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Interactions between sediment and water in a shallow and hypertrophic lake: a study on phytoplankton collapses in Lake Søbygård, Denmark

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Abstract

Short-term changes in phytoplankton and zooplankton biomass have occurred 1–3 times every summer for the past 5 years in the shallow and hypertrophic Lake Søbygård, Denmark. These changes markedly affected lake water characteristics as well as the sediment/water interaction. Thus during a collapse of the phytoplankton biomass in 1985, lasting for about 2 weeks, the lake water became almost anoxic, followed by rapid increase in nitrogen and phosphorus at rates of 100–400 mg N m^{-2} day^{-1} and 100–200 mg P m^{-1} day^{-1}. Average external loading during this period was about 350 mg N m^{-2} day^{-1} and 5 mg P m^{-2} day^{-1}, respectively.

Due to high phytoplankton biomass and subsequently a high sedimentation and recycling of nutrients, gross release rates of phosphorus and nitrogen were several times higher than net release rates. The net summer sediment release of phosphorus was usually about 40 mg P m^{-2} day^{-1}, corresponding to a 2–3 fold increase in the net phosphorus release during the collapse. The nitrogen and phosphorus increase during the collapse is considered to be due primarily to a decreased sedimentation because of low algal biomass. The nutrient interactions between sediment and lake water during phytoplankton collapse, therefore, were changed from being dominated by both a large input and a large sedimentation of nutrients to a dominance of only a large input. Nitrogen was derived from both the inlet and sediment, whereas phosphorus was preferentially derived from the sediment. Different temperature levels may be a main reason for the different release rates from year to year.

Introduction

Reduced nutrient loading is not always sufficient to reduce eutrophication, since nutrients accumulated in the sediment can be released and provide significant internal loading (Boström et al., 1982; Jacoby *et al.*, 1982). In particular phosphorus released from the sediment can severely prevent or delay the recovery of lakes (e.g. Bengtsson *et al.*, 1975; Peterson, 1982). In shallow lakes, where the input from the sediment is generally higher than in deeper lakes, this internal phosphorus loading sometimes can be a major contribution to the overall loading of the lake (Holdren & Armstrong, 1980; Lennox, 1984).

Traditionally, internal phosphorus loading has been regarded as a function of chemical and biological interactions, either within the sediment or between sediment and water. Less attention has been paid to how the biological structure in the lake water affects the internal loading. In shallow, small and hypertrophic lakes changes in the biological structure can be very rapid, and more or less dramatic collapses in phytoplankton biomass have been reported from many lakes (Barica, 1975; Fott *et al.*, 1980). These changes affect the chemical structure in the lake water, but it is an open question to what extent these collapses can affect the internal loading.

This paper describes collapses in phytoplankton biomass and changes in nutrient cycling that take place every summer in the shallow and hypertrophic Lake Søbygård, Denmark. The aim was to determine the impact of these changes on the interaction between sediment and water, especially concerning nitrogen and phosphorus dynamics. A related paper (Jeppesen *et al.*, 1989) discusses the biological interactions and factors controlling the collapses. The collapse observed in 1985 is used as a basis, supported by observations from 1986 and 1987.

Study area

Lake Søbygård is a small (0.39 km^2) and shallow (max. depth 1.9 m, mean depth 1.0 m) lake situated in the central part of Jutland, Denmark (9° 48′ E, 56° 15′ N) (see also Søndergaard *et al.*, 1987). Water residence time is 15 to 30 days, and one main inlet contributes 70–80% of the total water input. The remaining water comes from springs around the lake.

For several decades Lake Søbygård received large quantities of poorly treated municipal wastewater. Since 1976, however, the wastewater has been biological treated, and in 1982 a chemical treatment was introduced to reduce the input of phosphorus. The external phosphorus loading thereby decreased from about 30 to 5 g P m^{-2} year^{-1}. Correspondingly, phosphorus retention in the lake changed from highly positive to negative. Therefore, the internal phosphorus loading today accounts for about ⅔ of the total phosphorus loading. Measurements have revealed a large pool of phosphorus in the sediment, high enough to support an internal phosphorus loading for many years (Søndergaard *et al.*, 1987; Søndergaard, 1988). Phosphorus concentrations in the upper 15 cm of the sediment vary from 6 to 12 mg P g dw^{-1}. A major part of this phosphorus is bound to iron (extractable with NH_4Cl or NaOH).

Due to the high nutrient loading the lake is hypertrophic. Primary production is up to 1500 g C m^{-2} year^{-1}, and Secchi transparency <0.5 m most of the summer. Phytoplankton is dominated by diatoms during spring maxima, and by coccal green algae in summer and autumn. Cryptophytes are occasionally of importance (see Jeppesen *et al.*, 1989). The lake water is well-mixed, without any vertical or horizontal stratification. Because of its shallowness, wind action often induces resuspension of sediment which occasionally causes a considerable increase in lake water concentrations of nutrients and suspended matter (Jensen & Kristensen, 1986; Søndergaard *et al.*, 1987).

Rapid changes in phytoplankton biomass have not only been recorded in 1985 to 1987 as described in this paper, but also in the summers 1983 and 1984 (Andreasen *et al.*, 1984; Jeppesen *et al.*, 1989).

Methods

Concentrations of total phosphorus (tot-P), soluble reactive phosphorus (PO_4-P), total nitrogen (tot-N), and nitrite + nitrate (NO_{2+3}-N) have been monitored intensively during 1985–1987 in the main inlet, lake centre and in the outlet. Sampling frequency was 1–3 times a week. In periods with rapid changes samples were taken every day in the lake and every 4 hours in the outlet. Inlet and outlet water was collected by automatic sampler emptied every 1–4 days. The outlet concentrations were generally not different from those in the lake.

Orthophosphate was determined by the ascorbic acid-molybdenum blue method according to Murphy & Riley (1972), and total phosphorus as orthophosphate after persulphate digestion in an autoclave at 200 kPa for 30 min according to Koroleff (1970). Ammonium (NH_4-N) was determined by the phenol hypochlorite method according to Dansk Standard (1975) modified from Solórzano (1969), and nitrite + nitrate spectrophotometrically after reduction according to Dansk Standard (1975) and Dahl (1974). Usually nitrite concentrations are negligible compared to nitrate concentrations. Total nitrogen was measured as NO_{2+3}-N after potassium persulphate digestion according to Dansk Standard (1975) and Solorzano & Sharp (1980). Oxygen was measured continuously at 0.1 m depth using an oxygen probe. The probe was calibrated automatically once a day (Sortkjær & Jeppesen, 1987). Chlorophyll *a* was determined spectrophotometrically after extraction with ethanol according to Dansk Standard (1975) and Holm-Hansen & Riemann (1978).

Results

As described by Jeppesen *et al.* (1989), the collapses in phytoplankton biomass did not follow the same pattern from year to year. Furthermore, the collapses could be divided into different steps including a pre-clear-water period. The following results, however, focuse mainly on changes in nutrient concentrations during and shortly after a phytoplankton collapse.

In 1985 the variation during summer in the chemical and biological parameters of Lake Søbygård was especially characterized by one event. From the beginning of July to 20 July phytoplankton biomass, measured as chlorophyll *a*, decreased rapidly from about 800 to <50 μg chl-*a* l^{-1}. The decrease occurred in two steps, and most rapidly from 15 July, reaching a minimum of 12 μg chl-*a* l^{-1} on 23 July (Fig. 1). This clear-water period lasted for 3–5 days, after which the phytoplankton biomass returned to the original level.

Due to low primary production, but probably sustained respiration at the sediment/water interface, oxygen concentrations in the lake water decreased from a hypersaturated level of about 20 mg O_2 l^{-1} to 1 mg O_2 l^{-1} at the end of the clear-water period (Fig. 1). Lake water temperature during the clear-water period was between 17 and 19 °C.

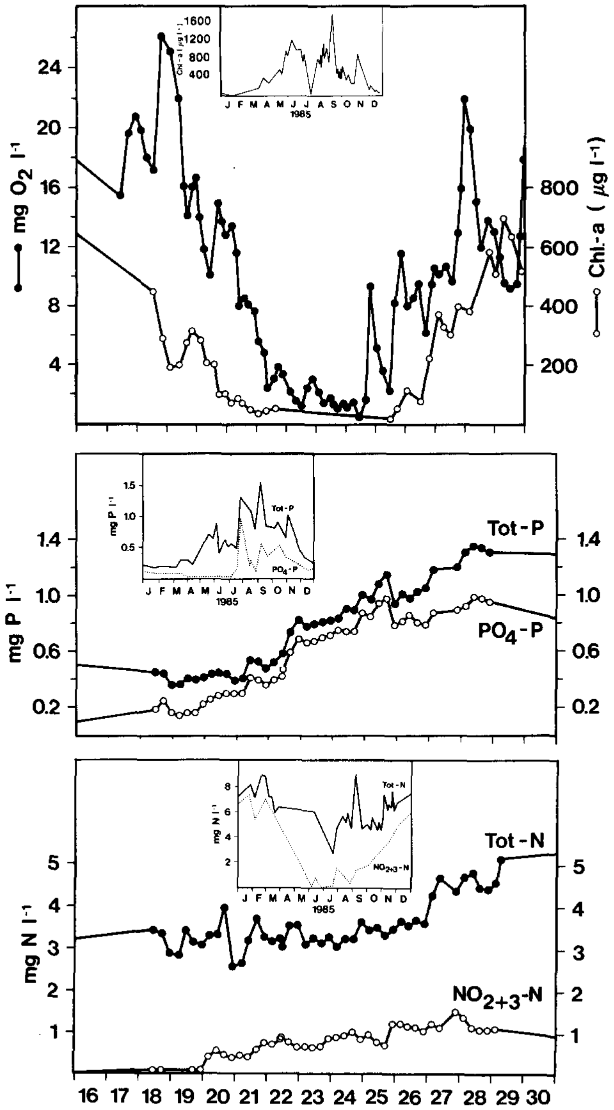

Fig. 1. Phytoplankton collapse from 18 to 30 July 1985. Upper: Chlorophyll *a* and oxygen concentrations in the outlet. Middle: Total N and NO_{2+3}-N in the outlet. Lower: Total phosphorus and PO_4-P in the outlet.

During the clear-water period both total nitrogen and nitrate increased markedly (Fig. 1). The increase in nitrate started on 20 July when the concentration of chlorophyll decreased to

<50 μg chl-*a* l^{-1}, and continued until 28 July when chlorophyll reached a level of 300–400 μg chl-*a* l^{-1} again. Apart from minor fluctuations, the increase rate of nitrate in this period was consistently about 130 mg N m^{-2} day^{-1}. External nitrogen loading during the collapse was about 350 mg N m^{-2} day^{-1} (Table 1).

At the time of the phytoplankton collapse the external input of phosphorus varied between 3.9 and 5.3 mg P m^{-2} day^{-1}, while the output of phosphorus from the lake increased from 10 to 53 mg P m^{-2} day^{-1}. This increase in net internal phosphorus loading was reflected in rapidly increasing lake-water concentrations of both orthophosphate and total phosphorus (Fig. 1). From 20 July to 28 July, orthophosphate thus increased from 0.24 to 0.96 mg P l^{-1}, and total phosphorus from 0.37 to 1.33 mg P l^{-1}. Corrected for input and output, the average net release of phosphorus from the sediment for an 8-day period during the phytoplankton collapse was 145 mg P m^{-2} day^{-1}.

Contrary to 1985, the development of phytoplankton in 1986 was characterized by several periods with rapid changes and relatively low biomass, although the phytoplankton biomass in 1986 did not reach the same low level as in 1985. The first and most complete phytoplankton collapse appeared at the end of June, followed by others in late August, September and October, respectively (Fig. 2). At the collapse in June chlorophyll *a* decreased from about 800 μg chl-*a* l^{-1} on 10 June to about 50 μg chl-*a* l^{-1} from 28 June to 1 July. Minimum biomass was reached on 29 June with 38 μg chl-*a* l^{-1}. The collapses that appeared later in the year were less marked.

Oxygen was not measured continuously during the collapse in June, but measurements indicate that oxygen concentrations may have been well below 5 mg O_2 l^{-1}. Ammonium increased at a rate of 65 mg NH_4-N m^{-2} day^{-1}. Lake water temperature during the collapse was from 22 to 24 °C.

Total nitrogen and nitrate did not increase to the same degree as during the collapse in 1985. Nitrate increased at a rate of 30 mg NO_3-N m^{-2} day^{-1} (Fig. 2). There are only few measurements of total nitrogen in this period, but at the end of the collapse total nitrogen began to increase concurrently with the increase in phytoplankton biomass. The increase-rate was about 150 mg N m^{-2} day^{-1}.

Concurrently with the decrease in phytoplankton biomass, phosphate concentrations increased from mid-June. The increase in total phosphorus did not start significantly until 28 June, when phytoplankton biomass had reached a level of 50 μg chl-*a* l^{-1}. The increase rate of both total phosphorus and phosphate was consistently about 0.20 mg P l^{-1} day^{-1} (Fig. 2). Corrected for input and output from the lake, average net release of phosphorus from the sediment in this

Table 1. Average P and N concentrations in main inlet and external P and N loadings during selected periods.

	tot-P		PO_4-P		tot-N		NO_{2+3}-N	
	mg l^{-1}	mg m^{-2} day^{-1}	mg l^{-1}	mg m^{-2} day^{-1}	mg l^{-1}	mg m^{-2} day^{-1}	mg l^{-1}	mg m^{-2} day^{-1}
1985	0.30	10.7	0.030	1.07	10.5	500	8.5	400
15–30 July	0.25	4.6	0.020	0.37	10.0	350	8.0	330
1986	0.25	12.6	0.020	1.0	9.5	440	8.5	400
24 June–4 July	0.20	4.8	0.015	0.38	10.0	250	9.5	220
1987	–	–	–	–	–	–	–	–
25 May–18 June	0.20	–	0.020	–	11.0	–	10.0	–

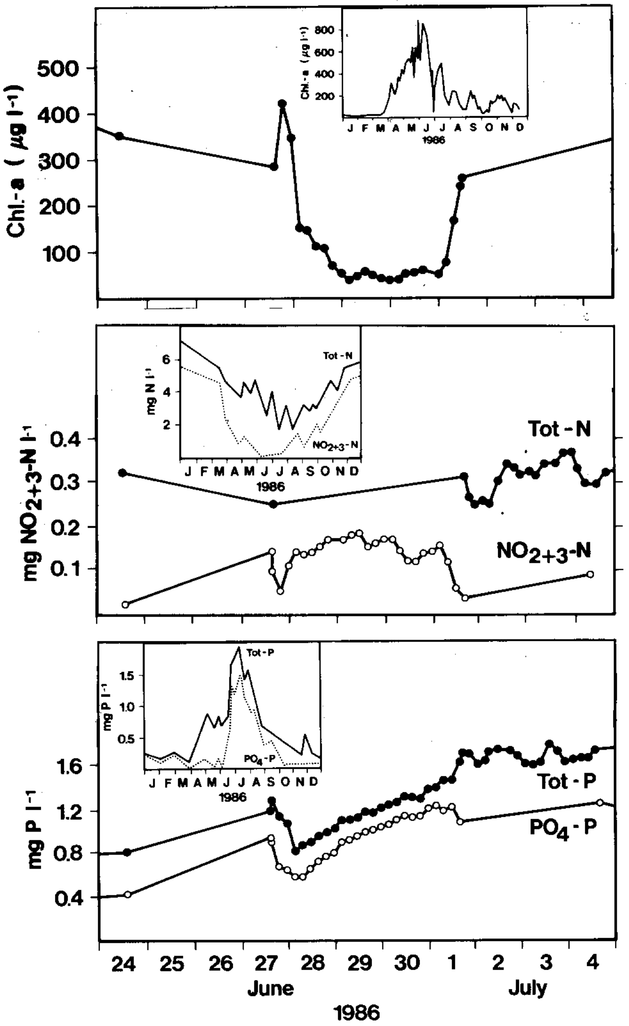

Fig. 2. Phytoplankton collapse from 24 June to 4 July 1986. Upper: Chlorophyll *a* concentrations in the outlet. Middle: Total N and NO_{2+3}-N in the outlet. Lower: Total phosphorus and PO_4-P in the outlet.

period was 240 mg P m^{-2} day^{-1}. Total phosphorus continued to increase for some time after the collapse, and remained high until mid-July.

In the first part of summer 1987 the seasonal development in phytoplankton was dominated by one major but relatively long-lasting collapse. This year it occurred already in early June, when chlorophyll *a* decreased from 430 µg chl-*a* l^{-1} on 20 May to <25 µg chl-*a* l^{-1} from 2 to 14 June (Fig. 3). Minimum concentrations of chlorophyll *a* were reached on 3 June with 3 µg chl-*a* l^{-1}, and on 11 June with only 1 µg chl-*a* l^{-1}. Lake water temperature during the collapse was from 13 to 15 °C.

Nitrate did not reach the same low concentrations before the collapse as in the previous years, probably because of the generally lower phytoplankton biomass in 1987. At the beginning of the clear-water period in late May concentrations were about 1.1 mg NO_3-N l^{-1}, but decreased to about 3.1 on 18 June (Fig. 3), corresponding to an increase rate of 90 mg NO_{2+3}-N m^{-2} day^{-1}. Total nitrogen increased at approximately the same rate. The ammonium increase rate was 75 mg NH_4-N m^{-2} day^{-1}.

Total phosphorus concentrations in lake water decreased during May until 3 June, after which the concentrations increased at a rate of 50 mg

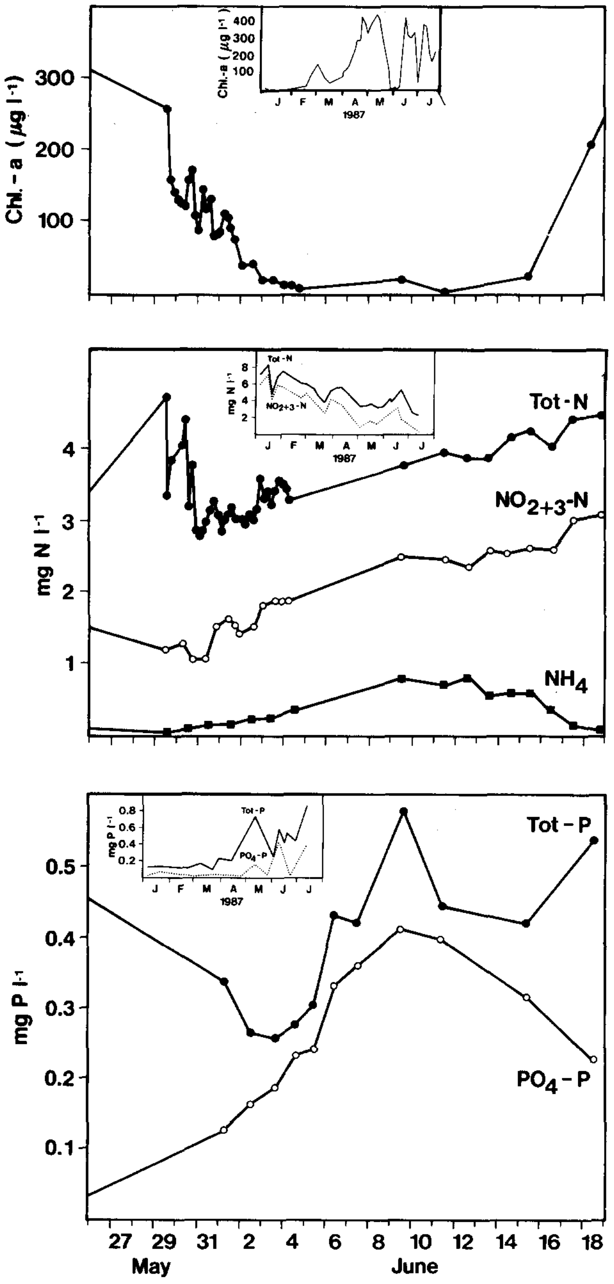

Fig. 3. Phytoplankton collapse from 26 May to 18 June 1987. Upper: Chlorophyll *a* concentrations in the outlet. Middle: Total N, NO_{2+3}-N and NH_4-N in the lake. Lower: Total P and PO_4-P in the lake.

tot-P m^{-2} day^{-1} (Fig. 3). Phosphate concentrations started to increase from 25 May, but most rapidly from 3 June at a rate of 40 mg PO_4-P m^{-2} day^{-1}.

Discussion

Marked seasonal variations in nutrient concentrations are not unusual in eutrophic lakes (Raaphorst & Brinkman, 1984; Yosida, 1982; Otsuki *et al.*, 1981). However, because of the very high nutrient level in both water and sediment, the variations in Lake Søbygård are large compared with most other lakes. This is also reflected in the rates of increase or decrease which take place in both the biological and chemical structure.

It is remarkable that the changes in phosphorus and nitrogen concentrations usually start almost exactly at or just prior to the date when phytoplankton biomass reaches its minimum – typically when chlorophyll *a* has decreased to < 100 µg chl-*a* l^{-1}. This supports the interpretation that the changes in nutrient concentration are related to the decreasing phytoplankton biomass. Average net increases of nitrogen and phosphorus during the periods of phytoplankton collapse are given in Table 2.

Increase of nitrogen:

Most of the nitrogen input to the lake, mainly in the form of nitrate, is either denitrified or incorporated as organic nitrogen in the phytoplankton. Denitrification may contribute significantly to the total removal of nitrogen in eutrophic lakes (Andersen, 1974; Kasper, 1985). Additionally, the very high primary production and nitrogen uptake by phytoplankton in Lake Søbygård, together with the shallow water, causes a high sedimentation of organic matter and thereby a removal of nitrogen from lake water to sediment. Secondarily, this sedimentation creates a potentially high consumption of oxygen and nitrate at the sediment water interface.

By use of sedimentation traps, the sedimentation of organic matter in Lake Søbygård, prior to the phytoplankton collapse in 1985, has been estimated as 4–6 g C m^{-2} day^{-1} (Kristensen & Jensen, 1987), and on average 800 mg N m^{-2} day^{-1}. Thus the external input of about 350 mg N m^{-2} day^{-1}, besides the outlet of organic nitro-

Table 2. Lake water temperature, average net increase of nitrogen and average net release of phosphorus during the collapses; in mg m^{-2} day $^{-1}$.

Period	Temp. °C	NO_{2+3}-N	tot-N	PO_4-P	tot-P
1985					
15–30 July	17–19	130	130–400	145	145
1986					
24 June–4 July	22–24	0–30	(150)	240	240
1987					
25 May–15 June	13–15	90	90	40	50

gen (average 120 mg N m^{-2} day^{-1}), is usually compensated by high rates of both denitrification and sedimentation. Depending on the denitrification rate, the recycling and release of nitrogen from the sediment must according to this mass balance be of the order of 600–800 mg N m^{-2} day^{-1}.

During the phytoplankton collapse, however, phytoplankton biomass and therefore sedimentation is low, and the nitrogen concentration in the lake water will increase due to continued input of nitrogen from both inlet and sediment. The increase of nitrogen in 1985 during the collapse was mainly due to an increase of nitrate. The increase rate of 130 mg N m^{-2} day^{-1} must be due to the input of nitrate from the inlet which is not further taken up by phytoplankton, and/or a nitrification of ammonium released from the sediment. Unfortunately, we have no measurements of ammonium in this period, but according to the sequence in following years there must have been a marked increase of ammonium concentration during the collapse. The start of the increase of nitrate about 20 July corresponds very well to the time when phytoplankton and thereby sedimentation reached very low levels. Problems concerning release rates of nitrogen from the sediment, nitrification and denitrification activities during the collapse are, however, not yet completely elucidated.

The enhanced increase rate of total nitrogen at the end of the collapse in 1985 may partly be explained by the development of anoxic conditions in the beginning of the clear-water period. Anoxia may shift a major part of the respiration at the sediment surface from using oxygen to using nitrate. Correspondingly, denitrification is increased. At the end of the collapse, however, when the lake water becomes oxic, part of the respiration will shift back to using oxygen, and thereby decrease the denitrification. Moreover, the increasing phytoplankton biomass at the end of the collapse with increased demand for nitrogen will tend to diminish the importance of denitrification.

The pattern of nitrogen increase in 1985 was supported by the development in both 1986 and in 1987, although the increase in those years was not as marked. Changes in temperature (Kamp-Nielsen, 1974), different phytoplankton minima and changed external nitrogen input (Table 1) may be reasons for the differences in nitrogen increase rates from year to year.

Increase of phosphorus:

The internal phosphorus loading in Lake Søbygård is usually restricted to the period from April to December. The net release of phosphorus in connection with phytoplankton collapses, and afterwards when phosphate is accumulated in the lake water, is therefore important for the overall internal phosphorus loading.

The increase in phosphorus concentration during phytoplankton collapses was very pronounced over all three years. The increase in PO_4-P usually starts before phytoplankton has reached its minimum, whereas the increase in total phosphorus does not start until the phytoplankton biomass is close to zero. This pattern reflects first a release of phosphate from decomposing phytoplankton combined with decreased phytoplankton phosphate uptake, and second an increase of total phosphorus due to decreased sedimentation of phosphorus. The same mechanism as proposed for the increase in nitrogen is thus valid also for phosphorus, although the increase in total phosphorus is solely caused by an internal loading.

The daily sedimentation of phosphorus prior to the phytoplankton collapses in 1985 has been calculated as 125 mg P m^{-2} (Kristensen & Jensen, 1987). During the collapse input from the inlet and output through the outlet have been calculated as respectively 4 and 17 mg P m^{-2} day^{-1}. If the gross release rate of phosphorus during the collapse is unchanged, and water concentration is corrected for in- and output, this means that in the absence of sedimentation of organic phosphorus the increase of phosphorus concentration in the lake water would be 130 μg P l^{-1} day^{-1}. This increase rate fits well the one actually observed. Therefore, during phytoplankton collapse the net release or increase of phosphorus approaches the gross release rate. Accordingly, the occurrence of phytoplankton collapses provides an excellent opportunity to study gross release rates of phosphorus in a natural system.

The net release rates or approximated gross release rates recorded in 1985 to 1987 during collapses varied from 50 to 240 mg P m^{-2} day^{-1}. These are very high rates compared to values from other lakes (e.g. Stevens & Gibson, 1977; Boström *et al.*, 1982), but are supported both by the measured sedimentation rates (Kristensen & Jensen, 1987) and by experiments with undisturbed sediment cores in the laboratory (Søndergaard, 1987; Søndergaard, 1989). The reason for the very high release rates is probably the unusually high phosphorus concentrations in the sediment, which create a potentially high release rate. Environmental conditions, such as a high decomposition rate due to a large sedimentation, frequent occurrence of resuspension, and a high proportion of iron-bound phosphorus sensitive to changes in redox potential and pH, are regarded as major factors causing the release (Søndergaard, 1988; Søndergaard, 1989).

The large variations in the release rates from year to year (Table 2) might partly be caused by the different temperature levels. Temperature can have a major effect on the release rate of phosphorus (Kamp-Nielsen, 1975; Lee, 1977; Kelderman & Van der Repe, 1982; Psenner, 1984). Above 15 °C Kamp-Nielsen (1975) found that an increase in temperature by 5 °C would lead to a doubling or more in the release rate of phosphorus. This strong temperature-dependence is comparable to Lake Søbygård in the temperature range 14-18 °C, although not 18–22 °C where the increase in release rate is less pronounced. The temperature-dependent release of phosphorus in Lake Søbygård signifies that a relatively large proportion of the net primary production in this shallow lake is decomposed in the sediment, and not in the lake water. This decomposition is very temperature-dependent, and if the release of phosphorus, as proposed by several authors (Lee, 1977; Psenner, 1984), is strongly affected by microbial and benthic activity, this might explain the temperature-dependent release. The temperature-dependence has been supported by experiments with undisturbed sediment cores (Søndergaard, 1987; Søndergaard, 1989). In these experiments the average release rate was determined to 20–30 mg P m^{-2} day^{-1} at 10 °C dependent on, e.g., pH, and to 130 mg P m^{-2} day^{-1} at 20 °C.

Besides the decreased sedimentation of phosphorus during the collapses, the low oxygen concentrations could promote a redox dependent release of phosphorus (Boström *et al.*, 1982). However, there are no indications that gross phosphorus release is enhanced during phytoplankton collapse. The increased net release seems solely to be a matter of reduced sedimentation.

To summarize, rapid changes of phytoplankton biomass occur more or less dramatically every summer in the shallow and hypertrophic Lake Søbygård. These changes lead to considerable changes also in the chemical structure mainly because of reduced sedimentation of organic nitrogen and phosphorus.

Nitrogen concentrations increase during the phytoplankton collapse because of decreased sedimentation of organic N but continuing high input of N from the inlet and sediment. The recycling of nitrogen between sediment and water is very important for the overall nitrogen pathway.

Usually gross release of phosphorus is several times greater than the net release, only counterbalanced by a large sedimentation. During a collapse, however, phosphorus sedimentation is reduced to near zero, and net release of phosphorus will be close to the gross release rate. The release rate of phosphorus seems to be temperature-dependent.

Thus lake water nitrogen and phosphorus concentrations during phytoplankton collapse are changed from being dominated by both a large sedimentation (output) and a large input (N from the inlet and sediment, and P from the sediment) to being dominated by only a large input of nutrients.

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References

Andersen, J. M., 1974. Nitrogen and phosphorus budgets and the role of sediment in six shallow Danish lakes. Arch. Hydrobiol. 74: 259–277.

Andreasen, K., M. Søndergaard & H. H. Schierup, 1984. En karakteristik af forureningstilstanden i Søbygård Sø – samt en undersøgelse af forskellige restaureringsmetoders anvendelighed til en begrænsning af den interne belastning. Publication No. 7 from The Botanical Institute, University of Århus, Denmark: 164 pp (in Danish).

Barica, J., 1975. Collapses of algal blooms in prairie pothole lakes: their mechanism and ecological impact. Verh. int. Ver. Limnol. 19: 606–615.

Bengtsson, L., S. Fleischer, G. Lindmark & W. Ripl, 1975. Lake Trummen restoration project I. Water and sediment chemistry. Verh. int. Ver. Limnol. 19: 1080–1087.

Boström, B., M. Jansen & C. Forsberg, 1982. Phosphorus release from sediments. Arch. Hydrobiol. Beih. Ergebn. Limnol. 18: 5–59.

Dahl, I., 1974. Intercalibrations of methods for chemical analysis of water. V. Results from intercalibrations of methods for determining nitrate and total nitrogen. Vatten 30: 180–186.

Dansk Standard, 1975. Vandundersøgelse. Dansk Standardiseringsråd, København (in Danish).

Fott, J., L. Pechar & M. Prazaková, 1980. Fish as a factor controlling water quality in ponds. In J. Barica & L. R. Mur (eds.): Hypertrophic ecosystems. Developments in Hydrobiology 2: 255–261.

Holdren, G. C. & D. Armstrong, 1980. Factors affecting phosphorus release from intact sediment cores. Envir. Sci. Technol. 14: 79–86.

Holm-Hansen, D. & B. Riemann, 1978. Chlorophyll *a* determination: improvements in methods. Oikos 30: 438–447.

Jacoby, J. M., D. D. Lynch, E. B. Welch & M. A. Perkins, 1982. Internal phosphorus loading in a shallow eutrophic lake. Wat. Res. 16: 911–919.

Jensen, P. & P. Kristensen, 1986. Sedimentation and resuspension measured by use of sedimentation traps. In: Physical processes in Lakes (ed. J. Virta), NHP-Report 16: 108–112.

Jeppesen, E., M. Søndergaard, O. Sortkjær, E. Mortensen & P. Kristensen, 1989. Interactions between phytoplankton, zooplankton and fish in a shallow, hypertrophic lake: a study on phytoplankton collapses in Lake Søbygård, Denmark. Hydrobiologia/Developments in Hydrobiology (this volume).

Kamp-Nielsen, L., 1974. Mud-water exchange of phosphate and other ions in undisturbed sediment cores and factors affecting the exchange rates. Arch. Hydrobiol. 73: 218–237.

Kamp-Nielsen, L., 1975. A kinetic approach to the aerobic sediment-water exchange of phosphorus in Lake Esrom. Ecol. Modelling 1: 153–160.

Kasper, H. F., 1985. The denitrification capacity of sediment from a hypertrophic lake. Freshwat. Biol. 15: 449–453.

Kelderman, P. & A. M. Van der Repe, 1982. Temperature dependence of sediment-water exchange in Lake Grevelingen, SW Netherlands. Hydrobiologia 92: 489–490.

Koroleff, F., 1970. Determination of total phosphorus in natural waters by means of persulphate oxidation. An Interlab. Report No. 3. Cons. int. Explor. Mer.

Kristensen, P. & P. Jensen, 1987. Sedimentation og resuspension i Søbygaard Sø. M.sc. thesis. Publ. No. 64 from The Freshwater Laboratory, The National Agency of Environmental Protection, Denmark, in cooperation with Botanical Institute, University of Århus, Denmark: 176 pp (in Danish).

Lee, G. F., 1977. Significance of oxic vs. anoxic conditions for Lake Mendota phosphorus release. In: Golterman, H. L. (ed.) Interactions between sediments and freshwater, Dr. W. Junk, B. V., The Hague: 294–306.

Lennox, L. J., 1984. Sediment-water exchange in Lough Ennell with particular reference to phosphorus. Wat. Res. 18: 1483–1485.

Murphy, J. & J. P. Riley, 1972. A modified single solution method for the determination of phosphate in natural waters. Analyt. Chim. Acta 27: 21–26.

Otsuki, A., K. Seiichi & K. Takkayoshi, 1981. Seasonal changes of the total phosphorus standing crop in a highly eutrophic lake: the importance of internal loading for shallow lake restoration.

Peterson, S. A., 1982. Lake restoration by sediment removal. Wat. Res. Bull. 18: 423–435.

Psenner, R., 1984. Phosphorus release patterns from sediments of a meromictic mesotrophic lake (Piberger See, Austria). Verh. int. Ver. Limnol. 22: 219–228.

Raaphorst, W. & A. G. Brinkman, 1984. The calculation of transport coefficients for phosphate and calcium fluxes across the sediment-water interface, from experiments with undisturbed sediment cores. Wat. Sci. Technol. 17: 941–951.

Solórzano, L., 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol. Oceanogr. 14: 799–801.

Solórzano, L. & J. H. Sharp, 1980. Determination of total dissolved nitrogen in natural waters. Limnol. Oceanogr. 25: 751–754.

Sortkjær, O. & E. Jeppesen, 1987. Hyppige feltmålinger øger forståelsen af lavvandede søers udvikling. In Annual Report 1986 from The Freshwater Laboratory, The National Agency of Environmental Protection: 21–28 (in Danish).

Stevens, R. J. & C. E. Gibson, 1977. Sediment release of phosphorus in Lough Neagh, Northern Ireland. In: Golterman, H. L. (ed.) Interactions between sediment and freshwater. Dr. W. Junk. B. V., The Hague: 343–347.

Søndergaard, M., 1987. Fosfordynamikken i lavvandede søer med udgangspunkt i Søbygård Sø. Report from The National Agency of Environmental Protection, The Freshwater Laboratory, Silkeborg, Denmark: 142 pp (in Danish).

Søndergaard, M., E. Jeppesen & O. Sortkjær, 1987. Lake Søbygård: a shallow lake in recovery after a reduction in phosphorus loading. GeoJournal 14: 381–384.

Søndergaard, M., 1988. Seasonal variations in the loosely sorbed phosphorus fraction of the sediment of a shallow and hypertrophic lake. Envir. Geol. Wat. Sci. 11: 115–121.

Søndergaard, M., 1989. Phosphorus release from a hypertrophic lake sediment: experiments with intact sediment cores in a continuous flow system. Arch. Hydrobiol. 116: 45–59.

Yosida, T., 1982. On summer peak of nutrient concentrations in lake water. Hydrobiologia 92: 571–578.