# Origin and production of phosphatases in the acid Lake Gårdsjön

Håkan Olsson
*Institute of Limnology, Box 557, 751 22 Uppsala, Sweden*

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**Abstract**

The activity of acid phosphatases was followed for one year in Lake Gårdsjön as well as in the inlet and the outlet of the lake. A budget of the phosphatases was calculated, including an estimation of the production of phosphatases. The phosphatase activity was also measured in two basins upstream of L. Gårdsjön: the north basin and the south basin of L. Stora Hästevatten.

The acid phosphatase activity was very high compared with reported alkaline phosphatase activities in other lakes. About 95% of the phosphatases in L. Gårdsjön was produced in the lake, and the production was highest in early summer.

Small *Chrysophyceae* (<10 μm) probably produced the majority of the acid phosphatases in the investigated lakes, and accordingly could be favoured in environments with low phosphorus supply due to their ability to produce large amounts of phosphatases.

## Introduction

Lake Gårdsjön, in southwestern Sweden, is an acidified and oligotrophic lake with very low phosphorus content. Phosphorus is also the nutrient which primarily restricts algal growth in the lake (Broberg & Persson 1981).

Very high acid phosphatase activity, compared with reported alkaline phosphatase activities in neutral lakes, existed in L. Gårdsjön (Jansson *et al.* 1981). Little information was found in the literature on the role of acid phosphatase (Jansson *et al.* 1981) and probably no further studies on phosphatases in acid lakes have been made. This justified a closer investigation of the origin, production and role of phosphatases in acid environments in the L. Gårdsjön area. In addition to this paper, two other parts of the study have been published (Jansson *et al.* 1981; Jansson 1981).

In Jansson *et al.* (1981) a characterization of the phosphatases by gel-filtration, the phosphatase activity at different pH and a preliminary budget of the phosphatase activity was presented. The phosphatases in L. Gårdsjön had a pH-maximum at 5.0 and the activity was inhibited by phosphate. At least four different types of acid phosphatases were found in the lake in July 1980. About 50% of the phosphatase activity was found in filtered water while 40% was found associated with seston smaller than 5 μm, including small algae (e.g. *Cromulina* and *Chlamydomonas*) and bacteria. Experiments to explain the extremely high phosphatase activity were presented by Jansson (1981). It was found that high concentrations of aluminum, a commonly observed feature of acid lakes, blocked the phosphorus esters in the lake, which was supposed to decrease the availability of phosphorus and in turn induced phosphatase production. Iron could probably have the same effect as aluminum, but existed in much lower concentrations and was therefore considered to be of less importance.

The present paper deals with phosphatases in

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three lakes, including variations during a whole year-cycle. The origin of the phosphatases and the regulatory factors of phosphatase activity is further analysed. A 'phosphatase budget' is presented for the whole investigation period. Production of phosphatases during different periods of the year was calculated from the budget and the connection between production, lifetime and activity of phosphatases is discussed.

## Characteristics of the studied lakes

The acidified Lake Gårdsjön is situated in the southwest of Sweden, about 45 km north of Gothenburg (Fig. 1).

The bedrock in the drainage area consists of gneiss and granite, and often lacks soil-cover. The soil consists mainly of till. Coniferous forest dominates the vegetation.

Upstream of L. Gårdsjön there are three smaller lakes (Fig. 1). L. Stora Hästevatten, which is included in this investigation, is divided into two basins by a road embankment and will be considered as two lakes, being referred to as the north basin and the south basin.

Table 1 gives morphometric characteristics and Table 2 chemical characteristics of L. Gårdsjön and the two basins of L. St. Hästevatten. The water renewal time of L. Gårdsjön is 2.3–2.7 years. The lakes are clear, poor in nutrients and have low pH. The aluminum content is high.

*Table 1.* Morphometric data of Lake Gårdsjön and of the two basins of Lake Stora Hästevatten.

| | Area ($km^2$) | Volume ($10^6$ $m^3$) | Mean depth (m) | Max. depth (m) |
|---|---|---|---|---|
| L. Gårdsjön | 0.31 | 1.5 | 4.9 | 18.5 |
| L. St. Hästevatten | | | | |
| The north basin | 0.03 | 0.1 | 3.2 | 6.5 |
| The south basin | 0.05 | 0.2 | 4.0 | 9.3 |

## Material and methods

### *Sampling*

Samples were taken in L. Gårdsjön and in the inlet and the outlet on 22 occasions from March 1980 to May 1981. During summer-stratification samples were taken from three different strata (epi-, meta- and hypolimnion), and during winter from two strata (epi- and hypolimnion). When the lake was isothermal one sample was taken from the whole water-column.

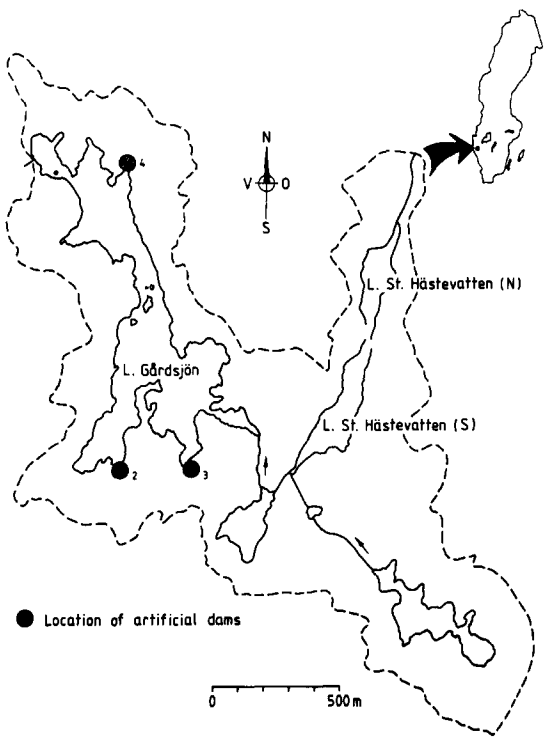


*Fig. 1.* The Lake Gårdsjön watershed.

Samples representing the water quality of diffuse inlets were taken on 18 occasions in three 'artificial dams' in the drainage area of L. Gårdsjön (Fig. 1). In both basins of L. St. Hästevatten, samples were taken from two strata during stratification and from the whole water-column during isothermal conditions.

Samples were frozen at –20 °C and were stored frozen until analysis after 8–219 days. On four occasions unfrozen samples were brought to the laboratory in Uppsala, immediately after sampling, for special studies.

### *Phosphatase activity assay*

Phosphomonoesterase activity, abbreviated to 'phosphatase activity' in the text, was analysed at 20 °C with the substrate 4-methylumbelliferyl

*Table 2.* Water-chemical data of Lake Gårdsjön, (epilimnion) and the two basins of Lake Stora Hästevatten, (mean for the whole water-column). All concentrations are given in $\mu g \cdot l^{-1}$.

| | L. Gårdsjön[a] | The north basin of[b] L. St. Hästevatten | The south basin of[b] L. St. Hästevatten |
|---|---|---|---|
| pH | 4.6 | 5.3 | 5.2 |
| Conductivity ($mS \cdot m^{-1}$) | 6.7 | 5.7 | 5.5 |
| Secchi disk transp. (m) | 8.9 | ~6.5 | 6.9 |
| Total-P | 5.4 | 3.6 | 4.5 |
| Part.-P | 3.5 | 2.7 | 3.1 |
| Total-N | 397 | 300 | 367 |
| $NO_2 + NO_3$-N | 114 | 84 | 49 |
| $NH_4$-N | 48 | 18 | 33 |
| Part.-N | 56 | - | - |
| Diss. org. C | 2 100 | 2 540 | 3 881 |
| Chlorophyll *a*[c] | 1.05 | 0.70 | 1.25 |
| Total-Al[c] | 270 | 90 | 150 |

[a] Mean for the period 1979–1980.
[b] Mean for the period 5 February 1980–18 November 1980.
[c] Mean for the whole water-column 28 April 1980–15 October 1980.

phosphate (Boehringer Mannheim) as described by Jansson *et al.* (1981). Samples from L. St. Hästevatten were analysed at pH 5.2 and the other samples at pH 4.6 in a Tris-malate-acetate buffer ($10^{-3}$ M with respect to each component). These pH-values were chosen in order to perform the analyses at a pH close to that in the analysed waters. The pH in the dams was about 4.15. The assay was conducted at pH 4.6 since the activity at the pH in L. Gårdsjön was the most relevant to budgeting phosphatases. The substrate concentration in the reaction tube was $1.1 \cdot 10^{-5}$ M.

The fluorescent product 4-methylumbelliferone was detected with a Turner 111 fluorometer equipped with Lamp No. 110-850, emitting UV light. As a primary filter Corning 7-60 was used, and Wratten 8 and 48 were used as secondary filters. A calibration curve (Jansson *et al.* 1981) was used to calculate the amount of product formed during the assay.

All activities in frozen samples were corrected according to the correction curve described below.

*Effects of freezing*

The effects of freezing on the phosphatase activity were investigated on 8 July 1980, 23 March (L. Gårdsjön), 25 March (L. Stora Hästevatten) and 18 May 1981. Phosphatase activity was analysed before freezing and at different time-intervals after freezing. The water was frozen in 20 ml aliquotes to avoid refreezing and thawing was done in a room-temperated waterbath.

In May 1981 tests were made on water from the metalimnion in L. Gårdsjön and the results were evaluated with non-linear least squares summary statistics. The curve obtained is presented in Fig. 2. When a sample was frozen at -20 °C for 20 days or more the phosphatase activity was reduced by about 60%.

No large differences were seen between different samples or in samples taken on different occasions.

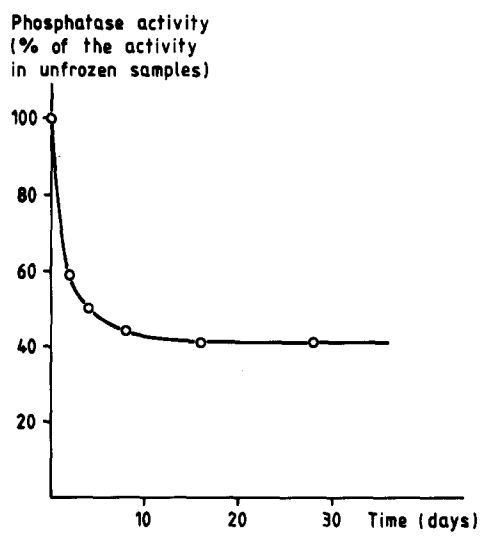


*Fig. 2.* The decline of phosphatase activity when samples were stored at -20 °C.

Therefore the curve presented in Fig. 2 was considered to be relevant as a correction curve for all frozen samples during the investigation.

*Budget calculations*

With the aim of obtaining information on the production of phosphatases in the lake, a factor describing the loss of phosphatase activity was introduced. The 'life-length' of phosphatases was studied in chloroform-treated water in July 1980 (Jansson *et al.* 1981). Data from that experiment were used to find an equation describing the losses of phosphatase activity with time by means of non-linear least squares summary statistics.

The 'decay curve' is presented in Fig. 3 and can be described with the equation

$$A_t = 100 \cdot (1 + a) \cdot (1 + a \cdot e^{b \cdot t})^{-1} \quad (1)$$

where $A_t$ is the phosphatase activity at the time t in per cent of the activity at the time zero; t is the time in days after adding chloroform; and a and b are constants that were estimated to 0.076 (SD = 0.042) and 0.071 (SD = 0.012) respectively. This equation was used in a model to estimate the phosphatase production.

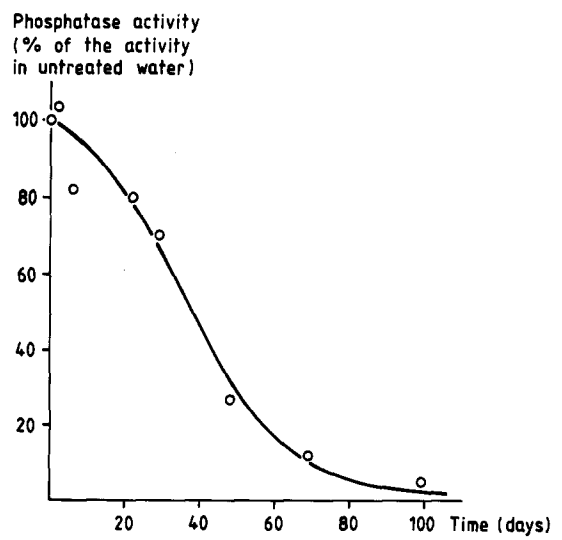


*Fig. 3.* The decline of phosphatase activity when adding chloroform to water from Lake Gårdsjön, 7 August 1980.

Transport of phosphatase activity has been calculated according to

$$A_i \cdot Q_i \quad (2)$$

for a certain time-period, i, of 14 days. $A_i$ is the phosphatase activity in the middle of the period and $Q_i$ is the accumulated water-flow during the same period. The phosphatase activity for periods with no sampling was extrapolated linearly from the two closest sampling events. The flows at the inlet and in the three dams have been calculated from the measured discharge in the outlet by factors proportional to the respective drainage areas. Phosphatase activity in precipitation was assumed to be zero.

The theoretical activity in the lake, after the period i, was calculated using the following equation:

$$\text{Theor}A_i = (V \cdot \text{Theor}A_{i-1} + A_{i,in} \cdot Q_{i,in} - A_{i,out} \cdot Q_{i,out}) \cdot V^{-1} \quad (3)$$

where A is the phosphatase activity and V is the lake volume. $A_{i,in} \cdot Q_{i,in}$ and $A_{i,out} \cdot Q_{i,out}$ represent the transport of phosphatase activity in the inflowing water and in the outlet according to (2), i indicating the number of the period.

For a certain period, the activity remaining from phosphatases produced and imported during previous periods, was calculated according to (1) and this activity was introduced as factor 'Theor $A_{i-1}$' in (3). The difference between the measured activity (mean for the whole water-body) and the theoretical activity gave the production of the phosphatases during the period. The model was run for 25 periods, from March 1980 to February 1981.

## Results

*Phosphatase activity budget and production of phosphatases*

From March to June 1980 no large differences were seen between the accumulated transport of phosphatases into and out of L. Gårdsjön. Later during the year, especially during November–December, output was higher than input.

From March 1980 until January 1981, 9 150 mmol · $min^{-1}$ of phosphatase activity had left and 5 900 mmol · $min^{-1}$ had entered the lake, and during the same period, the accumulated inflow of phosphatases was 5% of the accumulated production of phosphatases. Without correction for losses of phosphatase activity, the contribution from the inlets was about 11% of the production.

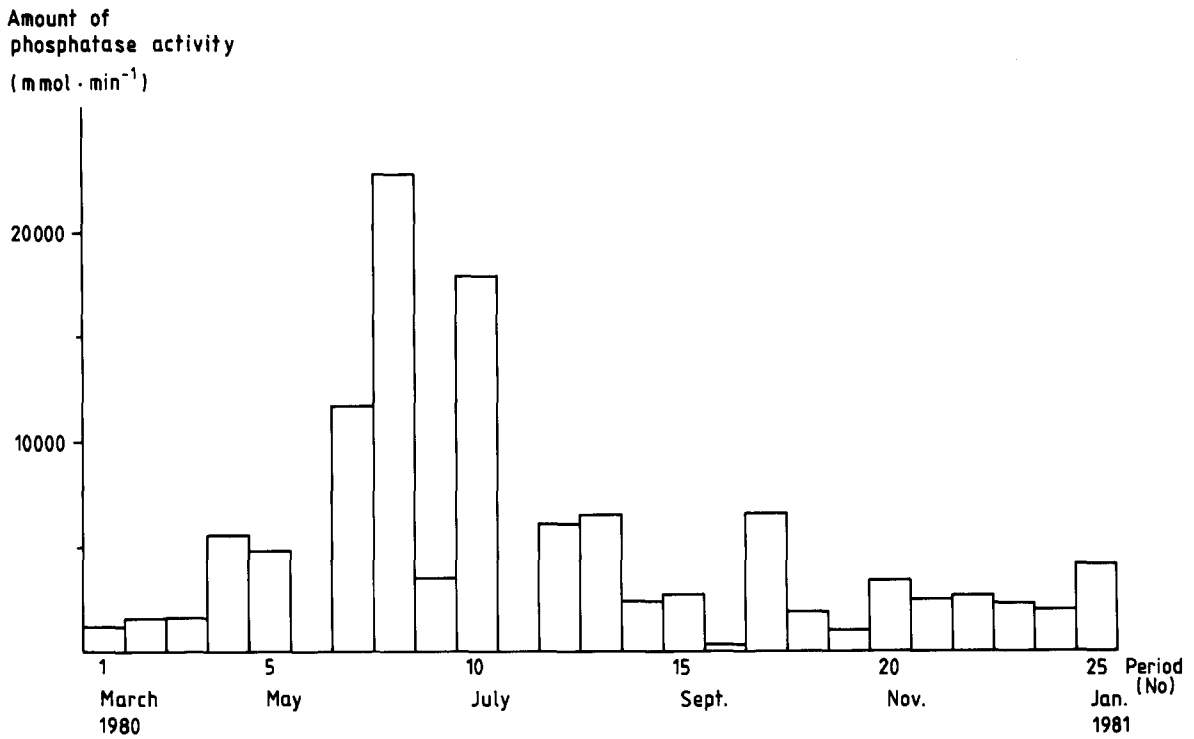


*Fig. 4.* The amount of phosphatase activity produced in Lake Gårdsjön during periods of 14 days, March 1980–January 1981.

The production of the phosphatases during each period of 14 days is shown in Fig. 4. The highest production (22 800 mmol · $min^{-1}$) occurred in early summer but there were large fluctuations during that time of the year. In periods 6 and 11 negative production values were achieved. These could be reduced or turned positive if the model was run with a higher 'decay rate' of the phosphatases.

The variations of the production of phosphatases broadly followed the variations of the phosphatase activity in L. Gårdsjön (see Fig. 5).

*Seasonal and spatial variations of the phosphatase activity*

The phosphatase activity in the studied waters is presented in Figs. 5–7.

In L. Gårdsjön and its outlet a peak in phosphatase activity was found from early June until late July. In the south basin of L. St. Hästevatten as well as in the inlet of L. Gårdsjön, a peak appeared half a month earlier, with the beginning in mid-May and the decline in early July.

In the dams and in the north basin of L. St. Hästevatten the phosphatase activity showed small variations over the investigated period. The lowest activities were found in the dams. The mean of the activity during the investigated period was 1.2 nmol · $l^{-1}$ · $min^{-1}$ (SD = 1.0) in the dams and 5.2 nmol · $l^{-1}$ · $min^{-1}$ (SD = 2.0) in the north basin of L. St. Hästevatten.

In the south basin of L. St. Hästevatten the activity was higher than in the north basin but the differences were small in autumn and winter. No summer peak was found in the north basin of L. St. Hästevatten. The north basin was isothermal during the whole summer, which contrasted to the south basin, where there was a well-developed thermocline. During the stratification period the activity was highest in the hypolimnion but vertical differences were generally small. In L. Gårdsjön the highest activity occurred in the metalimnion while the differences between the lower activities in the epi- and hypolimnion were small. The maximum activities in early summer exceeded the 'mean activities' during the rest of the year approximately 4–5 times in

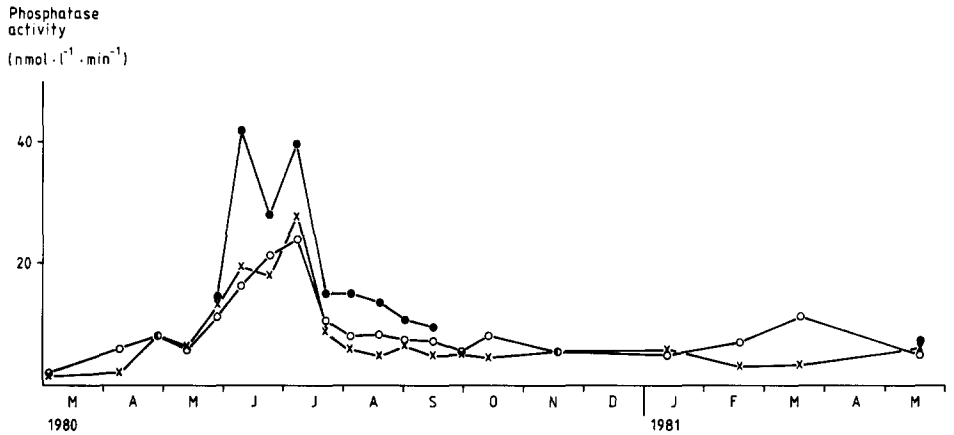


*Fig. 5.* Phosphatase activity in the epilimnion O, the metalimnion ●, the hypolimnion x and the whole water-column ◐ of Lake Gärdsjön, March 1980–May 1981.

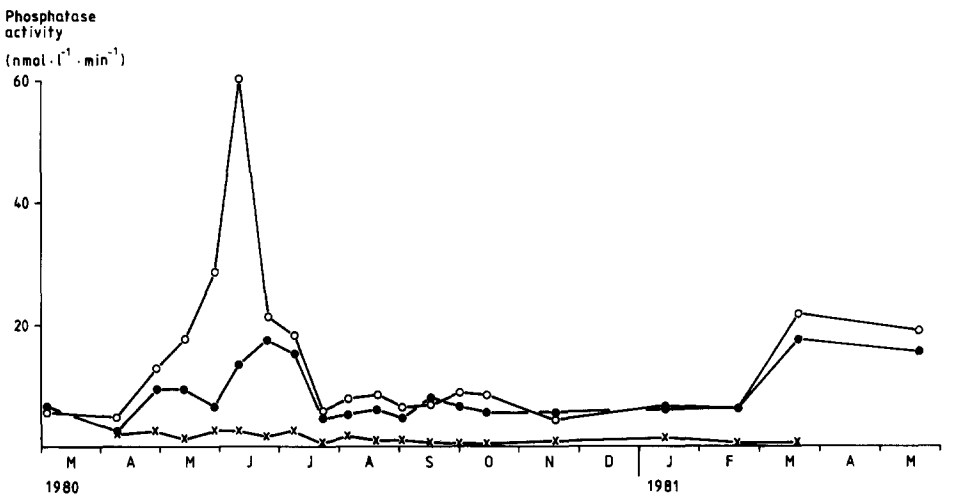


*Fig. 6.* Phosphatase activity in the inlet O and the outlet ● of Lake Gårdsjön and in the dams representing diffuse inlets x, March 1980–May 1981.

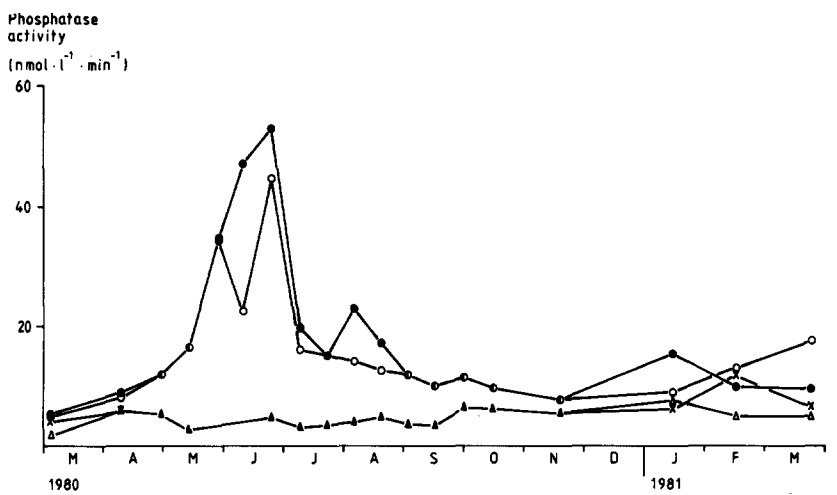


*Fig. 7.* Phosphatase activity in lake Stora Hästevatten, March 1980–March 1981. The epilimnion O, the hypolimnion ● and the whole water-column ◐ of the south basin. The epilimnion x, the hypolimnion △ and the whole water-column ▲ of the north basin.

both L. St. Hästevatten and L. Gårdsjön.

In March and May 1981 high activities were measured in both the inlet and outlet of L. Gårdsjön. The high activity in the outlet is difficult to explain when comparing it with the activity in L. Gårdsjön. On no other occasion did a significantly higher activity appear in the outlet compared with the lake.

*Phosphatase activity in relation to planktonic activity*

In order to further elucidate the influence of different planktonic organisms on the production of phosphatases the seasonal variation of phosphatase activity was compared with different plankton parameters.

In the north basin of L. St. Hästevatten the phosphatase activity as well as chlorophyll concentration (Broberg, in prep.) was lower during summer compared with the other lakes. The peak in phosphatase activity in the south basin of L. St. Hästevatten coincided well with a peak in chlorophyll *a* but in L. Gårdsjön a chlorophyll *a* maximum appeared earlier in spring. In both lakes chlorophyll *a* was high in autumn but the phosphatase activity showed no increase at that time of the year.

Data on primary production in L. Gårdsjön and in the north basin of L. St. Hästevatten (Grahn, in prep.) did not correlate with the phosphatase activity. Measurements of primary production were not made in the south basin of L. St. Hästevatten.

Bacterial biomasses in L. Gårdsjön (Andersson, in prep.) were highest in May and in autumn 1980 and no covariation with phosphatase activity was seen. Bacterial countings were not made in L. St. Hästevatten.

As regards algal countings (Larsson, in prep.), total biomasses gave the same temporal variation as chlorophyll *a*. Small *Chrysophyceae* (<10 μm) dominated the algal biomass in the south basin of L. St. Hästevatten during the biomass peak in June. The biomass of small *Chrysophyceae* mostly covaried well with the phosphatase activity in the south basin of L. St. Hästevatten and in L. Gårdsjön (Fig. 8a and b). In June–July when the biomass of *Chrysophyceae* (<10 μm) declined rapidly, the decrease in phosphatase activity was not noticed until 14 days later.

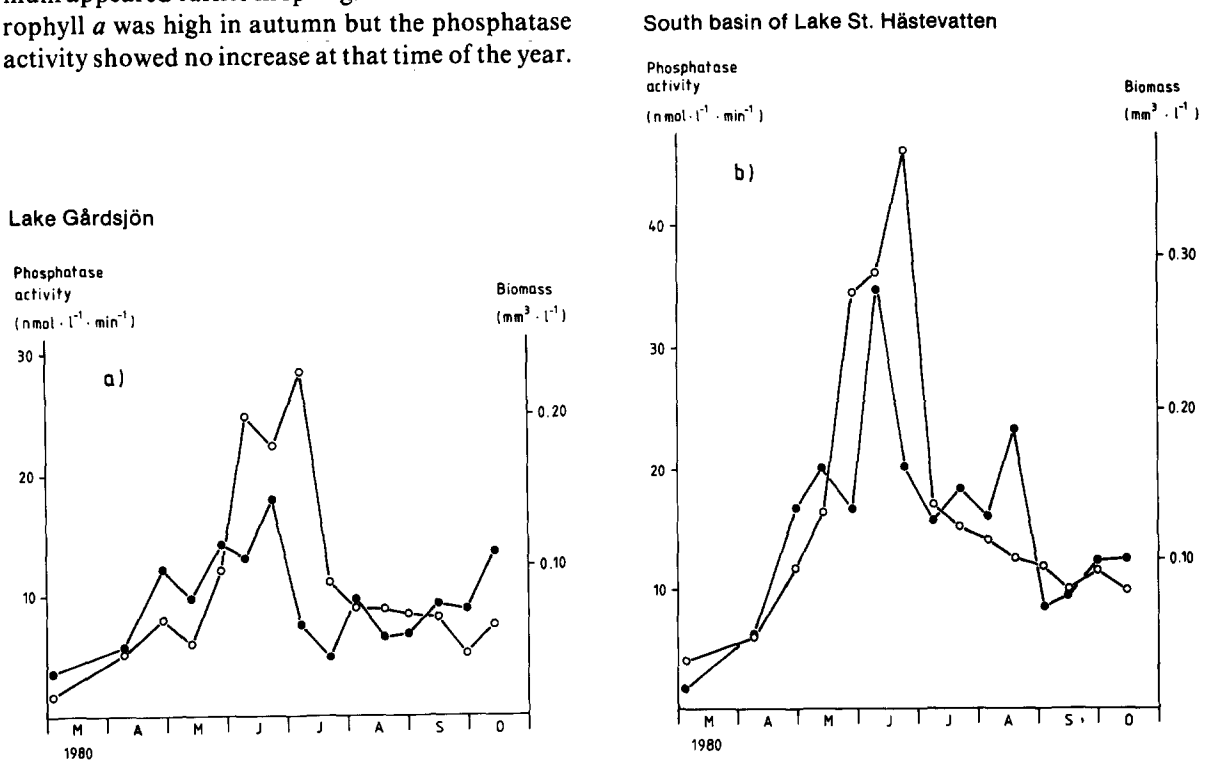


*Fig. 8.* Phosphatase activity ○ and biomass of *Chrysophyceae* (<10 μm) ●. Mean for the whole water-column.

Also vertical variations in phosphatase activity showed good agreement with vertical distribution of small *Chrysophyceae*. The highest phosphatase activity in the south basin of L. St. Hästevatten was found in the hypolimnion together with high biomass of *Chrysophyceae* (<10 μm). In L. Gårdsjön the phosphatase activity, as well as the biomass of *Chrysophyceae* (<10 μm), was highest in the metalimnion. In the hypolimnion the phosphatase activity was lower than expected from the biomass of *Chrysophyceae* (<10 μm). This was most pronounced in early May.

In the north basin of L. St. Hästevatten the biomass of *Chrysophyceae* (<10 μm) was lower during summer compared with the south basin. This was also the case with the phosphatase activity. No data from algal countings later than October 1980 were available when this paper was prepared.

*Phosphatase activity in relation to phosphorus fractions and aluminum*

No large differences in total and particulate phosphorus could be seen between the investigated lakes and there were no correlations, negative or positive, between phosphorus fractions and phosphatase activity.

Regarding the results from Jansson (1981) aluminum could be a factor regulating phosphatase activity in L. Gårdsjön. The aluminum concentrations during the period 28 April 1980–15 October 1980 in L. Gårdsjön, the south basin of L. St. Hästevatten and the north basin of L. St. Hästevatten were 270, 150 and 90 $\mu g \cdot l^{-1}$ respectively (Nilsson, in prep.), while the specific phosphatase activities (per biomass of small *Chrysophyceae*) were 160, 139 and 80 $nmol \cdot min^{-1} \cdot mm^{-3}$ respectively.

## Discussion

Budgeting of phosphatases gives important information on the origin of the phosphatases in a lake. Stevens & Parr (1977) found that the inlets could contribute 40% to the increased alkaline phosphatase activity in Lough Neagh during the investigated period (February–June 1974). One possible reason for this high input of phosphatases was suggested to be sewage effluents.

There are no sewage effluents affecting L. Gårdsjön. The lakes in the area are acid and oligotrophic. High input of phosphatases could be due to high production of phosphatases in the lakes upstream of L. Gårdsjön and/or in the soil profile of the catchment area. However, the budget calculations in L. Gårdsjön showed that the majority of the phosphatases (~95%) were produced in the lake. As will be discussed below, there are results indicating that the losses of phosphatase activity have been underestimated, which means that the contribution from the inlets could be even less important compared with the production in the lake.

During conditions of low phosphorus supply many investigations have reported that the phosphatase activity increases due to derepression or induction of enzyme synthesis. Consequently, the phosphatase production may give valuable information about the phosphorus conditions. The measured phosphatase activity is dependent on the phosphatase production but there may be a considerable timelag between the two variables depending on the longevity of the phosphatases in the water. A great step forward in ecological studies would therefore be made if the phosphatase production could be determined.

An attempt to estimate the production was made when budgeting phosphatases in L. Gårdsjön. The results seem reasonable and show that the methods used are applicable. In two periods during the summer negative values of production were however obtained, probably due to the actual elimination rate of phosphatase activity during these periods being higher than that observed under laboratory conditions.

The laboratory experiments estimating the lifetime of the phosphatases did not simulate or control all factors which could affect the phosphatases in the lake. Losses due to sedimentation of seston containing phosphatases, increased amount of hydrolytical enzymes or chemical substances with the property to break down phosphatases, and increased sunlight causing breakdown of organic substances, are some factors not included in the laboratory experiment. Furthermore, the equation describing losses of phosphatase activity in the model theoretically could only be applied on newly produced phosphatases, while the laboratory experiment was made on lake water which contained phosphatases of different ages. If it had been possible to perform the laboratory experiment with new-

ly produced phosphatases their lifetime would probably have been longer. However, the present results imply that of the factors not included in the experiment, those causing losses of phosphatases seemed to be most important. Since the estimated phosphatase production in different periods of the year gave very approximate values, seasonal changes of different parameters were only compared with the measured phosphatase activity.

The lakes with the lowest phosphatase activity in summer had the lowest biomass of phytoplankton, indicating that phytoplankton or bacteria associated with phytoplankton were the main producers of acid phosphatases. The pronounced phosphatase activity peak in L. Gårdsjön and in the south basin of L. St. Hästevatten coincided with the development of the biomass of *Chrysophyceae* (<10 μm) (Fig. 8a and b). Comparing the two variables in different strata of the lakes the results showed positive correlation. If it is assumed that small *Chrysophyceae,* at least during the summer, produced the same amount of phosphatase activity per biomass, the investigation indicates that a large part of the phosphatase activity in L. Gårdsjön and in L. St. Hästevatten came from algae among the group small *Chrysophyceae* (<10 μm). This is supported by results from the characterization of phosphatases in L. Gårdsjön with gel-filtration (Jansson *et al.* 1981). In July 1980 it was shown that the main part of seston-bound phosphatases were tied to particles passing a 5 μm filter. In this size fraction *Chrysophyceae* belonging to the genus *Chromulina* sp. were highly dominant.

*Chrysophyceae* have been shown to frequently dominate phytoplanktonic biomass in oligotrophic lakes (Schindler & Holmgren 1971; Ramberg 1979; Rosén 1981). *Chrysophyceae* was also shown to dominate in the eutrophic L. Erken during periods of low phosphorus supply, such as following the spring bloom (Pechlaner 1970; Pettersson 1980). Simultaneously the alkaline phosphatase activity was very high. Due to their ability to create a high phosphatase activity, *Chrysophyceae* could be favoured in environments of extremely low phosphorus availability.

In July the decline in phosphatases activity was delayed compared with the biomass of *Chrysophyceae* (<10 μm). A similar pattern was found by Petterson (1980) between the spring peak of chlorophyll *a* and the alkaline phosphatase activity in L. Erken in the years 1975–1978. Pettersson suggested the delay to depend on the algae containing surplus phosphorus in the beginning of growth and that the production of phosphatases increased when the surplus phosphorus was depleted after the biomass maximum.

In L. Erken the ratio surplus phosphorus/particulate phosphorus was at a minimum of about 0.07 in May and about 0.15 in April. In L. Gårdsjön the ratio was about 0.05 (mean) in 1979 with small variations (Broberg & Persson 1981). The ratio in 1980 should not be very different because phosphorus conditions were about the same as 1979. These figures indicate that the surplus phosphorus in L. Gårdsjön was constantly very low so the internal phosphorus supply should be depleted already at the onset of biomass increase. The maintained acid phosphatase activity in L. Gårdsjön can therefore hardly be explained as an effect of changed surplus phosphorus.

Considering the long 'survival' of phosphatase activity (Fig. 3) it is likely that the phosphatases can be active for 14 days after production. Since samples were taken fortnightly it is possible that the time-lag was shorter than 14 days. This means that the previously produced phosphatases could very well account for the observed delay. A long lifetime of alkaline phosphatases in lakes has been suggested by Healey (1973) but no information about lifetime of acid phosphatases in lakes has been found.

Jansson (1981) proposed that high concentrations of aluminum caused a high phosphatase activity in L. Gårdsjön. It was suggested that aluminum reacted with the phosphatase substrates and thereby protected the substrates against enzymatic hydrolysis. This inhibitory effect on recycling of phosphorus was compensated by an increased production of phosphatases.

A comparison between the investigated lakes, during the vegetation period, shows that the higher the concentration of aluminum the higher was the specific phosphatase activity (activity per biomass of small *Chrysophyceae*). If it is assumed that the lifetime of the phosphatases was the same in the three lakes it can be concluded that the highest phosphatase production took place in the lakes with the highest aluminum concentrations. My results thus support the experimental results of Jansson (1981) showing that aluminum inhibited recycling of phosphorus.

The main conclusions from this investigation are summarized below:

About 95% of the acid phosphatases in L. Gårdsjön were produced in the lake.

Small *Chrysophyceae* (<10 μm) were the major producers of acid phosphatases in the investigated lakes.

The determination of the production of phosphatases gave approximate values, but with a better estimation of the losses of phosphatases in the lake the method seems to be applicable in ecological studies.

Results from this investigation support the findings of Jansson (1981) that aluminum can be important in regulating the phosphorus availability in acid lakes. Further support for the effects of aluminum ought to be found from regional surveys of phosphatase activities and aluminum levels.

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