

Primary production in two shallow lakes with contrasting plant form dominance: A paradox of enrichment?

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Abstract

We estimated total lake plant biomass and primary net production in two shallow Swedish lakes that differ in nutrient loading and plant form dominance. In clearwater Lake Krankesjön ($10 \mu\text{g}$ chlorophyll *a* L^{-1}), submerged macrophytes contributed more than phytoplankton and epiphyton to the estimated plant biomass. Estimated net primary production during May to September was 90–130, 1.2, and 14 g C m^{-2} for phytoplankton, epiphyton, and submerged macrophytes, respectively. In turbid Lake Börningesjön ($60\text{--}80 \mu\text{g}$ chlorophyll *a* L^{-1}), primary production by submerged macrophytes and periphyton was negligible. Although gross primary production of phytoplankton was high close to the water surface, estimated areal net primary production during May to September was low, -40 to $+25 \text{ g C m}^{-2}$, as a result of self-shading and high respiration. Grazing pressure from zooplankton rarely exceeded $15\% \text{ d}^{-1}$ in both lakes, indicating that phytoplankton production was not limited by grazing. Low gross epiphyton production could result from high grazing by macroinvertebrates and thus higher trophic transfer efficiency through the benthic than through the pelagic food web. Provided that conditions in Lake Börningesjön reflect previous turbid state conditions in Lake Krankesjön, our results may explain why a shift to a clearwater state was followed by increased biomass of higher trophic levels. Our results also support the paradox of enrichment hypothesis, which predicts lower productivity at high nutrient loading. Contrary to former investigations, we found lower production at a higher nutrient loading already at the trophic level of primary producers.

It is now accepted that shallow, moderately eutrophic lakes can occur in two alternative stable states: a clearwater and a turbid state. Whereas the clearwater state is characterized by low turbidity and high density of submerged macrophytes, the turbid state is dominated by phytoplankton (Scheffer et al. 1993). Shifts between these states have vast effects on community structure and lake biodiversity, with consequences for ecosystem function and production (Scheffer et al. 2001). A number of studies of functional aspects of biotic structure have revealed several feedback mechanisms that stabilize or destabilize the alternative states (summarized by Scheffer et al. 1993). The quantitative aspects of primary production by the separate plant forms, however, have received less attention.

Lake Krankesjön, south Sweden, shifted spontaneously from the turbid to the clearwater state during the mid 1980s (Blindow et al. 1993; Hargeby et al. 1994). The reasons for this shift are not well understood. During the shift, a decrease of nutrients (nitrogen and especially phosphorus) was recorded and a biomass increase for different trophic levels including primary producers, primary and secondary consumers (zooplankton + macroinvertebrates), as well as fish and waterfowl at the third and fourth trophic levels (Table 1). The lake is situated within a military area. External nutrient loading is low and has probably not changed substantially during the last decades.

Similar differences in biomass of higher trophic levels between turbid and clearwater states as in Lake Krankesjön have been observed in other shallow lakes (Mitchell et al. 1988; Hanson and Butler 1994; Milberg et al. 2002) suggesting generally higher values in the clearwater than in the turbid state of shallow lakes. Because a shift from the clearwater to the turbid state often occurs accompanying increased nutrient loading (Scheffer et al. 1993), this phenomenon reminds strongly of the “paradox of enrichment” hypothesis (Rosenzweig 1971). Compared with this hypothesis, which was derived from Lotka-Volterra equations of simple food webs, a shift from turbid to clearwater state is characterized by a dominance shift among primary producers and a complex overall change of trophic web configurations. Instead of phytoplankton, submerged

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Table 1. Estimated changes in biomass and numbers for different trophic groups in Lake Krankesjön. Subm. macr. = submerged macrophytes.*

Trophic group		Before macrophyte expansion (1985–1987)	After macrophyte expansion (1990–1997)	Increase
Primary producers (g dry wt m ⁻²)	Phytoplankton	1.5	0.6	
	Subm. macr. + epiphyton	0.5	270	
	Total	2.0	271	×135
Primary + secondary consumers (g dry wt m ⁻²)	Macrozooplankton	0.15	0.06	
	Macroinvertebrates	2.2	5.0	
	Total	2.35	5.06	×2.2
Fish CPUE (kg net ⁻¹)	Benthi-/planktivores	1.3	4.1	
	Piscivores	0.5	1.6	×3.2
	Total	1.8	5.7	
Herbivorous waterfowl (n)	Mute swan	12	50	
	Coot	13	398	
	Total	25	448	×18
Omnivorous waterfowl (n)	Dabbling ducks	36	94	
	Diving ducks	36	57	
	Total	72	151	×2.1

* For phytoplankton, data on Chl *a* (seasonal averages of samples taken from 0- to 2-m depth; from Blindow et al. 2002) were converted to biomass according to Jeppesen et al. (1994) assuming a C:Chl *a* ratio of 30. For zooplankton (data in Blindow et al. 2000b), biomasses in the open water habitat were extrapolated for the whole lake. For macroinvertebrates, mean values were calculated for each habitat (data from Hargeby et al. 1994) over all years and used to calculate total biomass in the lake considering change of the different habitats among years. Fish abundance is given as average catch per unit effort (CPUE) in multimesh survey gill nets (for details, see Methods). Waterfowl data give mean numbers for countings during June and July (source: Hargeby et al. 1994; Blindow et al. 2000a).

macrophytes and/or periphytic algae become the main primary producers (Scheffer et al. 1993; Vadeboncoeur et al. 2001; Liboriussen and Jeppesen 2003), and the benthic food web gains in importance compared with the pelagic one (Vadeboncoeur et al. 2001).

One possible reason for this biomass increase of higher trophic levels in the clearwater state is more efficient energy transfer through the trophic web compared with the turbid state. Alternatively and/or additionally, annual net production of primary producers could be higher in the clearwater state than in the turbid state as a result of more efficient use of resources (nutrients, light): In the clearwater state, light reaches down to the sediment, giving primary producers attached to the substrate access to both nutrients and light, whereas in the turbid state, primary producers are either limited by nutrients (upper part of the water column) or light (lower part of the water column).

A comparison of whole-lake net primary production between the clearwater and the turbid state is necessary to test this hypothesis. Such comparisons have up to now rarely been published. Mitchell (1989) recorded a decrease of total net primary production during the shift from a turbid to a clearwater state in shallow Tomahawk

Lagoon. Liboriussen and Jeppesen (2003) found higher total annual primary production in the turbid than in the clearwater state when comparing two lakes. Calculation of primary production was, however, restricted to an area with low (0.5 m) depth, and to gross primary production only. Also Vadeboncoeur et al. (2001) who compared whole-lake primary production in several lakes, some of which had been subjected to artificial fertilization only measured gross primary production. This production increased with increasing nutrient loading, and a shift from epipelton to phytoplankton dominance took place.

Lake Krankesjön has been in the clearwater state since the shift in the 1980s (Blindow et al. 2002). Because there are not enough data available to allow for an estimation of whole-lake primary production for the turbid state, we compared data on whole-lake gross and net primary production of Lake Krankesjön in the clearwater state with data obtained from turbid Lake Börringesjön, which during our investigation had similar transparency as Lake Krankesjön during its turbid state in 1978 to 1985. Both lakes are situated in southern Scania, Sweden, have similar size and maximum depth and are unstratified. The mean depth is somewhat higher in Lake Börringesjön (Table 2).

Table 2. Morphological and chemical data for Lakes Krankesjön and Börringesjön surface open lake outside the reed belts.*

Lake	Surface (km ²)	Mean depth (m)	Retention time (months)	Volume (m ³ × 10 ⁶)	Calcium (mmol L ⁻¹)	tot-N (mg L ⁻¹)	tot-P (µg L ⁻¹)
Krankesjön	2.2	0.9	2.3	2.01	2.4	1.2	29
Börringesjön	2.7	1.5	8.3	4.09	2.3	1.4	160

* tot-N = total nitrogen; tot-P = total phosphorus. Chemical parameters: Mean values for samples taken during June to September of 1988–1997 (Lake Krankesjön) and 1998–2003 (Lake Börringesjön, as well as calcium values in Lake Krankesjön). Values for calcium (both lakes) and nitrogen and phosphorus (Lake Börringesjön) were obtained from the Swedish University for Agricultural Sciences, Uppsala.

Material and methods

Lake Krankesjön (55°42'N, 13°29'E) is surrounded by a military area and thus receives lower external nutrient loading than Lake Börringesjön. In opposite to Lake Börringesjön, this lake was dominated by dense charophyte vegetation during the 1940s (Almestrand and Lundh 1951) and stayed in the clearwater state for most of the time. A shift to the turbid state occurred in the mid 1970s, but a "spontaneous" shift back to the clearwater state started during 1985, which was accompanied by a significant decrease in nutrient concentrations in the water column (Hargeby et al. 1994; Blindow et al. 2002). Since about 1990, submerged vegetation has covered about 50% of the lake surface outside the reed belts, about 45% of which is dense vegetation of several winter-green species of *Chara* (*C. tomentosa*, *C. rudis*, *C. hispida*) (Blindow et al. 2002). Phytoplankton is dominated by small, noncolonial cyanobacteria, but also colonial, toxic cyanobacteria (*Microcystis* spp.) can be abundant during summer (G. Cronberg pers. comm.). During the previous period of turbid water, small, noncolonial cyanobacteria dominated (G. Cronberg pers. comm.), and Secchi depth was 20 to 40 cm during summer (Hargeby et al. 1994).

Lake Börringesjön (55°29'N, 13°20'E) had only sparse submerged vegetation (*Myriophyllum spicatum*, *Potamogeton pectinatus* and mats of *Chara* spp. down to about 50 cm depth) during the 1940s and was characterized by low Secchi depth of about 30 cm (Almestrand and Lundh 1951). During the last centuries, the lake received high nutrient loading from the surrounding agricultural area (Davidsson 2003). During recent years, the distribution of submerged vegetation is very similar to the former situation (own observations). The same is the case for summer Secchi depth values that vary between 20 and 40 cm (data obtained from Swedish University of Agricultural Sciences, Uppsala). Dense, low mats of *Chara aspera* occur on several locations around the lake where the reed belt is absent because of cattle grazing, but only to a water depth of about 25 cm. Sparse *Potamogeton pectinatus* and *Myriophyllum spicatum* can be found down to 70 cm depth. Phytoplankton is dominated by small, noncolonial chroococcal cyanobacteria (G. Cronberg pers. comm.).

During 1999, biomass and primary production of phytoplankton were estimated in both lakes. Because submerged macrophytes only occurred very sparsely in Lake Börringesjön (see previous), biomass and primary production of submerged macrophytes and epiphyton were estimated only in Lake Krankesjön. For estimates of maximum biomass, the peak values during summer (June to September) were selected for both lakes and the "relevant" groups of primary producers. Production estimates for phytoplankton and epiphyton cover the period from May to September.

Summer maximum biomass values were used as a rough estimate for annual production of submerged macrophytes in Lake Krankesjön. Because this vegetation is dominated by dense stands of *Chara* spp. (>90% of total macrophyte biomass) (Blindow 1992), other submerged macrophytes are neglected in the calculation of annual production. The

distribution of submerged macrophytes was estimated from boat during mid summer and combined with aerial photographs. For an estimation of summer biomass, 5 samples were taken with a Plexiglas corer (diameter 71 mm) within a dense, homogeneous stand of *Chara tomentosa* on 12 August. 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). Carbon content was assumed to be 45% of ash-free dry weight (Hart and Lovvorn 2000).

Underwater irradiance profiles were measured in duplicate at each sampling date by means of an underwater PAR meter (LI-COR 250) at sites where water depth was >2.5 m in 20-cm intervals. Vertical light attenuation (K) was calculated out of the slope of the log-transformed light measurements.

Data on global radiation were obtained from the Swedish Meteorological and Hydrological Institute (SMHI) for a station in Lund, about 15 km west of Lake Krankesjön and 35 km northwest of Lake Börringesjön, respectively, as hourly mean values of continuous global radiation (300–3,000 nm) measurements over the whole day from 01 April to 31 October 1999. Global radiation was converted to PAR assuming a 45% share of PAR in global radiation and using a conversion factor of 4.6 to convert $W m^{-2}$ (PAR) to $\mu mol photons s^{-1} m^{-2}$ (PAR).

Samples for chlorophyll and zooplankton were collected in both lakes during midday on 10 occasions throughout the vegetation period (May to September) when light measurements and estimation of phytoplankton primary production were also performed. In Lake Krankesjön, one additional sampling for chlorophyll and zooplankton took place on 20 April. For chlorophyll, phytoplankton and zooplankton collection, integrated water samples from 0- to 2-m depth were taken with a 2-m Plexiglas corer in the center of the lake at a water depth of >2.5 m. On 22 May, a nighttime sample was taken to assess the influence of diurnal vertical migration on zooplankton biomass and grazing rate in Lake Börringesjön.

For the analysis of chlorophyll *a* (Chl *a*), a known volume of the integrated sample was filtered through a GF/C filter. The filter was kept dark and frozen until analysis after extraction with methanol (Marker et al. 1980). These values were converted to biomass assuming a C:Chl *a* ratio of 30 and a dry wt:C ratio of 2.2 (Jeppesen et al. 1994).

For the analysis of zooplankton, a known volume of the integrated water sample was filtered through a 45- μm filter. The collected zooplankton was preserved with formalin (4%). Filtering microcrustacean zooplankton were determined, counted and measured under an inverted microscope. Biomass was calculated by 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.

Phytoplankton primary production was determined by means of light-dark bottles that were filled with natural water including phytoplankton (integrated water sample,

prefiltered through 150 μm to remove larger zooplankton) and incubated at 5 different depths (middle of the bottle 10, 25, 50, 95, and 140 cm below surface, respectively, one dark and one light bottle at each depth) in the open lake at a water depth of >2.5 m for 2–4 h. Oxygen was precipitated and determined according to the Winkler method in the original water sample and in all bottles after incubation. For calculation of net primary production the spread sheet model published by Walsby (1997) was used. In contrast to the conditions that the original model was designed for, we had to consider spatial limits. Therefore, we expanded the model by including volume-area versus depth functions in 0.1-m depth slices by using the hydromorphological data of the two lakes. Photosynthesis vs. irradiance parameters (i.e., P_{max} —maximum photosynthesis rate, R —respiration rate, α —term of light affinity, β —term of photoinhibition susceptibility) were calculated from the results of the bottle incubation by means of the formula of Webb et al. (1974). Irradiance values used for calculations were mean irradiances over the whole incubation period calculated for each 0.1-m depth slice on basis of converted SMHI data and vertical attenuation of the water (specified above). Because the spreadsheet of Walsby (1997) does not include respiration and attenuation values into the fitting procedure, a separate data set included both parameters into the fitting procedure to test for sensitivity to possible misdetermination of these two crucial parameters.

The data used for numerical analysis are (A) hourly integrals of irradiance, obtained from the SMHI, (B) fortnightly measurements of photosynthesis main parameters, and (C) fortnightly determinations of vertical light attenuation. Because of the different temporal resolutions of the parameters used, we interpolated B and C between the individual sampling dates by calculating smoothed averages on a hourly basis. The results are daily estimates of volume-based net primary production, which allow comparing net carbon production between the two lakes.

Epiphyton biomass was measured on artificial substrates (plastic strips) of about 75 cm length and 3.4 cm breadth that were placed within dense stands of *Chara* spp. in the western part of Lake Krankesjön over a period of about 2–3 weeks. A total of 10 incubation periods took place covering the whole investigation period with starting dates from 20 April to 11 September. After the incubation, two to five strips were collected and kept dark and frozen. Chlorophyll was analyzed and converted to carbon according to the method described above. To estimate epiphyton production, daily production was calculated for each incubation period. The mean value calculated out of these incubation periods was multiplied with the number of days (153) between 01 May and 30 September. Whole lake epiphyton biomass and production was estimated based on calculated surface area of submerged macrophytes as potential settling substratum by applying a surface:weight ratio of 1,205 $\text{cm}^2 \text{g}^{-1}$ dry weight measured by Sher-Kaul et al. (1995) for *Nitellopsis obtusa*, which has a similar size and architecture as *Chara tomentosa* (Hargeby 1990) and values for macrophyte biomass obtained as described previously.

Fish were caught by means of multiple-mesh gill nets. Lake Krankesjön was sampled in July–August each year 1985 to 1992; in 1996 (Hargeby et al. unpubl. data); and in August–September 1999 and 2003 (data obtained from the Swedish Fisheries Research Board). Lake Börringesjön was sampled in June 2000 (data obtained from the Swedish Fisheries Research Board) and September 2005 (T. Andersson unpubl. data). During 1985–1996, multifilamentous nylon nets were used, consisting of twelve panels with mesh sizes of 4–100 mm (knot to knot) in a geometric series. Each net (total length 48 m) consisted of 1.5-m high 4-m panels. Nets ($n = 7$ –14) were set out randomly for 24 h in sparsely vegetated areas and in *Chara* vegetation. Mean catch per net and day (CPUE) was calculated from the relative areal cover of these two habitat types each year. Sampling in 1999 and 2003 in Lake Krankesjön, and in Lake Börringesjön 2000 and 2005, followed another standard (Appelberg 2000). Each net then consisted of twelve 1.5-m-high 2.5-m panels of monofilament nylon net with 5–55-mm mesh following a geometric series. In both lakes, nets ($n = 12$ –24) were randomly distributed across the lake surface. All fish were identified to species, measured (total length) and weighed. The species were separated into piscivores (pike *Esox lucius* and perch *Perca fluviatilis*) and benthivores/planktivores (ruffe *Acerina cernuus*, roach *Rutilus rutilus*, rudd *Scardinius erythrophthalmus*, bream *Abramis brama*, white bream *Blicca bjoerkna*, bleak *Alburnus alburnus*, rain-bleak *Leucaspis delineatus*, crucian carp *Carassius carassius* and tench *Tinca tinca*). The maximum size of bream was used as an indirect and integrated measure of resource availability for benthivorous/planktivorous fish (Stenberg and Persson 2006 unpubl. data). The asymptotic maximum size of bream in each lake was estimated as the largest fish caught each year.

Results

Light attenuation—The diffuse vertical light attenuation coefficient in Lake Krankesjön varied from 2.37 to 3.49 m^{-1} (mean value 2.62 m^{-1}). In Lake Börringesjön the light attenuation ranged from 4.61 to 7.81 m^{-1} (mean value 5.87 m^{-1}).

Biomass and production of phytoplankton—In Lake Krankesjön, Chl *a* concentrations were highest (around 60 $\mu\text{g L}^{-1}$) during April and decreased to around 10 $\mu\text{g L}^{-1}$ from June to September. In Lake Börringesjön, Chl *a* concentrations were around 60–80 $\mu\text{g L}^{-1}$ until end of June and increased up to 145 $\mu\text{g L}^{-1}$ during September (Fig. 1).

Calculated phytoplankton net production between May and September was about 90–130 g C m^{-2} for Lake Krankesjön and about -40 to $+25 \text{ g C m}^{-2}$ for Lake Börringesjön. Because interpolation of monthly measurements inherits the risk of large deviations caused by single misdeterminations, different scenarios were tested to estimate a margin of uncertainties in determining phytoplankton net production rates (Fig. 2). Calculated phytoplankton net production was higher in Lake Krankesjön compared with Lake Börringesjön for all possible

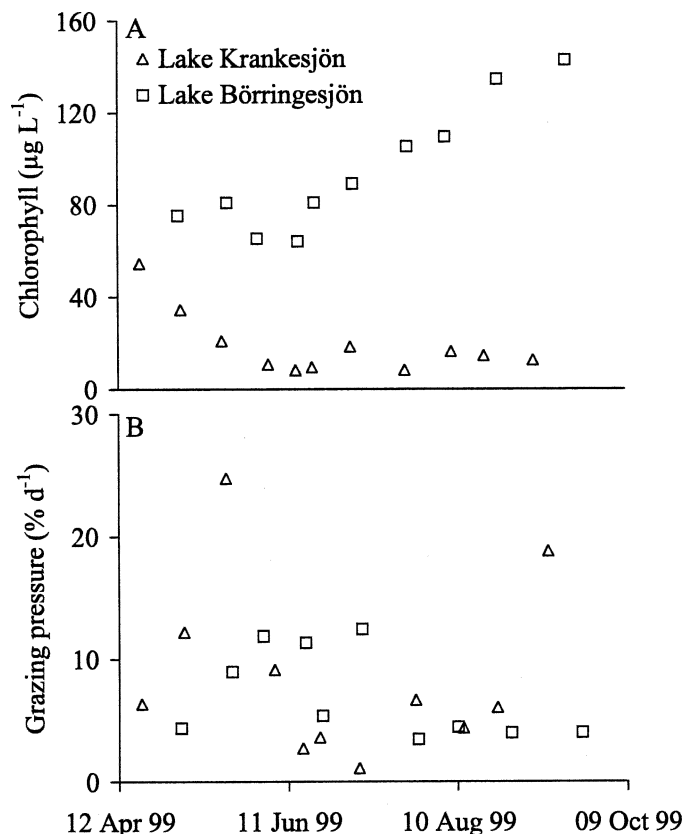


Fig. 1. (A) Chl *a* concentrations ($\mu\text{g L}^{-1}$) and (B) grazing pressure ($\% \text{d}^{-1}$) from macrozooplankton on phytoplankton in Lake Krankesjön and Lake Börringesjön during the vegetation period of 1999.

combinations of fitting and nonfitting of respiration and attenuation (Fig. 2).

Combining values for calculated phytoplankton production in Lake Krankesjön with the depth-volume function of Lake Börringesjön increased production by about 20–50% compared with production in the “original” Lake Krankesjön. Combining values for calculated phytoplankton production in Lake Börringesjön with the depth-volume function of Lake Krankesjön also increased production in the “original” Lake Börringesjön resulting in values somewhat lower or similar to Lake Krankesjön.

Lake Börringesjön had considerably higher gross production in the upper water layer during midday than Lake Krankesjön. A steep decrease of gross production with depth in combination with high respiration, however, resulted in a negative net production through most of the water column in Lake Börringesjön, whereas most of the water volume had positive net production in Lake Krankesjön. During August, the compensation depth was about 0.7 m in Lake Börringesjön but about 1.8 m in Lake Krankesjön (both attenuation and respiration fitted, Fig. 3).

Extrapolating phytoplankton net production to the period between 01 April and 31 October resulted in an increase from 91 to 102 g C m^{-2} in Lake Krankesjön and in a reduction from +19 to -61 g C m^{-2} in Lake Börringes-

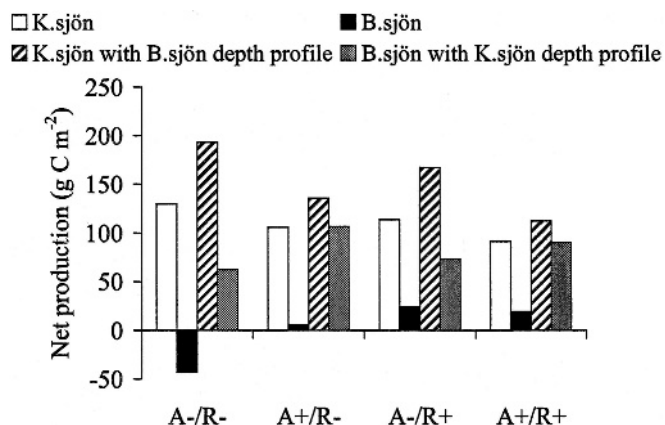


Fig. 2. Calculated phytoplankton net production in (from left to right) Lake Krankesjön, Lake Börringesjön, a model lake combining production characteristics of Lake Krankesjön with the depth profile of Lake Börringesjön (hatched bars) and a model lake combining production characteristics of Lake Börringesjön with the depth profile of Lake Krankesjön (gray bars). Parameter settings used are: A-/A+ attenuation not fitted/fitted, R-/R+ respiration not fitted/fitted. The data presented are accumulated net production for the whole vegetation period (01 May to 30 September).

jön, respectively, compared with the period of 01 May to 30 September (both attenuation and respiration fitted).

Biomass and production of epiphyton—Biomass of epiphyton on artificial substrates in Lake Krankesjön fluctuated between 0.1 and 1.8 $\mu\text{g Chl } a \text{ cm}^{-2}$ (2.6 and 54.1 $\mu\text{g C cm}^{-2}$) between sampling occasions, daily production between 0.006 and 0.106 $\mu\text{g Chl } a \text{ cm}^{-2} \text{ d}^{-1}$ (Fig. 4). Calculated for the whole lake surface, summer biomass was estimated as 5.1 g C m^{-2} , production during May–September as 12.9 g C m^{-2} (Fig. 5).

Biomass and production of submerged macrophytes—In Lake Krankesjön, *Chara* spp. covered around 21% of the lake area outside the reed belts during 1999. Maximum biomass of 375 g dry wt m^{-2} (147 $\text{g ash-free dry wt m}^{-2}$) was reached within dense stands of *Chara tomentosa* in August (Blindow et al. 2002) corresponding to about 79 g dry wt m^{-2} (31 $\text{g ash-free dry wt m}^{-2}$) for the total lake area outside the reed belts. Both peak biomass and annual production of *C. tomentosa* were estimated as 14 g C m^{-2} for the total lake area outside the reed belts (Fig. 5). Compared with previous estimates of biomass of submerged macrophytes in the clearwater state (1990–1997), both areal distribution and biomass of the vegetation were low in 1999 (Table 1; Blindow et al. 2002).

Zooplankton—During all sampling occasions but one, filtering rate of microcrustacean plankton was substantially higher in Lake Börringesjön than in Lake Krankesjön. Grazing pressure, however, was below 15% d^{-1} in both lakes for the whole sampling period apart from two occasions (20 May and 11 September) when grazing pressure was 25 and 19% d^{-1} , respectively, in Lake Krankesjön (Fig. 1). Microcrustacean filtering rates were

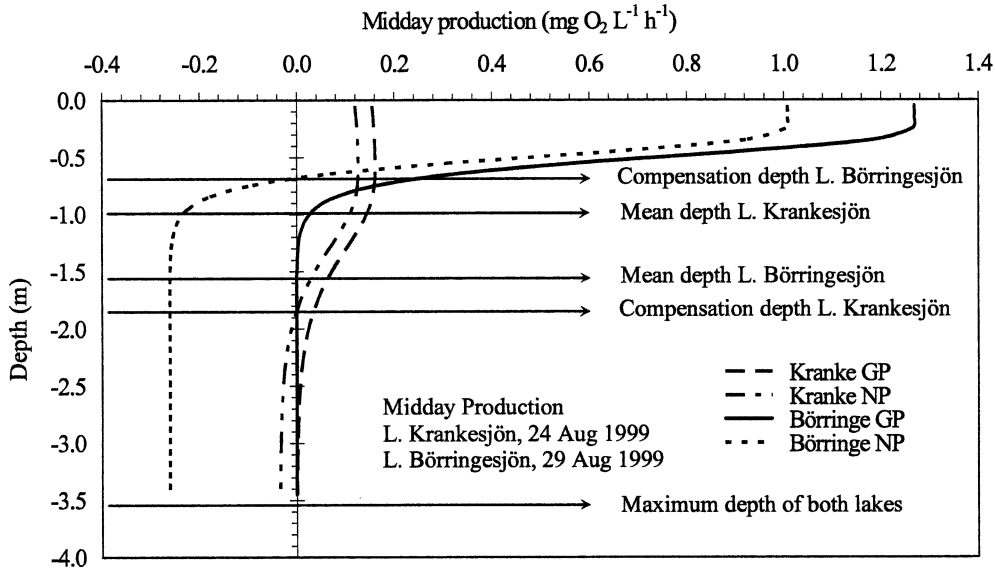


Fig. 3. Midday phytoplankton net (NP) and gross (GP) primary production in Lakes Krankesjön and Börringesjön, respectively. Both attenuation and respiration were fitted for the calculation.

similar (479 and 551 $\mu\text{g dry wt L}^{-1} \text{d}^{-1}$, respectively) for one sample taken during midday and one sample taken during midnight, respectively, in Lake Börringesjön on 22 May. In Lake Krankesjön, *Daphnia* biomass was low throughout the season (average: 31% of total Cladocera biomass) and never exceeded 8 $\mu\text{g dry wt L}^{-1}$ (Fig. 6). Biomass of *Daphnia* fluctuated throughout the season (average: 61% of total Cladocera biomass) and reached its highest value (324 $\mu\text{g dry wt L}^{-1}$) on 07 July (Fig. 6) in Lake Börringesjön.

Fish—The maximum size of bream increased in Lake Krankesjön, from an average of 1.0 ± 0.2 kg during the three turbid years 1985–1987 to 2.4 ± 0.2 kg during 1992–2003 (Fig. 7, $r_s = 0.86$, $p = 0.006$, Spearman rank correlation, $n = 11$). In Lake Börringesjön, maximum bream size was less than 1 kg at both sampling occasions (Fig. 7).

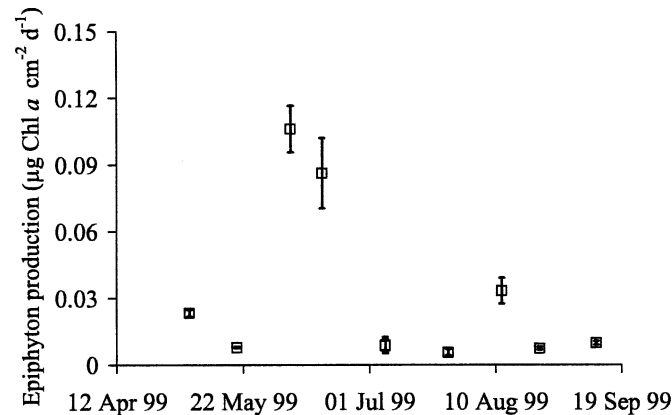


Fig. 4. Epiphyton daily net production (mean values \pm SE) on artificial substrates ($\mu\text{g Chl } a \text{ cm}^{-2} \text{ d}^{-1}$ of substrate); $n = 2$ to 5 for each sampling occasion.

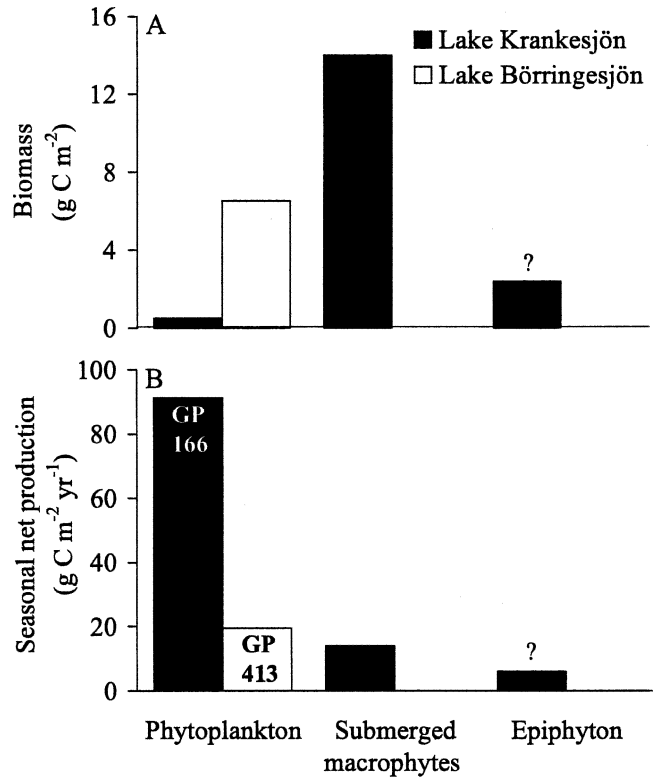


Fig. 5. Estimates of (A) peak biomass and (B) seasonal net production of phytoplankton in Lakes Krankesjön and Börringesjön and submerged macrophytes and epiphyton in Lake Krankesjön. Epiphyton biomass and seasonal production is marked with “?” because the absolute value of these items is uncertain (see text). For phytoplankton, values for seasonal gross production (GP) are added for both lakes.

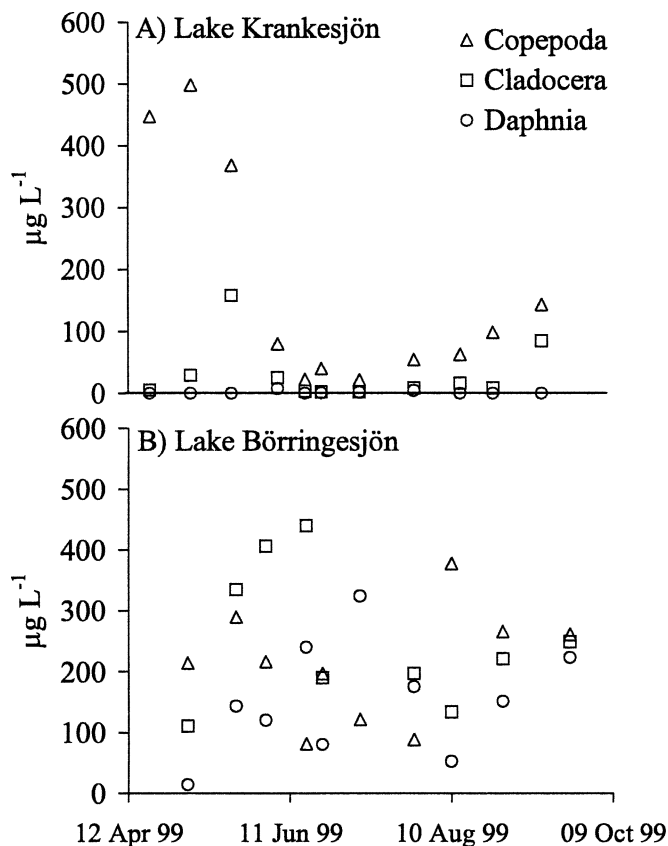


Fig. 6. Composition of macrozooplankton ($\mu\text{g dry wt L}^{-1}$) in Lake Börringesjön and Lake Krankesjön.

Discussion

In terms of phytoplankton gross primary production Lake Krankesjön and Lake Börringesjön differ in a manner expected for a less and a more eutrophic lake. A striking result of our investigation, however, is the fact that, despite far higher biomass and high rates of gross production during all sampling occasions, phytoplankton net production was lower in the highly eutrophic Lake Börringesjön than in the moderately eutrophic Lake Krankesjön. This low net productivity is most probably caused by low light availability due to self-shading: Even at times of high production, respiration, which should be regarded as “community respiration” because heterotrophic organisms like bacteria and microzooplankton contribute with an unknown proportion, outweighs photosynthesis already at low depths (midday compensation depth at about 0.7 m). Despite high rates of photosynthesis close to the surface, high respiration losses in deeper water and during the night hours result in a net primary production that was estimated as close to 0 for the investigation period between May to September. Extrapolation to the period between April to October, i.e., into the “dark” season, further reduces net primary production in Lake Börringesjön, while the same extrapolation further increases net primary production in Lake Krankesjön. These effects were not caused by different susceptibility to high light stress (β -term).

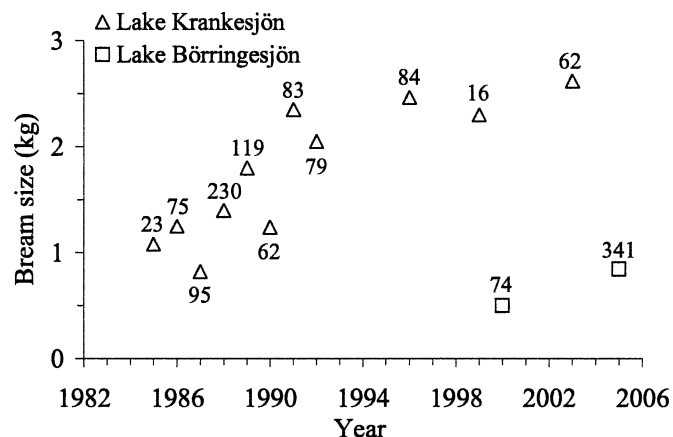


Fig. 7. Maximum weight of bream caught in gill nets in Lake Krankesjön and Lake Börringesjön during different years. The numbers above the symbols indicate the total number of bream caught.

Irrespective of the fact that, compared with Lake Krankesjön ($\sim 350 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), the average light saturation point was lower in Lake Börringesjön ($\sim 80 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), calculated beta-values were small and 15% higher for Lake Krankesjön than Lake Börringesjön. We therefore suggest that Lake Börringesjön has lower annual phytoplankton net production than Lake Krankesjön.

Both lakes are situated within the same climate zone and have similar size, but a somewhat different depth profile. Because of positive net primary production also in deeper water, an application of our data from Lake Krankesjön to a deeper lake with the profile of Lake Börringesjön would increase phytoplankton net production. An application of our data from Lake Börringesjön to a shallower lake with the profile of Lake Krankesjön would also increase net phytoplankton production due to reduction of the lake volume below the compensation depth. Any decrease of mean water depth would thus reduce the differences in total primary production between the turbid and the clearwater lake.

Low light availability most probably also caused the low density and maximum depth of submerged macrophytes in Lake Börringesjön. Consequently, epiphyton biomass is low in this lake, and epipelton can be expected to play a minor role in total primary production because only a very small part of the lake bottom is situated within the euphotic zone.

In contrast, submerged macrophytes and probably epiphyton are important contributors to biomass as well as annual primary production of Lake Krankesjön. Epipelton has not been included in this study but has been shown to contribute significantly to primary production in other lakes (Liboriussen and Jeppesen 2003) and in estuarine lagoons (Meyercordt et al. 1999). The same may be the case in Lake Krankesjön. During summer, benthic cyanobacteria often detach from the sediment and can be found floating in the water column in large quantities (pers. obs.). Another possibly important, but neglected contrib-

utor to total lake primary production is periphyton associated to other substrates like reed stems. Total primary production of Lake Krankesjön may thus be rather underestimated.

We have to admit that our estimates are all but precise. Apart from the fact that different methods have been used to estimate total seasonal production of phytoplankton, epiphyton and submerged macrophytes, the estimations of primary production for each of these life-forms are subject to a number of shortcomings (*see following*). For all parameter settings tested, however, total net production of phytoplankton is higher in Lake Krankesjön than in Lake Börringesjön. These different parameter settings allow us to estimate the size of possible miscalculations of phytoplankton production as a result of errors in the determination of vertical light attenuation or respiration, which both are not included in the fitting procedure of the original spreadsheet (Walsby 1997). Also, the fact that phytoplankton production within the dense submerged vegetation of Lake Krankesjön probably is considerably lower than the values measured in the open lake water does not cause a major error in the calculation of total lake phytoplankton net production because this vegetation only covered about 21% of lake surface during 1999.

Irrespective of its size, the production of submerged macrophytes and epiphyton in Lake Krankesjön adds up to the already higher net production of phytoplankton in this lake. Thus, our hypothesis is supported: Total lake net primary production is higher in the clearwater state than in the turbid state.

In Lake Krankesjön, dense mats of submerged macrophytes most probably contribute substantially to whole-lake production. *Chara tomentosa*, the dominant submerged macrophyte, hibernates as a green plant. Summer biomass is about four to six times higher than winter biomass (Blindow et al. 2002), and it appears reasonable to assume that an unknown, but probably low amount of biomass lost by grazing adds up to total annual production and that this production roughly corresponds to summer biomass. Apart from some specialized monophages, most macroinvertebrates feed on epiphyton rather than submerged macrophytes (Soszka 1975). Consequently, Rich et al. (1971) assumed annual production of *Chara* spp. to be about 1.4 times its peak biomass, and Trifonova et al. (2002) suggested that annual production of submerged macrophytes corresponded to about 1.2 times their peak biomass in two Russian lakes. Total annual production of submerged macrophytes (about $14 \text{ g C m}^{-2} \text{ yr}^{-1}$) is low compared with other investigations from lakes with abundant submerged vegetation (Rich et al. 1971; Adams and McCracken 1974; Trifonova et al. 2002) and may in fact have been underestimated. The year 1999 was rather “untypical” during the clearwater period of Lake Krankesjön with lower expansion and lower biomass of submerged macrophytes as well as higher turbidity (Blindow et al. 2002). A corresponding calculation of annual submerged macrophyte production for a “normal” clearwater year would result in about $55 \text{ g C m}^{-2} \text{ yr}^{-1}$, which is four times more than our estimation for 1999.

Our epiphyton biomass values are similar to those reported by Weisner et al. (1997) for artificial substrates in Lake Krankesjön, and our estimated epiphyton biomass values for *Chara* spp. in Lake Krankesjön ($18\text{--}379 \mu\text{g Chl } a \text{ m}^{-2}$ of vegetated lake area) are within the same range as values for epiphyton biomass on *Chara* spp. ($80\text{--}224 \mu\text{g Chl } a \text{ m}^{-2}$ of vegetated lake area) reported by Hart and Lovvorn (2000). However, the estimation of whole-lake epiphyton biomass and production certainly has serious shortcomings and could substantially differ from the “real” values. Total lake biomass and production of epiphyton were calculated by rather rough estimates of macrophyte biomass, macrophyte distribution and macrophyte surface: weight ratio. Furthermore, composition, biomass and productivity of epiphyton can differ substantially between submerged macrophytes and artificial substrates (Eminson and Moss 1980; Gough and Gough 1981). In opposite to phytoplankton biomass and production in Lake Krankesjön, the corresponding values for epiphyton are most probably an underestimation because they include grazing losses from macroinvertebrates that can limit epiphyton production more severely than resource availability (Jones et al. 2002). Epiphyton is the main food source for most macrophyte-associated macroinvertebrates (Soszka 1975), and dense charophyte vegetation in Lake Krankesjön harbors high biomass of these organisms (Hargeby et al. 1994). High importance of periphyton for total lake primary production was found by Liboriussen and Jeppesen (2003) and by Vadeboncoeur et al. (2003) for moderately eutrophic lakes, and a number of investigations (summarized in Wetzel 2001) have pointed out that epiphyton can be the main contributor to total primary production in lakes with abundant submerged vegetation.

The probable importance of epiphyton as food source in Lake Krankesjön is also indicated by changes in higher trophic levels after the expansion of submerged macrophytes. Growth rates of two-year (benthivorous) perch increased significantly after this expansion, and stable carbon isotope analyses of opercula taken from two-year perch indicate a shift at the base of the food chain, from phytoplankton to periphyton (Hargeby et al. 2005). Hecky and Hesslein (1995), who found high dependence of a number of fish species on benthic diet, assumed that the relative importance of attached algal primary production may be consistently underestimated.

In both lakes, grazing pressure from zooplankton on phytoplankton was low throughout the investigation period. Low food quantity and/or quality may have caused the low zooplankton densities that have been observed in Lake Krankesjön both during daytime and nighttime (Blindow et al. 2000b), while low predation pressure on phytoplankton by zooplankton in Lake Börringesjön confirms observations from many other highly eutrophic lakes. One possible explanation is dominance of inedible algae among phytoplankton, which, however, is not the case in Lake Börringesjön (G. Cronberg pers. comm.). High absolute and relative abundance of planktivorous fish is another common reason for low predation pressure on phytoplankton in highly eutrophic lakes (Persson et al. 1988; Jeppesen et al. 2000). Maximum size of bream, which

is positively correlated to both food availability (Stenberg and Persson 2006) and growth rate (Stenberg and Persson unpubl. data) and thus can be used as an indicator for competition among planktivorous/benthivorous fish, was low in Lake BÖrringesjön and during the turbid state of Lake Krankesjön. We therefore suggest that high predation pressure from fish is the most probable explanation for the low density of zooplankton in Lake BÖrringesjön.

Whatever the reason, low trophic transfer efficiency is the ultimate cause for the high rate of self-shading among phytoplankton in Lake BÖrringesjön, which has been described for many other highly eutrophic lakes (Erikson et al. 1998; Gervais and Behrendt 2003) and results in low amounts of carbon that could be transferred to higher trophic levels. Lower production with increasing nutrient concentrations in lakes has originally been predicted by the "paradox of enrichment" hypothesis and explained by increasing oscillations between predator and prey (zooplankton and phytoplankton) causing instability of the system (Rosenzweig 1971). The hypothesis has been supported by experimental studies (Holyoak 2000), but several investigations show that oscillations of the range predicted only rarely seem to occur under natural conditions. Persson et al. (1993) gave high predation pressure from higher trophic levels as possible explanation for reduction of these oscillations, Scheffer and de Boer (1995) spatial heterogeneity. Lake BÖrringesjön with its continuously high phytoplankton and low zooplankton densities throughout the investigation period is another example of small oscillations in a highly eutrophic system.

From the cited studies, which are based on either empirical results or model predictions, our results from Lake BÖrringesjön and Lake Krankesjön differ as the "paradox of enrichment" can be explained not by predator-prey interactions alone, but becomes obvious already on the level of primary production, i.e., within the prey level. Because of high self-shading and high respiration in deeper water, we expect that primary net production in lakes with a certain "critical depth range" often will decrease with increasing nutrient loading. Statements that phytoplankton primary production increases with increasing nutrient loading also in the hypertrophic range (e.g., Håkanson and Boulion 2001) have to be revised carefully, regarding the question whether net or gross primary production is under discussion. Investigations carried out by the ^{14}C method generally suffer from the drawback that net and gross production cannot be precisely distinguished in contrast to application of the oxygen method. Misinterpretations may be most serious under hypertrophic conditions because ^{14}C incubation periods can be kept very short and the results are close to gross production. With no information about respiration available, lake productivity in the sense of possible transfer to higher trophic levels may be seriously overestimated.

Neglecting respiration is a probable explanation for the fact that our results are different from other studies (Vadeboncoeur et al. 2001; Liboriussen and Jeppesen 2003) that show lower or equal primary production in the clearwater compared with the turbid state. Instead, we assume that net primary production generally decreases if

a lake switches from the clearwater to the turbid state. Because this shift in most cases takes place at a certain critical nutrient load (Hosper and Jagtman 1990; Jeppesen et al. 1990), this is, to our knowledge, the first example that lower nutrient loading is combined with higher primary net production and higher biomass of primary producers in a natural ecosystem.

As a consequence, increased nutrient loading to shallow lakes above a certain critical nutrient loading will probably not result in increased production of higher trophic levels. This assumption has already been made by Schiewer (1998) for shallow brackish water ecosystems and Kemp et al. (2001) after model calculations. Although higher fish CPUE with increasing nutrient concentrations has been reported for a number of shallow lakes (Jeppesen et al. 2000, 2005), incidental empirical evidence (*see* references summarized by Kemp et al. 2001) for lower fish yields under higher nutrient loading in both lakes and estuaries further supports this assumption. High fish biomass does not necessarily mean high fish production: Hypertrophic lakes are often characterized by high densities of cyprinids that consist of small, slowly growing individuals and consume their prey down to low densities (Stenberg and Persson 2006), thereby preventing an efficient energy transfer from phytoplankton to zooplankton. A switch from a turbid to a clearwater state is accompanied by a dominance shift from a pelagic to a benthic food chain and will increase the energy transfer to higher trophic levels (Hecky and Hesslein 1995). Generally, trophic transfer efficiency has been assumed to be optimal at intermediate nutrient conditions (Kemp et al. 2001; Jeppesen et al. 2003). We assume that this higher trophic transfer efficiency is the ultimate explanation for the increased production of higher trophic levels after the switch of Lake Krankesjön to the clearwater state.

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