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Deterministic and stochastic influence of nutrients on phytoplankton function and structure in coastal waters

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Abstract

Knowledge of how phytoplankton responds to nutrient inputs is essential for water management and for minimizing eutrophication. Only processes that are deterministic, i.e. that can respond as algorithms, are controllable. The study area is the chain of inshore waters (so-called Bodden) south of the Darss-Zingst peninsula – shallow eutrophic waters of estuarine character in the Southern Baltic. Monitoring programmes and laboratory experiments have revealed an annual periodicity of the phytoplankton and of the physico-chemical factors influencing it. On the basis of these results, experiments were carried out in enclosures to study the effects of nutrient loading on phytoplankton. The purpose was to test the feasibility of influencing phytoplankton development under field conditions during the transition period from late spring to mid-summer.

This contribution presents results from the 1985 shallow water enclosure experiments (FLAK 85) which demonstrate that

- the scale of phytoplankton reactions and the species involved are stochastic in character and are governed by stochastic interactions between meteorological events and water exchange processes in the chain of Bodden;
- all processes affecting phytoplankton growth are deterministic in character, conforming to simple batch theories: simultaneous addition of nitrogen and phosphorus favours green algae, and in exceptional cases one algal species became dominant;
- nutrient loadings do not affect the time of transition to the mid-summer phytoplankton population, the most important regulating factor obviously being temperature.

Introduction

The term eutrophication denotes a more intensive growth of algae and higher plants as a result of overloading of waters with plant nutrients. This is usually a normal process in the development of freshwater ecosystems; during the past few decades, however, it has accelerated considerably as a result of the more intensive exchange of matter between nature and human society. This applies not only to freshwaters, estuaries and coastal regions of the Baltic, but to an increasing extent to the Baltic Sea itself (LARSSON et al. 1985).

Phytoplankton in particular responds rapidly to changes in nutrient loads in the pelagic zone, the benthic zone and the sediment acting rather as a buffer. Regulation of nutrient loads, and thus rational management of waters, demands exact knowledge of phytoplankton reactions in the different types of water bodies. In this respect KILHAM and KILHAM (1984), REYNOLDS (1984) and SOMMER (1984) have added much to our understanding of this problem.

Despite this progress, our theoretical knowledge of phytoplankton responses is still far from comprehensive, especially with respect to the causes of seasonal phytoplankton periodicity and succession. At every turn, experimenters are confronted with the fact that deterministic processes which can be formulated as simple algorithms, are accompanied by stochastic processes. Since the latter cannot be described in terms of algorithms, regulation is impossible. The task of future research must therefore be to reduce the stochastic component to a minimum. This is one of the aims of our investigations in a shallow eutrophic estuarine system of the Baltic.

Here we present results of a mesocosm experiment on the effects of nutrient loading on phytoplankton growth and periodicity during the transition period from late spring to mid-summer.

Material and methods

The investigation area was Kirr Bucht, a shallow bay near the field laboratory of the Department of Biology located at the chain of waters (Bodden) south of the Darss-Zingst Peninsula (Fig. 1). The waters form a brackish estuarine system with an area of 200 km² on the southern coast of the Baltic Sea. The chain of eutrophic waters has a mean depth of 2.0 m and is connected to the Baltic Sea by a narrow channel at the eastern end.

The results presented here were obtained during an interdisciplinary shallow water enclosure experiment in 1985 (FLAK 85). The enclosures consisted of polyethylene cylinders with a diameter of 2 m which were open at the top and bottom. The bottom of each cylinder was encased in a metal ring (45 cm high), which was driven 35 to 40 cm deep into the sediment, to anchor the enclosure and to isolate the interior of the enclosure from the surrounding water. Floats were attached to the upper part to provide the necessary buoyancy and to prevent water from entering over the top. The enclosed area was about 3.1 m². Since the mean water depth was 0.5 m, the enclosed water volume was about 1.6 m³. The enclosure walls were brushed weekly to prevent fouling. As shown by the results presented below, the enclosures are suitable for experiments on eutrophic brackwater communities up to 75 days in duration. PARSONS (1982) and KUIPER et al. (1983) came to similar conclusions regarding the use of enclosures in experiments with enclosed marine communities.

The experiment began on May 31, 1985, when the water bodies were isolated. Loading with additional nutrients started on June 4, 1985, and the experiment ended on August 13, 1985.

Owing to the isolation of the enclosed water bodies from the surrounding water, they were cut off from horizontal transport processes, and vertical mixing was reduced. In the control (enclosure I), this led to "mesotrophic" conditions due to an increase in the previously existing nitrogen limitation. As proved by the enclosure III, this lack can be compensated for by the addition of nitrogen. Hypertrophic conditions were induced in enclosure II by the simultaneous addition of NH₄Cl and NaH₂PO₄. Total input in the course of the experiment was 12.3 g N as NH₄Cl and 1.68 g P as NaH₂PO₄ per m³. The nutrients were given in intervals (see Fig. 6, arrows) in single portions of up to 150 mmol NH₄Cl and 100 μmol NaH₂PO₄ per enclosure.

Samples from the enclosures and from the surrounding water were taken daily at 05.30 hours (Central European Summer Time for two months.) The samples were analyzed for, among other things, chlorophyll-a content (methanol extraction after RIEMANN 1978, and analysis after LORENZEN 1967), ¹⁴C fixation in the light incubator with light saturation (P_{max}) and *in situ* (¹⁴C activity: 3.7 x 10⁵ Bq x 100 ml⁻¹), and the qualitative and quantitative

composition of the phytoplankton (UTERMOEHL 1958). The assimilation numbers (P_{max}^B in $\text{mg C} \times (\text{mg Chl a})^{-1} \times \text{h}^{-1}$) were calculated from the active chlorophyll-a content and the ^{14}C fixation rate.

Parallel studies were used to record the structure and function of the bacterial, ciliate and zooplankton populations in the pelagic zone. Other work dealt with the micro-, macrophyto-, meio- and macrozoobenthos, and with the total activity of the sediment. Details of the results obtained were given by ARNDT et al. (in press) and SCHIEWER et al. (in press). The following relevant physico-chemical parameters were measured routinely: irradiation (global irradiation and photosynthetically active radiation at wave lengths of 425, 545, 660 nm and as white light measured with the LM2 radiation meter; WALTER 1981), temperature, transparency, water motion, O_2 saturation, salinity, pH (WALTER 1981) and inorganic phosphorus and nitrogen concentrations (phosphate, nitrate nitrite and ammonium) were analyzed immediately after sampling. Analyses were done by standard methods (see ROHDE and NEHRING 1979) using flow-through analyzers from VEB MLW Medingen, Freital. Common statistics methods (standard deviation, confidence interval, correlation coefficient) were used to analyse the results.

Results

For several years, monitoring programmes and laboratory experiments have supplied data regarding the periodicity of the phytoplankton, and the physico-chemical factors affecting it. Fig. 2 shows the percentage distributions of the different phytoplankton groups from April 1981 to July 1983, based on biomass levels (BÖRNER 1984), together with a generalized view of the seasonal changes in limiting factors (SCHIEWER, unpub.).

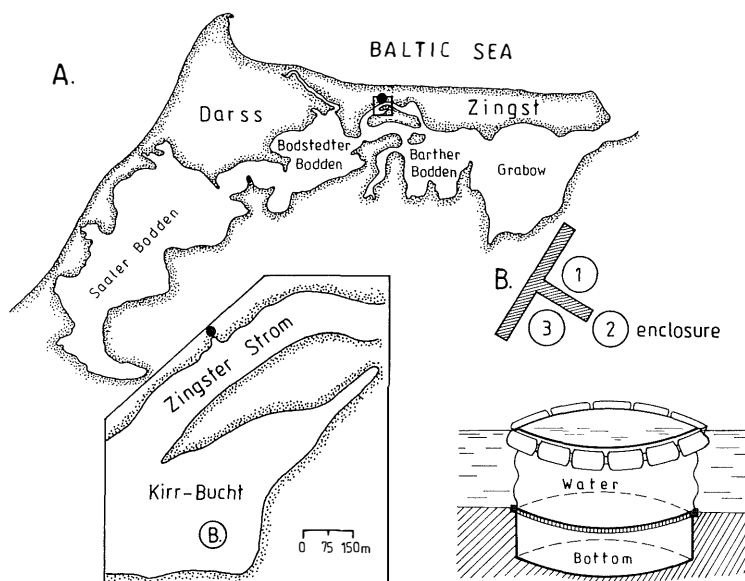


Figure 1

Investigation area and enclosure design.

A: Chain of waters (Bodden) south of Darss-Zingst Peninsula.

B: Kirr Bucht and enclosure design.

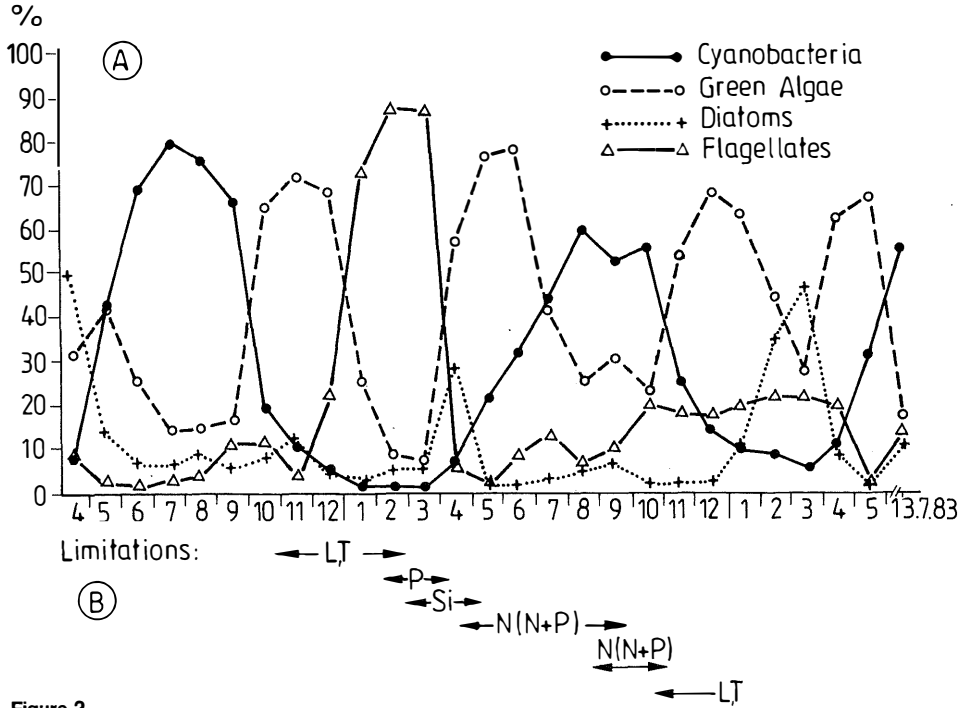


Figure 2

Phytoplankton periodicity in the investigation area

A: Relative frequency of the phytoplankton groups in percent calculated on biomass levels and their seasonal distribution (BÖRNER 1984)

B: Generalized scheme, showing the main limiting physico-chemical factors (L = light, T = temperature, N = nitrogen, P = phosphorus, N+P = phosphorus and nitrogen alternately owing to lack of nutrient reserves. N(N+P) = at first N-limitation which shifts later to a more alternately nitrogen and phosphorus limitation due to lack of stored nutrients. Si = silicon)

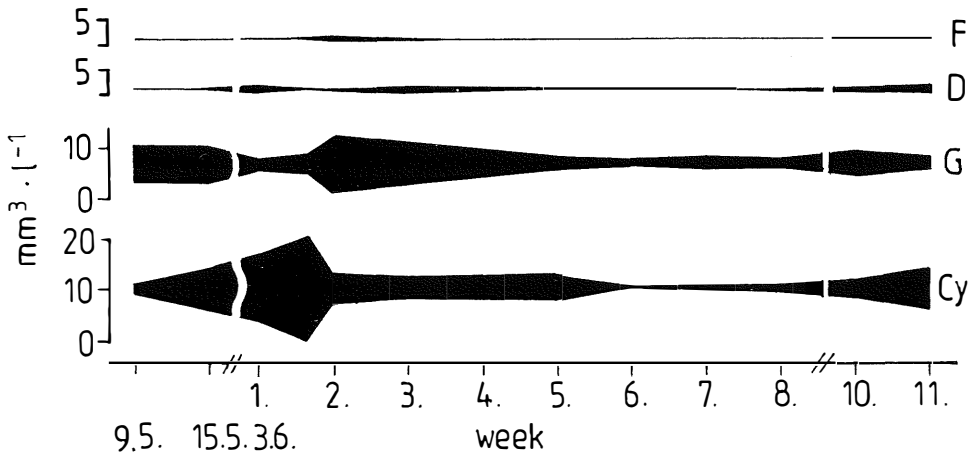


Figure 3

Phytoplankton development in Kirr-Bucht during the investigation period May 9 to August 13, 1985. Volume given as $\text{mm}^3 \cdot \text{l}^{-1}$. Cy = cyanobacteria, D = diatoms, G = green algae, F = flagellates

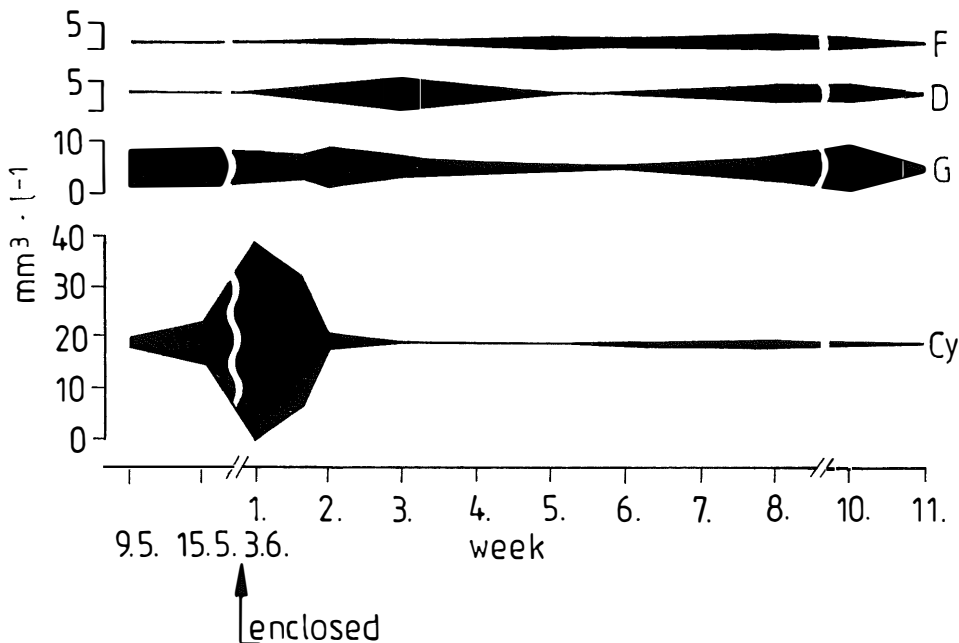


Figure 4

Phytoplankton development in control enclosure. See Fig. 3 for further details.

The experiment started at the time when the green algae are usually replaced by cyanobacteria as the dominant group. This initial situation is shown in Figs. 3, 4 and 5. In 1985 it was characterized by an increase in the chroococcal cyanobacteria *Gomphosphaeria pusilla*. The limitation status of the phytoplankton became apparent by additional enrichment experiments in separate flasks during the whole FLAK-experiment. These experiments confirmed that N was the limiting factor. The P reserves of the phytoplankton enabled the total population to double. Initially, the development of the chroococcal cyanobacteria continued despite the additional nutrient load, the population of *Microcystis* species also clearly increasing in the enclosures (especially in the control enclosure). The subsequent development in the surrounding water and the control enclosure was characterized by a decline in phytoplankton biomass, which reached a minimum between weeks 5 and 6 of the experiment (Figs. 3, 4). The phytoplankton development that followed did not lead to the dominance of summer cyanobacteria (*Anabaena spiroides*, *Nodularia harveyana*) because the water temperatures of 16°C in August were too low.

The simultaneous addition of nitrogen and phosphorus to enclosure II led to a significant change in the dominance structure in the second week of the experiment: the green algae were dominant (Fig. 5). *Scenedesmus quadricauda*, *Monoraphidium contortum* and *Kirchneriella irregularis* proliferated, *Scenedesmus* becoming increasingly dominant during the following weeks and accounting for 89% of the biomass in the 6th week.

This rapid development of *Scenedesmus* was accompanied by distinct changes in their shape: coenobia broke down into individual cells, which became increasingly round.

The *Scenedesmus* population collapsed almost instantaneously from the 6th to 7th week. The algae formed aggregations, showing a strong tendency to adhere to the polyethylene

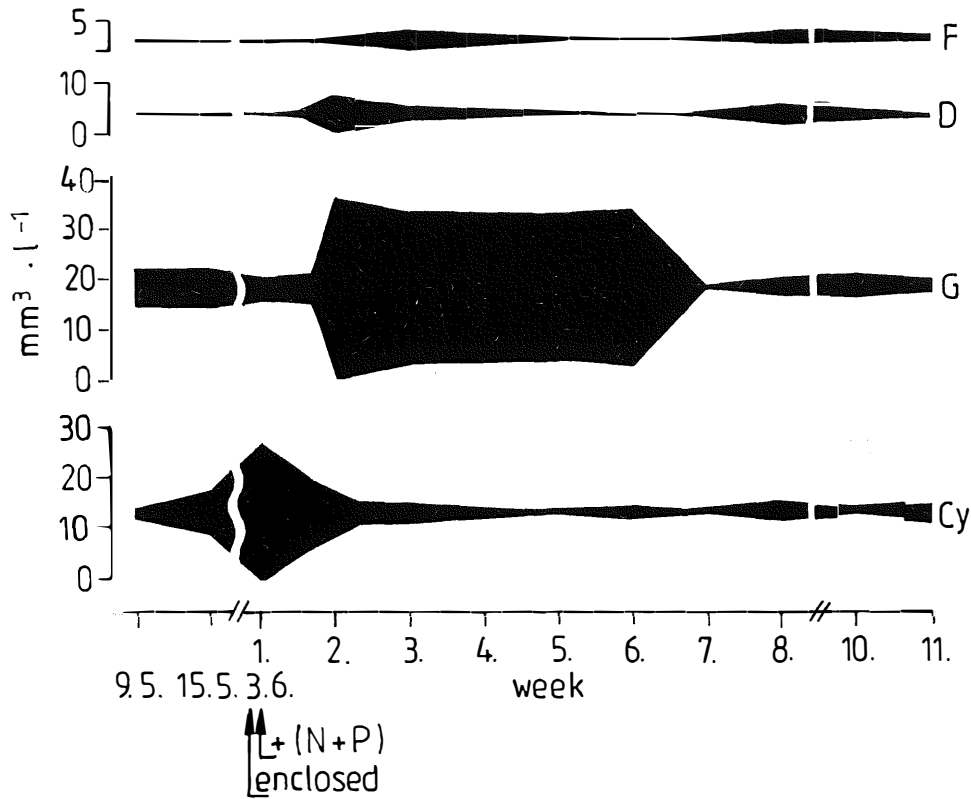


Figure 5

Phytoplankton development in (N+P) loaded enclosure. See Fig. 3 for further details.

sides, and finally sank completely to the bottom, as could be shown by presediment analysis. Measurements of grazing activities and respiration rates have shown that major grazing and respiratory losses can definitely be precluded. It is also striking that despite its large biomass the dominance of the green algae, which lasted over four weeks, had no significant effect on the further development of the phytoplankton in enclosure II. On the contrary, it was almost identical to phytoplankton development in the control enclosure and surrounding water.

A detailed analysis of chlorophyll-a development in enclosure II together with nutrient input and meteorological data (irradiation and temperature) reveals the links between these factors (Fig. 6). The nutrient input triggered off a logarithmic growth process from the very start, similar to that observed in batch cultures, regardless of the species that were developing. Lower nutrient input levels from June 14 to 27 caused losses, but these were compensated for when the "normal" nutrient input level was resumed. The whole phytoplankton population was limited by light when the chlorophyll-a values reached their maximum of $1271 \text{ mg} \times \text{m}^{-3}$ (see later). The abrupt collapse of the *Scenedesmus* population was not a result of nutrient deficiency, but of a major rise in temperature accompanied by more intense irradiation at the onset of phosphorus deficiency. Similar phenomena must have taken place from May 9 to June 3, 1985. Following a period of cool

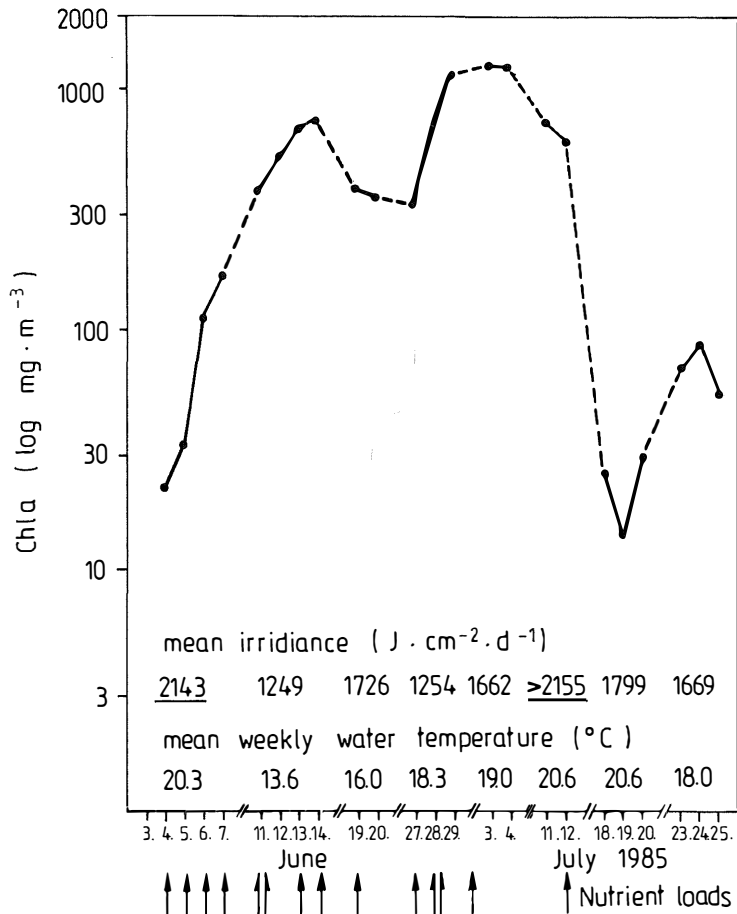


Figure 6

Chlorophyll-a content (mg m^{-3}) given on a logarithmic scale. Additional data: weekly mean irradiance per day and mean weekly water temperature. Arrows = time of nutrient input. Total nutrient input: $12.3 \text{ gN} \cdot (\text{m}^{-3})^{-1}$ as NH_4Cl and $1.68 \text{ gP} \cdot (\text{m}^{-3})^{-1}$ as NaH_2PO_4

weather, the water temperature in the shallow areas rose from about 14°C to 23°C in only a few days. In the open water this led to a major increase in algal biomass (Fig. 7). Comparison of chlorophyll-a development in the enclosures and the surrounding water shows clearly that chlorophyll-a development was initially almost the same in all cases. Nutrient inputs (enclosure II) and nutrient supply by horizontal transport in the open water delayed the reduction in chlorophyll-a concentrations for short periods, but by the 8th week these differences had vanished.

The changes in assimilation numbers (Fig. 8) are also striking. Under nutrient-limited conditions (control enclosure) the assimilation index varied inversely with biomass development. When the limitation is reduced, it follows the biomass development, as it had earlier in the surrounding water and in nutrient-saturated enclosure II. Major changes in chlorophyll-a concentrations were accompanied by significant reductions in the assimilation indexes in both May (all samples) and in July (enclosure II).

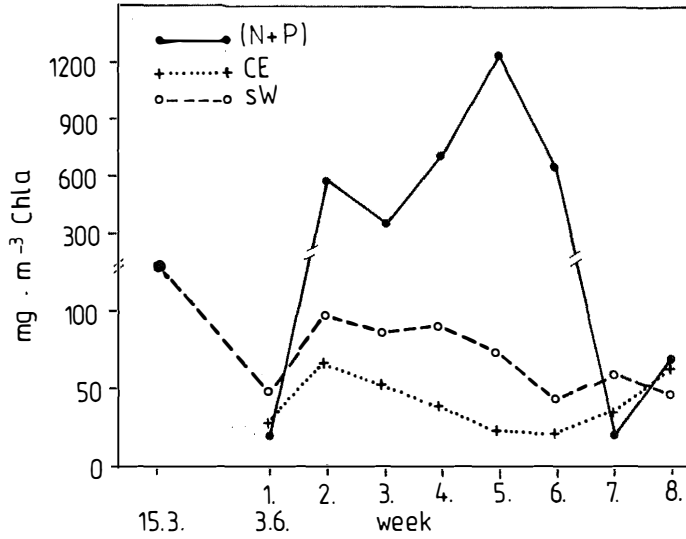


Figure 7
Development of chlorophyll-a content of open water and in enclosures (weekly means). SW = open water, CE = control enclosure, (N+P) = enclosure with nitrogen and phosphorus loading

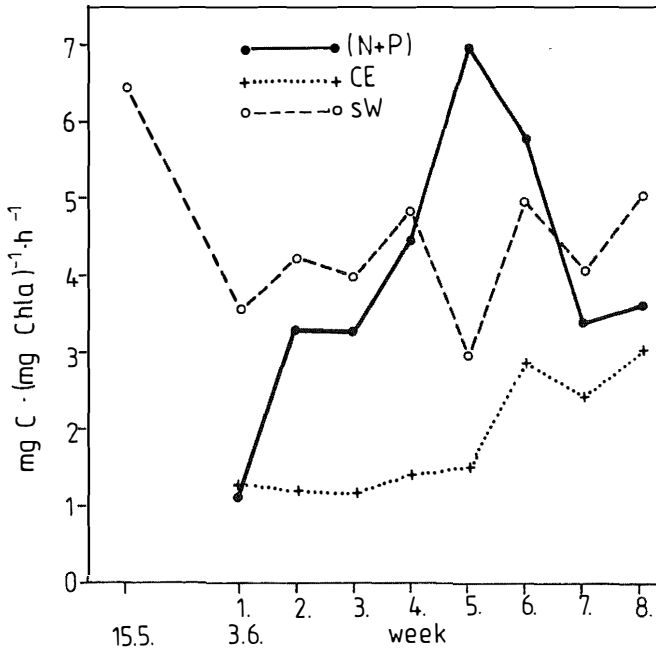


Figure 8
Assimilation numbers (P_{max}^B in $mg\ C \cdot mg\ Chl\ a^{-1} \cdot (c \cdot mg)^{-1} \cdot h^{-1}$). Incubator experiment with light saturation. See Fig. 7 for further details.

The mean assimilation index for the open water during the investigation period was 4.31 ± 1.25 (95 % confidence interval), about the same as the values of 4.0 found in July 1980 (SCHIEWER 1984). Nutrient limitation caused major reductions: 1.27 ± 0.32 (95 % confidence interval) in the control enclosure from June 3 to July 4, 1985. The assimilation index can obviously only rise above 4.0 when light is the limiting factor during a long period (May 1985 in the open water, 5th and 6th weeks of the experiment in enclosure II).

Discussion

The size of enclosure we used proved suitable for studying the main components of the shallow aquatic ecosystem concerned. Significant differences between the control enclosure and the surrounding open water appeared during the first four weeks. These were caused by the absence of nutrients supplied by horizontal transport and by reduced turbulence. After about 8 weeks the differences disappeared. The purpose of our work was to reduce the stochastic component in the processes involved in phytoplankton development, thus making the processes more easily controlled. According to REYNOLDS (1984) phytoplankton is subject to two basic kinds of change: autogenic unidirectional sub-sequences (successions) and allogenic seasonal periodicities. The former result from specific reactions to critical changes in resource-ratio gradients, whereas the latter stem from the variability of the physical environment. Our results clearly show that the phytoplankton periodicity (end of May to August) itself was not influenced by nutrients. Regardless whether the situation is characterized by nutrient limitation or saturation, the same status was achieved by the end of July. The influence of the physical environment predominates, and of the factors we studied, temperature and light were the most important. In other words, changes in successions need long-term, enduring nutrient changes.

Taking into account the nature of the waters we studied, we can make the following general conclusions:

1. Nutrient inputs to shallow eutrophic waters are generally consumed by the phytoplankton during the vegetation period and converted into biomass. Nutrient limitation (nitrogen limitation in our case) occurs owing to the imbalance between nutrient supply and uptake. Greater inputs of both phosphorus and nitrogen permit biomass production to increase until limited by light. Under these circumstances the response of the phytoplankton follows simple batch laws.
2. In the brackish (2 to 8 ‰ salinity) biotope we studied, simultaneous loading with phosphorus and nitrogen favours mainly the green algae. This phenomenon is obviously not specific to the waters we studied, as it has often been described in freshwater biotopes (for instance by DE NOYELLES and O'BRIEN 1978, KRZECZKOWSKA-WOLOSZYN and KYSELOWA 1979, HOLMGREN 1984).
3. The development of the phytoplankton follows its normal seasonal periodicity; regardless whether growth is nutrient-limited or not. The effects of temperature and light are much greater than that of nutrient levels. This also applies to the transitional period we studied despite the results shown in Fig. 2B. The factors responsible for the striking decrease in biomass and for the disruption of the seasonal periodic changes in species composition of the phytoplankton in shallow waters of this kind are not nutrient-related, but are rather related to the length of the insolation period and the too rapid increase in temperature. A period of good weather lasting at least about one week is required to change the development. Prolonged periods of good weather and water temperatures above 16°C are necessary for the full development of the typical summer cyanobacterial population.

4. It is therefore evident that in field experiments it is impossible to base precise long-term predictions of algal biomass and species composition of the phytoplankton community on known responses of the phytoplankton. This also applies to the seasonal course of phytoplankton development. Variations of one or two months must be considered normal for the type of waters we studied, but these variations in time do not affect the basic course of development, since compensatory mechanisms subsequently operate to restore the normal periodicity. Stable changes in the succession can obviously be achieved only by modifying environmental conditions in the same direction for a period of many years.
5. Sedimentation is the most important cause of losses during the vegetation period in the waters we investigated (see above), and in addition to purely physical factors such as water temperature and turbulence, physiological processes are also involved. Light, and the utilization of carbohydrates synthesized for algal growth in the light, obviously play an important role in this respect. In view of the decrease observed in the assimilation index when the chlorophyll-a concentration was still quite high, it seems likely that there is some kind of feedback between assimilate accumulation and photosynthesis. Changes in the structure of the phytoplankton (see COTE and PLATT 1983) also have some significance in connection with the assimilation indices.

The fact that uncontrollable large-scale external forces such as seasonal changes, temperature and light all affect the phytoplankton populations in the same direction, greatly reduces the possibility of regulating such populations by nutrients.

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