INVESTIGATIONS ON THE SEASONAL SUCCESSION OF WADDEN SEA INHABITING DIATOMS AT DANGAST (NORTH SEA, GERMAN BIGHT) OVER A ONE YEAR PERIOD

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DIATOMS (BACILLARIOPHYCEAE)
DIATOM ASSEMBLAGES
SEASONAL SUCCESSION
WADDEN SEA
SEDIMENTS

ABSTRACT – The subject of the study was the diatom flora of the tidal flat sediments at Dangast (Wadden Sea, German Bight). Special attention was paid to the seasonal succession of diatoms inhabiting the tidal flat sediments over a growing season (March/April to November). Results of the light microscopic analyses, concerning the relative abundance of diatoms during 8 sampling periods, were treated by means of multivariate mathematical techniques including analyses of similarity (Ranked similarity matrix based on the Bray-Curtis similarity index), biodiversity, and ordination. The results clearly show the succession pattern of the diatom assemblages over a vegetation season. The groupings distinguished corresponded to early spring, late spring, mid-summer, late summer and autumn. Although the number of the taxa is relatively high (over 250), the major component of the diatom assemblages included a group of only 33. However, only several taxa out of the latter group were responsible for diversification of the similarity and the MDS diagrams.

INTRODUCTION

Large surface areas of shallow marine and estuarine intertidal and subtidal habitats are covered by biofilms composed of cyanobacteria, diatoms and/or euglenoids (e.g. Kingston 1999a, 1999b, Paterson 1986, Paterson 1995, Round 1971). Those found on muddy sediments are often dominated by diatoms (Underwood & Kromkamp 1999) and although the overall species richness of marine benthic diatoms is high, only a few taxa usually represent most of the biomass within these assemblages (Admiraal & Peletier 1980, Paterson 1986, Underwood 1994, Witkowski et al. 2000).

Diatom-rich biofilms play an important role in ecosystem functioning. Their primary production can be very high, and this can constitute a significant proportion of the carbon fixation (Underwood & Kromkamp 1999). Diatom-rich biofilms also

Similar to what is found for planktonic diatoms, diatom-dominated biofilms are subject to changes in species composition over the short- and long-term time scales. The reasons for this are manifold: several physical and chemical parameters vary within hours, days, months or years and thus might have a great impact on the fitness (metabolism, reproduction rate, survival) of certain taxa. Endogenous, species-specific factors and rhythms might also influence species abundance. Changes in species composition, on the other hand, might lead to significant changes in nutrient cycling, nutrient flow, sediment stability and erosion.

One might get the impression from the literature that a certain discrepancy exists between taxonomic and functional studies on diatoms and diatom-rich biofilms. Taxonomic studies often focus on the description of (new) species and their distribution and abundances, and describe the habitats mostly on the basis of physical and/or chemical parameters, i.e. nutrient concentrations, salinity, pH and temperature. These parameters are then taken as a valid description of potential niches of distinct species, without any regard to the variable nature of these and other parameters over short, medium and long-term time scales. Functional studies, on the other hand, often ignore species composition, and treat the entire assemblage as the “object of interest”. They thus neglect short- and long-term changes in species composition of the investigated biofilm. More recent functional studies, however, clearly demonstrate significant differences in the behaviour and physiology of different taxa even within the same biofilm, and show that species respond differently to the external nutrient environment (Oxborough et al. 2000, Thornton et al. 2002, Underwood 2002).

The current study was undertaken as a necessary step in combining both approaches. The Wadden Sea sediments of Dangast are dominated by diatoms (Sauer et al. 2002). In previous studies, molecular and biochemical methods were applied to the diatom-rich biofilms at this particular field site. Short-term experiments revealed that the diatom assemblages adapt to changes in light intensity on the protein and mRNA levels (Hust et al. 1999, Meyer et al. 2003). Currently, no data on the seasonal succession and the abundances of distinct species are available for this sampling site. We therefore investigated the seasonal succession and species abundances over the period of one year. Future, functional, molecular and biochemical studies undertaken within the same area can be interpreted more precisely when both functional and taxonomical data are known and combined.

**MATERIAL AND METHODS**

*Field sampling:* Sampling was performed in 2001 at a single sampling site on the North Sea shore near the harbour of Dangast (Germany). Its geographic location is shown in Fig. 1. Samples, i.e. muddy intertidal sediments were collected within a defined area of approximately 10 m² throughout the entire period. The sampling dates and some physical parameters measured on these days are compiled in Table I. At least three patches, 15-20 cm in diameter and homogeneously brownish in colour were chosen. For sampling, the uppermost 4-8 mm of the sediment surfaces of these patches, which consisted mainly of brownish diatom layers, were scratched off with a spatula, placed into Petri dishes, homogenized, and transferred to the laboratory.

![Fig. 1. – Geographic location of the sampling site on the North Sea shore near the harbour of Dangast (Germany). Its position is marked by an arrow.](image-url)
luted with water so that after placing a drop of sample onto glass slides the diatom valves were evenly spread on the slides. The drops were allowed to air dry, covered with Naphrax (Beyersdorfer, Mandelbachtal, Germany), prewarmed to 60°C and sealed with cover glasses. Finally, they were allowed to dry over night at room temperature. At least 15 to 20 slides were made for each sediment sample and examined. The slides and the aliquots of some samples are deposited in the diatom collection of A Witkowski (Univ Szczecin, Poland).


Light microscopy (LM) and scanning electron microscopy (SEM): Light microscopic studies were carried out with a Leica DMLB microscope equipped with ×100/1.4 PlanAPO oil immersion objectives. For SEM, small aliquots of the suspensions of cleaned frustules were allowed to air dry on aluminium stubs, sputter-coated with approximately 10-20 nm of Au and finally examined in a scanning electron microscope operated at 5 kV (Hitachi S4500). SEM stubs have been deposited in the Botanical Institute of JW Goethe University, Frankfurt am Main in Coll. Lange-Bertalot.

Measurement of relevant physical parameters: Photon flux rates, temperature, humidity and pH were measured with an Almemo 2290-2 measuring device (Ahlborn Mess- und Regeltechnik, Germany) equipped with the relevant sensors. Salinity was measured with a hand refractometer (American Optical Corporation).

Statistical treatment: The structure of the Dangast tidal flat diatom flora and the mutual relationships between assemblages in particular sampling periods were determined by means of multivariate mathematical analysis applying PRIMER software (Plymouth Routines in Multivariate Ecological Research, Clarke & Warwick 1995). Data from 8 sampling sessions during 2001 were used to compare the similarity of the diatom assemblages at different sites using relative abundance. The analyses included only those taxa which occurred in at least one sample with an abundance of 1%. To reduce discrepancies between abundant and less abundant taxa, the data were fourth-root transformed. Ranked similarity matrices were constructed using the Bray-Curtis similarity measure and group-average sorting (Lance & Williams 1967). Hierarchical classification of abundances was performed using PRIMER’s CLUSTER procedure and identification of homogenous groups. In order to separate periods with similar diatom assemblages, diatom counts were subjected to similarity analysis using the Bray-Curtis index, whereby sorting was performed by means of a group-average, i.e. average similarity indices for successively created groups of samples. The procedure of multi-dimensional scaling (MDS) was applied to construct a 2-dimensional diagram of sampling periods distribution within a multi-dimensional space, where distances between particular sampling periods and their mutual distribution reflect similarity or dissimilarity of diatom assemblages.

RESULTS

Altogether 36 slides were analysed in LM. From the first two sampling dates (April 2001) diatom counts included 11 and 6 slides respectively. As the results were very closely matched in several slides, the number of slides analysed was reduced to three for the following samples. For statistical analyses the average of three countings was used for each taxon. The number of taxa identified in the material studied amounted to 258. Identification of a very small centric, structureless diatom (2-3 µm in diameter) and its proper identification was only possible by SEM.

The number of taxa in the individual samples ranged from 25 (in early April) to 60 (in mid July). The number of taxa increased throughout the vegetation season, the lowest occurring in spring. The highest number was reached in early summer and counts remained at this level until late autumn. The selection of taxa for statistical treatment was based...
on their percentages and only those with an average 1% content in at least one of the sampling periods were taken into consideration. The list of taxa included in the statistical treatment encompassed only 33 (for the abundances of particular taxa see Table II) out of the total of 258 species. Some of the most abundant or interesting taxa are illustrated in Plate I. In the material studied we have found three interesting taxa i.e. *Navicula spartinetensis* S. Sullivan et Reimer, *Navicula cf. flanatica* Grunow (Pl. I; Fig. 19-20) and *Pleurosigma sterrenburgii* Stidolph. They are interesting because of either their biogeography or taxonomy.

*Navicula spartinetensis* was originally described by Sullivan & Reimer (1975) from Delaware salt marsh on the Atlantic coast of USA, while *P. sterrenburgii* was originally recorded from an antipodal locality in New Zealand (Stidolph 1993), but was recently found at the Jadebusen in the North Sea (Sterrenburg 2003). In addition, in all samples a small admixture of *Chaetoceros* spp. resting spores was recorded. The similarity analyses of the diatom assemblages at particular sampling dates are shown in the diagram for relative abundance (Fig. 2, top). The similarity regarding abundance is moderate, as the differentiation of the dendrogram begins with a similarity index above 50%. Nevertheless, several groups of sampling dates (A, B, C, D) were distinguished. They all show distinct seasonal characteristics.

Group A encompassed samples from early spring (beginning and end of April). Characteristic for these samples is the very strong dominance of *Nitzschia filiformis* W. Smith var. *conferta* (Richter) Lange-Bertalot (Pl. I; Fig. 1-7) and of several other less abundant taxa including *Navicula spec. 4* (Pl. I; Fig. 23-26), *Navicula phyllepta* Kützing (Pl. I; Fig. 16-18), *Thalassiosira profunda* (Hendey) Hasle (Pl. I; Fig. 28), *Nitzschia pusilla* Grunow (Pl. I; Fig. 8-9) and *Cymatosira belgica* Grunow in Van Heurck. Accessory taxa in this sample were: *Navicula spartinetensis* (Pl. I; Fig. 21-22), *Delphineis minutissima* (Hustedt) Simonsen, *Gyrosigma fasciola* (Ehrenberg) Griffith et Henfrey, *Paralia sulcata* (Ehrenberg) Cleve and *Pleurosigma sterrenburgii*. Group B included samples collected during the late summer (August, September, subgroup B1) and late autumn (end of

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October and beginning of December, subgroup B2). All samples were dominated by *Navicula cf. phyllepta* Kützing (Pl. I; Fig. 11-12; 14-15), *Thalassiosira profunda*, *Cymatosira belgica* and *Delphineis minutissima*. Less abundant, but constantly occurring were: *Fragilaria gedanensis* Witkowski, *Navicula digitoradiata* (Gregory) Ralfs, *N. phyllepta*, *N. phylleptosoma* Lange-Bertalot (Pl. I; Fig. 13), *Gyrosigma* spec. 1, *Nitzschia constricta* (Kützing) Ralfs, and *N. aequorea* Hustedt (Pl. I; Fig. 10). The distribution pattern of some of the latter taxa (i.e. *Gyrosigma* spec. 1 and *Navicula phyleptosoma*) was responsible for the differentiation of subgroups B1 and B2. Their content showed a rather strong decreasing tendency. *Nitzschia filiformis var. conferta*, the most abundant taxon in group A, was absent in group B. Group C included only one sampling period, which was completed in June, i.e. late spring. Dominant taxa were *Navicula phylepta*, *Thalassiosira profunda*, *Cymatosira belgica*, *N. phyleptosoma*, *Delphineis minutissima*, and *N. spartinetensis*. Less abundant were *Navicula cf. phylepta*, *Nitzschia constricta*, *Paralia sulcata* and *Nitzschia aequorea*. The hitherto dominating taxa i.e. *Nitzschia filiformis var. conferta*, *P. sterrenburgii* and *Navicula spec. 4* showed a very strong decrease and the latter taxon was not even found in June. Group D, similarly to the preceding one, included only one sampling period – mid summer (July). In this sample dominant taxa were *Cymatosira belgica*, *Thalassiosira profunda*, *Navicula phylepta*, *Nitzschia constricta*, *Paralia sulcata*, *Navicula cf. phylepta*, *Nitzschia sigma* (Kützing) W. Smith and *Navicula spartinetensis*. Accessory taxa included *Dimeregramma minor*, *Fragilaria gedanensis*, *Navicula digitoradiata*, *Staurophora amphioxys* (Gregory) D.G. Mann, *P. sterrenburgii* and *Planothidium delicatum* (Kützing) Round et Bukhtiyarova. When compared to the preceding group, *C. belgica*, *N. constricta* and *P. sulcata* showed a strong increase in abundance, while *N. phylepta*, *Thalassiosira profunda* and *N. phyleptosoma* decreased. In Fig. 2, bottom the results of the Multi-Dimensional Scaling (MDS) analysis are illustrated. It is a two-dimensional diagram, which corresponds to the distribution of the sampling periods in a multi-dimensional space. A stress index value of 0.01 for the frequency of occurrence indicates that the sampling
site configuration provides a useful two-dimensional image regarding the real relationships between the sampling periods (corresponding to the groupings of sampling periods as revealed by Bray-Curtis similarity analysis).

**DISCUSSION**

The results of our study clearly show the phenomenon of seasonal succession of the diatom flora of the tidal flat sediments at Dangast. Although relatively easily to derived solely from the LM analyses it was tested by means of multivariate mathematical techniques. The most useful in this case appeared to be the similarity dendrogram supplemented with the MDS diagram.

General studies of the tidal flat, salt marsh and estuarine diatom flora are numerous (e.g. Riznyk 1973, Sullivan 1975, 1978, Amspoker 1977, Amspoker & McIntire 1978, McIntire 1978, Admiraal 1984, Admiraal & Peletier 1980, Admiraal et al. 1984, Paterson 1989, Sauer et al. 2002). However, the problem of seasonal succession of the diatom flora in tidal flat sediments has been less exhaustively studied and fewer relevant publications exist (e.g. Hendey 1964, Oppenheim 1991, Laird & Edgar 1992, Underwood & Paterson 1993, Underwood 1994). Hendey (1964) studied a seasonal distribution of numerous taxa inhabiting British coasts. Several of diatom taxa identified in our material were also observed by Hendey (1964). Included in this group were e.g. *Gyrosigma fasciola*, *G. littorale*, *Navicula digitiradiata*, *Nitzschia sigma*, *Paralia sulcata*, *Staurophora amphioxys* and *S. salina*. One of the most extensive studies on seasonal and spatial changes in diatom flora from Severn Estuary (UK) was completed by Underwood (1994).

A comparison of our study with other studies of tidal flat diatom floras shows distinct differences with respect to species composition and their sea-
sonal distribution. The data summarised by Underwood (1994) indicate the seasonal distribution of some epipellic species. From the group of 7 species with determined seasonality (Underwood op. cit.) only two belonged to the dominant taxa in our material. These were Delphinites minutissima and Cymatosira belgica. They were relatively frequent all round the year and D. minutissima reached its maximum in autumn, while the second species in question was abundant in late spring, summer and autumn. Some species did not show any seasonal pattern as they were present the year round. NAVICULA PHYLLEPTA, Paralia sulcata and Thalassiosira profunda belonged to this group. On the other hand the occurrence of Nitzschia conferta was subject to very strong seasonality. It occurred in early spring as a strongly dominant species and then almost disappeared.

From the research hitherto it is clearly visible that diatoms very strongly dominate the microphytobenthic community of the tidal flats of Dangast and that a very strong domination of only a few taxa within the diatom flora is characteristic for this habitat, contributing to more than 90% of diatom counts (e.g. Admiraal & Peletier 1980, Underwood 1994). In the case of Admiraal & Peletier (1980) seven taxa contributed to 95% of the epipellic diatom assemblage, while in the case of Underwood (1994) 11 taxa contributed for 99%. Underwood (1994), referring to Sullivan (1975, 1978), Laird & Edgar (1992), his own study and to Admiraal & Peletier (1980) pointed out differences in diversity of diatom assemblages from salt marsh and tidal flat respectively. He noticed that diatom assemblages from tidal flats were less diverse. In contrast to the studies of the former authors, in our study the number of taxa was rather high (as typi-
cally for instance for the marine littoral zone, e.g. Snoeij s et al. 1989, Witkowski 1991, 1994, Busse & Snoeij s 2002). On the other hand, with such a high number of taxa (usually exceeding 40 in individual samples) the number of dominant taxa remained low, as in other tidal flats studied. However, as also shown by Amspoker (1977) and Amspoker & McIntire (1978) the species richness of a diatom flora may greatly vary depending on locality. Amspoker (1977) identified 93 taxa at Scripps Beach, La Jolla in California, while Amspoker & McIntire (1978) recorded 390 diatom taxa in Yaquina Estuary in Oregon, USA. The latter study encompassed a transect along a very wide range of salinity from marine to pure freshwater, however.

When compared to other studies on tidal flat diatoms our study shows that a feature characterising the Dangast site (possibly also the whole area) is the species composition. Although in general the species identified at Dangast belong to the common list of taxa inhabiting tidal flats, the domi-
nant species, with few exceptions, were site-spe-
cific. An interesting finding is mass occurrence of Thalassiosira profunda and of two somewhat less abundant “non-European” taxa. These are Pleurosigma sterrenburgii, which may have been misidentified as some populations of P. rhomboeum Grunow (see Sterrenburg 2003). This species was recently discovered in the Jadebusen (German Wadden Sea, Sterrenburg 2003) and its presence is confirmed in our study. The second interesting specie s is Navicula spartinetensis, first described by Sullivan & Reimer (1975) from Delaware salt marshes. Our study indicates that it belongs to the dominant forms in the area we studied. The previously published studies on the tidal flat diatoms along the European coasts did not illustrate this species (e.g. Hustedt 1939, 1959, Brockmann 1950, Hendey 1964, Aleem 1973, Witkowski et al. 2000). This might indicate that this characteristic species has reached the European coasts very recently. This and other taxonomic and biogeographic questions will be the subject of a further publication (Witkowski et al. in prep).

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