Seasonal changes of mechanisms maintaining clear water in a shallow lake with abundant *Chara* vegetation

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Abstract

The study is based on monitoring data on the seasonal variation during four (1996–1999) vegetation periods, as well as long-term summer data on submerged vegetation, nutrients, light, phytoplankton and zooplankton in Lake Krankesjön, a shallow, calcium-rich, moderately eutrophic lake in southern Sweden.

The lake has been in the clear water state with abundant submerged vegetation since the end of the 1980s. Somewhat lower summer biomass of submerged macrophytes during 1997 and 1999 indicates a temporary instability of the clear water state. During these 2 years, summer transparency was about 1.2–2.1 m, while concentrations of total phosphorus and chlorophyll (Chl) a were about 26–40 and 8–18 µg l⁻¹, respectively.

Summer biomass of submerged macrophytes was higher during 1996 and 1998. In both years, a distinct increase in light availability and decrease in concentrations of nutrients and chlorophyll occurred simultaneously with the development of dense *Chara* vegetation. Summer values for transparency were about 2.0–2.5 m, while concentrations of total phosphorus and Chl a were about 20–32 and 4–11 µg l⁻¹, respectively.

Summer biomass of crustacean zooplankton was below 250 µg l⁻¹ during all 4 years. A peak abundance of Cladocera (mainly *Bosmina longirostris*) during May or June caused only a short-term reduction in chlorophyll concentrations that was more pronounced in 1997 than in 1996.

Measured light attenuation during 1999 was closely correlated with light attenuation calculated from the amount of suspended solids, chlorophyll concentrations, and water colour. Detritus contributed most to the total amount of suspended solids, while chlorophyll was the main contributor to light attenuation.

A long-term decrease of the ratios between chlorophyll and total phosphorus suggests that phytoplankton in the clear water state is limited by factors other than total phosphorus concentrations.

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Increased sedimentation rate, carbon limitation, allelopathy and a lower bioavailable fraction of the total amount of phosphorus are possible explanations, while nitrogen limitation and grazing from zooplankton probably are of minor importance.

Possible reasons for the “instability” of the clear water state during 1997 and 1999 are discussed. Unusually high water level as well as cold and windy weather during the spring of 1996–1999 may have caused a slow and late growth of the plants and thus a temporary instability. However, a tendency for an increase in total phosphorus concentrations and sediment accumulation along the wind-protected shores during the clear water state indicate the possibility of a long-term destabilization which contradicts the alternative stable states model. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Alternative stable states; Shallow lakes; Submerged macrophytes; Charophyta; Light

1. Introduction

Shallow, moderately eutrophic lakes are suggested to occur in two alternative stable states, one characterized by high transparency and abundant submerged vegetation (clear water state), the other by low transparency and high phytoplankton densities (turbid state) (Scheffer et al., 1993; Scheffer, 1998). Light availability is a key factor for the outcome of interactions between submerged macrophytes and phytoplankton, and submerged macrophytes are able to improve their own light availability by different feedback mechanisms (Scheffer et al., 1993). Dense submerged vegetation can store a large part of the lake’s nutrient pool (Blindow, 1992; Kufel and Ozimek, 1994). Furthermore, this vegetation offers refuges to zooplankton like *Daphnia* spp. (e.g. Lauridsen and Buenk, 1996) which has been suggested to be an important mechanism for the maintenance of the clear water state in shallow lakes (Timms and Moss, 1984). Thus, submerged macrophytes can reduce phytoplankton biomass by both bottom-up and top-down mechanisms.

Physical mechanisms such as the inhibition of sediment resuspension by submerged macrophytes have also been suggested to be important for the maintenance of the clear water state in shallow lakes (Scheffer et al., 1993). Numerous studies have shown that sediment resuspension is one of the major factors influencing turbidity and thus light availability in shallow, wind-exposed lakes (e.g. Jónasson and Adalsteinsson, 1979; Bengtsson et al., 1990; Hamilton and Mitchell, 1996). Decreased sediment resuspension was suggested to be the cause for increases in water transparency observed after expansion of submerged macrophytes (Hanson and Butler, 1994). Recently, the reduction of wind-induced turbidity in the presence of submerged macrophytes has been statistically proven (Hamilton and Mitchell, 1996).

Lake Krankesjön (55°42′N, 13°28′E), a 2.9 km² shallow (mean depth 1.5 m, maximum depth 3.0 m), moderately eutrophic lake in southern Sweden (Table 1) switched from a turbid to a clear water state during the mid-1980s when submerged macrophytes started to expand. *Potamogeton pectinatus* L. was dominant during the first years but was later replaced by charophytes (Blindow et al., 1993; Hargeby et al., 1994). This paper focuses on the feedback mechanisms which stabilize the clear water state with dominance of charophytes. Thereby, we combine long-term monitoring data (1985–1999) with a more intensive field study
Table 1
Chemical characteristics of Lake Krankesjön

<table>
<thead>
<tr>
<th>Period</th>
<th>Tot-P (μg l⁻¹)</th>
<th>Tot-N (μg l⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1985–1987</td>
<td>54 ± 4 (19)</td>
<td>1500 ± 100 (12)</td>
</tr>
<tr>
<td>1988–1997</td>
<td>29 ± 1 (48)</td>
<td>1200 ± 100 (15)</td>
</tr>
</tbody>
</table>

*a Nutrient concentrations (total phosphorus: Tot-P and total nitrogen: Tot-N) are shown for both the turbid state (1985–1987) and the clear water state (1988–1997). Summer (June to September) mean values ± S.E. are given for nutrient concentrations. Numbers of observations are given in brackets.

(1996–1999) in order to discuss possible mechanisms that maintain the clear water state as well as possible reasons for a shift.

2. Material and methods

2.1. Sampling and analysis procedures

For the documentation of the long-term trends, the distribution of submerged vegetation was estimated by mapping from boat during July or August once a year since 1984 as well as from aerial photographs (available for several years). Plant biomass was determined by means of a steel or sharpened plexiglass core. Within the dense and homogeneous stands of charophytes (mainly *Chara tomentosa* L.), a small core (diameter 10 cm) was used. Within the sparse and more scattered stands of vascular plants (mainly *P. pectinatus*) larger tubes (diameter 10–75 cm) were used. Enclosed plants were collected and weighed. Average biomass was calculated for each plant species out of a larger number of samples taken. Values for biomass and distribution were combined to calculate the average biomass of submerged macrophytes per lake area.

For the documentation of seasonal variation, biomass measurements of submerged macrophytes were restricted to the dominant species, *C. tomentosa*. Five replicate samples per occasion were taken with a plexiglass core (diameter 71 mm) in a dense meadow of this species situated about 300 m south of the deepest part of the lake during 1996, 1997 and 1999. In 1999, samples taken during the beginning of the vegetation period have been omitted due to a drawback of the vegetation from the previous sampling site. Only maximum biomass values obtained from the centre of the *Chara* meadow are thus given for this year. The samples were sieved (mesh size 2 mm) and kept frozen until dry and ash-free dry weight were determined after drying at 105 °C (24 h) and ignition at 525 °C (1–2 h).

Water samples (0–2 m) for chemistry, suspended material and plankton were taken in the deepest part of the lake (3 m) with a 2 m plexiglass tube about once a month (June to September) during 1985–1995, but more frequently during 1996–1999. Samples taken for nutrient analysis were preserved with HgCl₂ (1985–1997) or frozen (1998 and 1999). Thereby, samples for analysis of nitrate nitrogen were filtered (GF/C) prior to freezing. The nutrient concentrations obtained did not differ between these two preservation treatments. All nutrient analyses were performed on an autoanalyzer according to standard procedures. Total nitrogen was calculated as the sum of Kjeldahl and nitrate nitrogen.
For the analysis of chlorophyll (Chl) a, a known volume of water was filtered through a GF/C filter. The filter was kept dark and frozen until analysis after extraction with methanol (Marker et al., 1980). Dry weight of phytoplankton was calculated assuming a C:Chl a ratio of 30 and a DW:C ratio of 2.2 (Jeppesen et al., 1994).

For the analysis of zooplankton, a known volume of water was filtered through a 45 μm filter and preserved with formaldehyde (4%). Filtering microcrustacean zooplankton were determined, counted and measured under an inverted microscope. Biomass was calculated using formulae given by Dumont et al. (1975) and McCauley (1984). Crustacean potential filtering rate and grazing pressure on phytoplankton were calculated according to Jeppesen et al. (1994), assuming that copepods and cladocerans ingest 50 and 100% of their biomass per day, respectively.

Suspended material was determined only in 1999. A known volume of lake water was filtered through a preweighed GF/C filter. The filter was kept dark and frozen. The amount of suspended material was determined after drying for 4 h at 105 °C (dry weight) and ignition for 1 h at 525 °C (ash weight). The amount of detritus was calculated as the difference between measured ash-free dry weight and phytoplankton dry weight.

Transparency was measured as Secchi depth in the deepest part of the lake (3 m). Light was measured at 0 and 40 cm depth during 1996 and 1999 with a photometer (LI-COR and Windaus) over the deepest part of the lake. Out of three replicate measurements, the vertical light attenuation (E) was obtained out of the slope of the log-transformed light measurements. Calculated values for E were obtained using the formula for “combined field data” (Scheffer, 1998, Table 2) which had been modified for Swedish lakes (unpublished results) keeping the background value (0.70) given in this formula, but adding a constant for water colour

\[ E_{\text{cal}} = 0.70 + [0.022 \times \text{Chl}] + [0.029 \times \text{Det}] + [0.030 \times \text{Iss}] + [14 \times \text{colour}] \]

where Chl is the concentration of chlorophyll a (μg l\(^{-1}\)); Det is amount of detritus (mg l\(^{-1}\)); Iss is amount of inorganic suspended solids (mg l\(^{-1}\)); color is the water colour (absorbance at 420 nm, 5 cm cuvette, GF/C filtered lake water).

The contribution of different seston fractions (inorganic material, detritus, phytoplankton) to the vertical light attenuation was calculated according to the same formula.

Table 2
Wind velocities measured at Hörby and air temperature at Lund, 20 km NE and 17 km W of Lake Krankesjön, respectively*

<table>
<thead>
<tr>
<th>Month</th>
<th>Wind velocity (m s(^{-1}))</th>
<th>Temperature (°C)</th>
<th>Mean 1961–1990</th>
</tr>
</thead>
<tbody>
<tr>
<td>April</td>
<td>3.3 3.8 3.9 3.6</td>
<td>7.8 5.6 7.3 8.2</td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>3.5 3.5 3.6 3.0</td>
<td>9.7 10.3 12.9 11.2</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>2.4 3.3 3.0 2.7</td>
<td>14.7 15.9 14.9 15.2</td>
<td></td>
</tr>
<tr>
<td>July</td>
<td>3.0 2.7 2.9 2.7</td>
<td>15.7 18.4 15.6 18.9</td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>3.5 2.8 3.0 2.6</td>
<td>18.6 20.9 15.3 17.3</td>
<td></td>
</tr>
</tbody>
</table>

* Wind velocities are monthly mean values calculated from two daily measurements (00.00 and 12.00 p.m. UTC). Temperature values are monthly mean values. Data are obtained from the Swedish Meteorological and Hydrological Institute (SMHI).
3. Results

3.1. Long-term trends

Both biomass and distribution of submerged macrophytes increased between 1985 and 1989, remained relatively constant between 1990 and 1998, but decreased considerably during 1999 (Fig. 1). After 1989, charophytes were dominant among submerged macrophytes regarding biomass and distribution. Between 1990 and 1998, they formed dense beds covering about 50% of the bottom area of the lake outside the reed belts. During 1995–1998, *C. hispida* L. and *C. rudis* v. Leonh. expanded and were as common as *C. tomentosa* during 1999. All three species are perennial and hibernate as green plants (Blindow, 1992, unpublished data).

Summer (June to September) values of transparency increased from about 50 cm during 1985–1987 to about 150–250 cm during 1989–1999. Summer concentrations of chlorophyll decreased simultaneously from about 20–30 to about 10 μg l⁻¹.

During the same period, summer concentrations of total phosphorus decreased from 50–70 to about 20–30 μg l⁻¹ (Fig. 2). There was a tendency for concentrations to increase between 1990 and 1999 (Spearman rank, $R_S = 0.64$, $P = 0.056$, $n = 10$). Total nitrogen decreased from about 1400–1800 μg l⁻¹ during 1985–1987 to about 1000–1200 μg l⁻¹ during 1988–1999. Ratios between chlorophyll and total phosphorus were around 0.40–0.49.

Fig. 1. Distribution (A) and biomass (B) of submerged macrophytes in Lake Krankesjön during 1984–1999. Dark hatched area: Charophyta. Grey areas: vascular plants. Transparency (C) and chlorophyll *a* concentrations (D) in Lake Krankesjön during 1985–1999. Mean summer (June to September) values ± S.E. are shown.
Fig. 2. Total phosphorus (A), total nitrogen (B), N/P ratio (C) and ratio of chlorophyll a and total phosphorus (D) in Lake Kranksjön during 1985–1999. Mean summer (June to September) values ± S.E. are given.
between 1985 and 1990, decreased to values around 0.20–0.33 during 1991–1998 and increased to about 0.35 during 1999. The decrease between 1985 and 1999 is significant (Spearman rank, $R_S = -0.73$, $P = 0.0087$, $n = 13$).

3.2. Seasonal development

3.2.1. Weather conditions and water level during 1996–1999

Mean wind velocities during April to June were somewhat higher in 1997 and 1998 compared to 1996 and 1999 (Table 2). Major deviations from long-term average temperature values occurred during all 4 years. Thus, April temperatures were 1.8, 1.3 and 2.2 °C higher during 1996, 1997 and 1999, respectively. May mean temperatures were 1.7 and 1.1 °C lower during 1996 and 1997, respectively, and 1.5 °C higher during 1998. June temperatures did not differ from long-term average values for any of the 4 years. July temperatures were about 1.1 °C lower during 1996 and 1.6 and 2.1 °C higher during 1997 and 1999, respectively. August temperatures were about 2.1 and 4.4 °C higher during 1996 and 1997, respectively, and 1.2 °C lower during 1998.

During all of the years 1996–1999, the water level during May to June was between 5 and 15 cm higher compared to the average water level during 1985–1994 (Fig. 3).

3.2.2. Plant biomass

Both in 1996 and 1997, *C. tomentosa* biomass started to increase during the end of May/beginning of June (Fig. 4). In 1996, the plants reached maximum biomass values
of about 700–800 g d.w. m\(^{-2}\) during July and August. In 1997, biomass values fluctuated during the spring probably because of patchy distribution of the vegetation at the sampling site. The maximum biomass was lower (around 550 g d.w. m\(^{-2}\)) compared to 1996. In 1999, *C. tomentosa* reached a maximum biomass of about 375 ± 243 g d.w. m\(^{-2}\) (mean ± S.E.) during August.

During 1996, plant biomass was significantly correlated with transparency, and there was a tendency for negative correlations with concentrations of total phosphorus as well as chlorophyll in the water column (Table 3). During 1997, no such correlations were found.

### 3.2.3. Physico-chemical variables

In 1996, the transparency increased from 120 and 125 cm during April to the beginning of May to 165–270 cm during June to September (Fig. 5). Concentrations of chlorophyll

<table>
<thead>
<tr>
<th></th>
<th>Secchi depth</th>
<th>Total phosphorus</th>
<th>Chlorophyll</th>
</tr>
</thead>
<tbody>
<tr>
<td>1996</td>
<td>0.64 (9)**</td>
<td>0.43 (9)*</td>
<td>0.40 (9) ns</td>
</tr>
<tr>
<td>1997</td>
<td>0.01 (14) ns</td>
<td>0.02 (14) ns</td>
<td>0.06 (14) ns</td>
</tr>
</tbody>
</table>

\* Numbers of observations are given in brackets. Significance of regression denoted as \** P < 0.01, * P < 0.05, ns: not significant.
increased to 15 μg l⁻¹ during mid-June and dropped again to lower concentrations (4–10 μg l⁻¹) which were maintained throughout the summer. Total phosphorus, total nitrogen and zooplankton filtering rate explained 64, 0 and 0%, respectively, of the variation in chlorophyll concentrations (Table 4). Values for total phosphorus decreased from

22 μg l⁻¹ at the end of April to about 4 μg l⁻¹ during the end of May, increased to 15 μg l⁻¹ during mid-June and dropped again to lower concentrations (4–10 μg l⁻¹) which were maintained throughout the summer. Total phosphorus, total nitrogen and zooplankton filtering rate explained 64, 0 and 0%, respectively, of the variation in chlorophyll concentrations (Table 4). Values for total phosphorus decreased from
Table 4

$R^2$ values for simple regressions between concentrations of chlorophyll $a$ and concentrations of total phosphorus, concentrations of total nitrogen (positive correlations), and zooplankton filtering rate, respectively (negative correlations), as well as maximum grazing pressure (daily filtering rate as percentage of phytoplankton biomass) during 1996 through 1999$^a$

<table>
<thead>
<tr>
<th>Year</th>
<th>Total phosphorus</th>
<th>Total nitrogen</th>
<th>Filtering rate</th>
<th>Max. grazing press.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1996</td>
<td>0.64 (13)$^{**}$</td>
<td>0.00 (10) ns</td>
<td>0.00 (13) ns</td>
<td>160</td>
</tr>
<tr>
<td>1997</td>
<td>0.37 (15)$^*$</td>
<td>0.11 (15) ns</td>
<td>0.08 (15) ns</td>
<td>540</td>
</tr>
<tr>
<td>1998</td>
<td>0.39 (7) ns</td>
<td>0.79 (6)$^*$</td>
<td>0.01 (7) ns</td>
<td>38</td>
</tr>
<tr>
<td>1999</td>
<td>0.75 (11)$^{***}$</td>
<td>0.07 (11) ns</td>
<td>0.40 (11)$^*$</td>
<td>25</td>
</tr>
</tbody>
</table>

$^a$Numbers of observations are given in brackets. Significance of regression denoted as $^{***}P<0.001$, $^{**}P<0.01$, $^*P<0.05$, ns: not significant.

38 $\mu$g l$^{-1}$ during April to 23–32 $\mu$g l$^{-1}$ during the summer. Concentrations of total nitrogen decreased from 1250 to 920–1100 $\mu$g l$^{-1}$. The N/P ratio decreased from 52 to 34–40 during the summer. The chlorophyll/total phosphorus ratio varied from 0.16 to 0.58. The lowest values were obtained during end of May to end of June, the highest value during April.

In 1997, transparency varied between 110 and 170 cm during the beginning of the vegetation period and was thus comparable to 1996. Apart from two occasions, however, summer transparency varied between 120 and 210 cm and was thus lower than during 1996 (Fig. 5). Summer chlorophyll concentrations were higher (8–15 $\mu$g l$^{-1}$) than during 1996. A rapid decline occurred in the beginning of the vegetation period from 23 and 31 $\mu$g l$^{-1}$ during March to beginning of May to 4–10 $\mu$g l$^{-1}$ during mid-May to June. Total phosphorus, total nitrogen and zooplankton filtering rate explained 37, 11 and 8%, respectively, of the variation in chlorophyll concentrations (Table 4). Total phosphorus concentrations decreased from 35 to 40 $\mu$g l$^{-1}$ during March to May to 26–40 $\mu$g l$^{-1}$ during the summer. Concentrations of total nitrogen decreased from 1800 to 900 $\mu$g l$^{-1}$. The N/P ratio increased from 24 and 50. The chlorophyll/total phosphorus ratio was highest (0.6) during April.

In 1998, the transparency increased from 180 cm in April to 190–270 cm during May to September (Fig. 6). Summer concentrations of chlorophyll were about 4–11 $\mu$g l$^{-1}$, summer concentrations of total phosphorus about 23–34 $\mu$g l$^{-1}$. Total phosphorus, total nitrogen and zooplankton filtering rate explained 39, 79 and 1, respectively, of the variation in chlorophyll concentrations (Table 4). Concentrations of total nitrogen remained relatively constant (1000–1300 $\mu$g l$^{-1}$) throughout the season. The N/P ratio increased from 26 to 47 during the summer. The chlorophyll/total phosphorus ratio was highest (0.6) during April. Lower values (0.15–0.3) were obtained during May to September.

In 1999, the transparency was 100–125 cm during April and May, increased to 180–250 cm in June and decreased to 165–190 cm during July to September (Fig. 6). Chlorophyll concentrations had their minimum value (8–9 $\mu$g l$^{-1}$) during June after high values (55 $\mu$g l$^{-1}$) during April. Concentrations of total phosphorus were higher (about 60 $\mu$g l$^{-1}$) than during the years before during the beginning of the season, but decreased to summer values of about
30–40 μg l⁻¹. Total nitrogen concentrations were relatively constant (900–1400 μg l⁻¹) throughout the season. Total phosphorus and zooplankton filtering rate explained 75 and 40%, respectively, of the variation in chlorophyll concentrations (Table 4). The chlorophyll/total phosphorus ratio decreased rapidly from 0.9 in April to 0.3–0.5 during June to September.
Fig. 7. Biomass and composition of microcrustacean zooplankton in the open water of Lake Kranksjön during 1996–1999.
3.2.4. Zooplankton

During 1996, biomass of Cyclopoida reached a peak (about 970 μg d.w. l\(^{-1}\)) during the end of April to the beginning of May, while Cladocera reached their maximum biomass (about 720 μg l\(^{-1}\)) during beginning of June due to a mass occurrence of *Bosmina longirostris*, *Ceriodaphnia quadrangula*, chydorids, *Alona* spp., *Sida crystallina*, *Diaphanosoma brachyurum* and Calanoida occurred in low abundances (Fig. 7).

During 1997, biomass of Cyclopoida was lower and never exceeded 260 μg l\(^{-1}\), while biomass of Cladocera reached high values (1050–1570 μg l\(^{-1}\)) during mid-May to beginning of June due to a mass development of *B. longirostris*. *Daphnia* spp., *C. quadrangula*, chydorids, *S. crystallina*, *D. brachyurum* and Calanoida were found in low abundances.

During 1998, biomass of both Cyclopoida and *B. longirostris* reached a peak during mid-May (about 330 and 160 μg l\(^{-1}\), respectively). Compared to 1996 and 1997, Calanoida reached higher biomass of up to 115 μg l\(^{-1}\). *C. quadrangula*, chydorids and *D. brachyurum* occurred in low abundances.

Cyclopoida reached a peak during April and beginning of May of 1999 (about 360–370 μg l\(^{-1}\)), while *B. longirostris* reached its peak abundance during mid-May (155 μg l\(^{-1}\)). At the same time, biomass of Cyclopoida and Calanoida also were high (220 and 125 μg l\(^{-1}\), respectively). *C. quadrangula*, *D. brachyurum* and phytoplankton occurred in low abundances.

3.2.5. Light and suspended material

In 1996, measured light attenuation decreased from about 1.8 m\(^{-1}\) during April and May to about 1.2–1.4 m\(^{-1}\) from beginning of June to July (Fig. 8). In 1999, measured light attenuation decreased from about 3 m\(^{-1}\) during April to about 1.7–2.3 m\(^{-1}\) during July and September. Calculated light attenuation was close to the measured values apart from one occasion (5 July).

The total amount of suspended material during 1999 decreased from about 11 mg d.w. l\(^{-1}\) during April to 3–4 mg d.w. l\(^{-1}\) during June and increased again to values around 4–6 mg d.w. l\(^{-1}\) during the summer (Fig. 9). Detritus represented the largest seston fraction, while inorganic material contributed to around 15–30% and phytoplankton to around 10–30%. Phytoplankton, however, contributed most of the different seston fractions to light attenuation.

During 1999, measured light attenuation was significantly correlated to both concentrations of chlorophyll and amount of suspended material (Table 5). Concentrations of

<table>
<thead>
<tr>
<th>Table 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>( R^2 ) values for simple regressions between different variables in Lake Krankesjön during 1999 (all positive correlations)*</td>
</tr>
<tr>
<td>Chlorophyll (a)-inorganic s.s.</td>
</tr>
<tr>
<td>( E )-chlorophyll (a)</td>
</tr>
<tr>
<td>( E)-total s.s.</td>
</tr>
<tr>
<td>Total phosphorus–total s.s.</td>
</tr>
<tr>
<td>Total nitrogen–total s.s.</td>
</tr>
</tbody>
</table>

*Numbers of observations are given in brackets. \( E \) = light attenuation (m\(^{-1}\)), s.s. = suspended material. Significance of regression denoted as ** \( P < 0.001 \), ns: not significant.
Fig. 8. Measured light attenuation \((E, \text{m}^{-1})\) in Lake Krankesjön during 1996 (A). Measured light attenuation \((E, \text{filled symbols})\) and calculated light attenuation \((E_{\text{cal}}, \text{open symbols})\) in Lake Krankesjön during 1999 (B).
Fig. 9. Amount and composition of seston (A) and contribution of the different seston fractions to the vertical light attenuation (B) in Lake Krankesjön during 1999.
chlorophyll correlated well to the amount of inorganic suspended material. The amount of suspended material was significantly correlated with total phosphorus, but not nitrogen.

4. Discussion

The development of dense submerged vegetation in Lake Krankesjön is closely related to changes in chemical, physical and biological variables. This has earlier been shown both from the development during the shift from turbid to clear water state (Blindow et al., 1993, 2000a) and is now shown also for the seasonal development of the plants. While 1996 and 1998 represented “typical” clear water years, plant maximum biomass and/or areal coverage was lower during 1997 and especially 1999. These differences among years are reflected in the physical and chemical variables measured. During 1996 and 1998, an increase in transparency and a decrease in the concentrations of chlorophyll and total phosphorus occurred simultaneously with the start of the growing season for the dense Chara meadows that covered about half of the lake area outside the reed belts. Compared to these 2 years, summer values of transparency were lower during 1997 and 1999, while concentrations of total phosphorus and chlorophyll were higher. The difference is also obvious from the higher values for light attenuation in 1999 compared to 1996.

We assume that biomass and areal coverage of submerged macrophytes must reach a certain threshold in order to create clear water conditions in the open water. During the first years of the expansion of Chara aspera in Lake Veluwemeer, “clear water conditions” were observed only within this vegetation, while “turbid state conditions” occurred outside the plant beds (Van den Berg et al., 1998). During 1997, Chara had expanded further and covered about 60% of the lake area, which is comparable to the situation in Lake Krankesjön during 1996–1998, and clear water was observed also outside the dense vegetation (Van den Berg, 1999). Jeppesen et al. (1994) estimated 30% of a lake’s area must be covered by submerged vegetation at a minimum, to create stable clear water conditions.

Among the numerous mechanisms to maintain clear water conditions (Scheffer et al., 1993), physical processes and nutrient limitation are most important in Lake Krankesjön, while grazing from zooplankton is of limited importance. Apart from long-term data on biomass of macrozooplankton during the summer months (Blindow et al., 2000b), the results presented in this study give further evidence for our suggestion that grazing from zooplankton is of minor importance for the limitation of phytoplankton in the clear water state of Lake Krankesjön. Thus, lower zooplankton peak biomass and lower maximum grazing pressure were observed during the “typical” clear water year of 1996 compared to the “unstable” year of 1997, and the decrease in both chlorophyll concentrations and the chlorophyll/total phosphorus ratio during and following the zooplankton peak occurrence was more pronounced in 1997 compared to 1996. In 1998 and 1999, we may have missed the peak abundance of zooplankton due to lower number of sampling occasions. This may explain the lower maximum grazing pressure observed during these years. Zooplankton filtering rate was not significantly correlated to chlorophyll concentrations in any of the 4 years except for the “unstable” year 1999.

Instead, we suggest that nutrient availability is the main limiting factor for growth of phytoplankton in Lake Krankesjön. This assumption is supported by the close correlation
between chlorophyll and nutrients (especially phosphorus) in all of the 4 years. Phosphorus is probably the most limiting nutrient, which is also indicated by the overall high N/P ratios in the lake.

Ratios of chlorophyll and limiting nutrient are suggested to be constant over a wide range of climate zones and salinity if grazing and light availability are considered (Mazumder and Havens, 1998; Meeuwig et al., 1998). Thus, a probable explanation for the decrease in chlorophyll/phosphorus ratios in Lake Krankesjön during May/June is grazing from zooplankton. However, this ratio was generally low during the summer of all 4 years in spite of low biomass of zooplankton and high water transparency. In our long-term data, summer mean values of the ratio of chlorophyll and total phosphorus are significantly lower during the clear water state than during the turbid state, but increased during the “unstable” year 1999. With respect to the lower filtering capacity of zooplankton (Blindow et al., 2000b) and the higher transparency in the clear water state, the opposite should be expected. Similarly, Faafeng and Mjelde (1998) found lower chlorophyll to total phosphorus ratios in clear water lakes than in turbid lakes in Norway. Ratios of chlorophyll and total phosphorus in Lake Krankesjön both during clear water and turbid state correspond well to the values given by Faafeng and Mjelde (1998), and during the clear water state, our values correspond well to results from other lakes dominated by dense vegetation of *Chara* spp. (Kufel and Ozimek, 1994; Hough and Putt, 1988).

Several different explanations for this decrease in ratio between chlorophyll and limiting nutrient (phosphorus) in the presence of dense submerged vegetation in Lake Krankesjön can be given. Increased sedimentation due to reduced mixing has been suggested to cause reduced phytoplankton numbers in lakes dominated by submerged plants (Jones et al., 1996). Carbon limitation of phytoplankton is another possibility. Concentrations of bicarbonate decreased during the springs of 1996–1998 to minimum values around 60–70 mg l$^{-1}$ measured in the open water of the lake (unpublished data), but were above 90 mg l$^{-1}$ at all sampling occasions of 1999, when ratios of chlorophyll and total phosphorus were higher.

Inhibition of microalgae by allelopathic substances excreted from charophytes has been shown in the laboratory (Blindow and Hootsmans, 1991), but the quantitative importance of this effect in the field is not known. Forsberg et al. (1990) found the same ratio between chlorophyll and total phosphorus in lakes with abundant *Chara* spp. as in lakes where these plants are absent. They concluded that low phytoplankton densities often observed in lakes with abundant *Chara* vegetation are not caused by allelopathy. Their results, however, contrast with our own findings that low ratios of chlorophyll to total phosphorus occur in Lake Krankesjön during periods of high biomass of *Chara* spp.

An alternative explanation is that only part of the total phosphorus is available for phytoplankton, and that the unavailable fraction is larger in the presence of dense submerged vegetation when phosphorus concentrations decrease. As Lake Krankesjön is calcium-rich, a large fraction of total phosphorus may be precipitated as apatite-bound phosphorus. Similarly, Meeuwig et al. (1998) explained low yield of chlorophyll in turbid estuaries by an unusually high proportion of phosphorus unavailable for algae.

In agreement with the situation in other shallow lakes (Jónasson and Adalsteinsson, 1979; Bengtsson et al., 1990; Hamilton and Mitchell, 1996; Scheffer, 1998; Bachmann et al., 1999), we assume that one of the main mechanisms affecting light availability in Lake Krankesjön is wind-induced resuspension of the sediments rather than external nutrient
Phytoplankton is the main contributor of light attenuation in Lake Krankesjön. Apart from the fact, however, that also detritus and inorganic material contribute to up to almost 40% of the light attenuation, chlorophyll concentrations during 1999 were positively correlated with inorganic suspended material, which indicates that phytoplankton biomass increases during periods of strong wind. Increased internal nutrient loading by resuspended seston (Hamilton and Mitchell, 1997; Noges et al., 1998) is a probable explanation for this correlation. Thus, total phosphorus concentrations during 1999 were closely correlated to the total amount of suspended material.

High transparency in Lake Krankesjön occurs generally during periods with dense submerged vegetation. Both phytoplankton biomass and amount of tripton (=inorganic suspended solids + detritus) decrease during summer when submerged vegetation is well developed. Extinction coefficients measured during 1996 were closely correlated with biomass of submerged macrophytes but only weakly with concentrations of chlorophyll. A large data set from Danish lakes (Jeppesen et al., 1994) shows higher (about 1 m) transparency values than in Lake Krankesjön (about 0.5 m) at the total phosphorus concentration (about 50 μg l⁻¹) which was observed during the turbid state in Lake Krankesjön. All this indicates that sediment resuspension has a strong impact on light availability in Lake Krankesjön, and that submerged vegetation increases light availability both by inhibition of phytoplankton and by reduction of sediment resuspension.

A temporary decrease of the biomass of *C. tomentosa* occurred during 1997, and a strong decline of the submerged macrophytes was observed during 1999. Several possible explanations can be given for this destabilization during the last years. The higher water level during the last 4 years decreased light availability in the lower layers of the water column, which may have reduced the growth of submerged macrophytes but only weakly with concentrations of chlorophyll. A large data set from Danish lakes (Jeppesen et al., 1994) shows higher (about 1 m) transparency values than in Lake Krankesjön (about 0.5 m) at the total phosphorus concentration (about 50 μg l⁻¹) which was observed during the turbid state in Lake Krankesjön. All this indicates that sediment resuspension has a strong impact on light availability in Lake Krankesjön, and that submerged vegetation increases light availability both by inhibition of phytoplankton and by reduction of sediment resuspension.

Alternatively, the recent development in Lake Krankesjön can be explained by a long-term destabilization of the clear water state. Thus, gradual decrease in water depth since 1985 in the shallow areas along the southern shore of the lake (own observations) indicates enhanced sedimentation within and behind the dense beds of *Chara* spp. Our long-term data show a slow, but continuous increase of summer concentrations of total phosphorus. Enhanced sedimentation and reduced sediment resuspension as well as nutrient accumulation within the dense submerged vegetation, i.e. the same mechanisms that are suggested to be the most important for the maintenance of the clear water state, may thus cause a long-term destabilization of the clear water state. If this explanation is true, the alternative stable state...
model may not be valid for shallow lake ecosystems. Long-term studies of lakes in the clear water state are necessary to prove this possibility.

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