Environmental conditions and the development of *Planktonema lauterbornii* Schmidle in phytoplankton of Karhijärvi, a lake in SW Finland

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In the warm summer of 1999, the filamentous green alga *Planktonema lauterbornii* Schmidle appeared among dominants in the phytoplankton of Karhijärvi, a lake located in SW Finland. In the cool and rainy summer of 2000, the species almost disappeared from the lake again. *P. lauterbornii* was found in Karhijärvi for the first time in 1994 when it appeared in small numbers. The occurrence of *P. lauterbornii* in fresh waters in the Baltic Sea region is known only in a few cases whereas more records are from brackish waters. This paper describes the chemical and physical environment of Karhijärvi and the species composition of phytoplankton in summer 1999 in comparison with long-term monitoring data of the lake. A general increase of air temperature and especially the mild winters during the 1990s probably favoured the northward invasion of the warm water species *Planktonema lauterbornii*.

Introduction

There are several statements in the literature of unexpected appearance and mass development of some phytoplankton species in lakes where these species have been earlier unknown or rare. On only a few occasions, this phenomenon could clearly be attributed to a single factor like the eutrophication of waterbodies (appearance of *Limnothrix redekei* (van Goor) Meffert in Lough Neagh described by Gibson (1993)), or to climatic warming (northward expansion of subtropical *Cylindrospermopsis raciborskii stated* by Padisak (1995)). In most cases the reasons for such outbursts have remained unclear. Besides factors directly favouring the development of

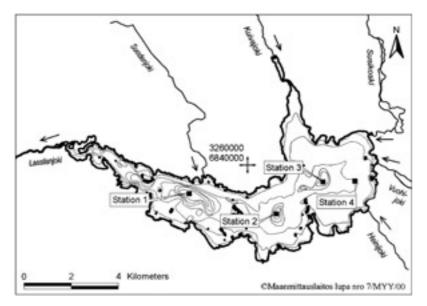


Fig. 1. Karhijärvi, connecting rivers and sampling stations.

particular species, the mechanisms are often much more complex and based on interspecific trophic relations or competition where the external factors play only a tuning role.

Karhijärvi is a shallow, comparatively young lake in the south-western part of Finland (Fig. 1 and Table 1). The lake was formed as a result of lowering the Litorina sea level less than nine thousand years ago (Alhonen 1991). The bedrock in the area of Lavia municipality, where the lake is located, is represented mainly by porphyritic granite, slate, grey granite and gneiss. Mineral soil is mostly coarse moraine, although there are vast plains of clay around Karhijärvi (Tarmio *et al.* 1971).

The Susikoski river is the most important inflow, which brings water to the north-east basin of Karhijärvi (Fig. 1). The Vuohijoki, a river coming from a series of narrow but quite deep lakes, enters about one kilometre south from the Susikoski river. The Heinijoki discharges from the south-west. The Kuivajoki

 Table 1. The main morphometric characteristics of Karhijärvi.

Area, km ²	34
Volume, 10 ⁶ m ³	75
Mean depth, m	2.2
Maximum depth, m	8
Catchment area, km ²	161.5

enters the northern bay of the lake, Riihonlahti, and the Suodenjoki from the north discharges to the narrower west part of the lake (Wartia 1907). These are the most important inflows, which, together with numerous smaller streams, collect water from the 161.5 km² area to Karhijärvi. The only outflow from the lake is via the Lassilanjoki from the western bay.

The water level has decreased considerably in the past. The first change was about 200 years ago and the latest in 1968 (Wartia 1907, anonymous 1978). The water in Karhijärvi is very turbid because of clay, which makes the water grey at high wind velocities (Wartia 1907). The lake is nowadays eutrophic. Diffuse loading from non-point sources together with effluent waters from the sewage treatment plant of Lavia Commune have been considered the main nutrient (N, P) inputs to the lake (Podsetchine and Huttula 1994). However, an intensive monitoring carried out from April to September 1993 (K. Krogerus and P. Ekholm, unpubl.) revealed that only less than 0.5% of the 6000 kg external load of P and 2% of the 81000 kg load of N was coming from the sewage treatment plant.

The present paper documents the occurrence and seasonal development of the filamentous green alga *Planktonema lauterbornii* Schmidle in the phytoplakton of Karhijärvi until the year 2000. The possible reasons of its unexpected mass development in 1999 are discussed, on the one hand, on the basis of monitored environmental conditions in the lake and, on the other hand, the facts published on ecological requirements and the distribution pattern of the species.

The phytoplankton species composition of Karhijärvi described in this paper was studied within the frames of a larger project aimed at following the formation, transportation and fate of phytoplankton patchiness.

Material and methods

The long-term data on water quality analysed in this paper have been collected in the course of routine monitoring by Pirkanmaa Regional Environment Centre (earlier Häme Regional Environment Centre) and Water Protection Association of the Kokemäenjoki. Older phytoplankton data from 1971 to 1990 were derived from monitoring records of Finnish Environment Institute. In 1993–1994 phytoplankton was analysed by Eija Salovaara and the unpublished results are used with her permission. Four of the sampling stations (named as Stations 1-4 in Fig. 1) were sampled more regularly. The most extensive time-series starting from 1964 and consisting of 194 records originates from Station 2 located at a 6.3 m deep site in the middle of the lake, between the islands Isosalo and Selkäsaari. Air temperature and wind data were obtained from Tampere-Pirkkala airport located at a distance of about 60 km from Karhijärvi.

Seasonal data were collected at the 7.4 m deep Station 1 from June to October 1999 and from May to October 2000. In August of both years, additional samples were taken from Stations 2 and 3. Chlorophyll a and phytoplankton samples were taken with a sampling tube, which integrated the 0-2 m surface layer. Altogether 29 quantitative phytoplankton samples were analysed. Water for other analyses was taken at 2 m from the surface and 1 m above the bottom. Temperature was measured at the depth of 1 m. The following variables were analysed: temperature, Secchi depth, turbidity, conductivity, pH, colour, oxygen, chlorophyll a, total phosphorus, total nitrogen, ammonium nitrogen and the sum of nitrite and nitrate nitrogen.

CTD-profiles were made twice, in the morn-

ing and in the afternoon of 17 August 1999 at Sampling Stations 1, 2 and 3 using the Hydrolab MiniSonde, which measured depth, temperature, salinity, conductivity, turbidity and oxygen.

Phytoplankton samples were fixed with Lugol solution and counted at $600 \times$ magnification using the Utermöhl (1958) technique. Algae were counted in transect along the chamber diameter until reaching the number of 400 counting units (cells, filaments, colonies). Large cells like those of *Ceratium hirundinella* were counted separately in the whole chamber. The mean volume of each species was estimated in all samples by approximating the shape of species to the closest simple geometric form. As the diameter of *Aulacoseira* filaments was very variable (from 2.5 to 30 μ m), it was divided for counting into 12 different size classes.

Results

Environmental conditions in the lake in 1999 compared with the long-term data

Turbid water and eutrophic conditions presented by several parameters analysed (Table 2) are distinctive features of Karhijärvi. The values given in Table 2 are from one metre depth. Deeper the colour, turbidity, and nutrient concentrations were normally higher.

All turbidity values measured in 1999 exceeded 5 FTU, which is considered to be the limit for turbid water (Oravainen 1987). The highest values were perceived in July whereas water at the depth of six metres was much more turbid than at two metres. Conductivity was within the common range for Finnish waters: around 5.7 mS m⁻¹ during summer with a slight increase in autumn. Long-term data show a slight decreasing trend in the conductivity in Karhijärvi (Fig. 2).

The pH was higher than 7 in 1999 and reached its maximum in September together with chlorophyll *a* indicating high phytoplankton production. The water colour at two metres varied between 60 and 120 Pt mg l^{-1} decreasing during the sampling period. At six metres the colour was 150 Pt mg l^{-1} in the beginning of July, otherwise it was quite similar at both depths.

According to Oravainen (1987) these values are typical for highly humic, brown waters. Secchi depth was changing between 0.7 and 1.1 m. The chlorophyll *a* values varied between 17 and 31 μ g l⁻¹ during the three summer months, but the highest value (41 μ g l⁻¹) was measured in September. Chlorophyll *a* values perceived are typical for eutrophic and highly eutrophic waters (Oravainen 1987).

Increasing trends in air temperature could be revealed in the time-series from the last quarter of the 20th century (Fig. 3). During the period 1988-2000 both the summers and winters were on average significantly warmer than in the period 1975–1987 (two-sided *t*-test, p = 0.0454for summer, p = 0.0009 for winter). The summer of 1999 was warm and the water temperature exceeded the long-term mean value. The highest temperature of 22.7 °C was measured on the 1st of July. During the intensive sampling campaign in August 1999, the temperature was almost the same at all sampling stations; there was no distinctive vertical stratification either. The difference between surface and bottom temperatures was usually less than 1 °C. The weakness of thermal stratification also explains the similarity of other parameters measured at the depths of two and six metres. The lake was well oxygenated with a saturation level usually exceeding 80% at six-metre depth except on 1st of July, when the saturation was only 16%.

The concentration of total phosphorus (TP) was also typical for highly eutrophic waters (Oravainen 1987). The mean value at two-metre depth was 59 μ g l⁻¹ during the sampling period

in 1999. The lowest value (38 μ g l⁻¹) was measured in October and the highest (76 μ g l⁻¹) at the end of June. Values were normally slightly higher at the depth of six metres. The total nitrogen (TN) values were typical for humic waters, around 700 μ g l⁻¹. In summer the values of inorganic nitrogen were low (4–45 μ g l⁻¹; 1%–7% of TN) indicating effective uptake by phytoplankton. The TN:TP ratio at two-metre depth varied between 10 and 18 (mean 13). The ratio increased during summer, but still neither of the nutrients clearly proved to limit phytoplankton growth.

The weather was calm (wind speed $0-5 \text{ m s}^{-1}$) before and during the measurement campaign on 16–18 August. However, there were big changes in the wind direction: during 11–13 August it blew nearly from the west, i.e. across the longer axis of the lake, but just before sampling it turned north-east and kept this direction from evening 14th until noon 17th of August. Then it suddenly turned back west.

The CTD-profiling made on 17th of August 1999 showed big changes in turbidity (Fig. 4). In the morning of 17th of August, the turbidity was the lowest at Station 3 but in the afternoon it was the most turbid of the three stations. Station 2 had a slight turbidity peak at the depth of 1 m in both measurements. The profiling showed a constant salinity of 0.03 ppt and conductivity of 5 mS m⁻¹ at all stations and at all depths, except the bottom layer at the deepest Station 1 where it reached 6 mS m⁻¹. The oxygen saturation was high and fell below 90% only in the deepest layers at Station 1.

included).						
Variable	Unit	Depth (m)	Range	Average	Number of samples	
Colour	mg Pt I⁻¹	1	27–200	96	81	
Secchi depth	m		0.3–2.6	1.1	82	
Turbidity	FTU	1	1.5–17	6.2	59	
Conductivity	mS m⁻¹	1	4.8–11	7.3	82	
Total phosphorus	µg l⁻¹	1	15–83	43	56	
Total nitrogen	$\mu g I^{-1}$	1	500-2 000	945	59	
Chlorophyll a	mg m⁻³	0–2	10–63	33	25	

 Table 2.
 Water quality parameters as measured at Station 2 in Karhijärvi in 1964–1993 (winter data included).

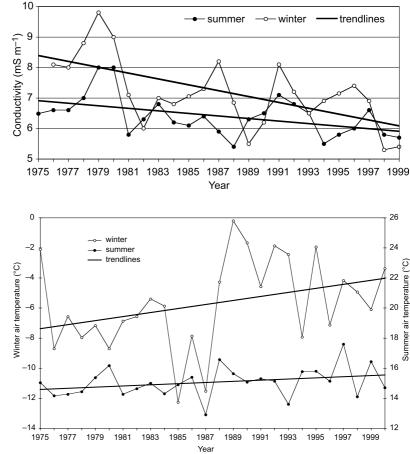
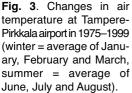


Fig. 2. Changes in conductivity at 1 m depth in Karhijärvi in 1975–1999 (winter = January or February, summer = July or August).



Phytoplankton assemblage

General composition and seasonal dynamics

The phytoplankton composition of Karhijärvi was rather diverse. Altogether 105 taxa were identified in 29 samples taken in 1999–2000. In the profound analysis by E. Salovaara, 142 taxa were identified in 1993 and 176 taxa in 1994. No single species achieved a monodominant position. Species of higher biomass, further named the dominating species, belonged to different algal phyla (Table 3).

Diatoms showed similar dynamics in all four years when phytoplankton was studied seasonally (Fig. 5). In May, the biomass of diatoms (around 5 g m⁻³) made up 80% or more of the total phytoplankton biomass and was nearly

totally built up by species of the genus Aulacoseira (A. granulata, A. granulata v. angustissima, A. islandica, A. italica, A. italica v. tenuis, A. ambigua). In summer, the proportion of diatoms fell below 20% while centric diatoms from genera Aulacoseira, Cyclotella and Stephanodiscus remained important within the group. In some periods, species with a delicate frustule (Acanthoceras zachariasii, Rhizosolenia spp.) could reach remarkable numbers. In autumn the relative role of diatoms increased again. In the cool summer of 2000, the biomass of diatoms was higher than in other years from which seasonal data were available (Fig. 5).

Among chlorophytes the role of *Planktonema lauterbornii* will be discussed separately. The remainder part of green algae, consisting of a variety of chlorococcales, some conjugates and

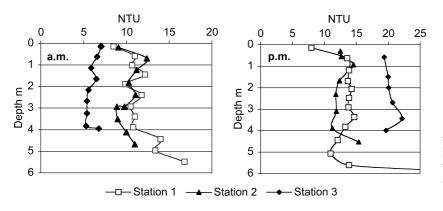


Fig. 4. Turbidity profiles from three stations in Lake Karhijärvi in the morning and in the afternoon of 17 August 1999.

Mougeotia sp., formed a minor group never exceeding 3% of the total biomass. The biomass and composition of this group remained unchanged in the *Planktonema*-rich year of 1999.

Planktonema lauterbornii appeared in Karhijärvi for the first time in 1994. It has not been recorded in the earlier material (35 summer phytoplankton samples from the period 1963–1993). In 1994, the species was found in small amounts (up to 0.015 g m⁻³) from the middle of July to October. In 1999, *Planktonema lauterbornii* developed a biomass of 4.6 g m⁻³ and was clearly one of the phytoplankton dominants in summer (Table 3). In the cool summer of 2000, the species almost disappeared again, reaching a biomass of only 0.24 g m⁻³.

Cyanobacteria increased during the diatom decline in June and contributed more than a half of the total biomass of the warm water phytoplankton community. Different species, mainly of filamentous form, built up the bulk of the biomass in different years. *Planktothrix agar-dhii* and *Aphanizomenon gracile* were the main dominants in 1993, *Anabaena mendotae* and

A. solitaria in 1994, while Planktolyngbya limnetica was the most abundant cyanobacterium in both 1999 and 2000. Actually, two species P. limnetica and P. subtilis occurred in 1999, but as they had an overlap in filament size, they were not distinguished but counted together as Planktolyngbya spp. In the year 2000, only P. limnetica was found. The role of chroococcales was variable: they were more numerous in the warm summers of 1994 (Aphanothece minutissima, Cyanodictyon imperfectum) and 1999 (C. imperfectum and Microcystis pulverea). Comparing the years 1999 and 2000 by weather conditions, different Anabaena species were favoured by the warm summer in 1999, whereas Planktolyngbya seemed to get an advantage in the cool and windy summer of 2000 (Table 3).

A small peak of dinoflagellates, caused mainly by *Ceratium hirundinella* or *C. furcoides* (in 1994), developed every year in the period of maximum temperature. Other phytoplankton groups like chrysophytes, cryptophytes and euglenophytes were usually represented in small numbers. Only in the year 2000, *Mal*-

Table 3. The percentage (average, minimum and maximum) of some algal groups and species in phytoplankton biomass in the years 1999 (warm summer) and 2000 (cool summer).

Algal group or species	1 Jul12 Oct. 1999	28 Jun.–21 Sept. 2000	
Aulacoseira spp.	14 (4–40)	19 (4–31)	
Cyanobacteria	42 (26–58)	45 (6-84)	
Anabaena spp.	6 (0–12)	3 (1–6)	
Planktolyngbya spp.	22 (1–38)	40 (14–66)	
Planktonema lauterbornii	30 (1–44)	0 (0–1)	
Chlorophyta without Planktonema	2 (0–3)	2 (1–3)	

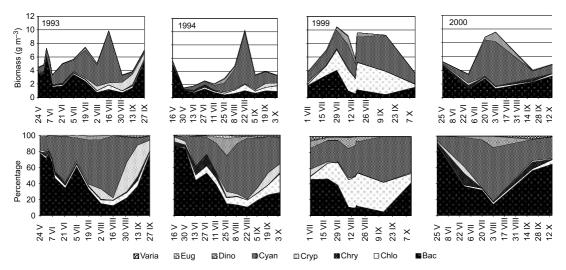


Fig. 5. Seasonal dynamics of phytoplankton biomass in Karhijärvi and the percentages of taxonomic groups. *Bac* – diatoms; *Chlo* – chlorophytes; *Chry* – chrysophytes; *Cryp* – cryptophytes; *Cyan* – cyanophytes (= cyanobacteria, blue-green algae); *Dino* – dinophytes; *Eug* – euglenophytes; *Varia* – unidentified small flagellates and spherical cells + some minor groups as Prymnesophyceae and Raphidophyceae.

lomonas spp. reached relatively high abundance in June and September.

filament length ($C_{var} = 8\%$).

Temporal pattern in 1999

The total phytoplankton biomass varied from 3.7 to 10.5 g m⁻³ (Fig. 5). The contribution of P. lauterbornii to the total biomass was only 1% at the first sampling on 1st of July but increased rapidly and remained at 30-40% until the middle of September. Daily measurements from 16th to 18th of August revealed rapid changes in the biomass of single species as well as in the total biomass. During 2 days the total biomass almost doubled. The increase could be observed at all three stations and in all dominating species except for Ceratium hirundinella, the biomass of which remained almost unchanged. The biomass increase in P. lauterbornii coincided with the decrease in the length of its filaments which are rather fragile and have a pronounced seasonal variation ($C_{var} = 18\%$) (Fig. 6). The broken filaments looked half decomposed in fixed samples. The sheathed filaments of Planktolyngbya were more endurable and did not break easily as indicated by the smaller variability of their

Horizontal pattern in 1999

Although the temporal variability exceeded the spatial one, there were some systematic differences between the three main stations. The highest biomass of *P. lauterbornii* and *C. hirundinella* but the lowest biomass of *Planktolyngbya* spp. occurred at Station 1 in the western part of the lake. The longest filaments of *P. lauterbornii* and *Planktolyngbya* spp. were found at Station 2 in the middle of the lake that might refer to the weakest resuspension. At Station 3 the biomass of *P. lauterbornii* was the smallest. All these differences could be followed also in the year 2000.

Discussion

Phytoplankton in Karhijärvi showed a species succession typical to eutrophic lakes. With increasing temperature the spring diatoms were replaced by a warm water community dominated usually by cyanophytes. In warm sum-

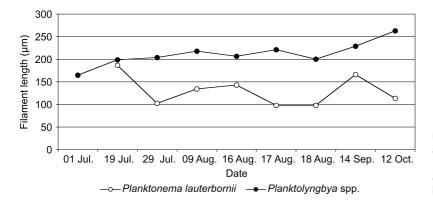


Fig. 6. Changes in average filament lengths of *Planktonema lauterbornii* and *Planktolyngbya* spp. in Karhijärvi in 1999.

mers (1994 and 1999) *Planktonema lauterbornii* appeared and gained a remarkable role in the summer community. In autumn, the proportion of diatoms increased again.

The large share of filamentous species and frequent occurrence of specimens of large sized benthic diatoms (*Surirella biseriata, Gyrosigma acuminatum*) in the plankton was due to strong wind mixing of the lake. Frequent mixing is the likely reason why scum-forming species like *Anabaena* were rare (Paerl 1988).

Year-to-year changes in dominating species are probably a sign of instability of the ecosystem. In the case of Karhijärvi it is remarkable that the newcomer among dominants was Planktonema lauterbornii, a species which is uncommon in Finnish fresh waters in general. P. lauterbornii is a nearly cosmopolitan species but seems to prefer warmer regions. Its occurrence has been reported from Lake Balaton in Hungary (Uherkovich 1989, Padisak et al. 1990), from Lake Grande de Estanya in Spain (Avila et al. 1984), from Lake Turkana in Kenya (Harbott 1982), from reservoirs on the Negro River in Uruguay (Bonilla 1997), from some high altitude lakes in the Ecuadorian Andes (Rott 1981), but also from Lake Alexandrina in Australia (Geddes 1984). The northernmost finding places of P. lauterbornii are located in the Baltic Sea region: Skuja (1956) reported it from Norrviken and some Swedish lakes. P. lauterbornii is more common in brackish waters (Tikkanen 1986). In 1984-1996, this species appeared among the dominants in the Curonian Lagoon, Lithuania (Olenina 1998). Hällfors (1984) describes P. lauterbornii as one of the dominating filamentous algae in intertidal rockpools in the Tvärminne archipelago, south coast of Finland. The hypothesis of the preference for more saline environment does not seem to be valid in the case of Karhijärvi where the conductivity has been decreasing during last 25 years (Fig 2).

The location of the main distribution area of the species in warmer regions, as well as the mass occurrence in shallow rock pools in which the water temperature exceeds the air temperature in summer by 6-10 °C (Hällfors 1984), reveal the termophilic character of the species. Its success in Karhijärvi in 1999 could probably be connected with the general trend of warming (Fig. 3), with the extraordinary warm summer and perhaps with the eutrophic status of the lake.

P. lauterbornii is a typical K-strategist: in all above cited cases the species was usually a coor subdominant in a phytoplankton community. In Lake Alexandrina (Australia), P. lauterbornii was even the monodominant accounting for more than 95% of algal cells (Geddes 1984). P. lauterbornii can co-dominate with several species of diatoms, cyanophytes, chlorophytes and dinophytes. So in the Curonian lagoon the principal species co-occurring with P. lauterbornii were Aphanizomenon flos-aquae, Stephanodiscus hantzschii and Diatoma tenuis (Olenina 1989), in Lake Balaton A. flos-aquae f. klebahnii, Planktolyngbya limnetica, Coelosphaerium kuetzingianum, Cyclotella comta, Nitzschia sp. and Crucigenia quadrata (Padisak et al. 1990), in the reservoirs of the Negro River Anabaena planktonica and Aulacoseira granulata (Bonilla 1997), in Lake Turkana Microcystis spp. and Botryococcus braunii (Harbott 1982) and in Lake Grande de Estanya different Chlorococcales. Hence, all species co-dominating with *P. lauterbornii* in Karhijärvi have been observed in one or another combination in different lakes except *Ceratium hirundinella*, a widely distributed dinoflagellate in fresh waters.

In Karhijärvi, the strongest competition seemed to occur between *P. lauterbornii* and another K-strategist, the cyanobacterium *Planktolyngbya limnetica*. In cooler summer the niche left free by *P. lauterbornii* was occupied by *P. limnetica*.

Moed and Hoogveld (1982) described a similar event of excluding competition between P. lauterbornii and filamentous blue-green algae in shallow, eutrophic, alkaline and peaty Lake Tjeukemeer. In 1970, 1975 and 1977, P. lauterbornii exceeded a density of 1000 filaments ml-1 in July-August when the usually abundant bluegreens failed to grow. Planktothrix agardhii capable of maintaining high numbers during summer was almost absent in July 1975 and August 1977, i.e. in the periods when considerable amounts of P. lauerbornii were observed. The figure added by the authors shows that two other species of blue-greens, Limnothrix redekei and Planktolyngbya limnetica, totally disappeared during mass occurrence of P. lauterbornii.

At the moment we can only speculate about the mechanism hidden behind the success of *P. lauterbornii* against blue-greens. It can hardly be light limitation as the blue-greens have been shown to be the superior competitors under conditions of low light, and also able to promote such conditions, as they can cause a higher turbidity per unit of phosphorus than other algae (Scheffer *et al.* 1997). However, the important role of *P. lauterbornii* in the benthic community of turbid Lake Balaton (Uherkovich 1989) indicates the ability of *P. lauterbornii* to grow at low light levels. Another explanation could be that the algae found on the bottom had sedimented from the overlying water column.

Scheffer *et al.* (1997) suggested photoinhibition as a mechanism that could explain the absence of filamentous blue-green algae in clear water. In sunny warm summers photoinhibition of blue-greens growth could favour other algae. However, the maintenance of a rather constant maximum biomass level in Karhijärvi, despite the change in dominating species, indicates nutrient limitation. Harbott (1982) suggested a relationship between riverine nitrogen supply and the biomass of generally N-limited phytoplankton in Lake Turkana where *P. lauterbornii* was a subdominant. Resistance to N-limitation might explain also the more frequent occurrence of *P. lauterbornii* in brackish waters, which are more often N-limited compared to fresh-water lakes (Valiela 1991). Both high temperature and rich nutrient conditions favour the development of *Planktonema* in eutrophic rock-pools fertilized by seabirds (Hällfors 1984).

According to Chiaudani and Vighi (1974) nitrogen is limiting phytoplankton when the TN:TP ratio is less than 10 and phosphorus, when the ratio is over 17. The TN:TP ratio in Karhijärvi changing from 10 to 18 implied neither of the nutrients to be clearly limiting.

The simultaneous increase in the biomass of dominating species and the shortening of the filaments of *Planktonema* during three days could probably be attributed to resuspension of already settled algae as it was observed at all stations. Certainly, the effect was combined also with the exchange of water masses at sampling stations. The change in wind direction could explain the rapid biomass increase between 16 and 18 August.

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