DISTRIBUTION AND DYNAMICS OF PROTIST COMMUNITIES IN A FRESHWATER TIDAL ESTUARY

VERSPREIDING EN DYNAMIEK VAN PROTISTENGEMEENSCHAPPEN IN EEN ZOETWATERGETIJDENGEBIED

Chapter 3. *Aulacoseira subborealis* stat. nov. (Bacillariophyceae): a common but neglected plankton diatom from eutrophic waters

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Summary

Aulacoseira subarctica f. *subborealis* differs from *A. subarctica* var. *subarctica* by a number of morphological features (less elongate linking spines and smaller spine grooves, discus always areolated, shallower mantle and different 'Formwechsel', considerably finer structure), and its ecological preferences. It is therefore considered to represent a separate species: *A. subborealis*. Differential characteristics with respect to the next most resembling species, *A. alpigena*, include the non-spathulate linking spines, each one originating from two pervalvar ribs, more numerous areolae on the disci, smaller dimensions, finer areolation of the mantle and, in LM, absence of more marked mantle areolae next to the collum. In LM, confusion may further arise with *A. laevissima*, *A. distans* or *A. nygaardii*, which also show some superficial resemblance. *A. subborealis* is widely distributed in rivers and lakes in W-Europe and Australia, and presumably occurs in New Zealand and Michigan as well, but was reported only rarely because of confusion with other taxa. It appears to develop especially well in more alkaline and rather eutrophic, highly turbid fresh water.

Introduction

Aulacoseira species are important diatoms in freshwater systems throughout the world. They often attain high biomass in eutrophic rivers (e.g. Hotzel & Croome 1996, Yang *et al.* 1997) and lakes (e.g. Haberyan 1985, Håkansson 1989, Donar *et al.* 1996), but are also an important component of the diatom communities in oligotrophic waters (e.g. Haworth *et al.* 1988, van Dam & Mertens 1995, Hall & Smol 1996). As the dominant *Aulacoseira* species vary with lake trophic status, they are particularly useful indicator organisms in actuo-ecological and palaeolimnological studies (e.g. Sabater & Haworth 1995, Donar *et al.* 1996, Bradbury & Van Metre 1997, Kling 1998). Obviously, this requires a firm taxonomic basis, which has not yet been attained for all known members of the genus in spite of several recent comprehensive studies, such as by e.g. Camburn & Kingston (1986), Haworth (1988) and Krammer (1991a, 1991b).

Aulacoseira subarctica (O. Müller) Haworth f. *subborealis* (Nygaard) Haworth is one of those taxa that remained in relative obscurity, so far. Since its decription by Nygaard (1956) from the sediments of Lake Gribsø (Denmark) as *Melosira italica* Ehrenberg var. *subborealis* Nygaard, it was reported only occasionally in the literature. Renberg (1976, 1978) recorded the taxon in some lake stratigraphies from northern Sweden, whereas Haworth (1988) mentions its occurrence from a Scottish lake, and presumably Michigan and New Zealand as well. The latter author recombined the taxon as a form of *Aulacoseira subarctica*, argueing that its basic morphology agrees entirely with that of *A. subarctica* var. *subarctica* and that only differences in size and spine length are observed. Krammer & Lange-Bertalot (1991) consider *Aulacoseira subarctica* f. *subborealis* to be an insufficiently described taxon and provide no clues to its identification.

Recent observations by the authors indicate that *Aulacoseira subarctica* f. *subborealis* can be an important phytoplankton diatom in W.-European rivers and lakes, and that it is also widely distributed elsewhere. This suggests that *Aulacoseira subarctica* f. *subborealis* often remains unidentified or is mistaken for other taxa, due to identification problems and its absence in standard reference works. In order to prevent further confusion, we present a detailed morphological study of this taxon based on collections from different localities and discuss relations to neighbouring or similar taxa. The results of this study provide arguments for raising *Aulacoseira subarctica* f. *subborealis* to the species level. Furthermore, an overview of the distribution and ecology of this diatom is given on the basis of published and new observations.
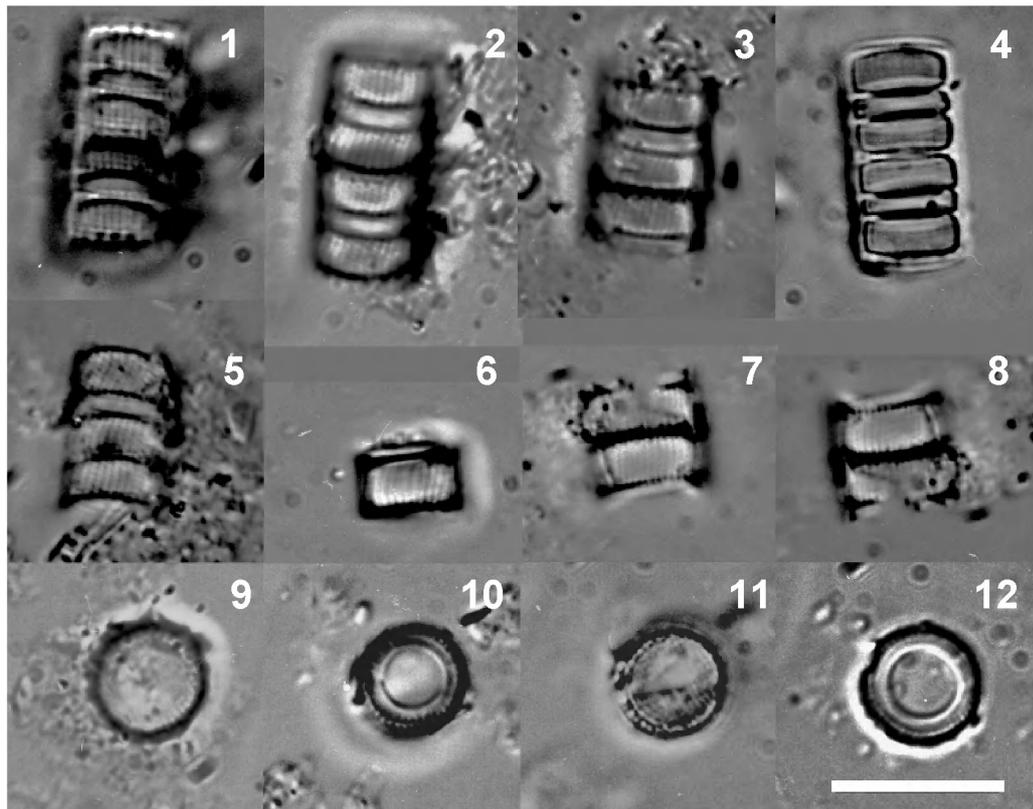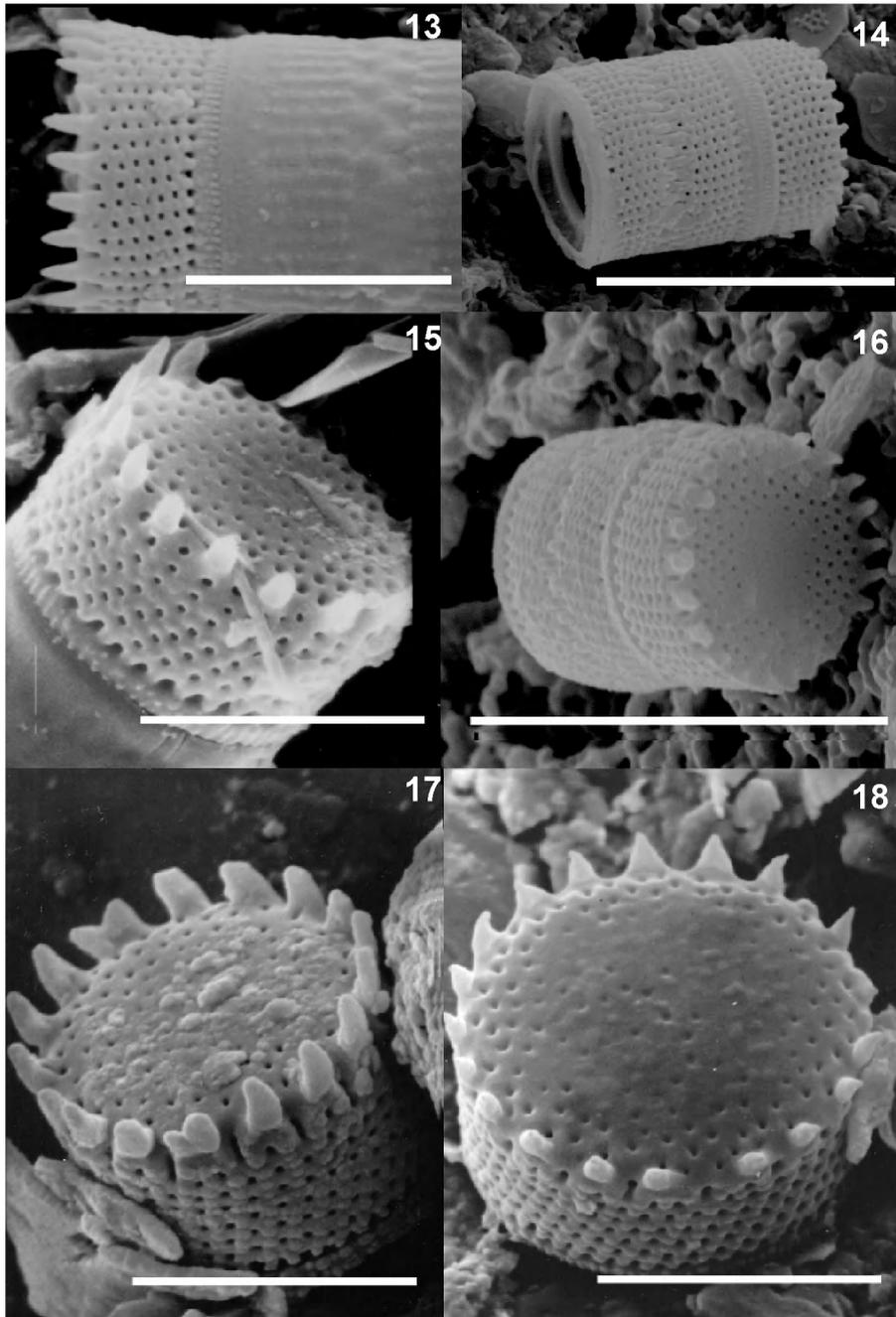
Figs 1-12. *Aulacoseira subborealis* Denys, Muylaert & Krammer stat. nov., Blankaart (LM). Figs 1-8: Mantle views at different focus in the LM. Figs 8-12: Valve face views at different focus in the LM. Scale bar = 10 μm.

Materials and methods

Morphological observations of *Aulacoseira subarctica* f. *subborealis* were conducted on the subfossil type material from Lake Gribsø (Denmark), on a sediment-core sample taken in the Blankaart Reservoir (Woumen, Belgium), and on recent phytoplankton and surface sediment collections from the rivers Schelde (Belgium), Maas and Rijn (The Netherlands), the Lac Chauvet (Massif Central, France), a lake at Asserbos (The Netherlands) and billabongs in the River Murray Basin (Australia).

Samples were cleaned with concentrated hydrogen peroxyde or sulphuric acid. Cleaned residue was mounted in water, Naphrax or Hyrax, and observed with Leitz Orthoplan and a Zeiss Universal light microscopes (LM). For scanning electron microscopy (SEM), Philips SEM 515 and JEOL JSM-840 microscopes were used. Nomenclature and most of the terminology follow Krammer & Lange-Bertalot (1986, 1988, 1991a, 1991b). Following Haworth (1988), 'Ringleiste' and pseudoseptum are considered synomyms.

Figs 13-18. *Aulacoseira subborealis* Denys, Muylaert & Krammer stat. nov., Blankaart (Figs 13, 14, 16), Asserbos (Fig. 15), Murray billabong (Fig. 17) and Schelde estuary (Fig. 18) (SEM).
Figs 13, 14: Mantle views. Figs 15-18: Oblique views showing the external valve face.
Scale bar 5 (Figs 1, 16-18) or 10 μm (Figs 14, 15).

Observations

Aulacoseira subborealis Denys, Muylaert & Krammer stat. nov.

Basionym: *Melosira italica* f. *subborealis* Nygaard (1956, p. 74, Plate 1, Fig. 8, Plate 2, Figs 13-19, Plate 6, Figs 24-25).

Synomyms: *Aulacoseira subarctica* (O. Müller) Haworth f. *subborealis* (Nygaard) Haworth (Haworth, 1986), also reported as *M. distans* (Ehrenberg) Kützing in Cassie (1981), *M. distans* in Eloranta (1986) and *A. distans* var. *distans* by Siver & Kling (1997)

Valve morphology
(Figs 1-23, Table 1)

Only vegetative cells, often still in short filaments of 2 to 4 cells, are observed. Their frustules are cylindrical and measure *ca.* 5.5 to 9 μm in diameter (mostly 6-7 μm) and are about 2.5 to 4 μm high (Figs 1-8). The ratio between mantle height and diameter varies from 0.39 to 0.55, increasing with size. The inner and outer sides of the mantle are slightly convex; both being parallel to each other. At its edge with the valve face, the mantle is more or less rounded off. The pseudosulcus is shallow and opens with an angle of about 30° (Fig. 4). The discus is flat or just very slightly sunken in the middle. In the LM, a shallow but distinct sulcus groove can be seen, continuing inwards into a solid pseudoseptum of about 1-1.5 μm wide (Figs 4, 9, 10, 12). The ratio between pseudoseptum width and valve diameter is fairly constant (0.23-0.25). The pseudoseptum bears an enforced inner rim (Figs 14, 20, 21, 23), making it T-shaped in section. This rim is also conspicuous in the LM (Figs 9, 10, 12). The collum is only *ca.* 0.5 to 1 μm high; the ratio between its height and the rest of the mantle varies from 0.2 to 0.43. In the SEM its regular surface ornamentation with low and closely spaced transverse ridges, often partly dissolved into small warts, becomes apparent (Figs 13-19, 23). The areolae on the mantle are fairly distinct and appear as more or less round in the LM. The SEM observations confirm this shape (Figs 13-19). Their density amounts to *ca.* 35 to 40 in 10 μm. The pervalvar rows of areolae, 23.5 to 28 in 10 μm, are generally somewhat inclined (up to ca. 20°) and curved, but may sometimes be almost straight and parallel to the pervalvar axis as well. In the LM all the mantle areolae appear equally large. With the SEM, however, it can be seen that those adjacent to the sulcus are somewhat enlarged (Figs 13, 15, 19). The areolae are closed by simple rotae (see Round *et al.* 1990), slightly sunken beneath the mantle surface (Fig. 22). The pervalvar ribs bear low, rounded knobs; one at each crossing with a connecting rib, so that each areola is surrounded by four knobs (Figs 15-19). The linking spines are rather small, but distinct in the LM. Their density amounts to *ca.* 12-14 in 10 μm. The spines, which all appear to be of the same type (linking spines) do not appear to be completely straight, even when cells have not yet been separated, but are slightly curved inwards. They are pointed, tapering from the base, and without anchors or projections (Figs 15-19). Occasionally, their base may be somewhat broadened (Fig. 18). The spines are about 2.5 times as long as wide, giving them a rather stout appearance. Their length does not exceed *ca.* 1.2 μm. SEM observations show that they emanate from two pervalvar ribs, a feature also discernable in the LM. In material from the Murray river billabongs, spines emerging from 3 or 4 pervalvar
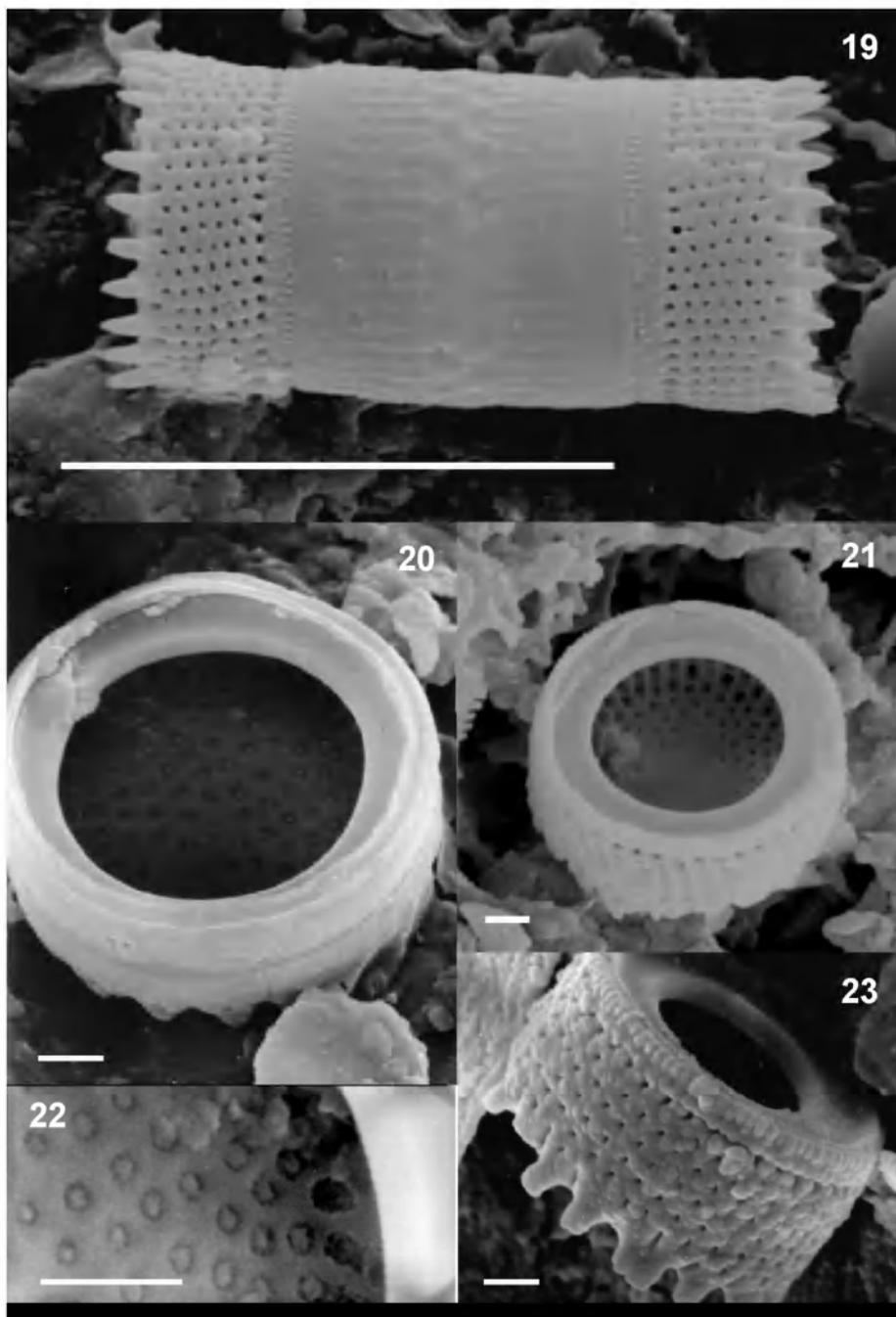
Figs 19-23. *Aulacoseira subborealis* Denys, Muylaert & Krammer stat. nov., Blankaart (Figs 19, 21), Schelde estuary (Figs 20, 22) and Murray billabong (Fig. 23) (SEM).
Fig. 19. Mantle view of two sibling frustules with cingulum. Figs 20, 21, 23: Oblique views showing part of the valve interior. Note the enforced rim of the pseudoseptum. Scale bars = 1 μm. Fig. 22. Detail of the valve face areaolae. Scale bar 10 (Fig. 19) or 1 μm (Figs 20-23).

ribs were sometimes observed, in which case the spines were bifurcated (Figs 17, 23). Sometimes, an areola occurs on the base of a spine. Between the spines, short spine grooves are present (Figs 13, 17, 18). Pervalvar rows of areolae end both at the base of each spine and in the spine grooves. Fine areolae are present on the entire

valve face, where they are often placed in a more or less radial pattern in continuation of the rows af areolae on the mantle. In some valves the areolae are occluded towards the exterior ('blind') in the central part of the discus, in which case only a broad marginal zone is fully areolated (Figs 16, 18). Towards the center the areolae become progressively smaller. So far, no observations are available on the rimoportula(e).

Occurrence

Sediment records

On the basis of the inferred pH values for the period of maximum development and subsequent waning in the Holocene record from Lake Gribsø, *A. subborealis* was already provisionally classified as alkaliphilous by Nygaard (1956). The high abundances of the species in the post-isolation phases of Lake Prästsjön and Lake Rudetjärn observed by Renberg (1978) also point to a preference for alkaline and relatively nutrient-rich conditions.

A more precise impression of the trophic range of *Aulacoseira subborealis* is given by its occurrence in the sediment record of the shallow (< 2 m) Blankaart Reservoir, Belgium, which underwent severe eutrophication and pollution in the course of this century due to the inflow of untreated sewage and agricultural drainage (Denys 1994). Fig. 24 gives a summary diatom diagram from the core in which it was most abundant. From 26 to 32 cm depth *Aulacoseira subborealis* attains a frequency of 0.2 to 6.8 % in a transition phase from an assemblage dominated by epiphytic and epipelic diatoms (*Achnanthes lanceolata* subsp. *frequentissima* Lange-Bertalot, *Cocconeis placentula* Ehrenberg, *Gomphonema micropus* Kützing, *Gyrosigma acuminatum* (Kützing) Rabenhorst, *Navicula* spp.) and small *Fragilaria* spp. (*F. brevistriata* Grunow, *F. construens* (Ehrenberg) Grunow and *F. construens* f. *venter* (Ehrenberg) Grunow) to a plankton-dominated assemblage typical of hyper-eutrophic and polluted conditions (*Cyclotella atomus* Hustedt, *C. meneghiniana* Kützing, *Nitzschia* spp., *Stephanodiscus hantzschii* Grunow, *S. parvus* Stoermer & Håkansson, *Thalassiosira pseudonana* Hustedt). *Aulacoseira subborealis* culminates at the same level as *Cyclostephanos dubius* (Fricke) Round, a species indicating alkaline and nutrient-enriched water (Clarke 1989, van Dam *et al.* 1994) for which Bennion (1994) observed a TP (total phosphorus) optimum of 215 µg l^{-1}.
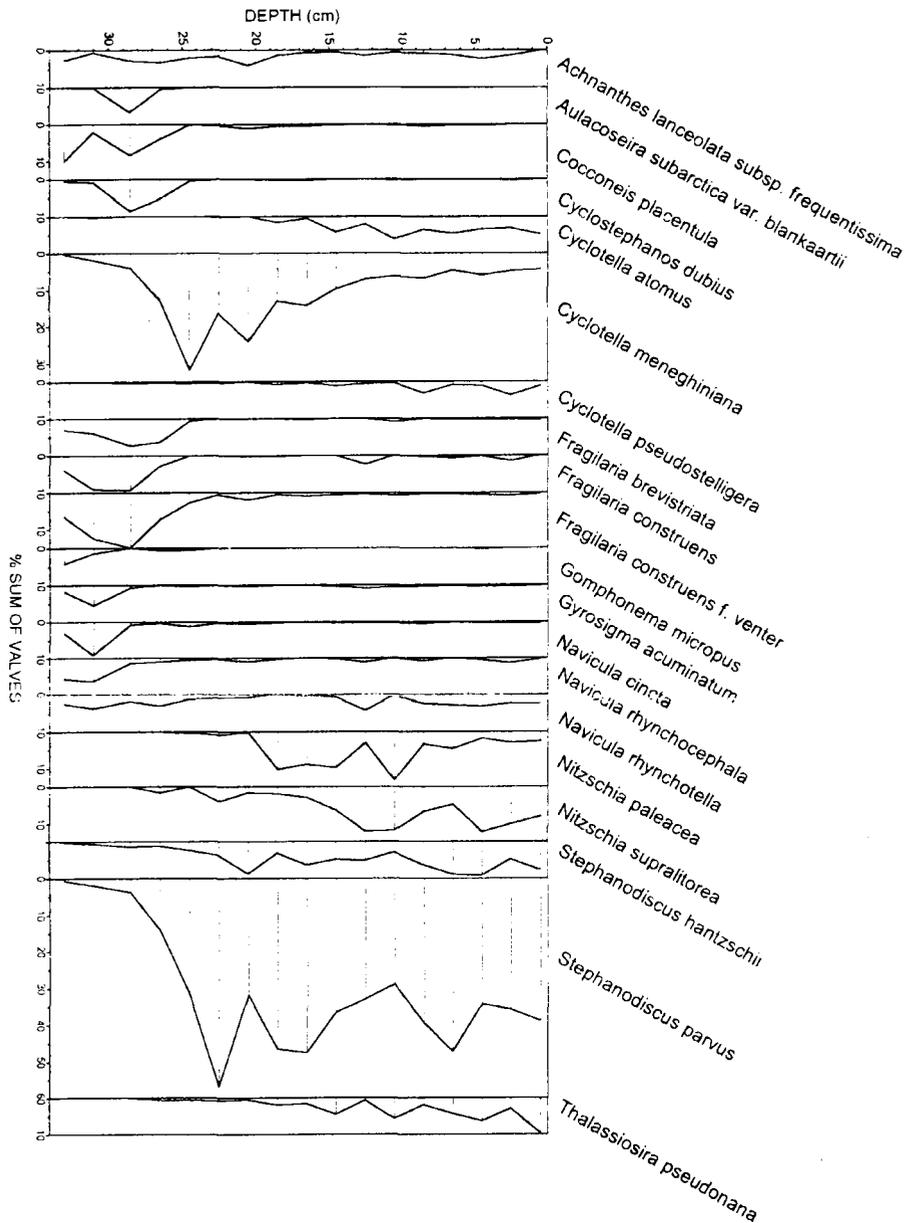
Fig. 24. Diatom diagram of core 5, Blankaart (selected taxa only; percentages are based on counts of at least 500 valves).

Recent observations

Aulacoseira subborealis is a minor constituent of the phytoplankton communities in the freshwater tidal reaches of the Schelde estuary. It was found mainly in the uppermost estuarine zone during autumn, contributing less than 1 % to the total phytoplankton biomass with a maximum of 180 cells ml^{-1} (Fig. 25). *A. subborealis* occurred in the most upstream reaches of the Schelde estuary together with *A. granulata* (Ehrenberg) Simonsen, which contributed on average 5 % to the total phytoplankton biomass and occurred in winter and from late summer to early autumn (Fig.25). The spatial

distribution of the latter species suggests that it was autochthonous within the estuary. The accompanying dominant was *Cyclotella scaldensis* Muylaert & Sabbe. In the freshwater tidal estuary, TP concentration ranges between 75 and 235 µg l^{-1} and turbidity is very high (Secchi depth 20-40 cm and SPM concentrations of about 100 mg l^{-1}). In the tributaries, turbidity is lower (Secchi depth > 50 cm) while phosphorus concentrations are comparable (average 110 µg l^{-1}) (data from Muylaert *et al.* 1997).
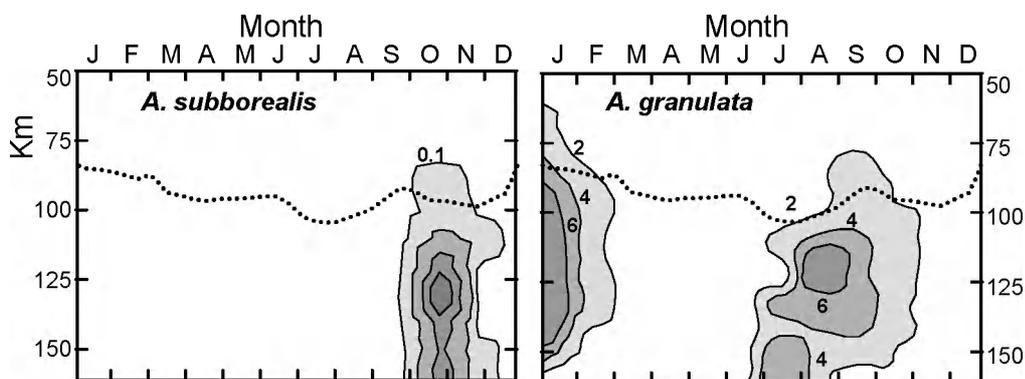

Fig. 25. Spatio-temporal distribution of *Aulacoseira granulata* and *A. subborealis* in the upper reaches of the Schelde estuary, Belgium (in mg C l^{-1}); months are indicated along the horizontal axis while distance from the mouth of the estuary is displayed along the vertical axis. The position of the 0.5 psu isohaline (broken line) is indicated to show the relation of diatom distribution to salinity.

In the Dutch part of the River Maas, *A. subborealis* was observed together with the closely related *A. subarctica*. Neither species was dominant. *A. subborealis* bloomed at the most upstream station sampled (Eijsden) in late summer (Fig. 26). At the more downstream situated stations, it occurred in much lower numbers but densities were highest in the same period. *A. subarctica* was not observed at the most upstream station but occurred at the more downstream situated stations (Belfeld) and diplayed a bloom at station Keizerveer in spring. Both species were also present in the Dutch part of the River Rijn, again never as a dominant component of the phytoplankton. As in the Maas, both species displayed different optima in space and time.

In The Netherlands, *A. subborealis* was also found in several eutrophic lakes in the catchment area of the Rivers Maas and Rijn. In neighbouring Belgium, *A. subborealis* was noted in surface sediment samples from five eutrophic ponds. It occurred within a count of 500 valves (max. 2 %) in waters ranging in average pH from 6.5 to 7.9 and in TP from 110 to 160 µg l^{-1}.

In a survey of diatoms in the surface sediments of 57 billabongs in the River Murray basin, *A. subborealis* was found to be an important component of the diatom community. It occurred in 42 billabongs, contributing to more than 10 % of total abundance in 24 of these, and was the most abundant species in 11. It was most common in the billabongs along the middle to lower reaches of the Murray River, where it often occurred together with *A. granulata*, the dominant phytoplankter in this
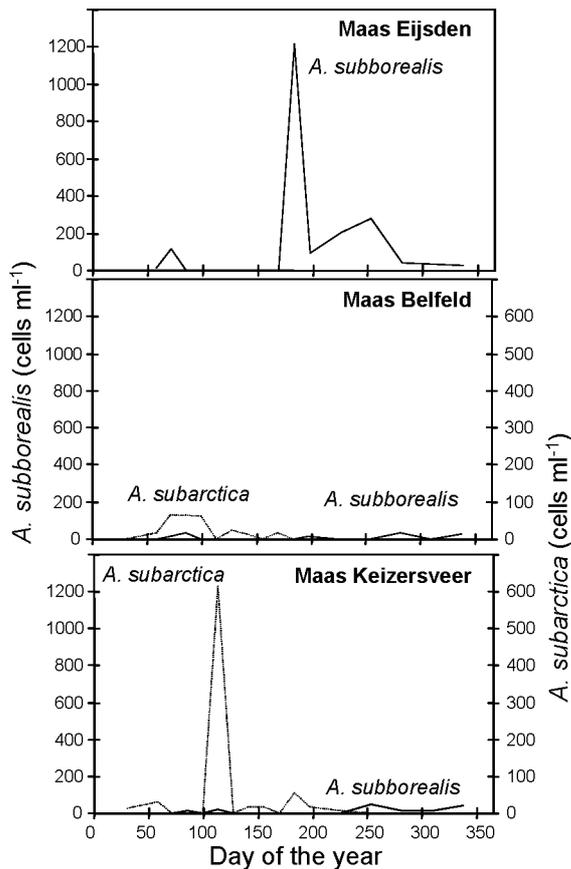
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Fig. 26. Seasonal occurrence of *Aulacoseira subborealis* and *A. subarctica* in the River Maas, The Netherlands at three sampling stations: Eijsden (most upstream), Belfeld and Keizersveer (most downstream).

river (Hotzel & Croome 1996). The billabongs where *A. subborealis* occurred are characterised by shallow depth (< 4 m), high turbidity and very high phosphorus concentrations (TP concentrations 67 to 1680 μg l⁻¹). In those billabongs which receive summer irrigation flows of the River Murray, *A. granulata* was usually the dominant species, whereas in lakes receiving no riverine inputs, *A. subborealis* often dominated.

A study in the French Massif Central revealed *A. subborealis* in six lakes. Highest abundance was noted in the plankton and sediments of the Lac Chauvet, a 66 m deep crater lake at 1166 m above sea level, where it occurred together with mainly *Aulacoseira ambigua* (Grunow) Simonsen, *Asterionella formosa* Hassall, *Cyclotella pseudostelligera* Hustedt and *C. glomerata* Bachmann. In these lakes, the TP-optimum calculated by weighted averaging obtained for *Aulacoseira subborealis* amounted to 100 μg l⁻¹. *A. subarctica* sometimes co-occurred in vey low proportions with *A. subborealis*, but displayed a different distribution pattern, occurring more abundantly at higher nitrate and total alkalinity levels.

Discussion

Taxonomy

Electron microscopic observations on the valve morphology of *A. subarctica* var. *subarctica* have been published by, among others, Crawford (1979), Haworth (1988), Canter & Haworth (1991), Krammer & Lange-Bertalot (1991a) and Le Cohu (1996). They reveal a large similarity in the structure of this species and that of *A. subborealis*, e.g. with regard to the form and arrangement of mantle areolae, and the overall shape as well as the implantation of the linking spines. As in *A. subborealis*, the mantle areolae of *A. subarctica* are surrounded by four knobs each. Similar knobs, are observed in other *Aulacoseira* species, but with different arrangements (e.g. Davey & Crawford 1986, Haworth & Sabater 1993, Krammer 1991, Le Cohu 1991). Apart from these similarities, however, the linking spines are considerably longer and more slender in *A. subarctica*, and the spine grooves correspondingly extend further on the mantle. According to Le Cohu (1991, personal communication 1997) and personal observations, *A. subarctica* presents two types of spines: separation spines, with a somewhat widened base and a length of about 2.8 µm, and longer linking spines of 3.3 to 4 µm. Only one type of spines (interlocking or linking spines) is observed in *A. subborealis*. Due to the limited length of these spines, sibbling cells separate easily and filaments remain short, making separation spines redundant. The abundant terminal cells of *A. subarctica* show unperforated disci. Normal cells, however, have disci that are areolated as in *A. subborealis* (cf. Le Cohu 1997, personal communication R. Le Cohu 1997, and unpublished observations K. K.). Cells with unperforated disci were not observed in *A. subborealis*. Variation in the areolation of the valve face was also noted in other *Aulacoseira* species (cf. Haworth & Sabater 1993) and a varying degree of importance is attributed to the areolae pattern of the valve face (e.g. Haworth 1988, Krammer & Lange-Bertalot 1991a). A more straightforward distinction between both taxa is found in the density of mantle areolae, with *A. subarctica* having only 17-22 pervalvar areolae and 17-21 pervalvar striae in 10 µm (Krammer & Lange-Bertalot 1991a, Table 1). Although some populations of *A. subborealis* show somewhat more heavily silicified cells, no overlap is observed with regard to this feature. We acknowledge that environmental conditions, such as light or nutrient availability, may affect pore size and the degree of silicification in *Aulacoseira* spp. (see e.g. Stoermer *et al.* 1985; Kilham *et al.* 1986), but this does not appear to explain the observed variation beween *A. subarctica* and *A. subborealis*. Moreover, the cells of *A. subarctica* tend to have less convex mantle margins and are usually longer in relation to their width. The valve heigth to diameter ratio tends to vary substantially in *A. subarctica* populations (Krammer & Lange-Bertalot 1991a, Jewson 1992, Siver & Kling 1997). In a detailed morphometrical study, Jewson (1992) reported that while cell diameter was highly variable, cell height remained more or less constant. Thus, small cells of *A. subarctica*, of which the cell diameter might overlap with that of *A. subborealis*, will usually have a valve height to diameter ratio exceeding 1 (Krammer & Lange-Bertalot 1991, Siver & Kling 1997), whereas this ratio is always markedly below 1 in *A. subborealis*. Consequently, *A. subborealis* is not merely a small form of *A. subarctica*. A final morphological difference is found in the structure of the pseudosulcus, of which the inner margin is not or less conspicuously thickened in *A. subarctica* (R. Le Cohu, personal communication 1995). Finally, *A. subborealis* also

differs from *A. subarctica* in its ecological requirements, since the latter is more typical of oligo- to mesotrophic conditions and more or less acid water (Krammer & Lange-Bertalot 1991a; van Dam *et al.* 1994). All these differences indicate that *A. subborealis* is quite distinct from *A. subarctica* var. *subarctica*.

Characteristics of some other taxa which could give rise to confusion are gathered in Table 1. In the LM, *A. subborealis* resembles *A. alpigena* (Grunow) Krammer rather strongly; both having cells which are more wide than high, convex mantle margins, inclined/curved rows of mantle areolae, and small linking spines. The latter, however, has a distinctly coarser mantle areolation (15-22 striae in 10 μm and areolae of similar density; Krammer & Lange-Bertalot, 1991a). Another distinction, visible in the LM, is that in *A. alpigena*, the areolae in the row next to the collum appear distinctly larger than the remaining ones, and that collum and mantle are separated by a more strongly refractive ring (the pseudoseptum). In valve view, *A. alpigena* is distinguished easily by having only one or two rows of marginal areolae. In the SEM, the very different linking spines (spathulate or with marginal anchors), their different implantation and the absence of spine grooves are important differential characteristics (see Haworth 1988; Marciniak 1988; Krammer & Lange-Bertalot 1991a). *A. laevissima* (Grunow) Krammer presents an almost equally fine areolation and similar cell shape as *A. subborealis*. Generally, however, it has a larger diameter and the collum is higher relative to the remainder of the mantle. Also, the valve face presents more marked and equally large areolae over the entire surface, the linking spines posess small terminal anchors, and the pseudoseptum is less well developed (Haworth 1988; Krammer 1991b; Krammer & Lange-Bertalot 1991a). The less known N-American *Melosira nygaardii* Camburn has longer cells, only 20-22 striae in 10 μm, which also run parallel to the pervalvar axis, and an unperforated valve face (Camburn & Kingston 1986). *Aulacoseira distans* (Ehrenberg) Simonsen should also be mentioned here, because *A. subborealis* repeatedly has been reported under this name. *A. distans* was described (as *Galionella distans*) by Ehrenberg (1836) from fossil samples ('Biliner Polierschiefer'). Material from the type location is also present in other collections, e.g. in the Kützing collection (sample nr. 107 from the BM (NH)). Krammer (1991a) presents a series of light-microscopical photographs of the type material from the Ehrenberg collection. Material from both the Ehrenberg and Kützing collections has been examined by D. Crawford. Both collections were found to contain morphologically identical *Aulacoseira* species (Crawford, personal communication 1998). SEM photographs of *A. distans* from the Kützing collection are published in Haworth *et al.* (1986) and Haworth (1988). *A. distans* specimens from the type locality differ substantially from *A. subborealis* in having mantle areolae arranged in straight rows, a pervalvar striae density of 12-15 in 10 μm, larger areolae on the entire surface of the discus and spines which emerge from a single pervalvar rib. Thus, confusion between these two taxa seems unlikely. Up to recently, however, diatoms possessing marginal spines that emerge from two pervalvar ribs in stead of one and with mantle areolae arranged in curved rows were often identified as *A. distans* (see e.g. Cassie 1981, Eloranta 1986, Krammer 1991, Krammer & Lange-Bertalot 1991a, Siver & Kling 1997). These specimens clearly differ from the *A. distans* type material but show similarities to *A. subborealis*, particularly the specimens illustrated by Cassie (1981) and Eloranta (1986), which appear identical.

Ecology

We observed *Aulacoseira subborealis* in recent and subrecent material from rivers and lakes in the northern as well as the southern hemisphere. Previous studies have reported this taxon from Scandinavian lakes (Renberg 1976), Scottish lake sediments (material from Pennington *et al.* 1972, re-identified by Haworth 1988) and lakes in Canada (Siver & Kling 1997), Michigan and New Zealand (Cassie 1981; Haworth 1988). It therefore seems to be a widespread and common taxon of cosmopolitan distribution.

Like many other members from the genus *Aulacoseira*, *A. subborealis* may be a useful indicator species for trophic conditions. Based on the present data *A. subborealis* appears to indicate fairly nutrient-rich conditions, especially with TP concentrations of ca. 100 µg l^{-1} or more. In the Schelde and Murray basins, it co-occurs with *A. granulata*, which also reflects more eutrophic conditions (e.g. Donar *et al.* 1996, Kling 1998). Interestingly, *A. subborealis* was found to mark the onset of hyper-eutrophication in the Blankaart Reservoir. In the Rivers Maas and Rijn, it was observed with the closely related *A. subarctica*, a species marking the onset of nutrient enrichment in oligotrophic systems (Haworth 1988, Sabater & Haworth 1995), but generally occurring in less eutrophic environments than *A. granulata* (Krammer & Lange-Bertalot 1991a, van Dam *et al.* 1994). Both taxa occurred separated in time and space, which demonstrates that, despite close relationships, substantial differences in their ecological requirements exist. This is also apparent from the subfossil records and present distribution of *A. subborealis* and *A. subarctica* in European lakes.

Although *A. subborealis* occurs in the Schelde estuary, this does not imply adaptation to increased salinities, since is was only found in the freshwater tidal zone and disappeared rapidly even before a notable increase in salinity occurred. Moreover, its distribution suggests that it originates from the Schelde River, as it was most common in the most upstream part of the estuary and occurred in periods when river discharge was highest. *A. subborealis* was also found in the lower reaches of other rivers (Rijn, Maas), as well as in shallow turbid lakes (Blankaart Reservoir and Murray River billabongs), and deeper crater lakes (Lac Chauvet). Lowland rivers are strikingly similar in terms of light climate to turbid shallow lakes (Reynolds 1994, Reynolds *et al.* 1994), suggesting that *A. subborealis* is particularly well adapted to low-light environments.