Seasonal dynamics and depth distribution of *Planktothrix* spp. in Lake Steinsfjorden (Norway) related to environmental factors

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To investigate factors and mechanisms regulating toxin-producing populations of *Planktothrix*, we conducted a field study (2001–04) in the mesotrophic Lake Steinsfjorden, South-eastern Norway. The occurring species, *Planktothrix rubescens* and *P. agardhii*, had similar depth distributions and seasonal dynamics, both forming metalimnetic blooms in 10–14 m depth. By comparing the resource availability and temperature in Lake Steinsfjorden with demands determined in laboratory studies, temperature and light were identified as the most important factors controlling growth and depth distribution of *Planktothrix* spp. In addition, macronutrients, especially nitrogen, may have limited growth in periods. A lowering of nutrient supplies over time could in addition to the prevailing suboptimal temperature and light conditions prevent the population of *Planktothrix* spp. from forming blooms. On two occasions, a major decrease in *Planktothrix* spp. abundance in the open water could be linked to a transport towards the banks of Lake Steinsfjorden with subsequent decomposition in the littoral zone. Our results show that the depth distribution and seasonal dynamics of *Planktothrix* spp. in Lake Steinsfjorden is controlled by environmental factors in a similar way as in other Nordic, Central European and North American lakes.

**INTRODUCTION**

Cyanobacterial blooms have become a worldwide phenomenon, and are associated with a number of problems, mainly due to their production of toxic compounds. These so-called cyanotoxins have caused adverse effects in wild and domestic animals, and have led to human fatalities (Chorus and Bartram, 1999). Blooms of toxin-producing cyanobacteria receive increased attention when developing in municipal water supplies and inland waters used for recreational activities.

Most planktonic cyanobacteria contain gas vesicles enabling cells to regulate their buoyancy, and to maintain a certain vertical position in response to physical and chemical factors (Reynolds, 1987). Because cyanobacteria can accumulate at a certain depth, the populations are often observed as blooms in a layer of a stratified water column (Reynolds et al., 1987; Walsby, 1994). According to Mur et al. (Mur et al. 1999), various physiological properties have given rise to different ecostrategists of bloom-forming cyanobacteria. The most common type forms blooms in the epilimnion of eutrophic lakes and is represented by various genera, including *Microcystis*, *Anabaena* and *Aphanizomenon*. Cyanobacteria adapted to low light conditions, especially the red variants producing the pigment phycoerythrin, may bloom in the metalimnion.
These blooms are usually dominated by toxin-producing filamentous species of the genus *Planktothrix*, and is typically encountered in sub-alpine lakes in Europe, exemplified by Lake Zürich (Thomas and Märki, 1949) and Lake Lucern (Zimmermann, 1969) in Switzerland, Lake Mondsee (Dokulil and Jagsch, 1992) in Austria, Lac du Bourget (Jacquet et al., 2005) and Lake Nantua in France (Feuillade, 1994), as well as in several lakes in Germany (Wiedner et al., 2001; Padišák et al., 2003) and in the Nordic countries (Skulberg, 1978; Lindholm and Meriluoto, 1991; Willén and Mattsson, 1997). This phenomenon is also known from North American lakes (Edmondson, 1970; Klemê, 1976; Konopka, 1982a; Konopka et al., 1993). Metalimnetic blooms of toxin-producing *Planktothrix* have raised some concern as they often appear as a response to lake restoration or they remain a problem despite costly measures to increase water quality (Feuillade and Druart, 1994; Buergi and Stadelmann, 2000; Ernst et al., 2001; Jacquet et al., 2005).

In addition, surveys of toxic cyanobacterial blooms have shown that metalimnetic blooms dominated by *Planktothrix* produce the highest level of toxins per biomass (Fastner et al., 1999).

*Planktothrix* can grow and survive in the metalimnetic zone because its requirements for irradiance and temperature are low compared to other phototrophic organisms (Van Liere, 1979; Feuillade et al., 1992). Also, in this layer the availability of nutrients may be good, and there is limited competition with other photosynthetic organisms. Since *Planktothrix* can grow under low irradiances, it can also maintain a population under low light conditions and/or deep circulation in autumn and winter (Walsby and Schanz, 2002). However, due to the limiting irradiance, and temperature conditions of the metalimnion, the growth rate of *Planktothrix* is slow (exemplified by an average net specific growth rate of 0.48 day⁻¹ for the population of *Planktothrix rubescens* in Lake Mondsee, Austria, Dokulil and Teubner, 2000).

Most studies on the environmental factors that control the growth and distribution of *Planktothrix* populations have been done in central-Europe. However, differences in climatic conditions raise the question of whether the growth and distribution of such populations in Norwegian lakes are regulated in the same manner. Answering this question is of importance since these lakes are often used for public water supply and/or recreational purposes.

The present study was carried out in Lake Steinsfjorden in South-eastern Norway. It has a natural population of red and green forms of *Planktothrix* spp. that form blooms in the metalimnion during summer, and sometimes accumulate in association with the ice cover in winter (Skulberg, 1964; Edvardsen, 2002). Lake Steinsfjorden has also been the object of extensive limnologically investigations, see e.g. (Strom, 1932; Skogheim and Rognerud, 1978). The lake is no longer used as a drinking water supply, but agricultural irrigation, fishing and several recreational purposes are important. A continuous monitoring programme was initiated by the Norwegian Institute for Water Research (NIVA) in 1997 to observe the occurrence of cyanobacteria and cyanotoxins in the lake (Edvardsen, 2002). Strains of both *P. rubescens* and *P. agardhii* isolated from Lake Steinsfjorden have been shown to produce toxins of the type microcystins, in addition to other bioactive peptides (T. Rohrlack, B. Edvardsen, R. Skulberg, et al., unpublished results). A need for a risk assessment has evolved. In order to be able to make predictions about the occurrence and distribution of toxic *Planktothrix*, this study aims to improve understanding of environmental factors that control them.

**METHOD**

**Study site**

Lake Steinsfjorden is situated in the South-eastern part of Norway (60°05’N, 63 m altitude). It is a dimictic, mesotrophic and elongated lake (7.9 km long and 2.6 km wide) with an area of 13.9 km², a total volume of 142 × 10⁶ m³, maximum and average depths of 24 and 10.2 m, respectively, and with a water retention time of 4.6 years (Strøm, 1932; Skogheim and Rognerud, 1978). During the period of thermal stratification, the lake is divided into three layers: epilimnion (0–7 m), metalimnion (8–14 m) and hypolimnion (15–20 m) which hold, in average, 60, 29 and 11%, respectively, of the total lake volume. The catchments area is 63.7 km². Lake Steinsfjorden is connected to the larger and deeper Lake Tyrifjorden (121 km², maximum depth of 293 m) through a narrow and shallow passage with a low rate of water exchange (typically 1 m³ s⁻¹).

**Sampling**

Sampling (n = 33) was done at different time intervals in the deepest part of the lake (60°05’N, 10°19’E) in the period March 2001 to September 2004. Water samples were taken from every meter with a 3.4 L Limmnos water sampler (Limmnos Oy, Turku, Finland). Volume weighted composite samples for the epilimnetic and metalimnion layers were prepared according to the bathymetry of Lake Steinsfjorden in the laboratory the same day. Aliquots of the integrated samples were used for chemical
measurements and the analysis of the phytoplankton composition other than *Planktothrix* spp.

**Physical measurements and chemical analysis**

Vertical profiles of water temperature and dissolved oxygen concentration were measured by a model 58 oxygen probe (YSI, Yellow Springs, OH, USA) on each sampling date. Photosynthetically active radiation (PAR) was measured by a combination of a LI-190 quantum sensor (air), a LI-192 underwater quantum sensor and a LI-1000 data logger (LI-COR, Lincoln, NE, USA). Data of global radiation in the range 300–3000 nm, reported as hourly means (W m$^{-2}$, measured with a pyranometer, Kipp & Zonen CM 11, The Netherlands), were kindly provided by Bioforsk, station Hønefoss (60° 14′ N, 10° 26′ E). Nutrients were analysed by scalar autoanalysers according to Norwegian and ISO-standard methods; ammonia (NS-EN ISO 14911), nitrate (NS-EN ISO 10304-1), phosphorus (NS 4724) and particulate P (NS 4725), or by Carlo Erba elemental analyser 1106 for particulate N.

**Phytoplankton measurements**

Samples for the counting and identification of other phytoplankton than *Planktothrix* spp. were preserved with Lugol’s solution and 10 mL were sedimented for the inverted microscope technique according to Olrik et al. (Olrik et al., 1998). The taxonomic classification used herein followed the Süßwasserflora von Mitteleuropa, volume 1–24 (Ettl and Gaertner, 1985–99). The concentration of *Planktothrix* spp. was determined from filters and not from sedimented samples because green and red trichomes were not distinguishable when fixed with Lugol’s solution and secondly because the presence of gas vesicles hampered the sedimentation process. Samples were taken from every depth sample, by filtrating 100 mL of lake-water on a cellulose nitrate membrane filter with a pore size of 0.45 μm and a diameter of 40 mm (Sartorius AG, Göttingen, Germany). The filters were dried at room temperature overnight and stored in darkness until used. *Planktothrix* species were identified according to Suda et al. (Suda et al., 2002). Filament lengths of 750 μm were counted directly on the filters using a stereo microscope at 100× magnification (Nikon SMZ-10, Japan). The mean diameters of *Planktothrix* spp. were determined once by microscope measurements of 100 filaments for each species. Filament lengths unit counts and the mean filament diameter were used to determine the biovolume concentration.

The net specific growth rate of *Planktothrix* spp. in Lake Steinsfjorden 2001–04 was calculated as the natural logarithm of the phytoplankton biovolume increase from one sampling date to the next and dividing it by the number of days in between.

**Estimation of resources available to *Planktothrix* spp.**

**Irradiance**

In order to assess whether *Planktothrix* spp. in Lake Steinsfjorden was limited by irradiance at any time, underwater light climate was estimated for the period March 2001 to September 2004 based on measured vertical profiles of PAR ($n = 33$) and hourly means of global radiation, assuming that PAR constitutes 45% of global radiation (Kalf, 2002). Measurements of irradiance at different depths were expressed as fraction of surface irradiance and fitted to a log-linear model of depth, corresponding to the Lambert-Beer’s law of light attenuation. We assumed that the vertical light attenuation coefficient changed slowly compared to the fast daily fluctuations of irradiance, so that the light attenuation coefficient could be interpolated linearly between dates of measurements. Combining interpolated vertical light attenuation with time series of global irradiance allowed calculation of light at any depth and any time. The resulting matrix of irradiance as a function of depth and time was compared with the light demand of *Planktothrix* spp. for growth at half the maximum rate, 1 W m$^{-2}$ (Van Lier and Mur, 1979) and for 90% of the maximum growth rate, 10 W m$^{-2}$, calculated from the half saturation constant given by Van Lier and Mur (Van Lier and Mur, 1979) assuming Monod’s kinetics.

**Nutrients**

The availability of nitrogen and phosphorus to *Planktothrix* spp. was determined in two ways. One was the concentration of the dissolved inorganic macronutrients N and P in the water as ammonia, nitrate and phosphorus. The other was the particulate N and particulate P per biovolume *Planktothrix* spp. Values were compared with the cellular amount necessary for growth ($Q_0$) and for 90% of maximal growth rate ($Q_{90}$) according to the Droop-model from batch culture experiments run with the *P. agardhii* strain PT2 (Rohrlack and Utkilen, 2007). This method assumes that phytoplankton were the major source of particulate N and P in Lake Steinsfjorden and that the different phytoplankton groups have the same cellular amount of N and P.
RESULTS

General, physical and chemical conditions
In the period for the study (2001–04), Lake Steinsfjorden was ice covered from the end of December to the beginning of April followed by a period of vertical circulation. A thermal stratification started to build up in May and a stable thermocline could be identified from June to September (Fig. 1a). The epilimnion had surface temperatures above 20°C in July and August, while temperatures ranged from 10 to 14°C in the metalimnion during the same period. Autumnal cooling increased the thickness of the mixed layer gradually until the thermocline disappeared in October, followed by another complete overturn of the water column.

The oxygen saturation varied between 70 and 100% in the epilimnion and never declined below 20% in the meta- and hypolimnion.

The dissolved inorganic fractions of the macronutrients N and P were highly variable during the investigation period (Figs 2 and 3). The level of nitrate and ammonium were relatively high in March 2001 (Figs 2a and 3a, 21.1 μM in the epilimnion and 22.5 μM in the metalimnion) due to heavy rainfalls during the autumn of 2000. These levels decreased throughout the investigation period. The sum of nitrate and ammonium in the epilimnion was on average 2.8 ± 4.7 μM (mean value ± SD, n = 33) and under the detection limit (0.36 μM for ammonium and 0.07 μM for nitrate) on five occasions (Fig. 2a). The average phosphate level in the epilimnion (Fig. 2b) was 0.05 ± 0.04 μM and on six occasions phosphate was below the detection limit (0.03 μM). For the metalimnion, the sum of nitrate and ammonium (Fig. 3a) was on average 5.2 ± 5.1 μM and under the detection limit on two occasions, while the phosphate level (Fig 3b) was on average 0.06 ± 0.04 μM and undetectable at three occasions.

Phytoplankton community
The phytoplankton community in Lake Steinsfjorden was dominated by members of Cyanophyta, Chrysophyceae, Bacillariophyceae and Cryptophyta (Fig. 4). Planktothrix was often the only filamentous cyanobacterial genus found. Other cyanophytes found in addition were members of the genera Anabaena, Aphanocapsa, Snowella and Woronichinia. The Planktothrix spp. population was composed of the red form P. rubescens and the green form P. agardhii.

The average total phytoplankton biovolume was 0.7 ± 0.9 cm³ m⁻³ (mean value ± SD, n = 18) in the epilimnion and 1.5 ± 0.9 cm³ m⁻³ in the metalimnion in the period of summer stratification (June–September). The Planktothrix spp. fraction of the phytoplankton biovolume in the epilimnion was highly variable ranging from 0.4% in August 2002 (after a collapse of the population) to 98% in November 2003 with a mean of 38 ± 31% (mean value ± SD, n = 22) for the period 2001–2004 (Fig. 4a). In the metalimnion, the Planktothrix spp. fraction was higher on average (63 ± 27%) although it ranged from 8% in May 2001 to 97% in November 2003 (Fig 4b).

The seasonal dynamics of Planktothrix spp.
Planktothrix spp. were present on all sampling days through the years 2001–2004. In the middle of May, when a stable temperature gradient started to build up, the population of Planktothrix spp. accumulated in the metalimnion in 10–14 m depth, and was confined to this layer from June to August. As the upper mixed layer progressively reached higher depths through September, the population became transferred up into the surface layer. The metalimnietic peak flattened out and the population was evenly distributed in the water masses during circulation periods (Fig. 1c) in spring and autumn.

The maximum biovolume concentration of Planktothrix spp. recorded in the period 2001–04 was 4.1 cm³ m⁻³ at 11 m depth in November 2003. This population was decreased to less than half in January 2004 and accumulations of filaments were observed both floating just underneath and frozen into the ice cover. Probably filaments had floated up from below and entered into pockets of water inside the ice. In the microscope, the Planktothrix spp. appeared as an entanglement of filaments. After ice melting in April, large quantities of viable Planktothrix spp. filaments were observed in shallow areas and piling up on banks. A similar event took place between the sampling dates at the end of July and the beginning of August 2002, when the Planktothrix spp. biovolume at the deepest part of Lake Steinsfjorden was reduced from 0.70 to 0.06 cm³ m⁻³ and accumulations were observed along beaches at the southern end of the lake.

The net specific growth rate of Planktothrix spp. in Lake Steinsfjorden 2001–04 was estimated to a maximum of 0.07 day⁻¹ (doubling time of 7.7 d) in September 2002 and a minimum of −0.13 day⁻¹ in July–August 2002 following a collapse of the population (Fig. 5). The Planktothrix spp. population in Lake Steinsfjorden was dominated by P. rubescens (60–70%), while P. agardhii constituted around 30–40% in the period 2002–04 (Fig. 6). Both species had a similar depth distribution at
all times during the investigation period, although the \textit{P. agarðhii} fraction of the population increased to 50–70\% in 2004.

**Seasonal dynamics of \textit{Planktothrix} spp. in relation to environmental factors**

**Irradiance**

During the period of thermal stratification, the major part of the \textit{Planktothrix} spp. population was mostly found at depths receiving \(\leq 1\) W m\(^{-2}\) (Fig. 1b and c), the irradiance needed for half of maximal growth rate. The irradiance needed for 90\% of maximal growth rate, 10 W m\(^{-2}\), reached to about 5 m depth and just a minor part of the \textit{Planktothrix} spp. population. When the population circulated through the whole water column during circulation periods in spring and autumn, only the upper layer of 2–3 m received \(\geq 10\) W m\(^{-2}\), while the metalimnion received \(\leq 1\) W m\(^{-2}\).

**Nutrients**

On several occasions, the dissolved fractions of nitrogen and phosphorus were under or close to the detection limits in both the epi- and metalimnion (Figs 2a and b, 3a and b). This indicates a potential for nitrogen and/or phosphorus deficiency for the population of \textit{Planktothrix} spp. in Lake Steinsfjorden. However, although external resources of N and P were low, \textit{Planktothrix} spp. may grow on internal resources. The particulate fractions of N and P per biovolume of \textit{Planktothrix} spp. can be used to assess these storage levels, which in the epilimnion were under the \(Q_0\)-limits three and two times, respectively \((n = 22)\), and at the same time in July 2001 (Fig. 2c and d). This indicates that there have been occasions of N and/or P
deficiency for the phytoplankton in the epilimnion during 2001–04. Also in more than 50% of the sampling dates, the internal storages of N and P per biovolume of *Planktothrix* spp. were under the Q90-levels indicating suboptimal nutrient conditions. In the metalimnion, the internal storages of N and P were never under the Q90-limit, but under the Q90-levels 14 and 7 times, respectively (Fig. 3c and d).

**Fig. 2.** The epilimnetic availability of nitrogen and phosphorus to *Planktothrix* spp. in Lake Steinsfjorden, 2001–04. (a) The sum of ammonium and nitrate. (b) Phosphate. Stars indicate dates when concentrations were below the detection limit (0.36 μM for ammonium, 0.07 μM for nitrate and 0.03 μM for phosphate). Particulate N (c) and P (d) per biovolume of *Planktothrix* spp. The cellular amount necessary for growth (Q90) and for 90% of maximal growth rate (Q90) according to culture studies is represented as dashed and solid horizontal lines, respectively.

**Fig. 3.** The metalimnetic availability of nitrogen and phosphorus to *Planktothrix* spp. in Lake Steinsfjorden, 2001–04. See further text under Fig. 2.
DISCUSSION

The maximum specific growth rate obtained in culture experiments with *P. rubescens* (strain NIVA CYA 406) isolated from Lake Steinsfjorden was 0.75 day\(^{-1}\) (C. B. Halstvedt, T. Rohrlack, H. C. Utkilen, et al., unpublished results). In other culture studies, the maximum specific growth rate for *Planktothrix* spp. strains ranged from 0.12 to 1.15 day\(^{-1}\), depending on growth conditions and type of strain (Van Liere and Mur, 1979; Bright and Walsby, 2000; Davis and Walsby, 2002). Dokulil and Teubner (Dokulil and Teubner, 2000) calculated positive net biovolume changes of *P. rubescens* in Lake Mondsee, Austria from field data (net specific growth rate, day\(^{-1}\)) and it ranged from 0.001 to 0.316 with an average of 0.048 day\(^{-1}\). Based on field data in this study, the maximum net specific growth rate was estimated to 0.07 day\(^{-1}\) (Fig. 5), indicating growth limitations of the population of *Planktothrix* spp. in Lake Steinsfjorden in the period 2001–04, although loss processes were not studied in detail in this study.

When we compare light-energy demands from culture studies (Van Liere and Mur, 1979) with estimated available irradiance in the field, it can be assumed that the population of *Planktothrix* spp. in Lake Steinsfjorden was growing under limiting irradiance levels (Fig. 1b and c). During summer, the population in
Fig. 5. The net specific growth rate of the *Planktothrix* spp. population in Lake Steinsfjorden 2001–04.

Fig. 6. Depth profiles of biovolume concentration of (a) *P. rubescens* and (b) *P. agardhii* in Lake Steinsfjorden 2002–04. Yellow triangles mark the dates of sampling.
the metalimnion received only enough irradiance to grow at half of maximal growth rate. The irradiance was also shown to control the distribution of *Planktothrix* populations in other lakes, such as Crooked Lake, Indiana, USA (Konopka, 1982a) and Lake Zürich, Switzerland (Walsby and Schanz, 2002). At the same time, *Planktothrix* is known to be a low irradiance specialist that is adapted to grow at low irradiances. This ability provides an advantage not only for the *Planktothrix* filaments that aggregate in the stratified metalimnion during summer, but also for those in the epilimnion with decreasing irradiance during autumn when days become shorter, and for filaments transported into greater depths during winter (Walsby and Schanz, 2002; Davis et al., 2003).

Among cyanobacterial species, *Planktothrix* tend to tolerate the widest range of temperatures compared to *Microcystis*, *Anabaena* and *Aphanizomenon* (Foy et al., 1976; Post et al., 1985). However, in culture studies the optimum temperature for growth was 20–30°C (Foy et al., 1976; Van Liere and Mur, 1979; Davis and Walsby, 2002; Suda et al., 2002). In Lake Steinsfjorden, it was only in the upper meters of the epilimnion during the period of summer stratification that the temperatures reached 20°C or more (Fig. 1a). Most of the *Planktothrix* spp. population, however, was then to be found in the metalimnion which held 10–14°C. Thus, most of the population was growing at 6–20°C below optimal temperature conditions in the warmest period, which is comparable to the conditions in other European lakes with *Planktothrix* spp., such as Lake Zürich, Switzerland (Micheletti et al., 1998), Lake Pusiano, Italy (Legnani et al., 2005), Lake Geneva, Switzerland and France and Lac du Bourget, France (Jacquet et al., 2005).

In enrichment, experiments run with *Planktothrix* spp. from Lake Steinsfjorden, Lovstad (Lovstad, 1983) found indications of N limitation. Compared to minimum levels of N and P for maximal growth rate in culture studies (Rohrlack and Utkilen, 2007), the conditions of both the epi- and metalimnion in Lake Steinsfjorden 2001–04 were often below the limit necessary to achieve maximal growth rate. This was especially the case for the sum of nitrate and ammonium, also indicating N limitation (Figs 2c and 3c). However, one should take into account that the Q-values used in this evaluation are based on culture experiments run under optimal light and temperature conditions. Under the suboptimal conditions of Lake Steinsfjorden from 2001 to 2004, it is likely that the nutrient demand of the cells were lower than under optimal conditions of culture experiments, and therefore the population of *Planktothrix* spp. might have had enough N and P for growth after all. Reynolds (Reynolds, 1987) suggested that the stratification of *Planktothrix* spp. provides a means of maintaining biomass with minimum energy expenditure through a period in which growth in the epilimnion is severely limited by nutrient deficiencies.

Hitherto, the focus has been on environmental factors influencing growth and biovolume of the *Planktothrix* spp. population in Lake Steinsfjorden, but loss processes must also be considered. In the period January to March 2004, the population in the deepest part of the lake was decreased by 87% (Fig. 1c). When the ice melted in the beginning of April 2004, accumulations of *Planktothrix* spp. filaments were observed along the bank at the North-eastern part of the lake. A possible explanation is that the ice melting started in this part of the lake, heating the <4°C surface water and causing downwelling in this area. A compensatory current assumingly brought surface water from underneath the remaining ice, thereby transporting the part of the *Planktothrix* spp. population that was floating under the ice to the North-eastern part of the lake.

During the period of summer stratification of 2002, a 90% drop in the population biovolume of *Planktothrix* spp., from 0.70 to 0.06 cm³ m⁻³ was observed over three weeks. In the same period, *Planktothrix* spp. accumulated along beaches in the southern end of the lake, indicating that filaments had floated to the surface and drifted by wind to the banks. A similar collapse was observed in Lake Steinsfjorden during the summer of 2000 (Edvardsen, 2002), and Walsby et al. (Walsby et al., 1998) also observed that the population of *P. rubescens* in Lake Zürich decreased by 90–99% from May to June. Possible explanations on the cause of these population collapses include failure in buoyancy regulation, intensive grazing, parasite and virus attack.

These collapses cause profound changes in the population, but there are also loss processes on a smaller scale. We have not studied the phytoplankton biovolume loss through processes such as sedimentation, grazing, parasitism or dilutions, processes which vary with season and species and are therefore difficult to quantify (Reynolds et al., 1984). During the periods of summer stratification in 2001–04, around 10–20% of the *Planktothrix* spp. population was found in the hypolimnion (Fig. 1c), but the question is whether these filaments were dying and sinking out or if they later could have regained buoyancy and returned to the metalimnetic depth of 10–12 m. Since *Planktothrix* spp. are able to maintain their position in the metalimnion, one can assume that the loss by sinking out of the euphotic zone is small (Walsby, 1994). It is also suggested that *Planktothrix* is poorly grazed and rarely a subject to viral attack (Kurmayer and Jütten, 1999; Suttle, 2000). In
general, filamentous cyanobacteria are difficult to ingest for zooplankton because of the mechanical interference with the feeding apparatus (Gliswicz, 1990). The production of microcystins seems to be involved in the resistance to grazing (Blom et al., 2001).

In Lake Steinsfjorden, *P. rubescens* and *P. agardhii* coexisted and followed the same depth distribution pattern in the period 2002–04 (Fig. 6). This is an interesting finding since it is thought that the ability of *Planktothrix* to grow under low irradiance is related to the occurrence of the pigment phycoerythrin. From the results of the present study it appears likely that growth under low irradiances conditions and formation of blooms in the metalimnion do not necessarily require phycoerythrin. Besides, production of phycoerythrin consumes energy, and does not necessarily lead to a higher growth rate (Raven, 1984). Stomp (Stomp et al., 2004) demonstrated by culture experiments with a red and green form of marine Synechococcus-type picocyanobacteria that they coexisted because of different pigment composition enabling them to exploit their own niche of the underwater light spectrum.

There is disagreement in the literature on whether *Planktothrix* spp. have their main growth period when the lake is stratified in summer (Micheletti et al., 1998; Bright and Walsby, 2000), or when the lake is circulating in spring and autumn (Reynolds et al., 1984; Feuillade, 1994). Reynolds (Reynolds, 1987) suggested that *Planktothrix* spp. accumulate in the metalimnion due to nutrient limitation in the epilimnion in the summer, and that little growth occurs as it ‘aestivates’ between main periods of growth in spring and autumn when the lake is vertically mixed and nutrients become more available. Both in Lake Nantua, France (Feuillade, 1994) and in Crooked Lake, Indiana, USA (Konopka, 1982b) the peak in the *Planktothrix* spp. biovolume was not at the same depth as that of maximum photosynthesis. Micheletti et al. (Micheletti et al., 1998) on the other hand estimated a significant growth of the metalimnetic *P. rubescens* population in Lake Zürich, Switzerland during the period of summer stratification and showed that without this metalimnetic growth, little or no biovolume would have survived to support the autumnal increase. Davis et al. (Davis et al., 2003) concluded that *Planktothrix* spp. are not simply a low-irradiance specialist of either the summer metalimnion or during autumn mixing, but of both these periods. Growth of the population of *Planktothrix* spp. in Lake Steinsfjorden from 2001 to 2004 seems to be in agreement with the conclusions of Davis et al. (Davis et al., 2003) that the net growth rate estimated from the field could be positive during periods of both circulation and thermal stratification (Fig. 5).

This study has shown that to survive in a mesotrophic lake like Lake Steinsfjorden, *Planktothrix* spp. have developed adaptations to accumulate in the metalimnion during periods of thermal stratification and maintain a viable population all year round in the water column. This special adaptation/lifestyle seems to be the same as described for other *Planktothrix* spp. populations in Nordic, European and North-American lakes, despite significant differences in climatic conditions. Another indication of the similarity of these *Planktothrix* spp. lakes are the maximal population biovolume. The total population biovolume concentration in the water column can be calculated using the method of Walsby and Schanz (Walsby and Schanz, 2002) and for Lake Steinsfjorden in the period 2001–04; it varied from 0.6 cm$^3$ m$^{-2}$ in August 2002 up to 73 cm$^3$ m$^{-2}$ in November 2003. This is in the same order of magnitude as for the populations in Lake Zürich, 120 cm$^3$ m$^{-2}$ (Walsby and Schanz, 2002) and Blelham Tarn, 100 cm$^3$ m$^{-2}$ (Davis et al., 2003).

As already mentioned, *Planktothrix* is one of the bloom-forming genera of cyanobacteria with the highest toxicity potential (Fastner et al., 1999) and it is therefore important to know how to manage these populations, for preventing further blooms and predicting situations of high toxin production. This work shows that *Planktothrix* spp., although they are adapted to the limiting temperature and irradiance conditions of Lake Steinsfjorden, have very low net growth rates. It is likely that the occurrence of an additional stress factor, such as a limitation by nutrients, would exceed the ability of *Planktothrix* spp. to compensate loss processes and to form metalimnetic blooms.

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