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The spring development of phytoplankton in Lake Erken: species composition, biomass, primary production and nutrient conditions – a review

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Abstract

In Lake Erken climatic factors such as duration of ice cover, snow-depth and insolation govern the phytoplankton development and the species composition during the spring, with significant variations from year to year.

Generally the small diatom, *Stephanodiscus hantzschii var. pusillus* creates a conspicuous peak at ice-break. In some years motile dinoflagellates start to develop under the ice already in early March, which results in a much longer spring bloom.

The highest biomasses were recorded in 1954–1955 with values up to 11 mg l^{-1} of fresh weight. The chlorophyll *a* concentrations have at most reached an epilimnetic average of 30 $\mu g\,l^{-1}$.

The primary production reached a maximum value of 2200 mg C $m^{-2}\,d^{-1}$ in 1955 and the average production for two months during the spring varied from 30 to 64 mg C $m^{-3}\,d^{-1}$.

Concerning nutrients, phosphorus was shown to be the limiting nutrient at the end of the spring bloom. This fact was confirmed by orthophosphate concentrations, algal surplus phosphorus content and alkaline phosphatase activity, as well as estimations of inorganic N : P and C : P ratios and nutrient enrichment experiments.

Introduction

From the early fifties and onwards the spring development of phytoplankton and its conditions have been a central theme for limnological research at the Erken laboratory. Already in 1954 and 1955 the biomass development and the primary production were measured intensively (Rodhe *et al.*, 1958). Nauwerck (1963) continued with a year-round study in 1957 of phytoplankton and zooplankton biomass, species composition and production. Pechlaner visited the laboratory in 1960 in order to follow the outburst of phytoplankton during the spring in relation to nutrient conditions and climatic factors (Pechlaner, 1970). During the 1970's considerable effort was made to estimate the phosphorus situation during the spring, and this work was continued during the early 1980's (Boström & Pettersson, 1977; Pettersson, 1979a, b; 1980, 1985; Eriksson & Pettersson, 1984). The nitrogen cycle was also followed (Boström, 1981; Tirén & Boström, 1983).

In 1983 Bell and Kuparinen assessed phytoplankton and bacterioplankton production during early spring (Bell & Kuparinen, 1984). The information given in these papers is here summarized and some new results from more recent years are included.

Lake Erken

Lake Erken (59° 51′ N, 18° 35′ E) is situated 11.1 m above sea level and has an area of 24 km^2. The mean depth is 9 m and the water residence time about 7 years (Widell, 1970).

The lake is regularly covered with ice for 16 to 18 weeks from late December/early January to late April/early May. After the spring overturn the summer stratification starts to develop in late May.

The conductivity (at 20 C) in the epilimnion is about 27 mS m^{-1} and the pH within 7.9–8.7. The alkalinity of the lake has according to yearly averages decreased from 1.8 mequ l^{-1} in the 1960's to 1.4 mequ l^{-1} twenty years later as shown in Fig. 1 (Rodhe, 1981).

Nitrate is accumulated in the whole water column during autumn and winter and reaches a level of around 300 μg N l^{-1}. Ammonia, however, is not accumulated and the concentration is less than 10 μg N l^{-1}, except at certain deep sites. Phosphate has a concentration of around 10 μg P l^{-1} during winter, but is rapidly taken up by the phytoplankton in spring.

About a month before ice-break the transparency is about 10 m and then it decreases to 3 m as a minimum during the spring peak of phytoplankton.

A common sampling point situated above the deepest point has been used by all investigators of the phytoplankton spring bloom.

In some cases comparisons cannot be made due to differences in technique and approach. For

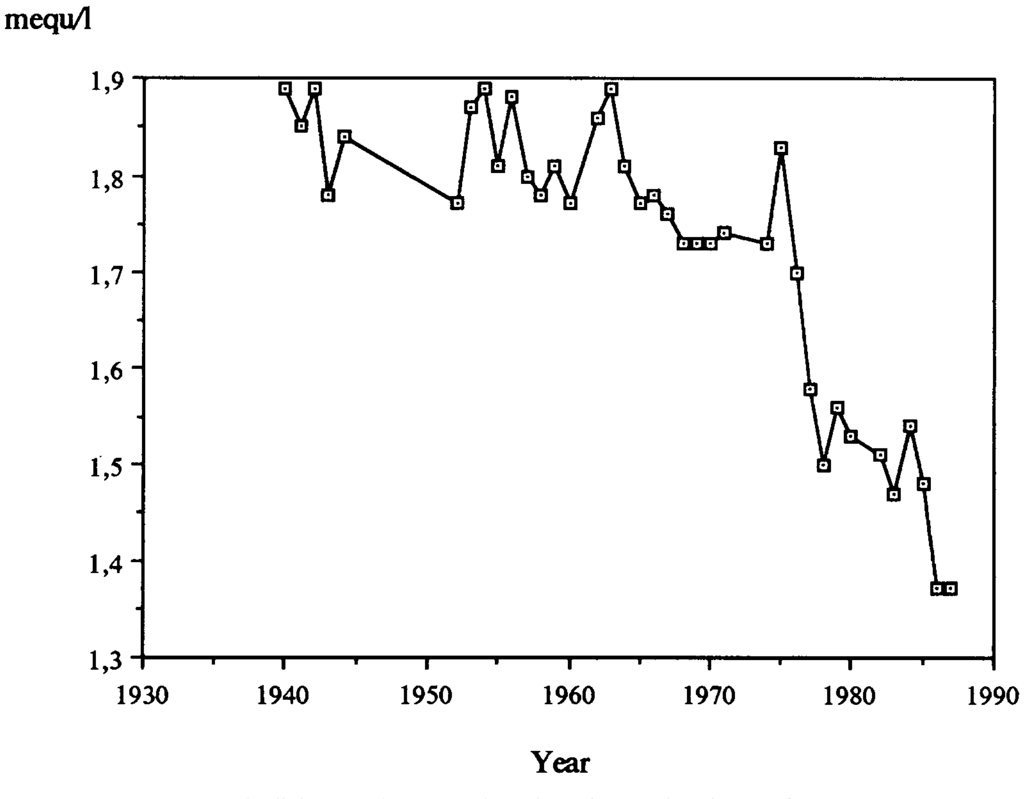

Fig. 1. The alkalinity (yearly means) in Lake Erken during the last forty years.

the determination of primary production several incubation times have been used as well as 'reduced series' with measurements at one or two depths. The earliest chlorophyll measurements were made with a fluorometric technique, which gave too high values. The methodological problems in chemical analyses used at the Erken laboratory are discussed by Boström & Pettersson (1973).

Results and discussion

Algal abundance

Stephanodiscus hantzschii var. pusillus dominated the spring outburst of phytoplankton during most of the investigation period (Rodhe *et al.*, 1958; Nauwerck, 1963; Pechlaner, 1970; Boström, 1981; Bell & Kuparinen, 1984). Regular winters with a snow- and ice-cover, which efficiently extinguishes the light, create conditions favourable for this small-size (150 μm^3 – Nauwerck, 1963; 85-235 μm^3 – Blomqvist, pers. comm.) diatom to develop exponentially around ice-break, when the light conditions improve.

Atypical climatic conditions, however, affect the species composition of phytoplankton during the spring severely. In the winter of 1973, with only 10 weeks of ice-cover and almost no snow, autumnal diatoms could persist and the large species *Stephanodiscus rotula* (Ehr.) Grun. (800-4000 μm^3 – Blomqvist, pers. comm.) and *Asterionella formosa* (280-1000 μm^3 – Blomqvist, pers. comm.) were dominant already in early March; the biomass maximum was reached on 1 April (Boström & Pettersson, 1977).

In 1979 the ice-cover lasted for 21 weeks, but the light conditions improved somewhat in early March due to a snow-melting period. This year motile dinoflagellates developed just under the ice and intensive vertical migration was shown (Pettersson, 1985). Similar migrations were well followed by Nauwerck (1963) in 1957. The dinoflagellates *Woloszynskia ordinata* and *Peridinium aciculiferum* were dominant during the entire spring development in 1979, a phenomenon not recorded before. In 1984 *Melosira islandica* ssp. *helvetica* was more abundant than in earlier years (Eriksson, pers. comm.). A similar increase in number for this species was reported by Pechlaner (1970) for the spring of 1960, although the biomass value of 1984 (1.1 mg l^{-1}) was not reached.

The species composition of phytoplankton affects the form of the spring peak as shown in Fig. 2. It is a well-known fact that the sedimentation of diatoms is very rapid; at the traditional outburst of diatoms during the spring in Lake Erken, they have decreased significantly a few days after the peak.

The average chlorophyll *a* concentrations in the epilimnion have never exceeded 30 $\mu g\ l^{-1}$ and the

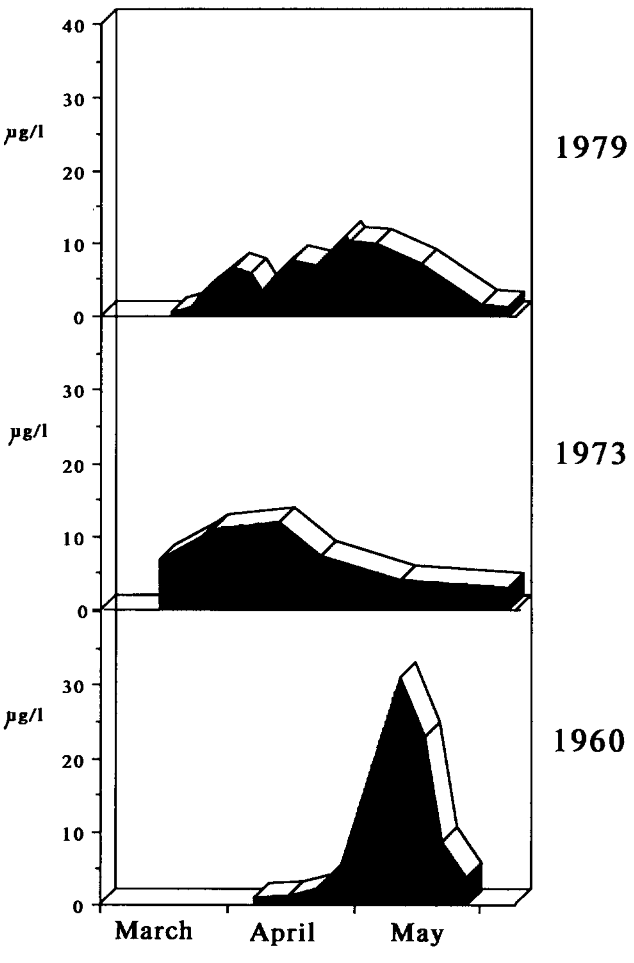

Fig. 2. Temporal change in the average (0–10 m) phytoplankton biomass (expressed as μg chl *a* l^{-1}) in Lake Erken during springs with different species composition.

range for recorded maxima is 11 to 30 $\mu g\ l^{-1}$. The reported fresh weight maxima vary from 4 to 11 $mg\ l^{-1}$. However, in thin layers beneath the ice up to 75 μg chl *a* l^{-1} was measured in 1980 (unpubl. data). The fresh weights recorded by Rodhe *et al.* (1958) for the springs of 1954 and 1955 are still the highest reported for Lake Erken.

Primary production

The primary production has been measured during several springs from 1954 onwards with the ^{14}C-method (Rodhe *et al.*, 1958; Nauwerck, 1963; Pechlaner, 1970; Boström & Pettersson, 1977; Eriksson & Pettersson, 1984; Bell & Kuparinen, 1984). The maximum production rates of the different springs are presented in Fig. 3. The highest primary production rate yet measured was recorded in May 1955, as 2200 $mg\ C\ m^{-2}\ d^{-1}$. However, a value of 2700 $mg\ C\ m^{-2}\ d^{-1}$ was calculated by Boström & Pettersson (1977) as a maximum for the spring of 1960.

The mean probable primary productions during two months of the spring, as calculated by Boström & Pettersson (1977), are shown in Fig. 4. There was a twofold variation in average production.

Bell & Kuparinen (1984) described Lake Erken as a batch culture during the spring outburst of phytoplankton – a good comparison since the grazing from zooplankton is negligible (Nauwerck, 1963; Pechlaner, 1970). They also estimated the bacterioplankton production to 1.2–1.7 $mg\ C\ m^{-3}\ d^{-1}$ during the spring of 1983 from ^{3}H-thymidine incorporation. Under the assumption of similar bacterioplankton production throughout the water column this corresponds to 11–15 $mg\ C\ m^{-2}\ d^{-1}$. The gross bacterioplankton production (production plus respiration) was 20% of gross primary production, when calculated per square meter of surface area.

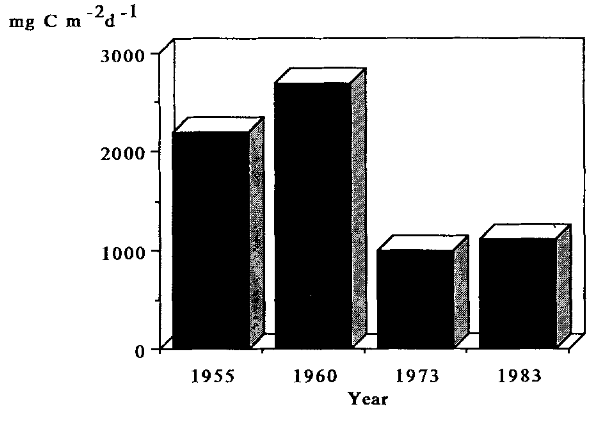

Fig. 3. The maximum primary production (recorded or calculated) for one day in Lake Erken during four springs.

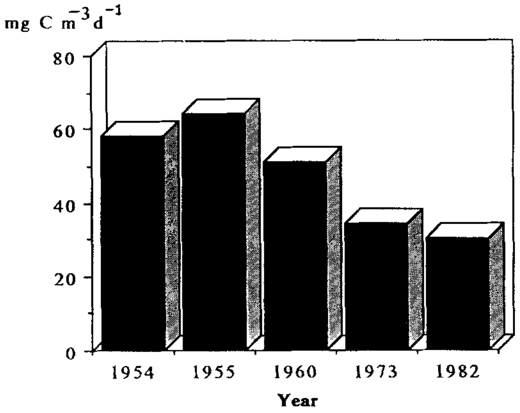

Fig. 4. Comparison of the mean probable primary production (see Boström & Pettersson, 1977) in Lake Erken during two months in the springs of five years.

Nutrients

The nutrient supply and availability during the spring development of phytoplankton were followed intensively from 1975 to 1984.

Nitrogen cycling was studied by determination of nitrate, nitrite and ammonia concentrations regularly and by laboratory experiments on nitrification and denitrification (Boström, 1981; Tirén & Boström, 1983). Nitrate has a markedly regular seasonal variation in Lake Erken. The formation of nitrate by nitrification occurs mainly in the surface sediment and nitrate is accumulated during the turnover period in autumn with low primary production. Under these conditions the denitrification process is inhibited. The concentration of nitrite is negligible during the whole year. Ammonia is never accumulated in high concentrations in the whole water column. Inflowing water occasionally causes high concentrations of 100–200 μg NH_4–N l^{-1} (Boström, 1981).

In order to investigate the phosphorus conditions, measurements of total phosphorus, particulate phosphorus and enzymatically determined orthophosphate (Pettersson, 1979a) were combined with determinations of biomass-related physiological parameters such as surplus phosphorus content and specific alkaline phosphatase activity (for methods and results see Pettersson, 1979b, 1980, 1985). Laboratory experiments on nutrient enrichment were performed during 1982–1984 with a completely randomized factorial design (Eriksson & Pettersson, 1984; Eriksson, in prep.).

The results presented in the above mentioned papers can be summarized as follows:

The orthophosphate concentration decreased from about 10 μg P l^{-1} to below the detectable level (0.1 μg P l^{-1}) by late April, after a rapid uptake by phytoplankton starting in late March/early April.

A luxury uptake of phosphorus was shown by high surplus phosphorus content in the particulate matter. The maximum content registered, 10 μg P per mg C, appeared in March 1979, when the dinoflagellates dominated the biomass beneath the ice. This figure was twice as high as any previously measured value.

Surplus phosphorus can also be expressed as concentration in the water, to be compared with orthophosphate, particulate phosphorus and total phosphorus. In 1979 and 1980, 12 μg P l^{-1} was measured as surplus phosphorus beneath the ice in late March due to a dense dinoflagellate bloom. In 1983 and 1984 more moderate concentrations, around 3.5 μg P l^{-1}, were registered in the middle of April, before the phytoplankton outburst. This was in agreement with the results obtained during the years 1975 to 1978. However, surplus phosphorus determination turned out to be useful in showing luxury phosphorus storage by phytoplankton before the logarithmic growth began around ice-break. When related to particulate phosphorus, surplus phosphorus decreased from more than 30% to 15% in 1979. The minimum values for the specific surplus phosphorus content, reached in May, were about 0.4 μg P per mg C, i.e. one order of magnitude less than in March/April.

As recommended by several authors (see Pettersson, 1985), alkaline phosphatase activity was used as an indicator of phosphorus deficiency in phytoplankton. In Lake Erken, measurements of the alkaline phosphatase activity were performed during the spring of the years 1975 to 1984. The specific activity increased in 1979 from 0.4 nmol (mg C)$^{-1}$ min^{-1} in March and April to 7 nmol (mg C)$^{-1}$ min^{-1} in late May. This picture was also valid for the years before as well as after. Also, as shown in Eriksson & Pettersson (1984), the actual activity (nmol l^{-1} min^{-1}) increased drastically after the spring peak of phytoplankton in 1982 (see also Pettersson, 1980). In the latter paper it was also noticed that the proportion of free enzymes was high, 40% to 70% of the total activity, when the phosphorus deficiency was severe in late May.

In 1976 it was possible to calculate the Michaelis constant of the alkaline phosphatases, which decreased to a minimum of 0.3 μmol l^{-1} in May, when the algae were phosphorus-limited. It was concluded that the phytoplankton compensated the phosphorus deficiency with an increase in enzyme production, liberation of free exoenzymes and with an improved ability to use low substrate concentrations (Pettersson, 1980).

Additional information from N : P and C : P ratios as well as nutrient enrichment experiments confirmed the statement that phosphorus limitation ended the spring outburst of phytoplankton in Lake Erken (Pettersson, 1980, 1985; Eriksson & Pettersson, 1984). In some years also nitrate was depleted, but generally phosphorus is the controlling factor. Pechlaner (1970) stated that depletion of inorganic nutrients was the obvious cause for the end of the spring outburst. He also concluded that silicon did not decrease enough to limit the growth of diatoms. This was verified by all later investigations. The concentration of molybdate reactive silicon very rarely decreased below 0.5 mg Si l^{-1}. The concentrations of micronutrients have not been followed in Lake Erken.

However, selenium has been studied and shown to have significant effect on algal growth in laboratory enrichment experiments with natural algal assemblages (Eriksson & Pettersson, 1984) as well as algal cultures (Eriksson, 1982).

Conclusion

The spring development of phytoplankton is an event which has been followed more or less intensively on a number of occasions in Lake Erken during the last thirty years.

The form of the spring bloom varies, mainly due to climatic factors such as duration of ice- and snow-cover and thus light conditions at the end of the winter stratification affecting the species composition. A sharp phytoplankton peak with the small diatom *Stephanodiscus hantzschii var. pusillus* as the dominant species is most often occuring, but exceptions are not uncommon.

Studies of the nutrient conditions, including usage of physiological indicators of algal phosphorus status, have shown phosphorus to be the factor ending the spring peak. The studies of the pelagial community in Lake Erken are to be continued; emphasis will be put on improvements in primary production estimates, automatic continuous measurement of *in vivo* fluorescence and determination of phosphorus turnover.

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