COMPARISON OF BRACKISH WATER PLANKTON ASSEMBLAGES OF IDENTICAL SALINITY RANGES IN AN ESTUARINE TIDAL (WESTERSCHELDE) AND STAGNANT (LAKE VEERE) ENVIRONMENT (S.W.-NETHERLANDS). I. PHYTOPLANKTON *)

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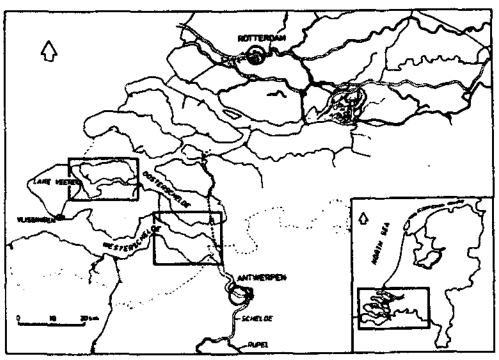
INTRODUCTION

In this study a comparison is made between the phytoplankton of the brackish water region of the Westerschelde estuary and Lake Veere, southwestern Netherlands between Antwerpen and Rotterdam (Fig. 1), based on investigations made by BAKKER (1972) and DE PAUW (1971).

Lake Veere is a man-made brackish water lake. Originally it formed a portion of the sea-arm Oosterschelde and was separated from the sea by dams in 1960 and 1961. During the first years after the closure chlorinity fluctuated between 9.5 and 12.5 °/oo. Then the lake passed a mesohaline stage (6 to 10 °/oo Cl') during the years 1965/66 (Fig. 2). This was caused partly by high Rhine discharges influencing the whole Delta area, and especially lowering the salinity of the Oosterschelde, connected with Lake Veere via locks in the eastern dam. However, relatively large quantities of water from the neighbouring polders, discharged on the lake, must be seen as the main factor responsible for



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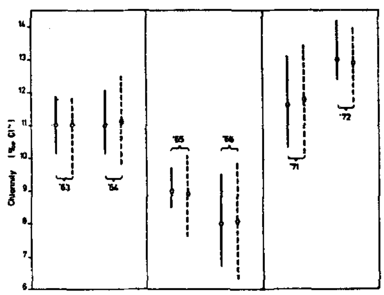

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Fig. 1. Map of the areas investigated (rectangles) in the S.W.-Netherlands.

Fig. 2. Means and ranges of chlorinity in Lake Veere during the periods '63/'64, '65/'66 and '71/'72. Solid lines: western part; broken lines: eastern part.

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the low salinity. During the last years, on the other hand, chlorinity varied between 10 and 14°/oo, characterizing the lake as polyhaline.

Lake Veere is flushed once to twice a year, while residence times in the Westerschelde, on the contrary, may fluctuate between several months during summer and some weeks in winter, depending on river discharge.

We have chosen the 6 to 10 to 14°/oo Cl' stages of Lake Veere as a basis for comparison with the same chlorinity ranges of the Westerschelde.

We are fully aware that comparison of the immature mesohaline stages 1965/66 of the recently created brackish Lake Veere with the permanent mesohaline ranges of the aged estuarine ecosystem of the Westerschelde, is perhaps not completely justified. Nevertheless, the possibility to compare a brackish water tidal area with a stagnant brackish water of the same salinity in order to investigate the role of salinity as "ecological masterfactor" (KINNE, 1971), seems promising and has therefore been utilized in this study.

RESULTS

1. Some environmental factors

The factors suspended matter, transparency and nutrients will be briefly discussed.

a. Suspended matter (Fig. 3A)

High suspended matter contents may be found in the brackish waterzone of an estuary, the brackish zone acting as a sediment trap (POSTMA and KALLE, 1955). Moreover, the Westerschelde is heavily polluted. Average sediment content in the 6-10°/oo Cl' range is 50-60 mg/l, in the 10-14°/oo Cl' range 30-60 mg/l. These values correspond very well with those of the same salinity ranges of the Elbe estuary (NÖTHLICH, 1972).

Lake Veere values differ strongly from those of the Westerschelde. In the Westerschelde the turbulent tides continuously whirl up sand and silt, in amounts depending on the current velocity (WARTEL, 1972); much organic and inorganic material is transported downstream from the strongly polluted oligohaline zone of Antwerpen; only a small part of the sediment is represented by living material. The Lake Veere sediment on the contrary, is composed for the greater part of organic (planktonic) substance throughout the year (only during stormy weather some bottom sediment may be brought into suspension). Suspended matter values in this area amount to an average of 10 mg/l or less during the last years in the polyhaline stage and to 10-20 mg/l in the mesohaline stage.

Differences between the eastern and western lake section are generally small. During the years 1965/66 on the other hand, sediment content was higher in the eastern sampling locality caused by high discharges of polderwaters here. Discharge of polderwater in the area of the western sampling station does not occur.

b. Transparency (Fig. 3B)

In estuaries high sediment values are coupled with low transparencies. Secchi disc visibility in the mesohaline range of the Westerschelde is usually less than 0.5 m and varies in the polyhaline range from 0.5 to 0.8 m. Average transparency in Lake Veere in the polyhaline

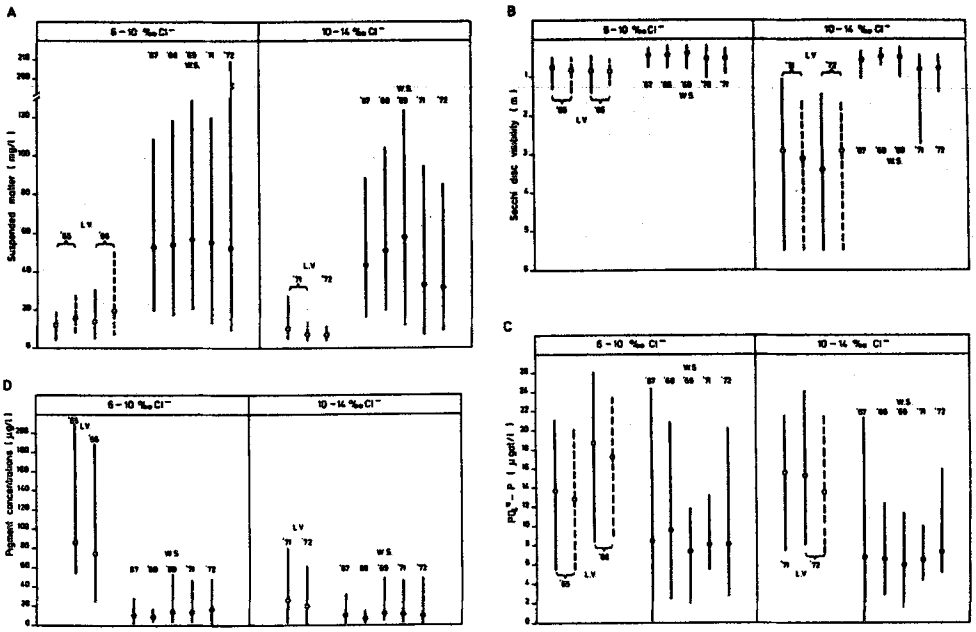


Fig. 3. Means and ranges of suspended matter (Fig. 3A), Secchi disc visibility (Fig. 3B), dissolved inorganic phosphate (Fig. 3C) and pigment concentrations (Fig. 3D) in Lake Veere (L.V.) and the Westerschelde (W.S.) in mesohaline (6-10^{o}/oo Cl') and polyhaline (10-14^{o}/oo Cl') ranges. The western part of Lake Veere is represented by solid, the eastern part by broken lines. (Fig. 3D: pigment extraction in methanol 96%, spectrophotom. measurements at 665 μu, calibration with pure chlorophyll a).

stage is about 3 m. The relatively low visibilities of 1 to 1.5 m during those periods always have been measured during the springblooms of phytoplankton. In the polyhaline range average transparencies in the Westerschelde proved to be less than minimum visibilities in Lake Veere.

As a result of systematical sampling at lower current velocities (high water slack tide) during 1971 and 1972, higher average Secchi values and lower average suspended matter content were found, notably in the polyhaline range. In upstream direction stronger pollution supersedes tidal influences. Sampling occurred at different stages of the tidal cycle during the period '67-'69.

The mesohaline stage of Lake Veere presents quite another picture. Visibilities were very low, about 0.8 m, throughout the year. In this period low visibilities were combined with low suspended matter content (compare Figs. 3A and 3B): the suspended particles were represented quantitatively by very small algae of 1 to 5 μ diam. (ultraplankton, μ-algae). Decreasing grain sizes of suspended particles cause increasing specific extinction (POSTMA, 1961).

c. Nutrients (Fig. 3C)

During the last years the average orthophosphate contents of Lake Veere varied between the very high values of 13 and 16 μgat/l, against 6 to 8 μgat/l in the Westerschelde (i.e. about 50% of the values of

Lake Veere). Values are slightly higher in the mesohaline ranges. Dissolved phosphorus increases to 50 μgat/l in the freshwater zone of the Westerschelde upstream of Antwerpen.

Phosphorus is present in excess and has never been limiting for algal growth in Lake Veere. In the Westerschelde only the year 1967 showed minimum values below 1 μgat/l.

A similar detailed figure for nitrogen compounds cannot be given because less values are available from Lake Veere. However, values for total dissolved inorganic N in the Westerschelde (DE PAUW, in preparation) are mostly in the order of magnitude of 5 mg/l (i.e. NO_2 + NO_3 + NH_4), while in Lake Veere N-levels always are lower, 1-2 mg/l, even during winter and spring (measurements of F. VEGTER, Yerseke, pers.comm.). During dry summers nitrate can disappear completely from the water of Lake Veere and thus become limiting factor for algal growth. Great differences exist, therefore, in the N/P ratios. N/P ratios in the Westerschelde varied from 35 to 172 in the mesohaline range, the average being 71; from 26 yo 112 in the polyhaline range with an average of 45. (The N/P ratio of normal seawater is about 15). In Lake Veere, on the contrary, N/P ratios fluctuated between 0.5 (during summer) and 7 (in spring).

2. Composition of the phytoplankton

Fig. 4A and 4B are illustrating the occurrence, relative abundance and seasonal distribution of the most characteristic phytoplankton species in the two salinity ranges in Lake Veere and the Westerschelde. It is clearly visible that the phytoplankton assemblages of Lake Veere and the Westerschelde show hardly any similarity in the mesohaline range: the distribution of dominant species is entirely different in both areas, while they have only a few species in common (Fig.4A). The dominating brackish water species in the Westerschelde is *Coscinodiscus commutatus*, character species of the estuarine mesohaline zone (cf. SCHULZ, 1961). The other predominant species in the Westerschelde nearly all prove to be marine diatoms: the degree of euryhalinity of these species is striking. Diatoms of coastal seawater are usually euryhaline to some degree. The remarkable euryhalinity of *Actinocyclus ehrenbergii* has to be mentioned particularly. Although living specimens often have been observed in waters of very low salinity, we did not find data in literature about mass occurrence of this species under mesohaline conditions as we met in the Westerschelde (2600 cells/l).

The dominating species of Lake Veere in the mesohaline stage are mainly non-diatoms: Cryptophycean flagellates (*Rhodomonas* sp.), a ciliate with zoöxanthellae (*Mesodinium rubrum*) and u-algae. Contrary to the other species μ-algae flowered throughout the year. Marine diatoms are scarce in Lake Veere in this stage, with the exception of *Sceletonema costatum*, character species of nutrient-enriched seawater (HORSTMANN, 1972) and *Detonula confervacea*.

Fig. 4B, showing the main phytoplankton species present in the polyhaline range, is very different from Fig. 4A. The most important spring species of the mesohaline stage of Lake Veere did persist, but at a glance it is clear that the number of species in the polyhaline stage has increased strongly. The broken lines indicate presence of marine species (mainly diatoms) in surface waters of the eastern lake section, penetrating into the lake from the sea through the locks. Evidently the

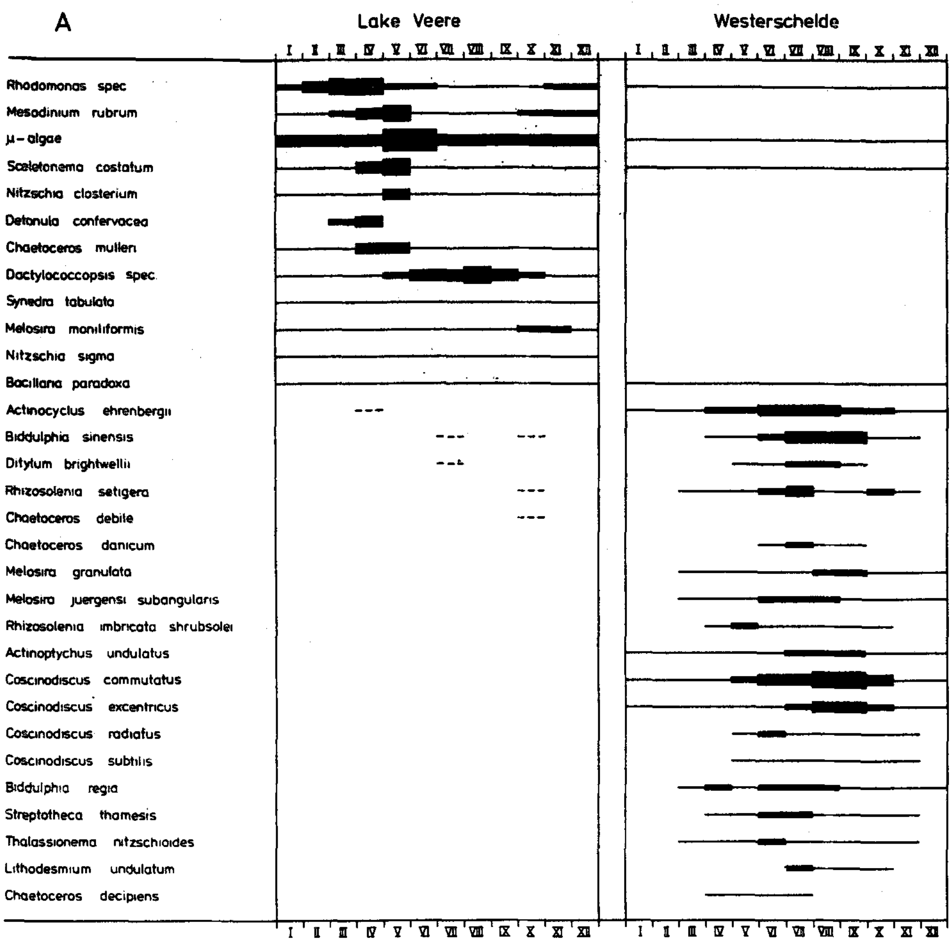


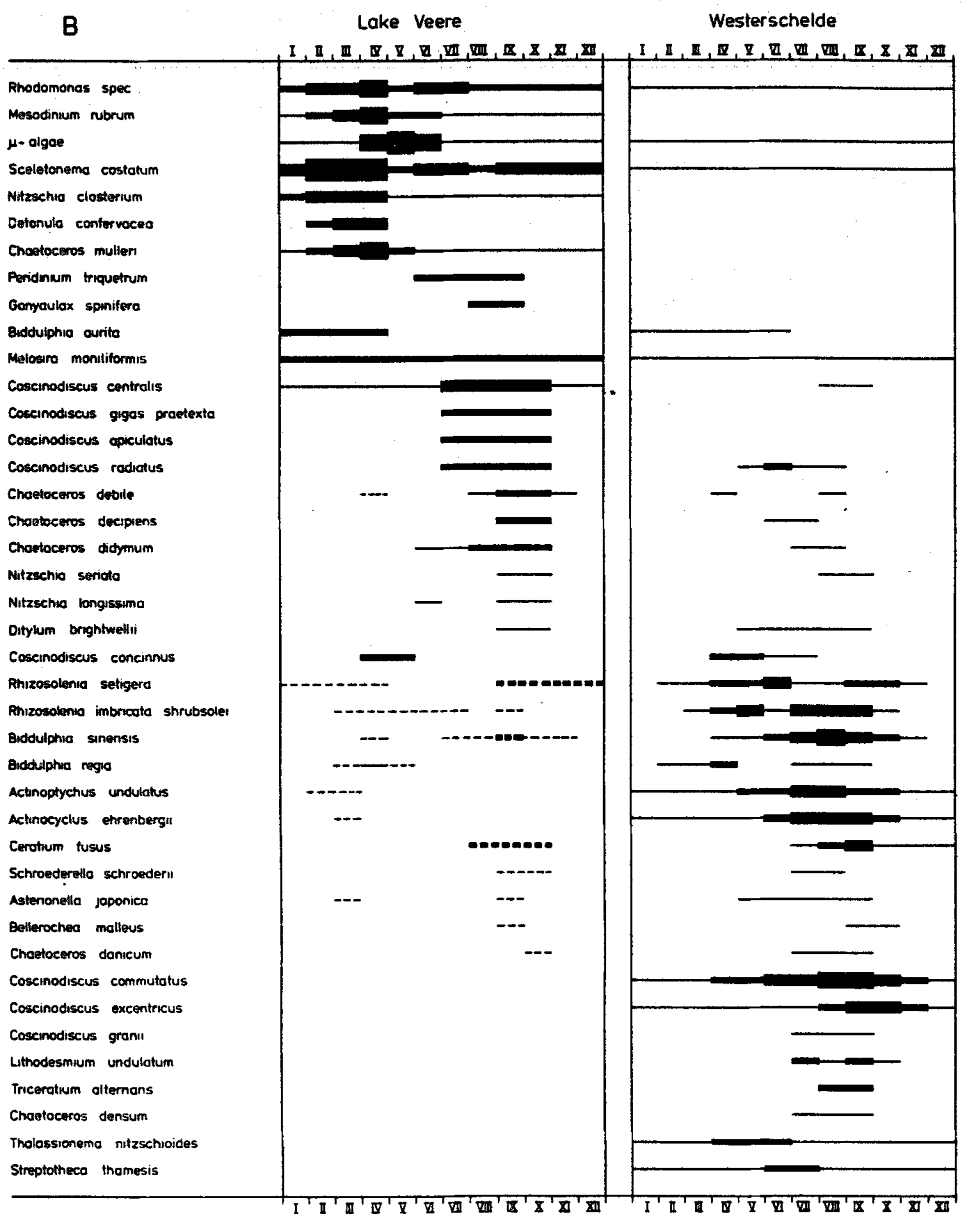
Fig. 4. Characteristic species composition, relative abundance and seasonal distribution of phytoplankton in mesohaline (Fig. 4A) and polyhaline (Fig. 4B t.o.p.) ranges of Lake Veere and the Westerschelde. Further explanation in the text.

higher chlorinity gave several species the opportunity to grow in the lake.

The Westerschelde assemblage differs much less from the mesohaline one than the Lake Veere community does.

3. Size of the standing stocks

The density of the standing stocks of phytoplankton, expressed in micrograms green pigment/l, is presented in Fig. 3D. Average densities in the Westerschelde always prove to be smaller than in Lake Veere. Very great differences were seen in the mesohaline range: Westerschelde



values 10 to 15 μg/l, Lake Veere values 70 to 90 μg/l (averages). Maximum values in Lake Veere were higher than 200 μg/l. In the polyhaline stage average standing stocks of Lake Veere have decreased strongly (20 to 30 μg/l) and the maximal values were lower too (60 - 80 μg/l).

The year cycle of chlorophyll concentration has been given in Fig.5. In Lake Veere evidently strong blooms develop in spring in the mesohaline as well in the polyhaline stage. In the Westerschelde spring de-

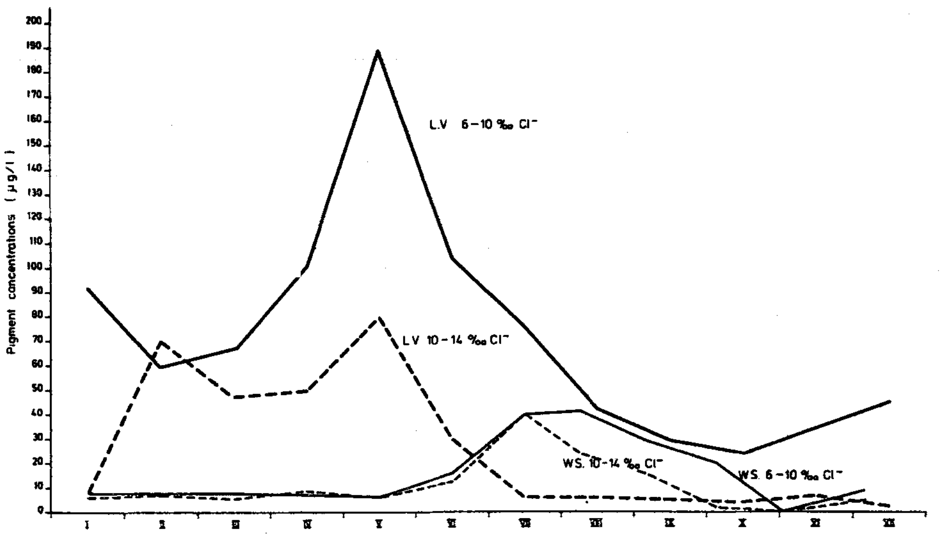


Fig. 5. Seasonal evolution of pigment concentration in Lake Veere (L.V.) and the Westerschelde (W.S.) in meso- (6-10 ^{o}/oo Cl') and polyhaline (10-14 ^{o}/oo Cl') ranges.

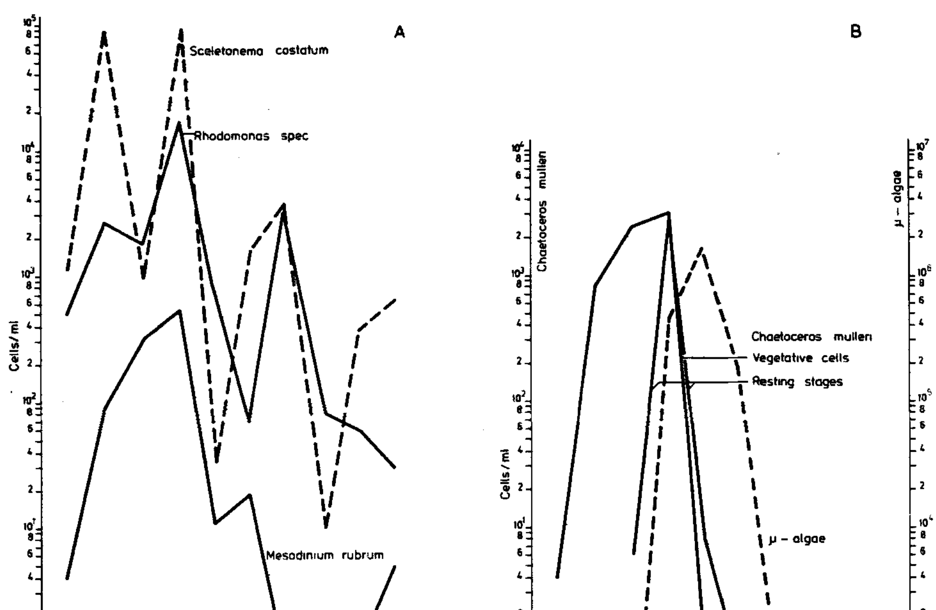


Fig. 6. Seasonal evolution of standing stocks of *Sceletonema costatum*, *Rhodomonas sp.* and *Mesodinium rubrum* (Fig. 6A); *Chaetoceros mulleri* and μ-algae (Fig. 6B). Lake Veere, 1971.

velopment of phytoplankton within the chosen salinity ranges was not significant. Maximum phytoplankton stocks in the Westerschelde are found during summer. Standing stocks in the mesohaline range of the Westerschelde never reached the level of the mesohaline stage of Lake Veere. Summer levels of the polyhaline range of the Westerschelde on the other hand sometimes exceed those of Lake Veere.

The growth curves of some predominant species responsible for the demonstrated pigment values in Lake Veere are depicted in Fig. 6. All values have been given on a logarithmic scale. The diatom *Sceletonema costatum* (Fig. 6A) demonstrates spring peaks of 100.000 cells/ml. Summer and fall densities are always lower than those in spring. Cryptophycean flagellates *(Rhodomonas spec.)* and a ciliate with algal symbionts (*Mesodinium rubrum*) show a similar picture (Fig. 6A). Fig. 6B presents the development of the diatom *Chaetoceros mulleri*. At the end of the exponential phase of this species a strong increase is found in the number of resting stages. Very characteristic for Lake Veere is the enormous development of the ultraplankton (u-algae). In the mesohaline stage these cells flowered throughout the year, in the polyhaline stage (Fig. 6B) they occur especially during the breakdown of the spring blooms (1 to 2 millions of cells/ml). The dynamics of these blooms in Lake Veere and their interdependence with nutrients and grazing activity of zooplankton shall be dealt with in another paper (BAKKER and VEGTER, in preparation).

The summer populations of some abundant discoid diatoms in the Westerschelde are given in Fig. 7A. The meshohaline brackish water diatom *Coscinodiscus commutatus* is the most abundant species, so the highest numbers are counted in the mesohaline range (53.000 cells/l). The marine diatom *Biddulphia sinensis* too reached maximum density during July (27.000 cells/l), enormous numbers for such a big diatom), this time in the polyhaline range (Fig. 7B).

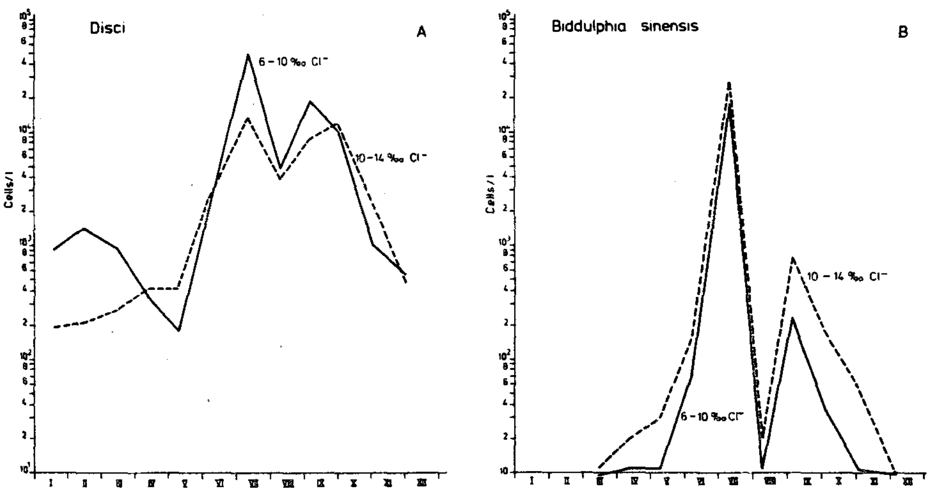


Fig. 7. Seasonal evolution of standing stocks of discoid diatoms (Fig. 7A) and *Biddulphia sinensis* (Fig. 7B). Westerschelde, 1972.

DISCUSSION

It follows from our results that tidal and stagnant brackish waters within the same salinity range differ strongly in composition and size of the standing stocks of phytoplankton in relation to other environmental factors.

Both habitats are strongly eutrophicated. Lake Veere especially in relation to the phosphates, the Westerschelde in relation to nitrogen compounds. Con equently, the N/P ratios in the Westerschelde are always higher, mostly far higher, than in Lake Veere. Low N/P ratio's were very favourable for the blooming of μ-algae in the mesohaline range. Also RYTHER (1954) made this observation in great South Bay and Moriches Bay along the eastern coast of the U.S.A. Moreover he found that μ-algae flourish on numerous nitrogen substrates and especially on ammonia, which explains the strong increase in numbers of these small forms during the breakdown of the spring peaks of phytoplankton.

Salinity proves to be an all-important ecological factor in the stagnant brackish water of Lake Veere. The difference in phytoplankton composition of the two stages is striking. The number of marine species increased strongly in the polyhaline stage.

In the brackish water tidal area of the Westerschelde, on the contrary, salinity is evidently less important than in Lake Veere. Differences in phytoplankton composition between the polyhaline and mesohaline zones of the Westerschelde are much smaller than those between the similar stages of Lake Veere. Transitions in the Westerschelde estuary proceed gradually in space and slowly in time as a consequence of the predominant marine influences on this well-mixed estuary. The gradual decrease in salinity along the axis of the estuary levels down differences in phytoplankton composition. The polyhaline zone, therefore, harbours a marine planktonic diatom flora, though impoverished. The mesohaline zone is occupied by a few typical brackish water species in mass occurrence (*Coscinodiscus commutatus*), but comprises furthermore many marine diatoms in fairly large numbers. The continuous transport of marine species into the brackish water zone of the estuary has resulted in extreme adaptation, in the course of geological time, of several of these species (notably diatoms) to lowered salinities. Many marine species have reached in this way a very high degree of euryhalinity.

Tidal brackish waters are always characterized by high sediment contents, low tranparencies and, consequently, unfavourable light conditions. Direct influences of turbidity on phytoplankton are hardly known (HAGMEIER, 1971). The turbidity of these waters is seldom caused by dense concentrations of living phytoplankton, but mainly by inorganic and dead organic material (detritus) from the bottom and littoral zone, kept in suspension by the tides. Besides salinity, turbulence therefore proves to be a master factor, influencing environment and plankton of an estuary. Turbulence prevents settlement of large and heavy forms, especially diatoms. The already mentioned continuous transport of marine species from the sea in upstream direction is made possible by tidal turbulence. Under these circumstances heavily silicified diatoms are able to maintain themselves in the plankton. Strong euryhalinity, continuous resuspension and relatively long residence times are the conditions estuarine brackish water phytoplankton need for its maintenance and growth. The clearest illustration is the mass occurrence of *Coscinodiscus commutatus* in the Westerschelde.

Stagnant brackish waters are found to show low transparencies too, but the cause is always strong blooming of nannophytoplankton. Here unfavourable light conditions always result from phytoplankton development itself, very dense springblooms leading sometimes to selfshading as TALLING (1960) reported for the diatom *Asterionella formosa* growing in freshwater lakes.

Absence of tidal turbulence creates the opportunity for stabilization of the watermass and, consequently, for development of small pelagic (often motile) phytoplankton species (cf. also GILLBRICHT, 1955; and HICKEL, 1967). Lake Veere waters stabilize quickly in spring and summer, although wind-induced turbulence, however, is able to destroy stratifications within short time. Motile species like flagellates and ciliates find optimal conditions for blooming in Lake Veere, as well as small pelagic diatoms like *Sceletonema*, *Detonula* and several *Chaetoceros* species. Absence of continuous (tidal) turbulence explains why Lake Veere is lacking several diatoms occurring abundantly in the same salinity range in the Westerschelde. Such diatoms quickly settle in the lake and die off soon if no resuspension follows. Summer diatoms of Lake Veere are less coarsely structured, like *Coscinodiscus centralis* (the counterpart of *C.commutatus* in the Westerschelde), or are characterized by favourable surface - volume ratios as the flatshelled *Coscinodiscus radiatus* and - *gigas praetexta*.

In the Westerschelde turbulence permanently prevents stabilization. Consequently, small motile phytoplankton do hardly occur or, when occurring, development is hampered by turbulence and does not proceed logarithmically.

Shorter residence times and turbulence conditions therefore seem to be the explanation of the differences in quantitative relationships of phytoplankton in Lake Veere and the Westerschelde. Lake Veere blooms are shown to develop in spring, summer and fall, but especially in spring. Phytoplankton development in the brackish water zone of the Westerschelde proceeds only in summer, when relatively long residence times and high temperatures enable some diatom species to develop in the estuarine environment.

SUMMARY

Species composition, abundance and seasonal distribution of the phytoplankton of brackish water ecosystems depend not only on salinity but on several other environmental factors too.

In stagnant brackish waters (Lake Veere) the easily established stability of the water masses proved to be an ecological masterfactor in relation to phytoplankton development, equaling salinity in importance.

In tidal brackish waters (Westerschelde estuary) turbulence acts as an ecological masterfactor in relation to phytoplankton development, dominating salinity in importance within the chosen salinity ranges.

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