proschkina-Lavrenko
Opephora perminuta (Grunow *in* Van Heurck) Frenguelli
Grunoviella perminuta (Grunow *in* Van Heurck) Peragallo & Peragallo
Sceptroneis marina var. *perminuta* Grunow *in* Van Heurck

Similar species:
Staurosira elliptica (Schuman) Round & Williams

Morphometrics:
Biovolume (µm^3): 85
Frustule geometry: elliptic prism
Length (µm): 13.9 – (15.1) – 17.1 (n=6)
Width (µm): 2.2 – (2.4) – 2.6 (n=5)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 12 – (14) – 16 (n=6)

Description: valves usually heteropolar with cuneate to obtusely rounded apices. The valve face is flat, gradually tapering to the mantle. A lanceolate axial area is present, usually occupying half of the valve width. The striae are parallel to slightly radiate in the centre, becoming more radiate towards the apices. They more or less alternate and are composed by areolae that become increasingly apically elongate towards the margin. A ring of spines interrupts the striae in the margin but these continue, descending the mantle. In the cuneate foot-pole there is a large apical pore field, with the pori organized in more or less parallel rows. Apparently, in the other pole there also exists a smaller pore field.

Notes: this taxon is very reminiscent of *P. perminuta* as it is described and illustrated in Sabbe & Vyverman (1995). The most typical features of that species, namely the marginal ring of spines, interrupting the striae which continue below the spines and the lanceolate axial area can clearly be attested in the SEM micrograph. However, this is not the case of the additional accompanying siliceous granules or spines (*cf.* Sabbe & Vyverman 1995, Snoeijs & Balashova 1998). We therefore restrained ourselves to make a positive identification of this species without further studies. It was however easily distinguished form the co-occurring *O. mutabilis* and *O. guenter-grassii* by its larger axial area, the almost opposite striae (indistinct in LM) and the marginal ring of spines.
For discussion of close and similar taxa, as well as the nomenclatural history of *P. perminuta*, please see Sabbe & Vyverman (1995).

Distribution & Ecology: like *O. mutabilis*, *P. perminuta* is a stalked epipsammic species that forms short, ribbon-like colonies. *Pseudostaurosira perminuta* is referred for brackish and marine sediments in the North

Sea coasts and for the Baltic Sea (Witkowski *et al.* 2000). According to Sabbe (1997), *O. perminuta* prefers higher salinities, being more abundant in poly- and euhaline reaches of the Westerschelde estuary. In our study, *P.* cf. *perminuta* was found almost exclusively in the upper shore sandy station (10 occurrences) where it was present throughout the study period but never at high abundances (max. abundance < 1.4%).

References:
Sabbe & Vyverman (1995) – pg. 237; figs. 1-12, 54-60
Snoeijs & Balashova (1998) – # 481
Witkowski (1994) – pg. 128; figs. 10/1-13 (*F. neoelliptica*)
Witkowski *et al.* (2000) – pg. 76; figs. 25/35-37

Incertae sedis

Micrographs: Pl. 3: 25-27

Similar species:
Fragilaria amicorum Witkowski & Lange-Bertalot

Morphometrics:
Biovolume (µm^3): 30
Frustules geometry: elliptic prism
Length (µm): 4.1 (n=1)
Width (µm): 2 (n=1)
Pervalvar axis (µm): 5 (estimated)
Striae in 10 µm: 72 (n=1)

Description: valves very small and almost elliptical. In LM, they look structureless but a close observation shows that the valves are covered by fine striae, above the density that could make them resolvable in LM.

Notes: this extremely small diatom was impossible to identify with only a few observations in LM. It should be noted that it was not confused with close copulae of very small species (*e.g. F.* cf. *sopotensis*) because of their outline and thickness of the margin. Additionally, the changing of the focal plane in LM clearly showed that the specimens possessed a valve face. Without SEM studies it is not possible to even determine the genus. A relation to the araphid species *Fragilaria amicorum* is, nonetheless, an avenue that may be explored in future studies, given the similar size range, outline (it is linear elliptical), probable ecology and the barely resolvable (in LM) transapical striae.

Distribution & Ecology: epipsammic, probably interstitial. In this study it was only found in the upper shore station of the sandy transect where it was found in just two samples and at very low abundances (max. abundance <0.27%).

ORDER RHAPHONEIDALES

Fam. Rhaphoneidaceae Forti

Neodelphineis Takano 1982

Genus description: Round *et al.* (1990); Takano (1982)

Neodelphineis pelagica Takano 1982

Micrographs: Pl. 3: 22-23; Pl. 40: 6

Similar species:
Delphineis ovata Andrews (fossil)
Delphineis penelliptica Andrews (fossil)

Morphometrics:
Biovolume (µm^3): 100
Frustule geometry: box
Length (µm): 6.5 – (10.0) – 13.8 (n=10)
Width (µm): 4.4 – (5.1) – 6.0 (n=10)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 16 – 18 – 21 (n=10)
Punctae in 10 µm: 17 – (20) – 25 (n=5)

Notes: Takano (1982) and Hernández-Becerril (1990) explain in detail the main differences between *Neodelphineis* and the closely related genera *Delphineis* and *Ra-*

phoneis. The most striking differences are: the clear discontinuity of the transverse striae across the axial area; the striae almost do not radiate and seem to alternate; spinulae occur on the edge of the margin between the striae. *Neodelphineis pelagica* has typically one rimoportula at each apex to one side of the sternum, as it is clearly visible in Pl. 40: 6 in one of the apices. The apical pore fields are reduced to a single small pore occurring adjacent to each rimoportula, between it and the valve apex.

Distribution & Ecology: this species forms zigzag colonies in the estuarine and coastal marine plankton. Originally described for Japan by Takano (1982), where it was also found living in mudflats (Ohtsuka 2005). It is probably interstitial and thycoplanktonic. Frequently found in southern North American coasts (*e.g.* Hernández-Becerril 1990, Round *et al.* 1990) but also occurring in Chesapeake Bay (Cooper 1995). To our knowledge, this is the first report for Europe. In our study, this species was rare, with only 7 occurrences and always at very low abundances (<0.5%).

References:
Cooper (1995) – figs. 32a-b, 48
Hernández-Becerril (1990) – figs. 1-13
Round *et al.* (1990) – pg. 412; figs. a-i
Takano (1982) – figs. 1-34

ORDER THALASSIONEMATALES

Fam. Thalassionemataceae Round

Thalassionema Grunow *ex* Mereschkowsky 1902

Genus description: Round *et al.* (1990)

Thalassionema nitzschioides (Grunow) Mereschkowsky 1902

Micrographs: Pl. 3: 24

Synonyms:
Synedra nitzschioides Grunow
Thalassiothrix nitzschioides Grunow *in* Van Heurck
Thalassionema nitzschioides (Grunow) Van Heurck

Morphometrics:
Biovolume (µm^3): 291
Frustule geometry: box
Length (µm): 29.1 – (31.1) – 34.5 (n=3)
Width (µm): 2.9 – (3.1) – 3.5 (n=3)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 8 – (9) – 10 (n=3)

Notes: this taxon is described in detail elsewhere (*e.g.* Hasle & Syversten 1996, Bérard-Therriault *et al.* 1999).

Distribution & Ecology: *Thalassionema nitzschioides* is a common neritic planktonic species that forms zigzag or stellate colonies. It is a cosmopolitan species, widespread in coastal areas but with the apparent exception of the Polar Regions (Hasle & Syversten, 1996). Frequently found in estuarine phytoplankton and in the Portuguese coast where it is part of the spring bloom (*e.g.* Resende *et al.* 2007) but with only one occurrence in our samples.

References:
Bérard-Therriault *et al.* (1999) – pg. 58; figs. 48/d,e,g
Hasle & Syvertsen 1996, pg. 257; figs. 56/2, 57/b
Poulin *et al.* (1984c), p. 363, fig. 92, 9
Snoeijs & Vilbaste (1994) – #194

ORDER LYRELLALES

Fam. Lyrellaceae Mann

Petroneis Stickle & Mann 1990

Genus description: Round *et al.* (1990)

Petroneis humerosa (Brébisson *ex* W. Smith) Stickle & Mann 1990

Micrographs: Pl. 5: 1-2

Synonyms:
Navicula humerosa Brébisson

Similar species:
Petroneis latissima (Gregory) Stickle & Mann
Petroneis marina (Ralfs) Mann

Morphometrics:
Biovolume (µm^3): 29779
Frustule geometry: box
Length (µm): 55.9 – (70.5) – 96.1 (n=4)
Width (µm): 34.5 – (35.2) – 35.7 (n=4)
Pervalvar axis (µm): 12 (estimated)
Striae in 10 µm: 10 – (11) – 12 (n=4)
Lineolae in 10 µm: 10 – (13) – 15 (n=4)

Notes: recently, Jones *et al.* (2005) published a very detailed account of the valve and protoplast morphology, cell division and sexual reproduction of *P. humerosa* and other species of the genus *Petroneis*.

Distribution & Ecology: *Petroneis humerosa* is a marine and brackish water species, widespread along European coasts and the Baltic Sea (Witkowski *et al.* 2000) but also elsewhere (*e.g.* South Africa, Skinner *et al.* 2006). It preferably occurs in fine to medium sandy intertidal sediments, although usually in low numbers (*e.g.* Sabbe 1997). It is a typical example of a large epipelic species which colonizes sandflats. Occurring in our sandy transect samples, it was extremely rare during counts (only 3 occurrences). However, when examining the slides at low magnifications numerous cells were observed. Given its biovolume and apparent rareness, its importance in the sandflat diatom communities is probably underestimated.

References:
Germain (1981) – pg 216; pl. 82/1
Hendey (1964) – pg. 206; fig. XXXI/14
Jones *et al.* (2005) – figs. 1-3, 15, 17, 23, 30-32
Round *et al.* (1990) – pg. 462, figs. a-i
Snoeijs & Vilbaste (1994) – #180
Witkowski *et al.* (2000) – pg 327, figs, 101/2-3, 102/3

ORDER CYMBELLALES

Fam. Anomoeoneidaceae Mann

Dickieia Berkeley *ex* Kützing 1844

Genus description: Cox (1985), Mann (1994a)

***Dickieia* sp.1**

Micrographs: Pl. 6: 1-4; Pl. 40: 7-10

Similar species:
Dickieia ulvacea Berkeley *ex* Kützing
Dickieia subinflata (Grunow *in* Cleve & Möller) Mann
Navicula pseudoinflata Giffen

Morphometrics:
Biovolume (µm^3): 638
Frustule geometry: elliptic prism
Length (µm): 20.3 – (23.9) – 32.5 (n=10)
Width (µm): 4.8 – (5.7) – 6.7 (n=10)
Pervalvar axis (µm): 6 (estimated)
Striae in 10 µm: 11 – (13) – 14 (n=10)
Lineolae in 10 µm: 33 – (48) – 58 (n=4)

Description: valves linear-elliptical, apices broadly rounded. Valve face is almost flat, curving into a rather deep mantle. The valve is slightly thicker near the apices. Axial area is straight and narrow, central area transapically expanded and slightly asymmetrical, with two smaller striae, giving it a stauros-like facet. Striae radiate from the centre becoming parallel and narrowly spaced, halfway to each apex. In the apices, the striation becomes very dense. Their structure is irresolvable in LM. In SEM, the striae are finely but distinctly punctuate. They are composed by dense uniseriate rows of rounded poroids, which have a simple external opening but seem to be internally occluded (FIGX). Raphe is straight, with central raphe endings pore-like and slightly deflected. Internally, terminal raphe endings are straight and finish near a narrow rib-like or helictoglossa-like structure. Externally, the terminal raphe fissures are curved over the valve apex, with the curve opening towards the secondary side, but with an initial angular deflection. The valvocopulae have two transverse rows of round poroids. The plastid shape was not determined.

Notes: this taxon most probably belongs to the genus *Dickieia* which was resurrected by Mann (1994) to harbour *Navicula ulvacea* (Berkeley) Cleve, *Navicula subinflata* Grunow in Cleve and its close relatives. It is certainly very reminiscent of *Dickieia ulvacea* with which it shares many morphological characters, described in detail in Hanic & Lobban (1979) and in Cox (1985). However, *Dickieia* sp.1 is narrower than *D. ulvacea*, it has a slightly lower striae density and the striae are more finely punctate. *Navicula subinflatoides* Hustedt bares even more similarities to the taxon found in Tagus estuary but it was found to be a large form of *D. ulvacea,* through morphological and auxospore formation studies carried out by Cox (1985).
The striation pattern and the stauros-like central area are similar to the ones found in *Dickieia subinflata* but this species has more coarsely punctate striae and the polar raphe curvature turns in opposite directions. Another similar taxon is *Navicula pseudoinflata* Giffen (not yet formally transferred to *Dickieia*) but it has a higher striae density and very strongly marked central striae, which are also much more distinctly widely spaced. This taxon can only be confidently placed in the genus *Dickieia* after the structure and morphology of the plastid is determined.

Distribution & Ecology: very common and frequent in coarse/medium sandy muddy stations. It was especially abundant during summer (September) with over 10 % of relative abundances. Probably epipelic but it may be tube-dwelling. The exact life-form is not yet determined. Considering the close taxa, *Dickieia subinflata* is a free-living species living in sandy sediments (*e.g.* Hustedt 1961-1966, Cox 1985), but *D. ulvacea* is known to live in mucilage sacs (Cox, 1985) or even in foliose colonies (Hanic & Lobban 1979), although it can also be epipelic.

***Dickieia* sp.2**

Micrographs: Pl. 6: 5

Similar species:
Dickieia ulvacea Berkeley *ex* Kützing 1844

Morphometrics:
Biovolume (μm^3): 103
Frustule geometry: elliptic prism
Length (μm): 8.3 (n=2)
Width (μm): 3.2 (n=2)
Pervalvar axis (μm): 6 (estimated)
Striae in 10 μm: 22 (n=2)

Description: small elliptical valves, slightly asymmetrical, almost bean-shaped in valve view. Valve face curves in an apparently deep mantle. Axial area is straight and narrow. Striae slightly radiate, being more widely spaced at the central area. Raphe straight, with central raphe end slightly expanded.

Notes: just a few valves were observed (in the LM) making identification only tentative. The valve shape (with a deep mantle) and the striation pattern recalls *D. ulvacea*, especially *sensu* Witkowski *et al.* (2000). However, it has much smaller valves and a higher striae density than what is given in works that studied the type of *D. ulvacea* (*i.e.* Hanic & Lobban 1979) and others (*e.g.* Cox 1985, Witkowski *et al.* 2000). Even if the identification here is only tentative without further information, there are enough reasons to believe this taxon rightfully belongs to the genus *Dickieia*.

Distribution & Ecology: present in medium/coarse sandy muddy stations. Very rarely found in our samples, with only 4 occurrences and at very low abundances (< 0.3%). It is most probably small motile epipsammic species but the exact life-form is unknown.

References:
Witkowski *et al.* (2000) – pg. 181

Staurophora Mereschkowsky 1903

Genus description: Round *et al.* 1990

Staurophora salina (W. Smith) Mereschkowsky 1903

Micrographs: Pl. 6: 6-8; Pl. 41: 1-3

Synonyms:
Navicula salina (W. Smith) Schütt
Schizonema salinum (W. Smith) Kuntze
Stauroneis salina W. Smith

Similar species:
Staurophora amphioxys (Gregory) Mann *in* Round, Crawford & Mann
Staurophora wislouchii (Poretzky & Anisimova) Mann *in* Round, Crawford & Mann

Morphometrics:
Biovolume (μm^3): 2278
Frustule geometry: elliptic prism
Length (µm): 26.0 – (42.5) – 58.2 (n=17)
Width (µm): 7.4 – (9.8) – 14.2 (n=17)
Pervalvar axis (µm): 7 (estimated)
Striae in 10 µm: 18 – (20) – 21 (near central area, n=18); 24 (near apices, n=2)
Punctae in 10 µm: 40 – (47) – 52 (n=5)

Notes: the distinction between *Staurophora amphioxys* and the very similar *S. salina* is very problematic. When the literature is consulted (*e.g.* Hustedt 1931-1959, Hendey 1964, Krammer & Lange-Bertalot 1986), it becomes evident that *S. amphioxys* (syn. *Stauroneis gregorii* Ralfs in Pritchard), *S. salina* (syn. *Stauroneis salina* Smith) and *S. wislouchii* (see below) are all euryhaline species that have overlapping size ranges (*i.e.* 38 to 100 µm, although *S. amphioxys* is considered to be the largest). These species also have similar striae densities (around 20 in 10 µm) and striation patterns (slightly radiate to parallel). The main differences these authors mention are slight changes in the shape of the valves and valve ends, like an apparently narrower stauros in *S. salina*, a species that also seems to have a "somewhat more delicate structure". Hustedt (1931-1959) also pointed out for the existence in *S. gregorii* of "rudimentary pseudosepta" in the valve ends.
Our specimens do not look very distant from *S. salina*, as it is illustrated in the above mentioned works and from type material specimen illustrated in Cox (1988). Additionally, we failed to see, in LM and SEM, the apical thickenings that might correspond to Husted's "pseudosepta" of *S. amphioxys.* This led us to identify the specimens found in our study as *S. salina.* This said, it should be noticed the SEM micrographs (Pl. 41: 1-3) correspond quite well to the illustrations given in Round *et al.* (1990) of specimens (apparently) of *S. amphioxys*, the lectotype of the genus *Staurophora*, although this is not explicitly said in the text (pg. 482). Therefore, a thorough investigation of type material of these taxa is necessary. See Sabbe (1997) for other taxonomical problems concerning this genus.

Distribution & Ecology: *Staurophora amphioxys* and *S. salina* taxa are found in brackish-marine sediments worldwide (Hustedt 1931-1959, Witkowski *et al.* 2000) and have the same solitary epipelic life-style. With 27 occurrences, it was a very common species in our samples. It was especially common in coarse/medium sandy muddy stations, during summer, when it had its maximal abundance (around 15% of relative abundances).

References:
Cox (1988) – fig. 44
Hendey (1964) – pgs. 218-219; figs. XXXVII/13-14
Hustedt (1931-1959) – pgs. 787, 790; figs. 1133/a-d, 1135/a-d
Krammer & Lange-Bertalot (1986) – pg. 250; figs. 91/14-15
Snoeijs & Balashova (1998) – #485
Round *et al.* (1990) – pg. 482; figs. a-i

Witkowski *et al.* (2000) – pg. 353; figs. 149/13

Staurophora wislouchii (Poretzky & Anisimova) Mann *in* Round, Crawford & Mann 1990

Micrographs: Pl. 6: 9-11; Pl. 41: 4-5

Synonyms:
Stauroneis wislouchii Poretzky & Anisimova

Similar species:
Staurophora salina (W. Smith) Mereschkowsky
Staurophora amphioxys (Gregory) Mann *in* Round, Crawford & Mann
Stauroneis tackei (Hustedt) Krammer & Lange-Bertalot

Morphometrics:
Biovolume (µm^3): 2116
Frustule geometry: elliptic prism
Length (µm): 30.4 – (36.6) – 41.9 (n=6)
Width (µm): 9.5 – (10.5) – 13.3 (n=6)
Pervalvar axis (µm): 7 (estimated)
Striae in 10 µm: 20 – (23) – 26 (n=6)
Punctae in 10 µm: 43 (n=2)

Notes: this taxon is also very similar to the above mentioned *S. salina* and *S. amphioxys*. The main differences seem to be their relatively smaller size, the slightly more protracted bluntly rounded ends and slightly denser striation. These very faint differences make it very plausible that all these three species are, in fact, part of the same size continuum and only reflect the morphological variability of the same taxon. This hypothesis was already put forward by Krammer & Lange-Bertalot (1986). The taxonomic significance of these species, as well as other close ones, should be investigated (*viz.* Sabbe 1997). Auxosporulation studies, as the ones realized by Cox (1985) and Mann (1984) on the closely related genus *Dickieia*, seem particularly useful in order to clarify these questions.

Distribution & Ecology: *Staurophora wislouchii* has been mostly described for saline inland waters of Eurasia (Hustedt 1931-1959, Krammer & Lange-Bertalot 1986) but it was also found as a solitary epipelic species in the Baltic Sea (Snoeijs & Balashova 1998). Very rarely found in our samples (only 4 occurrences) but it attained almost 4% of relative abundance in one sandy station in September 2004.

References:
Hustedt (1931-1959) – pg. 792; figs. 1137
Krammer & Lange-Bertalot, 1986 – pg. 250; figs. 91/16-17
Snoeijs & Balashova (1998) – #487

ORDER ACHNANTHALES

According to the classification proposed by Round *et al.* (1990), the order Achnanthales was placed within the raphid diatoms and grouped all monoraphid families and genera. Quite recently, in a cladistic analysis including protoplast and frustule characters, Cox and Williams (2006) reinstated the hypothesis that monoraphid genera have arisen independently from different naviculoid diatoms and that *Achnanthes sensu stricto* should be transferred to the Mastogloiales (see also Cox 2006). Molecular analyses (Medlin & Kaczmarska 2004) also have shown that marine and freshwater species within the Achnanthales have evolved separately, thus reinforcing the notion of paraphyly of this group. Although acknowledging monoraphid diatoms are in need of having their systematics reassessed, it was decided, for the sake of convenience to maintain the *Achnanthales sensu* Round. The relatives of the monoraphid taxa, other than *Achnanthes sensu stricto*, still have to be found among naviculoid diatoms.

The nomenclature chosen describe the frustule of monoraphid diatoms (see above, section 7.1) designates the valve with raphe as

"Raphe-sternum valve" (= RSV or RS-valve) and the rapheless valve as "Sternum-valve" (= SV or S-valve).

Fam. Achnanthaceae Kützing

Achnanthes Bory de Saint-Vincent 1822

Genus description: Round *et al.* (1990); Toyoda *et al.* (2005) (*sensu stricto*)

Achnanthes sensu stricto, as defined in Round *et al.* (1990), should be a monophyleptic group of robust marine species close to *A. brevipes* Agardh and *A. longipes* Agardh. That is, monoraphid heterovalvar diatoms which are flexed in girdle view, usually with two H-lobed plastids with a central pyrenoid, that have valve and girdle band areolae occluded by cribra or volae (never by hymenes) and with internal raphe fissures coaxial, simple or slightly hooked to the same side. For this reason, in recent years the *Achnanthes sensu lato* (*e.g.* Hustedt 1931-1959, Patrick & Reimer 1966, Lange-Bertalot & Krammer 1989) has been consistently split and many new genera have erected (*e.g. Achnanthidium*, *Planothidium*, *Pauliella*). However, there are still a number of species, within the genus, that are not "true" *Achnanthes* but have not yet been sufficiently studied to merit transfer to a new genus. Therefore, it is explicitly stated when the species assigned here do not belong to *Achnanthes sensu stricto*.

Achnanthes cf. ***amoena*** Hustedt 1952

Micrographs: Pl. 8: 17-23

Synonyms:
Kolbesia amoena (Hustedt) Kingston
Achnanthes biceps sensu Takano
Achnanthes orientalis Hustedt non Petit
Achnanthes triconfusa VanLandingham

Similar species:
Achnanthes kolbei Hustedt
Achnanthes lemmermannii var. *obtusa* Hustedt
Achnanthes biasolettiana var. *linearis* Grunow

Morphometrics:
Biovolume (µm^3): 111
Frustule geometry: elliptic prism
Length (µm): 11.2 – (13.2) – 17.7 (SV, n=7); 10.7 – (12.4) – 15.0 (RSV, n=6)
Width (µm): 4.0 – (4.5) – 5.8 (SV, n=7); 4.0 – (4.4) – 5.7 (RSV, n=6)
Pervalvar axis (µm): 2 (estimated)
Striae in 10 µm: 14 – (16) – 18 (SV, n=7); 16 – (18) – 19 (RSV, n=6)

Notes: our specimens, particularly the RS-valves, are very reminiscent of *A. amoena*. This species was described and illustrated in detail by Chang (1992) and Krammer & Lange-Bertalot (1991b). The main morphological features of this taxon are the characteristic lateral sterna that interrupt the striae of the rapheless valve and the clear differences in striation density between the RS-valves and the S-valves.
This was not the case of the specimens found in our study. They do have lateral sterna in the S-valves but the RS-valves do not have a much higher striation density (*i.e.* 20-26 in 10 µm, Krammer & Lange-Bertalot 1991b) although the striae seem to be continuous. The few RS-valves observed during our study were part of complete frustules and, since they have a very short pervalvar axis, a shade effect of the overlying coarser striae of rapheless valve could be causing an illusion of coarser striae in the RS-valve face. In any case and until further studies are made, this taxon was only tentatively identified as *A.* cf. *amoena*.
Regarding *A. amoena*, Chang (1992) and Krammer & Lange-Bertalot (1991b) consider it to be closely related to *A. lemmermannii* var. *obtusa* Hustedt and to *A. biasolettiana* var. *linearis* Grunow (see also remarks below on *A. lemmermannii* var. *obtusa*). Apart for not having clear differences in stria density between the RS- and the S-valves, these species also lack characteristic lateral sterna in the rapheless valve. Conversely, the slit-like areolae with no visible

internal occlusions (see fig. 6/3 in Krammer & Lange-Bertalot 1991b) are quite close to the continuous "alveolate" striae of *A. lemmermannii* var. *obtusa* (Sabbe 1997).

Achnanthes amoena is also quite reminiscent of the freshwater species *A. kolbei*, a synonym of *Kolbesia kolbei* (Hustedt) Round & Bukhtiyarova which was transferred to the genus *Kolbesia* by Kingston (2000). However, this transfer, as well as the relation between *K. kolbei* and *A. amoena*, needs to be further investigated. As Sabbe (1997) pointed out, the North American freshwater specimens seem to have distinctly punctate striae making them, also in our opinion, even more similar to *Kolbesia* but different from *A. amoena,* as illustrated in Krammer & Lange-Bertalot (1991b). In any case, this taxon is not an *Achnanthes sensu stricto*.

Distribution & Ecology: the life-form and distribution of this uncommon species in not very clear. Chang (1992) and Krammer & Lange-Bertalot (1991b) reported it for brackish/marine waters and Snoeijs (1993) described it as a stalked species found mainly in the Bothnian Sea (salinities ~5‰). Sabbe (1997) found it rarely in fine sandy sediments at higher salinities (18 ‰). Krammer & Lange-Bertalot (1991b) also refer it as common in "electrolyte-rich freshwater", which is in accord with the North American observations (but see above). It was extremely rare in our samples (only two occurrences).

References:
Chang (1992) – figs. 2-5
Krammer & Lange-Bertalot (1991b) – pg. 44; figs. 26/7-23, 6/3
Lange-Bertalot & Krammer (1989) – pg. 21; figs. 43/30-45, 44/1-2
Simonsen (1987) – pg. 385; fig. 583/21-24
Snoeijs (1993) – #1
Witkowski *et al.* (2000) – pg. 85; fig. 51/34-36

Achnanthes cf. ***fogedii*** Håkansson 1978

Micrographs: Pl. 8: 24-35; Pl. 41: 6

Similar species:
Achnanthes fogedii Håkansson
Achnanthes holsatica Hustedt
Fistulifera saprophila (Lange-Bertalot & Bonik) Lange-Bertalot
Navicula difficillimoides Hustedt
Navicula indifferens Hustedt

Morphometrics:
Biovolume (μm^3): 97
Frustule geometry: elliptic prism
Length (μm): 6.8 – (10.4) – 12.3 (SV, n=15); 6.5 – (9.5) – 13.0 (RSV, n=11)
Width (μm): 3.9 – (5.0) – 5.9 (SV, n=15); 3.2 – (4.7) – 6.5 (RSV, n=11)
Pervalvar axis (μm): 3 (estimated)
Striae in 10 μm: 29 – (32) – 36 (SV, n=13)

Description: the frustules are saddle-shaped, being slightly folded along the transapical axis. Valves are elliptical to rhombic-lanceolate with cuneately-obtuse apices and seem to be extremely delicate and unornamented. Only the SV has striae visible in the LM and these are limited to the edge of the valve. They are composed by a single transapically oriented elliptical areola, occluded internally by a velum. The rapheless valve (SV) has a slightly silicified sternum that is only easily seen in phase-contrast LM. In the RSV, the axial area is narrow and linear-lanceolate and central area small and roundish. The raphe is straight and apparently lies on a heavily silicified raphe-sternum. The central raphe endings are straight, expanded and fairly distant. The central nodule is particularly bright in LM. The distal raphe endings are located at the margin of the apices and seem to be deflected to the same side, near the apical margin. The striae are irresolvable in LM.

Notes: this taxon is extremely reminiscent of *A. fogedii.* Both valves, particularly the rapheless one, have very similar features to the valves of that species (see Håkansson 1978, Snoeijs & Kasperoviciene 1996; Witkowski *et al.* 2000). However, the striation density in the SV is slightly higher and, more importantly, the RSV striae are not visible in LM. *Achnanthes fogedii*, as described by Håkansson (1978), has striae in the RSV with a density of 22-25 in 10 μm and which are interrupted on the valve. Since there were no SEM images of the RS-valves from specimens collected in this study, we could not attest if the putative transapical striae were also interrupted on the RS-valves. Conversely, the raphe structure seems to be very similar to what is observed in the LM micrographs available in the literature (see references below). Even so, when a single RSV is observed in LM, it might be confused with valves from freshwater species *N. indifferens* (see Krammer & Lange-Bertalot 1996, pg. 213) or even *F. saprophila*. The study of the incinerated slides confirmed that the SV and RSV belonged together. As it is the case of *A. fogedii* and *Achnanthes* sp.1, this taxon is not part of *Achnanthes sensu stricto*.

Distribution & Ecology: small epipsammic species, probably a small motile or adnate diatom. In our study, it was only found in the sandy stations where it was fairly common (31 occurrences), particularly in the medium-coarse sands, albeit never very abundant (max. abundance <1.75 %). *Achnanthes fogedii* was initially described for sub-fossil sediments in the Baltic Proper, accompanied by other brackish water species (Håkansson 1978). Witkowski *et al.* (2000) considered *A. fogedii* as an extant species, having frequently found it in Mediterranean material and concluded that is probably a widespread (but overlooked) species.

References:
Håkansson (1978) – figs. A-G
Snoeijs & Kasperoviciene (1996) – #302
Witkowski *et al.* (2000) – pg. 89; figs. 51/11-15

Achnanthes lemmermannii var. ***obtusa*** Hustedt 1939

Micrographs: Pl. 8: 11-16

Synonyms:
Achnanthes biasolettiana var. *linearis* Grunow

Similar species:
Achnanthes lemmermannii var. *lemmermannii* Hustedt
Achnanthes amoena Hustedt
Achnanthes minuscula Hustedt

Morphometrics:
Biovolume (µm^3): 53
Frustule geometry: elliptic prism
Length (µm): 7.5 – (8.9) – 11.2 (SV, n=7); 7.5 – (8.9) – 10.3 (RSV, n=5)
Width (µm): 2.9 – (3.9) – 4.4 (SV, n=7); 2.8 – (3.6) – 4.4 (RSV, n=5)
Pervalvar axis (µm): 2 (estimated)
Striae in 10 µm: 20 – (21) – 23 (SV, n=7); 21 – (22) – 23 (RSV, n=5)

Notes: *Achnanthes lemmermannii* var. *obtusa* was described by Hustedt (1939) but, according to Krammer & Lange-Bertalot (1991b), it has nothing to do with the nominate variety *A. lemmermannii* var. *lemmermannii*. The same authors defend it is conspecific with *A. biasolettiana* var. *sublinearis* which, again, is not related to the nominate variety of *A. biasolettiana.* Although very reminiscent of *A. lemmermannii* in LM, it has a finer striation and the striae structure is completely different. *Achnanthes lemmermannii* var. *lemmermannii* has multiseriate triangular striae, reason for its recent transfer to the genus *Planothidium* (Morales 2006 and see below), whereas the striae of *A. lemmermannii* var. *obtusa* are quite similar to the ones in *A. amoena* (see above). According to Sabbe (1997), the striae are composed of “alveoli” (this term is not used as in *Pinnularia*) but are not interrupted by lateral sterna (*i.e.* like *A. amoena*). With the transfer of the nominate variety to the genus *Planothidium* (see below), the taxonomic position of *A. lemmermannii* var. *obtusa* remains unresolved. It cannot be transferred to this genus, for the reasons explained above, and even its position in the *Achnanthes* may be put in question if the hymenate occlusions in the striae are confirmed.

Distribution & Ecology: solitary, adnate or small motile epipsammic species. It has been described for intertidal estuarine sandflats of the Schelde estuary and of the German Wadden Sea (Lange-Bertalot & Krammer 1989; Sabbe 1997). Found in the same sandy stations has *P. lemmermannii*, although not as abundant (20 occurrences in 40 samples and 1.9 % of max. relative abundance). No clear seasonality was found.

References:
Lange-Bertalot & Krammer (1989) – pg. 95; figs. 43/32-32'
Sabbe (1997) – pg. 115; fig. 8/8-11, 42/2,7
Simonsen (1987) – pg. 254; fig. 376/15-20

Achnanthes s.l. **sp.1**

Micrographs: Pl. 8: 36-47; Pl. 41: 7- (?) 9

Similar species:
Achnanthes fogedii Håkansson 1978
Platessa bavarica Lange-Bertalot & Hofman
Platessa holsatica (Hustedt) H. Lange-Bertalot

Morphometrics:
Biovolume (µm^3): 55
Frustule geometry: elliptic prism
Length (µm): 7.4 – (8.8) – 10.8 (SV, n=11); 7.4– (8.8) – 11.2 (RSV, n=18)
Width (µm): 2.9 – (3.8) – 4.4 (SV, n=11); 3.3 – (4.1) – 5.4 (RSV, n=18)
Pervalvar axis (µm): 2 (estimated)
Striae in 10 µm: 29 – (31) – 33 (SV, n=8); 30 – (32) – 36 (RSV, n=10)

Description: valves lanceolate with broadly rounded, slightly produced, rostrate apices. Both valves seem very delicate. The raphe-sternum valve (RSV) is flat and has a straight raphe, with simple, more or less distant, central endings, which are only slightly expanded. The raphe apical endings have external fissures bent towards the same side. The axial area is narrow and linear and the central area asymmetrical and slightly expanded transapically. Since the striae are very fine, only the raphe and the central nodule are easily discernible in LM. The striae radiate throughout the valve, particularly at the centre. In SEM, it can be seen that they are composed by slit-like areolae, which are transapically orientated near the margins and sometimes are biseriate. The striae then become monoseriate and change to apically orientated and almost rounded towards the axial area. Internally, the separation between the poroids forming the striae becomes less clear towards the margins, with a probable fusion of the vimines. The rapheless valve (SV) only has striae near the margin, radiating throughout the valve. These are composed by a single, large slit-like poroids, oriented towards the centre. They are slightly coarser than in the RSV but usually are clearly visible in LM. The sternum is also easily discernible visible in LM. In SEM, it is externally marked by what appears to be small longitudinally aligned impressions, along the length of the sternum.

Notes: this species is quite unique and unlike anything described in the literature consulted. It clearly does not belong to *Achnanthes sensu stricto*, as defined in Round *et al.* (1990), but it is also not obvious to which achnanthoid genus it may belong. The marginal striation in the SV is reminiscent of *P. holsatica* (syn. *A. holsatica* Hustedt) or *P. bavarica* but the striae ultrastructure is quite different. The biseriate striae and the strong virgae of *Platessa* are closer to the striae found in *Planothidium* (*cf.* Krammer & Lange-Bertalot 2004; pl. 92) than to what is observed in our specimens. Additionally, the RS valves are quite different from those two genera and only superficially resemble the RSV of the *Psammothidium* species (*cf.* Bukhtiyarova & Round 1996). The closest related taxon seems to be *Achnanthes fogedii,* which has similar striae ultrastructure in the rapheless valve (*viz.* Håkansson 1978, Snoeijs & Kasperoviciene 1996). However, the taxon found in our study differs in valve outline, in the pattern of the striae of the RSV and in the striae ultrastructure.

Distribution & Ecology: small epipsammic species, probably adnate. This species was present in all sandy stations (31 occurrences), thus seemingly indifferent to silt content and sand grain size. Even though it was never very abundant (max. abundance < 1.3%) a slight increase in numbers during winter was detected.

Achnanthes s.l. **sp.2**

Micrographs: Pl. 12: 1-11; Pl. 41: 10

Similar species:
Pauliella taeniata (Grunow) Round & Basson
Astartiella bahusiensis (Grunow) Witkowski, Lange-Bertalot & Metzeltin
Astartiella bremeyeri (Hustedt) Witkowski, Lange-Bertalot & Metzeltin

Morphometrics:
Biovolume (µm^3): 270
Frustule geometry: elliptic prism
Length (µm): 12.6 – (15.9) – 19.0 (SV, n=5); 13.2 – (17.3) – 21.4 (RSV, n=10)
Width (µm): 4.9 – (5.1) – 5.3 (SV, n=5); 3.9 – (5.1) – 5.9 (RSV, n=10)
Pervalvar axis (µm): 4 (estimated)
Striae in 10 µm: 25 – (28) – 30 (SV, n=5); 21– (29) – 34 (RSV, central area n=6)

Description: valves broadly elliptical with broadly rounded apices. Raphe-sternum valve has a straight raphe, with simple central raphe endings and apical raphe ending also straight and distant from the apical margins. The axial area (sternum) is parallel-sided to the raphe and slightly expanded at the centre. Striae of the RSV are uniseriate, slightly radiating and almost invisible in LM, with the exception of the ones delimiting the roundish central area. Rapheless valve (SV) with a more or less broad sternum, linear to lanceolate, but it is never very narrow. Striae parallel at the centre to slightly radiating and visible throughout the valve face in LM.

Notes: this taxon does not belong to *Achnanthes s.s.* (*sensu* Round *et al.* 1990) and seems to be closer to the genera *Pauliella* (see Round & Basson 1997) and *Astartiella* (see Moser *et al.* 1998), that were recently created with taxa formerly in *Achnanthes s.l.*. The taxon to which it seems to have the greater similarities is the benthic coastal species *Astartiella bremeyeri* [former *Achnanthes bremeyeri*, see Lange-Bertalot & Krammer (1989) for a thorough discussion of this species]. However, it lacks the very narrow sternum in the SV, typical of *A. bremeyeri* and *A. bahusiensis*. Additionally, the striae seem to be composed by slit like areolae, instead of rounded poroids occluded by hymenate vela. The relation to the arctic planktonic species *Pauliella taeniata* (former *Achnanthes taeniata*) should also be explored in future studies.

Distribution & Ecology: solitary, epipsammic species, with unknown life-form, but probably motile. Recurrently found in samples of the medium coarse sandy stations, especially during late autumn and winter. Never very abundant (max. abundance < 2%)

Vikingea Witkowski, Lange-Bertalot & Metzeltin 2000

Genus description: Witkowski *et al.* (2000)

The systematic position of this recently described monoraphid genus is uncertain. However, as the authors (Witkowski *et al.* 2000) pointed out several similarities to the group of "taxa around *Achnanthes brevipes*" (*i.e.* to *Achnanthes s.s.*), we tentatively placed this genus in the family Achnanthaceae.

Vikingea **sp.1**

Micrographs: Pl. 7: 38-40

Similar species:
Vikingea gibbocalyx (Brun) Witkowski, Lange-Bertalot & Metzeltin

Morphometrics:
Biovolume (µm^3): 310
Frustule geometry: elliptic prism
Length (µm): 11.8 (SV, n=1)
Width (µm): 6.7 (SV, n=1)
Pervalvar axis (µm): 5 (estimated)
Striae in 10 µm: 17 (SV, n=1)

Description: only the raphe-sternum valve is described. RS-valve is convex and heavily silicified with a marginal rib surrounding the whole valve. The apices are slightly depressed, indicating that the convexity of the apical axis is not very strong. The sternum is narrow and linear. The striae slightly radiate throughout and are composed by three or more large areolae, almost quadrangular. The exception is the central striae, where an extremely large, transapically expanded areola occupies most of the space.

Notes: this unknown species definitively belongs to *Vikingea*, since it shares many morphological features to both *V. gibbocalyx* and *V. promunturii*; the only two known species attributed to this recently described genus (see Witkowski *et al.* 2000).

Distribution & Ecology: this species only occurred once in this study. The ecology is unknown.

Fam. Achnanthidiaceae Mann

Achnanthidium Kützing 1844

Genus description: the concept of *Achnanthidium*, as used here, follows that proposed by Round and Bukhtiyarova (1996), rather than that adopted by Round *et al.* (1990).

Achnanthidium exiguum (Grunow) Czarnecki 1994

Micrographs: Pl. 7: 35-36

Synonyms:
Achnanthes exigua Grunow *in* Cleve & Grunow

Morphometrics:
Biovolume (µm^3): 120
Frustule geometry: elliptic prism
Length (µm): 12.5 (n=1)
Width (µm): 4.9 (n=1)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 26 (n=1)

Notes: only one RS-valve of this periphytic freshwater taxon was found. Valve outline, morphometrics and morphological characters, such as the very narrow sternum and the central hyaline area in one side of the valve, correspond to the descriptions and illustrations given by Lange-Bertalot & Krammer (1989) and Krammer & Lange-Bertalot (1991b). It is most probably allochtonous.

References:
Krammer & Lange-Bertalot (1991b) – pg. 38; fig. 23/1-27, 6/4
Lange-Bertalot & Krammer (1989) – pg. 51; figs. 45/4-36

Achnanthidium minutissimum (Kützing) Czarnecki 1994

Micrographs: Pl. 7: 37

Synonyms:
Achnanthes minutissima Kützing

Morphometrics:
Biovolume (µm^3): 53
Frustule geometry: elliptic prism
Length (µm): 9.0 (n=1)
Width (µm): 3.0 (n=1)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 30 (n=1)

Notes: *Achnanthidium minutissimum* is a large species-complex of common benthic freshwater taxa (*e.g.* Krammer & Lange-Bertalot 1991b). Due to its importance in water quality surveys it has been extensively studied in the pasts 15 years (*e.g.* Potapova & Hamilton 2007). With only one occurrence, its presence in an intertidal estuarine environment can only be considered allochtonic.

References:
Krammer & Lange-Bertalot (1991 b) – pg. 56; figs. 32, 34, 35/1-3
Potapova & Hamilton (2007) – figs. 4/a, 8/a-am

Planothidium Round & Bukhtiyarova 1996

Genus description: Round & Bukhtiyarova (1996)

The genus *Planothidium* was erected by Round & Bukhtiyarova (1996) to accommodate achnanthoid taxa that presented typical "fasciculate" striae, composed of bundles of tiny areolae, which are separated by ribs visible in the valve interior. This group of species was formerly included in the genus *Achnanthes s.l.* and, later, in *Achnanthidium sensu* Round *et al.* (1990). Lange-Bertalot (1997b) created the genus *Achnantheiopsis*, to accommodate the same group of species, but it is a later synonym of *Planothidium*. This publication remains, nonetheless, an excellent morphological and ultrastructural description of these taxa. Lange-Bertalot separated them in two main groups: one group around the freshwater species *Achnanthes lanceolata* Brébisson ex Kützing, with a characteristic hoof-mark or cavum in the central region of the RS-valve and another group, around the marine/brackish species *Achnanthes delicatula* (Kützing) Grunow in Cleve & Grunow, that does not possess this cavum but can have a central interruption of the striation in one side of the RS-valve. Recently, Morales (2006) made a revision of the North-American freshwater species of *Planothidium* and organized them in 4 main groups based mainly on features of the central region of the rapheless valve.

Planothidium delicatulum s.l. (Kützing) Round & Bukhtiyarova 1996 **morphotype 1 (m.1)**

Micrographs: Pl. 7: 1-7; Pl. 42: 1-5

Synonyms:
Achnanthidium delicatulum Kützing
Achnanthes delicatula (Kützing) Grunow *in* Cleve & Grunow
Achnantheiopsis delicatula (Kützing) Lange-Bertalot

Similar species:
Planothidium minutissimum (Krasske) Morales

Morphometrics:
Biovolume (µm^3): 140
Frustule geometry: elliptic prism
Length (µm): 5.3 – (11.3) – 19.0 (SV, n=18); 5.9 – (10.3) – 18.2 (RSV, n=16)
Width (µm): 3.9 – (5.9) – 9.1 (SV, n=17); 3.5 – (5.4) – 8.5 (RSV n=16)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 10 – (14) – 19 (SV, n=17); 9 – (14) – 19 (RSV n=16)

Description: valves elliptic to lanceolate with slightly produced, subrostrate apices. Valve face flat abruptly curving into a shallow mantle. RS-valve has a straight raphe with pore-like, slightly expanded, central endings and external distal terminal fissures that are bent to the same side. The raphe sternum is rather narrow, with a roundish, slightly expanded central area. In the S-valve, the sternum is wider, varying from the lanceolate to rhombic and always with a central hyaline area, in one of the sides of the valve, caused by widely spaced striae central. In both valves the striae slightly radiate and are multiseriate, being distinctly wedge-shaped in the centre of the valve. The striae are composed by 4-5 rows of areolae (near the mantle) and are separated, internally, by costate virgae.

Notes: most of the "*Planothidium delicatulum*" specimens found in our samples do not completely correspond to any formal species or varieties of the "*Achnanthes delicatula*-Sippenkomplex", proposed by Kramer & Lange-Bertalot (1991), nor to the four species referred by Round & Bukhtiyarova, (1996), for the same group of species (*i.e. P. delicatulum*, *P. hauckianum*, *P. engelbrechtii*, *P. septentrionalis*). In fact, only *P. septentrionalis* could be easily identified in our samples (see below). The taxonomy and nomenclature of this group species is extremely complex and is discussed thoroughly in Kramer & Lange-Bertalot (1991b).
Most of the valves observed showed characters that are more close to *P. hauckianum* than to *P. delicatulum*, such as radiating striae and a broader, lanceolate, sternum in the S-valve (Lange-Bertalot & Kramer

1989). Conversely, the striae density, another character that separates both species, is above the range given for *P. hauckianum*, which is of about 8-11 in 10 µm (*e.g.* Witkowski *et al.* 2000). Concerning valve outline, Tropper (1975) demonstrated that it can be extremely variable in natural populations where elliptic valves (*i.e. A. hauckiana* var. *elliptica*) can coexist with lanceolate valve with subrostrate (*i.e. A. hauckiana* var. *rostrata*) or cuneate (*i.e. A. hauckiana* var. *hauckiana*) ends, further hindering identification. Finally, it should be mentioned that there is no certainty that the specimens from brackish sites commonly identified as *A. hauckiana* have anything to do with the specimens from the type locality, according to Lange-Bertalot & Krammer (1989). Therefore, the specimens found in our study could not be assigned to a known species, other than *P. delicatulum sensu* latissimo (see Krammer & Lange-Bertalot 1991b).

Nonetheless, there was a persistent morphological consistency of some of the forms encountered in our study. Therefore, informal, easily recognized morphotypes were created to designate the specimens found during the study. The criteria that were chosen may or may not reflect differences of taxonomical significance. They mainly refer to valve outline in combination with the presence/absence of an interruption in the striae in one of the sides of the central RS-valve (*viz.* Morales 2006).

Morphotype 1 (m.1) is very similar to *A. hauckiana* var. *rostrata* Schulz (*sensu* Patrick & Reimer 1966) but with a very clear space on one side of the centre of the S-valve. This makes it very close to the freshwater *P. minutissimum*, both in outline and striation pattern. The main differences seem to be the size range as well as the fact that the striae are composed of maximum of 3 rows of areolae.

Distribution & Ecology: *Planothidium delicatulum sensu* latissimo was one of the most common epipsammic taxa, appearing in all samples from sandy sediments with maximal relative abundances up to 15% of the total diatom assemblage. It seems to be indifferent to average grain size of sand and even to the presence of silt, especially in the case of morphotype 1. *Planothidium delicatulum* seems to be an extremely common and cosmopolitan diatom (*e.g.* Witkowski *et al.* 2000), being often identified as *A. hauckiana*, *A delicatula* and their varieties (Laws 1988, Kuylenstierna 1989-1990, Sabbe 1993, Snoeijs 1993, Méléder *et al.* 2007). Morphotype 1 seems particularly similar to the specimens found in intertidal flats of the Westerschelde estuary by Sabbe (1997). We have considered it as an adnate species but it may as well be a small motile epipsammic species.

References:
Krammer & Lange-Bertalot (1991b) – pg. 72
Lange-Bertalot & Krammer (1989) – pg. 44; figs. 80/1-23, 87/14-23’, 90/1-2, 90/5-6
Patrick & Reimer (1966) – pg. 269, fig. 17/33-34
Sabbe (1997) – pg. 129; figs. 9/1-10, 43/3
Snoeijs (1993) – #3
Sundbäck & Snoeijs (1991) – fig. 8/a
Witkowski *et al.* (2000) – pgs. 118, 120; figs. 46/28-29, 48/1-2, 48/39-41

Planothidium delicatulum s.l. **(**Kützing) Round & Bukhtiyarova 1996 **morphotype 2 (m.2)**

Micrographs: Pl. 7: 8-13; Pl. 42: 6 (?) -9

Similar species:
Planothidium deperditum (Giffen) Witkowski, Lange-Bertalot & Metzeltin

Morphometrics:
Biovolume (µm^3): 62
Frustule geometry: elliptic prism
Length (µm): 4.9 – (8.0) – 10.4 (SV, n=11); 5.7 – (6.6) – 9.0 (RSV, n=9)
Width (µm): 3.7 – (4.4) – 5.4 (SV, n=11); 2.9 – (4.1) – 5.4 (RSV, n=9)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 12 – (15) – 18 (SV, n=11); 16 – (19) – 23 (RSV, n=9)

Description: valves flat, elliptical with broadly rounded apices. RS-valve has a narrow raphe-sternum with a very small asymmetrical central area. Raphe straight with pore-like, slightly expanded, central endings and external distal terminal fissures clearly bent to the same side (*cf.* morphotypes 1). The S-valve has a large, lanceolate sternum and the lateral hyaline area is caused by the lack of two central striae, in one side of the valve, and not by a wider distance between the central striae, as it seems to be the case in morphotype 1. The striae are wedge-shaped in the centre and radiate throughout the valve. They are composed by rows of 3-4 tiny areolae, near the mantle, that are occluded by hymens. The costate virgae that separate the striae seem similar to morphotype 1, hence they are less deep and reinforced than in morphotype 3 (see below).

Notes: for a general discussion on *Planothidium delicatulum* see morphotype 1. Apart from the elliptical valve outline, morphotype 2 looks very similar to morphotype 1. It has the same size range, striae density and orientation, as well as the same lateral gap in the centre of the S-valve. The ultrastructural details observed in SEM, such as the similar raphe structure or striae composition, shape and density confirm the closeness between these two morphotypes.
Also the lateral hyaline area does not have a depression, which is a feature common to other forms around *P. delicatulum* group. Therefore, a simple difference in valve outline is probably not sufficient to give this morphotype any taxonomical recognition, other than a probable synonymy to *Achnanthes hauckiana* var. *elliptica* or to *Achnanthes* var. *hauckiana*, both of dubious taxonomical validity (Krammer & Lange-Bertalot 1991b).
Conversely, it is interesting to notice that morphotypes m.1 and m.2 have practically the same size range and similar median length and width values. This means that small lanceolate valves may coexist with larger elliptical valves. However, no in-depth morphological study was made in this natural population and Tropper (1975) concluded that quantified change in shape with size of *Achnanthes hauckiana* actually obeys to Geitler's generalizations that state that the apical axis decreasing more rapidly than the transapical axis and the valve outlines becoming smoother with the decrease in size (Geitler 1932, but see Round *et al.* 1990). The fact that both morphotypes coexist naturally in our studied sites makes this kind of research promising.

Distribution & Ecology: it has the same life-form and ecology as morphotype 1 (see above). However, when separating the counts and comparing the distribution of both morphotypes, it can be seen that morphotype 2 is slightly more abundant and has a considerable preference for the fine-medium sandy site with low mud content. Conversely, the very slight temporal variations in relative abundances were more or less parallel in both morphotypes, with a minor increase in spring, followed by a short collapse in late summer. This morphotype was also found in San Francisco Bay (Laws 1988) and in the Baltic Sea (Witkowski 1994).

References:
Laws (1988) – Fig. 17/14 (as *Achnanthes hauckiana*)

Planothidium delicatulum s.l. (Kützing) Round & Bukhtiyarova 1996 **morphotype 3 (m.3)**

Micrographs: Pl. 7: 14-19; Pl. 42: 10 (?) - 12

Similar species:
Planothidium conspicuum (Mayer) Morales

Morphometrics:
Biovolume (µm^3): 91
Frustule geometry: elliptic prism
Length (µm): 5.8 – (8.6) – 10.7 (SV, n=14); 7.3 – (10.2) – 13.3 (RSV, n=12)
Width (µm): 3.9 – (4.9) – 7.7 (SV, n=14); 3.5 – (5.2) – 7.7 (RSV, n=12)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 13 – (15) – 18 (SV, n=14); 12 – (15) – 19 (RSV, n=12)

Description: valves elliptical with broadly rounded apices. RS-valve with a narrow raphe-sternum, only slightly expanded in the central area due to the smaller central striae. Raphe straight, barely non-coaxial, with simple central nodules and distal raphe ends just slightly deflected to the same side. S-valve has a large, lanceolate and slightly asymmetrical sternum. There is no lateral interruption of the striae in the centre of the valve. The striae are parallel at the centre, where they are wedge-shaped, and radiate towards the ends. They are composed by rows of 3-5 tiny areolae, near the mantle, that are occluded by hymenes. The costate virgae that separate the striae seem to be deeper and reinforced, when compared with the other morphotypes of *P. delicatulum* (see above).

Notes: in many ways, this morphotype is the most reminiscent of *P. hauckianum*, as it is presented in the literature (*e.g.* Witkowski *et al.* 2000, Krammer & Lange-Bertalot, 1991b), because it has an elliptical valve outline and no lateral interruption of the striae. In addition it has reinforced costate virgae and slight differences in raphe features (*e.g.*no pore-like central nodules and distal ends barely bent), making it distinct from the other two morphotypes described above. It should be noted, however, that it is extremely hard to distinguish the elliptical RS-valves of morphotypes 2 and 3 in LM and that it has similar size range and striae density to the above mentioned morphotypes of *P. delicatulum* (*i.e.* m.1 and m.2). Therefore, it was decided to maintain it as one of the forms within the *P. delicatulum sensu* latissimo.

The RS-valve of *A. delicatulum* illustrated by Kuylenstierna (1989-1990) seems to be almost identical to our specimens in SEM, although the S-valve illustrated there and in Sundbäck & Snoeijs (1991) has a narrower, linear sternum. The specimens illustrated in Witkowski *et al.* (2000) as *Planothidium* cf. *hauckianum* (Pl. 48/39-41) seem to be the most similar ones (including striae density) to the specimens of this morphotype found in our study. *Planothidium conspicuum* is, apparently, the freshwater equivalent of this morphotype (see Morales, 2006), with the same striae density and size range.

All morphotypes of *P. delicatulum* were found in the same environment. The relation between them and the different species (found in different freshwater environments) that deserved taxonomical recognition should be further explored. When following the rules established by Morales (1996) the three *P. delicatulum* morphotypes described here could have justified the rank of species. The group around *P. delicatulum* sorely needs a complete revision and research including molecular data.

Distribution & Ecology: similar life-form and ecology to the above mentioned morphotypes. When cell counts of the different morphotypes of *P. delicatulum* are separated, this morphotype was the least common of the three (maximal relative abundance of 1.9%) and occurred mainly in the sandy transect, showing no preference between fine and coarser sands. As mentioned above, this morphotype seems to be only illustrated in Kuylenstierna (1989-1990) and Witkowski *et al.* (2000) but most likely has a much wider distribution than the Baltic Sea.

References:
Krammer & Lange-Bertalot – figs. 40/9-13
Kuylenstierna (1989-1990) – figs. 35/348-349
Sundbäck & Snoeijs (1991) – fig. 8/b-c
Witkowski *et al.* (2000) – figs. 48/39-41

Planothidium deperditum (Giffen) Witkowski, Lange-Bertalot & Metzeltin 2000

Micrographs: Pl. 7: 20-25

Synonyms:
Cocconeis deperdita Giffen

Similar species:
Planothidium delicatulum s.l. (Kützing) Round & Bukhtiyarova morphotype 2

Morphometrics:
Biovolume (µm^3): 54
Frustule geometry: elliptic prism
Length (µm): 7.7 – (8.2) – 8.8 (SV, n=5); 8.4 (RSV, n=2)
Width (µm): 3.6 – (4.2) – 4.6 (SV n=5); 4.3 (RSV, n=2)
Pervalvar axis (µm): 2 (estimated)
Striae in 10 µm: 14 – (16) – 21 (SV, n=5); 17 (RSV, n=2)

Notes: only S-valves were found. According to Witkowski *et al.* (2000) this species is related to the group around *P. delicatulum*, as the multiseriate striae and the absence of a depression in the hyaline lateral area seem to indicate. The higher striae density and narrow central sternum on the S-valve distinguishes this species from the very similar morphotype 2 of *P. delicatulum* (see above).

Distribution & Ecology: epipsammic and probably adnate species. In our study, it was very rare (just 3 occurrences and max. abundance of 0.6 %), only occurring in the medium/fine sandy site. Sabbe (1997) reported for the Westerschelde estuary, stating it had a different autoecology of *P. delicatulum*, as it mainly appeared in fine sandy sediments but never in sediments with higher silt content, thus agreeing with our distribution. Cosmopolitan, it was originally described for the Saldanha Bay in South Africa (Giffen 1975), but it was also reported for the Thames estuary (Juggins 1992, as Achnanthes sp.2) and by Witkowski (1994a) for the gulf of Gdansk and the Mississippi Delta.

References:
Giffen (1975) – fig. I/26-28
Juggins (1992) – fig. A1/3
Sabbe (1997) – pg. 131; fig. 9/17-18, 43/8-9 (as *Achnanthidium* sp.1)
Witkowski (1994a) – fig. 18/4 (as *A. delicatula*)
Witkowski *et al.* (2000) – pg. 119; fig. 36/31-33, 49/12-13

Planothidium lanceolatum (Brébisson *ex* Kützing) Lange-Bertalot 1999

Micrographs: Pl. 7: 30-34

Synonyms:
Achnanthes lanceolata (Brébisson *ex* Kützing) Grunow in Cleve & Grunow
Achnanthidium lanceolatum Brébisson *ex* Kützing
Planothidium lanceolatum (Brébisson) Round & Bukhtiyarova

Morphometrics:
Biovolume (µm^3): 96
Frustule geometry: elliptic prism
Length (µm): 10.4 – (11.4) – 12.7 (SV, n=3); 11.2 (RSV, n=2)
Width (µm): 5.0 – (5.3) – 5.9 (SV, n=3); 4.5 (RSV, n=2)
Pervalvar axis (µm): 2 (estimated)
Striae in 10 µm: 13 – (14) – 16 (SV, n=3); 14 (RSV, n=2)

Notes: *Planothidium lanceolatum* is a freshwater species. As *P. delicatulum* it shows considerable morphological variation, although retaining its typical lateral "hoof-mark". A thorough discussion of this taxon can be found in Krammer & Lange-Bertalot (1991b). Considering the several varieties of P. *lanceolatum* that may correspond to this specimen, the var. *rostrata* seems to be the most plausible one.

Distribution & Ecology: only a small number of valves of this cosmopolitan freshwater epipsammic species were found. Juggins (1992) reported it as common in the freshwater sandy tidal reaches of the Thames estuary and Sabbe (1997) also found few valves in the Westerschelde estuary, supposing they were washed away from the freshwater areas.

References:
Lange-Bertalot (1989) – pg. 83; figs. 84, 85, 86, 87/1-13
Krammer & Lange-Bertalot – pg. 75; figs. 41, 42, 43, 44

Planothidium cf. ***lemmermannii*** Hustedt (Morales) 2006

Micrographs: Pl. 8: 1-10

Synonyms:
Achnanthes lemmermannii Hustedt

Similar species:
Achnanthes lemmermannii var. *obtusa* Hustedt
Achnanthes minuscula Hustedt
Planothidium daui (Foged) Lange-Bertalot

Morphometrics:
Biovolume (µm^3): 75
Frustule geometry: elliptic prism

Length (µm): 8.0 – (10.3) – 17.6 (SV, n=6); 7 – (11.6) – 17.3 (RSV, n=6)
Width (µm): 3.4 – (4.1) – 6.1 (SV, n=7); 3.7 – (4.8) – 6.3 (RSV, n=6)
Pervalvar axis (µm): 2 (estimated)
Striae in 10 µm: 13 – (18) – 19 (SV, n=5); 14 – (16) – 19 (RSV, n=6)

Notes: this taxon has a complex taxonomy and an ambiguous ecological status. Originally described for a freshwater site (Hustedt 1931-1959) as *Achnanthes lemmermannii* var. *lemmermannii*, it has been commonly found in the type locality (Krammer & Lange-Bertalot, 1991b) but also in North American freshwater sites (*e.g.* Morales 2006). Conversely, a brackish water morphospecies with a very similar valve outline, striation density and size range has been found recurrently in European estuarine and coastal sediments (*e.g.* Sundbäck 1983, Kuylenstierna 1989-1990, Sabbe 1997, Witkowski *et al.* 2000) and even by Hustedt (1939), in North Sea sandflats. This morphospecies has been commonly designated by *Achnanthes* cf. *lemmermannii* and corresponds well to specimens observed in our samples. Hustedt (1939) suggested that *A. lemmermannii* was actually a coastal diatom that "migrated" to the freshwater areas but did not explain the abundance in the type locality. Both Krammer & Lange-Bertalot (1991b) and Sabbe (1997) doubt that it is the same species, given the differences in autoecology, but admit that the morphological differences are subtle and, apparently, only limited to the (sub)-rostrate (and not capitate) apices of the brackish water species (see figures 26/30-40 in Krammer & Lange-Bertalot 1991b). The relation with *A. minuscula* Hustedt is also not clear (Krammer & Lange-Bertalot 1991b).

Observations in the SEM of coastal forms of *A. lemmermannii*, made by Kuylenstierna (1989-1990) and Sabbe (1997), show that the striae are constituted by rows of poroids just as in *Planothidium* species (Round & Bukhtiyarova 1996b). Recently, Morales (2006) demonstrated that the freshwater *A. lemmermannii* var. *lemmermannii* also has multiseriate triangular striae and transferred it to the genus *Planothidium*. When comparing these SEM micrographs, *i.e.* the ones presented in by Morales (2006), and the ones from the former coastal studies, the morphological differences become even less clear, making the case for conspecificity between the freshwater and brackish water strains more tenable. Only SEM examination of the type material and access to molecular data of both ecotypes can help clarify this situation.

Distribution & Ecology: solitary, epipsammic species frequently found in European coastal fine and medium sandy sediments (see references above) but also in brackish water "salinas" in Chile (Krammer & Lange-Bertalot 1991b). An alternate freshwater ecology cannot be excluded (see above). It is probably an adnate diatom. In our samples, it was common in the sandy stations (28 presences in 45 samples), occurring throughout the year, usually at low abundances (max. abundance 1.4%).

References:
Krammer & Lange-Bertalot (1991) pg. 44; fig. 26/33-40
Kuylenstierna (1989-1990) – pg. 77; figs. 32/312, 34/336-337
Lange-Bertalot & Krammer (1989) – pg. 94-9; fig. 79/1-10
Morales (2006) – figs. 85-90
Sabbe (1997) – pg. 132; figs. 9/11-16, 43/1-2 (as *Achnanthidium* sp.2)
Simonsen (1987) – figs. 220/10-12
Snoeijs & Kasperoviciene (1996)– #305
Witkowski *et al.* (2000) – pg. 97; figs. 48/35-41, 51/32-33

Planothidium septentrionalis (Østrup) Round & Bukhtiyarova 1996

Micrographs: Pl. 7: 26-29

Synonyms:
Achnanthes septentrionalis Østrup
Achnanthes delicatula subsp. *septentrionalis* (Østrup) Lange-Bertalot

Similar species:
Planothidium delicatulum s.l. (Kützing) Round & Bukhtiyarova

Morphometrics:
Biovolume (µm^3): 300

Frustule geometry: elliptic prism
Length (µm): 15.0 – (17.2) – 19.2 (SV, n=6); 11.0 – (14.0) – 18.4 (RSV, n=6)
Width (µm): 6.9 – (8.8) – 9.8 (SV, n=6); 5.3 – (7.6) – 9.6 (RSV, n=6)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 9 – (11) – 14 (SV, n=6); 9 – (11) – 13 (RSV, n=6)

Notes: complete descriptions of the morphology, taxonomy and ecology of this taxon can be found elsewhere (*e.g.* Krammer & Lange-Bertalot 1991b). This species is very close to *P. delicatulum* (see above) being mainly distinguished by its larger broadly elliptic valves, its narrow sternum and by the drawn out apices.

Distribution & Ecology: cosmopolitan, marine and brackish water species. Probably adnate in our study it was mainly found in the sandy transect, especially in the finer sandy station. Never very common it increased to a maximal abundance of 3.7 % at the end of the study period (*i.e.* winter 2004).

References:
Krammer & Lange-Bertalot (1991b) – pg. 71; figs. 39/15-19
Lange-Bertalot & Krammer (1989) – pg. 46; figs. 80/24-31, 82/ 1-24, 90/3-4
Witkowski *et al.* (2000) – pg. 124; figs. 46/20-22

***Planothidium* sp.1**

Micrographs: Pl. 8: 48-55

Morphometrics:
Biovolume (µm^3): 42
Frustule geometry: elliptic prism
Length (µm): 7.2 – (7.8) – 8.8 (SV, n=7); 6.9 (RSV, n=2)
Width (µm): 3.3 – (3.6) – 3.8 (SV, n=7); 3.0 (RSV, n=2)
Pervalvar axis (µm): 2 (estimated)

Description: valves lanceolate-rhombic with slightly protracted blunted apices. Both valves are delicate and structureless. Only the slight expansions of the median costa (*i.e.* raphe-sternum) in the central area and on the poles are perceivable in LM. In the SV, the central sternum is even more perceivable in LM. The striae are irresolvable in LM. The central raphe endings on the RSV are straight and simple.

Notes: the identity of this peculiar diatom is not at all clear. Superficially it looks like a taxon belonging to the genus *Fistulifera*, given the obvious similarities, in LM, to the freshwater species *F. saprophila* or *F. pelliculosa* (see Lange-Bertalot 2001). However, observations of the incinerated slides indicated that it is most probable that this unknown species is a monoraphid diatom. The hypothesis that these could be the raphid valves of Achnanthes sp.1 (see above), with a similar valve outline, was abandoned after the observation of intact frustules of that taxon, in which the raphid valve lacks the prominent raphe-sternum. In fact, this taxon is very reminiscent of an unknown species described by Sabbe (1997) and tentatively identified as *Achnanthidium* sp.4 (but *Achnanthidium sensu* Round *et al.* 1990). He was fortunate to observe is species on SEM and concluded the RSV were related to *Achnanthes* cf. *delicatissima* (*sensu* Sundbäck & Snoeijs 1991), and *Achnanthes* sp. C (*sensu* Kuylenstierna 1989-1990). All these taxa have striae composed of alveoli, which is typical of the striae structure in *Planothidium*. Therefore, even though it was not confirmed with direct observations this species is provisionally considered as *Planothidium* sp.1.

Distribution & Ecology: small motile, probably epipsammic, species. Even though it was never very abundant (max. abundance < 0.7%), this species was fairly frequent in the sandy station but it was also found in a few mudflat samples (21 occurrences). Sabbe (1997) reported this taxon for the Westerschelde estuary, found mainly in the medium sandy sediments in the lower reaches and the mouth of that estuary.

Fam. Cocconeidaceae Kützing

Anorthoneis Kützing 1844

Genus description: Sterrenburg (1988), Round *et al.* 1990, Hein (1991)

Anorthoneis excentrica (Donkin) Grunow 1867

Micrographs: Pl. 11: 1-4

Synonyms:
Cocconeis excentrica Donkin
Orthoneis excentrica (Donkin) Peragallo & Peragallo

Similar species:
Anorthoneis minima Foged
Anorthoneis hummii Hustedt
Anorthoneis vortex Sterrenburg
Anorthoneis pulex Sterrenburg

Morphometrics:
Biovolume (µm^3): 2522
Frustule geometry: elliptic prism
Length (µm): 22.3 – (26.8) – 29.4 (SV, n=4); 21.2 – (27.2) – 33.9 (RSV, n=6)
Width (µm): 19.8 – (22.9) – 27.2 (SV, n=4); 20.2 – (24.2) – 29.8 (RSV, n=6)
Pervalvar axis (µm): 5 (estimated)
Striae in 10 µm: 9 – (10) – 13 (SV, n=4); 11 – (12) – 12 (RSV, n=6)

Notes: according to Sterrenburg (1988), *Anorthoneis excentrica* distinguishes itself from other *Anorthoneis* species, namely *A. vortex* and *A. pulex*, by the lack of a hyaline area on either of the valves, coarser striation and larger size. The specimens illustrated by Witkowski (1994) correspond to *A. vortex*, as the author corrected latter (Witkowski *et al.* 2000). Likewise, the specimen illustrated by Snoeijs & Vilbaste (1994) seems also to be *A. vortex*.

Distribution & Ecology: cosmopolitan, marine and brackish water species occurring in coastal sandy sediments. Although sometimes referred as free living among sand grains and present in “foam from the beach”, Sterrenburg (1988) established that this species is mainly epipsammic, probably adnate. An epiphytic life-style was also discarded. In our samples, it was very rare (max. abundance 0.53%), occurring only in a few sandy sediment samples. The low abundances of *Anorthoneis* taxa seem to be recurrent in the literature (*e.g.* Foged 1975, Garcia & Talgatti 2008), as Sterrenburg (1988) points out.

References:
Hendey (1964) – pg. 182, fig. XXXVIII/10
Poulin *et al.*(1984a) – fig. 4
Round *et al.* (1990) – pg. 510
Sterrenburg (1988) – figs. 1/3,5-6, 4/24-27
Witkowski *et al.* (2000) – pg. 97; figs. 42/20, 54/9-10

Anorthoneis cf. ***tenuis*** Hustedt 1955

Micrographs: Pl. 11: 5-14; Pl. 43: 1

Similar species:
Anorthoneis dulcis Hein
Anorthoneis pulex Sterrenburg
Anorthoneis vortex Sterrenburg
Cocconeis tenuis Hustedt

Morphometrics:
Biovolume (µm^3): 309
Frustule geometry: elliptic prism
Length (µm): 11.1 – (13.1) – 15.8 (SV, n=11); 10.8 – (13.8) – 17.3 (RSV, n=12)
Width (µm): 7.9 – (9.5) – 12.0 (SV, n=11); 6.2 – (9.8) – 12.6 (RSV, n=12)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 13 – (16) – 18 (SV near sternum, n=11); 14 – (17) – 20 (RSV near sternum, n=10); 17.0 – (21) – 23 (RSV near margin, n=11)
Punctae in 10 µm: 13.8 – 17.3 – 19.7 (SV, n=4); 19.7 – 23.3 – 26.2 (RSV, n=5)

Notes: of the three groups Sterrenburg (1988) created to sort out the valid species of *Anorthoneis*, this taxon belongs to group III (*i.e.* “with dilated central hyaline area on both valves”). This group includes *A. pulex*, *A. vortex*, *A. dulcis* and *A. tenuis*, as illustrated by Simonsen (1987), which are also part of the lower size range group (with the exception of *A. vortex*). The distinction between them is quite difficult, as a result of several factors. Firstly, they have quite similar S-valves and the low pervalvar height of the frustules makes it very difficult to discern the fragile RS-valves. It is seemingly impossible to determine the complete structure of the frustule without SEM examination of the material. Secondly, there are only a few, often incomplete studies regarding this genus. For example, for some species (*e.g. C. tenuis* and *A. tenuis*) the holotype consists of only one RS-valve and an S-valve. Finally, the morphological variation in most of these taxa is little known and the taxonomical relevance of morphological features, such as size and shape of central area, striation density or the presence and shape of the punctae in the marginal zone are largely undetermined (see Hein 1991, Sterrenburg 1988 and Sabbe 1997).

The specimens found in our study seem to be the same as the one described as *A.* cf. *tenuis* by Sabbe (1997). Even though it is very similar to *A. pulex* and *A. dulcis* in size range and, especially, when considering the S-valve, it can be distinguished from these taxa by several ultra-structural aspects.

The most conspicuous difference to *A. pulex* is that the RS-valves do not correspond at all to the one illustrated and described by Sterrenburg (figs. 19-21, 1988). However, as Sabbe (1997) remarked, Sterrenburg's illustrations probably refer to whole frustules, with the depicted raphe system belonging to a finely areolated RS-valve that was hidden by the S-valve and, therefore, were not correctly described. It was also it very difficult to photograph RS-valves in complete frustules, in the slides of incinerated material. Sabbe (1997) described and illustrated two types of RS-valves, of the same size range of *A. pulex*, that were previously unreported, and that he attributed to *A.* cf. *pulex* and *A.* cf. *tenuis.* The latter ones are very similar to the RS-valves found in our slides, with the central striae having a lower density than the ones attributed to *A.* cf. *pulex* but close to the ones attributed to *A.* cf. *tenuis* (*sensu* Sabbe 1997). Additionally, and as Sabbe (1997) remarked, the distinct striation pattern in the marginal zone is not only due to the insertion of short striae but it seems rather independent and composed by more elongated, square areolae, in opposition with the more rounded ones in the central area. Considering the rapheless valve, there is a small or absent central hyaline area, often filled with "faint" striae up to the sternum, where a vestigial raphe is frequently present. Both features are clearly visible in our SEM micrographs and seem to be rarer in *A. pulex* (Sterrenburg 1988), which has a much larger hyaline central area and also has a slighter finer striation in the RSV, near the sternum. As for *A. dulcis*, the fact that it has a higher similarity between both valves, allows a simple distinction between both species (Hein 1991, Garcia & Talgatti 2008).

Sabbe (1997) considered this taxon to be very close to *A. tenuis* but the identity of the latter species is also problematic. The protologue is based only in a single S-valve (see Simonsen 1987), that has a striation density of 18-20 in 10 µm and no vestigial areolae. Following Sabbe's (1997) rationale, this S-valve does not correspond to the RS-valve of *C. tenuis* (as suggested by Simonsen 1988), which he further considered as a putative synonym of *A. pulex*. Our observations confirm that the RS-valve *A.* cf. *tenuis* is different from *C. tenuis* and from *A. pulex*. Unfortunately Sterrenburg (1988) could not examine the type material of both these taxa when he described *A. pulex*. A complete LM and SEM study of the complete frustules (including type material) is necessary to discern the relationships between all these taxa.

Distribution & Ecology: as most species of *Anorthoneis*, this taxon seems to be part of the adnate, epipsammic fraction of estuarine/marine sandy sediments. Similar specimens were found in the polyhaline reaches of the Westerschelde estuary (Sabbe 1997), Chesapeake Bay (Cooper 1995) and probably also in Tanzania (Witkowski *et al.* 2000). In our samples it was very rare (only 5 occurrences; max. abundance of 0.3 %) and only present in sandy sediments.

References:

Cooper (1995) – fig. 71
Sabbe (1997) – pg. 120; figs. 10/9-12, 10/13(?), 10/16 (?), 44/4-6
Simonsen (1987) – pg. 405; figs. 603/15-20

Witkowski *et al.* (2000) – fig. 51/2? (as *A. pulex*)

Cocconeis Ehrenberg 1837

Genus description: Lange-Bertalot & Krammer (1989); Krammer & Lange-Bertalot (1991b), Round *et al.* (1990)

Cocconeis cf. **discrepans** A. Schmidt *in* Schmidt *et al.* 1894

Micrographs: Pl. 9: 17-22; Pl. 43: 3

Synonyms:
Raphoneis tenuis Hustedt

Similar species:
Amphicocconeis disculoides (Hustedt) De Stefano & Marino (syn. *Cocconeis disculoides* Hustedt)
Amphicocconeis debesi (Hustedt) De Stefano
Psammococconeis brasiliensis Garcia

Morphometrics:
Biovolume (µm^3): 110
Frustule geometry: elliptic prism
Length (µm): 8.5 – (11.0) – 14.5 (SV n=8); 9.0 (RSV n=2)
Width (µm): 5.0 – (5.5) – 6.0 (SV n=8); 4.8 (RSV n=2)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 13 – (16) – 18 (n=8); 21 (RSV n=5)
Punctae in 10 µm: 11 – (12) – 14 (n=5)

Description: valves elliptic to narrowly elliptic, with acute apices. The S-valve has a narrow, very slightly lanceolate sternum. The striae are coarse, composed by transapically elongated poroids, arranged in longitudinal rows. The poroids are, apparently, located at the bottom of crater-shaped external openings. The striation is parallel at the centre and slightly radiating towards the apices. RS-valve has striae that radiate throughout the valve and that seem to be interrupted by two lateral areas. The raphe-sternum is narrow with a circular central area. Raphe is straight with the central endings approximate.

Notes: the specimens found in our study show clear resemblances to *C. discrepans* as it is depicted and described in Witkowski *et al.* (2000) and Witon & Witkowski (2006), specially when considering the sternum valve, where there was total agreement regarding the morphometric data. This valve is also very reminiscent of *Raphoneis tenuis* Hustedt (see Simonsen 1987, Cooper 1995) which was considered a synonym of *C. discrepans* by Witkowski *et al.* (2000). Sabbe (1997) also found a similar taxon in the Westerschelde estuary (*Cocconeis* sp.5) but most of his specimens had lower striation density (with the exception of Figs. 11/21-22). However, the raphe-sternum valves described and illustrated in the above mentioned works have always very fine striation, barely resolvable in LM. In our study, we were only capable of finding two RS-valves still part of complete frustules. The striation visible in the RS-valves could be caused by the reflection of the coarser striation on the S-valve standing below, since the pervalvar axis is very short. Conversely, the RS-valves seem to have a slightly more radiating striation pattern and lateral interruption of the striae. It was, therefore, decided not to make a definitive positive identification as *C. discrepans* without further studies.
The only valve depicted in the SEM micrograph (Pl. 43: 3) had slightly lower striation density (13 in 10µm) than the ones observed in LM, but within the striae density range of *Cocconeis sp.5 sensu* Sabbe. If further studies confirm that all these taxa (including C. *discrepans sensu* Schmidt) have poroids located at the bottom of crater-like external openings, it will be advisable to transfer them to either *Psammococconeis* or *Amphicocconeis* (see Garcia 2001, De Stefano & Marino 2003, Sar *et al.* 2003a). However, at this moment there is not enough information. For example, it was impossible to determine if the poroids are occluded internally by fimbriate hymenes (*viz. Psammococconeis*) or simple hymenes (*viz. Amphicocconeis*).

Distribution & Ecology: Epipsammic, probably adnate species. It was extremely rare in our study, only present in medium/coarse sandy stations and with very few occurrences (4), always at very low abundances (max. abundance < 0.3 %). Cocconeis discrepans is reported for coasts of the Atlantic and Indian oceans.

References:
Cooper (1995) – figs. 31/a-c
Simonsen (1987) – pg 369, figs. 554/1-4
Witon & Witkowski (2006) – figs. 133, 134
Witkowski *et al.* (2000) – pg. 106; figs. 41/35-40, 42/26-27

Cocconeis cf. ***distans*** Gregory 1857

Micrographs: Pl. 9: 1-7; Pl. 43: 2

Similar species:
Cocconeis distans Gregorii
Cocconeis guttata Hustedt & Aleem
Cocconeis nitida Gregory

Morphometrics:
Biovolume (µm^3): 1845
Frustule geometry: elliptic prism
Length (µm): 18 – (20.9) – 26 (SV, n=6); 16.8 – (22.6) – 26 (RSV, n=11)
Width (µm): 14.3 – (16.7) – 21.8 (SV, n=6); 13.9 – (18.9) – 26.3 (RSV, n=11)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 7 – (9) – 11 (SV near sternum, n=6); 13 – (15) – 16 (RSV near sternum, n=11)

Description: valves broadly elliptic, almost flat and with a narrow mantle. RS-valve has a slightly eccentric and narrow raphe-sternum and small rounded central area. The raphe is simple, almost straight but it is non-coaxial, with the central endings turning slightly to opposite sides, internally. The distal endings finish near the apices. The striae radiate throughout and are uniseriate up to the valve margin. They are composed by rounded areolae internally occluded by non-perforated hymenes. Near the mantle fold there is a marginal row of simple elliptical, transapically elongated, punctae that are also occluded by non-perforated hymenes. The sternum valve has completely different transapical striae, which are composed by rounded, robust areolae, more or less irregularly spaced and loosely delineating the radiating striae. The sternum is very slightly eccentric and it is linear to slightly lanceolate. There is also a marginal ring of finer poroids.

Notes: the complex and confusing taxonomical history of *Cocconeis distans* has been recently revised by De Stefano *et al.* (2006), where historical collections and live material were analysed. Our specimens do not correspond completely to the description given there and in Hustedt (1931-1959) because the RS-valves lack the characteristic submarginal hyaline area, reinforced by a thickened rim. Additionally, it has slightly coarser striation. However, many other morphological features show that both taxa are very closely related. Several authors, including Hustedt (1955); Kuylenstierna (1989-1990) and Witkowski *et al.* (2000) seem to have found exactly the same type of specimens we encountered in our study and identified them as *C. distans* or *C.* cf. *distans*. It is most probably a variety, but further studies are needed to determine its taxonomical validity.

Distribution & Ecology: epipsammic, probably adnate species. This taxon was very rare in our study and it was only present in samples of the medium/coarse sandy stations (7 occurrences), always at very low abundances (max. abundance <0.55%). It has been reported as rare in sandy sediments for the Southern and Western Baltic Sea (*e.g.* Kuylenstierna 1989-1990, Witkowski 1994) and for the Gulf of Saint Laurent (Poulin *et al.* 1084). *Cocconeis distans* has a more cosmopolitan distribution either in sandy sediments (*e.g.* Hustedt 1931-1959) or as epiphyte in seagrasses (*e.g.* De Stefano *et al.* 2006).

References:
Hustedt (1955) – fig. 5/4-5 (as *C. distans*)
Kuylenstierna (1989-1990) – fig. 37/361-362 as *C. distans*)
Poulin *et al.* (1984a) – pg. 51; fig. 29-32 (as *C.* aff. *distans*?)

Witkowski (1994a) – fig. XIV/6 (as *C. distans*)
Witkowski *et al.* (2000) – fig. 38/31-34 (as *C.* cf. *distans*)

Cocconeis hauniensis Witkowski *emend.* Witkowski 2000

Micrographs: Pl. 10: 1-5; Pl. 43: 4-5

Similar species:
Cocconeis sp.1
Cocconeis peltoides Hustedt

Morphometrics:
Biovolume (µm^3): 54
Frustule geometry: elliptic prism
Length (µm): 5.4 – (7.8) – 11.5 (SV, n=24); 6.1 – (7.4) – 8.7 (RSV, n=6)
Width (µm): 3.4 – (4.6) – (5.6) (SV, n=25); 2.1 – (4.1) – 4.9 (RSV, n=6)
Pervalvar axis (µm): 2 (estimated)
Striae in 10 µm: 21 – (26) – 32 (SV, n=26); 24 – (25) – 27 (RSV, n=7)
Punctae in 10 µm: 32 – (46) – 58 (SV, n=5)

Notes: a detailed morphological description was made by Witkowski (1993a) and, with corrections relatively to the RS-valve, by Witkowski *et al.* (2000). The delicate raphe-sternum valve of *Cocconeis hauniensis* shows close resemblances to the RS-valve of *C. peltoides*, *C. pelta* and even *Cocconeis* sp.1. All these taxa lack a distinct placentuloid submarginal ring of silica in their RS-valve. Conversely, the S-valves, which are more robust, can be distinguished from the other similar species by their size, striation density, the lack of lateral hyaline areas (*viz. C. peltoides*) or by the absence of poroids on the mantle (*viz. Cocconeis* sp.1). Other important characters are the uniseriate striae and the existence interstria fimbriate projections on the valvocopulae. *Cocconeis* sp.2 described by Sabbe (1997) is probably conspecific to *C. hauniensis*, since it has the same size range, similar striae density in the sternum valves and seems to be indistinct in the LM. Nevertheless, when comparing the SEM micrographs of the external RS-valves (*i.e.* Figs. 45/7, Sabbe 1997; 55/1; Witkowski *et al.* 2000), the Westerschelde specimens seem to be slightly different. They have higher marginal striae density (approximately 70 in 10 µm) and non-coaxial raphe branches, with central raphe endings deflected in opposite directions. Unfortunately, in our study no external views of the RS-valves were found in the SEM.

Distribution & Ecology: solitary, epipsammic and probably adnate species. Witkowski *et al.* (2000) describes this species as widespread in the Baltic Sea. Sabbe (1997) refers to *Cocconeis* sp.2 as very common in fine sandy to silty sediments, throughout the Westerschelde estuary. In our study *C. hauniensis* was very common, occurring in all samples from the sandy stations throughout the study period. Maximal relative abundances (max. abundance <5.5%) were registered in medium coarse sands, especially in late spring/early summer.

References:
Sabbe (1997) – pg. 126; figs. 10/17-22, 45/7-8
Witkowski (1993) – figs. 1/E-N, 2/A-C, 3/A-D
Witkowski *et al.* (2000) – pg. 108, fig. 42/1-7, 55/1

Cocconeis cf. ***hauniensis*** Witkowski 1993

Micrographs: Pl. 10: 6-11

Similar species:
Achnanthes levanderi Hustedt

Morphometrics:
Biovolume (µm^3): 60
Frustule geometry: elliptic prism
Length (µm): 8 – (8.4) – 8.8 (SV, n=5); 9.8 (RSV, n=2)
Width (µm): 3.8 – (4) – 4.2 (SV, n=5); 4.7 (RSV, n=2)
Pervalvar axis (µm): 2 (estimated)
Striae in 10 µm: 22 – (24) – 26 (SV, n=5); 25 (RSV, n=1)

Notes: only RS-valves were found. This taxon is probably conspecific to *C. hauniensis* (see above) because it has the same size, striation density and orientation of the striae. However, the RS-valves are consistently more narrowly elliptic (*i.e.* with less broadly rounded ends) and with a considerably wider and longer lanceolate sternum. In addition, the striae seem to be more robust, with almost distinct punctae in LM, and limited to the valve margin. The axial area and striation make this taxon very reminiscent of the freshwater oligotrophic species *Achnanthes levanderi* (*e.g.* Krammer & Lange-Bertalot 1991b). Witkowski (1993a) admits the RS-valve of *C. hauniensis* can have either small axial areas, irregularly widened in the centre of the valve, or large lanceolate axial areas. Finally, figure 10/17 in Sabbe (1997) displays a specimen of *Cocconeis* sp.2 (see above in *C. hauniensis*) very similar to the specimens found in our study. Therefore, further studies are needed to fully understand the relations and morphological variability of these small taxa.

Distribution & Ecology: solitary, epipsammic and, probably, adnate species. Less common than *C. hauniensis*, it mainly occurred in the sandy transect stations (29 of 45 sandy sediment samples) and at much lower abundances (max. abundance < 1.8%).

References:
Sabbe (1997) – pg. 126; figs. 10/17-22, 45/7-8
Witkowski (1993) – figs. 1/E-N, 2/A-C, 3/A-D

Cocconeis pelta Schmidt 1874

Micrographs: Pl. 10: 12-17; Pl. 43: 10-11

Similar species:
Cocconeis fluminensis (Grunow) Peragallo & Peragallo
Cocconeis cf. *pelta* (see below)
Cocconeis peltoides Hustedt

Morphometrics:
Biovolume (µm^3): 221
Frustule geometry: elliptic prism
Length (µm): 11.3 – (12.8) – 14 (SV, n=6); 14.2 (RSV, n=2)
Width (µm): 7.1 – (8.5) – 9.8 (SV, n=6); 9.0 (RSV, n=2)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 19 – (22) – 26 (SV, n=8); 25 (RSV, n=2)
Punctae in 10 µm: 50 (n=3)

Notes: the sternum valves of *C. peltoides* and *C. fluminensis* resemble *C. pelta* in its characteristically large lanceolate axial area, bordered by marginal costae. Frequently overlooked, due to their fine structure, our observations show that the fragile RS-valves of *C. peltoides*, *C. pelta* and *C.* cf. *pelta* are virtually indistinguishable in LM (see description below, *Cocconeis* cf. *pelta*)

Distribution & Ecology: epipsammic adnate species. Cosmopolitan, marine, common in European estuaries (*e.g.* Baltic Sea), but also present in Patagonian coast (Sar 2003). In our study, *C. pelta* was very common in the sandy sediment samples (40 occurrences out of 45 samples) but with low abundances (max. abundances < 3.3 %).

References:
Hendey (1964) – pg. 181
Hustedt (1931-1959) – pg. 361; fig. 815
Peragallo & Peragallo (1897-1908) – pg. 10; fig. II/6
Sar *et al.* (2003a) – pg. 91; fig. 33
Witkowski *et al.* (2000) – pg. 111; fig. 41/7-10

Cocconeis cf. ***pelta*** Schmidt 1874

Micrographs: Pl. 10: 18-22; Pl. 43: 9

Similar species:
Cocconeis fluminensis (Grunow) Peragallo & Peragallo
Cocconeis pelta Schmidt

Morphometrics:
Biovolume (µm^3): 166
Frustule geometry: elliptic prism

Length (µm): 9.0 – (11.2) – 13.0 (SV, n=6); 11.3 (RSV, n=2)
Width (µm): 6.4 – (7.5) – 8.3 (SV, n=6); 7.8 (RSV, n=2)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 21 – (23) – 25 (SV, n=6); 28 (RSV, n=2)
Punctae in 10 µm: 63 (SV, n=1)

Description: valves elliptical with a narrow mantle. S-valves have a large, broadly lanceolate, axial area bordered by delicate marginal costate virgae, radiating throughout the valve. The striae are located in the intercostae; they are uniseriate and composed by rounded poroids, occluded internally by non-perforated hymenes. Sometimes an elevated, broadly lanceolate central sternum is present and a vestigial raphe is frequently visible in the middle of this sternum. Although very reminiscent of *C. pelta*, the random drop-like depositions of silica on the axial area of the S-valve do not occur. RS-valves are very fragile and undulate longitudinally. Axial area is narrow and raphe simple and straight. Distal raphe ends near the apices, central raphe ends quite approximate and central area small and circular. Striae are barely visible in the LM and only near the sternum, probably becoming biseriate (and irresolvable in LM) closer to the valve margins.

Notes: very reminiscent of *C. pelta*, the main differences are the lack of any drop-like patterns caused by silica deposition in the central area of the RS-valve, a slightly higher marginal striae density and the apparently less reinforced costate virgae. It is also slightly smaller than *C. pelta* but still only a few specimens were measured. The S-valves look extremely similar to *Cocconeis* sp.3 depicted in Sabbe (1997), but this taxon has even denser striation. Probably a morphotype of *C. pelta*, but without more complete studies, such as ultra-structural investigations of the different valves in the SEM, it is not possible to determine the relations of these close taxa.

Distribution & Ecology: epipsammic, probably adnate. This taxon is extremely rare, with only 5 occurrences in our samples (in sandy stations) and always at very low abundances (max. abundance < 0.5%). Not referred in the consulted literature, with the possible exception of Sabbe (1997) for the sandy sediments of the Westerschelde estuary. It has been probably overlooked and/or identified as *C. pelta.*

References:
Sabbe (1997) – pg. 127; fig. 11/16-17

Cocconeis peltoides Hustedt 1939

Micrographs: Pl. 10: 23-30; Pl. 43: 6-7

Similar species:
Cocconeis fluminensis (Grunow) Peragallo & Peragallo
Cocconeis pelta Schmidt

Morphometrics:
Biovolume (µm^3): 175
Frustule geometry: elliptic prism
Length (µm): 9.6 – (12.7) – 16.3 (SV, n=8); 6.2 – (11.2) – 20.7 (RSV, n=15)
Width (µm): 6.3 – (8.3) – 9.7 (SV, n=8); 4.5 – (7.2) – 9.6 (RSV, n=15)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 15 – (16) – 17 (SV, n=8); 20 – (27) – 30 (RSV, n=10)
Areolae in 10 µm: 20 – (25) – 27 (SV, n=7)

Notes: common and very easily distinguishable species with its coarsely punctate S-valves, which have lateral hyaline areas, caused by raised sections of the valve. However, it has seldom been illustrated in the SEM (*e.g.* Sabbe 1997, Snoeijs & Vilbaste 1994). The internal views of our specimens closely match the ones depicted by Sundbäck & Snoeijs (1991). In both cases, the specimens have small rounded poroids at the end of each stria, near the mantle, with well developed rim. This feature was also remarked by Sar *et al.* (2003, fig. 39). The RS-valves of *C. peltoides* are very reminiscent of *C. pelta* (see discussion above). In LM, the striae are only visible in a more or less lanceolate area near the raphe-sternum because they become biseriate as they are closer to the valve margin (Sabbe 1997).

Distribution & Ecology: *Cocconeis peltoides* is a cosmopolitan epipsammic, adnate species found in sandy sediments of estuaries and coastal areas of Northern and Western Europe but also in North America (*e.g.* Hustedt 1955), South America (Sar *et al.* 2003) and South Africa (Giffen 1975). Fairly common in the sandy stations studied (22 occurrences in 45 samples) it was never very abundant (max. abundance < 1.9 %).

References:
Brockmann (1950) – fig. 6/5,7
Cooper (1995) – fig. 49
Hendey (1964) – pg. 181
Hustedt (1939 (1939)) – pg. 606; fig. 23-27
Kuylenstierna (1989-1990) – pg. 81; fig. 37/364-366
Sabbe (1997) – pg. 122; figs. 11/1-4, 43/5, 44/1-3
Sar *et al.* (2003) – pg. 91; fig. 34-41
Simonsen (1987) – pg. 253; fig. 376/1-10
Snoeijs & Vilbaste (1994) – # 119
Sundbäck & Snoeijs (1991) – figs. 9/a-c
Witkowski *et al.* (2000) – pg. 111; fig. 41/7-10

Cocconeis cf. ***peltoides*** Hustedt 1939

Micrographs: Pl. 10: 31-34; Pl. 43: 8

Similar species:
Cocconeis fluminensis (Grunow) Peragallo & Peragallo
Cocconeis pelta Schmidt

Morphometrics:
Biovolume (μm^3): 146
Frustule geometry: elliptic prism
Length (µm): 7.4 – (10.9) – 14.5 (SV, n=10)
Width (µm): 5.3 – (6.8) – 8.2 (SV, n=10)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 13 – (16) – 17 (SV, n=10)
Punctae in 10 µm: 23 (n=2)

Notes: only sternum valves were found. These specimens have the same general morphology as *C. peltoides* (see above) but with one main difference: the typical longitudinal hyaline lines, delimiting the lanceolate depressed central area, are not clearly visible in the LM. In *C. peltoides*, these are formed not only by the lateral undulation of the valve face, but also by external siliceous thickenings that form longitudinal costae and transverse interstriae in the valve surface (see Snoeijs & Vilbaste 1994). The SEM external view of the S-valve shows that the longitudinal elevation, halfway between the sternum and the valve margin is less developed and longitudinal costae and interstriae are much less silicified, being almost completely disorganized and imperceptible. Sar *et al.* (2003) found similar features in specimens of the Gulf of San Matías (Argentina) and decided to maintain them in *C. peltoides*. It may be that the specimens found in our study are only morphotypes, included the range of variation existing within this species However, they do not correspond completely to the ones depicted in that study (figs. 37 and 38, Sar *et al.* 2003). Since they lack the longitudinal lines and were clearly distinct from typical *C. peltoides* in LM, it was decided to name them *C.* cf. *peltoides*.

Distribution & Ecology: epipsammic, probably adnate species, quite common in the sandy stations (37 occurrences in 45 samples) it was more frequently found than *C. peltoides*, although with the same abundances (max. abundance 1.7%). Besides the possible reports referred above, Cooper (1995) found very similar R-valve in Chesapeake Bay sediments.

References:
Cooper (1995) – figs. 35a-b
Sar *et al.* (2003) – pg. 91; fig. 34-41

Cocconeis cf. ***placentula*** Ehrenberg 1838

Micrographs: Pl. 10: 35-44

Similar species:
Cocconeis neodiminuta Krammer
Cocconeis neothumensis Krammer
Cocconeis neothumensis var. *marina* De Stefano Marino & Mazzella
Cocconeis placentula var. *euglypta* (Ehrenberg) Grunow

Morphometrics:
Biovolume (µm^3): 96
Frustule geometry: elliptic prism
Length (µm): 5.8– (9.2) – 12.2 (SV, n=20); 7.7 – (9.0) – 10.8 (RSV, n=9)
Width (µm): 3.4 – (4.8) – 6.0 (SV, n=19); 4.4 – (5.3) – 6.2 (RSV, n=9)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 22 – (25) – 30 (SV, n=20); 19 – (24) – 28 (RSV, n=9)
Punctae in 10 µm: 19 – (22) – 25 (SV, n=11)

Description: valves elliptic, with broadly rounded apices. RS-valve has a very narrow, linear and slightly raised raphe-sternum. An obvious submarginal rim encircles the valve, interrupting striae near the margin of the valve. The striation has a slightly radiating pattern but the striae are almost parallel in the centre. The raphe is straight and it is not easy to distinguish the central and distal ends in LM, as the distal ends seem to finish close to the submarginal ring. Central area very small and central raphe endings approximate. S-valve has a narrow, linear central sternum. Striae are slightly radiating (as in the RS-valve) and formed by transapically elongate poroids (more than 5 in each hemivalve). Between the striae, there are siliceous ribs that create wavy longitudinal lines (seen in LM) across the striae.

Notes: the same taxon was reported and described by Sabbe (1997) for the poly- and euhaline reaches of Westerschelde estuary As he states in his remarks, even though it largely corresponds to the description of *C. placentula* (*sensu* Krammer & Lange-Bertalot 1991b) this species has a different striae density and a different autoecology, being typical of freshwater or slightly brackish water (*e.g.* Juggins 1992, Snoeijs 1993). The variety *C. placentula* var. *euglypta* is thought to be more estuarine (*e.g.* Cooper, 1995, Kuylenstierna 1989-1990, Snoeijs & Balashova 1998) but it is much larger and has coarser striation (Krammer & Lange-Bertalot 1991b, but see below).
The marine taxon *Cocconeis neothumensis* var. *marina* is another species that closely resembles *C.* cf. *plancentula* in its general appearance, especially when considering the S-valves of *C. placentula* var. *euglypta*, (De Stefano *et al.* 2000). However, the RS-valve of *C. neothumensis* var. *marina* is quite different, as it lacks the typical submarginal hyaline line, common to all placentuloid varieties, including our described taxon. Other important differences are discussed in two studies by De Stefano *et al.* (2000) and Sar *et al.* (2003a).While considering it to be most probably a variety of *C. placentula*, we decided to follow Sabbe (1997) and hesitate to make a definitive identification of this taxon without further studies.

Distribution & Ecology: one of the most common adnate epipsammic species found in our study, occurring in 37 of 45 samples from the sandy stations. It was particularly common in the medium/coarse sandy stations where it achieved its relative maximal abundance (<4.1%). Sabbe (1997) reports this taxon as common in fine sandy sediments throughout the Westerschelde estuary. Besides this study, well documented and illustrated, it is difficult to access where the taxon described here might have been occurring with certainty, as there are many reports of *C. plancentula* and its varieties from freshwater to fully marine conditions (see Cooper 1995, for references list).

References:
Sabbe (1997) – pg. 123; figs. 11/12-12, 46/5-6

Cocconeis scutellum Ehrenberg var. ***parva*** (Grunow) Cleve in Van Heurck 1880

Micrographs: Pl. 10: 45-46

Synonyms:
Cocconeis aggregata Kützing
Cocconeis consociata Kützing
Cocconeis transversalis Gregory
Cocconeis scutellum var. minor Schmidt

Similar species:
Cocconeis scutellum var. *scutellum* Ehrenberg
Cocconeis diminuta Pantosek
Cocconeis stauroneiformis (W. Smith) Okuno
Cocconeis neothumensis Krammer

Morphometrics:
Biovolume (µm^3): 532
Frustule geometry: elliptic prism
Length (µm): 19.7 (SV, n=2)
Width (µm): 11.5 (SV, n=2)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 13 (SV, n=2)
Punctae in 10 µm: 12 (SV, n=1)

Notes: a revision of this species and its varieties has been recently published by De Stefano *et al.* (2008). Although only a few sternum valves were found, the size range and striae density point to one of the smaller varieties of *C. scutellum*, the var. *parva*. According to De Stefano *et al.* (2008), this variety can also be distinguished "by the absence of biseriate striae on the mantle, submarginal hyaline areas in both valves and papillae on RS-valve". Regarding the S-valve, the monoseriate striae seem to end near the mantle in large apically elongated poroid areolae (Figs. 91-92 in De Stefano *et al.* 2008), making the marginal ring more difficult to discern than in other varieties. *Cocconeis scutellum* var. *parva* can also be easily confused with *C. diminuta* Pantosek, which has the same size range, but this species has transapically elongated poroids and lacks the characteristic marginal ring of fine punctuate striae (Poulin *et al.* 1984a).

Distribution & Ecology: *Cocconeis scutellum* var. *parva* has a cosmopolitan distribution (*e.g.* Witkowski 2000) often co-occurring with the nominate variety (Hendey 1964) being especially abundant in brackish and estuarine environments (De Stefano *et al.* 2008). This adnate species has been commonly reported as epiphytic in phanerogam leaves or even other (larger) diatoms (De Stefano *et al.* 2008). It has also been reported for hard substrates (Poulin *et al.* 1984b) and, more rarely, as epipsammic in intertidal flats (Riaux-Gobin 1991). In our study, it was fairly frequent in the sandy station samples (12 occurrences in 45 samples) but always at very low abundances (max. abundance < 0.9 %).

References:
Archibald (1983) – pg. 76; fig. 168
De Stefano *et al.* (2008) – pg. 530; figs. 90-105
Hendey (1964) – pg. 180
Krammer & Lange-Bertalot (1991b) – pg 93; figs. 57/5-7
Poulin *et al.* (1984a) – pg. 56; figs. 49–53
Riaux-Gobin (1991) – pg. 129, figs. 2/9–11
Snoeijs (1993) – # 25 (nominate variety)
Witkowski *et al.* (2000) – pg. 114; figs. 38/10, 42/17-19

Cocconeis sp.1

Micrographs: Pl. 9: 8-13; Pl. 44: 1-2

Similar species:
Cocconeis hauniensis Witkowski emend. Witkowski
Cocconeis peltoides Hustedt

Morphometrics:
Biovolume (µm^3): 109
Frustule geometry: elliptic prism
Length (µm): 8.5 – (10.5) – 13.7 (SV, n=10); 8.4 – (8.8) – 9.4 (RSV, n=3)
Width (µm): 2.7 – (5.9) – 8.3 (SV, n=10); 3.9 – (4.4) – 5.0 (RSV, n=3)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 15 – (17) – 20 (SV, n=10); 24 – (25) – 26 (RSV, n=3)
Punctae in 10 µm: 27 (SV, n=2)

Description: valves elliptical with broadly rounded apices. The RS-valve with a very narrow raphe-sternum; central raphe endings approximate and transapical striae quite faint in LM, parallel at the centre to strongly radiate at the ends. The S-valve has a more robust striation, radiating throughout; central sternum more or less wide and lanceolate. The SEM micrograph of S-valve internal view shows that striae are uniseriate, composed by rounded poroids, which are occluded by hymenate vela. At the end of each stria, near the valve face-mantle junction, there is a very small pore.

Notes: The raphe-sternum valve is similar to the one of small specimens of *Cocconeis peltoides* but the sternum valve is closer to *Cocconeis hauniensis*, which has the same size range but finer and denser striation. A unique character is the marginal ring of small pores, at the end of the striae, which was only found in *Cocconeis* sp.1, described and illustrated by Sabbe (1997). The latter taxon S- and RS-valves correspond very well to the specimens found in our study, with the exception of the co-existence of uniseriate and biseriate striae in the RS-valve in Sabbe's taxon.

Distribution & Ecology: Sabbe (1997) reports this taxon as common for fine sandy sediments of the Westerschelde estuary, also referring that Juggins (1992) found it in the outer sandy stations of the Thames estuary. Epipsammic diatom, it is probably an adnate species. In our study, it appears infrequently and only in the samples of the sandy stations (12 occurrences in 45 samples), always at low abundances (max. abundance < 0.9%) and throughout the year.

References:
Juggins (1992) – pg. 206; fig. A.1/2
Sabbe (1997) – pg. 125; figs. 11/5-10, 45/4-5

Cocconeis sp.2

Micrographs: Pl. 9: 14-17

Similar species:
Cocconeis neodiminuta Krammer = *Cocconeis diminuta* Pantosek
Cocconeis stauroneiformis (W. Smith) Okuno
Cocconeis neothumensis Krammer
Cocconeis sp. *sensu* Sar *et al.* (2003)

Morphometrics:
Biovolume (µm^3): 110
Frustule geometry: elliptic prism
Length (µm): 7.8 – (10.2) – 14.9 (SV, n=11)
Width (µm): 4.3 – (5.5) – 6.9 (SV, n=11)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 15 – (16) – 17 (SV, n=5 m.1); 24 (SV, n=4 m.2)
Punctae in 10 µm: 13 – (14) – 19 (SV, n=4)

Description: only sternum valves were found. Valves elliptical with rounded to slightly cuneate-obtuse apices. The S-valves have a linear-lanceolate central sternum. The S-valve striae are fairly coarse, uniseriate and are almost parallel at the valve centre, becoming more radiate towards the valve ends. They are composed by circular to quadrangular areolae, more or less aligned in at least four longitudinal rows in each hemivalve. The central stria in one of the sides of the valve is reduced to one large areola, near the mantle, thus giving the impression of an half of a "stauros".

Notes: our specimens were particularly similar to *C. diminuta*, but this name was considered *nomen dubium* by Krammer (1990), who pointed out several problems with the original description. Additionally, *C. diminuta* was originally described by Pantosek as a freshwater species of Lake Balaton (Slovakia) and Hustedt (1931-1959) followed this autoecology. Finally, Krammer and Lange-Bertalot (1991b) considered it as a possible synonym of the freshwater taxon *C. neodiminuta* Krammer. Nevertheless, it has been frequently reported for coastal and estuarine waters (*e.g.* Taylor 1972, Poulin *et al.* 1984a, Laws 1988, Cooper 1995, MOLTEN 2004), although these specimens depicted in those works do not completely match the morphology of the valid species *C. neodiminuta*. This is also the case of *Cocconeis* sp. in Sar *et al.* (2003; pg. 83, Figs 9-12) and means that the true identity of all these marine taxa remains problematic.
The specimens found in our study have also a lanceolate sternum, the same size range and/or the same striation density as the taxa referred above. Conversely, the sternum valve has, typically, a short stria in the centre of the valve, which is very reminiscent of some *C. stauroneiformis* (see Figs. 42/10-11 in Witkowski *et al.* 2000). The ultrastructure of the valves of *C. stauroneiformis* is, however, completely different (*e.g.* Romero 1996) as well as the morphometry.
A final note should be added. Two groups of S-valves with different striae densities were found. This fact and given that we were unable to find the RS-valves meant that this taxon remained unidentified.

Distribution & Ecology: epipsammic, probably adnate species. It was quite infrequent in our samples (7 occurrences and only present in stations with coarse/medium sands, always at very low abundances (max. abundance <0.7 %).

ORDER NAVICULALES

Suborder Neidiineae

Fam. Amphipleuraceae Grunow

Frustulia Rabenhorst 1853

Genus description: Lange-Bertalot (2001), Round *et al.* (1990)

Frustulia interposita (Lewis) De Toni 1891

Micrographs: Pl. 13: 13-14; Pl. 44: 10-11

Synonyms:
Brebissonia interposita (Lewis) Kuntze
Navicula interposita Lewis

Morphometrics:
Biovolume (µm^3): 22066
Frustule geometry: elliptic prism
Length (µm): 109.1 – (152.6) – 228.0 (n=4)
Width (µm): 13.7 – (20.7) – 24.8 (n=4)
Pervalvar axis (µm): 9 (estimated)
Transversal striae in 10 µm: 19 – (20) – 21 (n=3)
Longitudinal striae in 10 µm: 13 – (21) – 19 (n=3)

Notes: a detailed LM description of this species is given by Patrick & Reimer (1966).

Distribution & Ecology: epipelic. The ecology and geographical distribution is unclear. According to Patrick & Reimer (1966), the type locality is uncertain (South America) and the authors described it for low mineral content water in Eastern USA and California. However, it has been reported as common for hypersaline waters (*e.g.* Servant-Vildary *et al.*1990) or as part of estuarine benthic diatom communities (*e.g.* DeFelice & Lynts 1978, Laws 1988). In the Tagus estuary it has been frequently found in mudflat epipelic assemblages (*e.g.* Ribeiro *et al.* 2003). In our study it was extremely rare, with only 3 occurrences (max. abundance < 0.8%).

References:
Laws (1988) – fig. 19/13
Patrick & Reimer (1966) – pg. 305; figs. 22/5
Servant-Vildary *et al.*(1990) – figs. 39-45

Fam. Berkeleyaceae Mann

Berkeleya Greville 1862

Genus description: Cox (1975a, 1975b, Round *et al.* (1990)

Berkeleya rutilans (Trentepohl *ex* Roth) Grunow 1880

Micrographs: Pl. 12: 12-15

Synonyms:
Conferva rutilans Trentepohl *ex* Roth
Amphipleura rutilans (Trentepohl *ex* Roth) Cleve

Morphometrics:
Biovolume (µm^3): 347
Frustule geometry: elliptic prism
Length (µm): 22.8 – (27.3) – 34.7 (n=5)
Width (µm): 4. – (5.4) – 6.4 (n=5)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 24 – (26) – 25 (n=5)

Notes: a detailed description of this taxon, both in LM and SEM is given by Cox (1975a, 1975b)

Distribution & Ecology: cosmopolitan tube-dwelling species in estuarine to marine waters worldwide. In our study, this species was very infrequent (5 occurrences) and present only in muddy sands at very low abundances (max. abundance < 1.5%).

References:
Cox (1975a) – figs. 8-12, 15, 31-32
Cox (1975b) –figs. 3-4, 8, 12-13, 20, 30-35
Houpt (1994) – figs. 3-4
Snoeijs (1993) – # 13
Witkowski *et al.* (2000) – pg. 157; fig. 62/14-17

Climaconeis Grunow 1862

Genus description: Cox (1982); Round *et al.* (1990)

Climaconeis fasciculata (Grunow *ex* Cleve) Cox 1982

Micrographs: Pl. 12: 32-33

Synonyms:
Navicula fasciculata (Grunow *in* Cleve & Möller) M. Peragallo
Navicula scopulorum var. *fasciculata* Grunow in Cleve & Möller
Okedenia scopulorum var. *fasciculata* (Grunow in Cleve & Möller) Mereschkowsky

Similar species:
Berkeleya scopulorum (Brébisson) Cox

Morphometrics:
Biovolume (µm^3): 18079
Frustule geometry: box
Length (µm): 167.4 (n=1)
Width (µm): 12.8 – (13.5) –14.6 (n=3)
Pervalvar axis (µm): 8 (estimated)
Striae in 10 µm: 15(n=3)
Punctae in 10 µm: 16 (n=2)

Notes: when only considering the frustule morphology, this taxon can be easily confused with smaller specimens of *Berkeleya scopulorum*, which have similar valve outlines and striation density. There are, nevertheless, important differences in striation pattern and shape of the valve ends as well as undulations of the valve margin in C. *fasciculata*, as Hustedt (1961-1966) pointed out. Furthermore, there are clear differences when the chloroplast structure is taken into account. *Berkeleya* spp. have one plastid, formed by two plates appressed to the girdle and united by a narrow isthmus (Cox 1979a), whereas this taxon possesses four to six pairs of H-shaped chloroplasts, each with a pyrenoid, arranged along the length of the valve (Jesus, pers. comm.). This means this taxon was correctly transferred to the genus *Climaconeis* by Cox (1982) in spite of lacking the characteristic transapical craticular bars, typical of some species of this genus (Cox, 1982, Round *et al.* 1990).

Distribution & Ecology: epipelic, euryhaline saltwater species. This taxon has been seldom reported since its original description from material collected at Elephant Point, Bengal (Cox 1982). According to this author, Mereschkowsky found it in California in 1901. Recently, Park *et al.* (2007) reported and illustrated an extremely similar *Climaconeis* sp., which we consider to be conspecific to *C. fasciculata*. In their report, they state that this taxon occurs in estuarine tidal flats in Korea but it is also present in Japanese and Chinese coasts. Since Hustedt (1961-1966) states that *C. fasciculata* was not present in European coasts and given the paucity of reports on this species, we believe this constitutes the first report for Europe. In our study, it occurred only once, in a mudflat sample, and at an extremely low relative abundance (0.3%). It has been, however, recurrently found in other samples from mudflats of the Tagus estuary and identified as *Berkeleya* sp. (*e.g.* Ribeiro *et al.* 2003).

References:
Cox (1982) – figs. 10; 16-17
Hustedt (1961-1966) – pg. 28, fig. 1187
Park *et al.* (2007) – figs. 3-5

Lunella Snoeijs 1996

Genus description: Snoeijs (1996)

Lunella cf. ***garyae*** Ulanova & Snoeijs 2006

Micrographs: Pl. 12: 16-17

Similar species:
Lunella bisecta Snoeijs
Lunella ghalebii Witkowski, Lange-Bertalot & Metzeltin
Lunella sp.1 (*sensu* Sabbe 1997)

Morphometrics:
Biovolume (µm^3): 22
Frustule geometry: half-elliptic prism
Length (µm): 6.9 (n=1)
Width (µm): 2.7 (n=1)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 29 (n=1)

Notes: only one valve was found during our study, in the upper shore fine-medium sandy station. Its morphology seems to correspond fairly well to the recently described *Lunella garyae* (Ulanova & Snoeijs, 2006), since it has the same catenuloid shape and it is of about the same size and striation density. *Lunella* is a very small genus of marine epipsammic diatoms with only 3 species described at the moment (Fourtanier & Kociolek 2007). Sabbe (1997) found a similar unidentified *Lunella* species in the fine sandy sediments of the Westerschelde estuary but the striation of his specimens is coarser (*i.e.* 18-25 str./10 µm) and the central raphe endings are turned towards the dorsal side. It is possible that both taxa are conspecific (see figs. 46/1-2, Sabbe 1997), in spite of the difference in stria density and habitat, but further studies are necessary. Since *L. garyae* was described for hypersaline supralittoral rock pools the only valve we studied was cautiously identified as *L.* cf. *garyae*. The life form and ecology are unknown.

References:
Sabbe (1997) – pg. 135; figs. 12/1-3, 46/1-2
Ulanova & Snoeijs (2006) – figs. 4-55

Parlibellus Cox 1988

Genus description: Cox (1988); Round *et al.* (1990)

Parlibellus berkeleyi (Kützing) Cox 1988

Micrographs: Pl. 13: 1-3; Pl. 44: 3-4

Synonyms:
Navicula comoides (Dillwyn) Peragallo & Peragallo
Navicula grevillei var. *comoides* Aleem
Navicula pseudocomoides Hendey
Micromega berkeleyi Kützing
Schizonema berkeleyi (Kützing) Rabenhorst

Similar species:
Parlibellus hendeyi Witkowski, Lange-Bertalot & Metzeltin
Parlibellus bennikei Witkowski, Lange-Bertalot & Metzeltin

Morphometrics:
Biovolume (µm^3): 625
Frustule geometry: elliptic prism
Length (µm): 13.7 – (18.5) – 25.9 (n=10)
Width (µm): 5.2 – (6.1) – 7.1 (n=9)
Pervalvar axis (µm): 7 (estimated)
Striae in 10 µm: 20 – (23) – 25 (n=10)
Punctae in 10 µm: 29 (n=2)

Notes: For a complete morphological description of this species, as well as of its complicated taxonomic history, two works by Cox (1978, 1988) should be consulted.

Distribution & Ecology: *Parlibellus berkeleyi* in one of the best known examples of endotubular (*i.e.* tube-dwelling) diatoms that colonize the intertidal areas of the European and North American coasts (*e.g.* Lobban 1984). In our study, it was never very abundant (max. abundance <1.6%) as hard substrates are a better habitat for the fronds than soft sediments (Houpt, 1994), but it was fairly frequent (12 occurrences). It was present in all stations but it was more common in the coarser sandy stations.

References:
Cox (1988) – pg. 21; figs. 6-10, 16
Hendey (1964) – pg.192; fig. XXX/2 (as *N. pseudocomoides*)
Hustedt (1961-1966) – pg. 304; fig. 1423 (as *N. comoides*)
Houpt (1994) – pg. 2, 8, 15, 17
Peragallo & Peragallo (1897-1908) – fig. VIII/13
Snoeijs & Vilbaste (1994) – #176
Witkowski *et al.* (2000) pg. 320; figs. 104/24-26, 105/26-29

Parlibellus cf. ***calvus*** Witkowski, Metzeltin & Lange-Bertalot 1996

Micrographs: Pl. 13: 4-5

Morphometrics:
Biovolume (µm^3): 252
Frustule geometry: elliptic prism
Length (µm): 10.1 – (15.0) – 18.7 (n=3)
Width (µm): 3.7 – (4.3) – 4.7 (n=3)
Pervalvar axis (µm): 6 (estimated)
Striae in 10 µm: 22 – (23) – 24 (n=3)
Punctae in 10 µm: ~25 (n=1)

Description: valves lanceolate, with broadly rounded apices. Valve face is flat, gently curving to a deep mantle. Axial area narrow, central area expanded transapically, almost reaching the margin, giving it a “stauros”-like facet. The central area is asymmetrical and bordered by one short stria in one side and by two short striae on the other side of the valve. Raphe is straight with the central raphe endings distant and slightly expanded. Raphe distal ends are placed very near the apical marginal and seem to be deflected to the same side. Striae slightly radiate throughout the valve and become parallel near the apices. In the centre, the striae are more widely spaced, particularly on the side where the proximal raphe ends deflect. The punctae composing the striae are barely visible in LM.

Notes: specimens found in our study correspond fairly well to the *P. calvus,* a taxon described by Witkowski *et al.* (Metzeltin & Witkowski 1996). Size range and striae density are the same but there are also important differences such as the lack of short striae, bordering the fascia margin, in *P. calvus* and also the existence of slight constriction, seen in girdle view, which was not confirmed in our specimens. Finally, *P. calvus* seem to be a mainly Arctic species (see below). The identification remains, therefore, only tentative.

Distribution & Ecology: *Parlibellus* cf. *calvus* only occurred in the medium/coarse sandy stations (14 occurrences) and always at extremely low relative abundances (max. abundance < 0.6%). *Parlibellus calvus* was originally described for the marine sediments of the Bear Island (Barents Sea) but it was also found in the West Baltic Sea (Witkowski *et al.* 2000). Life-form and ecology are unknown but it could be epipelic or tube-dwelling.

References:
Metzeltin & Witkowski (1996) – pg. 24; figs. 54/10-14
Witkowski *et al.* (2000) – pg. 320; figs. 104/18-19, 105/17-21

Parlibellus **sp.1**

Micrographs: Pl. 13: 11-12

Similar species:
Navicula protracta f. *elliptica* Hustedt
Navicula sp.R (*sensu* Kuylenstierna 1989-1990)
Navicula utlandshoerniensis Van Landingham
Parlibellus protracta (Grunow) Witkowski, Lange-Bertalot & Metzeltin
Parlibellus sp.2 (*sensu* Sabbe 1997)
Stauroneis legleri Hustedt

Morphometrics:
Biovolume (µm^3): 2672
Frustule geometry: elliptic prism
Length (µm): 23.2 – (25.8) – 28.5 (n=12)

Width (µm): 5.3 – (6.6) – 8.9 (n=11)
Pervalvar axis (µm): 19.9 (n=1)
Striae in 10 µm: 14 – (17) – 20 (n=12)

Description: valves lanceolate to linear-lanceolate, with slightly cuneately-round apices. Valve face slightly curved. Axial area is narrow, central area slightly expanded and elliptical. Raphe is straight, central raphe endings fairly distant and expanded. Raphe apical ends usually not clearly visible in LM but seem to be deflected to the same side. Striae slightly radiate throughout the valve and parallel near the apices. In the centre of the valve, the striae are more widely spaced; sometimes the striae pattern is not symmetrical at the centre. The striae become more densely packed near the apices and their structure is indistinct in LM.

Notes: even though the plastid type and the valve ultrastructure of this unknown diatom was not observed, this taxon shows very strong similarities to species of the genus *Dickieia* and *Parlibellus*, namely the striae and raphe structure. It is very reminiscent to the unidentified diatoms *Navicula* sp.R *sensu* Kuylenstierna (1989-1990) and, in a lesser degree, to *Parlibellus* sp.2 *sensu* Sabbe (1997). The curved valve face and striae structure exclude all three taxa from *Navicula sensu stricto.* Referring to his taxon, Sabbe (1997) pointed out to the similarities it shared with group around *N. protracta* and to *S. legleri* but also to the fact that it had a butterfly-shaped single chloroplast, which is typical of the genus *Parlibellus* (Round *et al.* 1990). *Navicula protracta*, for example, was also later transferred to the genus *Parlibellus* by Witkowski *et al.* (2000). *Navicula utlandshoerniensis* is also quite similar to our specimens but more studies are needed to check if *N. utlandshoerniensis* belongs or not to the *Navicula sensu stricto*.

It should be noted that the structure of the plastid was not checked in the specimens found in our study which, additionally, do not correspond completely to *Parlibellus* sp.2 *sensu* Sabbe (1997) because they lack the shorter striae in the centre of the valves. We believe, however, that they belong to this genus, rather than to *Dickieia* (the other possibility), but further studies are needed.

Life form & Ecology: this taxon was rarely found during our study (15 occurrences), almost exclusively in the sandy stations and mainly in the medium/coarse sandy sediments, but always at very low abundances (max. abundance <0.9%). Life-form is unknown, probably epipelic.

References:
Krammer & Lange-Bertalot (1991b) – pg. 163; figs. 55/5-10
Kuylenstierna (1989-1990) – pg. 120, figs. 723-724
Sabbe (1997) – pg. 138, figs. 12/6-13, 47/5
Witkowski *et al.* (2000) – pgs. 311, 324; figs. 108/8-9, 134/13-18

***Parlibellus* sp.2**

Micrographs: Pl. 13: 6-10

Similar species:
Parlibellus adnatus (Heiden) Witkowski, Lange-Bertalot & Metzeltin
Parlibellus bennikei Witkowski, Lange-Bertalot & Metzeltin
Parlibellus berkeleyi (Kützing) Cox

Morphometrics:
Biovolume (µm^3): 736
Frustules geometry: elliptic prism
Length (µm): 16.9 – (20.1) – 22 (n=3)
Width (µm): 4.1 – (4.7) – 5.0 (n=3)
Pervalvar axis (µm): 10 (estimated)
Striae in 10 µm: 17 – (18) – 19 (n=3)

Description: valves elliptic with cuneate apices. Valve face gently curves to a rather deep mantle. Axial area is narrow and the central area is elliptical, more or less expanded. Raphe is straight, central raphe endings fairly distant and expanded. Raphe distal ends are deflected to the same side. Striae very slightly radiate throughout the valve and parallel near the apices. The punctae composing the striae are resolvable in LM.

Notes: during our study, a few specimens were found that did not quite correspond to *P. berkeleyi*, although there were many resemblances. Some of these similar morphological features were: the stria areolae structure, the raphe shape and size range. The striation density and pattern were also similar but the shape of the central area is notoriously different. Some specimens had in fact, a small elliptical central area, as in *P. adnatus* (Fig.104/16-17, Witkowski *et al.* 2000); others had a larger, almost circular central area, as in *P. bennikei* (Fig.104/16-17, Witkowski *et al.* 2000). However, both these two species have much larger frustules. Since only a few valves were observed, it was not possible to further advance the identification of these specimens.

Distribution & Ecology: with only 8 occurrences, *Parlibellus* sp.2 was mainly found in the sandy transect lower shore stations (medium/coarse sands) and with low abundances (max. abundance <1.5 % but in the rest of occurrences with < 0.4 %). Diatom with unknown ecology but it is probably tube-dwelling and/or epipelic.

References:
Witkowski *et al.* (2000) – pg. 319; figs. 104/11-17 (*P. adnatus* & *P. beninikei*)

Fam. Cavinulaceae Mann

Cavinula Mann & Stickle *in* Round, Crawford & Mann 1990

Genus description: Round *et al.* (1990)

Cavinula sp.1

Micrographs: Pl. 12: 19-31; Pl. 44: 5

Similar species:
Cavinula jaernefeltii (Hustedt) Mann & Stickle
Cavinula mollicula (Hustedt) Lange-Bertalot in Lange-Bertalot & Metzeltin

Morphometrics:
Biovolume (µm^3): 98
Frustule geometry: elliptic prism
Length (µm): 6.9 – (9.0) – 11.5 (n=17)
Width (µm): 4.0 – (4.6) – 5.5 (n=17)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 24 – (29) – 33 (n=16)

Description: valves elliptical with broadly rounded apices. Axial area is thickened, narrow and linear-lanceolate, extending all the way to the valve ends. Central area is transversely expanded and slightly asymmetrical. Raphe straight, central raphe ends expanded and somewhat distant; the distal raphe ends, not clearly seen apparently turning in opposite (?) directions. Striae probably finely punctate with confluent poroids aligned inside the striae (Pl. 44: 5, to be confirmed). The striae radiate throughout the valve. In the centre of the valve the striae are shorter and slightly more distant but there is no alternation between shorter and longer striae.

Notes: *Cavinula* is described as a freshwater genus (Round *et al.* 1990) and it was erected to accommodate the species-group around *Navicula cocconeiformis* Gregory which, among other features, has finely punctate radiating striae, a thickened raphe-sternum, ending short of the apices, and expanded central raphe endings. Two species, *C. jaernefeltii* and *C. mollicula*, are very reminiscent of the taxon found in our study and, although it is considered a freshwater taxa, Witkowski *et al.* (2000) reported *C. mollicula* for the brackish reaches of the Baltic Sea (as *N. mollicula*, pg. 291, figs. 109/1-3). The specimens found in our samples do not correspond entirely to its description, particularly in the central area, which is slightly enlarged transapically and with no alternation of short and long striae.
Literature research showed that the taxon that had more morphological similarities with our own was, apparently, *Navicula subatomoides* Hustedt which is, in fact, the raphe-sternum valve of a freshwater oligotrophic species of Achnanthidiaceae (see discussion in Krammer & Lange-

Bertalot 1991b, pg. 24-25). Nonetheless, the taxon found in our study is undoubtedly biraphid (see Pl. 12: 26 and 29).
In conclusion, the taxon described here is of uncertain identity without further studies, namely SEM observations. Given it cannot be a *Navicula sensu stricto* and it shared several common features with *Cavinula*, it was decided to assign it provisionally to this genus.

Distribution & Ecology: unknown but it is probably a small motile epipsammic species. Not very abundant (max. abundance < 3.6%), but occurring consistently in almost all samples from the medium-coarse sandy stations, particularly in the first year of the study (only 3 in 34 occurrences were in other stations).

Fam. Scoliotropidaceae Mereschkowsky

Biremis Mann & Cox 1990

Genus description: Round *et al.* 1990

Biremis ambigua (Cleve) Mann *in* Round, Crawford & Mann 1990

Micrographs: Pl. 14: 1-5

Synonyms:
Pinnularia ambigua Cleve

Morphometrics:
Biovolume (µm^3): 5286
Frustule geometry: elliptic prism
Length (µm): 37.6 – (47.3) – 65.0 (n=11)
Width (µm): 8.6 – (9.6) – 10.2 (n=3)
Pervalvar axis (µm): 15 (n=1)
Striae in 10 µm: 7 – (7) – 8 (n=11)

Notes: a very complete morphological description and historical background of this taxon is given in Cox (1990). It is also well illustrated in Round *et al.* (1990) and compared with *B. lucens* in Sabbe *et al.* (1995)

Life form & Ecology: it is a common, cosmopolitan and epipelic diatom living in sandy sediments (Cox 1990, Witkowski *et al.* 2000). Sabbe (1997) reported that this species was mainly found in rather coarse sandy sediments, which had a higher median grain size than the optimum grain size attributed for the epipsammic adnate *B. lucens* (see below). In our study, it was rather infrequent, with 6 occurrences in the medium-coarse sandy stations and low abundances (max. abundance < 1.6 %).

References:
Cox (1990) – fig. 1-28
Hendey (1964) – pg. 223; fig, XXXIV/5-8
Round *et al.* (1990) – pg. 548
Sabbe *et al.* (1995) – fig. 34, 35, 38, 51, 52
Sabbe (1997) – pg. 142; figs. 14/1-3, 46/3,8
Snoeijs & Kasperoviciene (1996) – #323
Witkowski *et al.* (2000) – pg. 158; fig. 155/2-6

Biremis lucens (Hustedt) Sabbe, Witkowski & Vyverman 1995

Micrographs: Pl. 14: 6-10; Pl. 44: 6-9

Synonyms:
Navicula lucens Hustedt
Fallacia lucens (Hustedt) Mann

Morphometrics:
Biovolume (µm^3): 439
Frustule geometry: elliptic prism
Length (µm): 8.4 – (16.6) – 30.0 (n=25)
Width (µm): 2.9 – (4.0) – 5.4 (n=18)
Pervalvar axis (µm): 5.8 – (8.4) – 12.6 (n=4)
Striae in 10 µm: 14 – (15) – 17 (n=8, morphotype 1), 10 – (12) – 13 (n=12, morphotype 2)

Notes: a very complete morphological description, as well as a detailed taxonomic and ecological discussion, is given by Sabbe *et al.* (1995b). As the authors of the mentioned work, we were aware of the existence of two morphotypes of *B. lucens* co-occurring in our samples. One morphotype had a striae density of 14-17 striae in 10 µm (m.1) and another with 10-13 striae /10 µm (m.2), as Figure 25 shows. The latter one seemed to dominate but no consistent counts of both morphotypes were made. This co-occurrence of both morphotypes is a known phenomenon in other European estuaries and coasts (see Sabbe *et al.* 1995b).

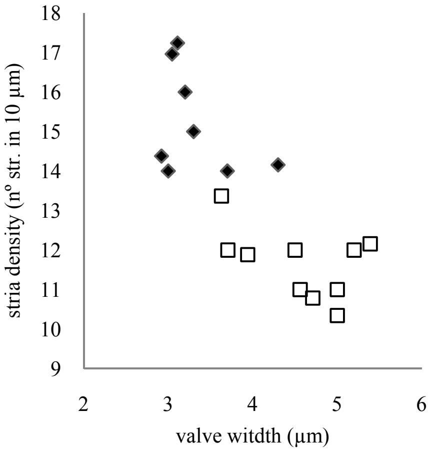

Figure 25 – Transapical striae density *vs.* valve width of *B. lucens* m.1 (♦) and *B. lucens* m.2 (□).

Life form & Ecology: cosmopolitan species present in marine and brackish sandy sediments (Witkowski *et al.* 2000). Epipsammic with an adnate life-form, it adheres to the sand grains by the girdle. Solitary, it can also form small ribbon-like colonies (Sabbe *et al.*1995). In our study, it was one of the most frequent and common species in the sandy sediments. It occurred in all samples from the sandy stations (total 48 occurrences) being also present in 3 samples from mudflats but in very low numbers. It was quite abundant, ranging from 1.1% to 13.8 %, representing one of the co-dominant taxa of the sandy stations. This conforms to the observations given by Sabbe (1997), who reported the largest abundances of *B. lucens* for the middle reaches stations of the Westerschelde estuary (salinity 10 - 25 ‰).

In our study, *B. lucens* seemed to show a slight preference for the lower shore medium/coarse sandy stations of the sandy transect and for sandy station in the muddier transect (Table 12, but see also section 4.3). The lower abundance in the fine sands station was, therefore, a bit surprising. However, Sabbe *et al.* (1995b) investigated the ecological preferences of both morphotypes of *B. lucens* and concluded that the morphotype 2 (which apparently dominates in our samples) seems to thrive well in sands with a certain amount of silt content. Station A1 has the lowest mud content, whereas the other stations had always a significant mud fraction. Since morphotype 2 seemed to be the dominant form in our samples (albeit unconfirmed!) this may explain spatial distribution found in our study. Additional work will be needed to confirm this pattern. Sabbe *et al.* (1995b) raises interesting points on the relationship between spatial and seasonal distribution of these morphotypes and should be consulted. Even though it is not very obvious, there was a small seasonal pattern in *B. lucens* numbers, with a slight peak in its relative abundance in late spring - early summer.

Table 12 – Occurrence (%), average relative abundance (%) of *B. lucens* and average mud content (%) per sampling station. Standard deviation given within brackets.

Station	Occurrence	Abundance	Mud content
A1	100	2.5 (1.2)	2.3 (1.0)
A2	100	7.9 (3.0)	5.4 (2.4)
A3	100	8.5 (1.8)	7.7 (3.1)
V1	100	5.9 (3.6)	13.5 (9.3)
V2	18	0.1 (0.1)	90.0 (7.3)
V3	8	0.0(0.1)	96.5 (2.2)

References:
Hustedt (1961-1966) – pg. 171; fig. 1311
Sabbe *et al.* (1995) – figs. 1-33, 39-53
Simonsen (1987) – pg. 174; fig. 275/27-29
Snoeijs & Kasperoviciene (1996) – #324
Witkowski *et al.* (2000) – pg. 159; figs. 155/9-15

Suborder Sellaphorineae

Fam. Sellaphoraceae Mereschkowsky

Fallacia Stickle & Mann 1990

Genus description: Round *et al.* (1990)

Fallacia aequorea (Hustedt) Mann 1990

Micrographs: Pl. 15: 1-3

Synonyms:
Navicula aequorea Hustedt
Navicula misella Hustedt (but see Simonsen 1987)

Similar species:
Fallacia cryptolyra Brockman
Fallacia cassubiae Witkowski

Morphometrics:
Biovolume (µm^3): 120
Frustule geometry: elliptic prism
Length (µm): 9.8 – (10) – 10.3 (n=3)
Width (µm): 5.0 – (5.1) – 5.2 (n=3)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 23 – (25) – 26 (n=3)
Punctae in 10 µm: 50 (n=1)

Notes: the small lyratae taxa are extremely difficult to study due to the minuteness of the valve details in LM. As an example, Simonsen (1987) considered one holotype of *N. misella* Hustedt as conspecific of *N. cryptolyra* Brockman and another as conspecific of *N. aequorea* Hustedt.
In our study, during the cells counts, both species (*i.e. F. cryptolyra* and *F. aequorea*) were also confused and counted together. There are, however, a few morphological features that allow an easier discrimination between both taxa: *F. aequorea* has straight raphe branches, with straight distal raphe ends; it does not have areolae within the area enclosed by the lateral areas and it has an orbicular central area. The lyra is, therefore, limited to rudimentary lateral sterna, almost parallel to the raphe. For a complete description, as well as for a discussion on the relations with morphologically similar taxa, Sabbe *et al.* (1999) should be consulted.

Distribution & Ecology: cosmopolitan, brackish to marine species (Sabbe *et al.* 1999, Witkowski *et al.* 2000). Solitary, epipsammic diatom, the exact life-form is unknown, either adnate or a small motile epipsammic form. Sabbe (1997) reported as common in fine sandy sediments in polyhaline reaches of the Westerschelde estuary. In our study, it was scored with *F. cryptolyra* during counts (see below).

References:
Hustedt (1961-1966) – pg. 184; figs. 1318
Simonsen (1987) – pg. 256; figs. 379/8-14 (pg.415, fig. 617/21-23 as *N. misella*)
Sabbe *et al.* (1999) – pg. 9; figs. 7-10, 60, 61
Witkowski *et al.* (2000) – pg. 200; figs. 71/35-36

Fallacia amphipleuroides (Hustedt) Mann 1990

Micrographs: Pl. 15: 4-6; Pl. 45: 2-3

Synonyms:
Navicula amphipleuroides Hustedt
Navicula margin-ornata Salah
Navicula fenestrella Hustedt
Fallacia fenestrella (Hustedt) Mann

Similar species:
Fallacia margino-punctata Sabbe & Muylaert
Fallacia teneroides (Hustedt) Mann
Fallacia wuestii (Simonsen) Sabbe & Muylaert

Morphometrics:
Biovolume (µm^3): 85
Frustule geometry: elliptic prism
Length (µm): 7.8 – (8.0) – 8.2 (n=4)
Width (µm): 4.2 – (4.5) – 4.6 (n=4)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 19 – (21) – 22 (n=4)

Notes: For a complete description as well as for a discussion on the relations with morphological similar taxa Håkansson & Stabell (1977) and Sabbe *et al.* (1999) should be consulted.

Distribution & Ecology: cosmopolitan, brackish to marine species (Sabbe *et al.* 1999, Witkowski *et al.* 2000). Solitary, epipsammic diatom, the exact life-form is unknown, either adnate or small. In our study, it was very frequent, present in almost all samples from the sandy stations (41 occurrences). It was one of the common species of *Fallacia* in those assemblages (max. abundance < 3.2 %). There were very slight differences in abundance throughout the year; but it seems to be slightly more common in spring and autumn.

References:
Håkansson & Stabell (1977) – figs.1/A, D-E
Hustedt (1955) – pg. 30; figs. 5/33-34
Simonsen (1987) – pg. 415; figs. 619/20-26
Sabbe *et al.* (1999) – pg. 11; figs. 22-25
Witkowski *et al.* (2000) – pg. 200; figs. 71/43-44

Fallacia clepsidroides Witkowski 1994

Micrographs: Pl. 15: 10-12; Pl. 45: 4

Similar species:
Fallacia cassubiae Witkowski
Fallacia cryptolyra Brockman
Navicula suspirii Cholnoky

Morphometrics:
Biovolume (µm^3): 128
Frustule geometry: elliptic prism
Length (µm): 8.3 – (10.3) – 13.2 (n=5)
Width (µm): 4.3 – (5.1) – 6.5 (n=5)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 22 – (22) – 27 (n=5)
Punctae in 10 µm: 31 (n=2)

Notes: described by Witkowski (1994a), this taxon is very similar to the forms in the *F. cassubiae* / *F. cryptolyra* group (see discussion above). Both Sabbe (1999) and Witkowski *et al.* (2000) agree that this taxon does not belong in the above mentioned group. It can be distinguished by its lower striae density, the lack of conopeum, the shape of the central area (square in *F. clepsidroides*) but, primarily, by its pronounced lyra, which is clearly distinct in LM. The specimen shown in SEM completely corresponds to the figures in Witkowski (1994) but not to fig. 69 in Sabbe *et al.* (1999). A possible synonymy with *N. suspurii* should be investigated.

Distribution & Ecology: cosmopolitan brackish to marine species, found from the Baltic Sea to the Mediterranean (*e.g.* Witkowski *et al.* 2000). It is probably a small motile epipsammic diatom. In our study it was extremely rare, with only 3 occurrences in the sandy stations and at very low abundances (max. abundance <0.8 %).

References:
Garcia (2003) – pg. 311; figs. 1-13
Sabbe *et al.* (1999) – pg. 15; figs. 37-41, 73
Snoeijs & Potapova (1995) – # 239
Witkowski (1994) – pg. 120, fig. XXVI/1-12
Witkowski *et al.* (2000) – pg. 202; figs. 70/31-34

Fallacia cryptolyra (Brockmann) Stickle & Mann 1990

Micrographs: Pl. 15: 13-16; Pl. 45: 1

Synonyms:
Navicula cryptolyra Brockman
(?) *Fallacia cassubiae* Witkowski
Lyrella phyllohordae Guslakov
Navicula misella Hustedt (but see Simonsen 1987)

Similar species:
Fallacia aequorea (Hustedt) Mann
Fallacia clepsidroides Witkowski

Morphometrics:
Biovolume (µm^3): 87
Frustule geometry: elliptic prism
Length (µm): 6.9 – (9.1) – 10.3 (n=7)
Width (µm): 3.8 – (4.9) – 5.9 (n=7)
Pervalvar axis (µm): 3 (estimated)

Striae in 10 µm: 26 – (29) – 33 (n=7)
Punctae in 10 µm: 50 (n=1)

Notes: given that there was an early confusion with *F. aequorea* (see above), *F. cryptolyra* was interpreted in the broadest sense and no attempt was made to discriminate it from the extremely similar *F. cassubiae*. These two taxa may be distinguished by size, striae density, a more distinctive appearance of the lyra in LM and several morphological features observed in SEM (Witkowski 1991, 1994). They remain, however, very difficult to discern in LM and some authors (*e.g.* Sabbe *et al.* 1999) believe them to be conspecific. This question can only be answered when Brockman's original material is analysed in SEM. Unfortunately, during our study, these specimens were not found in the material selected for SEM analysis. We do have, however, a SEM micrograph from older Tagus estuary material (Ribeiro *et al.* 2003) that corresponds fairly well to the illustrations given by Witkowski (figs. XXVII/11-12, 1994) for *F. cassubiae*. Interestingly, this specimen does not correspond to others, given by Håkansson & Stabell (1977), Witkowski (1991), Snoeijs & Potapova (1995) and Sabbe *et al.* (1999) and that were identified either as *F. cassubiae* or as *F. cryptolyra*. A distinction based on fine ultrastructure may, therefore, be possible, but the identity of these taxa is still very confusing. The morphological differences concerning *F. clepsidroides* are much more obvious and explained above.

Distribution & Ecology: small motile epipsammic species. In our study occurred rather infrequently (only in 11 samples) and mainly in the upper shore fine/medium sandy station but it was never very abundant (max. abundance <1.4%). *Fallacia cryptolyra* is reported as a cosmopolitan species, particularly in brackish sediments (Sabbe *et al.* 1999, Witkowski *et al.* 2000). Sabbe (1997) reported it as "common in the epipsammon of medium sandy sediments in the eu- and polyhaline reaches of the Westerschelde estuary". *Fallacia cassubiae* is considered by Witkowski *et al.* (2000) as a brackish water species, very common in the Baltic Sea.

References:
Brockman (1950) – pg. 19; fig. 22, 23
Håkansson & Stabell (1977) – figs.2/A-C
Krammer & Lange-Bertalot (1986) – pg. 172; figs. 65/7-9
Sabbe *et al.* (1999) – pg. 13; 42-45, 70
Simonsen (1987) – pg. 415, fig. 617/18-20 (as *N. misella* Hustedt)
Snoeijs & Potapova (1995) – # 240
Sundbäck & Snoeijs (1991) – fig. 9/d-e
Witkowski (1991) – pg. 403; figs. 2-17
Witkowski (1994) – pgs. 119, 121; figs. 26/13-16, 26/11-12, 28/1 (*F. cassubiae*), 27/17-19 (*F. cryptolyra*)
Witkowski *et al.* (2000) – pgs. 201, 203; figs. 70/39-41 (*F. cassubiae*), 70/42-45 (*F. cryptolyra*)

Fallacia dithmarsica (König *ex* Hustedt) Mann 1990

Micrographs: Pl. 15: 8-9

Synonyms:
Navicula dithmarsica König *ex* Hustedt

Similar species:
Fallacia clipeiformis (König) Mann

Morphometrics:
Biovolume (µm^3): 185
Frustule geometry: elliptic prism
Length (µm): 12.5 – (14.4) – 15.8 (n=5)
Width (µm): 3.8 – (5.4) – 6.5 (n=5)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 19 – (19) – 20 (n=5)
Punctae in 10 µm: 19 (n=1)

Notes: a detailed description of this species is given elsewhere (Hustedt 1961-1966; Witkowski *et al.* 2000).

Distribution & Ecology: originally found in a sandflat of the Dithmarschen region in the German Wadden Sea. (Hustedt 1961-1966) but also known from the Bear Island (Witkowski *et al.* 2000). It is most likely an epipsammic form. In our study, it was also found the sandy stations (medium-coarse sands) but only twice and with an extremely low abundance (max. abundances < 0.31%).

References:
Hustedt (1961-1966) – pg. 550; fig. 1588
Kuylenstierna (1989-1989) – pg. 108; fig. 53/629
Witkowski *et al.* (2000) – pg. 204; figs. 71/21-22

Fallacia florinae (Moeller) Witkowski 1993

Micrographs: Pl. 15: 7; Pl. 45: 7-8

Synonyms:
Navicula florinae Moeller
(?) *Navicula sibayiensis* Archibald

Similar species:
Fallacia oculiformis (Hustedt) Mann
Fallacia zonata Hustedt Mann

Morphometrics:
Biovolume (µm^3): 113
Frustule geometry: elliptic prism
Length (µm): 7.2 – (10.2) – 13.9 (n=21)
Width (µm): 4.0 – (5.7) – 8.2 (n=21)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 22 – (29) – 34 (n=20)

Notes: this taxon is described in detail by Witkowski (1993b). It is very similar to *F. oculiformis* (see below) in the way that there is a clear demarcation between the striated marginal area and the axial area. In the case of *F. florinae*, the striae are limited to the marginal areas and the row of punctae along the internal edge of the lateral area does not occur (*viz. F. oculiformis*). The striae are more widely spaced at the centre of the valve (around 24 striae/10 µm) than in the apices (around 33/10). The SEM observations confirm and complete the ones by Witkowski (1993b), and it can be seen that the conopeum almost completely covers the valve face. Apart from the slits directly above the striae and some pores in the apices, the conopeum seems only to be perforated by small randomly placed pores, within the two longitudinal lateral areas, delimiting the axial area. Sabbe (1997) suggested that *Navicula sibayiensis* Archibald could be a possible synonym.

Distribution & Ecology: cosmopolitan**.** This taxon seems to be a typical component of brackish and marine intertidal and subtidal sandy assemblages in Europe and elsewhere (see Witkowski 1993a and references herein). Probably a small motile epipsammic diatom but it may as well be adnate. In our study, it was one of the most common *Fallacia* species (44 occurrences), being very frequent in all sandy stations. It showed a clear preference for the medium/fine sandy station, where it reached the highest abundances (average abundance 2.2%, max. abundance < 3.6%).

References:
Garcia (2003) – pg. 311; figs. 14-15, 17-23
Hendey (1964) – pg. 213; fig. XXXIII/6 (as *N. florinae*; fig. 7, *F. oculiformis*?)
Hustedt (1961-1966) – pg. 660, fig. 1660 (as *N. florinae*)
Kuylenstierna (1989-1990) – pg. 109; fig. 52/609 (as *N. florinae*)
Sabbe (1997) – pg. 150; fig. 13/8.
Snoeijs & Kasperoviciene (1996) – # 341
Witkowski (1993b)) – figs. 1-48
Witkowski (1994a) – pg. 121; figs. XXV/1-6, XXVIII/2
Witkowski *et al.* (2000) – pg. 204; figs. 71/45-49

Fallacia oculiformis (Hustedt) Mann 1990

Micrographs: Pl. 15: 21-26; Pl. 45: 5-6

Synonyms:
Navicula oculiformis Hustedt
Navicula pseudony Hustedt
Fallacia pseudony (Hustedt) Mann

Similar species:
Fallacia florinae (Moeller) Witkowski
Fallacia zonata Hustedt) Mann

Morphometrics:
Biovolume (µm^3): 136
Frustule geometry: elliptic prism
Length (µm): 8.8 – (12.3) – 18.2 (n=18)

Width (µm): 6.0 – (7.8) – 10.0 (n=18)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 23 – (24) – 29 (valve centre, n=18); 27 – (28) – 29 (valve ends, n=6)
Punctae in 10 µm: 28 – (33) – 40 (n=4)

Notes: one of the defining characters of this taxon is that the axial area is separated from the lateral areas by rows of short striae, allowing a simple distinction from similar taxa (*i.e. F. florinae*). This feature is not always easily seen, in particular in the constriction of the axial area in centre of the valve. The SEM internal views show that the areolae composing these striae may not reach the interior of the valve on the centre. Finally, *F. zonata* is also a similar taxon but it is considerably smaller.

Hustedt (1955) described *Navicula oculiformis*, along with *N. pseudony*, in his work on the marine littoral diatoms from the Beaufort Bay (USA). Simonsen (1987), when studying both types, believed them to be conspecific. He considered *N. pseudony* to be a synonym of the former but both taxa were transferred to *Fallacia* by Mann (Round *et al.* 2000). *Fallacia oculiformis* should be the preferable name, as Witkowski *et al.* (2000) suggested.

Distribution & Ecology: cosmopolitan species, found in European and North American coasts but also in the tropics (*e.g.* Coste & Ricard 1984, Garcia 2003). It is probably a small motile epipsammic species. In our study it was one of the most common *Fallacia* species, being present in almost all samples from the sandy stations (44 occurrences) and quite abundant for an epipsammic species (max. abundance < 4.5%).

References:

Garcia (2003) – pg. 314; fig. 51 (as *F. pseudony*)
Hustedt (1955) – pg. 22, fig. 8/6-7
Simonsen 1987, p. 408, fig. 61/12-24 (as *N. oculiformis* and *N. pseudony*)
Snoeijs & Kasperoviciene (1996) – # 343 (as *F. pseudony*)
Witkowski (1994) – pg. 122; figs. XXV/12-13, XXVVII/3-4 (as *F. pseudony*)
Witkowski *et al.* (2000) – pg. 210; figs. 71/30

***Fallacia* cf. *scaldensis* Sabbe & Muylaert 1999**

Micrographs: Pl. 15: 27-33; Pl. 45: 9

Similar species:

Fallacia pygmaea Kützing Stickle & Mann
*Fallacia forcipata (*Greville) Stickle & Mann
Fallacia clepsidroides Witkowski

Morphometrics:

Biovolume (µm^3): 230
Frustule geometry: elliptic prism
Length (µm): 9.6– (13.8) – 19.5 (n=13)
Width (µm): 5.7 – (7.1) – 8.5 (n=13)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 19 – (21) – 22 (n=13)
Punctae in 10 µm: 27 (n=2)

Description: valves lanceolate with broadly rounded apices. Axial area narrow and central area square to rectangular. The central area never extends laterally further than the branches of the lyra which is, therefore, constricted in the middle. The raphe is straight with central endings expanded and distant. Striae slightly radiate and are indistinct in LM. The external view of a frustule in SEM micrograph shows a flat valve, completely covered by the conopeum, the depressed lyra, the straight raphe with the central ending distant and the distal ones bending to the same side but the striae are still indistinct.

Notes: the specimens found during our survey agree almost completely with the description and illustrations given by Sabbe *et al.* (1999) which originally described this species, except in striae density. Our specimens have lower average striae density, as it was the case in Witkowski *et al.* (2000), and this was the reason we refrain from making a positive identification. The relations with similar taxa are carefully discussed in Sabbe *et al.* (1999), where the importance of the morphological features, such as lyra shape and striae structure, on the correct identification of these taxa is stressed.

Distribution & Ecology: this taxon was fairly recently described from the intertidal fine and medium sandy sediments of the

Westerschelde estuary (Sabbe *et al.* 1999) and there are still few reports. It was found in Hustedt's Beaufort material and in the Baltic Sea (Sabbe *et al.* 1999, Witkowski *et al.* 2000). It is most probably an epipelic species. In our study, it was fairly frequent (29 occurrences), particularly in the sandy transect where it reached its highest abundance (max. abundance < 2.5%).

References:
Sabbe *et al.* (1999) – pg. 18; fig. 52-58
Witkowski *et al.* (2000) – pg. 212; figs. 70/35-36

Fallacia subforcipata (Hustedt) Mann 1990

Micrographs: Pl. 15: 34-36

Synonyms:
Navicula subforcipata Hustedt

Similar species:
Fallacia brachium (Hustedt) Mann
Fallacia forcipata (Greville) Stickle & Mann
Fallacia pygmaea (Kützing) Stickle & Mann
Fallacia scaldensis Sabbe & Muylaert

Morphometrics:
Biovolume (µm^3): 204
Frustule geometry: elliptic prism
Length (µm): 10.2 – (12.4) – 13.7 (n=5)
Width (µm): 6.5 – (7.0) – 7.4 (n=5)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 17 – (18) – 19 (n=5)
Punctae in 10 µm: 18 (n=2)

Notes: this taxon is described in detail by Hustedt (1961-1966) and by Witkowski *et al.* (2000). It can be distinguished from similar taxa, like *F. forcipata* or *F. pygmaea*, by its size range and/or striae density and from *F. scaldensis* by the different shape of the lyra and the distinctly punctate striae. *Fallacia brachium* is larger, with twice the width and wider lateral areas.

Distribution & Ecology: marine species with a widespread distribution (Witkowski *et al.* 2000). A small motile epipsammic form, in our study appeared in the sandy stations, were it was fairly frequent (20 occurrences) but never abundant (max. abundance <1.61 %). This species mainly occurs in the medium/coarse sandy stations.

References:
Garcia (2003) – pg. 315; figs. 48-50, 52-53
Hustedt (1961-1966) – pg. 533, fig. 156
Laws (1988) – fig. 25/5
Simonsen (1987) – pg. 490, fig. 751/2-7
Witkowski *et al.* (2000) – pg. 213; figs. 72/20-23

Fallacia tenera (Hustedt) Mann 1990

Micrographs: Pl. 15: 37-39; Pl. 45: 10

Synonyms:
Navicula tenera Hustedt in Schmidt
Navicula uniseriata Hustedt
Navicula dissipata Hustedt
Navicula auriculata Hustedt
Navicula biseriate Brockmann
Navicula insociabilis var. *dissipatoides* Hustedt

Similar species:
Fallacia teneroides (Hustedt) Mann

Morphometrics:
Biovolume (µm^3): 103
Frustule geometry: elliptic prism
Length (µm): 6.7 – (9.3) – 11.0 (n=15)
Width (µm): 3.8 – (4.7) – 5.3 (n=14)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 18 – (21) – 24 (n=15)

Notes: detailed descriptions are given by Schoeman & Archibald (1976-1980), Sabbe *et al.* (1999), Krammer & Lange-Bertalot (1986) and by Witkowski *et al.* (2000). It is a highly variable species and it can be seen that the specimens found in our study do possess rows of punctae in both sides of the raphe branches (see Sabbe *et al.* 1999). The main difference to the very similar *F.* cf. *teneroides* is the presence of longitudinal ribs crossing the striae (see below) and the distinction to *F. arenaria* is the coarser striation.

Distribution & Ecology: cosmopolitan, present in marine and brackish waters in coastal areas (Witkowski *et al.* 2000). This species is epipelic and it can be found in both sandy and silty sediments (Sabbe *et al.* 1999). In our study it occurred mainly in the sandy stations being one of the most frequent (38 occurrences) *Fallacia* species but not one of the most abundant (max. abundance < 2.5%). In the station where it was more common, it had a slight peak during winter.

References:
Coste & Ricard (1982) – fig. 6/9
Krammer & Lange-Bertalot (1986) – pg. 175; figs. 66/19-23, 83/5
Sabbe *et al.* (1999) – pg. 18; figs. 1-4, 75, 78, 82
Simonsen 1987, p. 162, fig. 255: 6-10
Snoeijs & Potapova (1995) – # 242
Witkowski *et al.* (2000) – pg. 214; figs. 71/52-56

Fallacia cf. ***teneroides*** (Hustedt) Mann 1999

Micrographs: Pl. 15: 17-20; Pl. 45: 11-12

Synonyms:
Navicula teneroides Hustedt
Navicula umpatica Cholnoky
Fallacia umpatica (Cholnoky) Mann

Similar species:
Fallacia pulchella Sabbe & Muylaert
Fallacia tenera (Hustedt) Mann
Fallacia wuestii (Simonsen) Sabbe & Muylaert

Morphometrics:
Biovolume (μm^3): 87
Frustule geometry: elliptic prism
Length (µm): 5.7 – (8.5) – 10.6 (n=18)
Width (µm): 3.9 – (4.4) – 4.9 (n=18)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 20 – (21) – 26 (n=18)

Description: valves elliptical with broadly rounded apices. Axial area narrow, raphe with branches strongly curved. Central raphe endings expanded. Striae are parallel at the centre and radiate near the apices. They are interrupted by a wide, longitudinal, fan–shaped hyaline area. On the concave side of the raphe branches, the striae are composed by two distinct punctae (Pl. 45: 11-12), while on the convex side, there is usually just one row of punctae (but not always).

Notes: this taxon is almost certainly the same as the *F.* cf. *teneroides* described and illustrated in Sabbe *et al.* (1999). Our specimens are on average slightly smaller but we performed considerably more morphological measurements. The taxonomy of this species is discussed in detail in the above mentioned work and we renounced making a positive identification for the same reason as the authors: the central raphe ends were not widely spaced and sometimes additional punctae were detected in the convex side of the raphe braches, which never occurs in *F. teneroides* (Simonsen 1987, Sabbe *et al.* 1999). In our observations in SEM we failed to see the lyre-shaped depression, dividing the two internal punctae of the striae in the concave side of the raphe branches (fig 81, Sabbe *et al.* 1999). The relations with similar taxa (*e.g. F. tenera*, *F. wuestii*) are also discussed by the latter authors.

Distribution & Ecology: small motile epipsammic species. Sabbe *et al.* (1999) report *F.* cf. *teneroides* as mainly present in rather marine sandy sediments in the mouth of the Westerschelde estuary. In our study, which concerns a typical brackish area in the middle reaches of the estuary, this taxon was the most common and abundant *Fallacia* species in the sandy stations (45 occurrences, max. abundance < 6.9 %) and co-occurred with *F. tenera* (see above), a typical brackish species. However, it should be noted that it increased in abundance during the late spring and summer months, when the salinity peaked, and decreased in numbers when the salinity dropped during winter. *Fallacia teneroides* (Hustedt) Mann is considered as a truly brackish species and it is reported for South America (Hustedt 1961-1966) and in South Africa as *N. umpatica* (Schoeman & Archibald 1976-1980).

References:
Hustedt (1961-1966) – pg. 178; fig. 1312

Sabbe *et al.* (1999) –pg. 19; figs. 5, 6, 81
Simonsen (1987) – pg. 437; figs. 654/1-9
Witkowski *et al.* (2000) – pg. 215; figs. 71/?58-59

Navicula ponticula Giffen 1970

Micrographs: Pl. 15: 40-45

Similar species:
Fallacia clipeiformis (König) Mann 1990
Cocconeiopsis fraudulenta (Schmidt) Witkowski, Lange-Bertalot & Metzeltin

Morphometrics:
Biovolume (µm^3): 313
Frustule geometry: elliptic prism
Length (µm): 10.4 – (14.4) – 18.5 (n=11)
Width (µm): 6.9 – (9.2) – 11.0 (n=11)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 20 – (22) – 25 (n=11)
Punctae in 10 µm: 25 – (26) – 28 (n=3)

Notes: This taxon does not belong to *Navicula sensu stricto*. Witkowski *et al.* (2000) suggested it could be placed in the *Fallacia*, given its similarities to *F. clipeiformis*. In fact, the main difference between both taxa is the "distinctly finer valve structure" of *N. ponticula.* Our specimens are very similar to the illustration of *Navicula clipeiformis* König in Hustedt (fig. 1589, 1961-1966) and of *Navicula* (*Fallacia*?) *ponticula* Giffen in Witkowski *et al.* (2000) giving rise to questions of conspecificity between the two taxa, but neither the original descriptions nor the types were yet critically compared and analysed.

Another question this taxon raises is a possible transfer to the genus *Cocconeiopsis*. The striae structure appears to be very similar, with its distinctly punctate striae. The more distant areolae near the raphe sternum may appear to be a blurred lyra (*cf. Fallacia*) but it also occurs in *C. fraudulenta* (fig. 68/9 Witkowski *et al.* 2000). However, the main reasons for this possible transfer are the apparent lack of conopea and the raphe structure. The raphe is straight; the distal ends are not bending to one side of the valves and the central ends are distant, expanded and, apparently, placed in drop-like external depressions (*cf. C. breviata*). SEM studies are needed to enlighten these questions.

Distribution & Ecology: Marine brackish species reported for warm waters (Witkowski *et al.* 2000). Without considering its presumed conspecificity to *F. clipeiformis*, this is, to our knowledge, the first report for the European coasts. It is most likely an epipelic form. In our study, it only occurred in the sandy transect, mainly on the stations with coarser sands (12 occurrences) but always at very low abundances (max. abundance <0.83%).

References:
Witkowski *et al.* (2000) – pg. 211; figs. 67/21

Taxon of unknown affiliation

Cocconeiopsis Witkowski, Lange-Bertalot & Metzeltin 2000

This small genus was recently created (Witkowski *et al.* 2000) to accommodate the group of species around *Navicula orthoneoides* Hustedt which could not formally remain in the genus *Navicula sensu stricto*. One of the main reasons for this is that these species have distinctly punctate striae and composed by more or less circular areolae, externally covered by vela and internally occluded with hymens. Another main difference to the Naviculaceae is the raphe structure, which is straight and filiform and, typically, has completely straight central and terminal raphe endings. The latter ones usually terminate at a distance from the apical marginal and are bordered by two small parallel depressions.

Apparently, the position of this genus is not yet known and the plastid structure remains undetermined. Several details of striae and raphe structure show similarities to other members of the sub-order *Sellaphorineae* (*e.g. Cavinula*, *Diadesmis* or *Fallacia*) but further (possible molecular) studies are sorely needed to clarify the systematics of this genus.

Cocconeiopsis breviata (Hustedt) Witkowski, Lange-Bertalot & Metzeltin 2000

Micrographs: Pl. 14: 21-24; Pl. 46: 1-5

Synonyms:
Navicula breviata Hustedt

Similar species:
Cocconeiopsis pullus (Hustedt) Witkowski, Lange-Bertalot & Metzeltin

Morphometrics:
Biovolume (µm^3): 120
Frustule geometry: elliptic prism
Length (µm): 8.4 – (10.3) – 11.6 (n=22)
Width (µm): 4.7 – (5.9) – 6.7 (n=21)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 19 – (22) – 26 (22)
Punctae in 10 µm: 18 – (24) – 33 (15)

Notes: detailed descriptions of this rarely recorded species can be found elsewhere (Hustedt 1961-1966; Witkowski *et al.* 2000) to which the quite complete SEM examination of this species, our study permitted, is an addition.

Table 21 – Occurrence (%), average relative abundance (%) of *C. breviata* and average mud content (%) per sampling station. Standard deviation given within brackets.

Station	Occurrence	Abundance	Mud content
A1	100	2.2 (2.0)	2.3 (1.0)
A2	100	2.6 (1.4)	5.4 (2.4)
A3	100	3.6 (2.5)	7.7 (3.1)
V1	100	2.2 (1.5)	13.5 (9.3)
V2	36	0.1 (0.2)	90.0 (7.3)
V3	8	0.0 (0.0)	96.5 (2.2)

Distribution & Ecology: Small motile epipsammic species. According to Witkowski *et al.* (2000) this taxon is only described for the Indo-Malayan area and the Aegean Sea. Very recently it was also found in subtidal sandy sediments in Balaklava and Sevastopol bays in the Crimean coast (E. Nevrova, personal communication). This species was common in our study, being mainly in the sandy stations (Table 21) where it was one of the main components of the sandflat assemblages (max. abundance < 9.2%). This species was particularly abundant during late-summer and autumn.

References:
Hustedt (1961-1966) – pg. 637; figs. 1635
Simonsen 1987, p. 500, fig. 763: 4-6
Witkowski *et al.* (2000) – pg. 172; figs. 72

Suborder Diploneidineae

Fam. Diploneidaceae Mann

Diploneis (Ehrenberg) Cleve 1894

Genus description: Round *et al.* 1990

Diploneis didyma (Ehrenberg) Cleve 1894

Micrographs: Pl. 16: 6-7; Pl. 46: 7

Synonyms:
Navicula (*Pinnularia*) *didyma* Ehrenberg

Similar species:
Diploneis alpina Meister
Diploneis bombus Ehrenberg

Morphometrics:
Biovolume (µm^3): 3895
Frustule geometry: elliptic prism
Length (µm): 28.0 – (32.6) – 41.5 (n=6)
Width (µm): 13.3 – (15.2) – 18.6 (n=6)
Pervalvar axis (µm): 10 (estimated)
Striae in 10 µm: 9 – (10) – 10 (n=7)

Notes: detailed descriptions are given elsewhere (see references below). It is sometimes confused with the also very common *D. bombus*, of similar size range and outline.

In fact the two species are quite different: *D. bombus* has lateral longitudinal channels constricted in the middle, whereas in *D. didyma* they are slightly widened transapically.

Distribution & Ecology: cosmopolitan epipelic species, common in marine to brackish waters (*e.g.* Witkowski *et al.* 2000). In our study it was extremely rare, with only 4 occurrences, in one sandy station and always with very low abundances (max. abundance < 0.3%).

References:
Hendey (1964) – pg. 226; XXXII/12
Hustedt (1931-1959) – pg. 685; fig. 1075
Krammer & Lange-Bertalot (1986) – pg. 292; figs. 112/7
Patrick & Reimer (1966) – pg. 417
Round *et al.* (1990) – pg. 562; figs. b, f, g
Snoeijs (1993) – # 39
Tolomio *et al.* (1999) – fig. 25
Witkowski *et al.* (2000) – pg.185, figs. 87/17-19

Diploneis papula (A. Schmidt) Cleve 1894

Micrographs: Pl. 16: 1-5; Pl. 46: 6

Synonyms:
Navicula papula A. Schmidt

Similar species:
Diploneis notabilis (Greville) Cleve
Diploneis vetula (A. Schmidt) Cleve

Morphometrics:
Biovolume (µm^3): 754
Frustule geometry: elliptic prism
Length (µm): 12.8 – (16.8) – 22.9 (n=9)
Width (µm): 7.6 – (9.5) – 11.6 (n=9)
Pervalvar axis (µm): 6 (estimated)
Striae in 10 µm: 15 – (16) – 19 (n=8)

Notes: detailed descriptions can be found elsewhere (*e.g.* Husted 1931-1959, Witkowski *et al.* 2000). In these descriptions, a striation density of 10-14 str./10 µm is given. Sabbe (1997) noticed that in his study and in referenced papers from colder waters (Salah 1952, Giffen 1970, Droop 1994) *D. papula* specimens were characterized by higher stria density, well in the same range of the specimens found in our study. *Diploneis notabilis* is usually larger and, on average, has coarser striation. In *D. papula* the striae are composed by two transapically elongated areolae, separated by a short bar. The bars are more or less aligned, forming submarginal longitudinal ribs. In *D. notabilis*, the striae have several areolae, crossed bars, having several wavy longitudinal ribs.

Distribution & Ecology: epipelic species occurring mainly in sandy sediments. *Diploneis papula* has been mainly reported for warm waters (Hustedt 1931-1959, Sabbe 1997 and references herein) but it can be found in all oceanic coasts (Witkowski *et al.* 2000 and see above). In our study, this species was only found in the sandy transect, where it was quite rare (9 occurrences) and never abundant (max. abundance <0.32 %?).

References:
Hustedt (1931-1959) – pg. 680; fig. 1071
Sabbe (1997) – pg. 165; figs. 15/4-8, 49/2
Witkowski *et al.* (2000) – pg.190; figs. 86/14-15, 89/22-25

Diploneis cf. ***parca*** (A. Schmidt) Boyer 1927

Micrographs: Pl. 16: 10-11

Synonyms:
Navicula parca Schmidt
Navicula advena var. *parca* (Schmidt) Van Heurck
Schizonema parcum (A. Schmidt) Kuntze

Similar species:
Diploneis litoralis (Donkin) Cleve

Morphometrics:
Biovolume (µm^3): 1901
Frustule geometry: elliptic prism
Length (µm): 24.4 (n=1)
Width (µm): 12.4 (n=1)
Pervalvar axis (µm): 8 (estimated)
Striae in 10 µm: 15 (n=1)

Notes: only one tilted valve was found and the identification is only tentative. Size range, striae density and pattern and overall shape of the longitudinal channels point to *D. parca*. *Diploneis litoralis* (Donkin) Cleve is a similar taxon but it is usually much larger and has a coarser striation.

Distribution & Ecology: only one occurrence during our study. *Diploneis parca* is an epipelic, widespread marine species (Witkowski *et al.* 2000). According to Hustedt (1931-1959) it is common in English sandy coasts.

References:
Hustedt (1931-1959) – pg. 664; fig. 1061
Witkowski *et al.* (2000) – pg.191, figs. 89/4-5

Diploneis stroemi Hustedt 1937

Micrographs: Pl. 16: 8-9

Synonyms:

Similar species:
Diploneis interrupta (Kützing) Cleve

Morphometrics:
Biovolume (µm^3): 3763
Frustule geometry: elliptic prism
Length (µm): 30.6 – (37.1) – 40.5 (n=3)
Width (µm): 10.6 – (12.9) – 15.0 (n=3)
Pervalvar axis (µm): 10 (estimated)
Striae in 10 µm: 10 – (11) – 12 (n=3)

Notes: detailed descriptions given elsewhere (*e.g.* Husted 1931-1959, Witkowski *et al.* 2000). This species can be distinguished from the similar *D. interrupta* by the characteristic poroid outer layer of the striae, by the arrangement of the transapical ribs and, additionally, by the linear longitudinal channels (Husted 1931-1959).

Distribution & Ecology: epipelic species, commonly found in the sandy coast of the North Sea and Baltic Sea (Husted 1931-1959, Witkowski *et al.* 2000). In our study it was found only in one sample of a sandy transect station.

References:
Hustedt (1931-1959) – pg. 608; fig. 1022
Simonsen (1988) – pg. 225; figs. 331/5-8
Witkowski *et al.* (2000) – pg.194; figs. 86/4, 87/1-3

Suborder Naviculineae

Fam. Naviculaceae Kützing

Chamaepinnularia Lange-Bertalot & Metzeltin 1996

Genus description: Lange-Bertalot & Metzeltin (1996)

Chamaepinnularia cf. ***alexandrowiczii*** Witkowski, Lange-Bertalot & Metzeltin 2000

Micrographs: Pl. 14: 16-20

Similar species:
Chamaepinnularia clamans (Hustedt) Witkowski, Lange-Bertalot & Metzeltin
Navicula clamans var. *minor* Cholnoky

Morphometrics:
Biovolume (µm^3): 76
Frustule geometry: elliptic prism
Length (µm): 7.7 – (9.2) – 10.7 (n=6)
Width (µm): 3.4 – (4.2) – 5.2 (n=6)
Pervalvar axis (µm): (estimated)
Striae in 10 µm: 20 – (23) – 26 (n=6)

Notes: some specimens found during this study were very reminiscent of *C. alexandrowiczii*, a recently described species (Witkowski *et al.* 2000), which mainly differs from the very similar *C. clamans* by its smaller size and higher density striation.

However, without SEM observations to confirm this finding, we refrain to make a positive identification. Additionally, a possible conspecificity to *N. clamans* var. *minor* (Cholnoky 1959) should also be investigated.

Distribution & Ecology: small motile epipsammic species. According to Witkowski *et al.* (2000), *C. alexandrowiczii* has only been reported for its type locality (*i.e.* in the Red Sea), the Tanzania coast and the Adriatic Sea. In our study, it occurred almost exclusively in the sandy stations (19 occurrences) but it was never very abundant (max. abundance < 1.81%). It had a slight abundance increase in late summer and autumn, which means it had the same spatial and temporal distribution as *C. clamans* (see below).

References:
Witkowski *et al.* (2000) – pg. 168; figs. 69/1-6

Chamaepinnularia clamans (Hustedt) Witkowski, Lange-Bertalot & Metzeltin 2000

Micrographs: Pl. 14: 14-15

Synonyms:
Navicula clamans Hustedt

Similar species:
Chamaepinnularia alexandrowiczii Witkowski, Lange-Bertalot & Metzeltin

Morphometrics:
Biovolume (µm^3): 272
Frustule geometry:
Length (µm): 13.6 – (15.5) – 16.8 (n=4)
Width (µm): 6.3 – (6.4) – 6.5 (n=4)
Pervalvar axis (µm): 4 (estimated)
Striae in 10 µm: 20 (n=4)

Notes: a detailed description of this species can be found elsewhere (*e.g.* Hustedt 1961-1966, Hendey 1964, Witkowski *et al.* 2000).

Distribution & Ecology: small motile epipsammic species. This species is frequent in the North Sea coasts (Hendey 1964), although it is usually found with low abundances and mainly associated to sandflats (see Hustedt 1939, 1961-1966). It is most probably cosmopolitan, as the numerous reports for South Africa (Archibald 1983 and references herein) seem to indicate. In our study, it occurred almost exclusively in the sandy stations (21 occurrences) but it was never very abundant (max. abundance < 0.8%). It had a slight abundance increase in late summer and autumn.

References:
Archibald (1983) – pg. 153; figs. 257-259
Hendey (1964) – pg. 205;
Hustedt (1939) – pg. 624; figs. 75-77
Hustedt (1961-1966) – pg. 179; fig. 1313
Kuylenstierna (1989-1990) – pg. 106; fig. 772
Simonsen (1987) – pg. 257; fig. 379/20-22)
Snoeijs & Potapova – #251
Witkowski *et al.* (2000) pg 169; fig. 69/12

Geissleria Lange-Bertalot & Metzeltin 1996

Genus description: Lange-Bertalot (2001)

Geissleria cf. ***cummerowi*** (Kalbe) Lange-Bertalot 2001

Micrographs: Pl. 14: 11

Synonyms:
Geissleria schoenfeldii (Hustedt) Lange-Bertalot & Metzeltin
Navicula cummerowii Kalbe

Morphometrics:
Biovolume (µm^3): 65
Frustule geometry: elliptic prism
Length (µm): 8.1 (n=2)
Width (µm): 4.1 (n=2)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 22 (n=2)

Description: valves elliptic with bluntly rounded apices. Axial area is narrow and linear, central area small but widened transapically. Raphe straight with central raphe endings straight and slightly expanded. Striae radiate becoming almost parallel in the apices. In the centre, one of the two middle striae is typically much shorter than the other. The striae structure is indistinct in LM.

Notes: the few specimens found in our study seem to correspond quite well to the smaller, elliptical specimens of *G. cummerowi*, a freshwater species. However, we were unable to confirm, with only LM, the characteristic interruption of the last two apical striae in each apex (Lange-Bertalot 2000). Without further information this identification is only tentative.

Distribution & Ecology: this taxon only occurred once in this study. If it is later confirmed to be *G. cummerowi*, its origin is probably allochtonous.

References:
Lange-Bertalot (2001) – pg. 122; figs. 94/18-23

Geissleria decussis (Østrup) Lange-Bertalot & Metzeltin 1996

Micrographs: Pl. 14: 12-13

Synonyms:
Navicula decussis Østrup

Morphometrics:
Biovolume (µm^3): 469
Frustule geometry: elliptic prism
Length (µm): 21.6 (n=2)
Width (µm): 6.9 (n=2)
Pervalvar axis (µm): 4 (estimated)
Striae in 10 µm:18 (n=2)

Notes: a detailed description of this very distinct species can be found elsewhere (*e.g.* Germain 1981, Krammer & Lange-Bertalot 1986, Lange-Bertalot 2001).

Distribution & Ecology: this species only occurred once in this study. Since it is a freshwater species of oligosaprobic waters with average to moderately higher electrolyte content (Lange-Bertalot 2001) it is most probably allochtonous.

References:
Germain (1981) – pg. 194; fig. 73/6
Krammer & Lange Bertalot (1986) – pg. 141; figs. 47/10-18
Lange-Bertalot (2001) – pg. 123; figs. 95/1-17, 96/11

Haslea Simonsen 1974

Genus description: Round *et al.* (1990); Cox (1999b)

***Haslea* sp.1**

Micrographs: Pl. 17: 1-3

Similar species:
Haslea britannica (Hustedt & Aleem) Witkowski, Lange-Bertalot & Metzeltin
Haslea nautica (Cholnoky) Giffen
Navicula duerrenbergiana Hustedt

Morphometrics:
Biovolume (µm^3): 1085
Frustule geometry: elliptic prism
Striae in 10 µm: 40.5 – (45) – 49.1 (n=7)
Width (µm): 7.5 – (7.7) – 7.8 (n=7)
Pervalvar axis (µm): 4 (estimated)
Striae in 10 µm: 13 – (13) – 14 (n=7)
Lineolae in 10 µm: 22 – (24) – 25 (n=7)

Description: valves linear-lanceolate with cuneate apices, sometimes tapering rather brusquely. The central area is absent while the axial area is straight and very narrow. The raphe sternum is prominent and heavily silicified. The raphe is straight, with the central raphe endings approximate. The distal raphe endings are not clearly seen in LM but seem to be slightly bent to the same side. The transapical striae are parallel at the centre and slightly radiate near the apices. The striae have a typical "haslean" organisation, being uniseriate and composed by rectangular poroids separated by longitudinal lines, continuous from pole to pole (see Round *et al.* 1990).

Notes: this taxon is somewhat reminiscent of *Haslea britannica*, which has similar size range and density of the longitudinal lines. Conversely, that species, as described by Hustedt & Aleem (1951) has striae density of 20 in 10 µm, while our specimens have a coarser striation (around 13 in 10 µm). Witkowski *et al.* (2000) lowered the limit of the range of the stria density to 18 in 10 µm, most probably after measuring the type specimens depicted by Simonsen (1987). In any case the difference in striae density between *H. britannica* and our specimens is important. Additionally, the valve outline of *H. britannica* is much more lanceolate, with the margin clearly convex (Hustedt & Aleem 1951). *Haslea nautica* is another similar species, with the same size and striae density, but it has much coarser longitudinal ribs (around 15 in 10 µm, Witkowski *et al.* 2000).
The specimens found in our study seem to be very similar to ones depicted by Cox (1999b), which she considers to be a yet undescribed marine species of *Haslea*. The apices, raphe shape and striae structure are very similar and the morphometric data are within similar ranges, although her specimens are larger (62 µm long x 9 µm). Additionally, the areolae density, which we measured in SEM photos provided in her paper, are slightly denser (around 29 in µm). Cox (1999b) briefly discussed the similarities with *N. duerrenbergiana* which, according to her should also be transferred to *Haslea* and has slight differences in size and striae density. Both the taxon described by Cox (1999b) and *N. duerrenbergiana* seem to have striae composed by areolae more densely packed (and irresolvable in LM, Witkowski *et al.* 2000) than the diatom described here.

Distribution & Ecology: this taxon is a motile epipelic species. It occurred only in two samples of the muddy transect (one of them sandy) and it was never very abundant (max. abundance < 0.3%).

Hippodonta Lange-Bertalot, Witkowski & Metzeltin 1996

Genus description: Lange-Bertalot (2001)

This genus is defined by a combination of morphologic features (polythetic definition) which permit its separation from the very similar genus *Navicula*, namely a rather simplified raphe system and the recurrent heavy silicification of comparatively small cells (see Lange-Bertalot 2001). Even though acknowledging that there are differences to the type species of *Navicula*, *i.e. N. tripunctata* (Müller) Bory, Cox (1999) did not agree with the separation of *Hippodonta* from *Navicula sensu stricto*, stating that there is sufficient morphological variation within *Navicula s.s.*, to include the species transferred to *Hippodonta* (see also discussion below, *Navicula*).

Hippodonta caotica Witkowski, Lange-Bertalot & Metzeltin 2000

Micrographs: Pl. 18: 1-8; Pl. 46: (?) 8

Similar species:
Navicula cincta Ehrenberg

Morphometrics:
Biovolume (µm^3): 159
Frustule geometry: elliptic prism

Length (µm): 8.4 – (10.7) – 14.4 (n=15)
Width (µm): 3.8 – (4.7) – 5.7 (n=15)
Pervalvar axis (µm): 4 (estimated)
Striae in 10 µm: 10 – (13) – 15 (n=14)

Notes: the specimens found in our study are very reminiscent of *H. caotica*, described by Witkowski *et al.* (2000), having similar morphometric data, elliptical valves and a typically disorganized array of the striae. Witkowski (1994) originally identified his specimens as *N. ostreopii* Schulz non Cleve, but later separate them in two species of *Hippodonta*: *H. linearis* and *H. caotica* (Witkowski 1994, figs. 32/4, 6). We were unable to find in the literature SEM micrographs of *H. caotica* and, therefore, cannot confirm that Pl. 46: 8 is an internal view of that taxon.

There are striking similarities to *N. sjoersii* (see Busse & Snoeijs 2002, figs. 24-29), namely in the internal raphe structure, but this species has distinctly punctate striae, clearly seen in LM. Additionally the smaller specimens of *Navicula cincta* (see Lange-Bertalot 2001) are difficult to distinguish in LM from *H. caotica*, since they have similar striation density, densely packed lineolae and a conspicuous Voigt's fault, disorganizing the typical central-radiation/apical-convergence striation pattern in the larger specimens of *N. cincta*. Further studies are needed to clarify the identity of *H. caotica* which is morphologically somewhat borderline between *Hippodonta* and *Navicula*.

Distribution & Ecology:
Small motile epipsammic species, only described for the type locality in the gulf of Gdansk (Witkowski *et al.* 2000). In our study it was fairly frequent (29 occurrences), being mainly present in the lower shore muddy sandy stations of the sandy transect (max. abundance < 2.6%). It appeared throughout the study period.

References:
Witkowski (1994) – figs. 32/4, 6
Witkowski *et al.* (2000) – pg. 225; figs. 131/25-29

Navicula Bory de Saint-Vincent 1822

Genus description**:** Cox (1979b), Round *et al.* (1990), Cox (1999a) and Lange-Bertalot (2001)

In the past three decades, the formerly huge and heterogeneous genus *Navicula sensu lato* (*e.g.* Hustedt 1961-1966) has been split up into several new or resurrected genera (*e.g.* *Fallacia*, *Parlibellus*, *Biremis*, *Dickieia*, etc.). With the redefinition of *Navicula sensu stricto* by Cox (1979b), the genus was circumscribed to the group of species analogous to the generitype *Navicula tripunctata* (Müller) Bory which, after Round *et al.* (1990) continued this revision, should roughly correspond to the section Lineolatae. As Mann (1994) put it, *"Navicula* itself emerged (...) as a well-defined entity, with linear areolae, two girdle-appressed chloroplasts per cell (each containing an elongate, rod-like pyrenoid), and a characteristic type of raphe system".

Notwithstanding a clearer and narrower definition of a more homogenous *Navicula s.s.* there are still many species, within the genus, that do not correspond to the generitype. This seems to be particularly true for numerous marine and brackish water species (Lange-Bertalot 2001). As an example, Sabbe (1997) refers the species group around *Navicula crucifera* Grunow, which do not have flat valves. Other examples are given by Witkowski *et al.* (1998). Aware of this problem and wanting to prevent that a too narrow definition of *Navicula s.s.* would cause unnecessary splitting within the group, Cox (1999) further elaborated on the accepted morphological variability within the genus and made a more complete definition of *Navicula s.s.*, which extended her initial circumscription. An alternative solution was proposed earlier by Lange-Bertalot & Moser (1994), who described a new catch-all genus *Naviculadicta* to harbour temporarily all the taxa that cannot remain in *Navicula s.s.* but are of unknown generic affiliation. Albeit practical, this solution was rejected by many authors (*e.g.* Kociolek 1996) on the grounds that established a non-monophyletic (*i.e.* unnatural) group and that could eventually create insurmountable nomenclatural problems in the near future. A final decision could pass through one of the alternatives proposed in Lange-Bertalot (2001):

- Expanding the generic diagnosis
- Restructuring the expanded genus in revaluated subgenera
- Defining new genera from the section Lineolatae

The issue of this debate falls outside the scope of our study but it still directly affects it, as it was the case in other works in marine benthic diatoms (*e.g.* Sabbe 1997, Witkowski *et al.* 2000), since several of *Navicula* species we found did not fit into the current interpretation of *Navicula sensu stricto*. Following the example of the aforementioned authors, the broader interpretation (*i.e. Navicula s.l.*) was taken in those cases and it is explicitly stated if each taxon belongs to *Navicula s.s.* or not.

Navicula abscondita Hustedt 1939

Micrographs: Pl. 17: 4-10

Synonyms:

Similar species:
Navicula duerrenbergiana Hustedt
Navicula flagellifera Hustedt
Navicula subrostellata Hustedt
Navicula sp. 1 (see below)

Morphometrics:
Biovolume (µm^3): 642
Frustule geometry: elliptic prism
Length (µm): 24.4 – (32.3) – 38.1 (n=8)
Width (µm): 5.4 – (6.3) – 6.8 (n=8)
Pervalvar axis (µm): 4 (estimated)
Striae in 10 µm: 13 – (14) – 15 (n=8)

Notes: our specimens are in agreement with the protologue of *N. abscondita* in Hustedt (1939) and with the observations made by Sabbe (1997). The latter author clarified that there was an error in Simonsen's (1987) lectotypification and only the illustrations 16 and 17 (in Pl. 378, slide 267/3, "Linke nº 31") correspond to the type description. The other illustrations are from another taxa, yet undescribed, that both Sabbe (1997, as *Navicula* sp.8) and ourselves (*Navicula* sp1, see below), found in our respective material. Sabbe (1997) also found other misidentifications in Simonsen (1987) regarding other probable *N. abscondita* specimens (see references below).

Having very weakly silicified frustules, *N. abscondita* can be easily confused with very similar *N. duerrenbergiana* (Krammer &Lange-Bertalot 1986) but it has larger, more discrete central nodule, small roundish central area and indistinct striae (Sabbe 1997). Other species, such as *N. flagellifera* or *N. subrostellata* Hustedt also have striae with lineolae resolvable in LM.

Distribution & Ecology: according to Sabbe (1997) this species has only been reported from North Sea coasts (*e.g.* Hustedt 1939, Brockmann 1950) and the Mediterranean (Simonsen 1987, as *N. pavillardii*, see references below). Sabbe (1997) reported it as rare in silty sediments, while Hustedt (1939) and Brockman (1950) found it in sandy sediments from the Wadden Sea. In our study it was very infrequent but actually quite abundant (max. abundance <6.1%) in one of the seven samples from the sandy transect in which it occurred. It is most probably an epipelic form.

References:
Hustedt (1939) – pg. 620; figs. 53-54
Sabbe (1997) – pg. 169; figs. 17/7-8, 49/4
Simonsen (1987) – figs. 378/16-17 (not figs. 378/11-15), 380/12-12 (as *N. flagellifera*), 381/3-4 (as *N. pavillardii*)
Witkowski *et al.* (2000) – pg. 265; figs. 130/24, 33

Navicula aleksandrae Lange-Bertalot, Bogaczewicz-Adamczak & Witkowski 2003

Micrographs: Pl. 18: 19-23; Pl. 47: 1-3

Similar species:
Navicula biskanterae Hustedt
Navicula bozenae Lange-Bertalot, Witkowski & Zgrundo
Navicula germanopolonica Witkowski & Lange-Bertalot

Navicula paul-schulzii Witkowski & Lange-Bertalot

Morphometrics:
Biovolume (µm^3): 76
Frustule geometry: elliptic prism
Length (µm): 7.4 – (9.5) – 13.3 (n=32)
Width (µm): 2.4 – (4.1) – 5.2 (n=32)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 169 – (21) – 23 (n=32)
Lineolae in 10 µm: 39 – (43) – 47 (n=6)

Notes: *Navicula aleksandrae* is one of the several small-sized coastal *Navicula s.s.* that have been described in the recent years. These species have been probably overlooked in older studies since they are quite difficult to identify without detailed LM and SEM studies. Lange-Bertalot *et al.* (2003), who described this taxon, made comprehensive morphological comparison between these easily confused diatoms and this work should be consulted.

Navicula aleksandrae is particularly close to *N. germanopolonica* and to *N. bozenae,* which can co-occur in the same sandy sediments (Lange-Bertalot *et al.* 2003). It can be distinguished from *N. germanopolonica* by the closer central raphe endings, which are distinctly rounded (and not drop-like) and by curved terminal raphe fissures, but the main difference is the lineolae density. With approximately 30 lineolae in 10 µm, the striae of *N. germanopolonica* are still distinctly punctate in LM, whereas the striae of *N. aleksandrae* are irresolvable in LM (approximately 40 lineolae in 10 µm). The central area of *N. germanopolonica* is also manifestly larger and transapically expanded and there are also other minor differences in valve outline, striae orientation and shape of external slits of the areolae that should be taken into account. Regarding *N. bozenae*, it has coarser striae than *N. aleksandrae*, a distinctly radiating striation pattern in the centre of the valve and a clearly lanceolate valve outline. The differences in SEM are, nonetheless, less obvious, as they have the same high lineolae density and very similar raphe structure. As for other similar species, such as *N. paul-schulzii* or *N. biskanterae*, these taxa have a higher striation density as well as a clear radiating striae pattern in the middle of the valve. Before the formal description by Lange-Bertalot and colleagues, other authors have encountered this taxon. Sabbe (1997) reported it as *Navicula* sp.4 and the internal valve view, depicted in his work, clearly corresponds to ours and to the valve shown in Lange-Bertalot *et al.* (2003). All of them have a slightly thickened raphe-sternum in the central nodule, helictoglossae in the distal raphe endings but no accessory longitudinal rib. Regarding the striae, they all have more or less rectangular areolae and the semicircle of small punctae around the terminal nodules.

Distribution & Ecology: this species has only been reported for the Baltic Sea (*e.g.* Lange-Bertalot *et al.*, 2003), namely for the type locality (small freshwater creek in Sopot) and for sandy sediments of Puck Bay (brackish water). However it seems that Sabbe (1997) also found it in the Westerschelde estuary, especially in medium sandy intertidal sediments in the lower reaches of the estuary. As a small motile epipsammic species, it has been probably overlooked or only identified to the genus level in other works in European coasts. In our study it was one of the most common species, with 50 occurrences, most of them in sandy stations. The maximal abundances (almost 12% of relative abundance) were found in the medium/coarse sediments of the lower shore stations of the sandy transect. The temporal variations throughout the study were subtle but there was a slight but regular increase in numbers during spring, especially in the second year of the study.

References:
Lange-Bertalot *et al.* (2003) – figs. 1-20
Sabbe (1997) – pg. 198; 18/33-35, 52/2

Navicula cf. **aleksandrae** Lange-Bertalot, Bogaczewicz-Adamczak & Witkowski 2003

Micrographs: Pl. 18: 24-28

Similar species:
Navicula bozenae Lange-Bertalot, Witkowski & Zgrundo

Morphometrics:
Biovolume (µm^3): 47
Frustule geometry: elliptic prism
Length (µm): 4.4 – (8.2) – 9.5 (n=12)
Width (µm): 2.3 – (2.9) – 3.7 (n=12)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 18 – (21) – 23 (n=12)

Description: only LM description is given. Valves are flat and small, elliptical to narrowly elliptical-lanceolate with cuneately rounded apices, which are never protracted. Raphe is straight with expanded central endings and only slightly distant. The distal raphe endings are, apparently, both turned to the same (secondary?) side. Axial are narrow and central area very small and rounded. Striae are parallel or very slightly radiate, being always parallel near the apices. Their structure is indistinct in LM.

Notes: this taxon is very similar to *N. aleksandrae* (see above) in size range and in density and orientation of the striae. The only difference is the valve outline, which is elliptical to narrow-elliptical with bluntly rounded apices, instead of elliptical-lanceolate with shortly protracted ends. This outline is somewhat reminiscent of *N. bozenae* (see below) but the striae density and orientation are different. It is possible that the specimens found in our study are a morphotype of *N. aleksandrae* but SEM studies are needed for a detailed comparison. Furthermore, both taxa have very similar spatial distributions and in opposition to the distribution of *N. bozenae* (see below).

Distribution & Ecology: *Navicula* cf. *aleksandrae* is most probably a small motile epipsammic diatom. This taxon had a spatial-temporal distribution that mirrored the distribution of *N. aleksandrae.* Even though it was less abundant (max. abundance <6.55%) and frequent (40 occurrences) than *N. aleksandrae*, it was mostly found in the sandy stations, particularly in the medium-coarse sandy stations, lower shore in the sandy transect. Regarding the seasonal variation, it was more abundant during spring and in the second year of the study.

Navicula arenaria Donkin 1861

Micrographs: Pl. 19: 1-6; Pl. 46: 10-11

Synonyms:
Navicula lanceolata var. arenaria (Donkin) Van Heurck (syn. *N. arenaria* var. *arenaria*)
Navicula rostellata Kützing *sensu* Brockmann (1950), Hendey (1964)
(?) *Navicula normalis* Hustedt (possible synonyms of *N. arenaria* var. *rostellata*)

Similar species:
Navicula mollis (Smith) Cleve

Morphometrics:
Biovolume (µm^3): 3290
Frustule geometry: elliptic prism
Length (µm): 37.6 – (49.3) – 62.4 (n=22)
Width (µm): 5.6 – (8.5) – 9.7 (n=22)
Pervalvar axis (µm): 10 (estimated)
Striae in 10 µm: 9 – (11) – 12 (n=21)
Lineolae in 10 µm: 25 – (29) – 32 (n=16)

Description: only SEM ultrastructural details are given. Valve face is flat, gently curving into the mantle. Raphe-sternum distinct, becoming externally expanded in the centre. Internally, the raphe-sternum is broader and in the centre the accessory longitudinal rib is interrupted. Externally, the central raphe endings are hooked in the same direction (secondary side) although, in some eroded valves, this is not observed. The terminal raphe endings bend towards the primary side but the terminal fissures have a strong, angular, hook over the valve apex, opening towards the secondary side. The striae are composed by lineolae, occluded internally by hymenes. Externally they are slit-like and appear to be longitudinally aligned, except near the apices, where there are no terminal pores.

Notes: no distinction was made between *N. arenaria* var. *arenaria* Van Heurck and *N. arenaria* var. *rostellata* Lange-Bertalot during counts. The varieties differ mainly in valve outline and the shapes of the apices but have distinct taxonomic histories (caused by a misinterpretation of *N. rostellata* Kützing, see Krammer & Lange-Bertalot 1986). Our specimens showed a certain amount of morphological variability, especially in valve outline and in the shape of the central areas (both square and circular central areas were found) but most of them seem to be of the variety *rostellata*. Nonetheless, the specimens all correspond to *N. arenaria*, as the SEM micrographs attest (compare with Cox 1999). Even though it is common, this taxon is seldom illustrated by SEM (to our knowledge, only in Cox 1999 and Sabbe 1997) and for this reason a detailed description of the valves ultrastructure is given (see above).

Distribution & Ecology: *Navicula arenaria* is considered to be an epipelic, cosmopolitan species, common in both sandy and silty sediments, particularly in the North Sea coasts and the Baltic Sea (Krammer & Lange-Bertalot 1986). In our study it was present in all types of sediment (29 occurrences), but mainly in the sandy sediments. Although not very abundant it seemed to reach a seasonal peak in the winter/spring period (max. abundance < 5.2%).

References:
Brockmann (1950) – pg. 17; figs. 1/49,50,56
Cox (1999) – figs. 22, 37, 65 (SEM)
Hendey (1964) – pgs. 196, 200; figs. XXX/11,15
Krammer & Lange-Bertalot 1986, p. 118, fig. 39/1, 2
Kuylenstierna (1989-1990) – pg. 105, figs. 591
Sabbe (1997) – pg. 171; figs. 16/13-15, 49/5-6
Snoeijs & Balashova (1998) – # 452
Witkowski *et al.* (2000) – pg. 267; figs. 116/16-21, 129/29, 134/8-9

Navicula bozenae Lange-Bertalot, Witkowski & Zgrundo 2003

Micrographs: Pl. 18: 29-31; Pl. 46: 9

Similar species:
Navicula aleksandrae Lange-Bertalot, Bogaczewicz-Adamczak & Witkowski
Navicula biskanterae Hustedt
Navicula germanopolonica Witkowski & Lange-Bertalot
Navicula paul-schulzii Witkowski & Lange-Bertalot

Morphometrics:
Biovolume (µm^3): 91
Frustule geometry: elliptic prism
Length (µm): 7.0 – (10.1) – 14.7 (n=11)
Width (µm): 3.2 – (3.8) – 4.5 (n=11)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 16 – (18) – 20 (n=11)
Lineolae in 10 µm: 45 (n=1)

Notes: *Navicula bozenae* is one of small *Navicula s.s.* described by Lange-Bertalot *et al.* (2003). That work should be consulted for a detailed description and comparison with similar taxa. For further information the entries on *N. germanopolonica* and *N. aleksandrae* in our work should also be inquired. Considering the valve ultrastructure, as it is seen in SEM, the differences between *N. bozenae* and *N. aleksandrae* are quite minimal and seem limited to valve outline and to striae density and orientation. The only conspicuous difference found in the raphe structure is the marked longitudinal lines bordering the raphe-sternum externally (Lange-Bertalot *et al.* 2003). This is not seen in our specimens of *N. aleksandrae*, although they seem to be “suggested” in figs. 17-19 in Lange-Bertalot *et al.* (2003). Additionally, although not referred by the authors, both species have the same semi-circular row of punctae in the apices. This feature can be seen in SEM valve external views depicted by Lange-Bertalot *et al.* (2003) but also in SEM valve internal views depicted in Sabbe (1997) where both *N. bozenae* and *N. aleksandrae* were found and named *Navicula* sp.1 and *Navicula* sp.4, respectively. *Navicula paul-schulzii* also has the semicircle of areolae along the apical margin (Lange-Bertalot *et al.* 2003) but not *N. germanopolonica*, which also has different distal raphe endings, thus indicating that it is not as closely related to the other small *Navicula* species (see below).
In conclusion, the main differences between the two species seem to be, therefore, limited to the striation pattern (more parallel in *N. aleksandrae*) and density (slightly lower in *N. bozenae*). We therefore, speculate on the

possibility of *N. bozenae* and *N. aleksandrae* being varieties of the same species, in spite of their easy discrimination in LM.

Distribution & Ecology: to our knowledge, this species has only been found in the Baltic Sea, in the type locality (Sopot), in the sandy sediments of Puck Bay (Lange-Bertalot *et al.* 2003) and in the Westerschelde (Sabbe 1997), where it was one of the most common epipsammic diatoms in fine sandy intertidal sediments throughout the estuary. It is a small motile epipsammic species. In our study it was one of the most frequent species in the sandy sediments (39 occurrences). Interestingly, it had a complementary distribution to *N. aleksandrae* in the sandy transect (see above) as it was particularly abundant in the upper shore medium fine sandy station (max. abundance < 18.5%), thus confirming the observations by Sabbe (1997).

References:
Lange-Bertalot *et al.* (2003) – figs. 21-33
Sabbe (1997) – pg. 195; 18/28-32, 52/1

Navicula cf. ***celinei*** Witkowski, Metzeltin & Lange-Bertalot *in* Metzeltin & Witkowski 1996

Micrographs: Pl. 18: 51-52

Similar species:
Navicula salinicola Hustedt

Morphometrics:
Biovolume (µm^3): 122
Frustule geometry: elliptic prism
Length (µm): 10.7 – (12.4) – 16.5 (n=6)
Width (µm): 3.3 – (4.1) – 5.6 (n=6)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 15 – (17) – 18 (n=6)

Notes: this taxon is somewhat similar to *N. germanopolonica* or *N. salinicola* but it does not have striae composed by lineolae resolvable in LM and it has a clearly delineated central area, composed by the shortening of the two central striae. Together, with size range and striae density, these morphological features point to *Navicula celinei*, a taxon which has only been described for its type locality (Bear Island in the Barents Sea) and for the Norwegian Sea near Narvik (Witkowski *et al.* 2000). Without further studies we cautiously refrain ourselves to make a positive identification.

Distribution & Ecology: probably a small motile epipsammic species. In our study it was mainly found in sandy sediments (22 occurrences), particularly in medium-coarse sandy sediments on the lower shore stations of the sandy transect, but it was never very abundant (max. abundance < 2%). It was more commonly found in the second year of the survey and typically disappeared during summer.

References:
Witkowski *et al.* (2000) – pg. fig. 272; figs. 141/16-18

Navicula dilucida Hustedt 1939

Micrographs: Pl. 18: 47-50

Similar species:
Navicula dehissa Giffen

Morphometrics:
Biovolume (µm^3): 195
Frustule geometry: elliptic prism
Length (µm): 19.6 – (20.5) – 22.0 (n=5)
Width (µm): 3.2 – (3.5) – 3.8 (n=5)
Pervalvar axis (µm): 4 (estimated)
Striae in 10 µm: 19 – (20) – 21 (n=5)

Notes: there are not many species that have very narrowly lanceolate valves, with acutely rounded apices, central and axial areas narrow and striae that radiate throughout the valve. In fact only *N. dilucida* and *N. dehissa* seem to have this rather unique combination of morphological features. Our specimens fully correspond to the diagnosis given by Hustedt (1939) and to the lectotypes shown by Simonsen (1987). A direct comparison to Giffen's (1973) *N. dehissa* protologue was not made, but the specimens shown in Witkowski *et al.* (2000) are more broadly lanceolate and have a denser striation.

Distribution & Ecology: *Navicula dilucida* is an epipelic species that was rarely recorded since Hustedt (1939) described it for sandflats in Memmert Island (German Bight). Sullivan (1975a) reported it as part of the edaphic diatom community in a Delawarean saltmarsh (West Coast, U.S.A.) and in our study it was exclusively found in mudflat samples. It was extremely rare (4 occurrences) and scarce (max. abundance < 1.1%).

References:
Hustedt (1939) – pg. 627; figs. 53-54
Simonsen (1987) – pg. 258; figs. 379: 28-32
Witkowski *et al.* (2000) – pg. 274

Navicula diserta Hustedt 1939

Micrographs: Pl. 18: 9-14

Similar species:
Navicula hansenii Møller
Navicula perminuta Grunow *in* Van Heurck non Østrup
Navicula salinicola Hustedt

Morphometrics:
Biovolume (µm^3): 54
Frustule geometry: elliptic prism
Length (µm): 6.5 – (9.3) – 11.3 (n=13)
Width (µm): 2.6 – (2.9) – 3.4 (n=12)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 15 – (17) – 18 (n=13)

Notes: *Navicula diserta* is one of the many coastal and estuarine diatoms with small lanceolate naviculoid valves and shortened central striae that are similar and/or were synonymised to *Navicula perminuta* (*e.g.* Krammer & Lange-Bertalot 1986, Witkowski *et al.* 2000). This species group is extremely difficult to study given the fact that populations, found and indentified as *N. perminuta* (or its synonyms) in numerous studies, are rather character-poor (Witkowski *et al.* 2000). They have a highly variable morphology (*e.g.* striae density: 14-20 in 10 µm) and an additional difficulty is the fact that Grunow's type material of *N. perminuta* was never studied in SEM. Nonetheless, it was examined by Krammer & Lange-Bertalot (1985, 1986) who published LM micrographs of several lectotypes (Plate 35, figs. 14-16, Krammer & Lange-Bertalot 1986). Since then, these lectotypes have been critically compared with type slides of known synonyms (*e.g. N. hansenii*, *N. diserta*) or to newly described species, which have similar morphological features (*e.g. N. sjoersii*, *N. bossvikensis*). It should be noted that the lectotypes of *N. perminuta* have a high striae density (approximately 20 in 10 µm), a rectangular central area and the type material probably derives from an epiphyton sample (Sabbe 1997).

Regarding *N. diserta*, there is a great deal of taxonomic confusion, which is described in detail by Sabbe (1997) and also by Busse & Snoeijs (2003b). Briefly:

- Hustedt indicated Leybucht (near Dollar Bay, German Bight) as the type locality but placed the name *N. diserta* on the slide N6/23, from another locality (sandflat near Nessmersiel). This slide was interpreted by Archibald (1983) and Krammer & Lange-Bertalot (1985) as the type slide of this species. Later, Simonsen (1987) designated the correct type slide (N12/36, from Leybucht) and indicated another slide (397/75, from a sandflat in Memmert Island, East Frisia) where this species was also present.
- Archibald (1983) considered that *N. hansenii* and *N. pseudoincerta* Giffen were similar to the specimens of *N. diserta* he observed in the Nessmersiel slide and made them synonyms. Krammer & Lange-Bertalot (1985) compared that same Nessmersiel slide with Grunow's type slide of *N. perminuta* and concluded that *N. diserta* and *N. perminuta* too, were also synonyms. They followed Archibald (1983) and transferred the synonymies to *N. perminuta*.
- Sabbe (1997) studied the type slides selected by Simonsen (*i.e.* N12/36 and 397/75), performing additionally a SEM examination of material

from the type locality and finally compared it to his own material from the Westerschelde estuary. He determined that there was a problem in the lectotypification made by Simonsen (1987). The illustrated lectotype from the type slide (Pl. 379, Figs. 39-40) has slightly curved distal raphe endings and central raphe endings and actually concerns another species, *N. starmarchioides* Witkowski & Lange-Bertalot. The second illustrated lectotype (Pl. 379, Figs. 41-43) corresponds well with the original Hustedt description and was considered by Sabbe to be the "true" *N. diserta*. He found this taxon in both Hustedt's slides (N12/36 and 397/75), as well as in his own Westerschelde material. He also questioned the significance of the distinctiveness of the lineolate striae in LM, a main feature pointed by Hustedt (1939), as specimens with and without lineolate striae could be found within the same slide.

- The synonymy of *N. diserta* with *N. perminuta* was, therefore, challenged as *N. diserta* specimens have a lower striation density (14-18 in 10 µm) than the lectotypes of *N. perminuta*, a more lanceolate elliptic valve outline, a smaller average size, a central area that is not always rectangular and the terminal raphe fissures that are strongly hooked in sharp angles, instead of a the more "curved" hook in *N. perminuta* (*viz.* Busse & Snoeijs 2003). Sabbe further supports his claim that *N. diserta* is an independent species by the fact that it has a completely different ecology, being a small motile epipsammic species, common in intertidal sandflats, instead of a tube-dwelling species, common in the periphyton, as *N. perminuta* is suspected to be (Kuylenstierna 1989-1990, Snoeijs 1993, Witkowski 1994, Busse & Snoeijs 2003). Finally, and to give further support, other authors (*i.e.* Kuylenstierna 1989-1990, Witkowski 1994) also had independently discriminated *N. diserta*-like specimens from the *N. perminuta* specimens found in their studies.
- *N. hansenii* was also considered an independent species and cannot be referred as a synonym of *N. diserta* or *N. perminuta*. It has also a rather complex taxonomical history (see Kuylenstierna 1989-1990, Sabbe, 1997, Busse & Snoeijs 2002, Lange-Bertalot *et al.* 2003), with two different forms in its diagnosis, as a study of the type material by Kuylenstierna (1989-1990) demonstrated. One of the forms may be conspecific to *N. perminuta*, whereas the other formally designated as a lectotype of *N. hansenii* in Lange-Bertalot *et al.* (2003) is larger, with coarser striation, parallel margins and a rectangular central area, being different from both *N. perminuta* and *N. diserta*. Finally, the taxonomic status of *N. pseudoincerta* Giffen is uncertain.

We agree with the claim made by Sabbe (1997) and also consider *N. diserta* as an independent species. The specimens found in our study conform almost completely to his observations and it also occurred in sandy intertidal sediments. Most of specimens found did not have distinct lineolae in LM as well (but see below *N.* cf. *diserta*).

Distribution & Ecology: According to Sabbe (1997), *N. diserta* was one of the most common small motile epipsammic throughout the Westerschelde estuary. He also referred that this species has been observed with certainty in samples from the Baltic Sea, the Wadden Sea, the North Sea coasts of England and Netherlands and also in samples from the Somme estuary (France) and South America. In our study, it was also one of the most frequently found epipsammic diatoms with 37 occurrences, almost all in sandy stations. It was particularly abundant (max. abundance <5%) in the coarser grained lower shore stations of the sandy transect, where it had fairly constant numbers throughout the study period.

References:
Hustedt (1939) – pg. 627; figs. 78-79

Kuylenstierna (1989-1990) – pg. 118, figs. 58/718-719 (as *Navicula* sp.U)
Sabbe (1997) – pg. 175; figs. 18/10-18, 51/1-3,6
Simonsen (1987) – pg. 258; figs. 39-43
Witkowski (1994) – pg. 155; figs. XXXV/5-8 (as *N.* cf. *perminuta*)

Navicula cf. ***diserta*** Hustedt 1939

Micrographs: Pl. 18: 15-16; Pl. 47: 10-11

Similar species:
Navicula sjoersii Busse & Snoeijs

Morphometrics:
Biovolume (µm^3): 58
Frustule geometry: elliptic prism
Length (µm): 6.0 – (8.7) – 11.0 (n=12)
Width (µm): 2.8 – (3.4) – 4.0 (n=11)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 14 – (16) – 18 (n=12)
Lineolae in 10 µm: 30 – (32) – 34 (n=3)

Notes: Hustedt (1939), in his rather summarized diagnosis of *N. diserta*, said that this taxon "Von den übrigen kleinen Formen durch die deutlich linierten Streifen zu unterscheiden.", meaning that it could be differentiated from other small forms by its clearly lineolate striae. However, this feature is not very obvious in his drawings (figs. 78-79) or in the lectotypes of the species shown in Simonsen (1987). Sabbe (1997) minimized the importance of this criterion, as he found specimens with or without lineolate striae on the type slide (see above), mentioning that this feature may be influenced by the erosion in such small valves.

Even though *Navicula* cf. *diserta* is very similar to *N. diserta* (see above), as it can be inferred by the morphometric data, we used Hustedt's criterion to distinguish the specimens during the cell counts in order to determine if there were differences in abundance and distribution. It was also noticed that these specimens had invariably larger central areas, which were limited by one sole areola in both margins. Furthermore, a couple of specimens of this form were examined in SEM and there were slight differences to specimens illustrated by Sabbe (1997), namely the central raphe endings seem to be strongly hooked and deflected to the secondary side (as *N.* cf. *perminuta* in Cox 1999), instead of being pore-like. Also the smaller striae in the central area in *N. diserta sensu* Sabbe are quite variable and may be composed by more than one mantle areola. Finally, we could not discern any kind of rudimentary conopeum in the central area, nor its extension along the raphe branches. However, such minor differences in valve minutiae may not be sufficient to separate both morphotypes of *N. diserta*, but further studies will be needed.

Nevertheless, the SEM observations exposed very vividly the differences to what is presumed to be the true *N. perminuta* (see Busse & Snoeijs, 2002), namely the differences in the external raphe fissures and endings. Nor does *N.* cf. *diserta* conforms to *N. sjoersii*, which is also a small *N. perminuta*-like species with distinctly lineolate striae in LM, because of the fact that *N. sjoersii* has more broadly rounded apices, straight and expanded external central raphe endings and distal raphe endings that show a gentle curve hook to the secondary side (Busse & Snoeijs 2002).

Distribution & Ecology: probably a small motile epipsammic diatom, as *N. diserta*. This taxon was much rarer (only 8 occurrences) and less abundant (max. abundance <2.6%) than *N. diserta*. Nonetheless it mirrored the spatial distribution of *N. diserta* (see above) being more common in the lower shore stations of the sandy transect. This lower occurrence and abundance is also in agreement with the observations by Sabbe (1997), when he stated that the distinctly lineolate forms of *N. diserta* were much less abundant in the Westerschelde estuary than the typical form of *N. diserta* (see above).

References:
Cox (1999) – fig. 3 (?) (as *N.* cf. *perminuta*)

Navicula flagellifera Hustedt 1939

Micrographs: Pl. 20: 11-14

Similar species:
Navicula sp.3 (see below)
Navicula abscondita Hustedt

Morphometrics:
Biovolume (µm^3): 757
Frustule geometry: elliptic prism
Length (µm): 30.8 – (35.0) – 44.8 (n=4)
Width (µm): 5.7 – (6.9) – 8.0 (n=4)
Pervalvar axis (µm): 4 (estimated)
Striae in 10 µm: 11 – (12) – 13 (n=5)
Lineolae in 10 µm: 32 – (33) – 34 (n=3)

Notes: with raised apices, a small but distinct central area and lineolae density around 30 in 10 µm, these specimens correspond to *N. flagellifera*, as it is described and illustrated in Hustedt (1939), Simonsen (1987) and Witkowski *et al.* (2000). This taxon could, therefore, be easily distinguished from *Navicula* sp.3 (see discussion below). They seem to have, however, a slightly more broadly lanceolate valve outline than in the above mentioned descriptions.

Distribution & Ecology: *N. flagellifera* is a cosmopolitan epipelic species, reported for sandy littoral sediments (Hustedt 1939, Witkowski *et al.* 2000). In our study, it appeared only in the sandy stations (20 occurrences) in a complementary distribution to *Navicula* sp.3. It showed a strong seasonal peak in summer (max. abundance < 15.9%).

References:
Hustedt (1939) – pg. 628; figs. 94-95
Simonsen (1987) – pg. 258; figs. 380/9-10, 13-14 (not 11-12, see *N. abscondita*)
Witkowski *et al.* (1998) – figs. 69-70
Witkowski *et al.* (2000) – pg. 277; figs. 129/3, 6-8, ?19, 20

Navicula germanopolonica Witkowski & Lange-Bertalot 1993

Micrographs: Pl. 18: 39-46; Pl. 47: 4-6

Similar species:
Navicula aleksandrae Lange-Bertalot, Bogaczewicz-Adamczak & Witkowski
Navicula biskanterae Hustedt
Navicula bozenae Lange-Bertalot, Witkowski & Zgrundo
Navicula paul-schulzii Witkowski & Lange-Bertalot

Morphometrics:
Biovolume (µm^3): 132
Frustule geometry: elliptic prism
Length (µm): 8.7 – (12.2) – 17.4 (n=22)
Width (µm): 3.7– (4.7) – 5.7 (n=22)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 16 – (19) – 21 (n=22)
Lineolae in 10 µm: 25 – (29) – 32 (n=14)

Notes: *Navicula germanopolonica* is very reminiscent of *N. aleksandrae* and *N. bozenae* (see above) but it differs from both in having lower areolation density (around 30 in 10 µm) which is still resolvable in LM, and by the shape of the raphe endings. *Navicula biskanterae* and *N. paul-schulzii* also have higher areolation densities and the central striae are clearly curved radiate in valve centre. In fact, considering the raphe and other features observable in SEM, *N. germanopolonica* seems to be not as close to *N. viminoides*, as the above mentioned four *Navicula* species, being probably closer to the group around *N. gregaria* or *N. phyllepta* (Cox 1995), although further studies are needed.

Distribution & Ecology: this species has been reported for the Baltic Sea and North Sea coasts (*e.g.* Witkowski *et al.* 2000), where it seems to be a common member of the epipsammic communities in sandy sediments (*e.g.* Vilbaste *et al.* 2000, references listed below). It is a small motile epipsammic species that has been probably overlooked. Therefore it is possible that it has a much wider distribution. To our knowledge, the Tagus estuary is the first reported South-European location. In our study, *N. germanopolonica* was one of the most frequently encountered diatoms in the sandy transect (36 occurrences), being particularly abundant and common in the upper shore, medium fine sandy station (max. abundance < 20%).

References:
Lange-Bertalot (2001) – pg. 35, fig. 15/14-19

Lange-Bertalot *et al.* *(*2003) – figs. 34-48
Snoeijs & Potapova (1995) – # 255
Sundbäck (1983) – pg. 117; figs. 2/d,g (as *Navicula* sp.1)
Kuylenstierna (1989-1990) – pg. 118, figs. 60/761-763 (as *Navicula* sp. C)
Witkowski (1994) – pg. 148; figs. XXX/4-7
Witkowski *et al.* (2000) – pg. fig. 279; figs. 119/13-18

Navicula gregaria Donkin 1861 **morphotype 1 (m.1)**

Micrographs: Pl. 21: 13-14; Pl. 48: 1-5

Synonyms:
Navicula gottlandica Grunow *sensu* Hustedt
Navicula gregalis Cholnoky
Navicula phyllepta Kützing *sensu* Brockmann *et sensu* Hendey
Schizonema gregarium (Donkin) Kuntze 1898

Similar species:
Navicula cryptocephala Kützing
Navicula phyllepta Kützing
Navicula veneta Kützing

Morphometrics:
Biovolume (µm^3): 831
Frustule geometry: elliptic prism
Length (µm): 20.7 – (29.1) – 38.6 (n=40)
Width (µm): 4.9 – (7.3) – 8.4 (n=35)
Pervalvar axis (µm): 5 (estimated)
Striae in 10 µm: 15 – (17) – 19 (n=37)
Lineolae in 10 µm: 24 – (29) – 36 (n=36)

Notes: several authors (*e.g.* Brockman 1955, Hendey 1964) confused *N. gregaria* with *N. phyllepta* (see below), which can co-occur in the same brackish areas and has similar size and valve outline. Nonetheless, there are several clearly distinct features. *Navicula gregaria* has more or less diagonally off-set plastids; the apices are usually rather rostrate in *N. gregaria* and subrostrate in *N. phyllepta*; the central striae in *N. phyllepta* radiate, whereas in *N. gregaria* they are almost transverse and parallel and may be distinctly punctate and longitudinally aligned. Additionally, the central area of *N. gregaria* is typically asymmetrical, being rounded on one side and more square and transapically expanded on the other side, *i.e.* the primary side, to where the external central raphe endings are clearly pointing. Internally, in this area of the raphe, the axial siliceous rib, lying beside it, is also clearly asymmetrical and conspicuously thickened, expanding towards the primary side of the valve. Finally, there are two features of the central raphe endings, seen in SEM, which can also be used to separate both taxa. Externally, there is lightly broader siliceous thickening around the central raphe endings in *N. phyllepta*. Internally, there is a clear discontinuity between the fissures of the central raphe endings in *N. gregaria* (which are facing the secondary side), whereas in *N. phyllepta* a central groove creates the appearance of a continuous internal fissure (see also Cox 1995, for further differences). In the Tagus estuary, this taxon has been frequently confused with the freshwater species *N. cryptocephala* (*e.g.* Brotas & Plante-Cuny 1998, fig. 7/J).

A more complete description of *N. gregaria* and similar taxa can be found in Krammer & Lange-Bertalot (1986), Cox (1995) and Lange-Bertalot (2001). Cox (1987, 1995) and Lange-Bertalot (1993, 2001) studied in detail *N. gregaria* and discussed its rather confusing typification. Both authors agreed that there are several morphological forms within *N. gregaria* (Cox 1987). Lange-Bertalot considered it to be a complex of subspecies or even species (“Sippencomplex”, *viz.* Lange Bertalot 1993, 2001; Witkowski *et al.* 2000). However, the groupings established by Cox and Lange-Bertalot do not totally agree. One of them (Sippe nº 2 *sensu* Lange-Bertalot, *N. gregaria* sp B *sensu* Cox) concerns a smaller form, with denser and more finely punctuated striae (lineolae density > 40/10 µm), that has a freshwater ecological optimum but may also live in slightly brackish waters, in eutrophic conditions. Conversely, the “true” *N. gregaria* (form A, *sensu* Cox 1987), which corresponds to the type of *N. gregaria* and lives in truly brackish conditions, was interpreted differently by both authors. Cox (1987, 1995) established a wider morphological range for this form including specimens with and without distinctly punctuated striae in

LM. Conversely, Lange-Bertalot (2001) established a “Sippe nº1”, corresponding to the form similar to Donkin’s type, and a “Sippe nº 3”, which combines specimens with broader valves with relatively coarser lineolae and that live in the same brackish water conditions. Both “Sippen” are found in the type slide of *N. gregaria* (Lange-Bertalot, 2001). He later elevated “Sippe nº 3” to the rank of species, as *Navicula supergregaria* Lange & Rumrich (*e.g.* Lange-Bertalot, 2001) basing his decision on morphological differences (in LM), namely size-range and the more widely spaced lineolae, which is a constant morphological feature in many *Navicula* species.

Most of the specimens found in our study closely conform to *N. supergregaria* morphological features but it was decided not to identify them as *N. supergregaria*. The reasons for this decision are threefold: Firstly, SEM observations of several valve exteriors and interiors failed to encounter any differences to the ultrastructure description given in Cox (1995), as attested by the differential diagnosis to *N. phyllepta*, given above. This was also admitted by Lange-Bertalot (2001), when comparing the outer surface of the valves of both taxa. Secondly, a smaller and more finely punctuated morphotype (m.2, see below) was also found and co-occurred with the larger form in several samples. This morphotype conforms better to the type of *N. gregaria* (“Sippe nº1”, *sensu* Lange-Bertalot 2001) but, apparently, has the same ecology. Thirdly, some specimens had smaller valves but retained the distinctly punctuated striae, thus having an intermediate form between both morphotypes. Our morphotype 1 (m.1) has therefore, a wider morphological range (see above) than the one given in the diagnosis of *N. supergregaria* by Lange-Bertalot (*e.g.* striae, 13-15/10 µm; lineolae, 24-27/10 µm).

It is most possible that both morphotypes have also differences at the molecular level and they are actually different (*i.e.* not conspecific) taxa but, in view of the apparently similar ecological preferences, further studies are needed. However, since we could not effectively distinguish, in all confidence, between the *N. supergregaria*-like specimens and the ones more close to *N. gregaria s.s. sensu* Lange-Bertalot, it was decided to establish these two morphotypes of *N. gregaria*, where only the specimens with unmistakably denser lineolae (*i.e.* > 30 in 10 µm) were placed in morphotype 2 (see below).

Distribution & Ecology: *Navicula gregaria* is a cosmopolitan, motile epipelic species. It is one of the most common diatoms in Europe (Krammer & Lange-Bertalot 1986). It is euryhaline and mesohalobic and it is frequently encountered in samples from brackish water with silty sediments (Sabbe 1997, Witkowski *et al.* 2000). The formal distinction between both forms is quite recent and it is still not reflected frequently in the bibliography. Anyway, they seem to co-occur regularly (*e.g.* Lange-Bertalot 2001, Snoeijs & Vilbaste 1994). Also in our study it was one of the most frequently found species, with 64 occurrences in 68 samples. The spatial distribution of *N. gregaria* seems to be dependent of the sediment mud content but to a lesser extent than other typical mudflat free motile epipelic species (*e.g. N. spartinetensis, C. signata*) as it can be gathered from Table 13.

As one of the most important species in the mudflat diatom assemblages, it was equally abundant in the two sandy stations with higher mud content. Conversely, it was the epipelic species with the most marked seasonality (see section 4.5), peaking invariably during spring, both in muddy and sandy stations.

Table 13 – Occurrence (%), average relative abundance (%) of *N. gregaria* m.1 and average mud content (%) per sampling station. Standard deviation given within brackets.

Station	Occurrence	Abundance	Mud content
A1	73	0.7 (0.7)	2.3 (1.0)
A2	82	3.0 (3.8)	5.4 (2.4)
A3	100	11.4 (10.2)	7.7 (3.1)
V1	100	8.8 (8.3)	13.5 (9.3)
V2	100	11.7 (9.8)	90.0 (7.3)
V3	100	13.1 (13.5)	96.5 (2.2)

References:

Archibald (1983) – pg. 167, fig. 37
Cox (1995) – figs. 37-42, 67-62
Germain (1981) – pg. 170; fig. 63/7, 157/2
Krammer & Lange-Bertalot (1986) – pg. 116; figs. 38/10-15

Hendey (1964) – fig. 36/3 (as *N. phyllepta* Kützing)
Kuylenstierna (1989-1990) – pg. 109; figs. 52/610-613, 62/779
Lange-Bertalot (2001) – pg. 85; figs. 35/7-13 (as *N. gregaria*); pg. 92; figs. 38/19-25 (as *N. supergregaria*)
Sabbe (1997) – pg. 183; figs. 21/7-8, 19, 53/3-4
Snoeijs & Vilbaste (1994) – #160
Witkowski *et al.* (2000) – pg. 280; figs. 122/8-25, 129/9, 142/4-5

Navicula gregaria Donkin 1861 **morphotype 2 (m.2)**

Micrographs: Pl. 21: 15; Pl. 48: 6-8

Similar species: as above (see *N. gregaria* m.1)

Morphometrics:
Biovolume (μm^3): 271
Frustule geometry: elliptic prism
Length (μm): 15.9 – (18.3) – 23.6 (n=6)
Width (μm): 4.2 – (4.7) – 5.1 (n=6)
Pervalvar axis (μm): 4 (estimated)
Striae in 10 μm: 20 – (22) – 25 (n=6)
Lineolae in 10 μm: 33 – (35) – 37 (n=3)

Notes: this morphotype differs from *N. gregaria* m.1 by its smaller average size, by having more bluntly rounded to subrostrate apices (*cf. N. cryptocephala*), instead of the clearly rostrate apices of morphotype 1 and by having slightly more densely spaced striae. The striae are also much more finely punctate and barely visible in the LM (*i.e.* higher than 30 in 10 μm). Conversely, no notable differences were found between morphotypes in the external valve views observed in SEM, apart from the above mentioned striae and lineolae density.
The striation pattern of this morphotype is, actually, closer to the one observed in the lectotypes and in Kützing's material (figs. 37-42, Cox 95; figs. 8-9), as well as to the specimens from "Sippe 2" *sensu* Lange-Bertalot (= "*N. gregaria* B" *sensu* Cox). However, the valve outline is somewhat different, as the specimens found in our study were less broadly lanceolate and did not have so clearly drawn out apices.

Distribution & Ecology: for the worldwide distribution of *N. gregaria* see above. This morphotype is also motile epipelic diatom. Present in 23 samples, *Navicula gregaria* m.2 occurred in all stations but it was almost absent in the samples from the first year of study (only 4 occurrences). In the second year of sampling, it was more commonly found in medium-coarse sandy muddy stations and also in one of the mudflat sites. Never very abundant (max. abundance <5.7%), it was mainly found from January 2004 to July 2004, always co-occurring with morphotype 1.

References: as above (see *N. gregaria* m.1)

Navicula cf. ***gregaria*** Donkin 1861

Micrographs: Pl. 21: 16-18

Similar species:
Navicula litoris Salah
Navicula namibica Lange-Bertalot & Rumrich in Lange-Bertalot

Morphometrics:
Biovolume (μm^3): 275
Frustule geometry: elliptic prism
Length (μm): 13.3 – (19.7) – 29.0 (n=10)
Width (μm): 4.7 – (5.9) – 9.0 (n=10)
Pervalvar axis (μm): 3 (estimated)
Striae in 10 μm: 14 – (18) – 19 (n=10)
Lineolae in 10 μm: 23 – (28) – 33 (n=9)

Description: valves lanceolate with cuneately obtuse apices. Axial area is narrow and the central area transapically expanded and asymmetrical. Raphe straight with central endings distant, expanded and straight to very slightly deflected. In the central raphe endings area (central nodule?) there is a unilaterally thickening of the accessory rib towards the larger side of the central area (primary side). The distal raphe endings are expanded and deflected to the same (primary) side, apparently followed by a deflection of the raphe fissures to the secondary side. The striae are distinctly punctate, slightly radiating at the centre and convergent towards the apices.

Notes: this taxon is closely related to *N. gregaria*, particularly to the larger punctate form (*i.e.* "*N. supergregaria* form", see above *N. gregaria* m. 1). The main differences are the lack of produced apices, less obvious central unilateral thickening of the accessory rib and of the deflection of the central raphe endings. The wide range of cell sizes found in our study seems to indicate that the apical shape was not affected by size reduction, which seems also to be the case with *N. gregaria s.s.* (see Sabbe 1997 for other references).
Navicula cf. *gregaria* completely corresponds to "*N. gregaria* f.1" described by Sabbe (1997) for the Westerschelde estuary. This author remarked the reminiscence of this taxon to *N. namibia* (see Lange-Bertalot 2001), which has straight central raphe endings and slightly protracted ends. He also pointed out the similarities to *N. litoris* but we were unable to investigate this.

Distribution & Ecology: epipelic form. Sabbe (1997) reported this very taxon as very characteristic of fine sandy sediments throughout Westerschelde estuary, thus in contrast with *N. gregaria*, typically found in more silty sediments. In our study too, this taxon was almost exclusively found in the sandy stations (20 out of 21 total occurrences) and mainly in the sandy transect. It occurred throughout the study period but it was never very abundant (max. abundance < 1.5%).

References:
Sabbe (1997) – pg. 184; 21/1-6, 53/1-2

***Navicula* cf. *microdigitoradiata* Lange-Bertalot 1993**

Micrographs: Pl. 21: 22-29

Synonyms:
Navicula cincta f. *minuta* Van Heurck

Similar species:
Navicula digitoradiata (Gregory) Ralfs *in* Pritchard
Navicula "species 4" *sensu* Lange-Bertalot (2001) = *Navicula* "species 4" *sensu* Witkowski *et al.* (2004)

Morphometrics:
Biovolume (μm^3): 194
Frustule geometry: elliptic prism
Length (μm): 12.8 – (18.1) – 30.6 (n=37)
Width (μm): 4.1 – (4.6) – 5.4 (n=37)
Pervalvar axis (μm): 3 (estimated)
Striae in 10 μm: 15 – (17) – 19 (n=37)

Description: valves lanceolate to linear lanceolate with cuneately rounded apices. Valve face is slightly curved and strongly silicified. Axial area is narrow and sometimes slightly lateral (as seen in LM), probably because of the valve curvature. Central area small and somewhat asymmetrical thanks to the uneven shortening of the central striae. Raphe is straight or slightly curved. Central raphe endings quite proximate, slightly expanded, straight or (more frequently) slightly deflected to the (secondary?) side. Both distal raphe endings are deflected to the same side as the central raphe endings. The striae strongly radiate throughout the valve but become parallel to slightly convergent near the apices. The striae are finely punctate and the lineolae are imperceptible in LM. Virgae much more strongly silicified than the vimines (as in *N. digitoradiata*).

Notes: this taxon is very reminiscent of *N. microdigitoradiata*, having the same striae pattern and density (Lange-Bertalot 2001). However, it has a narrower valve outline (seen even in larger cells) and the central raphe ends seem to be slightly more distant than in *N. microdigitoradiata.* Based on these very characters, Lange-Bertalot (2001) separated a "*Navicula* species 4" from *N. microdigitoradiata* which additionally has a higher lineolae density. Since we were unable to observe these specimens in SEM, we could not confirm if they had more widely spaced lineolae than *N. microdigitoradiata*. Moreover, the striae density given in the short diagnosis of "Navicula species 4" is 12-15 in 10/μm and, therefore, is lower than the range given in our own measurements. Although we strongly suspect this taxon is not *N. microdigitoradiata s.s.*, we could not confirm with certainty that it is "*Navicula.* species 4" *sensu* Lange-Bertalot (2001). It was decided to name these specimens *Navicula* cf. *microdigitoradiata* until further studies confirm if they are conspecific to either *N. microdigitoradiata* or to the, yet not formally described, "*Navicula* species 4" *sensu* Lange-Bertalot (2001).

Distribution & Ecology: motile epipelic species. Found mostly in sandy muddy stations but it was extremely infrequent (5 occurrences) and rare (max. abundance < 0.32%). Both *N. microdigitoradiata* and "*N.* species 4" have been reported for coastal areas, estuaries and intertidal mudflats (*e.g.* Witkowski *et al.* 2004b, Forster *et al.* 2006).

References:

Kuylenstierna (1989-1990) – pg. 106; figs. 52/599 (*Navicula cincta* f. *minuta* = *N. microdigitoradiata*)
Lange-Bertalot (2001) – pg. 49, 68; fig. 52/1-7 (*N. microdigitoradiata*), 52/8-29 (*Navicula* spec. 4)
Sabbe (1997) – pg. 187; figs. 20/4-10, 53/5-6 (*N. microdigitoradiata*)
Snoeijs & Potapova (1995) - # 257 (*N. microdigitoradiata*)
Witkowski *et al.* (2000) – pg. 290; fig. 126/1-7 (*N. microdigitoradiata*), 126/29 (*Navicula* spec.)
Witkowski *et al.* (2004) – fig. 23-26 (*Navicula* spec. 4)

Navicula* cf. *mollis (W. Smith) Cleve 1895

Micrographs: Pl. 19: 7-9

Similar species:
Navicula ramosissima (Agardh) Cleve 1895

Morphometrics:
Biovolume (μm^3): 254
Frustule geometry: elliptic prism
Length (µm): 15.7 – (20.0) – 22.7 (n=5)
Width (µm): 3.9 – (4.6) – 5.6 (n=5)
Pervalvar axis (µm): 4 (estimated)
Striae in 10 µm: 13 – (15) – 16 (n=5)

Description: valves lanceolate with cuneate apices. Valve face apparently curved into a possible shallow mantle. Axial area is narrow, central area of variable size and usually rectangular. Raphe more or less straight, central raphe endings are expanded, straight or just slightly deflected to the same side. Terminal raphe endings deflected to the same side. Striae parallel to slightly radiate at the centre and slightly convergent near the apices. The structure of the striae is indistinct in LM.

Notes: Sabbe (1997) provisionally identified specimens extremely reminiscent to ours as *Navicula* cf. *mollis*. This identification was based on a common combination of features such as size range, striae density, an almost parallel striation pattern and the hooked distal raphe fissures. However, *N. mollis* has a distinctly rounded central area and a lanceolate valve outline, whereas *Navicula* cf. *mollis sensu* Sabbe has a more linear-lanceolate valve outline. There are also differences in ecological preferences: *N. mollis* is a tube dwelling diatom (*e.g.* Hendey 1964), whereas *N.* cf. *mollis* was found in sandy sediments in the Westerschelde estuary and in our study (see below).
Other taxa are also quite similar to *N.* cf. *mollis* but have one (or more) fundamental differences: *N. tripunctata* is larger and has coarser striation; *N. recens* has distinctly radiate striae at the valve centre; *N. ramosissima*, another tube-dwelling diatom, is larger and wider, and has a striation density of 12-13 striae in 10 µm (Witkowski *et al.* 2000).

Distribution & Ecology: epipelic motile diatom, living in sandy sediments. Sabbe (1997) reported as common in fine sandy sediments of the polyhaline reaches and in the mouth of the Westerschelde estuary. In our study it was extremely infrequent (2 occurrences) and rare (max. abundance < 0.65%). It was only found in lower shore stations of the sandy transect.

References:
Sabbe (1997) – pg. 188; figs. 20/15-18; 50/4, 51/7

Navicula paeninsulae Cholnoky 1963

Micrographs: Pl. 20: 1-5; Pl. 48: 11

Similar species:
Navicula stompsii Cholnoky
Navicula schroeteri Meister
Navicula pavillardii Hustedt

Morphometrics:
Biovolume (µm^3): 4159
Frustule geometry: elliptic prism
Length (µm): 47.3 – (59.8) – 67 (n=3)
Width (µm): 11.4 – (12.7) – 14.0 (n=3)
Pervalvar axis (µm): 7 (estimated)
Striae in 10 µm: 9 (n=3)
Lineolae in 10 µm: 18 – (20) – 21 (n=3)

Description: valves lanceolate with cuneate apices. Valve face is gently curving into a shallow mantle and with a slightly depressed central area. Axial area is narrow and linear, widening gradually to a rounded, lanceolate and asymmetrically expanded central area. Raphe is straight and in LM seems to be associated to a (bright) longitudinal siliceous rib. Central raphe endings are straight or just slightly defecting in the same direction. They are rather proximate, expanded and drop-like. The distal raphe endings slightly deflect to the same side. The striae strongly radiate throughout the valve, becoming parallel very near the apices. The striae are composed by large, apically elongated areolae and separated by strongly silicified virgae. The lineolae are more or less longitudinally aligned, except at the centre, where the striae radiate more strongly and the vimines form concentric lines. The areolae near the central area are smaller, giving a pointed shape to the shorter central striae.

Notes: this species was originally described by Cholnoky (1963) in his paper on littoral marine diatoms of South Africa. To our knowledge this is the first report of this species outside the type locality. For this reason, an adapted English version of the original diagnosis in German and Latin is given in this study. The identification was also confirmed through the comparison with micrographs of the type material kindly sent by R.E.M. Archibald (Pl. 20: 1-2). As Cholnoky (1963) refers, *N. paeninsulae* is rather similar to *N. stompsii*, but the latter species has a very small central area. Both species seem to be related to *N. pavillardii.*
The relations between *N. paeninsulae* and *N. schroeteri* should also be investigated as both taxa have similar size range, striae and lineolae density, raphe systems and an asymmetrical central area. The main differences seem to be the fact that *N. schroeteri* has linear lanceolate valves and the central area is more transapically expanded.

Distribution & Ecology: motile epipelic diatom. Like other large epipelic species living in sandy sediments (*e.g. P. humerosa*, see above) it was hardly ever encountered during the cells counts (5 occurrences). It was only found in the medium-coarse sands of the lower shore stations of the sandy transect, during autumn and winter (max. abundance < 2.3%).

References:
Cholnoky (1963) – pg. 63; fig. 67

Navicula pargemina Underwood & Yallop 1994

Micrographs: Pl. 18: 17-18

Similar species:
Proschkinia bulnheimii (Grunow) Karayeva

Morphometrics:
Biovolume (µm^3): 74
Frustule geometry: elliptic prism
Length (µm): 5.3 – (8.9) – 11.9 (n=5)
Width (µm): 3.7 – (4.0) – 4.2 (n=5)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 20 – (23) – 25 (n=5)

Notes: a complete description of *N. pargemina* is given in Underwood & Yallop (1994). The valves of this small naviculoid diatom typically remain in pairs after the acid treatment; reason for it could be confused with a small *Proschkinia* species, such as *P. bulnheimii*. However, the latter species has a higher striae count and multiple girdle bands (Underwood & Yallop 1994, Witkowski *et al.* 2000).

Distribution & Ecology: this species is typically a motile epipelic diatom, being reported for intertidal mudflats in several English estuaries (*e.g.* Paterson *et al.* 1998, Underwood *et al.* 1998, Underwood & Barnett 2006) and for the Narvik Coast (Witkowski *et al.* 2000). In our study, it was rarely found (6 occurrences) and only in the muddy transect, always at extremely low abundances (max. abundance < 0.64%).

References:
Underwood & Yallop (1994) – figs. 1-14
Witkowski *et al.* (2004) – pg. 295; fig. 142/35

Navicula phyllepta Kützing 1844

Micrographs: Pl. 21: 1-5; Pl. 49: 1-3

Synonyms:
Navicula lanceolata var. *phyllepta* (Kützing) Van Heurck

Similar species:
Navicula gregaria Donkin
Navicula cryptocephala Kützing
Navicula veneta Kützing

Morphometrics:
Biovolume (µm^3): 228
Frustule geometry: elliptic prism
Length (µm): 16.8 – (21.1) – 25.3 (n=17)
Width (µm): 4.0 – (5.6) – 7.0 (n=17)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 15 – (17) – 19 (n=17)
Lineolae in 10 µm: 44 – (49) – 54 (n=17)

Notes: this species has been frequently misidentified and confused with *N. gregaria* (see above for differential diagnosis) and with *N. cryptocephala*, a freshwater species with similar size and striation pattern. For a full description consult Germain (1981), Krammer & Lange-Bertalot (1986) or Cox (1995). The latter author also compares *N. phyllepta* with similar taxa. In the Tagus estuary, *N. phyllepta* has probably been confused as well as *N. gregaria* with the similar freshwater taxon *N. cryptocephala* (see above).
These specimens correspond to lectotype of *N. phyllepta* (see figs. 32/5 in Krammer & Lange-Bertalot 1986; fig. 28 in Cox 1995) as the valves are larger, wider and have coarser striae (17/10 µm in average) than other specimens found in our study, that were smaller and had higher striae density (22/10 µm in average) and were designated *Navicula* cf. *phyllepta.* For a detailed differential diagnosis between the two morphospecies, see below.

Distribution & Ecology: motile epipelic species, usually found in muddy sediments in brackish and coastal waters (*e.g.* Witkowski *et al.* 2000, Thornton *et al.* 2002, Haubois *et al.* 2005). Probably cosmopolitan (*e.g.* Sabbe *et al.* 2003) but due to frequent misidentification the exact distribution is not known with certainty (Lange-Bertalot 2001). Additionally, there are a series of conflicting reports on spatial and temporal distribution, with maximal abundances given for estuarine areas of higher (*e.g.* Underwood *et al.* 1998, Zong & Horton 1998) or lower salinities (*e.g.* Cox 1995, Thornton *et al.* 2002). Seasonal peaks have been reported for late spring/summer (*e.g.* Sabbe 1993), winter (Gätje 1992) but *N. phyllepta* has also been considered as common throughout the year (Peletier 1996, Haubois *et al.* 2005). These discrepancies have been associated to differences in organic waste and nutrient concentrations (Peletier 1996, Thornton *et al.* 2002) and recently to different forms of the species (Créach *et al.* 2006). *Navicula phyllepta s.s.* is probably a higher salinity brackish form (Sabbe *et al.* 2004) but for further information see below (in *N.* cf. *phyllepta*).
In our study it was not very abundant (max. abundance < 1.9%) nor was it very frequent (19 occurrences). It was found equally in mudflat samples and in samples from the lower shore stations of the sandy transect. These stations had a small but consistently present mud fraction. Abundances were low and fairly constant throughout the study period.

References:
Cox (1995) – figs. 28-29, 58-61
Germain (1981) – pg. 190; fig. 72/14-18, 157/5-5a
Krammer & Lange-Bertalot (1986) – pg. 104; figs. 32/5-(9?)-11
Kuylenstierna (1989-1990) – pg. 113; figs. 55/662-664, 62/775-776
Lange-Bertalot (2001) – pg. 56; figs. 46/1-9
Riaux & Germain (1980) – pl. 2 (except figs. 1'' & 2'')
Sabbe (1997) – pg. 193; figs. 21/1-(2?)-3, 52/3
Snoeijs & Potapova (1995) – #258, Form 1
Witkowski *et al.* (2000) – pg. 280; figs. 122/1-9
Witkowski *et al.* (2004b) –figs. 1/16-18

***Navicula* cf. *phyllepta* Kützing 1844**

Micrographs: Pl. 21: 6-12; Pl. 49: 4-9

Similar species:
Navicula phylleptosoma Lange-Bertalot *in* Lange-Bertalot & Genkal
Navicula salinarum Giffen (= *N. pseudosalinarioides* in Witkowski *et al.* 2000)

Morphometrics:
Biovolume (µm^3): 137
Frustule geometry: elliptic prism
Length (µm): 9.6 – (15.7) – 21.4 (n=60)
Width (µm): 3.5 – (4.5) – 7.0 (n=60)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 17 – (21) – 25 (n=60)
Lineolae in 10 µm: 44 – (49) – 54 (n=13)

Description: valves lanceolate, apices are cuneate or they are slightly produced and subrostrate. Axial area is narrow, slightly widening at the centre and externally thickened (SEM). Central area is very small, rounded and almost imperceptible in LM. Raphe is straight, central raphe endings are straight, slightly expanded and proximate. Internally, the central raphe endings are almost contiguous, placed at the centre of a boarder thickening of the raphe rib and facing the valve interior (as in *N. phyllepta*). The longitudinal siliceous additional rib, lying, beside the raphe, reduces its thickness near the central nodule and merges with the virgae at the apices. The distal raphe ends are turned towards the same (secondary) side and, internally, have helictoglossae. The striae slightly radiate in the centre and are parallel to slightly convergent in the apices. The striae are finely punctate and composed by slit-like lineolae, elongated apically.

Notes: this taxon has several features in common to *N. phyllepta s.s.*, *N. phylleptosoma* and *N. pseudosalinarum*. All of them have the same striation pattern, similar valve outlines and also have an externally raised sternum in the central nodule area, a feature also present in *N. cryptocephala*. Size range and striae and lineolae density are comparable to *N. phylleptosoma* (*viz.* Lange-Bertalot, 2001) but the overall ultrastructural appearance agrees more with the description and illustrations of *N. phyllepta s.s.* given in Cox (1995). Namely, the apically elongated lineolae and external raphe features look very similar to the ones depicted in this work. There is, however, one main character that separates the specimens found in our study from both *N. phyllepta s.s.* and *N. phylleptosoma*: the minuteness of the central area. This makes the combination of features in this taxon quite unique and easily distinguishable, even in LM.

A small parenthesis regarding the descriptions and illustrations of *N. phyllepta* and *N. phylleptosoma*, given in Cox (1995) and in Lange-Bertalot (2001), should be added: the SEM external views do not totally agree, as the central raphe fissures are slightly deflected to one side in the latter work and are almost straight in the former. Moreover, this feature was used by Lange-Bertalot (2001) do discriminate between *N. phyllepta* and *N. phylleptosoma*. In our opinion, the distinction between the two taxa needs to be better clarified, as well as the ecological status of *N. phylleptosoma.* It should be noted that *N. phylleptosoma*, although initially reported for Eurasian continental and desert salt-springs (Lange-Bertalot, 2001), has been increasingly referred for brackish coastal areas, such as salt marshes and intertidal flats (Witkowski *et al.* 2000, Lange-Bertalot, 2001), and seem to be especially abundant during winter (Witkowski *et al.* 2004).

Our specimens fully correspond, both morphologically and ecologically, to a pseudocryptic species of *N. phyllepta* found in the Westerschelde estuary and studied by Sabbe *et al.* (2004b), Créach *et al.* (2006) and, particularly, by Vanelslander *et al.* (2009a). Theses authors describe two clusters of strains of *N. phyllepta* that are molecular, morphological (*i.e.* size, valve width and striae density) and ecophysiologically distinct. One corresponds morphologically to *N. phyllepta s.s.* (see above) and has higher growth rates in higher salinities, being is particularly common in the polyhaline reaches of the estuary. The other one, precisely similar to *N.* cf. *phyllepta*, as described here has higher growth rates at lower salinities and is more abundant in the oligohaline reaches of the Westerschelde estuary. The morphological differences between *N. phyllepta* and *N.* cf. *phyllepta* found in our study can be clearly attested in the following plot (Figure 26) and confirm the results presented by Sabbe *et al.* (2004b) and Vanelslander *et al.* (2009a):

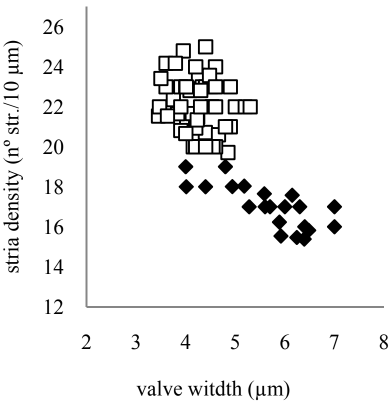

Figure 26 – Transapical striae density *vs.* valve width of *N. phyllepta* (♦) and *N.* cf. *phyllepta* (□).

Regarding the ill-known species *N. salinarum*, the main difference to the other similar taxa seem to be the higher valve width (7-9 µm) and length (24-35 µm), since the striae density is around 20 in 10 µm (Giffen 1975; Witkowski *et al.* 2000, where it is wrongly referred as *N. pseudosalinarioides* Giffen in pg. 300). Whether they correspond to the upper size limit of *N.* cf. *phyllepta* or *N. phylleptosoma* or, indeed to an independent species needs further study.

Therefore it was decided to name provisionally the taxon described here as *Navicula* cf. *phyllepta* but its relations to *N. phylleptosoma*, *N.* cf. *phyllepta sensu* Witkowski *et al.* (2004) and the taxa found in the Westerschelde estuary need to be further studied.

Distribution & Ecology: small motile epipelic diatom found mainly in mudflats. In our study, it was one of the most frequently found diatoms (57 occurrences in 68 samples), especially abundant in the mudflat stations, but also occurring in the sandy muddy stations.

We came to the conclusion that this taxon is the same as the semicryptic morphospecies of *N. phyllepta*, described for the oligohaline reaches in the Westerschelde estuary (see above) and that its ecological preference for lower salinities (Sabbe 1997, Sabbe *et al.* 2004b, Créach *et al.* 2006, Vanelslander *et al.* 2009a) may explain its rather peculiar temporal variation during period of our study. *Navicula* cf. *phyllepta* completely dominated the assemblages in the muddy transect in January and March 2003 (relative abundances up to 68%). The abundances were also high in the all sandy transect stations during those sampling periods (relative abundances: 6-8%), particularly when compared to the rest of the study period (relative abundances 0-2%). This initial dominance, in all sediment types, can only be explained by the low salinities observed during the particularly rainy winter of 2002/2003 (see Fig. 5, section 2.2.1). The numbers dropped with the salinity rise in spring and summer but, when the salinity decreased again in November 2003 the numbers of this taxon increased. However, this peak in numbers was not as important in the preceding winter, probably because the salinities did not drop to 10 psu, as in the preceding winter. Probably due to the fact that it lives mainly in the oligohaline reaches of the Westerschelde estuary, *N.* cf. *phyllepta* had different seasonal pattern from what was observed in the polyhaline sites of the Tagus estuary (this study): it peaks in late spring (Sabbe 1997, Créach *et al.* 2006), when the salinity rises in oligohaline areas of the Westerschelde.

References:

Riaux & Germain (1980) – 2/1''-2''
Sabbe (1997) – pg. 193; figs. 21/(2?)
Snoeijs & Potapova (1995) – #258, Form 2
Vanelslander *et al.* (2009a) – fig. 4A

Witkowski *et al.* (2004b) –figs. 1/11-12, 13-15(?)

Navicula platyventris Meister 1935

Micrographs: Pl. 18: 53-55; Pl. 48: 9-10

Similar species:
Navicula perrhombus Hustedt *ex* Simonsen
Navicula rhaphoneis (Ehrenberg) Kützing

Morphometrics:
Biovolume (µm^3): 172
Frustule geometry: elliptic prism
Length (µm): 10.0 – (12.4) – 15.0 (n=7)
Width (µm): 5.4 – (5.9) – 6.4 (n=7)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 10 – (11) – 12 (n=7)
Lineolae in 10 µm: 24 – (26) – 29 (n=5)

Notes: a description of *N. platyventris* can be found in Witkowski *et al.* (2000). It has some similarities to *N. perrhombus* but this species has usually rhombic valves with acute apices and not elliptic ones with capitate, produced apices. *Navicula rhaphoneis* (see Archibald 1983, pg. 198) has a similar valve outline to the taxon found in the Tagus but it is most probably conspecific to *N. perrhombus*, according to the same author.
The main differences to either *N. perrhombus* or to *N. rhaphoneis* is that the frustules are smaller and the striae have more densely packed lineolae than in *N. platyventris*. Additionally, the virgae seem much more developed, clearly delimitating each stria, in *N. perrhombus*. Finally, the SEM micrographs of our specimens correspond perfectly with the ones illustrated in Witkowski *et al.* (1998), although the valvocopulae with short outgrowths could not be confirmed. The shape and structure of the raphe and of the lineolae, and the semi circle of areolae in the apical margin may indicate a close relation with the group around *N. viminoides*.
Navicula aff. *perrhombus* (pl. 143/21-23, Witkowski *et al.* 2000) is also very reminiscent of the specimens found in our study, given the size and the presence of the capitate apices. However, the lineolae density (around 24/10 µm) and the heavily silicified virgae are similar to *N. perrhombus s.s.*

Distribution & Ecology: this taxon is mainly found in warm waters of tropical sea coasts, where it has been reported as a member of the periphyton in mangroves, saltmarshes and saltwater cenotes (*e.g.* Fernandes *et al.* 1999, Chen *et al.* 2005). It was never reported for the European coast, with the exception of the Mediterranean (Witkowski *et al.* 2000). In our samples it was almost exclusively found in the medium-coarse sandy stations, where it was probably a small motile epipsammic species. In the sandy stations, it was quite frequently found (24 occurrences) it was never abundant (max. abundance <1.6%).

References:
Witkowski *et al.* (1998) – 77-78
Witkowski *et al.* (2000) – pg. 299; figs. 143/16-19

Navicula recens (Lange-Bertalot) Lange-Bertalot 1985

Micrographs: Pl. 19: 10-11; Pl. 48: 12-13

Synonyms:
Navicula cari var. *recens* Lange-Bertalot

Similar species:
Navicula arenaria Donkin
Navicula cari Ehrenberg

Morphometrics:
Biovolume (µm^3): 1218
Frustule geometry: elliptic prism
Length (µm):34.8 – (38.8) – 48.3 (n=6)
Width (µm): 7.5 – (8.0) – 8.5 (n=6)
Pervalvar axis (µm): 5 (estimated)
Striae in 10 µm: 11 – (11) – 12 (n=6)
Lineolae in 10 µm: 29 – (30) – 32 (n=6)

Notes: we believe that our specimens correspond to *N. recens*, one of the many (linear)-lanceolate *Navicula* species with cuneate ends and striae that radiate at the centre, becoming parallel to convergent towards apices. The morphometric data is completely consistent with the author's description (*in* Kramer & Lange-Bertalot 1986, Lange-Bertalot 2001) and to other published reports of this taxon (*e.g.* Fukushima *et al.* 1990). The relations with similar taxa are discussed in Krammer & Lange-Bertalot (1986) and Lange-Bertalot (2001). Our SEM micrographs confirm its appurtenance to the group around *N. tripunctata*, namely due to the fact that the raphe-sternum is not raised externally (Cox 1979), as in *N. cari* for example. *Navicula mollis* seems also to be a close species but it has a higher striation density and is a tube-dwelling diatom.

Life form & Ecology: *Navicula recens* is an epipelic, cosmopolitan species, found mainly in brackish-waters and freshwaters with high electrolyte content (Kramer & Lange-Bertalot 1986, Witkowski *et al.* 2000). According to Lange-Bertalot (2001) it is a pollution tolerant species, living even in critical levels (β-α-meso-saprobic). In our study, it was extremely rare, with only two occurrences and at very low abundances (max. abundance < 0.63%).

References:

Fukushima *et al.* (1990) – figs. 1-6
Krammer & Lange-Bertalot (1986) – pg. 95; figs. 27/7-11
Lange-Bertalot (2001) – pg. 62; figs. 1/16-22
Witkowski *et al.* (2000) – pg. 301; figs. 142/28-31

Navicula spartinetensis Sullivan & Reimer 1975

Micrographs: Pl. 22: 1-23; Pl. 49: 10-13

Similar species:

Navicula flanatica Grunow
Navicula ammophila Grunow *sensu* Archibald (1983)
Navicula peregrinoides Muzafarov

Morphometrics:

Biovolume (µm^3): 299
Frustule geometry: elliptic prism
Length (µm): 17.4 – (25.9) – 35.0 (n=120)
Width (µm): 2.6 – (4.9) – 5.2 (n=120)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 13 – (15) – 17 (n=121)
Lineolae in 10 µm: 20 – (25) – 30 (n=114)

Notes: Witkowski (unpublished data) compared *N. spartinetensis* with similar taxa and concluded that it is indubitably an independent species. The true identity of *N. flanatica* is not yet clearly sorted out, but *N. spartinetensis* is clearly different from Grunow's original concept of *N. flanatica* as well as from the slightly different Hustedt's (1939) concept of the same taxon. *Navicula flanatica sensu* Hustedt has been widely followed by later authors (*e.g.* Brockman 1950, Hendey 1964, Krammer & Lange-Bertalot 1986, Sabbe 1997 and Witkowski *et al.* 2000). The differences to *N. flanatica sensu* Hustedt are a smaller average size, with less broader valves that lack slightly protracted apices and a higher striae density (11-15 striae in 10 µm, instead of 9-11 striae/10 µm in *N. flanatica*). Additionally, the central striae, immediately opposite to the central nodule are usually much shorter in *N. flanatica* (Hendey 1964).

Distribution & Ecology: *Navicula spartinetensis* is an epipelic species originally described as an edaphic diatom, living under the canopy of *Spartina alterniflora* Liosel, in a saltmarsh from the East Coast of the United States (Sullivan & Reimer 1975). Only recently, Witkowski *et al.* (2004) reported *N. spartinetensis* for an intertidal mudflat in Dangast (German North Sea Coast) followed by a subsequent finding by Méléder *et al.* (2007) in intertidal flats in Bourgneuf Bay (French Atlantic Coast).
This 30 years hiatus between published reports and the surprisingly recent discovery of an abundant species in the European Atlantic intertidal coasts led Witkowski (unpublished data) to review most of the floristic and ecological studies conducted in European and North American coasts, as well as to examine collection slides (*e.g.* Brockmann 1950, König 1959, Hendey 1977) and slides from material collected in recent studies in European coasts. He came to three surprising conclusions:

- *N. spartinetensis* is currently one of the most commonly found epipelic species in European Atlantic coasts, appearing exclusively in intertidal muddy sediments. It is apparently rarer in Danish, German and Dutch North Sea coasts and in the French coast of the English Channel, becoming increasingly more abundant in the French Atlantic coast and in the Tagus estuary (our study).

- This taxon is not present (*i.e.* illustrated) in any "classical" floristic study from the Wadden Sea (*e.g.* Hustedt 1939; Brockmann 1955), the Dutch and English North Sea coasts (*e.g.* Aleem 1950, Salah 1952, 1955, Hendey 1964, Sabbe 1997) prior to Witkowski *et al.* (2004). The absence *N. spartinetensis* in the well studied Baltic Sea is likely due to the lower salinities found there and also the lack of tidal flushing.
- *N. spartinetensis* was found in a slide from König's collection with material from a tidal flat form the Gulf of Arcachon (France) sampled in 1957, that is, almost 20 years before the formal description!

The historical presence of this taxon in the European coasts could not be completely assessed by Witkowski (unpublished data) as most ecological studies only include a species list and *N. spartinetensis* may have been wrongly identified as *N. flanatica*, *N.* cf. *flanatica* or placed in the *Navicula* spp. group, the fact remained undetected for so many years cannot be yet completely explained. As for North America, it was only detected again in slides of San Francisco Bay, from Hanna's collection (Witkowski, unpublished data), probably as a reflection on an even smaller number of floristic studies of saltmarsh and intertidal flats floras.

The biogeographical distribution of this species remains, therefore uncertain and is an excellent example of how the lack of floristic studies, illustrations in published ecological works and eventual force fitting in identifications hinders the study of the worldwide distribution and autoecology of marine benthic diatoms.

Navicula spartinetensis was one of the most common species found in our study, with 55 occurrences in 68 samples, it is one of the finest examples of how some epipelic species seem to be positively correlated to the sediment's mud content, as it can be seen in Table 14:

Table 14 – Occurrence (%), average relative abundance (%) of *N. spartinetensis* and average mud content (%) per sampling station. Standard deviation given within brackets.

Station	Occurrences	Abundances	Mud content
A1	27	0.1 (0.2)	2.3 (1.0)
A2	55	0.3 (0.3)	5.4 (2.4)
A3	100	1.6 (1.5)	7.7 (3.1)
V1	100	4.3 (3.3)	13.5 (9.3)
V2	100	25.0 (18.1)	90.0 (7.3)
V3	100	17.5 (7.0)	96.5 (2.2)

It was one of the most important components of the mudflats diatom flora but it was also relatively common in the sandy stations with higher mud content. Like other motile epipelic species, *N. spartinetensis* showed a marked seasonality. Although it was frequently found throughout all the study period, it was particularly common during summers, when it reached the maximal abundance (65% in V2). *Navicula flanatica*, to which it can be easily confused (see above), is known to reach its abundance peak during late winter-early spring (*e.g.* Admiraal *et al.* 1984, Sabbe 1997).

These observations differ from the original ecological parameters taken by Sullivan & Reimer (1975), when first described this species, which reported as particularly abundant during the cold winter months on a Delawarean saltmarsh (USA). It is more in accordance with other reports for European tidal flats (Méléder *et al.* 2007, Witkowski *et al.* 2004) where it occurred also throughout the year and peaked in abundance in spring and summer. It should be noticed that, as reported by Méléder *et al.* (2007), *N. spartinetensis* is not completely limited to strictly muddy sediments, but it can also occur (in lower abundances) in sandy muddy intertidal flats.

References:

Méléder *et al.* (2007) – S1/f

Sullivan & Reimer (1975b) – pg. 118; figs. 1/3, 2/3

Witkowski *et al.* (2004b) – fig. 21-22

Navicula viminoides **Giffen ssp.** ***cosmomarina*** Lange-Bertalot, Witkowski, Bogaczewicz-Adamczak & Zgrundo 2003

Micrographs: Pl. 18: 36-38; Pl. 47: 7-9

Synonyms:
Navicula viminoides Giffen *sensu* auct. nonnull.

Similar species:
Navicula viminoides Giffen ssp. *viminoides*

Morphometrics:
Biovolume (µm^3): 96
Frustule geometry: elliptic prism
Length (µm): 6.7 – (10.3) – 15.3 (n=19)
Width (µm): 3.9 – (4.8) – 5.4 (n=19)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 13 – (15) – 17 (n=18)
Lineolae in 10 µm: 15 – (22) – 26 (n=14)

Notes: the specimens found in our study fully correspond to *N. viminoides* ssp. *cosmomarina*, described by Lange-Bertalot and colleagues (2003). According to these authors, this subspecies differs from ssp. *viminoides*, described by Giffen (1975), on several features that warrant a ssp. status, at least until the type of nominate subspecies is found and studied. Basing their comparison on the detailed protocol given by Giffen, the authors considered that spp. *cosmomarina* has an elliptic-lanceolate valve shape (and not simply elliptical), raphe central endings that are more widely spaced, it possesses a distinct central area and striae with higher lineolae density and converging near the apices. The study of the type material of *N. viminoides* and its comparison to the ssp. *cosmomarina*, as well as to *N. viminea* Hustedt, will determine to which taxon it is more closely related, if ssp. *cosmomarina* merits the rank of an independent species or, by the contrary, if these taxa are conspecific.

It seems clear that *N. viminoides* ssp. *cosmomarina* is rather closely related to *N. aleksandrae, N. bozenae* and to *N. paulschulzii* (see above), as in our own observations (see above), as well as the illustrations of these taxa in Lange-Bertalot *et al.* (2003) demonstrate. All these species seem to have the same kind of raphe system with similar central and distal endings and helictoglossa, the same type of slightly elongate hymenate lineolae and all of them have a semi-circle of marginal areolae in the apices. *Navicula viminoides* ssp. *cosmomarina* distinguishes from these taxa by the distinctly punctate striae and by the raphe-sternum that is better developed externally, particularly in the centre. *Navicula germanopolonica* does not have any of these features, with the exception of the punctate striae.

N. viminoides ssp. *cosmomarina* has been recurrently found and identified as *N. viminoides*, particularly in the Baltic Sea sandy sediments (*e.g.* Snoeijs & Potapova 1995, Witkowski *et al.* 2000, Lange-Bertalot 2003). Sabbe (1997) encountered this species in the Westerschelde estuary and also separated it from *N. viminoides sensu* Giffen (1975) and also from *N. germanopolonica*. He named it *Navicula* sp.7, given its higher striae density and slightly different central area than *N. viminoides sensu* Giffen, which is “distinctly circular”.

Distribution & Ecology: *Navicula viminoides* ssp. *cosmomarina* has been reported for the Baltic Sea and the Mississippi delta (*e.g.* Witkowski *et al.* 2000) and also for the fine sandy to very fine sandy sediments in the mesohaline reaches of the Westerschelde estuary (Sabbe 1997). It is a small motile epipsammic species that was very frequently found during our study (46 occurrences). It was almost exclusively found in the sandy stations, particularly in the upper shore medium-fine sandy station of the sandy transect, where it reached the highest abundances (max. abundance <23.4%).

References:
Lange-Bertalot *et al.* (2003) – pg. 265; figs. 65-77
Sabbe (1997) – pg. 200; figs. 18/20-21, 52/4
Snoeijs & Potapova (1995) – # 261
Witkowski *et al.* (2000) – pg. 315; figs. 136/27-33, 141/13-15

Navicula **sp.1**

Micrographs: Pl. 20: 6-7

Similar species:
Navicula abscondita Hustedt

Morphometrics:
Biovolume (µm^3): 258
Frustule geometry: elliptic prism
Length (µm): 17.8 – (19.5) – 21.1 (n=4)
Width (µm): 4.4 – (4.8) – 5.0 (n=4)
Pervalvar axis (µm): 4 (estimated)
Striae in 10 µm: 17 – (19) – 20 (n=4)

Description: valves lanceolate, apparently slightly silicified, with a very flat valve face and cuneate apices. Axial and central areas narrow. Raphe straight, raphe-sternum very distinct, with distal and central nodules pronounced. Central raphe endings close together and expanded. Striae parallel throughout the valve or very slightly radiate in the centre and slightly convergent near the apices. The striae are irresolvable in LM.

Notes: this taxon corresponds to *Navicula* sp.8, described and illustrated by Sabbe (1997). As this author explains, this taxon was also illustrated by Simonsen (1987, figs. 378/11-15) where it was wrongly considered as the lectotype of *Navicula abscondita* Hustedt. Although they are both very similar, *Navicula* sp.8 has a higher striation density and lack the small and rounded central area. It therefore does not correspond to Hustedt's (1939) protologue and illustrations of *N. abscondita*, nor to the other specimens shown by Simonsen (1987, figs. 378/16-17) as types of that species.

Distribution & Ecology: to our knowledge this taxon was only found by Simonsen (1987) in a Hustedt's slide from silty sediments of the East Frisian Memmert Island littoral (German Bight coast) and by Sabbe (1997) in different sediment type on mesohaline reaches of the Westerschelde estuary. In our study it also appeared in muddy and sandy sediments, being extremely rare (4 occurrences and max. abundance < 0.58%). It is most probably an epipelic species.

References:
Sabbe (1997) – pg. 201; figs. 21/9-10 (as *Navicula* sp. 8)
Simonsen (1987) – figs. 378/11-15 (as *N. abscondita*)

***Navicula* sp.2**

Micrographs: Pl. 18: 32-35

Similar species:
Navicula biskanterae Hustedt
Navicula paul-schulzii Witkowski & Lange-Bertalot

Morphometrics:
Biovolume (µm^3): 74
Frustule geometry: elliptic prism
Length (µm): 5.3 – (9.3) – 11.9 (n=7)
Width (µm): 3.7 – (4.2) – 4.4 (n=7)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 20 – (23) – 25 (n=7)

Description: valves elliptic or elliptic-lanceolate with slightly produced, cuneately rounded apices. Axial area is narrow and central area small and variable in shape. Central raphe endings expanded and seem to be rather distant. Most specimens exhibited a peculiar striation pattern: the secondary side has parallel striation, whereas in the primary side the striae in the middle radiate and are almost parallel near the apices. In the primary side, the central area is slightly wider and the striae radiate pattern seems to be caused by the shortening of one of the central striae. The striae are composed by densely packed lineolae, irresolvable in LM.

Notes: apart from the consistently asymmetrical striation pattern, this taxon is very reminiscent of *N. paul-schulzii* and of *N. biskanterae*, given they all have similar size range, striae density and valve outline.
The relations between *N. biskanterae* and *N. paul-schulzii* are quite problematic and warrant further study. Besides the size range (where there is great overlap), minor differences in other features such as valve outline, striation pattern near the apices and the shape of the central area and of the central raphe ends have been used to separate these two species (Witkowski 1994, Witkowski *et al.* 2000, Lange-Bertalot *et al.* 2003).
In the protologue, Hustedt (1939) described *N. biskanterae*, as "elliptically to broadly elliptic-lanceolate with blunt rounded, not produced ends" and having striae that radiate slightly in the middle, becoming parallel

near the ends. His illustrations (Hustedt 1939, 1961-1966) only show elliptical valves with an almost imperceptible radiate striation pattern. Witkowski (1990) described *N. paul-schulzii*, in its protologue, as having lanceolate valves with acutely rounded ends and striae that distinctly radiate throughout the valve. Conversely, Simonsen's (1987) lectotype specimens of *N. biskanterae* have distinctly radiate striae, some of them also have slightly produced apices (Plate 379/18-19) and could be easily identified as *N. paul-schulzii.* There were no marked specimens in the slides with material from localities referred in Hustedt's protologue and Simonsen (1987) had to select one slide from Memmert as the lectotype. Therefore, the true identity still remains unclear as SEM studies on the types of *N. biskanterae* were not yet conducted to unravel its identity (Gaul *et al.* 1993, Henderson & Reimer 2003).

There are also some issues regarding *N. paul-schulzii* that need to be clarified. Witkowski (1994), in the description of SEM external valve views, refers the expanded central raphe endings as an important feature and later describes them as "distant", in opposition to the "approximate central endings" of *N. biskanterae* (Witkowski *et al.* 2000). However, in the comparison of both taxa made by Lange-Bertalot *et al.* (2003), it is the central pores of *N. paul-schulzii* that are described as "close-standing", being this feature used to separate the two taxa.

The true identity of *N. biskanterae* needs, therefore, to be assessed. If Simonsen lectotypification is confirmed, perhaps both taxa should be synonymised. If not, the differences between *N. paul-schulzii* and *N. biskanterae* can hereafter be more easily clarified.

We could not allocate, with absolute certainty, the specimens found in our samples to either one of these two taxa. But they seem to have more features in common with *N. paul-schulzii*, as illustrated in Lange-Bertalot *et al.* (2003) or Witkowski (1994) than with the specimens of *N. biskanterae* illustrated and described by Hustedt (1939, 1961-1966). The bizarre asymmetrical striation pattern does not seem sufficient to warrant a new species status to our specimens. The possibility that the specimens are only morpho- or ecotypes of one of the above-mentioned species is a more likely assumption. However, without SEM observations that would allow close comparison of morphological features, a positive identification cannot be confirmed.

Distribution & Ecology: Hustedt (1961-1966) considered *N. biskanterae* to be a marine species found frequently in (sandy) sediments of the North Sea German coast. As for *N. paul-schulzii,* is was reported as widespread in the Baltic sea (Witkowski *et al.* 2000), particularly in sandy sediments (Kuylenstierna 1989-1990, as *Navicula* sp.D; Lange-Bertalot *et al.* 2003). In our study, *Navicula* sp.2 appeared exclusively in the medium-coarse sandy sediments, particularly in the lower shore stations of the sandy transect (22 occurrences, max. abundance < 2.5%).

Navicula sp.3

Micrographs: Pl. 20: 8-10; Pl. 46: 14

Similar species:
Navicula flagellifera Hustedt

Morphometrics:
Biovolume (µm^3): 675
Frustule geometry: elliptic prism
Length (µm): 21.4 – (32.3) – 44.8 (n=23)
Width (µm): 4.3– (6.7) – 8.1 (n=22)
Pervalvar axis (µm): 4 (estimated)
Striae in 10 µm: 16 – (17) – 19 (n=24)
Lineolae in 10 µm: 47 – (53) – 58 (n=8)

Description: valves lanceolate with slightly produced rostrate apices. Valve face flat, curving abruptly into the mantle. Axial area is very narrow and the central area small. Raphe is almost straight, with pronounced distal and central nodules. Raphe-sternum slightly expanded in the centre, with central raphe fissures distinctly interrupted and facing the secondary side of the valve. In addition, a thick accessory rib runs alongside the raphe sternum. Central raphe endings approximate and expanded, drop-like and externally turning to the secondary side; distal raphe endings clearly bent towards the secondary side and with helictoglossae. Striae parallel throughout the valve or very slightly radiate in the centre and slightly convergent near the apices. The striae show a faint undulating pattern, especially in the middle of the valve and are irresolvable in LM.

Notes: this taxon shows many similarities to *N. flagellifera*, as it is described and illustrated in Hustedt (1939), Simonsen (1987) and Witkowski *et al.* (2000). However there are some fundamental differences: the apices are not raised (compare with figs. 69-70 in Witkowski *et al.* 1998) and the central area is much smaller and not distinctly rounded. Finally, even though the striae have a similar structure with the virgae more strongly silicified than the vimines, the density of the lineolae is much higher in *Navicula* sp.3 (approximately 50 in 10 µm and not circa 30 in 10 µm, as in *N. flagellifera*). *Navicula* sp.3 is also somewhat similar to *Navicula abscondita* (see above) but it has a slightly finer striation than that taxon and it has a less distinct central area.

Distribution & Ecology: epipelic species. In our study this species was quite frequent (26 occurrences) and it was mainly found in the muddy transect. Although more abundant in the mudflat stations, it occurred also in upper shore sandy station of the muddy transect, lower shore station of the sandy transect, that is, in sandy sediment with highest fractions of mud. This species showed a marked seasonality, mainly occurring during late summer and early autumn, when it reached the maximal abundance in the mudflat stations (12.4 %).

Navicula sp.4

Micrographs: Pl. 21: 19-21

Similar species:
Navicula cryptocephala Kützing
Navicula phyllepta Kützing
Navicula veneta Kützing

Morphometrics:
Biovolume (µm^3): 169
Frustule geometry: elliptic prism
Length (µm): 12.3 – (16.5) – 21 (n=6)
Width (µm): 3.4 – (4.3) – 5.0 (n=6)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 17 – (19) – 21 (n=6)

Description: valves lanceolate, with rounded, cuneate apices to very slightly produced and subrostrate. Axial area is narrow but central area is quite expanded transapically, butterfly-shaped and very slightly asymmetrical. In LM it gives the impression of being heavily silicified internally. Raphe is straight, central raphe endings are straight, slightly expanded and more or less proximate. The distal raphe ends are turned towards the same (secondary) side. The striae radiate throughout the valve but become parallel to slightly convergent near the apices. The striae are finely punctate and the lineolae are imperceptible in LM. A Voigt's discontinuity is usually present in the secondary side.

Notes: this taxon is similar to *N. cryptocephala* and allied species (Cox 1995, Lange-Bertalot 2001). In this group of species the valves have a moderately large central area, striae (composed by densely packed lineolae) radiating at the centre of the valve and converging at the apices. Some specimens were actually quite reminiscent to the brackish water species *N. veneta*, but they have slightly higher striae density, while others have more cuneate ends (as in *N. phyllepta*). Therefore, they do not correspond completely to any above-mentioned species. Additionally, there is a most remarkable and unique feature, which is the very bright and heavily silicified central area, not seen in other similar species. Whether this warrants a separation of from similar taxa needs further study, namely SEM studies.

Distribution & Ecology: motile epipelic diatom. This taxon was quite rare (12 occurrences) appearing mainly in mudflat samples and usually at very low abundances. It showed a strong temporal variability as its abundance numbers peaked (max. abundance < 2.6%) in the spring of both study years.

Eolimna Lange-Bertalot & Schiller 1997

Genus description: Schiller & Lange-Bertalot (1997)

Eolimna minima (Grunow *in* Van Heurck) Lange-Bertalot 1998

Micrographs: Pl. 12: 18

Synonyms:
Navicula minima Grunow *in* Van Heurck
Navicula atomoides Grunow *in* Van Heurck

Similar species:
Psammothidium subatomoides (Hustedt) Bukhtiyarova & Round
Sellaphora seminulum (Grunow) Mann

Morphometrics:
Biovolume (μm^3): 62
Frustule geometry: elliptic prism
Length (μm): 5.9 – (7.6) – 9.3 (n=8)
Width (μm): 2.9 – (3.4) – 4.6 (n=8)
Pervalvar axis (μm): 3 (estimated)
Striae in 10 μm: 25 – (29) – 34 (n=8)

Notes: only a few valves were found during our study and only in two samples, collected in the beginning of the survey (January and March 2003). These specimens were very reminiscent of *Eolimna minima*, with their small elliptical valves, fine striation and a large, rectangular, central area, bordered by very short striae. Given the size range the variety *atomoides* [syn. *Navicula minima* var. *atomoides* (Grunow in Van Heurck) Cleve] seem to be the form present in our sample. Additional SEM studies are necessary to positively confirm this identification.
E. minima is a cosmopolitan, freshwater species, considered to be mainly epilithic and aerophilic being found abundantly in rocky seepage areas (Germain 1981; Krammer & Lange-Bertalot, 1996). It is a eutrophic species usually associated to α-meso and polysaprobic conditions (*i.e.* high organic content and low oxygen). Considering its ecology, the valves encountered in our study were almost certainly washed in from nearby freshwater areas, during the exceptionally wet winter season of 2003. Therefore, it is probably allochtonous.

References:
Germain (1981) – pg. 232; figs. 85/41, 158/7
Krammer & Lange-Bertalot – 229; figs. 76/39-47

Fam. Plagiotropidaceae Mann

Plagiotropis Pfitzer 1871

Genus description: Paddock (1988), Round *et al.* (1990)

Plagiotropis vanheurckii Grunow *in* Van Heurck 1883

Micrographs: Pl. 26: 1-3; Pl. 50: 1-5

Synonyms:
Amphiprora vanheurckii (Grunow *in* Van Heurck) Pelletan
Tropidoneis vanheurckii (Grunow *in* Van Heurck) Cleve
Amphoropsis vanheurckii (Grunow) Mereschkowsky

Similar species:
Plagiotropis tayrecta Paddock
Plagiotropis vitrea (Smith) Kuntze

Morphometrics:
Biovolume (μm^3): 9078
Frustule geometry: prism on parallelogram
Length (μm): 28.2 – (56.6) – 69.8 (n=10)
Width (μm): 9.1 – (10.2) – 10.8 (valve mantle depth, n=3)
Pervalvar axis (μm): 20 (estimated)
Striae in 10 μm: 22 – (23) – 25 (n=7)
Punctae in 10 μm: 38 (n=3)

Notes: a detailed description of the isotypes of this taxon is given by Paddock (1988). It has been rarely observed in SEM (*e.g.* Paddock & Sims 1981, Paddock 1988, Méléder 2003). The raphe lays on top a eccentric keel and the valves are typically asymmetrical: on one side of the raphe the valve face is greater and deeper, with large hyaline margin (*i.e.* with no striae); on the other side of the raphe, the valve face is smaller, with the striae extending to the valve margin and it possesses two conspicuously arcuate lateral folds at each pole. The central and distal external raphe endings are deflected to the side with the lateral folds. *Plagiotropis vitrea* has a similar frustule architecture but the cells are larger, have coarser transverse striation and the distal raphe endings are unusually forked (Paddock 1988).

Distribution & Ecology: this species is referred as common in marine and brackish waters of North Sea coast and Baltic Sea (Witkowski *et al.* 2000). It is large motile epipelic species. In our study it was one of the most recurrently found species (41 occurrences) being present in all sampling stations (Table 15). It was particularly abundant in the sandy upshore muddy station (max. abundance < 12.5%) and during spring, late summer and autumn.

Table 15 – Occurrence (%), average relative abundance (%) of *P. vanheurckii* and average mud content (%) per sampling station. Standard deviation given within brackets.

Station	Occurrence	Abundance	Mud content
A1	36	0.1 (0.2)	2.3 (1.0)
A2	36	0.1 (0.2)	5.4 (2.4)
A3	73	0.7 (0.7)	7.7 (3.1)
V1	75	3.3 (3.6)	13.5 (9.3)
V2	73	0.7 (0.8)	90.0 (7.3)
V3	67	0.5 (0.6)	96.5 (2.2)

References:
Brockman (1950) – pg. 22
Hendey (1964) – pg. 256
Méléder (2003) – pg. vii; fig. 50 (as *P. vitrea*)
Paddock (1988) – pg. 24; figs. 1-7
Snoeijs & Kasperoviciene (1996) – #381
Witkowski *et al.* (2000) – pg. 340; figs. 174/4-5

Fam. Pleurosigmataceae Mereschkowsky

Gyrosigma Hassall 1845

Genus description: Cardinal *et al.* (1989); Round *et al.* (1990); Sterrenburg (1991a). A series of publications on systematics of *Gyrosigma* and *Pleurosigma* by Sterrenburg (*e.g.* 1990b, 1991a, 1992, 1993) and Reid & Williams (2003) should be consulted.

Gyrosigma acuminatum (Kützing) Rabenhorst 1853

Micrographs: Pl. 23: 1-5; Pl. 50: 6-7; Pl. 51: 1-2

Synonyms:
Frustulia acuminata Kützing
Gyrosigma spenceri (Quekett) Griffith & Henfrey
? *Pleurosigma acuminatum* var. *gallica* (Grunow in Van Heurck) Peragallo & Peragallo [= *Gyrosigma acuminatum* var. *gallica* (Grunow in Van Heurck) Cleve]

Similar species:
Gyrosigma attenuatum f. *hippocampus* (W. Smith) Brockmann
Gyrosigma distortum (Smith) Griffith & Henfrey
Gyrosigma enhippus (W. Smith) Sterrenburg & Ross
“Gyrosigma spenceri var. *curvula* (Grunow) Reimer 1966”
Gyrosigma wromleyi (Sullivant *in* Sullivant & Wormley) Boyer

Morphometrics:
Biovolume (µm^3): 20790
Frustule geometry: prism on parallelogram
Length (µm): 89.0 – (105.4) – 124.4 (n=10)
Width (µm): 14.6 – (15.7) – 18.4 (n=12)
Pervalvar axis (µm): 8 (estimated)
Striae in 10 µm: 20 – (21) – 22 (trans. str., n=11); 19 – (20) – 22 (long. str., n=11)
Longitudinal/transverse stria ratio: 0.90–(0.97) – 1.04 (n=11)

Notes: this species was described and illustrated in detail by Sterrenburg (1995a). This author determined that the type material of the well-known *G. spenceri* (Quekett) Griffith & Henfrey corresponds to the more slender specimens of *G. acuminatum* and, being a later synonym, is consequently a superfluous and illegitimate name (Sterrenburg 1994, 1995a). Through the careful study of bibliography and the type material, Sterrenburg also established that *G. acuminatum* is a freshwater to slightly brackish water species and that the numerous reports of *G. spenceri* from brackish to marine localities are not, forcibly, *G. acuminatum* (see discussion in Sterrenburg 1995a). In fact, Sterrenburg & Underwood (1997) later proposed that many of these records refer to *G. limosum* (see below).

In the case of the specimens found in our study, they were extremely abundant in the mudflat stations in a typically brackish area of the estuary (see below) but the morphological features matched to the ones of *G. acuminatum*. Namely, these features agreed completely with the criteria proposed by Sterrenburg (1991a) for identifying *Gyrosigma* species and the LM and SEM illustrations given in the references (see below):

- The longitudinal/transverse stria ratio is approximately 1.0 to 0.9, an indication that the specimens belong to section Acuminati *sensu* Peragallo (*e.g.* Sterrenburg 1995a)
- The frustules are heterovalvar and dimorphic, with the central raphe fissures curved in opposite directions but in one valve pointing to the concave side of the raphe-sternum and in the other valve pointing to the convex side (*i.e.* like mirror images).
- The terminal areas of the raphe have unilaterally dilated funnels, in a semilateral position.
- A crescent of apical microforamina is present around the helictoglossae in the hyaline terminal area.

This combination of features is only present in *G. acuminatum*. The only noticeable difference to the type material is the valve outline. The valves are slightly more linear-lanceolate, tapering less gradually to subacute apices. However, the valve outline is not a completely reliable criterion and can only be used in the general sense (Sterrenburg 1991a). Conversely, a similar outline can be seen in the reference material of *G. acuminatum*, presented by Sterrenburg (1995a, fig. 12). It also shows great similarities to *G. spenceri* var. *curvula sensu* Reimer (Patrick & Reimer 1966), particularly in valve outline, but this taxon is probably related to *G. limosum* (see Sterrenburg & Underwood 1997, for full discussion).

The morphological correspondence to *G. acuminatum* has been established but the ecological differences need to be further investigated. We propose that the following possibility could be explored:

- Peragallo & Peragallo (1897-1908) described and illustrated a *Pleurosigma acuminatum* var. *gallica* (syn. *G. acuminatum* var. *gallica*) which they referred as a variety “saumâtre” of *G. acuminatum*. The few morphometric data given corresponds to the specimens found in the Tagus estuary, namely the striae density: “diffère du type par ses extrémités un peu plus atténuées, subaiguëes et sa striation plus fine, 20 à 21 stries long., et trans.”.
- This variety could correspond to some of the reports of both *G. acuminatum* and *G. spenceri* in estuarine areas and to our own material. But first Grunow’s material of *Pleurosigma scalprum* var. *gallica* (*gallicum*) Grunow in Van Heurck, probably available in Van Heurck’s collection needs to be checked.

Almost all the illustrated references consulted during this study show *G. acuminatum* with the typical lanceolate, moderately sigmoid valves with gently tapering to fairly obtuse to subacute ends. They all refer to freshwater to slightly brackish areas.

The relations of *G. acuminatum*, *G. attenuatum* f. *hippocampus sensu* Brockman and its probable synonym *G. enhippus* (see Sterrenburg 1992) need to be further studied. The specimen depicted by Brockman (1955) does not have an offset central area (as in *G. attenuatum*) and it seems to be extremely similar to the specimens found in our study but have coarser striation (around 12 longitudinal striae in 10 µm).

Distribution & Ecology: Large motile epipelic species living mainly in mudflats.

Given the earlier confusions with *G. spenceri* the exact distribution of *G. acuminatum* is not well defined (see above). If the validity of the brackish variety *G. acuminatum* var. *gallicum* is confirmed, then this taxon has been reported at least, for the Normandy coast (see Peragallo & Peragallo 1897-1990) and for the Bourgneuf Bay (France West Coast, Méléder 2003). In our study, this taxon was almost exclusively found in the two mudflat stations (15 occurrences) being particularly abundant throughout the first year of the survey (max. abundance < 2.6%).

References:
Germain (1981) – pg. 132; figs. 49/2-5
Germain (1989) – figs. 1/6-7
Krammer & Lange-Bertalot (1986) – pg. 296; figs. 114/4,8
Laws (1988) – figs. 20/3-4
Méléder (2003) – fig. 47 (as *G. distortum*)
Peragallo & Peragallo (1897-1908) – pg. 168; fig. 34/13 (var. *gallica*)
Ribeiro (2000) – pg. 25; figs. 3/7, 10/1-4
Snoeijs & Vilbaste (1994) – #142
Schoeman & Archibald (1986) – figs. 49, 52, 53 (type material)
Sterrenburg (1995a) – figs. 1-6 (as *G. spenceri*); 7-16, 20-21, 23-30 (as *G. acuminatum*)

Gyrosigma balticum (Ehrenberg) Rabenhorst 1853

Micrographs: Pl. 23: 6-8

Synonyms:
Navicula baltica Ehrenberg

Morphometrics:
Biovolume (µm^3): 244295
Frustule geometry: prism on parallelogram
Length (µm): 352.9 (n=1)
Width (µm): 29.4 (n=2)
Pervalvar axis (µm): 14 (estimated)
Striae in 10 µm: 14 (trans. str., n=2); 13 (long. str., n=2)
Longitudinal/transverse stria ratio: 0.93 (n=3)

Notes: there are several taxa included in the *Gyrosigma balticum* species complex (see Sterrenburg 1995b, Reid & Williams 2003). Nonetheless, the specimens found during this study do conform to *G. balticum s.s.* in all morphological features, namely the offset central area and the "small crescent of apical foramina" (*viz.* Sterrenburg 1995b).

Distribution & Ecology: *G. balticum* is large motile epipelic species found worldwide, usually associated with cohesive sediments (Sterrenburg 1995b, Reid & Williams 2003). In certain conditions, this species can exhibit an erect life-form, standing upright and above the surface of the biofilm thanks to a mucilaginous stalk (Jönsson *et al.* 1994). In our study, it was extremely rare and it was only found in mudflat samples (2 occurrences) at very low abundances (max. abundance <0.27%).

References:
Cardinal *et al.* (1986) – pg. 171; fig. 15
Krammer & Lange-Bertalot (1986) – pg. 299; 115/5
Reid & Williams (2003) – figs. 45-50
Snoeijs & Vilbaste (1994) – #144
Sterrenburg (1995b) – figs. 1-4, 13-15 (neotype material)

Gyrosigma distortum (W. Smith) Griffith & Henfrey 1856

Micrographs: Pl. 25: 6-7; Pl. 51: 3-4

Synonyms:
Gyrosigma distortum (W. Smith) Cleve
Pleurosigma distortum W. Smith
Scalprum (Scalptrum) distortum (W. Smith) Kuntze

Similar species:
Gyrosigma acuminatum (Kützing) Rabenhorst
Gyrosigma wormleyi (Sullivant) Boyer [syn.: *G. distortum* var. *parkeri* (Harrison) Cleve]

Morphometrics:
Biovolume (µm^3): 7549

Frustule geometry: prism on parallelogram
Length (µm): 62.6 – (66.6) – 71.0 (n=5)
Width (µm): 13.0 – (14.4) – 15.2 (n=5)
Pervalvar axis (µm): 5 (estimated)
Striae in 10 µm: 26 – (27) – 28 (trans. str., n=5); 34 – (37) – 40 (long. str., n=5)
Longitudinal/transverse stria ratio: 1.3 – (1.4) – 1.5 (n=5)

Notes: detailed description of this species can be found elsewhere (*e.g.* Sterrenburg 1994). It can be easily distinguished from *G. acuminatum* by its finer striation, the more or less straight and simple central raphe endings, the distal raphe endings, which are laterally expanded (*i.e.* “flag-shaped”, Sterrenburg 1994) and that are bordered by a row of areolae curving along the apical margin. The specimens found in our study (both in LM and SEM) have slightly more dense striation than what is given in the literature (Patrick & Reimer 1966, Sterrenburg 1994) and the longitudinal/transverse stria ratio is also higher for a species, supposedly in the section Acuminati *sensu* Peragallo. The similar taxon *G. wormleyi* is a freshwater species and the references of its synonym “*G. parkeri*” for brackish waters are probably erroneous (Sterrenburg 1994).

Distribution & Ecology: *Gyrosigma distortum* is large motile epipelic diatom. It is a cosmopolitan, marine species, frequently found in mudflats (Sterrenburg 1994). In our study, it was fairly frequent (17 occurrences). It was found in the mudflat stations but mainly in the sandy muddy stations, where it reached its maximal abundance (4.2 %).

References:
Hustedt & Aleem (1951) – fig. 2/c
Patrick & Reimer (1966) – pg. 326; 24/6
Sterrenburg (1994) – pg. 232; figs. 29-32, 63-68
Ribeiro (2000) – pg. 27; figs. 3/1, 9/1-2

Gyrosigma fasciola (Ehrenberg) Griffith & Henfrey 1856

Micrographs: Pl. 25: 8-11; Pl. 51: 5-9

Synonyms:
Ceratoneis fasciola Ehrenberg
Pleurosigma fasciolum (Ehrenberg) W. Smith

Similar species:
Gyrosigma fogedii Stidolph

Morphometrics:
Biovolume (µm^3): 6614
Frustule geometry: prism on parallelogram
Length (µm): 66.5 – (82.0) – 99.4 (n=9)
Width (µm): 9.5 – (11.4) – 13.9 (n=9)
Pervalvar axis (µm): 5 (estimated)
Striae in 10 µm: 22 – (23) – 24 (trans. str., n=11); 20 – (25) – 29 (long. str., n=9)
Longitudinal/transverse stria ratio: 0.9 – (1.1) – 1.4 (n=9)

Notes: the taxonomic history of this taxon is given in detail by Stidolph (1994) and the differences between the main varieties of *G. fasciola* are given in Cardinal *et al.* (1986). Following the latter authors, the specimens found in our study may belong to the variety *G. fasciola* var. *arcuata* (Donkin) Cleve, which has a denser striation than the nominate variety. This taxon is also discussed and typified by Jahn *et al.* (2005).

Distribution & Ecology: *G. fasciola* is a common motile epipelic species in European (*e.g.* Hendey 1964, Krammer & Lange-Bertalot 1986), North American (*e.g.* Cardinal *et al.* 1986, Patrick & Reimer 1966) coasts, being also reported for the Southern Hemisphere (*e.g.* Stidolph 1980). In this study, it was one of the most common epipelic species (55 occurrences) and it was mainly found, but not exclusively, in the mudflat stations (Table 16) where it reached a maximum in abundance of approximately 50%. Like other dominant epipelic species, it had a very marked seasonality (Fig. 19, chapter 4) being the dominant epipelic species during late autumn and winter in the mudflats stations. Its presence was particularly important in the second year of the survey.

Table 16 – Occurrence (%), average relative abundance (%) of *G. fasciola* and average mud content (%) per sampling station. Standard deviation given within brackets.

Station	Occurrence	Abundance	Mud content
A1	18	0.0 (0.1)	2.3 (1.0)
A2	55	0.3 (0.6)	5.4 (2.4)
A3	82	1.6 (1.3)	7.7 (3.1)
V1	100	5.8 (5.5)	13.5 (9.3)
V2	100	17.4 (13.5)	90.0 (7.3)
V3	100	18.3 (11.1)	96.5 (2.2)

References:
Cardinal *et al.* (1986) – pg.
Krammer & Lange-Bertalot (1986) – pg. 300; fig. 116/5
Hendey (1964) – pg. 248
Patrick & Reimer (1966) – pg. 328; fig. 26/4
Stidolph (1994) – figs. 5-9 (as *G.* aff. *fasciola*)
Snoeijs & Kasperoviciene (1996) – #347

Gyrosigma cf. ***limosum*** Sterrenburg & Underwood 1997

Micrographs: Pl. 24: 6-10; Pl. 52: 1-2

Synonyms:
"*Gyrosigma spenceri*" *sensu* Hustedt (1930), Van der Werff & Huls (1957-1974) *et auctorum aliorum*

Similar species:
Gyrosigma exilis (Grunow) Reimer
Gyrosigma peisonis (Grunow) Hustedt
Gyrosigma wansbecki (Donkin) Cleve
Gyrosigma wansbeckii var. *minuta* Cardinal, Poulin & Bérard-Therriault 1986

Morphometrics:
Biovolume (µm^3): 7436
Frustule geometry: prism on parallelogram
Length (µm): 56.2 – (72.4) – 100.3 (n=23)
Width (µm): 7.2 – (8.8) – 11.0 (n=23)
Pervalvar axis (µm): 7 (estimated)
Striae in 10 µm: 20 – (22) – 25 (trans. str., n=26); 25 – (29) – 32 (long. str., n=25)
Longitudinal/transverse stria ratio: 0.67 – (0.78) – 0.89 (n=25)

Description: *Gyrosigma* cf. *limosum* has a slightly sigmoid valve with an almost linear outline, usually with little tapering and bluntly rounded ends. The longitudinal striation is conspicuously finer and the longitudinal/transverse stria ratio is < 0.85 (*i.e.* falling in the Strigiles section *sensu* Peragallo). The central area is rather small and the central raphe endings of this dimorphic species are deflected in opposite directions ("left-handed" crooks, Sterrenburg 1993a) that were easily seen in LM, using DIC microscopy.

Notes: This taxon is quite similar with *G. wansbeckii* (see below) but the latter species belongs to the section Acuminati *sensu* Peragallo, having longitudinal and transverse stria of similar density. Using this criterion, the specimens of both taxa found during our study were quite easily separated. *Gyrosigma exilis*, a freshwater species (Patrick & Reimer 1966, Sterrenburg 2005), is also very similar, especially to the smaller specimens of *G. limosum*. It is also in the section Strigiles, but it is more finely striated and the central area is larger and longitudinally expanded.
Conversely, the distinction between *G. limosum* and *G. peisonis*, seemed to us, to be rather difficult, using the available literature. Both taxa are described in detail by Sterrenburg & Underwood (1997) and Sterrenburg (1997) and they both belong to the section Strigiles *sensu* Peragallo, having similar transverse and longitudinal striae densities (striae ratio around 0.8), as well as comparable size ranges. Their ecology is also very similar: *G. peisonis* is found in estuaries and inland salt lakes (*i.e.* brackish to estuarine, Sterrenburg (1997)) and *G. limosum* is an estuarine to marine species (Sterrenburg and Underwood 1997). Most of specimens found in the samples studied have an almost linear valve outline and the oppositely deflected central raphe ending were easily seen in LM (as in *G. peisonis*). However, the central area is rather small as in *G. limosum*. The axial area (and raphe-sternum) was not clearly eccentric over half its length and its central portion was not clearly flexed like a large "S" (as in *G. peisonis*) nor was it practically median throughout the valve and with a straight central portion near the ends (as in *G. limosum*). Most of the specimens found

seemed to share more morphological features with *G. limosum*, but it is plausible that during counts both species were encountered. A similar case seems to have been detected by Hustedt (1955) in his Beaufort Bay samples but he decided to identify both forms as *G. peisonis*.

Distribution & Ecology: Sterrenburg and Underwood (1997) established that the many of the worldwide marine records of "*G. spenceri*", a late synonym of *G. acuminatum* (see above) do not refer to this freshwater species, thanks to ecological and morphological differences. They recommended that in the future the past reports of "*G. specieri*" should be attributed to *G. wansbecki*, *G. peisonis,* and particularly to *G. limosum*. The latter species seems to be typically found in cohesive sediments, as the ones present in mudflats. In our study, *G.* cf. *limosum* taxon also occurred in the sandy muddy stations but it was mainly found in the mudflat samples (8 of 14 occurrences) where it was more common (max. abundance <1.6%).

References:
Hustedt (1955) – pg. 34; fig. 10/4-5
Sterrenburg & Underwood (1997) – figs. 1-7 (*G. limosum*)
Underwood (1994) – fig. 12 (*G. limosum* as *G. spenceri*)

Gyrosigma wansbeckii (Donkin) Cleve 1894

Micrographs: Pl. 24: 1-5; Pl. 52: 4

Synonyms:
Pleurosigma balticum var. *wansbeckii* (Donkin) H. Peragallo
Pleurosigma wansbeckii Donkin
Gyrosigma balticum var. *wansbeckii* (Donkin) Heiden *in* Heiden & Kolbe

Similar species:
Gyrosigma balticum (Ehrenberg) Rabenhorst
Gyrosigma peisonis (Grunow) Hustedt

Morphometrics:
Biovolume (μm^3): 27104
Frustule geometry: prism on parallelogram
Length (μm): 68.8 – (130.8) – 176.5 (n=9)
Width (μm): 10.3 – (15.3) – 18.6 (n=11)
Pervalvar axis (μm): 7 (estimated)
Striae in 10 μm: 17 – (18) – 19 (trans. str., n=10); 18 – (19) – 21 (long. str., n=10)
Longitudinal/transverse stria ratio: 0.95 – (1.03) – 1.18 (n=10)

Notes: a detailed description of this species is given in Reid & Williams (2003). This taxon could be easily distinguished from *G. peisonis* (see above *G.* cf. *limosum*) because it has longitudinal and transverse striae with similar density (*i.e.* section Acuminati *sensu* Peragallo) and from G. *balticum*, thanks to its smaller size, finer striation and its elliptical but symmetric central area. Conversely, the specimens found in our study had a slightly lower striae density than the one given in other reports (*i.e.* transverse and longitudinal around 21-24, Cardinal *et al.* 1986; Reid & Williams 2003), but they definitively belong to the section Acuminati.

Distribution & Ecology: *G. wansbeckii* is a large motile epipelic diatom, probably cosmopolitan and especially common in brackish to marine waters (*e.g.* Hendey 1964, Hustedt 1931-1959, Sterrenburg 1997a). In our study it was rarely found and almost exclusively in mudflat samples (6 out of 7 occurrences) during winter and spring, but it was never very abundant (max. abundance < 0.54%).

References:
Cardinal *et al.* (1986) – pg. 179; fig. 45, 46 (*G. wansbeckii* var. *minuta*)
Brockmann (1950) – fig. 6/9
Hendey (1964) – pg. 248; fig. 35/5
Kuylenstierna (1989-1990) – pg. 103; fig. 579-580
Reid & Williams (2003) – figs. 23-29

Pleurosigma Smith 1852

Genus description: Cardinal *et al.* (1989); Round *et al.* (1990); Sterrenburg (1991b).

Pleurosigma angulatum sensu W. Smith emend Sterrenburg 1991

Micrographs: Pl. 25: 1-5; Pl. 52: 5-6

Synonyms:
Navicula angulata Quekett *pro parte quoad typum*
Navicula aestuarii Brébisson *ex* Kützing
Pleurosigma aestuarii (Brébisson *ex* Kützing) W. Smith
Pleurosigma angulatum var. *aestuarii* (Brébisson *ex* Kützing) Van Heurck
Pleurosigma quadratum W. Smith
Pleurosigma angulatum var. *quadratum* (W. Smith) Van Heurck,
Pleurosigma angulatum var. *undulatum* Grunow

Similar species:
Pleurosigma rhombeum (Grunow *in* Cleve & Grunow) H. Peragallo
Pleurosigma stidolphii Sterrenburg

Morphometrics:
Biovolume (µm^3): 38153
Frustule geometry: prism on parallelogram
Length (µm): 86.8 – (110.4) – 188.2 (n=7)
Width (µm): 17.1 – (24.4) – 46.1 (n=7)
Pervalvar axis (µm): 9 (estimated)
Striae in 10 µm: 20 – (20) – 21 (transverse striae, n=3); 17 – (18) – 19 (oblique striae, n=3)

Notes: the nomenclatural problems, morphological variability and references on *P. angulatum* and its presumed varieties were given in detail by Sterrenburg (1990a, 1991b). After studying several slides (including Smith's slides), this author came to the conclusion that there is no morphological discontinuity between the well known taxa *P. quadratum*, *P. angulatum* and *P. aestuarii*. This continuum was observed in size range, outline, width-length ratio, degree of valve silicification, stria angle and stria density. Regarding the valve outline, the "pinched" apices often considered as a character of *P. aestuarii* are probably a result of valve morphogenesis in narrower frustules and occurred also in "agulatum" specimens. Additionally, the terminal bipolar perpendicular stria occurs in all specimens studied by Sterrenburg and should be considered specific, as they do not exist in other known species of the genus (*e.g. P. rhombeum* or *P. stidolphii*). Finally, Sterrenburg gives an extended description of *P. aestuarii sensu* Smith, which includes all these individual entities.
The specimens found in our study could be allocated to either "*P. angulatum sensu* Smith" or to "*P. aestuarii*". However, the majority of the valves found were of an intermediate form between these two "morphotypes". This conforms to the observations made by Sterrenburg (1991b) in Dutch and British coast samples, where the larger *quadratum*, the medium *angulatum* and the smaller *aestuarii* forms should be considered as morphological stages of a vegetative cycle of a single organism.

Distribution & Ecology: large motile epipelic species thought to be cosmopolitan. However, Sterrenburg (1991b) casted some doubts on the correctness of the reports from the tropics. In the Northern Hemisphere, the Iberian Peninsula seems to be the southernmost limit. In our study, it was fairly common, with 20 occurrences, most of them during the second year of the survey and in all stations. However, it was much more abundant in the upper shore sandy muddy station of the muddy transect (max. abundance < 6.7% in March 2004).

References:
Hendey (1964) – pg 243, 245; figs. 35/1-3, 36/5, 41/5-6
Krammer & Lange-Bertalot (1986) – pg. 294; figs. 113/1-2, 114/1-2
Kuylenstierna (1989-1990) – pg. 122; fig. 581
Patrick & Reimer (1966) – pg. 331-332; figs. 27/1a-c,3a-c
Ribeiro (2000) – pg. 31-32; fig. 3/2-3, 9/5-6
Snoeijs & Kasperoviciene (1996) – #383, # 384

ORDER THALASSIOPHYSALES

Fam. Catenulaceae Mereschkowsky

Amphora Ehrenberg *ex* Kützing 1844

Genus description: Round *et al.* (1990), Nagumo (2003); Levkov (2009)

Amphora sensu lato is a large and heterogeneous genus, comprising more than 1400 names (Fourtanier & Kociolek 2007). This heterogeneity was recognised by Cleve (1895), who divided the genus in several subgenera (*e.g. Amphora*, *Halamphora*, *Cymbamphora*). However, he did not taken into account protoplast morphology and other cytological features and some subgenera were found to be heterogeneous (*e.g.* Mann 1994b, Sabbe *et al.* 2004a). Therefore, a major revision of the genus, in different lines from Cleve's suggestion, has long been advocated (*e.g.* Krammer & Lange-Bertalot 1986, Round *et al.* 1990).

Recently, Levkov (2009) revised the genus and established several new genus using in frustule and/or valve morphology, plastid morphology (according to the classification by Mereschkowsky 1903), raphe structure and areolae structure. For example, the species group around *Amphora coffeaeformis* was transferred to the new genus *Halamphora* (see below). A very complete description of *Amphora sensu stricto* is given by Levkov (2009) and also by Nagumo (2003, as a subgenus). It includes species close to *Amphora ovalis* Kützing with one butterfly-shaped plastid appressed to the ventral girdle (type 1 *sensu* Mereschkowsky 1903), uniseriate striae, and the raphe is usually biarcuate and raised above the rest of the valve. Other important features in *Amphora sensu stricto* is the way central raphe endings terminate internal, internally, in simple and narrow helictoglossae and the fact that are open and without any visible poroids in LM.

Amphora arenicola Grunow *in* Cleve 1895

Micrographs: Pl. 26: 4-8

Synonyms:
Amphora marina var. *arenicola* Grunow *in* Cleve & Möller

Morphometrics:
Biovolume (µm^3): 1109
Frustule geometry: half-rotational ellipsoid
Length (µm): 40.7– (43.1) – 45.3 (n=5)
Width (µm): 7.3 – (8.2) – 9.5 (n=3)
Pervalvar axis (µm): (estimated)
Striae in 10 µm: 12 – (12) – 14 (dorsal striae n=5); 11 – (12) – 12 (ventral striae n=5)

Notes: a detailed description of this species is given by Hendey (1964). Given its rather deep ventral side, the outline of the valve can vary considerably in LM, depending on the position of the valve.

Distribution & Ecology: this species is considered to be cosmopolitan (Witkowski *et al.* 2000). In our study it was extremely rare with only one occurrence in the upper shore station of the sandy transect (relative abundance = 0.27%). It is a large motile epipelic species that prefers sandy sediments.

References:
Hendey (1964) – pg. 262; fig. 38/10
Peragallo & Peragallo (1897-1908) –pg. 201; fig. 44/11
Witkowski *et al.* (2000) – pg. 129; figs. 162/1-2, 163/1-3

Amphora cf. ***helenensis*** Giffen 1973

Micrographs: Pl. 27: 14-16

Similar species:
Amphora pediculus (Kützing) Grunow

Morphometrics:
Biovolume (µm^3): 79
Frustule geometry: half-rotational ellipsoid
Length (µm): 8.1 – (9.3) – 10.1 (n=5)
Width (µm): 2.6 – (2.8) – 3.0 (n=5)
Pervalvar axis (µm): 6 (estimated)
Striae in 10 µm: 23 – (25) – 29 (dorsal striae, n=5); 20 – (23) – 27 (ventral striae, n=4)

Description: valves semi-elliptical with a convex dorsal margin and ventral margin straight to concave. Raphe is slightly biarcuate. Ventral striae interrupted in the centre and more or less parallel. The dorsal striae are parallel in the centre of the valve, becoming radiate near the apices. They are distinctly interrupted by longitudinal hyaline area in the middle of the dorsal side of the valve.

Notes: even though they are smaller and with a higher striae density, these specimens are very reminiscent of *A. helenensis*, especially from the specimens of that species reported for the Baltic Sea (*e.g.* Kuylenstierna 1989-1990, Snoeijs & Balashova 1998, Witkowski *et al.* 2000). SEM studies are necessary to confirm that they all belong to the same taxon.
It can be distinguished from *A. pediculus*, a similar species of comparable size, by the fact that the dorsal striae are interrupted longitudinally in the centre of the valve and not interrupted transversely as in that species (see below).

Distribution & Ecology: this taxon was extremely rare, with only 4 occurrences at very low abundances (max. abundance < 0.57%). Their ecological optimum is uncertain but it mainly occurred in sandy stations, being probably a small motile epipsammic species. This coincides with the observations by Sabbe (1997) for the Westerschelde estuary. As for *A. helenensis*, it is considered as a cosmopolitan marine species (Witkowski *et al.* 2000).

References:
Giffen (1975) – pg. 74, fig. 7-9
Sabbe (1997) – pg. 217; 23/10-14
Snoeijs & Balashova (1998) – # 409
Witkowski *et al.* (2000) – pg. 139, fig. 163/31-33

Amphora cf. ***pediculus*** (Kützing) Grunow in Schmidt *et al.* 1875

Micrographs: Pl. 27: 17-19; Pl. 52: 7 (Morphotype 1); Pl. 52: 8-9 (Morphotype.2)

Synonyms:
Amphora ovalis var. *pediculus* (Kützing) Van Heurck
Cymbella pediculus Kützing
Encyonema pediculus (Kützing) H. Peragallo

Similar species:
Amphora copulata (Kützing) Schoeman & Archibald
Amphora helenensis Giffen
Amphora iraniensis Krammer

Morphometrics:
Morphotype 1
Biovolume (µm3): 74
Frustule geometry: half-rotational ellipsoid
Length (µm): 6.7 – (8.7) – 11.5 (n=7)
Width (µm): 2.7 – (3.5) – 4.1 (n=6)
Pervalvar axis (µm): 6 (estimated)
Striae in 10 µm: 16 – (29) – 23 (dorsal striae, n=9); 17 – (20) – 23 (ventral striae, n=4)

Morphotype 2
Biovolume (µm3): 79
Frustule geometry: half-rotational ellipsoid
Length (µm): 6.1 – (7.9) – 10.1 (n=9)
Width (µm): 1.8 – (2.2) – 2.7 (n=9)
Pervalvar axis (µm): 6 (estimated)
Striae in 10 µm: 22 – (24) – 23 (dorsal striae, n=9); 23 – (24) – 25 (ventral striae, n=4)

Description: two different forms seemed to be present but were only distinguished with SEM. They look very similar in LM and both forms were scored together during counts. The SEM descriptions of both morphotypes are given separately.

In LM both forms have broadly elliptical frustules. The valves are semi-elliptical, with cuneate apices. The dorsal margin is convex and the ventral margin is straight to slightly concave or very slightly bi-arcuate. The raphe is straight with a narrow axial area and straight central raphe endings. The dorsal striae slightly radiate and have indistinct structure in LM (morphotype 1) or are faintly punctate (morphotype 2). The ventral striae radiate in the centre and are parallel to convergent near the apices. The central area is transapically expanded to both ventral and dorsal side (although not attaining the dorsal margin). A longitudinal hyaline bar can sometimes be seen in the dorsal side of the valve, interrupting the dorsal striae.

In SEM, both morphotypes have a flat valve face with the ventral and proximal dorsal side on the same plane. The distal dorsal side lies in an almost right angle and is delimited by a longitudinal hyaline bar. Morphotype 1 has striae which are composed by transapically elongated, slit–like punctae. The ventral striae are composed by a single punctum, while the ventral striae have one punctum in the proximal dorsal side and one in the distal dorsal side. The raphe is slightly bi-arcuate and the dorsal conopeum is only expanded near the apices. The distal raphe endings are dorsally deflected. The central area is limited to the ventral side and proximal dorsal side. A small punctum-like depression is present in the dorsal side of the central area, near the central nodule. It is probably a vestigial punctum of the central dorsal striae, since it is aligned with the punctum in the distal dorsal side. Morphotype 2 has punctate striae. The ventral striae are composed by just one punctum. The dorsal striae are composed by 2-3 punctae in the proximal side and 2 transversely elongated punctae in the distal dorsal side. The raphe is straight and the apical raphe endings are strongly dorsally deflected.

Notes: Given that there were two different forms, it was decided to designate these specimens as *Amphora* cf. *pediculus*. Both morphotypes belong to *A. pediculus* species complex and not to the group of species around *A. copulata* (see Nagumo 2003) or to the group around of *A. helenensis* (see above). The almost straight raphe and the transversely expanded central area, which is delimited in the ventral side at the central raphe endings level, are discriminating morphological features that separate both forms from the mentioned species groups.

With its punctate striae in LM, morphotype 2 is very similar to the *A. pediculus s.s.* (Schoeman & Archibald 1976-1980, Round & Bukhtiyarova 1996a, Nagumo 2003), whereas morphotype 1 is reminiscent of *A. inariensis*, apart from the fact that it seems to almost lack a dorsally expanded conopeum (*e.g.* Krammer & Lange-Bertalot 1986, Nagumo 2003) and to *A. pediculus* form B, described by Lee & Round (1989). Both *A. pediculus* and *A. inariensis* are considered to be common and typical freshwater species (Krammer & Lange-Bertalot 1986), but *A. pediculus* is often reported for brackish waters (Bérard-Therriault *et al.* 1986, Snoeijs 1993, Witkowski 1994b, Sabbe 1997). Interestingly, morphotype 1 corresponds almost completely to the specimens depicted in Snoeijs (1993) and Sabbe (1997) and collected in the Bothnian Sea and the Westerschelde estuary, respectively.

To our knowledge, whether the freshwater and brackish water specimens of *A. pediculus* do all belong to the same taxon has not yet been accessed. Since the morphological features do not seem sufficient, molecular studies are needed to clarify this question.

Distribution & Ecology: *Amphora* cf. *pediculus* is probably a small motile epipsammic species. In this study it was quite common (39 occurrences), being recurrently found in the sandy transect and it also occurred in the upper shore sandy station of the muddy transect. It was particular abundant (max. abundance <4.1%) in the upper shore station of the sandy transect, with fine to medium sands. This distribution agrees with the observations made by Sabbe (1997) for the Westerschelde estuary. Even though, it occurred throughout the year, as do most of the epipsammic species, it had a faint seasonal increase in numbers during summer and autumn of the two years surveyed.

References:
Lee & Round (1989) – figs. 16-17 (? as *A. pediculus* form B)
Sabbe (1997) – pg. 224; figs. 31/1-9, 56/4-7 (as *A.* cf. *pediculus* form 1)
Snoeijs (1993) – #10

Catenula Mereschkowsky 1903

Genus description: Round *et al.* (1990). This small genus has only three described species: *C. adhaerens*, *C. pelagica* Mereschkowsky and *C. robusta*, recently described by Witkowski and colleagues (Witkowski *et al.* 2000). The type of the genus, *C. pelagica*, has not yet been studied in detail and its relationship to C. *adhaerens* is not well established (Snoeijs 1996).

Catenula adhaerens (Mereschkowsky) Mereschkowsky 1902

Micrographs: Pl. 31: 4-7; Pl. 53: 9-11

Synonyms:
Navicula adhaerens Mereschkowsky
Amphora sabyii Salah

Similar species:
Lunella bisecta Snoeijs

Morphometrics:
Biovolume (µm^3): 34
Frustule geometry: half-elliptic prism
Length (µm): 5.1 – (9.8) – 14.7 (n=10)
Width (µm): 2.3 – (2.8) – 3.9 (n=10)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 28 – (31) – 34 (n=5)

Notes: this species is described in detail by Sundbäck & Medlin (1986). Even though it looks similar (in LM) to the lunate species of the genus *Lunella* (see above), it can be distinguished by the lack of poroids in the copulae and of striae in the valve face. The elongated transverse areolae in the mantle are also typical of this species. The morphology of the smaller specimens was slightly different with the raphe in a less eccentric position (Pl. 31: 4). These specimens were extremely rare (4 occurrences and max. abundance < 0.36%).

Distribution & Ecology: *Catenula adhaerens* is a cosmopolitan marine to brackish water species and commonly found attached to sand grains (*e.g.* Sundbäck & Medlin 1986, Witkowski *et al.* 2000). With a adnate lifeform, it typically forms ribbon-like colonies, attaching to the surface of the sand grains by the ventral margin, where the raphe is located in a fashion very similar to the freshwater species *Cymbelonitzschia diluviana* Hustedt (Jewson & Lowry 1993). It is one of the most frequently found epipsammic species in the European coasts (Hustedt 1939, Brockmann 1950). Sabbe (1997) reported it as especially abundant in fine to very fine sandy sediments of the Westerschelde estuary and indifferent to the amount of silt in the sediment. In our study, it was also one of the most frequently found epipsammic species in the sandy stations (42 occurrences), particularly along the sandy transect. It did not occur in the mudflat stations. With an average abundance of 1-2% throughout the study period, it had large peaks in abundance in the samples of late autumn in both years of the surveyed period (max. abundances of 6-9%).

References:
Brockmann (1950) – pg. 22; fig. 1/9
Cooper (1995) – pg. 66; fig. 44a-b, 52
Kuylenstierna (1989-1990) – pg. 95, figs. 490, 799
Round *et al.* (1990) – pg. 598
Salah (1955) – pg. 99; fig. 2/10
Simonsen (1962) – pg. 87
Snoeijs (1993) – #19
Sundbäck & Medlin (1986) – figs. 1-23
Witkowski *et al.* (2000) – pg. 168; fig. 170/1-12

Catenula sp.1

Micrographs: Pl. 31: 8-15; Pl. 54: 1-3

Similar species:
Amphora micrometra Giffen
Catenula adhaerens Mereschkowsky
Lunella bisecta Snoeijs

Morphometrics:
Biovolume (µm^3): 42
Frustule geometry: half-elliptic prism
Length (µm): 6.7 – (10.0) – 17.4 (n=11)
Width (µm): 1.7 – (2.7) – 3.0 (n=10)
Pervalvar axis (µm): 3 (estimated)
Mantle slits in 10 µm: 52 (n=2)

Description: valves are semi-lanceolate and have a clear dorsiventral symmetry. The ventral margin is almost straight and only slightly convex, while the dorsal margin is convex. In the smaller valves, the apices are weakly subrostrate whereas, in the larger valves the ends are subcapitate. In both cases, the apices always point to the ventral side of the valve. Valve face is flat with sharp transition, almost at a right angle to the comparatively deep mantle.

The raphe is close to the ventral valve margin. In LM, it seems to be straight, but only the branches near the central nodule are clearly visible. The central raphe ends are fairly distant and slightly expanded, separated by a bright, distinct central nodule. In SEM, the raphe looks rather simple and, in the external view, the central nodules are faintly turned to the dorsal side and the raphe branches are slightly sinusoidal, bending gently towards the ventral side and finishing near the mantle. The raphe distal endings are clearly within the apices but distant from the apical margin. The inside view confirms the simple structure of the raphe, with the only remarkable feature being the heavily silicified central nodule. There is no prominent helictoglossa in the apical raphe ends.

The striae are not visible in LM and only a bright "halo" is perceptible near the valve margin. They are uniseriate, parallel or radiating slightly and do not penetrate through the valve. They are filled by siliceous depositions in the valve face and are inexistent in the valve interior. The only true pores are seen near the dorsal and ventral mantles and seem to be associated to the transapically elongate mantle pores. In the internal view, it can be seen that every two inter-striae/pores are slightly reinforced internally, being responsible for the bright marginal "halo" seen in LM.

Notes: this taxon shows striking similarities to two small marine epipsammic diatoms, which also have a dorsiventral symmetry, small size a fine structure: *C. adhaerens* and *L. bisecta.* These two taxa belong to two very small genera that, although looking alike, are not closely related (Sundbäck & Medlin 1986, Snoeijs 1996). This taxon is virtually indistinguishable from *L. bisecta* in LM due to the same size range. The only features that may allow a correct identification in LM are slight differences in valve outline, such as the capitate apices and the brighter marginal "halo" in *Catenula* sp.1. The differences to *C. adhaerens* in LM are more evident, given the fact that this species has a straight ventral margin, bright distal raphe ends and the striae are usually discernible in LM.

However, the observations in SEM reveal that the taxon found in our study is a species of *Catenula*. Instead of having striae, composed by copulae with poroids that continue across the valve face mantle junction, cf. *L. bisecta* (Snoeijs 1996), the taxon described here has filled-in striae, practically identical to the ones of *C. adhaerens*, as well as the transapical elongate mantle poroids that exist in that species (see Sundbäck & Medlin, 1986). Another clear difference is the much simpler raphe structure while the thickened axial rib surrounding the raphe slits found in *Lunella* (see Snoeijs 1996) does not seem to exist.

A third taxon that has some similarities with this one is the small hyaline *Amphora micrometra* described by Giffen (1966) for the South African marine littoral. This species is well illustrated in Kuylenstierna (1989-1990), Snoeijs & Potopova (1995) and Archibald (1983) where the fine multiseriate striae, as shown in EM, clearly state that is an unrelated taxon.

Since this genus counts currently only these three species, the taxon described here is indubitable a new and yet undescribed species of *Catenula*.

Life form & Ecology: Epipsammic, probably adnate species. Very frequent, it occurred in almost all samples from the sandy stations (41 occurrences in 45 samples), appearing only once in the mudflat samples. It was never very abundant (max. abundance < 3.4%) and no clear seasonal pattern could be observed.

Catenula sp.2

Micrographs: Pl. 31: 16-21; Pl. 54: 4-6

Morphometrics:
Biovolume (µm^3): 65
Frustule geometry: half-elliptic prism
Length (µm): 13.7 – (15.6) – 19.0 (n=12)
Width (µm): 3.1 – (3.5) – 4.4 (n=12)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 13 – (14) – 15 (dorsal striae, n=12)
Puncta in 10 µm: 36 (n=1)

Description: valve lunate, with a flat ventral margin, a convex dorsal margin and rostrate apices. Valve face is flat with sharp transition, almost at a right angle to the comparatively deep mantle. The raphe is straight and very close to the ventral valve margin. The terminal raphe endings are close to the apices and the central raphe endings are conspicuously distant from each other (about a third of the valve length). In SEM, it can be seen that the central nodule is more heavily silicified that the rest of the valve, that both the central and terminal raphe endings are only very slightly deflected to the dorsal side and that they terminate in small helictoglossae.
The striae are very conspicuous and limited to the dorsal side. They slightly radiate and are more distant in the middle of the valve. Even though they have a more or less indistinct structure in LM, they are composed by transversely elongated occluded punctae, which are aligned in uniseriate rows burrowed between the heavily silicified interstriae. There are no apparent mantle poroids

Notes: this taxon is only tentatively allocated in the genus *Catenula*. It shares many morphological features with *C. adhaerens*, such as valve outline and symmetry and a rather simple raphe structure. Additionally, *C. adhaerens* also has dorsal striae (*e.g.* Sundbäck & Medlin 1986; Round *et al.* 1990), although they are much less conspicuous and invisible in LM. Conversely, there is one main difference that may determine the creation of a new genus to allocate this taxon: the apparent lack of mantle poroids. However, a more complete SEM study is needed (*e.g.* external valve views), as well as the observation of alive cells to determine plastid structure are necessary before this step can be pursued.

Distribution & Ecology: this species is epipsammic probably with an adnate lifeform. It was extremely rare (9 occurrences) and it was only found in the sandy transect, always at abundances below 1%. Like *C. adhaerens* it increased in numbers in November 2003 and 2004.

Halamphora (Cleve) Levkov 2009

The genus *Halamphora* was created by Levkov (2009), who recently revised the *Amphora sensu lato* and elevated the subgenus *Halamphora* Cleve to the genus status. A complete description of this genus is given there. This taxon includes species around *Amphora coffeaeformis,* which are characterised by having elliptical to lanceolate frustules, a girdle composed of numerous punctate bands, valves usually with rostrate or capitate ends and punctate striae, a straight or slightly curved raphe near the ventral margin, with a narrow raphe sternum (*cf.* Sala *et al.* 2006). The main differences to the genus *Amphora sensu stricto* (*i.e.* subgenus *Amphora* Cleve) are given by Levkov (2009) and report, for example, to the presence of a single H-shaped plastid (*i.e.* type 2 *sensu* Mereschkowsky) or to raphe ultrastructure: in most *Halamphora* species, the proximal raphe endings terminate internally with fused central helictoglossae, whereas in *Amphora s.s.*, each raphe branch terminates with separate central helictoglossae (*e.g.* Edlund *et al.* 2009).

***Halamphora* cf. *abuensis* (Foged) Levkov 2009**

Micrographs: Pl. 27: 20-21

Synonyms:
Amphora abuensis Foged
Cymbellopsis abuensis (Foged) Krammer

Similar species:
Amphora tenuissima Hustedt
Amphora cf. *tenuissima* Hustedt (see below)
Halamphora aponina (Kützing) Levkov
Halamphora gasseae Levkov
Halamphora luciae (Cholnoky) Levkov
Halamphora tenerrima (Aleem & Hustedt) Levkov

Morphometrics:
Biovolume (µm^3): 112
Frustule geometry: half-rotational ellipsoid
Length (µm): 9.4 – (11.7) – 16.6 (n=8)
Width (µm): 2.6 – (3.0) – 3.6 (n=8)
Pervalvar axis (µm): 6 (estimated)
Striae in 10 µm: 18 – (19) – 20 (dorsal striae, n=8); 29 (ventral striae, n=2)

Description: valves semi-elliptical with rostrate to slightly capitate apices and slightly ventrally bent. Dorsal margin is convex and the ventral margin more or less straight. In LM, ventral striae are invisible; the dorsal striae radiate throughout the valve, although only very slightly at the centre. Their structure is indistinct in LM.

Notes: this taxon is very reminiscent of *H. abuensis*, although the valves are slightly smaller (and narrower) than what is given by Levkov (2009) for that species.

The combinations of characters consisting of comparatively low dorsal striae density, non-punctuated dorsal striae (in LM) and apices ventrally bent, separates this taxon from *H. gasseae* (see Levkov 2009) and *H. luciae* (see Archibald 1983, Snoeijs & Balashova 1998, Witkowski *et al.* 2000, Levkov 2009). *Halamphora aponina* also has dorsal striae with irresolvable punctae in LM and similar striation density and but it has significantly larger valves and capitate ends (Archibald & Schoeman 1984; Levkov 2009).

The size range of this taxon overlaps the range of other small species with ventral striae that are irresolvable in LM, namely *H. tenerrima* and *Amphora* cf. *tenuissima* (see below) which was also found in our sample. The distinction between both species during cell counts was mainly based on a lower dorsal striae density (see Figure 27) and slight differences in valve outline (but see discussion below).

Given the lack of SEM observations of our own material, it was not possible to confirm several ultrastructure features of *H. abuensis*, namely the uniseriate striae, the central area fascia and the abrupt transition from the dorsal valve side to the dorsal mantle, were present in our specimens. This taxon is therefore only tentatively identified as *Halamphora* cf. *abuensis*.

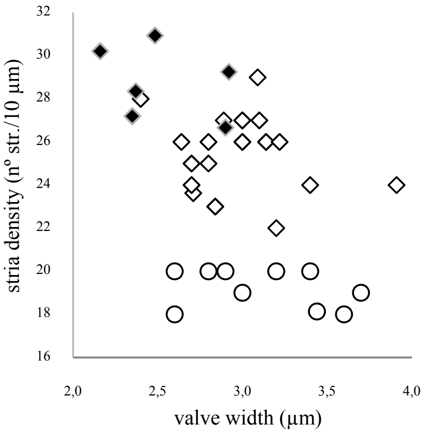

Figure 27 – dorsal striae density *vs.* valve width of *H.* cf. *abuensis* (○, LM) and *A.* cf. *tenuissima* (◊, LM; ♦, SEM).

Distribution & Ecology: this diatom is either an adnate or a small motile epipsammic species. It had a similar distribution to *A.* cf. *tenuissima*, although it was less abundant (max. abundance < 4%) and less frequent (34 occurrences). It was mainly found in the sandy transect stations. *Halamphora abuensis* has only been described for Ghana and it is probably a freshwater species (Levkov 2009).

References:
Levkov (2009) – pg. 166; 106/7-19, 238/5-6
Witkowski *et al.* (2000) – 161/14 (as *A. luciae*?)

***Halamphora* cf. *tumida* (Hustedt) Levkov 2009**

Micrographs: Pl. 53: 7

Similar species:
Halamphora acutiuscula (Kützing) Levkov
Halamphora ghanensis Levkov
Halamphora sabiniana (Reimer) Levkov
Halamphora sydowii (Cholnoky) Levkov

Morphometrics:
Biovolume (µm^3): 324
Frustule geometry: half-rotational ellipsoid
Length (µm): 18.4 (n=2)
Width (µm): 4.1 (n=2)
Pervalvar axis (µm): 10 (estimated)
Striae in 10 µm: 20 (dorsal striae, n=2); 42 (ventral striae, n=2)
Puncta in 10 µm: 44 (dorsal striae n=2)

Description: only a SEM description is given. Valves are semi-elliptical with slightly capitate apices. Dorsal margin is convex and the ventral margin more or less straight. The valves are vaulted and the dorsal striae are biseriate to about 1/2 or 2/3 of the length of the striae and become uniseriate towards the dorsal margin. The ventral striae are two times denser than the dorsal striae and are formed by transapically elongated single areolae. The ventral striae are not interrupted in the centre where they are reduced to extremely small puncta. The dorsal conopeum runs parallel to raphe branches, thus forming an obtuse angle. It is slightly expanded near the apices, just before it tapers abruptly near the distal raphe ends. The raphe branches are arranged in a weak but clear angle, with the central raphe endings approximate and very slightly deflected dorsally. The distal raphe endings are clearly turned to the dorsal side.

Notes: this specimen coincides with the descriptions and illustrations of *Halamphora* (*Amphora*) *tumida* given by Sar *et al.* (2004, type material), Garcia & Souza (2008) and Levkov (2009) but it is also very similar to *H. ghanensis* (Levkov 2009). In both mentioned taxa, the dorsal striae are biseriate near the raphe ledge and formed by two rows of alternating areolae, which are interrupted by longitudinal and fragmented siliceous thickenings towards the dorsal valve margin, thus giving a uniseriate-like facet to the striae. The main difference of our specimens to the ones illustrated in the above mentioned works seems to be the less thickened external costae (or inter-striae) which make the biseriate portion of the dorsal striae in those specimens to appear clearly sunken. Conversely, the ventral striae are uniseriate and transversely elongated as in the literature (where they appear with both round or elongated areolae) but are not completely interrupted on the central area and are slightly above the striae density range given by Sar *et al.* (2004). Finally, a last and minute difference is the fact that the specimens of *A. tumida* seems to have a rather straight raphe, with the central endings more distant from one another (Sar *et al.* 2004, Garcia & Souza 2008).

The angle of the raphe branches and the less thickened transverse dorsal costae makes the Tagus specimens all more similar to the freshwater western African species *H. ghanensis*, recently described by Levkov (2009). This author did not critically compare *H. ghanensis* to *H. tumida* and we find particularly difficult to distinguish between the two taxa, even with SEM, as both species share exactly the same ultrastructure of the dorsal striae and have uninterrupted ventral striae. The single row of dorsal areolar close to the raphe, typical in *H. ghanensis*, seems also to be present in *H. tumida*, as the observations made by Sar *et al.* (2004) and Garcia & Souza (2008) attest. *Halamphora ghanensis* diagnosis states that the dorsal striae are coarser (*i.e.* 14-16 in 10 µm) than in the Tagus estuary specimen and that the valves are larger (Levkov 2009).

The correspondence between specimens observed in SEM to the ones observed in LM can sometimes be very difficult, particularly in the case of the Catenulaceae. No match was found between this particular specimen and the ones encountered and micrographed in LM, in spite of coming from the same samples. Specimens of this taxon, when observed in LM, probably have invisible ventral striae and indistinctly punctate dorsal striae, slightly radiating throughout the valve, as is the case of *H. tumida* or *H. coffeaeformis*. *Halamphora* sp.1 (see below) has a similar size and also has dorsal striae with no distinct punctuations in LM, but it cannot be confused with this taxon, given the fact that it has slightly coarser dorsal striae density and visible ventral striae. Considering valve outline and striae density, this may mean that some of the larger specimens scored as *H. abuensis* could in fact correspond to this species. Therefore, the examination of a single specimen in SEM has proven to be insufficient to identify this taxon in light of the available literature. Therefore, this taxon is only tentatively identified as *Halamphora* cf. *tumida*.

Distribution & Ecology: unknown in our samples, but probably epipelic. *Halamphora tumida* is described as a brackish and marine, cosmopolitan species (Levkov 2009).

References:
Garcia & Souza (2008) – figs. 1-17
Levkov (2009) – pg. 239; figs. 102/9-16; 236/1-2,4
Sar *et al.* (2004) – figs. 1-14
Simonsen (1987) – figs. 654/12-19 (LM only)

Halamphora sp.1

Micrographs: Pl. 27: 1-6; Pl. 53: 1-4

Similar species:
Halamphora coffeaeformis (Agardh) Levkov
Halamphora acutiuscula (Kützing) Levkov
Halamphora exigua (Gregory) Levkov
Halamphora tumida (Hustedt) Levkov

Morphometrics:
Biovolume (µm^3): 951
Frustule geometry: half-rotational ellipsoid
Length (µm): 25.0 – (32.1) – 43.4 (n=13)
Width (µm): 4.3 – (5.3) – 7.0 (n=12)
Pervalvar axis (µm): 11 (estimated)
Striae in 10 µm: 15 – (16) – 19 (dorsal striae, n=13); 19 – (23) – 26 (ventral striae, n=10)
Puncta in 10 µm: 70 (dorsal striae, n=2)

Description: valves are semi-lanceolate, with the dorsal margin convex and the ventral margin usually slightly concave. Valve ends capitate. Axial area narrow and central area laterally expanded only towards the ventral side. In LM, the dorsal striae radiate slightly and have an indistinct structure, while the ventral striae are fairly conspicuous, formed by single, transversely elongated areola and are interrupted at the centre of the valve. A translucid longitudinal band covers the raphe and dorsal axial area. In SEM this structure is revealed as a wide partial conopeum (*cf.* Levkov 2009), running alongside the raphe, expanding to the dorsal side and covering the apices. The raphe more or less straight, with central raphe endings slightly deflected to the dorsal side. Internally, the distal raphe endings each finish in a small helictoglossa; while a tongue-like dorsal flap hides the central raphe endings (*i.e.* fused helictoglossae). The dorsal striae are formed by transapically elongated depressions which are perforated by a double row of fine pores throughout the whole length of the stria. The dorsal striae seem to be interrupted externally by a narrow longitudinal costa, running along the dorsal margin of the valve. Internally this siliceous expansion is not noticed. The ventral striae are probably uniseriate and are not completely interrupted in the centre of the valve, being reduced to very small round puncta in the central area.

Notes: the identification of this taxon proved to be extremely problematic and unsatisfactory. It is an excellent example of the difficulties that hinder the identification of many species belonging to the genus *Halamphora*. This has been brought about by the scarcity of EM studies of the type materials (see Archibald & Schoeman 1984; Clavero *et al.* 2000; Sala *et al.* 2006) but also by inconsistencies on the true identity of some well known taxa.
Considering the LM observations, the lack of punctuated dorsal striae, the valve outline and length makes the Tagus specimens very reminiscent of *Halamphora* (*Amphora*) *coffeaeformis sensu stricto* and *Halamphora* (*Amphora*) *aponina*. The former *A. coffeaeformis* var. *aponina*, considered a variety of *A. coffeaeformis* by Archibald & Schoeman (1984), was recently reassessed as a species on its own right, within the newly established genus of *Halamphora* (Levkov 2009). However there are patent differences between the Tagus specimens and both above

mentioned species, as they have a higher dorsal striae density (around 20 in 10 µm) and, in the case of *H. aponina*, the valves are considerably narrower when compared to the Tagus specimens.

In fact, the specimens found in our study correspond quite well to a type material specimen of *Amphora acutiuscula* (in Kützing's type slide BM 18173) depicted by Wachnicka & Gaiser (2007, fig. 15) and which they believe to be the correct characterization of the species. Their specimens seem to be very similar to the ones found in our study, in valve outline and length, striae density and the existence of a developed partial conopeum on the dorsal side of the raphe-sternum. In addition, the striae are not clearly punctate in LM and there is also an apparent dorsal marginal bar that may well correspond to the continuous longitudinal dorsal ridge seen in our material (see description above). However, our specimens seem to have slightly wider valves and, since Wachnicka & Gaiser (2007) did not provided SEM illustrations of *A. acutiuscula*, we could not infer with absolute certainty if the specimens found in the Tagus estuary correspond to the same taxonomic entity. As a matter of fact, Kützing's material of *A. acutiuscula* has not been yet studied in SEM.

Regarding *A. acutiuscula*, it should also be added that there is a considerable incongruence in the references concerning its true taxonomical identity. Archibald (1983), who also studied Kützing's type material of *A. acutiuscula* (type slide BM 18173) in LM, concluded that this confusion derives from the fact that there are different forms present in the type slide, none of which "had very clearly punctate striae" and , additionally, because there are two conflicting interpretations of *A. acutiuscula*. After studying Van Heurck's slide Nº 261 of *A. acutiuscula*, Archibald (1983) decided to follow the latter's definition of this taxon ,which restricts *A. acutiuscula* to specimens with distinctly punctate dorsal striae (in LM). This interpretation of *A. acutiuscula* became widely disseminated and it has been followed by many authors (*e.g.* Hustedt 1930, Bérard-Therriault *et al.* 1986, Snoeijs & Potopova 1995, Witkowski *et al.* 2000). Very recently, Levkov (2009) also preferred this interpretation when transferring this taxon to the new genus *Halamphora*. His SEM studies seem to conform with the EM observations of the "punctate taxon" made by Archibald (1983), which show the dorsal striae changing from a biseriate structure to a uniseriate one near the mantle, but neither Kützing's nor van Heurck's material were analysed in SEM. This feature of the dorsal striae is also common to *A. subholsatica* or to *A. tumida* (Sar *et al.* 2003b, Sar *et al.* 2004) and is clearly different from the biseriate dorsal striae found on the Tagus estuary taxon.

As for the specimens Archibald (1983) found in Kützing's putative type slide of *A. acutiuscula*, *i.e.* with no "clearly punctate striae" and with "distinct longitudinal band transversing the striae near the raphe" (possibly a partial conopeum), he did not clarify what the Kützing's specimens were, apart from being "closely allied to *A. exigua*". In fact, *A. exigua* does not seem to be closely related to either the Tagus estuary specimens or to the type specimen given by Wachnicka & Gaiser (2007). *A. exigua* lacks a developed conopeum and the raphe is very close to the ventral margin (Hendey, 1964).

Considering the SEM observations of the Tagus estuary material, these specimens are quite reminiscent of *A. coffeaeformis* type material, as it is described an illustrated by Archibald & Schoeman (1984). The fact that the dorsal striae are biseriate and the overall ultrastructure of the valves (seen in SEM) reinforce this closeness to *A. coffeaeformis*, particularly to the specimens illustrated by Bérard-Therriault *et al.* (1986), Sabbe (1997) and Sala *et al.* (1998). However, apart from the coarser dorsal striation mentioned above, such a conspicuous and continuous dorsal marginal ridge is not usually seen in that species (Archibald & Schoeman 1984).

The specimens depicted in the study by Bérard-Therriault *et al.* (1986) are probably conspecific to the Tagus estuary specimens and seem to share exactly the same difficulties in "fitting" in the accepted morphological variability of the type material of *A. coffeaeformis*, as shown by Archibald & Schoeman (1984), that is: coarser striation and a reinforced dorsal marginal ridge. Conversely, this last feature is commonly found in *H. aponina* (figs. 163-168, Archibald & Schoeman 1984; figs. 233/1-8, Levkov 2009). Additionally, numerous others similarities can be observed, especially when comparing striae ultrastructure, namely the fact that the dorsal interstriae striae are slightly reinforced in comparison to *A. coffeaeformis*. This is particularly true, when referring to the type material TEM observations made by Archibald & Schoeman (1984), who noticed that the valves had a "coarser appearance". A subsequent SEM study of the Kützing's *A. aponina* type material seems to be both promising and necessary. The SEM observations made by Levkov (2009) are from slightly different material which was not collected in the type locality.

In conclusion: a final identification of the Tagus estuary specimens was unattainable. The LM observations pointed in the direction of the original Kützing's type *A. acutiuscula* (and not to *A. acutiuscula sensu* van Heurck), both in valve size and striae density, while the SEM observations exposed the great ultrastructural similarities to *H. coffeaeformis* and, especially to *H. aponina*. Even though all the above mentioned species have been repeatedly studied (*e.g.* Archibald 1983, Archibald & Schoeman 1984, Wachnicka & Gaiser 2007, Levkov 2009) further work is still needed. Particularly SEM studies of Kützing's type material of both *A. acutiuscula* and *A. aponina* are direly required in order to finally determine the true nature of these taxa, as well as their relationship to the specimens found in the Tagus estuary.

Distribution & Ecology: *Halamphora* sp. 1 is probably a motile epipelic species. It was one of the most commonly found common *Amphora* species during our study with 27 occurrences and a maximal abundance of about 6%. Nevertheless, its distribution was restricted do the sandy stations, appearing throughout the sandy transect but also in the upper shore sandy station of the muddy transect, where it attained the maximal average abundance. It showed a seasonal peak in abundance in late winter and early spring.

References:

Bérard-Therriault *et al.* (1986) – pg. 408; figs. 12-14 (as *A. coffeaeformis*?)

Wachnicka & Gaiser (2007) – pg. 396; fig. 15-16 (as *A. acutiuscula*?)

***Halamphora* sp.2**

Micrographs: Pl. 27: 7-8, Pl. 53: 6 (Morphotype.1); Pl. 27: 9-13, Pl. 53:5 (Morphotype 2)

Similar species:
Amphora acutiuscula Kützing *sensu* Archibald
Amphora holsaticoides Nagumo & Kobayasi
Amphora pseudoholsatica Nagumo & Kobayasi
Halamphora holsatica (Hustedt) Levkov
Halamphora subholsatica Krammer
Halamphora tumida (Hustedt)

Morphometrics:

Morphotype 1
Biovolume (µm3): 345
Frustule geometry: half-rotational ellipsoid
Length (µm): 15.1 – (18.7) – 26.3 (n=12)
Width (µm): 3.8 – (4.2) – 4.6 (n=12)
Pervalvar axis (µm): 6 (estimated)
Striae in 10 µm: 17 – (19) – 22 (dorsal striae, n=9); 26 (ventral striae, n=1)

Morphotype 2
Biovolume (µm3): 799
Frustule geometry: half-rotational ellipsoid
Length (µm): 16.9 – (25.4) – 34.5 (n=17)
Width (µm): 3.8 – (5.5) – 6.7 (n=17)
Pervalvar axis (µm): 6 (estimated)
Striae in 10 µm: 14 – (17) – 20 (dorsal striae, n=17); 20 – (23) – 27 (ventral striae, n=17)

Description: valves semi-elliptical with rostrate to slightly capitate apices. Dorsal margin is convex and the ventral margin is more or less straight or slightly inflated. In some specimens the ventral striae are very conspicuous visible in LM and are interrupted at the centre, while in others the ventral striae were not visible in LM. In both cases, the dorsal striae radiate throughout the valve, although only very slightly at the centre. Their structure is clearly punctate in LM, particularly towards the dorsal margin.

Only two specimens, which were examined in SEM, could be tied to similar LM specimens in size and other morphometric parameters. In the case of the specimen in external valve view (Pl. 53: 6); the dorsal striae are composed mainly by a uniseriate row of rounded areolae, while the ventral striae consist of small single rounded puncta, probably invisible in LM. Below the dorsal partial conopeum, the proximal areolae of each dorsal stria is composed by several minute perforations (biseriate?), while the other areolae seem to be more simply structured and occluded internally. A well developed partial conopeum runs parallel to the raphe, with a constant breadth, until it tapers very abruptly in the apices. Externally, the central raphe endings are very slightly deflected dorsally, the distal raphe endings bend towards the dorsal side, skirting the conopeum end.

In the second specimen (Pl. 53: 5), we see only the valve interior and, in spite of similar size and striae densities, the ultrastructure details do not correspond completely to the former specimen's external view. The ventral striae are more conspicuous and composed by what seems to be transversely elongated areola. Additionally, the dorsal striae are only distinctly uniseriate near the dorsal margin and seem to start from the raphe ledge as biseriate. Near the raphe, there is an internal longitudinal rib, parallel to it, which separates the first row of areolae from the rest of the biseriate row of alternating puncta composing the biseriate portion of each dorsal stria.

Notes: as can be gathered from the description given above, at least two slightly different forms (species?) were scored together. The main criteria used during valve counts, *i.e.* valve size and density of the punctuated dorsal striae, were not sufficient to separate them. Further studies will be needed, both in LM and SEM, as it is still extremely difficult to tie the LM photos to a single interior valve view or an external view in SEM.

In any case, given the coincidence of morphometric parameters, it can be argued that most specimens with invisible ventral striae in LM correspond to the specimen with small rounded ventral areolae and are hereupon designated as morphotype 1. This diatom is very reminiscent of *H. holsatica*, with its clearly punctate, almost completely uniseriate dorsal striae and the distinctively convex dorsal margin. However, these specimens are smaller and have a higher dorsal striae areolae density than *H. holsatica*. Additionally, the areolae of the ventral striae are rounded, the central raphe endings are not distinctly dorsally bent and, just below the conopeum, the dorsal striae are biseriate and composed of small areolae, sunken in transapical depressions. This last feature does not occur in *H. holsatica* but it is quite typical of *H. sydowii*, as it is described and illustrated by Levkov (2009, Fig. 242/1-4). In addition, this taxon does not have ventral striae visible in LM and has dorsal striae with discernible punctuation in LM. It should be noted, nonetheless, that the areolae of the ventral striae of *H. sydowii* are transversely elongated; there is no interruption of the ventral striae on the central area and the dorsal striae seem to be more finely punctuated than in the Tagus estuary specimens.

Amphora sp. 6, described by Sabbe (1997), is also very reminiscent of the morphotype 1. The ventral striae are interrupted in the central area and have a density of around 26 striae in 10 µm (as in Pl. 27:6) but are not usually obvious in LM. The biseriate part of the dorsal striae is also limited to the area adjacent to the raphe ledge. Finally, they also have a clearly convex dorsal margin and are probably conspecific to our morphotype 1 specimens.

With regard to the specimens with visible, elongated areolae composing the ventral striae (clearly distinct in LM), they most probably match the second specimen described with SEM; hereupon designated as morphotype 2. A closer look on the dorsal striae of these specimens does seem to suggest that the dorsal striae near the raphe ledge are formed by compacted areolae and then turn to clearly individual punctae, near the margin (Pl. 27: 9-13; Pl. 53: 5). This last feature makes morphotype 2 close to the group of punctate species around *A. acutiuscula sensu* van Heurck (see discussion above *Halamphora* sp.1) but also to species that do not have punctate dorsal striae in LM, such as *H. ghanensis* or *H. tumida* (see above).

Morphotype 2 is very reminiscent to the punctate *A. acutiuscula* specimens, depicted by Archibald (1983, figs. 490-492). It also shows remarkable resemblances to the specimens to *A. subholsatica*, depicted by Witkowski *et al.* (2000). These morphological similarities include comparable size ranges, ventral and dorsal striae densities and the fact that the raphe shows a weak angle (*cf. A. subholsatica*, see Snoeijs & Balashova 1998).

Amphora subholsatica was originally described by Krammer (1997), being critically compared to *A. holsatica* and close species by this author, Sar *et al.* (2003) and Levkov (2009, as *Halamphora subholsatica*). Sar *et al.* (2003) stressed that the biseriate structure of the dorsal striae near the raphe ledge and the shift to a uniseriate portion near the margin (*i.e.* in a similar way to morphotype 2 specimens), could well indicate that *A. subholsatica* is conspecific, or at least closely related to the South African specimens of *A. acutiuscula* depicted by Archibald (1983, see *Halamphora* sp. 1 and discussion above). Conversely, the SEM observations of material from the Finish coast made by Levkov (2009) shows specimens in external view with uniseriate dorsal striae which are composed by large elongated areolae. Nonetheless, their internal structure is biseriate, which means the striae ultrastructure is different from *H. holsatica* but also from the group around *A. acutiuscula sensu* van Heurck and, therefore from our own material. It should be noted that the original text illustrations given by Krammer (1997) are not entirely conclusive on the exact ultrastructure of the dorsal striae and further research on the type material is advisable. If the observations made by Levkov (2009) are confirmed, then morphotype 2 or *A. acutiuscula* depicted by Archibald (1983) cannot be considered as *H. holsatica*.

In conclusion: even though it seems clear that two different entities were scored together during counts, it was not possible to determine with certainty the identity of either of them. The scarcity of SEM micrographs of the Tagus specimens, together with complex or incomplete studies of similar and closely-related taxa did not allow reaching a final and satisfactory decision on their respective identity.

Distribution & Ecology: probably a motile epipelic diatom. It occurred almost exclusively in the sandy stations (35 occurrences). They were not very abundant during the study period but, in January 2003, there was a peak in abundance on the medium/coarse sandy stations (3-5% in relative abundances). *Amphora subholsatica* is described has a brackish water species, found in inland saline waters and coastal areas (Witkowski *et al.* 2000, Levkov 2009), *A. acutiuscula sensu* van Heurck is considered a cosmopolitan species, present in marine to brackish-water coastal areas (Witkowski *et al.* 2000, but see discussion above). Sabbe (1997) reported his *Amphora* sp. 6 as common in the mesohaline reaches of the Westerschelde estuary and present in different sediment types. He also noticed it was present in Salah's material from Blakeney Point (North Sea coast, U.K.).

References:
Archibald (1983) – pg. 34; figs. 1/3-4, 3/89-92, 23/490-492 (morphotype 2(?), as *A. acutiuscula*)
Sabbe (1997) – pg. 233; figs. 25/1-6, 58/1-2 (morphotype 1(?), as *Amphora* sp. 6)
Snoeijs & Potopova (1995) – # 209 (morphotype 2(?) as *A. acutiuscula*)
Witkowski *et al.* (2000) – fig. 161/18-19 (morphotype 2(?) as *A. subholsatica*); figs. 161/10-13

Amphora cf. ***subacutiuscula*** Schoeman 1972

Micrographs: Pl. 27: 30-33; Pl. 53: 8

Similar species:
Halamphora acutiuscula (Kützing) Levkov
Halamphora coffeaeformis (Agardh) Levkov
Halamphora exigua (Gregory) Levkov
Halamphora salinicola Levkov & Diaz
Halamphora tumida (Hustedt) Levkov

Morphometrics:
Biovolume (µm^3): 190
Frustule geometry: Half-rotational ellipsoid
Length (µm): 11.5 – (17.2) – 25.2 (n=5)
Width (µm): 2.6 – (3.2) – 4.3 (n=5)
Pervalvar axis (µm): 9 (estimated)
Striae in 10 µm: 26 – (29) – 32 (dorsal striae, n=5)

Description: valves are semi-elliptical, with a convex dorsal margin and a somewhat linear ventral margin. The apices are only slightly produced and cuneate. The raphe is arcuate and, if the specimen observed in SEM was correctly allocated here, it appears that the central endings are proximate but separated by a distinct central nodule, a typical *Halamphora*-like fused helictoglossae. The ventral striae are invisible or barely visible in LM, whereas the dorsal striae are clearly coarser at the centre of the valve. They are parallel at the centre and slightly radiate at the ends.

Notes: these specimens were mainly identified by valve size and outline and the typically coarser central dorsal striae and the indistinct structure (in LM) of the ventral side of the valve. They correspond fairly well to the description and illustrations of *A. subacutiuscula* by Archibald (1983) and of *A.* cf. *subacutiuscula* by Sabbe (1997). Only a few individuals were found and, since Archibald (1983) pointed out that "the correct identity of *A. subacutiuscula* Schoeman (l.c.) is not certain", it was decided to follow Sabbe (1997) and refer to this taxon as *A.* cf. *subacutiuscula*.
Amphora cf. *subacutiuscula* shows close similarities to several members of the *Halamphora* genus, such as *H. coffeaeformis*. Likewise, *Amphora subacutiuscula* also has numerous *Halamphora* features but has not yet been formally transferred to the new genus recently created by Levkov (2009). The specimens from the Tagus estuary, as well as the type material of *Amphora subacutiuscula* need to be studied thoroughly in SEM.

Distribution & Ecology: Sabbe reported *Amphora* cf. *subacutiuscula* as common in fine sandy sediments of the Westerschelde estuary and considered it to be a motile epipelic diatom. In our study it was not very frequent (only 11 occurrences) and it was only found in the sandy stations but always at very low abundances (max. abundance < 0.62%). It occurred mainly in the lower shore stations of the sandy transect, composed mostly of medium and coarse sands.

References:

Archibald (1983) – pg. 56; figs. 134-136, 508-512.
Sabbe (1997) – pg. 227; figs. 26/8-16; 57/2,6
Wachnicka & Gaiser (2007) – pg. 409; fig. 71
Witkowski *et al.* (2000) – pg. 151; figs. 161/7

Amphora cf. ***tenuissima*** Hustedt 1955

Micrographs: Pl. 27: 22-29; Pl. 52: 10-14

Synonyms:
Amphora tenellula Giffen

Similar species:
Amphora luciae Cholnoky
Amphora tenerrima Aleem & Hustedt
Amphora tenuissima Hustedt

Morphometrics:
Biovolume (µm^3): 102
Frustule geometry: half-rotational ellipsoid
Length (µm): 7.5 – (10.8) – 18.6 (n=41)
Width (µm): 2.1 – (3.0) – 3.9 (n=40)
Pervalvar axis (µm): 5 (estimated)
Striae in 10 µm: 21 – (26) – 31 (dorsal striae, n=40); 35 – (41) – 47 (ventral striae, n=8)
Puncta in 10 µm: 35 – (42) – 46 (dorsal striae, n=3)

Description: valves semi-elliptical with rostrate to slightly capitate apices. Dorsal margin convex and ventral margin slightly inflated (*i.e.* convex) at the centre. In LM, ventral striae are invisible; the dorsal striae radiate throughout the valve, although only very slightly at the centre. Their structure is indistinct in LM. In SEM, the dorsal striae are composed by a uniseriate row of rounded to elliptical, irregularly positioned areolae, while each ventral stria consists of a single transversely elongated slit. In the dorsal striae, each areola seems to be composed by several perforations which, in the case of the first (*i.e.* proximal) areola, are usually fused in two kidney-shape holes per areola. The ventral striae are not interrupted in the central area but are reduced to very small slits, defining a half elliptical central area. A well developed dorsal conopeum is present and it is sometimes seen in LM, as a longitudinal line running parallel to the raphe. In SEM the valve is vaulted and the dorsal conopeum is placed over a shallow groove, close to the raphe, covering the proximal areolae of the dorsal striae. The conopeum is of equal breadth along the axial area but it tapers abruptly near the apices. Externally, the central raphe endings are very slightly deflected dorsally, the distal raphe endings bend towards the dorsal side, at the conopeum end. Internally, the central raphe ends are hidden beneath a tongue-like siliceous expansion (*i.e.* fused helictoglossae as in *H. coffeaeformis*) and the distal raphe endings terminate in small helictoglossae. The dorsal cingulum is composed by at least 6 copulae, each bearing two rows of small round poroids.

Notes: given its small average size, valve outline and the fact that the ventral striae are irresolvable in LM, *Amphora* cf. *tenuissima* belongs to the group of brackish marine taxa around *A. tenerrima* and *A. tenuissima*. This group has long been known for its extreme complexity (*e.g.* Aleem & Hustedt 1951, Sullivan 1979) and recently Clavero *et al.* (2000) characterized the type materials of the above mentioned taxa in SEM. As it was the case with other studies (Sullivan 1979, Bérard-Therriault *et al.* 1986), the specimens found in our study do not completely correspond to either *A. tenerrima* or *A. tenuissima*, or to others, such as the recently described species *A. pseudotenuissima* (Wachnicka & Gaiser 2007).

Levkov (2009) did not transfer *A. tenuissima* or *A. pseudotenuissima* to the new genus *Halamphora*, he only transferred *A. tenerrima*, which he personally studied. It is clear, however, that *A. tenuissima* (see figs. 32-33 in Clavero *et al.* 2000), as well as our specimens, do possess the tongue-like expansion, forming the fused central helictoglossae. A formal transfer to the new genus is, therefore recommended.

This taxon found in our study has similar dorsal striae density and the size range of *H. tenerrima*. Given the possibility of both taxa being present in the samples, they could have been scored together, during the cell counts, as they are particularly difficult to distinguish in LM. However, there are clear differences between the two taxa, but most of them refer to features only seen in SEM. In any case, *Amphora* cf. *tenuissima* has: 1) a finer poroid density in the connective bands; 2) dorsal margin is convex even in the larger specimens and never parallel to the ventral margin, which is usually slightly convex (not parallel as in *A. tenerrima*); 3) dorsal striae are monoseriate (not biseriate as in *A. tenerrima*) and not interrupted by a longitudinal costa in the dorsal margin; 4) ventral striae are slightly denser and are not interrupted in the central area, even though they are reduced to small rounded puncta; 5) the conopeum is not dorsally expanded and is truncated near the apices.

In fact, the taxon found in our study is very reminiscent of *A. tenuissima*, especially of *A. pseudotenuissima*. The main common features are the irregular, more or less elongated, puncta composing the monoseriate stria and the conopeum shape, with truncated distal ends. However, both species have striae densities clearly above 30 in 10 µm, which is the upper limit of the striae density of the specimens allocated to *Amphora* cf. *tenuissima* (Figure 27, see *H.* cf. *abuensis*).

Finally, it is also possible that these specimens correspond to Form B of *A. tenuissima*, described by Clavero *et al.* (2000) and selected by Simonsen (1987, pl. 664/9-11) to illustrate the type of *A. tenuissima* (Sabbe 1997; Clavero *et al.* 2000). This form has a striation density of 30 in 10 µm and the dorsal striae have irregularly spaced puncta, according to Clavero *et al.* (2000). However only two SEM micrographs of the valve interior of one specimen are depicted by Clavero *et al.* (2000) and although it corresponds quite well to the internal valve views of our specimens, it is not sufficient to make a positive match. The taxon *Amphora* sp. L06, described by Wachnicka & Gaiser (2007), probably also matches *A. tenuissima* form B, given its several similarities. The specimens studied by Sullivan (1979) are also very reminiscent of *A. tenuissima* and have irregular areolation of the dorsal striae; however, their connective bands do not have rounded areola (*cf. A. tenuissima* and our specimens). Finally the taxon mistakenly identified as *A. tenerrima* by Bérard-Therriault *et al.* (1986) has uniseriate dorsal striae and similar range, in several morphometric features, to the specimens found in the Tagus estuary. Needless to say that further studies are needed to clarify the actual relations between all these taxa.

Distribution & Ecology: this species is probably adnate or a small motile epipsammic diatom. It occurred almost exclusively in the sandy stations (45 out if 49 occurrences) being found throughout the study period, with a slight increasing in numbers during spring. It was one of the most commonly found *Amphora* species and it was particularly abundant in the medium/coarse sands of the lower shore stations of the sandy transect (max abundance < 8.5%).

ORDER BACILLARIALES

Fam. Bacillariaceae Ehrenberg

Bacillaria Gmelin (1788) *emend.* Schmid & Jahn 2007

Genus description: Round *et al.* (1990); Schmid (2007); Jahn & Schmid (2007)

As one of the oldest described diatom genus, *Bacillaria* has long been considered a monospecific, ubiquitous and cosmopolitan taxon (*e.g.* Hendey 1964, Krammer & Lange-Bertalot 1988, Witkowski *et al.* 2000, Ussing *et al.* 2004) with a unique and typical colony formation. Recently, Schmid (2007) established that there are at least three morphologically different groups that can produce *Bacillaria*-like colonies and that only the group comprising brackish-freshwater taxa belong to the revised *Bacillaria s.s.* (Jahn & Schmid 2007) given that it includes the type species *B. paxillifera*.

Bacillaria paxillifera (O. F. Müller) Hendey 1951

Micrographs: Pl. 29: 7, Pl. 54: 7

Synonyms:
Bacillaria paradoxa Gmelin
Vibrio paxillifer O.F. Müller

Morphometrics:
Biovolume (μm^3): 2721
Frustule geometry: box
Length (µm): 74.7 – (77.9) – 83.4 (n=3)
Width (µm): 6.6 – (7.0) – 7.4 (n=3)
Pervalvar axis (µm): 5 (estimated)
Striae in 10 µm: 23 – (24) – 25 (n=4)
Punctae in 10 µm: 53 (n=3)
Fibulae in 10 µm: 7 (n=1)

Notes: the specimens found in the Tagus estuary correspond to the description of *B. paxillifera* given in detail by Jahn & Schmid (2007) and Schmid (2007). Many morphological features such as the deep mantle, branched transapical ribs, uniseriate striae and the raphe structure (*e.g.* T-shaped external raphe endings, irregular flange) correspond completely to our observations.

Distribution & Ecology: According to Jahn & Schmid (2007) this taxon is colonial and epipelic or epiphytic, living in brackish water or in freshwaters with high electrolyte content, subject to great fluctuations on salinity. In our study it occurred only once but it is a commonly found species in other Tagus estuary intertidal flats (*e.g.* Ribeiro 2003). Apparently it is frequent in European coasts (*e.g.* Baltic Sea) and inland saline lakes (*e.g.* Neusiedler See), but the alleged worldwide distribution needs yet to be confirmed.

References:
Krammer & Lange-Bertalot (1988) – pg. 8; fig. 87/4-7
Jahn & Schmid (2007) – figs.1-4, 12-17
Round *et al.* (1990) – pg. 608, figs. a-b
Schmid (2007) – figs. 1/a,b,g, 4/a-f, 7/a,b, 8/a-c, 9/a,
Witkowski *et al.* (2000) – pg. 357, 212/9-12

Cylindrotheca Rabenhorst 1859

Genus description: Reimann & Lewin (1964); Reimann *et al.* (1965); Round *et al.* (1990).

Jahn & Kusber (2005) recently proposed the reinstatement of the genus *Ceratoneis*, which has priority over the name *Cylindrotheca*, using *Ceratoneis closterium* as the lectotype. However and despite of being incorrect according to the ICBN, Medlin & Mann (2007) proposed the conservation of *Cylindrotheca,* using *C. gerstenbergeri* Rabenh. Grunow (syn. *C. gracilis* Bréb. *ex* Kütz.) as the lectotype. The authors point several reasons for this measure, namely the 100-year consistency, although technically incorrect, of the use of *Ceratoneis* as an araphid freshwater diatom genus. The additional nomenclatural confusion brought to the ever growing literature of two model organisms, *C. fusiformis* and *C. closterium* which, in the latter case, is already hampered by this enduring use of the synonym *Nitzschia closterium* (*e.g.* Espinosa *et al.* 2008, Levy *et al.* 2009) should also be avoided and countered.

According to Round *et al.* (1990), "*Nitzschia* and *Cylindrotheca* are closely related but the reduced and slightly silicified valves, the spiral twist of the frustule (present in *C. closterium* but only near the poles), the fibula structure and the girdle together serve to separate *Cylindrotheca* from all other 'nitzschioid' genera". The fibulate raphe system is similar to the one found in *Bacillaria* (Schmid 2007), with the raphe fissure bordered by reinforced strips or ribs and by the arched (*i.e.* "arcuate") fibulae serving as clamps, holding the structure together (*viz.* Reimann *et al.* 1965). This type of raphe architecture is much simpler than the "canal-raphe" system, seen in the *Nitzschia sensu stricto*, *Epithemia* or *Surirella*, in which a more or less separate marginal cytoplasmic channel is clearly defined (sometimes forming keel) and linked to rest of the cell by a series of perforations (see Round *et al.* 1990, pg. 46, figs. 37).

Cylindrotheca closterium (Ehrenberg) Reimann & Lewin 1964

Micrographs: Pl. 28: 1-2

Synonyms:
Ceratoneis closterium Ehrenberg
Nitzschia closterium (Ehrenberg) W. Smith

Similar species:
Nitzschia longissima (Brébisson *in* Kützing) Grunow
Nitzschia reversa W. Smith

Morphometrics:
Biovolume (μm^3): 247
Frustule geometry: rotational ellipsoid
Length (μm): 53.8 – (70.8) – 100.4 (n=5)
Width (μm): 2.6 – (3.8) – 5.0 (n=5)
Fibulae in 10 μm: 12 – (14) – 16 (n=2)

Notes: this taxon is known by the synonym *N. closterium* in most of the major floras (*e.g.* Hustedt 1930, Germain 1981, Krammer & Lange-Bertalot 1988, Witkowski *et al.* 2000). The reason for this is its unique position among the other *Cylindrotheca* species, namely the horned-fusiform shape and, especially, the lack of twisting of the raphe in the mid-portion of the valve (*e.g.* Germain 1981). However, like Hasle & Syversten (1996) pointed out, *Cylindrotheca* does not belong to *Nitzschia sensu stricto* and several molecular studies have shown that they constitute an isolated cluster within the Bacillariaceae (*e.g.* Medlin 1990, Lundholm *et al.* 2002). It may well be a species complex (Haitao *et al.* 2007) which is an additional reason for not using this taxon as the lectotype of the genus (c.f. *Ceratoneis*, Jahn & Kusber 2005).

In estuarine and coastal waters it can be confused with weakly silicified *N. longissima* or with *N. reversa*. *Nitzschia longissima* usually has straight apical extremities and is very finely striated (*e.g.* Hendey 1964, Hasle & Syversten 1996), while *N. reversa* has the finely drawn ends typically bent in opposite directions (Germain 1981).

Distribution & Ecology: cosmopolitan species usually referred as marine planktonic (Hasle & Syversten 1996) even in estuarine

environments (*e.g.* Lucas *et al.* 2001, Coutinho 2005, Brogueira *et al.* 2007). Actually, it is a mainly epipelic diatom, as the other *Cylindrotheca* taxa (Reimann & Lewin 1964), but it is easily resuspended and spends some time in the plankton (Round *et al.* 1990). It is perfectly adapted to benthic environment being highly mobile and greatly responsible for the exopolysaccharide (EPS) production in the intertidal mudflats (*e.g.* Staats *et al.* 2000b, Underwood & Provot 2000). Our own microscopic observations of live material noticed that certain *C. closterium* individuals had the ability of actively bending and flexing the finely drawn apices.
The marine planktonic forms could correspond to cryptic species (Haitao *et al.* 2007), allocated within *C. closterium s.l.*, and not related to the specimens of *Ceratoneis closterium*, collected by Ehrenberg in the rising tide North Sea water, near Cuxhaven (Jahn & Kusber 2005).
The main reason for the lack of consistent reports of *C. closterium* in coastal benthic diatom studies is due to the fact that their fragile frustules are completely destroyed by the classic acid-cleaning methods and are, therefore, seriously underestimated in the benthic diatom assemblages (Sabbe 1997). They can only be accounted for in fresh material (Hustedt 1930), incinerated material slides or lugol preserved samples used, for example, in the Utermöhl technique (Hasle 1978a), applied in standard phytoplankton research.
Thanks to the use of slides of incinerated material (see section 3.1.2) we were able to estimate the contribution of *C. closterium* to the benthic assemblages. It was one of the most common epipelic species (49 occurrences), present in all sites (Table 17), particularly in the mudflat transect stations and the lower shore sand station. This spatial distribution, favouring the offshore stations near the channel, is probably not only linked to the presence of silt in the sediment but also to the deposition-resuspension cycle (*cf.* de Jonge & van Beusekom 1995) to which this species is strongly susceptible.

The species had a strong seasonal signal, being especially abundant in late spring and early summer (Figs. 18 and 19, section 4.5). This abundance peak is replicated in other studies in European coasts (Table 9, section 5.3.2). In the Sado estuary, south of the Tagus estuary, the seasonal bloom of *C. closterium* in the planktonic community was registered slightly later, *i.e.* August-September by Coutinho (2005).

Table 17 – Occurrence (%), average relative abundances (%) of *C. closterium* and average mud content (%) per sampling station. Standard deviation given within brackets.

Station	Occurrence	Abundance	Mud content
A1	36	0.9 (2.2)	2.3 (1.0)
A2	55	0.7 (0.9)	5.4 (2.4)
A3	91	4.7 (6.1)	7.7 (3.1)
V1	83	3.8 (3.0)	13.5 (9.3)
V2	91	3.0 (3.1)	90.0 (7.3)
V3	75	4.3 (5.9)	96.5 (2.2)

References:
Bérard-Therriault *et al.*(1999) – pg. 63; 55/d-e
Krammer & Lange-Bertalot (1988) – pg. 124; 87/1-2 (as *N. closterium*)
Reimann & Lewin (1964) – figs. 124/1-6, 125/1-8, 126/1-4,6
Round *et al.* (1990) – pg. 626, fig. a, c, h, i
Snoeijs (1993) – #33
Witkowski *et al.* (2000) – pg. 374; 212/4-6 (as *N. closterium*)

Cylindrotheca* cf. *gracilis (Brébisson *in* Kützing) Grunow *in* Van Heurck 1882

Micrographs: Pl. 28: 3-5, Pl. 54: 8

Synonyms:
Cylindrotheca gerstenbergeri Rabenhorst
Ceratoneis gracilis Brébisson *in* Kützing
Nitzschiella gracilis (Brébisson *in* Kützing) Rabenhorst

Similar species:
Cylindrotheca fusiformis Reimann & Lewin
Cylindrotheca signata Reimann & Lewin

Morphometrics:
Biovolume (µm^3): 639
Frustule geometry: rotational ellipsoid
Length (µm): 62.0 – (76.3) – 126.7 (n=7)

Width (µm): 2.8 – (3.6) – 4.0 (n=7)
Fibulae in 10 µm: 18 – (19) – 22 (n=9)

Notes: the three species of needle-shaped *Cylindrotheca* (*i.e. C. fusiformis*, *C. gracilis* and *C. signata*), described by Reimann & Lewin (1964), are not very easily distinguished and can all live in same habitat (*i.e.* marine littoral mud). *Cylindrotheca fusiformis* differs from the other two by the fact that it is slightly smaller and has slightly higher fibulae density but the main differences are the swelling of the frustule in the middle of the cell and two additional hyaline strips bordering the raphe, one at each side.

As for *C. gracilis* and *C. signata,* the discriminating feature is the silicified strips, bordering the raphe fissure, which are perforated in *C. signata*. Unfortunately, this can only be clearly seen in TEM (figs. 129/3b-4; Reimann & Lewin 1964). *Cylindrotheca signata* is slightly shorter and slender and has lower fibulae density than *C. gracilis*, in particular when considering *C. gracilis* var. *major*, but there is a large overlap in size range and fibulae density (Reimann & Lewin 1964, Krammer-Lange-Bertalot 1988). Our LM and SEM observations were insufficient to determine if the specimens found in our study are .*C. signata* or small *C. gracilis* specimens. As both taxa seem almost impossible to distinguish in LM, an interesting question on the distribution of both species in European coasts is raised. *Cylindrotheca gracilis* is commonly referred in most European floras (*e.g.* Germain 1981, Krammer & Lange-Bertalot 1988, Witkowski *et al.* 2000), including from the British Isles (Hendey 1964), while *C. signata* is a much obscure taxa, mainly appearing in ecological MPB studies on the British coasts (*e.g.* Paterson 1988, Underwood 1994, Bellinger *et al.* 2005) after the original description by Reimann & Lewin (1964). Whether *C. signata* is limited to the British Isles needs to be confirmed with TEM studies on British and continental material.

Our specimens do look extremely similar to *C. signata* as it is illustrated in MPB ecological studies from the British Isles (*e.g.* Underwood, 1994). However, it is impossible to validate this identification with only SEM and LM, therefore, we prefer to designate this taxon temporarily by *C.* cf. *gracilis*.

Distribution & Ecology: both *C. gracilis* and *C. signata* are referred as motile epipelic species living in marine littoral mud. Reimann & Lewin (1964) stated that the nominate variety of *C. gracilis* lives in freshwaters with high saline content (*e.g.* Neusiedler See), while the larger *C. gracilis* var. *major* lives in the marine littoral. However, Krammer-Lange-Bertalot (1988) raised some doubts on the validity of the separation of these two varieties and, consequently, on the spatial distribution of *C. gracilis/*C. *gerstenbergeri*. For instance, Van Heurck's authenticated "type" slide of *C. gracilis* (Type 417, Medlin & Mann 2007) was made from material collected in Wedel, downstream from Hamburg and probably was sampled in the brackish water reaches of the Elbe estuary, since the accompanying species is *Navicula pygmaea* Kützing.

In our study, *C.* cf. *gracilis* was one of the most common motile epipelic species (38 occurrences), even though it appeared almost exclusively in the muddy transect (Table 18). It was also one of the most abundant diatoms in the mudflat stations (max. abundance < 55.5%), showing a strong seasonal signal (*cf. C. closterium*), particularly in late summer and early autumn. As it was the case with *C. closterium*, the contribution of this species would have been completely underestimated if only the peroxide-cleaned slides were counted.

Table 18 – Occurrence (%), average relative abundance (%) of *C.* cf. *gracilis* and average mud content (%) per sampling station. Standard deviation given within brackets.

Station	Occurrence	Abundance	Mud content
A1	0	0.1 (0.3)	2.3 (1.0)
A2	9	0.1 (0.2)	5.4 (2.4)
A3	55	0.5 (0.7)	7.7 (3.1)
V1	67	1.4 (1.8)	13.5 (9.3)
V2	82	7.7 (7.4)	90.0 (7.3)
V3	100	22.5 (16.6)	96.5 (2.2)

References:

Germain (1981) – pg. 324; fig. 120/
Hendey (1964) – pg. 284
Krammer & Lange-Bertalot (1988) – pg. 134; 87/3
Reimann & Lewin (1964) – pl. 126-129

Underwood (1994) – fig. 24
Witkowski *et al.* (2000) – pg. 212; fig. 212/7

Nitzschia Hassall 1845

Genus description: Round *et al.* (1990)

Comprising more than 900 valid taxa (Lundholm & Moestrup 2000), *Nitzschia* is one of the largest and most difficult diatom genus. The reasons for this are multiple, many of them are discussed, for example, by Mann (1986), Lundholm & Moestrup (2000) or Witkowski *et al.* (2004a).
One of the reasons highlighted by these and other authors is the delicate structure and similar morphology of many species, which hinders a correct and easy identification. This seems to be especially true in the section "*Lanceolatae*" (see discussion below *N.* cf. *aequorea*). Another important reason pointed out, namely by Mann (1986) is the lack of a recent and comprehensive monograph of the genus, which particularly afflicts the marine taxa (Witkowski *et al.* 2004a).
Furthermore, there is a lack of con*sensu*s on the status of several sections within the Nitzschia *s.l.* (see discussion below *Tryblionella*). The genus *Nitzschia* has been traditionally divided in many sections, most of them established by Grunow (see Hendey 1964). Mann (1978) gives a detailed description and historical background of all sections of *Nitzschia sensu lato* established by Grunow.

Nitzschia cf. ***aequorea*** Hustedt 1939

Micrographs: Pl. 33: 12-15

Synonyms:
Nitzschia subfrustulum Hustedt
Nitzschia stimulus Cholnoky

Similar species:
Nitzschia agnita Hustedt
Nitzschia lanceolata W. Smith var. *minima* Peragallo & Peragallo
Nitzschia rosenstockii Lange-Bertalot
Nitzschia pusilla (Kützing) Grunow emend. Lange-Bertalot

Morphometrics:
Biovolume (µm^3): 145
Frustule geometry: prism on parallelogram
Length (µm): 9.4 – (17.1) – 28 (n=37)
Width (µm): 2.4 – (3.3) – 4.8 (n=32)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 31 – (34) – 37 (n=6)
Fibulae in 10 µm: 13 – (15) – 19 (n=35)

Description: valves typically lanceolate with convex margins and acute slightly produced weakly capitate apices. Raphe strongly eccentric with short fibulae, more or less evenly spaced. The central fibulae are not more widely spaced. The striae are barely visible in LM.

Notes: this taxon is part of *Nitzschia* sect. *Lanceolatae*, a section that also includes *N. aurariae*, *N. frustulum* and *N. valdestriata*. Most members of this section are very difficult to identify given the character poor frustule morphology in LM, the enormous number of species (more than 300, according to Mann, 1978) and the fact that many of them seem to grow in similar habitats. To this it should be added that many superfluous taxa were described and that some species descriptions have been based on the observation of very few specimens resulting in several species with similar valve outlines and overlapping striation and fibula densities (see comments by Sabbe 1997). An enormous effort was carried out in the past decades, particularly by Lange-Bertalot and colleagues (Lange-Bertalot 1976, Lange-Bertalot & Simonsen 1978, Lange-Bertalot 1980, Lange-Bertalot & Krammer 1987, Krammer & Lange-Bertalot 1988), in trying to sort out this "most problematic group of diatoms" (see discussion by Krammer & Lange-Bertalot 1988, pg. 76). This task was daunting, since it had to be mainly based in SEM studies of type materials, in a group where many species are known for their extreme plasticity in size range and/or striae and fibulae density (*e.g. N. intermedia*, Krammer & Lange-Bertalot 1988) and, for most cases, there is incomplete autoecological data. In spite of these great efforts many taxonomic problems concerning species of this group still remain unresolved, particularly in regard to marine or brackish-water species.

Such is the case of this particular taxon; it clearly belongs to the species-complex around *N. aequorea* and *N. agnita*, which includes many brackish water taxa (see discussion by Krammer & Lange-Bertalot 1998, pg. 116). The main difference between these two particular species seems to be striae density (*i.e.* higher than 35 striae in 10 µm in *N. agnita*; between 32-35/10 µm in *N. aequorea*). *Nitzschia rosentockii* and *N. lanceolata* var. *minima* are also likely candidates, particularly given the size-range. However, latter taxon is poorly defined and the type material is probably lost (Krammer & Lange-Bertalot 1988); whereas the former species is from electrolyte- rich freshwaters (Lange-Bertalot 1980).

It is possible that the specimens found in our study belong to a set of different species (with some specimens belonging *to N. pusilla* cf. Snoeijs & Potapova 1995, # 267) but we failed to seem any discontinuity in length *vs*. width, fibulae *vs*. length or fibulae *vs*. width plots, obtained from our morphometric data. Moreover, this fragile species was not studied in SEM. Therefore, this taxon can only be tentatively identified as *N.* cf. *aequorea*. The main reasons supporting this tentative claim are the fact that the striae are around 35 in 10 µm (see above) and the specimens are in average smaller than the that what has been reported for *N. agnita,* which has a size range of 18-40 µm (*viz.* Hustedt 1939, Hustedt 1957, Archibald 1983, Witkowski *et al.* 2000).

Table 19 – Occurrence (%), average relative abundance (%) of *N.* cf. *aequorea* and average mud content (%) per sampling station. Standard deviation given within brackets.

Station	Occurrence	Abundance	Mud content
A1	36	0.2 (0.3)	2.3 (1.0)
A2	55	0.2 (0.3)	5.4 (2.4)
A3	64	0.4 (0.4)	7.7 (3.1)
V1	83	1.4 (1.7)	13.5 (9.3)
V2	91	1.3 (1.1)	90.0 (7.3)
V3	42	0.3 (0.7)	96.5 (2.2)

Distribution & Ecology: motile epipelic species. According to Lange-Bertalot & Simonsen (1978), *N. aequorea* has been only occasionally recorded and even Hustedt (1939) found it rarely in the original material from sandy muddy flats of the North Sea coast ("im Schlicksandwatt", Simonsen 1987). Witkowski *et al.* (2000) considered this species to be "widespread" (cosmopolitan). Regarding *N. agnita,* it has been mainly reported for South Africa (see discussion by Archibald 1983, pg. 232). It is possible that this very taxon has also been identified as *N. lanceolata* var. *minima* (*viz.* Peragallo & Peragallo 1897-1990) or *N. rosenstockii* (*cf.* Sabbe 1997). In our study this taxon was one of the most frequently found species of *Nitzschia* (42 occurrences), being present in all stations (*i.e.* in muddy and sandy sediments) but it was more commonly found in the muddy transect (Table 19). It was never very abundant (max. abundance < 5%) being slightly more common during winter and spring.

References:

Hustedt (1939) – pg. 663; fig. 120
Krammer & Lange-Bertalot (1988) – pg. 117; 82/1-5
Kuylenstierna (1989-1990) – fig. 811
Lange-Bertalot & Simonsen (1978) – pg. 15; figs. 179-180
Simonsen (1987) – figs. 382/15-20
Witkowski *et al.* (2000) – pg. 367; fig. 210/14-15

Nitzschia angularis W. Smith 1853

Micrographs: Pl. 29: 5-6, Pl. 55: 3-5

Synonyms:
Homoeocladia angularis (W. Smith) Kuntze 1898

Morphometrics:
Biovolume (µm^3): 12016
Frustule geometry: prism on parallelogram

Length (µm): 112.5 – (118.2) – 122.5 (n=3)
Width (µm): 13.3 – (16.1) – 19.0 (n=3)
Pervalvar axis (µm): 8 (estimated)
Striae in 10 µm: 33 – (35) – 37 (n=3)
Fibulae in 10 µm: 5 – (6) – 9 (n=3)

Notes: this species was described in detail by Hendey (1964) or by Poulin *et al.* (1990), where SEM micrographs of this taxon can also be found.

Distribution & Ecology: Cox (1977) reported it as a tube-dwelling species in the Severn estuary (U.K) and Mann (1978) explained that *N. angularis* may live associated with two symbionts in these tubes: *N. lanceolata* W. Smith and *N. frustulum* (Kützing) Grunow. Kuylenstierna (1989-1990) found it as epiphyte of macroalgae and hydroids. In our study it occurred only once.

References:

Hendey (1964) – pg. 281; fig. 39/6
Mann (1978) – figs. 234-243
Poulin *et al.* (1990) – pg. 78; figs, 16-22
Peragallo & Peragallo (1897-1908) – pg. 284; fig. 73/6-7
Ricard (1987) – figs. 1073-1074
Witkowski *et al.* (2000) – pg. 368; figs. 199/5-6

Nitzschia cf. ***aurariae*** Cholnoky 1965

Micrographs: Pl. 28: 11, Pl. 56: 12-13

Synonyms:

Nitzschia elliptica var. *alexandrina* Cholnoky
Nitzschia alexandrina (Cholnoky) Lange-Bertalot & Simonsen

Morphometrics:

Biovolume (µm^3): 36
Frustule geometry: prism on parallelogram
Length (µm): 7.1 – (8.3) – 9.3 (n=6)
Width (µm): 2.5 – (2.8) – 3.0 (n=6)
Pervalvar axis (µm): 2 (estimated)
Striae in 10 µm: 52 – (55) – 57 (n=3)
Punctae in 10 µm: 56 (n=2)
Fibulae in 10 µm: 17 – (18) – 19 (n=5)

Notes: detailed descriptions of this taxon are given by Krammer & Lange-Bertalot (1988) and by Witkowski *et al.* (2000). The specimens found in the Tagus estuary are very similar to the ones described for the Baltic Sea (Sundbäck & Snoeijs 1991; Snoeijs & Potapova 1995) and have more elliptic-lanceolate outline, instead of the more linear-elliptic one found in Cholnoky's type material (Fig. 80/18-19, Krammer & Lange-Bertalot 1988). Besides the similar striae and fibulae density and the lack of central nodule, both forms also share the typical quincunx pattern of the areolae. It is easily distinguishable of the smaller specimens of *N. frustulum* by the fact that the striae are irresolvable in LM and the lack of central nodule. Trobajo (2007) also found very similar specimens (fig. 13/103) in the Empordà wetlands (NE Spain) but identified them as *N. pusila* Grunow. Even tough, the specimens found in SEM seem to be unquestionably *N. aurariae*, a more detailed study is necessary to confidently determine the identity of the specimens observed in LM.

Distribution & Ecology: cosmopolitan, widespread species, found in electrolyte rich freshwater and common in the Baltic Sea (Krammer & Lange-Bertalot 1988; Witkowski *et al.* 2000). Sundbäck & Snoeijs (1991) reported it as living in subtidal sand in the more brackish/marine areas of the Baltic (*viz.* in NE Skagerrak, Tjärnö, Sweden). The existence of two ecological morphotypes should be explored. It is a small motile epipelic species (*cf.* Snoeijs & Potapova 1995). In our study it was extremely rare, with only 4 occurrences and always at very low abundances (max. abundance < 0.45%).

References:

Krammer & Lange-Bertalot (1988) – pg. 113; 80/16-21
Ludes & Coste (1996) – fig. 29/20
Snoeijs & Potapova (1995) – #262
Sundbäck & Snoeijs (1991) – pg. 353; fig. 9i
Witkowski *et al.* (2000) – pg. 369; fig. 210/21

Nitzschia cf. ***dissipata*** (Kützing) Grunow 1862

Micrographs: Pl. 28: 6-10, Pl. 56: 2

Similar species:
Nitzschia distans Gregory 1857

Morphometrics:
Biovolume (µm^3): 193
Frustule geometry: prism on parallelogram
Length (µm): 12.7 – (19.3) – 29.5 (n=12)
Width (µm): 2.7 – (3.2) – 3.8 (n=12)
Pervalvar axis (µm): 4 (estimated)
Striae in 10 µm: 53 (n=2)
Punctae in 10 µm: 52 (n=1)
Fibulae in 10 µm: 6 – (8) – 10 (n=12)

Description: valves lanceolate or narrowly-lanceolate with slightly capitate apices. The canal-raphe is only slightly eccentric and the distance between two adjacent fibulae is not constant. The central fibulae are not widely spaced. The striae are finely punctate and are irresolvable in LM. In SEM, the striae are interrupted in the two longitudinal thickenings, on both sides of the canal-raphe, from which the fibulae stem.

Notes: this species is very similar to the freshwater species *N. dissipata* in outline, size-range and fibulae. It is possible that several *dissipata*-like species were lumped together in our study. The smaller specimens are extremely reminiscent of the small *N. dissipata* depicted by Krammer & Lange-Bertalot (1988, figs. 11/4-5) and Sabbe (1997, as *N.* cf. *dissipata*). However, in a larger valve, observed in SEM, the striae are interrupted near the canal-raphe, a feature that does not occur in *N. dissipata* (Mann 1978, figs. 808-811; Poulin *et al.* 1999, figs. 29; Snoeijs & Kasperoviciene 1996, #369). In spite of several reports (*e.g.* Poulin *et al.* 1990) the presence of *N. dissipata* in brackish and marine areas has been always problematic (Krammer & Lange-Bertalot 1988), although a certain tolerance to salinity has been acknowledged (*e.g.* Germain 1981). The specimens found in Tagus estuary seem to correspond to the *N.* cf. *dissipata* described by Sabbe (1997) for the Westerschelde estuary (see also his discussion on "*dissipata*-like" taxa) and, particularly, to *Nitzschia* sp.D described by Kuylenstierna (1989-1990) which has "two unmarked fields along the canal-raphe".

Distribution & Ecology: apart from the reports of Kuylenstierna (1989-1990) and Sabbe (1997) the geographical distribution of this taxon is unknown. As it was the case in the above mentioned works, this diatom was fairly rare in our study (20 occurrences), appearing in the muddy transect but also in the lower shore muddy sandy stations of the sandy transect. It was never very abundant (max. abundance < 1.61).

References:
Krammer & Lange-Bertalot (1988) – pg. 19; figs. 11/1-7
Kuylenstierna (1989-1990) – pg. 140; fig. 886
Sabbe (1997) – pg. 244; fig. 30/1-4

Nitzschia cf. ***distans*** Gregory 1857

Micrographs: Pl. 29: 3-4, Pl. 56: 1

Similar species:
Nitzschia affinis Grunow [syn. *N. angularis* var. *affinis* (Grunow) Grunow *in* Van Heurck)]

Morphometrics:
Biovolume (µm^3): 1343
Frustule geometry: prism on parallelogram
Length (µm): 31.4 – (42.3) – 73.1 (n=9)
Width (µm): 3.4 – (4.3) – 5.2 (n=4)
Pervalvar axis (µm): 10 (estimated)
Striae in 10 µm: 49 (n=1)
Punctae in 10 µm: 72 (n=1)
Fibulae in 10 µm: 4 – (6) – 7 (n=9)

Description: valves narrowly-lanceolate, with acutely rounded, slightly capitate apices. In girdle view, short wing-like expansions are clearly seen in the apices but are not as drawn-out as in *N. spathulata* (see below). The canal-raphe central to slightly eccentric, the central fibulae are not more widely spaced and the distance between adjacent fibulae is not regular. The striae are not resolvable in LM and are finely punctate. These areolae are continuous throughout the stria, which seems to end at the margin of the canal-raphe.

Notes: even though the specimens found in this study are very similar to *N. distans*, they are much smaller and with denser fibulae than the customary morphometric data given for that species (*e.g.* 130-220 µm in length and 1.5-3 fibulae in 10 µm, Witkowski *et al.* 2000). They correspond, however, to the taxa reported and illustrated by Giffen (1963), Kuylenstierna (1989-1990), Snoeijs & Kasperoviciene (1996), all of them identified as *N. distans* or *N.* cf. *distans.* According to Mann (1978), the only taxon on the "Spathulatae" section with similar morphometrics is *N. affinis* but this taxon was rarely recorded and has a more lanceolate valve outline (Peragallo & Peragallo 1897-1990). Both Mann (1978) and Kuylenstierna (1989-1990) acknowledge that a revision of this group is needed, as there are many intermediate forms between species.

Distribution & Ecology: motile epipelic species. It has been reported for subtidal sandy and muddy sediments from the marine/brackish water Skagerrak and Kattegat Swedish coast (Kuylenstierna 1989-1990, Snoeijs & Kasperoviciene 1996). The specimens reported by Giffen (1963, Trobajo 2007) also came from "strongly brackish water" of a Eastern Cape province estuary (South Africa). In our study, this taxon was infrequent (9 occurrences) and never very abundant (max. abundances < 0.94%) it was mainly found in the muddy transect.

References:

Giffen (1963) – pg. 245; fig. 85
Hendey (1964) – pg. 378
Kuylenstierna (1989-1990) – pg. 132; fig. 829-830
Poulin *et al.* (1990) – pg. 81; fig. 38-41
Snoeijs & Kasperoviciene (1996) – # 370
Witkowski *et al.* (2000) – pg. 378; 203/7-9

Nitzschia* cf. *dubia W. Smith 1853

Micrographs: Pl. 29: 1-2

Synonyms:
Homoeocladia dubia (W. Smith) Kuntze

Similar species:
Nitzschia bilobata W. Smith
Nitzschia commutata Grunow *in* Cleve & Grunow
Nitzschia *hybrida* Grunow *in* Cleve & Grunow

Morphometrics:
Biovolume (µm^3): 5529
Frustule geometry: prism on parallelogram
Length (µm): 62.2 – (83.3) – 110 (n=3)
Width (µm): 9.0 – (10.6) – 12 (n=3)
Pervalvar axis (µm): 8 (estimated)
Striae in 10 µm: 22 – (27) – 32 (n=4)
Fibulae in 10 µm: 11 – (12) – 12 (n=4)

Description: individual valves usually in girdle view and more or less linear-lanceolate, being slightly constricted in the middle. The apices are broadly rounded, slightly rostrate and asymmetric (*i.e.* turned towards the cingulum). Each fibula ends in one interstria and the central fibulae are only slightly more distant.

Notes: in spite of a slightly denser striation this taxon is very similar to *N. dubia* (for comparison see Witkowski *et al.* 2000). The middle constriction is not as pronounced as in related species, such as *N. bilobata* or *N. hybrida* and, additionally, the striae are not clearly punctate in LM as in *N. commutata*. The existence of smaller specimens of *N. dubia* with higher striae density in brackish waters was already noticed by Kuylenstierna (1989-1990, as *Nitzschia* sp.I)

Distribution & Ecology: large motile epipelic diatom. *Nitzschia dubia s.s.*, it is a cosmopolitan species living in brackish and marine waters. *Nitzschia* cf. *dubia* was found rarely in our study (8 occurrences), only during winter and, mainly, in the muddy transect.

References:
Germain (l981) – pg. 338; figs. 128/1,2
Krammer & Lange-Bertalot (l988) – pg. 55; figs. 41/1-2
Kuylenstierna (1989-1990) – pg. 132, 141; fig. 83
Sabbe (1997) – pg. 245; fig. 31/9
Snoeijs & Potapova (1995) – #264
Witkowski *et al.* (2000) – pg. 378; 190/7-8

Nitzschia frustulum (Kützing) Grunow *in* Cleve & Grunow 1880

Micrographs: Pl. 33: 4-8, Pl. 56: 6-11

Synonyms:
Homoeocladia frustulum (Kützing) Kuntze 1898
Nitzschia inconspicua Grunow (*sensu stricto* non *N. abbreviata* Hustedt)
Synedra frustulum Kützing 1844
See Trobajo *et al.* (2004) for full list of synonyms

Similar species:
Nitzschia *aurariae* Cholnoky

Morphometrics:
Biovolume (µm^3): 38
Frustule geometry: prism on parallelogram
Length (µm): 4.2 – (9.2) – 25 (n=41)
Width (µm): 2.0 – (2.7) – 4.0 (n=39)
Pervalvar axis (µm): 2 (estimated)
Striae in 10 µm: 22 – (28) – 32 (n=41)
Punctae in 10 µm: 32 – (39) – 46 (n=9)
Fibulae in 10 µm: 10 – (13) – 16 (n=38)

Notes: Wendker (1990) discussed in detail the morphology of this taxon and Trobajo & Cox (2006) described the type material of *N. frustulum*.

The conspecificity of *N. frustulum* and *N. inconspicua* has long been discussed (*e.g.* Lange-Bertalot & Simonsen 1978; Krammer & Lange-Bertalot 1988). The two species are traditionally only distinguished by size, the shape of the apices and autoecology (Sabbe 1997; Trobajo & Cox 2006): *N. frustulum* is reported for brackish water and has “longer, thinner” valves with cuneate/subrostrate apices; *N. inconspicua* occurs in freshwaters and has “shorter, fatter” valves, with broadly rounded apices.

Studying natural populations along the salinity gradient of the Schlei estuary (Germany), Wendker (1990) demonstrated that there is a morphological continuum between both species, with the “*inconspicua*“-form being more abundant in the freshwater reaches of the estuary and the “*frustulum*”-form more common in the brackish water reaches and the mouth of the estuary. Recently, Trobajo *et al.* (2006) established in a series of culture experiments that it was possible to obtain “*inconspicua*“-like cells from a “*frustulum*”-like clonal culture in different salinities, N:P ratios and water movements, all factors affected the length, width and/or fibula density of the frustules . Salinity was the main factor responsible for valve outline but increasing water movement may also augment cell width. These results corroborate the conspecificity of both species but also that the pattern found by Wendker (1990) is not necessarily always replicated in nature (Trobajo *et al.* 2006).

Conversely, Kuylenstierna (1989-1990) noticed that in his material for the Swedish west coast *N. inconspicua* had two rows of areolae on the mantle near the raphe, while *N. frustulum* had only one row. The latter feature can also be seen in the type material of *N. frustulum*, studied by Trobajo & Cox (2006). However, as our own SEM observations show, the number of rows areolae on the mantle near the raphe does not seem to be a stable morphological feature and small, “*inconspicua*”-like specimens, with only one row of pores were found (Pl. 56: 7). The taxonomical validity of this criterion is, therefore, questioned.

Finally, and still regarding the specimens found in our study, most of them had an “*inconspicua*” shape, in spite of being collected in a brackish water site. The fact that this species was most abundant in the sandy stations (see below), may imply that factors, other than salinity (*e.g.* water movement, cf. Trobajo *et al.* 2006) were likely responsible for an increase in average valve frustule width and a decrease in cell length and, therefore, for the “*inconspicua*” likeness of most specimens scored during counts.

Table 20 – Occurrence (%), average relative abundance (%) of *N. frustulum* and average mud content (%) per sampling station. Standard deviation given within brackets.

Station	Occurrence	Abundance	Mud content
A1	100	12.4 (2.9)	2.3 (1.0)
A2	100	3.9 (1.7)	5.4 (2.4)
A3	100	2.2 (0.9)	7.7 (3.1)
V1	92	1.3 (0.9)	13.5 (9.3)
V2	64	0.4 (0.5)	90.0 (7.3)
V3	8	0.0 (0.1)	96.5 (2.2)

Distribution & Ecology: *N. frustulum* is a common, cosmopolitan and markedly euryhaline species (*e.g.* Witkowski *et al.* 2000; Trobajo *et al.* 2006). This species was one of the most common and frequent (52 occurrences) *Nitzschia* found in our study. It was particularly abundant in the sandy transect, especially in upper shore fine sandy station (Table 20).

References:
Germain (1981) – pg. 352; fig. 134/1
Krammer & Lange-Bertalot (1988) – pg. 94-95; figs. 68/1-8 (*N. frustulum*), 69/1-13 (*N. inconspicua*)
Lange-Bertalot & Simonsen (1978)
Poulin *et al.* (1990) – pg. 84; figs. 44-48
Snoeijs (1994) – #76 (*N. inconspicua*), #78 (*N. frustulum*)
Trobajo & Cox (2006) – figs. 1-19 (type material)
Trobajo (2004) – figs. 7-14
Wendker (1990) – figs. 1-33
Witkowski *et al.* (2000) – pg. 382; figs. 209/13-17

Nitzschia littorea Grunow *in* Van Heurck 1881

Micrographs: Pl. 30: 1-3

Synonyms:
Hantzschia fogedii (Møller) Simonsen
Nitzschia thermalis var. *littoralis* Grunow *in* Cleve & Grunow
Nitzschia fogedii Møller

Similar species:
Nitzschia commutata
Nitzschia lacunarum Hustedt

Morphometrics:
Biovolume (μm^3): 6436
Frustule geometry: prism on parallelogram
Length (μm): 129.5 (n=2)
Width (μm): 9.0 (n=2)
Pervalvar axis (μm): 7 (estimated)
Striae in 10 μm: 30 (n=2)
Punctae in 10 μm: 23 (n=1)
Fibulae in 10 μm: 9 (n=2)

Notes: a detailed description of this species is given by Krammer & Lange-Bertalot (1998) or by Witkowski *et al.* (2000). It can be distinguished from the similar species by a clear quincunx striation pattern (Snoeijs & Kasperoviciene 1996).

Distribution & Ecology: large epipelic species. Common in marine European coasts (Krammer & Lange-Bertalot 1988, Witkowski *et al.* 2000), it has been reported several times for the Öresund and the Kattegat (*e.g.* Simonsen 1962, Kuylenstierna 1989-1990, Snoeijs & Kasperoviciene 1996), in the Swedish West coast. In our study, it was found once, in the upper shore station of the sandy transect.

References:
Krammer & Lange-Bertalot (1988) – pg. 67; 54/1-3a
Lange-Bertalot & Krammer (1987) – pg. 18, 34; fig. 23/4-5
Snoeijs & Kasperoviciene (1996) – #373
Simonsen (1962) – pg. 99 (as *H. fogedii*)
Witkowski *et al.* (2000) – pg. 391; fig. 197/11-16

Nitzschia lorenziana Grunow *in* Cleve & Möller 1879

Micrographs: Pl. 30: 4

Synonyms:
Homoeocladia lorenziana (Grunow *in* Cleve & Møller; Grunow *in* Cleve & Grunow) Kuntze

Nitzschiella lorensiana (Grunow in Cleve & Møller; Grunow *in* Cleve & Grunow) Peragallo & Peragallo

Morphometrics:
Biovolume (µm^3): 1914
Frustule geometry: prism on parallelogram
Length (µm): 75.0 (n=1)
Width (µm): 6.5 (n=1)
Pervalvar axis (µm): 5 (estimated)
Striae in 10 µm: 16 (n=1)
Fibulae in 10 µm: 7 (n=1)

Notes: this species is described in detail by Krammer & Lange-Bertalot (1988) and Poulin *et al.* (1990). As we found very few specimens we abstain of determining the variety of *N. lorenziana* found in our samples.

Distribution & Ecology: cosmopolitan brackish water species, found also in marine coasts (Krammer & Lange-Bertalot 1988; Witkowski *et al.* 2000). Large motile epipelic species, also reported as pelagic in coastal areas (Snoeijs & Balashova 1998). In this study, this species was only found in one sample.

References:
Krammer & Lange-Bertalot (1988) – pg. 125; figs. 86/6-10
Poulin *et al.* (1990) – pg. 87; figs. 63-72
Snoeijs & Balashova (1998) – #464
Witkowski *et al.* (2000) – pg. 392; figs. 210/24-25, 211/3, 212/1-3

Nitzschia sigma (Kützing) W. Smith 1853

Micrographs: Pl. 30: 5-7, Pl. 56: 3-5

Synonyms:
Homoeocladia sigma (Kützing)
Sigmatella sigma (Kützing) Frenguelli
Synedra sigma Kützing

Morphometrics:
Biovolume (µm^3): 15304
Frustule geometry: prism on parallelogram
Length (µm): 57.6 – (107.8) – 225.3 (n=8)
Width (µm): 5.7 – (7.5) – 13.2 (n=8)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 25 – (28) – 34 (n=10)
Punctae in 10 µm: 18 – (24) – 34 (n=5)
Fibulae in 10 µm: 7 – (9) – 11 (n=7)

Notes: detailed descriptions of this species are given by Germain (1981) or by Krammer & Lange Bertalot (1988). It is most probably a species complex (Witkowski *et al.* 2000)

Distribution & Ecology: large motile epipelic taxon. Cosmopolitan species, it is widespread in most marine coasts and estuaries (Witkowski *et al.* 2000). In our study, it was fairly rare (18 occurrences) being mainly found in the lower shore stations of both transects. It had very low abundances (max. abundance < 0.8%), but its relative numbers increased during summer.

References:
Germain (1981) – pg. 368; pl. 139/1-6
Krammer & Lange-Bertalot (1988) – pg. 32; figs. 23/19
Ohtsuka (2005) – pg. 146; figs. 44-45
Poulin *et al.* (1990) – pg. 92; figs. 90-92
Snoeijs & Vilbaste (1994) – # 173
Witkowski *et al.* (2000) – pg. 404; figs. 206/1-10

Nitzschia spathulata Brébisson *ex* W. Smith 1853

Micrographs: Pl. 31: 1-3, Pl. 55: 1-2

Synonyms:
Homoeocladia spathulata (Brébisson *ex* W. Smith) Kuntze 1898

Similar species:
Nitzschia distans var. *tumescens* Grunow
Nitzschia angularis W. Smith

Morphometrics:
Biovolume (µm^3): 8327
Frustule geometry: prism on parallelogram
Length (µm): 82.0 – (87.8) – 92.0 (n=5)
Width (µm): 5 (estimated)
Pervalvar axis (µm): 15 (n=4)
Striae in 10 µm: 40 (n=1)
Fibulae in 10 µm: 5 – (6) – 10 (n=9)

Notes: this taxon is described and illustrated in detail by Mann (1978) but also by Hendey (1964) and Witkowski *et al.* (2000). It can be distinguished from the other species on the "*Spathulatae*" group not only by its dimensions but also by the very large wing-like expansions in the apices.

Distribution & Ecology: this species is widespread in the European marine coasts (Witkowski *et al.* 2000) but it also occurs in South Africa (Giffen 1963), in the North-American Pacific coast (Riznyk 1973) or in New Zealand (Chapman *et al.* 1957). It is a large motile epipelic species. The specimens studied by Brockmann (1950), Giffen (1963), Riznyk (1973) and Mann (1978) were found in intertidal sand. Round (1979) referred *N. spathulata* as an associated species of the epipelic assemblages living below the surface of intertidal sandflats. In the present study, it was found only once but I found it frequently in other samples from sandy sediments of the Tagus estuary.

References:
Brockmann (1950) – pg. ; fig. 4/23
Giffen (1963) – pg. 248; fig. 94
Hendey (1964) – pg. 281
Mann (1978) – pg. 222; figs. 247-252, 815-831 (except 817)
Peragallo & Peragallo (1897-1908) – pg. 284; fig. 73/4
Witkowski *et al.* (2000) – pg. 405; fig. 206/19-20

Nitzschia valdestriata Aleem & Hustedt 1951

Micrographs: Pl. 33: 9, Pl. 56: 14

Similar species:
Nitzschia frustulum Kützing
Nitzschia valdecostata Lange-Bertalot & Simonsen

Morphometrics:
Biovolume (μm^3): 39
Frustule geometry: prism on parallelogram
Length (μm): 6.3 – (9.5) – 18.2 (n=7)
Width (μm): 2.0 – (2.6) – 3.7 (n=7)
Pervalvar axis (μm): 2 (estimated)
Striae in 10 μm: 14 – (18) – 22 (n=6)
Punctae in 10 μm: 53 (n=1)
Fibulae in 10 μm: 6 – (10) – 15 (n=6)

Notes: this taxon is described in detailed by Lange-Bertalot & Simonsen (1979) or by Krammer & Lange-Bertalot (1988). *Nitzschia valdestriata* differs from the small forms of *N. frustulum* (see above) by the more linear outline, the blunt ends and the rougher structure (Aleem & Hustedt 1951). This structure, where each fibula spans two interstriae, is also replicated in *N. valdecostata*, with the exception of the central fibulae (see Lange-Bertalot & Simonsen 1979; Krammer & Lange-Bertalot 1988).

Distribution & Ecology: small motile species, cosmopolitan and widespread in brackish waters (Krammer & Lange-Bertalot 1986, Witkowski *et al.* 2000). In our study it was fairly frequent (22 occurrences) although it was never very abundant (max. abundance <1.8%). It occurs in both mudflat and sandflat stations but it was more frequent and abundant in sandy sediments.

References:
Aleem & Hustedt (1951) – pg. 19; figs. 5a-b
Kuylenstierna (1989-1990) – pg. 139; fig. 864-865
Krammer & Lange-Bertalot (1988) – pg. 121; figs. 89/9-11
Lange-Bertalot & Simonsen (1978) – pg. 58; figs. 254-259, 271, 272
Simonsen (1987) – figs. 551/9-13
Snoeijs & Vilbaste (1994) – #174
Witkowski (1994) – pg. 172; fig. 61/21
Witkowski *et al.* (2000) – pg. 407; figs. 203/19-21, 207/14-16

***Nitzschia* sp.1**

Micrographs: Pl. 32: 1-4, Pl. 55: 6-7

Morphometrics:
Biovolume (μm^3): 3493
Frustule geometry: prism on parallelogram
Length (μm): 69.9 – (82.6) – 92.0 (n=4)
Width (μm): 10.0 – (10.8) – 11.2 (n=4)

Pervalvar axis (µm): 5 (estimated)
Striae in 10 µm: 29 – (30) – 31 (n=4)
Punctae in 10 µm: 51 (n=1)
Fibulae in 10 µm: 13 – (13) – 14 (n=3)

Description: valves broadly linear-lanceolate, with a slight central constriction of the margin bearing the raphe. The apices are acutely-rounded, slightly rostrate and asymmetric (*i.e.* turned towards the cingulum). The fibulae are relatively small and separated by two to three striae, except in the middle, where they are more distant. The SEM shows that the striae are monoseriate and composed by round occluded punctae. They are parallel throughout the valve and separated, externally, by transversal costae, with the exception of the marginal canal-raphe.

Notes: we were unable to identify this quite unique taxon. It may belong to the *Nitzschia* sect. *Dubiae*, given its overall valve outline and shape. However, the external structure of the striae was not observed in other members of this section (*cf.* Mann 1978; Lange-Bertalot & Krammer 1987). Further studies are needed.

Distribution & Ecology: large motile epipelic species. In our study it occurred only once.

Nitzschia sp.2

Micrographs: Pl. 33: 1-3, Pl. 54: 9-11

Similar species:
Nitzschia hummii Hustedt

Morphometrics:
Biovolume (µm^3): 3393
Frustule geometry: prism on parallelogram
Length (µm): 179.4 – (183.5) – 185.6 (n=3)
Width (µm): 2.5 – (6.5) – 9.0 (n=4)
Pervalvar axis (µm): 5 (estimated)
Striae in 10 µm: 31 (n=2)
Punctae in 10 µm: 46 (n=1)
Fibulae in 10 µm:16 (n=2)

Description: frustules are arcuate, extremely long, and narrow and distinctively curved, which gives them a bow-like appearance. The apices taper progressively and, depending on the valve position, seem to be slightly turned towards the concave side. The transverse striae are clearly seen in LM but their punctate structure is only perceived in SEM as monoseriate rows of rounded punctae. The most conspicuous structure of each valve is the huge canal-raphe. It is simple and shallow but the heavily silicified and expanded fibulae clearly separate the canal-raphe from the rest of the cell lumen (*cf.* Round *et al.* 2000). The canal-raphe ultrastructure is rather complex: the fibulae are large in relation to the transapical costae and have two longitudinal ridges. These two ridges are separated by a few poroids, since the striae continue through both the proximal and distal (outer) sides of the raphe (near the raphe slit). The inside portulae are elliptical and better defined than the secondary, outer portulae of the second ridge. This corresponds to raphe-type vii (*cf.* Mann 1978).

Notes: this species is rather unique and we were not able to find anything like it in the references consulted. Perhaps the most similar species is *Nitzschia hummii*, described by Hustedt (1955) for the Beaufort Bay (USA). This species, however, has wider valves and striae more coarsely punctate (see figs. 634/1-4, Simonsen 1987). The raphe ultrastructure (see above) appears to be very similar to what is found in sect. *Nitzschia* (*e.g. N. sigma, N. sigmaformis*), at least according to the criteria established by Mann (1978)

Life form & Ecology: large epipelic species probably motile. In our study it only occurred in 3 samples from the muddy transect (max abundance < 0.63%). However, this large and conspicuous diatom has been detected in other samples from the Tagus estuary, mainly from sandy sediments. Apart from the Tagus estuary, this diatom has also been found in estuarine intertidal mudflats in Southern Brittany (France) by M. Loir (pers. communication).

Nitzschia sp.3

Micrographs: Pl. 28: 12-13

Morphometrics:
Biovolume (μm^3): 46
Frustule geometry: prism on parallelogram
Length (µm): 7.9 – (8.7) – 9.3 (n=3)
Width (µm): 3.2 – (3.4) – 4.0 (n=3)
Pervalvar axis (µm): 2 (estimated)
Striae in 10 µm: 29 (n=3)
Fibulae in 10 µm: 16 (n=3)

Description: valves broadly lanceolate with cuneately round apices. The canal-raphe is eccentric with relatively large fibulae, which are more or less equidistant. The striae are barely visible in LM and are parallel in the middle and slightly radiant near the apices.

Notes: this taxon clearly belongs to the *Nitzschia* sect. *Lanceolatae*, as do *N. aequorea*, *N. aurariae* and *N. valdestriata* (see above). Contrary to the mentioned species, it has cuneate apices, which are not even slightly rostrate or subcapitate. It is somewhat reminiscent of *N. frustulum* (see above) but the valves are much wider and the striation is finer. As only a few specimens were found, we were unable to identify them.

Distribution & Ecology: motile epipelic species. In our study, it was extremely rare (4 occurrences) and found only in the muddy transect, with very low abundances (max. abundance < 0.4%).

Nitzschia sp.4

Micrographs: Pl. 33: 19-21

Morphometrics:
Biovolume (μm^3): 1166
Frustule geometry: prism on parallelogram
Length (µm): 42.5 (n=2)
Width (µm): 7.8 (n=2)
Pervalvar axis (µm): 5 (estimated)
Fibulae in 10 µm: 11 (n=2)

Description: valves broadly linear-lanceolate, with a very slight central constriction of the margin bearing the raphe. The apices are acutely-rounded, slightly rostrate and asymmetric. The canal-raphe is very eccentric, with relatively small fibulae unevenly distributed. The median fibulae are more distant than the others and the striae are irresolvable in LM.

Notes: this taxon seems to belong to the *Nitzschia* sect. *Dubiae*, as do *N. dubia* and *Nitzschia* sp.1 (see above). However, since only a few specimens were found, we were unable to identify this taxon.

Distribution & Ecology: motile epipelic species. In our study it occurred only in 3 samples and at extremely low relative abundances (max. abundance 0.2%).

Tryblionella Smith 1853

Genus description: Round *et al.* (1990) but see Mann (1978) for an detailed historical review of the *Nitzschia* sect. *Tryblionella*.

This genus is defined by a combination of morphologic features, such as the very eccentric raphe and the longitudinal fold of the valve. The reestablishment of this genus made by Round *et al.* (1990) is still not followed by all main authors (*e.g.* Krammer & Lange-Bertalot 1988, Witkowski *et al.* 2000) and many taxonomical transfers from *Nitzschia* to *Tryblionella* still remain to be correctly done (see below). Interestingly, we could not find any reference to molecular phylogenetics works, within the Bacillariophyceae, that included *Tryblionella*. Therefore, the relationships between *Nitzschia*, *Tryblionella* and *Psammodictyon* still remain to be elucidated.
We decided to accept the reestablishment of the genus *Tryblionella* and its validity. We also include in this section the entries of two *Nitzschia* species (*N. parvula*; *N. pararostrata*) that still await a proper nomenclatural transfer to the genus *Tryblionella*.

Tryblionella apiculata Gregory 1857

Micrographs: Pl. 34: 2-6; Pl. 57: 1-7

Synonyms:
Nitzschia constricta (Kützing) Ralfs non (Gregory 1855) Grunow
Nitzschia apiculata (Gregory) Grunow
Tryblionella constricta (Kützing) Poulin non Gregory

Similar species:
Tryblionella acuminata Smith
Tryblionella hungarica (Grunow) Mann
Tryblionella marginulata (Grunow *in* Cleve & Grunow) Mann

Morphometrics:
Biovolume (µm^3): 863
Frustule geometry: elliptic prism
Length (µm): 20.9 – (31.2) – 45.5 (n=25)
Width (µm): 5.9 – (7.0) – 8.5 (n=23)
Pervalvar axis (µm): 5
Striae in 10 µm: 16 – (17) – 20 (n=25)
Punctae in 10 µm: 61 – (64) – 69 (n=4)
Fibulae in 10 µm: 16 – (17) – 19 (n=21)

Notes: *Tryblionella apiculata* has a complex nomenclatural history that is explained in detail by Krammer & Lange-Bertalot (1988) and Sabbe (1997). It is still frequently named by its most common synonym *Nitzschia constricta* (Kützing) Ralfs (*e.g.* Witkowski *et al.* 2000) but it should not be confused with a different species, *Psammodictyon constrictum* Gregory (Mann), which has a common synonym with the same specific epithet: *Nitzschia constrica* (Gregory 1855) Grunow 1880. *Tryblionella apiculata* has a very obvious transverse striation formed by ribs separating the striae. It can be distinguished from *T. acuminata* and *T. hungarica*, which are also common species in brackish-marine waters, because it is smaller than the former and does not have an unequal number of striae and fibulae, as the latter. Finally, the striae have 3-4 rows of punctae (Schoeman & Archibald 1976-1980, Archibald 1983) as could be seen in the SEM. A detailed description of *T. apiculata* and close taxa is given by Mann (1978).

Distribution & Ecology: *Tryblionella apiculata* is a common, cosmopolitan and widespread species in freshwater (electrolyte-rich), estuarine and marine sediments worldwide (Hendey 1964, Admiraal 1984, Krammer & Lange-Bertalot 1988, Cox 1996, Witkowski *et al.* 2000). It is a large motile epipelic species that, in our study, occurred in samples of all stations (34 occurrences), especially in the muddy sandy sediments and in one of the mudflat stations. It had relatively low relative abundances (max. abundance <2.2 %) and appeared throughout the 2 sampling years. It has been recurrently found in the Tagus estuary (*e.g.* Brotas 1995, as *N. tryblionella* Hantzsch; Ribeiro 2000, 2003; Jesus 2006).

References:
Germain (1981) – pg. 336 fig. 127/8
Krammer & Lange-Bertalot (1988) – pg. 43; figs. 35/1-6
Mann (1978) – pg. 162; figs. 174-175, 742-743
Ribeiro (2000) – pg. 37; figs. 5/10, 14/5-7
Sabbe (1997) – pg. 253; fig. 60/2
Snoeijs & Vilbaste (1994) – #196
Witkowski *et al.* (2000) – pg. 377; figs. 187/8-12

Tryblionella levidensis W. Smith 1856

Micrographs: Pl. 34: 1

Synonyms:
Nitzschia levidensis '*salinarum*'-Sippen *sensu* Krammer & Lange-Bertalot
Nitzschia tryblionella var. salinarum Grunow *in* Cleve & Grunow
Tryblionella salinarum (Grunow *in* Cleve & Grunow) Pelletan

Similar species:
Tryblionella calida (Grunow *in* Cleve & Grunow) Mann in Round, Crawford & Mann
Tryblionella gracilis W. Smith
Tryblionella victoriae Grunow

Morphometrics:
Biovolume (µm^3): 386
Frustule geometry: elliptic prism

Length (µm): 16.0 (n=2)
Width (µm): 7.7 (n=2)
Pervalvar axis (µm): 4 (estimated)
Striae in 10 µm: 15 (n=2)
Fibulae in 10 µm: 9 (n=2)

Notes: a detailed description of this taxon is given by Krammer & Lange-Bertalot (1988) and Sabbe (1997). The specimens found in our study have no discernible striae in LM and the valve is crossed by numerous transapical ribs, as it is the case of the similar species *Tryblionella victoriae* and the nominate variety of *T. levidensis*. However, we believe that these specimens belong to the variety *salinarum*, which can be distinguished from the nominate variety by the narrower and denser transapical ribs and for the indistinct zigzag-shaped contact line between neighbouring ribs (Krammer & Lange-Bertalot, 1988). Sabbe (1997) did not raise this taxon to species level (*Tryblionella salinarum*) on the grounds that the morphological variability within *T. levidensis* is still not sufficiently clear but he proposed a new combination: *Tryblionella levidensis* var. *salinarum* (Grunow in Cleve & Grunow) Sabbe comb. nov. prov. To our knowledge, this new combination has not yet been formally published.

Distribution & Ecology: *Tryblionella levidensis* var. *salinarum* (syn. *Nitzschia tryblionella var. salinarum*) is a common, cosmopolitan and widespread species in estuarine and marine sediments worldwide (Snoeijs & Potapova 1995, Witkowski *et al.* 2001). Only a couple of specimens were observed in our material and only in a sample from a mudflat station. It is a motile epipelic species.

References:
Sabbe (1997) – pg. 257; fig. 31/2
Snoeijs & Potapova (1995) – # 299
Krammer & Lange-Bertalot (1988) – pg. 37; figs. 28/5-10, fig. 29/1-5
Witkowski *et al.* (2000) – pg. 389; figs. 181/6-9

Tryblionella littoralis (Grunow *in* Cleve & Grunow) Mann *in* Round, Crawford & Mann 1990

Micrographs: Pl. 34: 7-8; Pl. 57: 11-12

Synonyms:
Nitzschia littoralis Grunow in Cleve & Grunow
Nitzschia tryblionella var. *littoralis* (Grunow) Grunow in Van Heurck

Similar species:
Tryblionella circumsuta (J.W. Bailey) Ralfs *in* Pritchard
Tryblionella gracilis W. Smith
Tryblionella debilis Arnott *ex* O'Meara
Tryblionella levidensis W. Smith
Tryblionella plana (W. Smith) Pelletan

Morphometrics:
Biovolume (µm^3): 4940
Frustule geometry: elliptic prism
Length (µm): 48.6 – (60.5) – 67.5 (n=4)
Width (µm): 14.6 – (14.8) – 15.0 (n=3)
Pervalvar axis (µm): 7 (estimated)
Striae in 10 µm: 34 (n=3)
Fibulae in 10 µm: 8 (n=3)

Notes: a detailed description of this species is given by Krammer & Lange-Bertalot (1988). *Tryblionella littoralis* has transapical rib-like thickenings irregularly spaced across the valve (as in *T. debilis*, *T. gracilis*, *T. levidensis*) but these ribs are denser and much less developed than in those species. Another difference is the fact that the striae are barely resolvable but usually detectable in the LM. *Tryblionella circumsuta* and *T. plana* are also quite similar to *T. littoralis*, but the valves totally lack transapical ribs and the striae are coarser.

Distribution & Ecology: *Tryblionella littoralis* is a common, cosmopolitan and widespread species in intertidal zones of estuaries and marine coasts worldwide (*e.g.* Krammer & Lange-Bertalot 1988, Witkowski *et al.* 2000). It is a large motile epipelic species. Only a couple of specimens were observed in our material. It has been previously reported by the author (Ribeiro 2000, 2003) as frequent in another mudflat in the Tagus estuary (*i.e.* Pancas) but it was mistakenly identified as *T. gracilis.*

References:

Germain (1981) – pg. 334; figs. 125/3-5
Hustedt (1930) – fig. 762
Krammer & Lange-Bertalot (1988) – pg. 41; figs. 30/6-10
Ribeiro (2000) – pg. 38; figs. 5/11-13, 14/1-2
Snoeijs & Vilbaste (1994) – #199
Witkowski *et al.* (2000) – pg. 390; figs. 182/7-11

Nitzschia cf. ***pararostrata*** (Lange-Bertalot) Lange-Bertalot 2000

Micrographs: Pl. 33: 10-11

Synonyms:

Nitzschia compressa var. *pararostrata* Lange-Bertalot

Similar species:

Nitzschia compressa (J.W. Bailey) Boyer
Nitzschia hustedtiana Salah
Tryblionella punctata W. Smith
Tryblionella granulata (Grunow) Mann *in* Round, Crawford & Mann

Morphometrics:

Biovolume (µm^3): 224
Frustule geometry: prism on parallelogram
Length (µm): 13.6 (n=1)
Width (µm): 7.0 (n=1)
Pervalvar axis (µm): 4(estimated)
Striae in 10 µm: 16 (n=1)
Punctae in 10 µm: 17 (n=1)
Fibulae in 10 µm: 16 (n=1)

Description: valves broadly lanceolate-elliptic with short rostrate apices. The raphe is eccentric and not easily seen in LM, apparently with evenly spaced fibulae and no central break or nodule. The striae are punctate and in the same number as the fibulae. An apical fold in the centre of the valve is quite indistinct.

Notes: this taxon belongs to the species group around *Nitzschia compressa* and *Tryblionella granulata*. These species have an equal number of fibulae and transapical costae and also lack conspicuous central raphe endings (Mann 1978). Considering its small size, striae/fibulae density and the fact that the apical fold and canal-raphe are less visible than in the larger members of this species group, *Nitzschia hustedtiana* (see Archibald 1983) and *N. pararostrata* (see Witkowski *et al.* 2000) are the most likely candidates. The relations between these two taxa have not yet been established and deserve further study. It is possible that they are conspecific. Since only very few specimens were found during our study this taxon is only tentatively identified as *N.* cf. *pararostrata*, the taxon with the earliest synonym (Lange-Bertalot *et al.* 1996). A detailed study of this species group is needed to determine if they belong to the genus *Psammodictyon*, *Tryblionella* or, in the case of these smaller taxa above mentioned, *Nitzschia* sect. *Lanceolatae* (*viz.* Mann 1978).

Distribution & Ecology: motile epipelic species. Found only once during this study. *Nitzschia pararostrata* is reported for the Icelandic coast and for tidal flats in the Netherlands and elsewhere in the North Sea (Witkowski *et al.* 2000). *Nitzschia hustedtiana* was reported for the type locality (*i.e.* Blakeney Point, Norfolk, U.K) by Salah (1952) and for the South Africa coast (see Archibald 1983 and references herein).

References:

Archibald (1983) – pg. 262; figs. 392-394, 554 (*N. hustedtiana*)
Lange-Bertalot *et al.* (1996) – pg.164; figs. 48/6-6’ (*N. compressa* var. *pararostrata*)
Salah (1952) – pg. 166; fig. 2/9
Trobajo (2007) – fig. 109
Witkowski *et al.* (2000) – pg. 398; figs. 185/14-16

Nitzschia cf. ***parvula*** W. Smith 1853 non Lewis 1862

Micrographs: Pl. 33: 16-18; Pl. 57: 8-10

Synonyms:
Homoeocladia parvula (W. Smith) Kuntze
Tryblionella parvula (W. Smith) Sabbe comb. nov. prov.

Similar species:
Nitzschia schweikertii Witkowski, Lange-Bertalot, Ruppel & Kociolek
Nitzschia ligowskii Witkowski, Lange-Bertalot, Kociolek & Brseznińska
Tryblionella marginulata var. *subconstricta* f. *minuta* (Poulin)
Tryblionella apiculata Gregory

Morphometrics:
Biovolume (µm^3): 219
Frustule geometry: prism on parallelogram
Length (µm): 14.3 – (21.7) – 30.0 (n=37)
Width (µm): 3.4 – (4.3) – 4.8 (n=37)
Pervalvar axis (µm): 3 (estimated)
Striae in 10 µm: 28 – (31) – 34 (n=36)
Punctae in 10 µm: 40 (n=3)
Fibulae in 10 µm:12 – (14) – 17 (n=35)

Description: valves linear slightly constricted in the middle and with weakly rostrate apices. The raphe is strongly eccentric and the fibulae evenly spaced (separated by one interstria and two striae), with the exception of the more widely spaced central ones (two interstriae and three striae). The transapical striae are finely punctate and composed by round to elliptical occluded poroids which are irresolvable in LM. A very distinct apical fold in the centre of the valve interrupts the striae.

Notes: given the slight constriction in the middle of the valve this taxon is very reminiscent of *N. parvula*. However, it is smaller and has a higher striae and fibulae density than reported by Krammer & Lange-Bertalot (1998) and Witkowski *et al.* (2004a), who studied the type material of *N. parvula*. It corresponds completely to the specimens of *T. parvula* found by Sabbe (1997) in the Westerschelde estuary.

Recently, Witkowski *et al.* (2004a) described four new species, similar to *N. parvula*, as well as summarized the morphometric data of several other taxa belonging to the group of taxa around that species. Of the species referred in that article only *N. schweikertii* has a similar fibulae and striae density range to the specimens found in the Tagus estuary but it is considerably larger. *Nitzschia ligowskii* is also quite similar and it has a comparable size range; Conversely, the striation is slightly coarser and the valves are more distinctly constricted.

Given the similitude to *N. parvula*, particularly *sensu* Sabbe (1997), we decided to name this taxon provisionally *Nitzschia* cf. *parvula* until additional studies are made. It should be noted that it is not possible to study the type material of on *N. parvula* in EM (Lange-Bertalot & Simonsen 1978; Witkowski *et al.* 2004).

All the above mentioned species are very close to *T. apiculata* or to *T. hungarica*, *i.e.* belonging to the sect. "Apiculatae" *sensu* Grunow (*viz.* Mann 1978) and could be formally transferred to the genus *Tryblionella*. To our knowledge, the new combination *Tryblionella parvula* (W. Smith) Sabbe comb. nov. prov. proposed by Sabbe (1997) has not yet been formally established.

Distribution & Ecology: motile epipelic species. In this study, it was one of the most frequent nitzschioid diatoms (34 occurrences), being present in all stations. It was mainly common in the two upper shore stations of the muddy transect (max. relative abundance <9.4 %) and but also in the lower shore muddy sandy stations of sandy transect. This species had a particularly strong seasonal signal: it was almost completely absent during summer and autumn and reach its abundance peak in winter.

References:
Krammer & Lange-Bertalot (1988) – pg. 44; figs. 51/10-11
Lange-Bertalot & Simonsen (1978) – pg. 42; figs. 54-57
Sabbe (1997) – pg. 259; figs. 31/5-6
Witkowski *et al.* (2000) – pg. 398; figs. 195/8-9
Witkowski *et al.* (2004a) – pg. 582; figs. 7-9

Fam. Entomoneidaceae Reimer 1975

Entomoneis (Ehrenberg) Ehrenberg 1845

Genus description: Round *et al.* (1990); Patrick & Reimer (1975)

Entomoneis paludosa var. ***paludosa*** (W. Smith) Reimer in Patrick & Reimer 1975

Micrographs: Pl. 34: 9-10

Synonyms:
Amphicampa paludosa (W. Smith) Rabenhorst
Amphiprora paludosa W. Smith
Amphitropis paludosa (W. Smith) Rabenhorst

Similar species:
Entomoneis gigantea (Grunow) Kennett
Entomoneis paludosa var. *duplex* (Donkin) Makarova & Akhmetova
Entomoneis pseudoduplex Osada & Kobayasi

Morphometrics:
Biovolume (μm^3): 2869
Frustule geometry: half-elliptic prism
Length (μm): 34.0 – (39.1) – 45.5 (n=7)
Width (μm): 8.9 – (10.4) – 11.5 (n=3)
Pervalvar axis (μm): 12 (estimated)
Striae in 10 μm: 20 – (22) – 24 (n=7)
Punctae in 10 μm: 40 (n=3)

Notes: this well-known species is described in detail by Osada & Kobayasi (1990) or by Krammer & Lange-Bertalot (1986). It is very fragile and only a few specimens were found in sufficient good condition to be identified. Some of them (not included in the morphometrics) had a markedly denser striation (around 29 in 10 μm) and probably belonged to either *Entomoneis paludosa* var. *duplex* or to *Entomoneis pseudoduplex* but the valves were too damaged for a sound identification. In any case it is probably that they were scored together with the more common *E. paludosa*.

Distribution & Ecology: motile epipelic species, cosmopolitan and common worldwide in brackish waters on marine coasts (Witkowski *et al.* 2000). In our study this species was extremely rare, with only two occurrences and very low abundances (max. abundance < 0.32%). Due to the fragility of the frustules it was probably underestimated during cell counts.

References:
Osada & Kobayasi (1990) – pg. 162; figs. 1-2, 32-4
Krammer & Lange-Bertalot (1986) – pg. 439; figs. 204/2-4
Snoeijs & Potapova (1995) – #235
Witkowski *et al.* (2000) – pg. 199; figs. 109/26-27, 173/8

Fam. Surirellaceae Kützing 1844

Petrodictyon Mann *in* Round, Crawford & Mann 1990

Genus description: Round *et al.* (1990)

Petrodictyon gemma (Ehrenberg) Mann *in* Round, Crawford & Mann 1990

Micrographs: Pl. 35: 4-6, Pl. 58: 1-2

Synonyms:
Novilla gemma (Ehrenberg) Heiberg
Surirella gemma Ehrenberg

Morphometrics:
Biovolume (μm^3): 22764
Frustule geometry: elliptic prism
Length (μm): 44.5 – (59.8) – 93.7 (n=49)
Width (μm): 20.0 – (25.5) – 37.1 (n=4)
Pervalvar axis (μm): 19 (estimated)
Striae in 10 μm: 24 (n=3)
Punctae in 10 μm: 28 (n=3)

Transapical costae (primary ribs) in 10 µm: 2 – (3) – 4 (n=4)
Secondary ribs in 10 µm: 8 (n=1)

Notes: this well-known species is described in detail elsewhere (*e.g.* Krammer & Lange-Bertalot 1988; Witkowski *et al.* 2000). The specimens found in this study are shorter, thinner and have denser striation than the usual morphometrics given for this species in the literature (*e.g.* 72- 140 µm for length *in* Hendey 1964). However, other authors have also recorded smaller specimens of this taxon in their studies (see Archibald 1983).

Distribution & Ecology: large motile epipelic species, with a cosmopolitan distribution in marine and brackish waters (Witkowski *et al.* 2000). In our study, this species was very rare (4 occurrences, 3 in the mudflat stations) and never very abundant (max. abundance < 1.4 %)

References:
Archibald (1983) – pg. 312
Hendey (1964) – pg. 288; figs. 50/5, 52/4
Krammer & Lange-Bertalot (1988) – pg. 191; 140/1-3
Round *et al.* (1990) – pg. 638
Sabbe (1997) – pg. 261; fig. 59/3
Snoeijs & Vilbaste (1996) – # 179
Witkowski *et al.* (2000) – pg. 413; figs. 216/8-9

Surirella Turpin 1828

Genus description: Lange-Bertalot & Krammer (1987); Round *et al.* (1990)

The different sections of this genus used in this study were defined by Peragallo & Peragallo (1897-1990). It should be noted that Sect. *Fastuosae sensu* Peragallo has less restricted interpretation that it is perceived from the taxonomic keys constructed by Krammer & Lange-Bertalot (2000), but see discussion below (in *Surirella* sp.1)

Surirella atomus Hustedt 1955

Micrographs: Pl. 34: 11- (?) 13; Pl. 58: 8-9

Similar species:
Surirella brebissonii Krammer & Lange-Bertalot
Surirella minuta Brébisson *ex* Kützing
Surirella ostentata Cholnoky
Surirella ovalis Brébisson

Morphometrics:
Biovolume (µm^3): 294
Frustule geometry: elliptic prism
Length (µm): 6.1 – (11.6) – 17.0 (n=6)
Width (µm): 4.2 – (6.4) – 8.8 (n=6)
Pervalvar axis (µm): 5 (estimated)
Striae in 10 µm: 59 (n=2)
Punctae in 10 µm: 185 (n=1)

Notes: the specimens found in the Tagus estuary clearly correspond to the original description by Hustedt (1955) and to the LM micrographs of type specimens, provided by Simonsen (1987). This minute species can be distinguished from the small specimens of *S. brebissonii*, *S. minuta* or *S. ovalis* by the lack of rib-like fibulae, tapering and extending from the margin, in the internal side of the valves, and the fact that the striae are irresolvable in LM. The valve face is only very slightly undulate and the structural details of the valves (*e.g.* fibulae) can only be seen in SEM. It is also very similar to the freshwater species *S. ostentata* (see Archibald 1983)

Distribution & Ecology: small motile epipelic species. Since the original description by Hustedt (1955), who found it in a muddy sediment sample of Beaufort Beach (USA), this species has been rarely recorded. Apart from this reference and Archibald (1983) we were unable to have access to other references or reports of this taxon. According to Henderson *et al.* (2003) there are only two other works that provide SEM micrographs of this species, but we could not confirm if they corresponded to our own observations. In this study, only a couple of valves of this species were found in the muddy transect. The author (Ribeiro, 2000; Ribeiro *et al.* 2003) had already recorded this species for another Tagus estuary mudflat but wrongly identified it as *S. brebissonii.* In that study it was a much more common species and occurred mostly in winter and spring.

References:
Admiral (1983) – pg. 311; figs. 459-460
Hustedt (1955) – pg. 48; fig. 16/23
Simonsen (1987) – pg. 425; figs. 628/15-16
Ribeiro (2000) – pg. 41; figs. 7/7, 15/7-8

Surirella curvifacies Brun 1895

Micrographs: Pl. 36: 1-4; Pl. 59: 1-9

Synonyms:
Surirella traunsteineri Hustedt

Similar species:
Surirella brebissonii Krammer & Lange-Bertalot
Surirella fluminensis Grunow
Surirella striatula Turpin

Morphometrics:
Biovolume (µm^3): 14697
Frustule geometry: elliptic prism
Length (µm): 53.6 – (76.0) – 101.5 (n=13)
Width (µm): 28.2 – (35.2) – 45.0 (n=13)
Pervalvar axis (µm): 7 (estimated)
Striae in 10 µm: 22 – (23) – 24 (n=4)
Punctae in 10 µm: 19 (n=3)

Notes: this species has been barely recorded since it was described by Brun (1895) and it was identified with the help of A. Witkowski and E. Ruck (pers. communications). According to Hustedt (see Simonsen 1987), *S. traunsteineri* is described for the Indian Ocean (Schmidt 1874-1959) and is probably conspecific to *S. curvifacies*. This taxon has a quite unique structure given, for example, the slight helicoid torsion of the frustule about the apical axis (the torsion is not complete as in *S. spiralis*), irregularly shaped longitudinal sternum in the centre of the valves and clearly alveolate striae.

Distribution & Ecology: large motile epipelic species. The worldwide distribution is unknown and we were unable to find more references on both *S. curvifacies* and *S. traunsteineri*. The type locality of *S. curvifacies* is in the Japanese coast, according to its Index Nominum Algarum card (http://ucjeps.berkeley.edu/cgi-bin/porp_cgi.pl?652510). Therefore, this may well be the first confirmed report for the European coast and probably the first time it was observed in SEM. In this study it was the most commonly found *Surirella* (16 occurrences), being almost completely limited to the mudflat station and to winter samples, when it reached its maximal relative abundance (4.7%, in January 2004). It has been recurrently found in Tagus estuary samples (*e.g.* Ribeiro 2000, fig. 7/6 as *Surirella* sp.)

References:
Brun (1895) – figs. 15/36-37
Schmidt *et al.* (1874-1959) – heft 70, year 1912; fig. 283/12 (as *S. traunsteineri*)
Simonsen (1987) – pg. 28; fig. 19/1-4 (as *S. traunsteineri*)

***Surirella* sp.1**

Micrographs: Pl. 35: 1-3; Pl. 58: 3-7

Synonyms:
Surirella punctata (Grunow *in* Schmidt *et al.*) M. Peragallo

Similar species:
Surirella brebissonii Krammer & Lange-Bertalot
Surirella brightwelli var. *baltica* (Schumann) Krammer
Surirella fastuosa var. *cuneata (*A. Schmidt) Peragallo & Peragallo
Surirella fastuosa var. *punctata* Grunow *in* Schmidt *et al.* 1877

Morphometrics:
Biovolume (µm^3): 3529
Frustule geometry: elliptic prism
Length (µm): 34.2 – (37.1) – 40.7 (n=4)
Width (µm): 20.7 – (21.1) – 21.4 (n=4)
Pervalvar axis (µm): 6 (estimated)
Punctae in 10 µm: 87 (n=1)

Description: frustules in girdle view are more or less clavate. Valves are heteropolar, obovate, with one broadly rounded apex and the other apex more or less cuneate. Raphe system is marginal and small. Wing absent. Fibulae are marginal and only clearly visible in SEM. The surface is extremely undulated and composed by marginal domes, arranged concentrically. The elevated central area (sternum) is narrowly lanceolate. Striae concentric, multiseriate and finely punctate; they are barely visible in LM and seem to be only present in the valve interior, inside the domes but also extending towards the sternum. The external surface of the valve is sparsely covered by siliceous warts or spines.

Notes: this taxon is particularly interesting since it combines morphological features that define two different sections of the genus *Surirella*. Since it does not possess wings and is somewhat similar to *S. ovalis* Brébisson, it could well belong to the sect. *Pinnatae sensu* Peragallo (*cf. S. brebissonii*, S. *brightwelli*). Conversely, it has to be excluded from this section because of the conspicuous presence of an elevated central sternum (see Krammer & Lange-Bertalot 1988, 2000). This "central crown shaped field" (*viz.* Krammer & Lange-Bertalot 2000) and the overall shape and size makes it very reminiscent of some species of the sect. *Fastuosae sensu* Peragallo, namely *S. fastuosa* var. *cuneata* and especially *S. fastuosa* var. *punctata.* However, it lacks the infundibula, characteristic of most members of this section (see Krammer & Lange-Bertalot 1988, 2000b), particularly the species cluster around *S. fastuosa*.

The sect. *Fastuosae* needs further study or, maybe even, a major revision in order to determine the taxonomic status of most of these marine species and varieties. For example, Peragallo & Peragallo (1897-1990) refer a subsection of the Fastuosae that included species that are similar to *S. fastuosa* but that do not have a central band of striae (*i.e.* the infundibulae are "absentes ou rudimentares"). This group includes *S. fluminensis* (and probably *S. curvifacies*, see above) but also *S. intercedens*. Interestingly, when Schmidt (1874-1959) defined *S. fastuosa* var. *punctata*, he clearly stated that "ist nach des Autors Ansicht seiner *S. intercedens* nähernd". This closeness to *S. intercedens* needs to be confirmed and, in that case, this variety should be taken off the *S. fastuosa* group. For the moment, and without additional information, we refrain ourselves of identifying this taxon.

Distribution & Ecology: large motile epipelic species. Found rarely in this study (4 occurrences) and never very abundant (max. abundance < 0.32%). It has been recurrently found in other mudflats of the Tagus estuary (*e.g.* Ribeiro 2000, Ribeiro *et al.* 2003) where it was tentatively but wrongly indentified as S. cf. *brightwelli*.

References:

Schmidt *et al.* (1874-1959) – heft 14, year 1877; figs. 56/7

7.3. Diatom taxa list

The diatom taxa list enumerates all 184 diatom taxa observed during this study. It provides details of their average biovolume (µm^3), valve length/width ratio (L/W) and size-class (A: < 100 μm^3; B: 100 – 250 μm^3; C: 250 – 1000 μm^3; D: > 1000 μm^3). Ecological affiliations are divided in 2 columns: Functional groups [Epipelic (Eplc); Epipsammic (Epsmc); Undefined (Other)] and Life-forms [Adnate (Adnt); Stalked (Stal); Small motile epipsammic (Mo<20es), Small motile epipelic (Mo<20pl), Large motile (Mo>20); Tychoplanktonic (Tych); Planktonic (Plank); Epiphytic (Epiph); Undefined (Other). For more information on the different life-form and functional group definitions, see above section 3.5. In the last column, species that were selected for SPECIES-DATASET 2 and 3 (D.S. 2/3), used in the multivariate analyses, are marked with an x.

Species	**Biovolume (µm^3)**	**L/W**	**Size-class**	**F. group**	**Life-form**	**D.S. 2/3**
Achnanthes cf. *amoena*	111	2.9	B	Epsmc	Stal (?)	
Achnanthes cf. *fogedii*	97	2.0	A	Epsmc	Adnt	x
Achnanthes lemmermannii var. *obtusa*	53	2.3	A	Epsmc	Mo<20es	x
Achnanthes s.l. sp.1	55	2.2	A	Epsmc	Adnt	x
Achnanthes s.l. sp.2	270	3.3	C	Epsmc	Mo<20es	x
Achnanthidium exiguum	120	2.6	B	Other	Other	
Achnanthidium minutissimum	53	3.0	A	Other	Other	
Actinocyclus normanii	2788	1.0	D	Other	Plank	
Actinoptychus senarius	6923	1.0	D	Other	Tych	
Amphora arenicola	1109	5.3	D	Eplc	Mo>20	
Amphora cf. *helenensis*	79	3.3	A	Epsmc	Mo<20es	
Amphora cf. *pediculus*	82	2.5	A	Epsmc	Mo<20es	x
Amphora cf. *subacutiuscula*	190	5.3	B	Eplc	Mo<20pl	
Amphora cf. *tenuissima*	102	3.6	B	Epsmc	Mo<20es	x
Anorthoneis excentrica	2522	1.1	D	Epsmc	Adnt	
Anorthoneis cf. *tenuis*	309	1.4	C	Epsmc	Adnt	
Aulacoseira granulata	568	1.0	C	Other	Plank	
Aulacoseira islandica	362	1.0	C	Other	Plank	
Aulacoseira subartica	302	1.0	C	Other	Plank	
Bacillaria paxillifera	2721	11.1	D	Eplc	Mo>20	
Berkeleya rutilans	347	5.1	C	Other	Other	x
Biremis ambigua	5286	4.9	D	Eplc	Mo>20	x
Biremis lucens	439	4.1	C	Epsmc	Adnt	x
Catenula adhaerens	34	3.5	A	Epsmc	Adnt	x
Catenula sp.1	42	3.8	A	Epsmc	Adnt	x
Catenula sp.2	65	4.5	A	Epsmc	Adnt	
Cavinula sp.1	98	1.8	A	Epsmc	Mo<20es	x
Chamaepinnularia cf. *alexandrowiczii*	76	2.2	A	Epsmc	Mo<20es	x
Chamaepinnularia clamans	272	2.4	C	Epsmc	Mo<20es	
Climaconeis fasciculata	18079	12.4	D	Eplc	Mo>20	
Cocconeiopsis breviata	120	1.7	B	Epsmc	Mo<20es	x
Cocconeis cf. *discrepans*	110	2.0	B	Epsmc	Adnt	
Cocconeis cf. *distans*	1845	1.2	D	Epsmc	Adnt	
Cocconeis hauniensis	54	1.7	A	Epsmc	Adnt	x
Cocconeis cf. *hauniensis*	60	2.1	A	Other	Adnt	x
Cocconeis pelta	221	1.5	B	Epsmc	Adnt	x
Cocconeis cf. *pelta*	166	1.5	B	Epsmc	Adnt	
Cocconeis peltoides	175	1.6	B	Epsmc	Adnt	x
Cocconeis cf. *peltoides*	146	1.6	B	Epsmc	Adnt	x
Cocconeis cf. *placentula*	96	1.7	A	Epsmc	Adnt	x

Species	**Biovolume (μm^3)**	**L/W**	**Size-class**	**F. group**	**Life-form**	**D.S. 2/3**
Cocconeis scutellum var. *parva*	532	1.7	C	Other	Ephy	
Cocconeis sp.1	109	1.8	B	Epsmc	Adnt	
Cocconeis sp.2	110	1.9	B	Epsmc	Adnt	
Cyclotella cf. *ambigua*	1191	1.0	D	Other	Plank	
Cyclotella atomus	57	1.0	A	Other	Plank	
Cyclotella meneghiniana	957	1.0	C	Other	Tych	
Cylindrotheca closterium	247	8.3	B	Eplc	Mo>20	x
Cylindrotheca cf. *gracilis*	639	19.1	C	Eplc	Mo>20	x
Cymatosira belgica	295	2.5	C	Other	Tych	
Cymatosira sp.1	325	2.5	C	Other	Tych (?)	
Dickieia sp.1	638	4.2	C	Eplc	Mo>20	x
Dickieia sp.2	103	2.6	B	Epsmc	Mo<20es	
Dimeregramma minor	916	2.7	C	Epsmc	Stal	
Diploneis didyma	3895	2.1	D	Eplc	Mo>20	
Diploneis papula	754	1.8	C	Eplc	Mo<20pl	
Diploneis cf. *parca*	1901	2.0	D	Eplc	Mo>20	
Diploneis stroemi	3763	2.9	D	Eplc	Mo>20	
Entomoneis paludosa var. *paludosa*	2869	3.8	D	Eplc	Mo>20	
Eolimna minima	62	2.2	A	Eplc	Mo<20pl	
Eunotogramma dubium	120	3.1	B	Epsmc	Adnt	
Fallacia aequorea	120	2.0	B	Epsmc	Mo<20es	n.a.
Fallacia amphipleuroides	85	1.8	A	Epsmc	Mo<20es	x
Fallacia clepsidroides	128	2.1	B	Epsmc	Mo<20es	
Fallacia cryptolyra	87	1.9	A	Epsmc	Mo<20es	x
Fallacia dithmarsica	185	2.7	B	Epsmc	Mo<20es	
Fallacia florinae	113	1.8	B	Epsmc	Mo<20es	x
Fallacia oculiformis	136	1.8	B	Epsmc	Mo<20es	x
Fallacia cf. *scaldensis*	230	2.0	B	Epsmc	Mo<20es	x
Fallacia subforcipata	204	1.8	B	Epsmc	Mo<20es	x
Fallacia tenera	103	2.0	B	Eplc	Mo<20pl	x
Fallacia cf. *teneroides*	87	1.9	A	Epsmc	Mo<20es	x
Fragilaria cf. *cassubica*	81	4.8	A	Epsmc	Stal	
Fragilaria cf. *sopotensis*	63	1.2	A	Epsmc	Stal	
Fragilaria sp.1	104	2.1	B	Epsmc	Stal	
Frustulia interposita	22066	7.3	D	Eplc	Mo>20	
Geissleria cummerowi	65	1.9	A	Eplc	Mo<20pl	
Geissleria decussis	469	3.1	C	Eplc	Mo>20	
Gyrosigma acuminatum	20790	6.7	D	Eplc	Mo>20	x
Gyrosigma balticum	244295	12.0	D	Eplc	Mo>20	
Gyrosigma distortum	7549	4.6	D	Eplc	Mo>20	x
Gyrosigma fasciola	6614	7.2	D	Eplc	Mo>20	x
Gyrosigma cf. *limosum*	7436	8.3	D	Eplc	Mo>20	x
Gyrosigma wansbeckii	27104	9.1	D	Eplc	Mo>20	x
Halamphora cf. *abuensis*	112	3.9	B	Epsmc	Mo<20es	x
Halamphora cf. *tumida*	324	4.5	C	Eplc	Mo>20	n.a.
Halamphora sp.1	951	6.0	C	Eplc	Mo>20	x
Halamphora sp.2	799	4.6	C	Eplc	Mo>20	x
Haslea sp.1	1085	5.9	D	Eplc	Mo>20	
Hippodonta caotica	159	2.3	B	Epsmc	Mo<20es	x
Incertae sedis	30	2.0	A	Epsmc	Other	
Lunella cf. *garyae*	22	2.6	A	Other	Other	
Minidiscus chilensis	75	1.0	A	Other	Plank	

Species	Biovolume (μm^3)	L/W	Size-class	F. group	Life-form	D.S. 2/3
Navicula abscondita	642	5.1	C	Eplc	Mo>20	x
Navicula aleksandrae	76	2.3	A	Epsmc	Mo<20es	x
Navicula cf. *aleksandrae*	47	2.8	A	Epsmc	Mo<20es	x
Navicula arenaria	3290	5.8	D	Eplc	Mo>20	x
Navicula bozenae	91	2.6	A	Epsmc	Mo<20es	x
Navicula cf. *celinei*	122	3.0	B	Epsmc	Mo<20es	x
Navicula dilucida	195	6.2	B	Eplc	Mo<20pl	x
Navicula diserta	54	3.2	A	Epsmc	Mo<20es	x
Navicula cf. *diserta*	58	2.6	A	Epsmc	Mo<20es	x
Navicula flagellifera	757	5.1	C	Eplc	Mo>20	x
Navicula germanopolonica	132	2.7	B	Epsmc	Mo<20es	x
Navicula gregaria m.1	831	4.0	C	Eplc	Mo>20	x
Navicula gregaria m.2	271	3.9	C	Eplc	Mo<20pl	x
Navicula cf. *gregaria*	275	3.3	C	Epsmc	Mo<20es	x
Navicula cf. *microdigitoradiata*	194	4.0	B	Eplc	Mo<20pl	
Navicula cf. *mollis*	254	4.3	C	Eplc	Mo>20	
Navicula paeninsulae	4159	4.7	D	Eplc	Mo>20	x
Navicula pargemina	74	5.4	A	Eplc	Mo<20pl	
Navicula phyllepta	228	3.7	B	Eplc	Mo>20	x
Navicula cf. *phyllepta*	137	3.5	B	Eplc	Mo<20pl	x
Navicula platyventris	172	2.1	B	Epsmc	Mo<20es	x
Navicula ponticula	313	1.6	C	Eplc	Mo<20pl	
Navicula recens	1218	4.9	D	Eplc	Mo>20	
Navicula spartinetensis	299	5.3	C	Eplc	Mo>20	x
Navicula viminoides ssp. *cosmomarina*	96	2.2	A	Epsmc	Mo<20es	x
Navicula sp.1	258	4.1	C	Epsmc	Mo<20es	
Navicula sp.2	74	2.3	A	Epsmc	Mo<20es	x
Navicula sp.3	675	4.8	C	Eplc	Mo>20	x
Navicula sp.4	169	3.8	B	Eplc	Mo<20pl	x
Neodelphineis pelagica	100	2.0	B	Other	Tych	
Nitzschia cf. *aequorea*	145	5.5	B	Eplc	Mo<20pl	x
Nitzschia angularis	12016	7.4	D	Eplc	Mo>20	
Nitzschia cf. *aurariae*	36	3.0	A	Eplc	Mo<20pl	
Nitzschia cf. *dissipata*	193	6.1	B	Eplc	Mo<20pl	x
Nitzschia cf. *distans*	1343	10.5	D	Eplc	Mo>20	
Nitzschia cf. *dubia*	5529	7.9	D	Eplc	Mo>20	x
Nitzschia frustulum	38	3.5	A	Epsmc	Mo<20es	x
Nitzschia littorea	6436	14.3	D	Eplc	Mo>20	
Nitzschia lorenziana	1914	11.5	D	Eplc	Mo>20	
Nitzschia sigma	15304	14.3	D	Eplc	Mo>20	
Nitzschia spathulata	8327	10.9	D	Eplc	Mo>20	
Nitzschia valdestriata	39	3.7	A	Epsmc	Mo<20es	x
Nitzschia cf. *pararostrata*	224	1.9	B	Eplc	Mo<20pl	
Nitzschia cf. *parvula*	219	5.0	B	Eplc	Mo<20pl	x
Nitzschia sp.1	3493	7.7	D	Eplc	Mo>20	
Nitzschia sp.2	3393	31.2	D	Eplc	Mo>20	
Nitzschia sp.3	46	2.6	A	Eplc	Mo<20pl	
Nitzschia sp.4	1166	5.5	D	Eplc	Mo>20	
Opephora guenter-grassii	62	4.0	A	Epsmc	Stal	x

Species	**Biovolume (μm^3)**	**L/W**	**Size-class**	**F. group**	**Life-form**	**D.S. 2/3**
Opephora mutabilis	167	3.5	B	Epsmc	Stal	x
Opephora pacifica	443	2.9	C	Epsmc	Stal	x
Opephora sp.1	137	2.6	B	Epsmc	Stal	x
Parlibellus berkeleyi	625	3.0	C	Other	Other	x
Parlibellus cf. *calvus*	252	3.5	C	Other	Other	
Parlibellus sp.1	2672	3.9	D	Eplc	Mo>20	
Parlibellus sp.2	736	4.3	C	Other	Other	x
Petrodictyon gemma	22764	2.3	D	Eplc	Mo>20	x
Petroneis humerosa	29779	2.0	D	Eplc	Mo>20	
Pierrecomperia catenuloides	51	3.5	A	Epsmc	Tych	x
Plagiogrammopsis minima	113	3.9	B	Epsmc	Stal	x
Plagiotropis vanheurckii	9078	5.5	D	Eplc	Mo>20	x
Planothidium delicatulum s.l. m.1	140	2.0	B	Epsmc	Adnt	x
Planothidium delicatulum s.l. m.2	62	1.7	A	Epsmc	Adnt	x
Planothidium delicatulum s.l. m.3	91	1.9	A	Epsmc	Adnt	x
Planothidium deperditum	54	2.0	A	Epsmc	Adnt	
Planothidium lanceolatum	96	2.1	A	Epsmc	Adnt	
Planothidium cf. *lemmermannii*	75	2.5	A	Epsmc	Mo<20es	x
Planothidium septentrionalis	300	1.9	C	Epsmc	Adnt	x
Planothidium sp.1	42	2.2	A	Epsmc	Adnt	
Pleurosigma angulatum	38153	4.5	D	Eplc	Mo>20	x
Pseudopodosira sp.1	589	1.0	C	Other	Tych	x
Pseudostaurosira cf. *perminuta*	85	6.3	A	Epsmc	Stal	x
Staurophora salina	2278	4.4	D	Eplc	Mo>20	x
Staurophora wislouchii	2116	3.5	D	Eplc	Mo>20	x
Surirella atomus	294	1.8	C	Eplc	Mo<20pl	
Surirella curvifacies	14697	2.2	D	Eplc	Mo>20	x
Surirella sp.1	3529	1.7	D	Eplc	Mo>20	
Thalassiocyclus lucens	236	1.0	B	Other	Tych	x
Thalassionema nitzschioides	291	10.0	C	Other	Plank	
Thalassiosira angulata	796	1.0	C	Other	Plank	
Thalassiosira binata	99	1.0	A	Other	Plank	
Thalassiosira minima	201	1.0	B	Other	Plank	
Thalassiosira cf. *profunda*	35	1.0	A	Other	Tych	x
Thalassiosira proschkinae	88	1.0	A	Other	Tych	
Thalassiosira cf. *pseudonana*	50	1.0	A	Other	Tych	x
Thalassiosira cf. *visurgis*	333	1.0	C	Other	Plank	
Thalassiosira sp.1	468	1.0	C	Other	Plank	
Tryblionella apiculata	863	4.4	C	Eplc	Mo>20	x
Tryblionella levidensis	386	2.1	C	Eplc	Mo<20pl	
Tryblionella littoralis	4940	4.1	D	Eplc	Mo>20	
Vikingea sp.1	310	1.8	C	Other	Other	

Chapter 8

Concluding Remarks

8. Concluding Remarks

The synergy between diatom taxonomy and ecology is the guiding principle behind the present thesis. Ecological studies have great to gain if they apply consistent and correct taxonomy for it provides accurate diversity and abundance estimates (Kociolek 2005). This helps the data analysis in the immediate study but it also allows a sound comparison with other ecological studies (Kociolek & Stoermer 2001). Conversely, illustrated floristic studies, associated to ecology-oriented research projects, could function as regional floras, thus giving important information to taxonomists on species biogeography and ecological preferences (*e.g.* Kociolek 2006). This greater interplay between taxonomy and ecology in diatom studies is clearly perceived by the three main objectives this thesis intended to accomplish. The illustrated floristic account of the diatom taxa (**chapter 7** and **volume 2**) should serve as a complement to studies on MPB ecology already published (Cartaxana *et al.* 2006, Jesus *et al.* 2006b, Jesus *et al.* 2009). The use of fine-grained taxonomy, according to the consistent criteria documented in the floristic study, allowed a detailed taxonomic description of the structure of the benthic diatom communities, their spatial-temporal distribution and the relationships with environmental variables (**chapters 3, 4** and **5**). In addition, other metrics were used to describe the communities, such as size-classes and life-forms, thus allowing a more sophisticated community description. The high-resolution species abundances dataset was the departure point of the third and final aim of this thesis: to investigate if there are any valid alternatives to species-level identification that could be available to MPB ecologists, with low expertise in diatom taxonomy, but interested in community structure description. **Chapter 6** consists of an exercise that aims to objectively compare and test the effects that these alternatives could have on the results and interpretation of multivariate analysis, used in the description of community spatial-temporal patterns and in the linkage to environmental variables.

Arguably, the most important chapter of this thesis is the Diatom Identification Guide (**chapter 7** and **volume 2**). The main ambition was to create an accessible tool that could be useful for future researchers, such as ecologists and geologists, working in the Tagus estuary or elsewhere. For this reason, we tried to collect a maximum of information on each taxon (*e.g.* on morphometrics and autoecology) and to provide as many LM and SEM micrographs as possible. In addition, the procedure leading to the identification of each taxon is, generally, explained in a way that is reproducible by other researchers. Possible errors or misinterpretations made during identifications can, therefore, be easily detected (and corrected) by future users of this guide.

During this study 185 diatom taxa were observed. While 108 taxa were identified to species (or infraspecific) level, it was not possible to determine the identity of 77 taxa (42% of all taxa). In this second group, 45 taxa (24% of all taxa) were assigned to a known species and are indicated by the abbreviations "cf." or "aff.". This group comprises taxa that closely resembles a known species but may differ from the type description (for example, in size or striae density). Within the scope of this study, we could not always establish whether theses specimens belonged or not to the morphological continuum of the nominate species. The remaining 32 taxa (27 % of all taxa) could not be unambiguously identified. They were given a serial number in the genus we believe they belong to. A few taxa included in this group (species and genera) are most likely new to science (*e.g. Catenula* sp.1 e *Catenula* sp.2), although still further research is needed.

This guide is the most extensive and detailed report on the Tagus estuary benthic diatoms to date, but is by no means an exhaustive account of all intertidal diatoms of the Tagus estuary. It should be noted that a limited number of samples was studied and were all collected in a small area of the estuary. The intertidal areas downstream and upstream from the Alcochete flats, are most probably colonized by diatom taxa that were not reported in the present study due to role of salinity in determining the taxonomic composition of benthic estuarine diatoms. In addition, it is now well established that saltmarsh benthic diatom communities, in the upper intertidal zone, are floristically distinct from the unvegetated intertidal flats (*e.g.* Oppenheim 1991, Zong & Horton 1998, Sullivan 1999). The periphytic flora, growing on stems of halophytes and on rocks, also remains to be studied. In order to determine the biodiversity of these important communities, an ambitious, whole estuary survey could be envisaged in the future, particularly if it covered the yet unexplored fresh-water tidal area, upstream from Vila Franca de Xira.

Many species encountered in this work, particularly the ones most frequently found in the mudflat and sandflat assemblages, are also often reported for other intertidal and subtidal areas of North-West Europe, from the Baltic Sea to the English and the French West coast (*e.g.* Hustedt 1939, Brockmann 1950, Sundbäck & Persson 1981, Sundbäck 1983, Juggins 1992, Rincé 1993, Underwood 1994, Witkowski 1994a, Sabbe 1997, Méléder *et al.*

2007). There are also great similarities to the diatom floras found in North American (*e.g.* Hustedt 1955, Laws 1988) and South African coasts (*e.g.* Giffen 1971, Giffen 1975), thus supporting the long accepted perception of the cosmopolitan nature of estuarine and marine diatoms (*e.g.* McIntire & Moore 1977). However, the "ubiquity hypothesis" (cf. Finlay 2002, Fenchel & Finlay 2004), which advocates the global distribution of diatoms species and other protists, has recently been challenged for freshwater diatoms (*e.g.* Vanormelingen *et al.* 2008). Given the morphological variability associated to brackish water diatoms, the widespread practice of force-fitting diatom taxa into known entities and the general lack of specialized floras, it seems hard to access at present the biogeography of brackish water and coastal diatoms. The cosmopolitan nature of the majority of estuarine and coastal diatoms should, therefore, be considered with great care. A cautionary example is brought by a study on *Skeletonema costatum*, a "ubiquitous" species that is frequently reported all over the world. Based on morphological and molecular data on the species, that study concluded that there were several *S. costatum*-like entities, which had distinct ecological characteristics (*e.g.* different blooming seasons) and geographical distribution, thus putting into question the recurrent worldwide reports for this species (Sarno & Kooistra 2005). Conversely, the recent discovery of *Navicula spartinetensis* as common and even dominant component of the mudflat assemblages of several European mudflats (see section 7.2), although it was only reported before for its type locality (in Delaware, USA), is another reminder of the fractional information we still have for most coastal benthic diatom species.

A single tidal area (circa 1 km^2), composed by a mosaic of sediment types from sandflats with different sand textures to extremely silty mudflats, was studied in this thesis. Multivariate analysis established that temporal variation patterns of the diatom communities were clearly subordinate to spatial ones and mud content was the environmental variable that was more closely related to the biotic spatial-temporal patterns. The structure of the intertidal diatom communities could be roughly divided in two functional groups: the epipelon and the epipsammon. The epipelon is composed of large or medium-sized motile species, capable of endogenous migrations to the sediment surface; and small immotile species (*e.g. Cymatosira belgica*), which are easily resuspended. The epipsammon is composed by species that live in close association to individual sand grains and can be divided in three groups: stalked species, attached to the surface by a short stalk; adnate species, which are strongly attached to the sand grains; and small motile biraphid diatoms. These two latter lifeforms probably form a continuum of small prostrate diatoms that trade high adherence and lower dispersion rates (low-risk strategy) for higher motility but also higher resuspension/dispersal rates (high-risk strategy). The epipelon completely dominated the sampling stations of the sheltered areas (*i.e.* mudflats) whereas the epipsammon was the dominant functional group in the sandy transect (*i.e.* sandflats). However, both functional groups co-existed in two sandy stations with low mud contents (8 and 14 %, in average). The epipelic communities found in this study were mainly composed by medium sized motile diatoms (*e.g. Navicula gregaria*. *N. spartinetensis*) while the epipsammic were composed by a mix of the three life-forms referred above. The spatial distribution of these three life-forms was not uniform, whereas the temporal variation of epipsammic assemblages was very limited. The co-existence of different life-forms within the epipsammon and the epipelon is a phenomenon rarely studied (*e.g.* Miller *et al.* 1987, Jewson *et al.* 2007) but the way these different life-strategies cope with a changing benthic environment has important implications on their ecology, function and distribution (Sabbe 1997).

Since diatoms of all species are constantly redistributed over intertidal areas by tidal action, their absence from any area indicates an inability to survive there (cf. Riznyk & Phinney 1972, Sullivan 1999). This apparently self-evident or trivial observation is absolutely essential to fully understand why benthic diatom communities are not uniformly distributed within a tidal flat. Most motile epipelic diatoms are larger than epipsammic ones and are more prone to be destroyed by the collision with sand grains. They are, therefore, less likely to survive in exposed sediments and are directly controlled by the intensity, duration and frequency of sediment physical disturbance. Conversely, the epipsammon is well adapted to cope with the frequent abrasion and burial that occurs in non-cohesive sediments. Physical stress may still play an important role, particularly with regard to the occurrence of stalked species. Nevertheless, the presence of epipsammon seems to be mainly determined by the availability of a suitable substrate to grow (*i.e.* sand grains). Few epipsammic species occur in mudflats because any available sand grains are quickly covered by settling silt. Physical disturbance of the sediment seems, therefore, to be the primary structuring factor of the intertidal benthic diatom communities. The mosaic of sediment textures found in this study was mainly created by the complex interaction of tidal currents, wind-induced waves and bioturbation, which had site-specific intensities and frequencies. Epipelic diatoms also contribute to the cohesiveness of the mudflat sediment by the continuous production of EPS. Consequently, mud content should be seen as a good indicator of the degree of sediment exposure and a predictor of the presence of epipelic species.

When considering the whole estuary, salinity and nutrient concentrations should play a more important role as they influence the taxonomic composition of the communities. The bloom of *Navicula* cf. *phyllepta* in early 2003, when salinities were very low, is an example of these effects. Even if the assemblages change their taxonomic composition throughout the estuary, the physiognomy of benthic diatom communities continues to be mainly determined by physical stress as life-forms have a different resistance and resilience to physical disturbance.

By directly comparing diversity, taxonomic structure and physiognomy, this study stressed the ecological differences of both epipelic and epipsammic communities in intertidal benthic environments. Ecological models must take into account their fundamental differences, namely in diversity and temporal patterns. However, still much research is needed on life strategies and autoecology of individual diatom species. Experimental studies exploring the effect of species richness and identity on epipelic biomass (*e.g.* Vanelslander *et al.* 2009b) or describing in detail cell attachment or the formation and recovery of resting cells of epipsammic species (Jewson *et al.* 2007) should be pursued in the future. Further development of these lines of research will help to determine with more certainty which combination of factors (*e.g.* nutrients, grazers and light conditions) is behind the actual taxonomical composition of any given assemblage of estuarine benthic diatoms.

Chapter 6 demonstrated that less time-consuming alternatives are able to replicate the major multivariate patterns given by species-level analysis. The most consistent alternative approaches to species-abundance data were: (1) maintaining a high taxonomic resolution but not performing cell counts; (2) lowering the taxonomic resolution to genus-level, while counting the diatom cells. These two user-friendly approaches could, therefore, be confidently used by ecologists only interested in describing the major shifts in intertidal benthic diatom community structure. However, temporal patterns were clouded by the decrease in taxonomical resolution or the loss of abundance data. Given that most of the temporal signal in the intertidal benthic diatom communities is given by the succession of species-specific seasonal blooms of epipelic diatoms, identification to the species level is mandatory to detect temporal variations. Sharp spatial discontinuities, caused by distinct sediment types, were always detected. Nonetheless, some approaches failed to correctly access more subtle structural changes caused by slight differences in sediment textures. Consequently careful consideration of the appropriate approach to be chosen must take into account the sediment characteristics of sampling area and the study objectives. The good performance obtained by the 29 *Navicula* species-abundance dataset is an important reminder of the amount of information on community structure and distribution contained within a single species.

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