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Local environment overrides regional climate influence on regime shift in a north temperate lake

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Abstract Regime shifts in shallow lakes are typically characterized by submerged macrophyte (clear water regime) or phytoplankton (turbid regime) dominance. Climate warming is expected to affect water quality and facilitate turbidity in lakes, but we may also expect synergistic effects on organisms' interactions from climate and local specific dynamics in lakes. We here examined long-term changes in phytoplankton composition in July and August from 1980 to 2011 in a temperate shallow lake, Lake Krankesjön, a dataset including 21 years throughout a 31-year period. We hypothesize that although effects of the ongoing climate change are visible in our long-term data set, local specific dynamics override climate effects. We found that cyanophytes were the most abundant phytoplankton taxa among which small-sized colonial cyanobacteria were dominant. Both population density of small-sized colonial cyanobacteria and maximum water temperature increased over the period of study. However, the variations in the phytoplankton assembly were likely mainly related to three principal factors, including the local availability of nutrients, grazing from zooplankton, and possibly, an increasing trend in temperature. The first two factors are associated with the local specific dynamics, while the last with regional climate. Our long-term study showed that although there were potential climate warming effects on the phytoplankton community, local factors, such as biotic interactions and nutrient availability, were likely stronger drivers than climate warming in Lake Krankesjön at least over the last 30-year period.

Keywords Regime shift · Climate warming · Phytoplankton community · Biotic interaction · Nutrient availability

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Introduction

The relative roles of climate and local environments on regime shifts between submerged macrophyte and phytoplankton dominance under global warming have rarely been empirically quantified in lake ecosystems.

Regime shifts in shallow lakes are typically characterized by a shift in dominance between submerged macrophytes and phytoplankton (Brönmark et al. 2010; Carpenter et al. 2003; Genkai-Kato et al. 2012; Xu et al. 2014). Most studies on shallow lakes have focused on understanding the mechanisms behind alternative states (Jeppesen 1998; Moss et al. 1996; Scheffer 2004), but little work has been done so far to disentangle the mechanisms behind natural regime shifts in shallow lakes under regional or global climate envelopes (Brönmark et al. 2010; Scheffer and Jeppesen 2007).

At a local scale, the processes determining lake biological regimes include both top-down and bottom-up interactions, and thus, it is crucial to examine the relative roles of different factors at different levels (Bayley et al. 2007; Brönmark et al. 2010; Hargeby et al. 2007; Scheffer and Jeppesen 2007; Xu et al. 2012). In terrestrial grassland ecosystems, local food web interactions have been shown to override temperature effects (Suttle et al. 2007), and similarly, it has been experimentally demonstrated that changes in the local food web composition may alter the response to climate change (Hansson et al. 2013).

At a regional scale, freshwater lakes are recognized as sensitive indicators of environmental change, and many studies have confirmed the existence of a significant increase in temperature in aquatic ecosystems over the world (Gille 2002; Levitus et al. 2000; Schindler and Smol 2006). In temperate regions, temperature is predicted to increase 2–5 °C during the lifetime of the coming generation (IPCC 2013). Temperature increases are generally associated with altered standing stocks of biomass for primary producers (Blenckner et al. 2007), and a general prediction for lakes in a warmer world is that the spring phytoplankton biomass will increase (Gerten and Adrian 2002) and cyanobacteria will dominate over the seasons (Hyenstrand et al. 1998; Kosten et al. 2012; Robarts and Zohary 1987).

Lake Krankesjön is situated in southern Sweden (55°42′N, 13°28′E) approximately 20 km east of the city of Lund. Temperature series from Stockholm and Uppsala in southern Sweden indicate that summer climate warming happened in this region during the last century (Moberg et al. 2003), indicating the lake is under the stress of global warming. In most years during the recent two decades, the major part of the lake bottom was covered with submerged vegetation, mainly Charophytes. Vegetation community shifts have been recorded in Lake Krankesjön (Blindow et al. 1993; Hargeby et al. 1994, 2007), where one state was characterized by submerged vegetation and clear water, and the other by turbid water and sparse submerged vegetation. A major objective with this study was to examine the relative importance of climate versus local environmental factors to disentangle which drivers are responsible for the regime shift (and consequent changes in phytoplankton community), emphasizing on long-term changes. We examined the effects of nutrient and grazers on phytoplankton assembly, based on a long-term (31 years) data set. We hypothesize that although the effects of the ongoing climate change (increased temperature) are visible in our long-term data set, local specific dynamics (nutrient and grazing) override climate effects.

Materials and methods

Study sites

The drainage area of Lake Krankesjön covers 53 km^2, consisting mainly of open fields (about 70 %) and forests (15 %). The lake covers a surface of 3.4 km^2 and has a mean depth of 1.5 m and a maximum depth of 3 m (Hargeby et al. 1994, 2007). The planktivorous fish roach (*Rutilus rutilus*) is the most abundant fish species in the lake. Other common benthivorous species in Lake Krankesjön are rudd (*Scardinius erythrophtalmus*), tench (*Tinea tinea*), bream (*Abramis brama*), and white bream (*Blicca bjoerkna*). Piscivorous fish species common in Lake Krankesjön are perch (*Perca fluviatilis*) and pike (*Esox lucius*) (Hansson et al. 2007).

Monitoring data

We analyzed summer samples (July and August) from the lake in two periods: In the period 1980–1995, water samples were collected monthly, while during 2000–2011, samples were collected every 2 weeks. Sampling was performed in the water above the deepest point of the lake throughout the study (Fig. 1). The collected data set includes water chemistry and plankton density and biomass. We used maximal summer water temperature as an indicator of

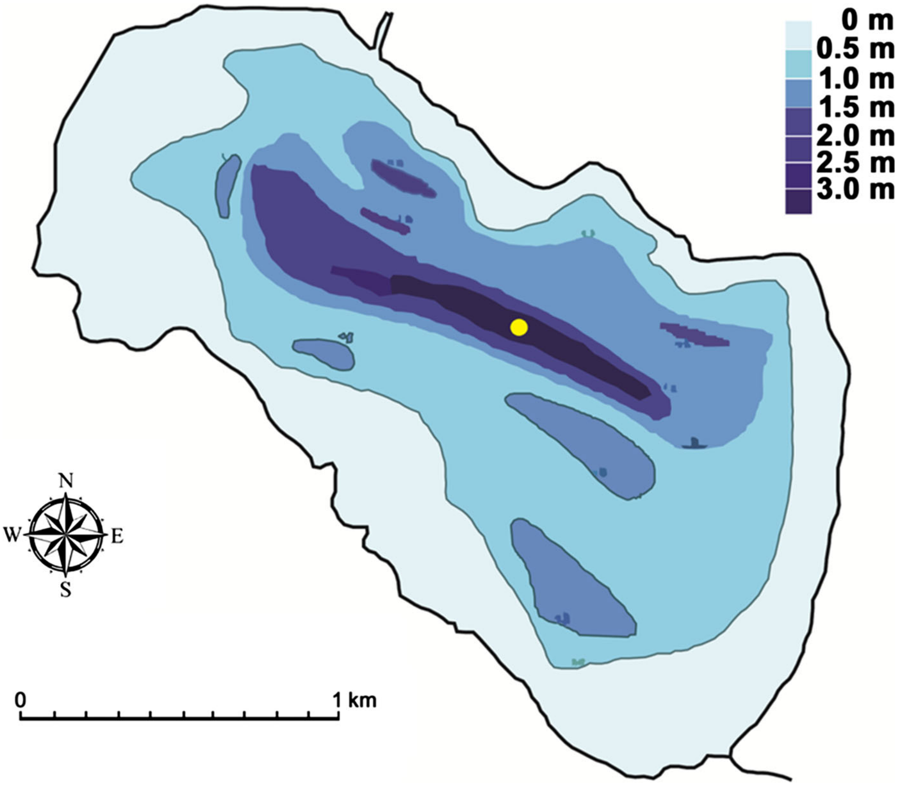

Fig. 1 Map of Lake Krankesjön in southern Sweden. The *yellow circle* represents the location of the long-term field collection of this study. (Color figure online)

regional climate warming. We used mean water clarity between July and August, measured as Secchi depth, as a state variable to differentiate between the clear and turbid regimes, because there was a significantly negative relationship between total phytoplankton density and Secchi depth in Lake Krankesjön ($r = -0.85, p < 0.01$). We defined turbid state as mean Secchi depth lower than 0.5 m, transient water state as Secchi depth between 0.5 and 1 m, and clear water state as Secchi depth larger than 1 m.

Water chemistry was analyzed according to standard procedures (auto-analyzer) on samples preserved frozen in 1 L polyethylene bottles and analyzed according to Blindow et al. (2000). Nutrients (total phosphorous and nitrogen concentrations, hereafter TN and TP) were analyzed on Aquatec Autoanalyzer. Chlorophyll *a* was analyzed on a fluorometer after extraction in 95 % ethanol (TD 700, Turner Design). Zooplankton was sampled using a 50-μm plankton mesh with 10 L of water and preserved with Lugol's acid solution for later enumeration at 20× magnification (Olympus SZ-40). After counting and length measurement of zooplankton, crustacean biomasses were calculated from either length-dry weight (Bottrell et al. 1976) or length-carbon regressions (Vasama and Kankaala 1990).

Phytoplankton sampling and enumeration

Water samples for phytoplankton analysis were taken with a 1.2-m-long Plexiglas tube with a diameter of 36 mm, filled into a 100-mL glass bottle, and preserved in Lugol's acid solution for further analysis in the laboratory. We selected summer (July and August) phytoplankton samples for analyses from 1980 to 2011. Samples from 1986, 1992–1994, and 1996–2002 are lacking, and total up to 21 years' samples are analyzed. Phytoplankton were examined at 400× magnification (Olympus CK 2 microscope) and determined to genus level using the Utermöhl method (Paxinos and Mitchell 2000). Phytoplankton were analyzed at the group level (i.e., cyanophytes, cryptophytes, chrysophytes, diatoms, chlorophytes, colonial cyanobacteria) and are expressed and plotted as cell/colony number per liter. The dinophytes and xanthophytes were identified but never exceeded 1 %

of the relative abundance and were therefore excluded from further analyses. Within Cyanobacteria, we assessed the abundance for small cell-sized colonies and filaments, and the counting accuracy was controlled by randomly recounting the sample by a coauthor, with the difference never exceeded 3 % relative abundance.

Statistics

We performed multiple linear regression using local (zooplankton biomass, TN and TP) and climate (maximum water temperature in July and August) variables as independent variables and phytoplankton density as dependent variables. The variables corresponding to each year in this long-term dataset were selected into the analysis, and the number of sample sizes reduced to sixteen for the linear regression. We then performed variable selection for best model (stepwise selection with both forward and backward methods) by exact Akaike information criterion. Finally, relative importance of local and climate variables on the phytoplankton density was estimated. Relative importance metrics for the linear model are based on the method of LMG, e.g., R^2 partitioned by averaging over orders (Lindeman et al. 1980), and the confidence intervals were calculated based upon 1,000 bootstrap datasets. Statistical analyses were performed using the R statistical computing package (R Development Core Team 2014).

Results

During the study period, the maximum water temperature (July–August) significantly increased ($r = 0.54$, $p < 0.01$, Fig. 2a). The mean Secchi depth was below 0.5 m before 1987 when the lake was at a turbid regime, and it increased after 1987 when the lake shifted to a clear water regime (Fig. 2b). TP and TN decreased from 1978 to 1987 and then fluctuated at relatively low levels during more than 15 years, from 1988 to 2004. Thereafter, both TN and TP showed an increasing trend until the end of the time series (Fig. 2c, d). Chlorophyll *a* (Fig. 2e), and the total phytoplankton density (Fig. 2f) was also higher during the turbid than during the clear water regime. The increasing trend of TP, TN, and chlorophyll *a* at the end of our time series may indicate another shift back to a more turbid state. Total zooplankton biomass showed higher values during the turbid, than during the clear, regime, and accordingly, zooplankton biomass was considerably higher at the end of the time series (2011), again suggesting a tendency for a regime shift.

The most abundant phytoplankton group in Lake Krankesjön was cyanophytes (Fig. 3a), accounting for 74–99 % of the total phytoplankton abundances throughout the monitoring period. The density of cyanophytes, diatoms, and chlorophytes showed similar long-term patterns (Fig. 3a, d, e). Cryptophytes was characterized by an opposite long-term trend compared with cyanophytes (Fig. 3b), whereas chrysophytes did not show any obvious trends (Fig. 3c).

Among the cyanophytes, the small cell-sized colonial cyanobacteria was the dominant group throughout the study period (mean = 82.5 %, Fig. 4). Next to small cell-sized colonial cyanobacteria, *Lyngbya* spp. was the dominant taxon in the beginning of 1980s, with maximum density of 53.5 % in 1981. After this period, the population of *Lyngbya* collapsed (Fig. 4) and did not recover during the investigation period.

Multiple linear regression further suggested that the local factors, such as nutrient availability (bottom-up effects) and zooplankton biomass (top-down grazing effect), significantly contributed to the phytoplankton density (Fig. 5), which is indicated by a measure of goodness of fit of linear regression (R^2) and its confidence intervals. Average temperature played a lesser role than the local variables (grazing and nutrients); nevertheless, the coefficients of determination of temperature were significantly greater than zero according to confidence intervals.

Discussion

Lake Krankesjön has shifted “spontaneously” from the turbid regime to clear water regime during our study period without any obvious manipulation or large-scale alteration in land use or nutrient input (Blindow et al. 1993; Hargeby et al. 2007). The turbid regime persisted for about 10 years and then shifted permanently to a clear state for 20 years. At the end of the investigation period, it showed a trend to shift toward turbid state again. Monitoring data on water chemistry during the shift show that the transient time

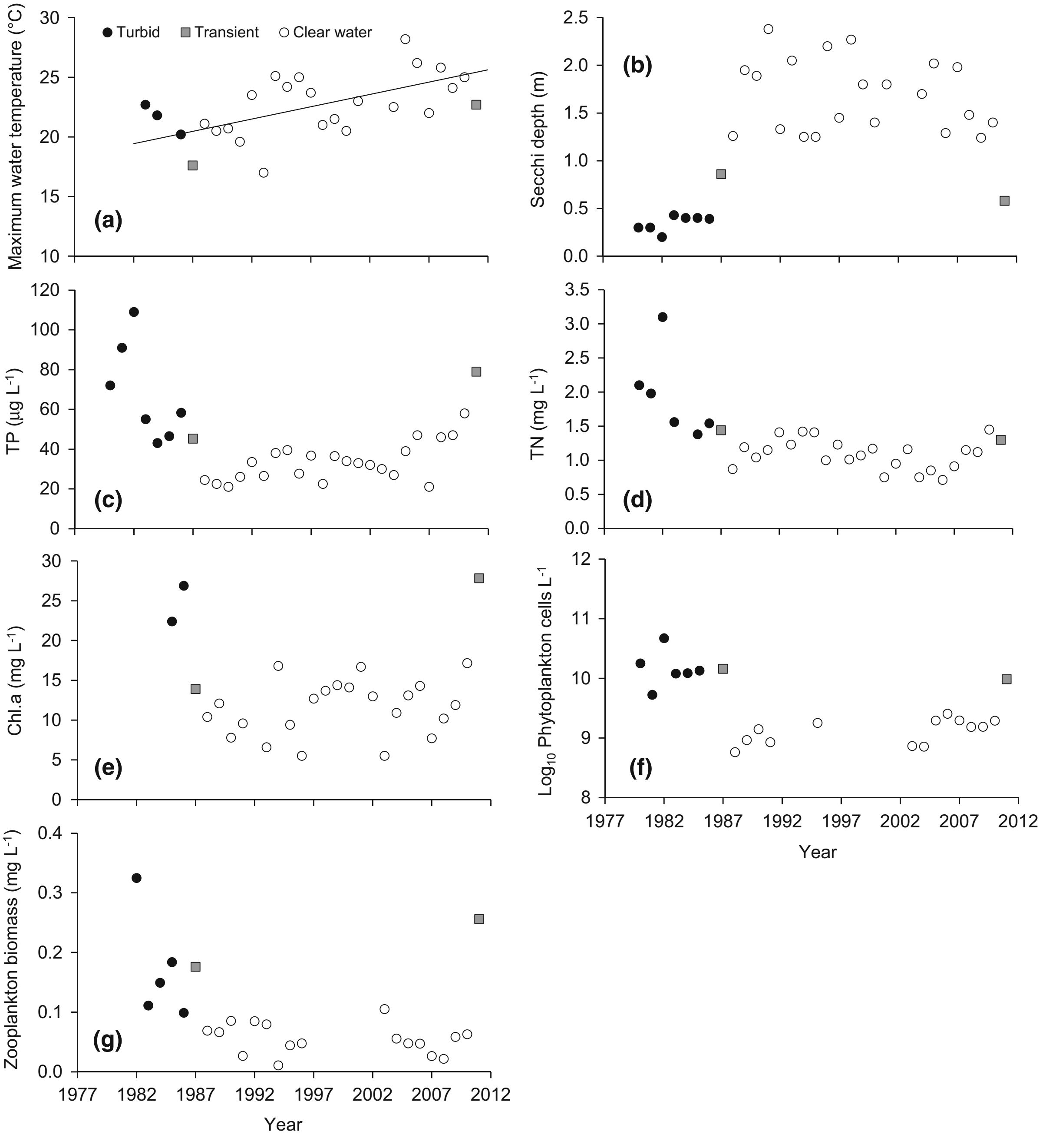

Fig. 2 Long-term dynamics of **a** maximum water temperature ($N = 26$), **b** Secchi depth ($N = 30$), **c** total phosphorous concentration ($N = 32$), **d** total nitrogen concentration ($N = 31$), **e** chlorophyll *a* ($N = 26$), **f** total phytoplankton density ($N = 21$), and **g** total zooplankton biomass ($N = 24$) in summer from 1980 to 2011 in Lake Krankesjön. Turbid years (*filled circles*) denote years of Secchi depth between 0 and 0.5 m, transient years (*gray squares*) denote years of Secchi depth between 0.5 and 1 m, and clear water years (*open circles*) denote years of Secchi depth larger than 1 m

periods between the clear water and turbid regimes were short compared with periods during which the system remained in a certain regime. The clear water regime showed significantly lower concentrations of TP and TN than the turbid period. Since there were no alterations in land use or nutrient input to the lake, a

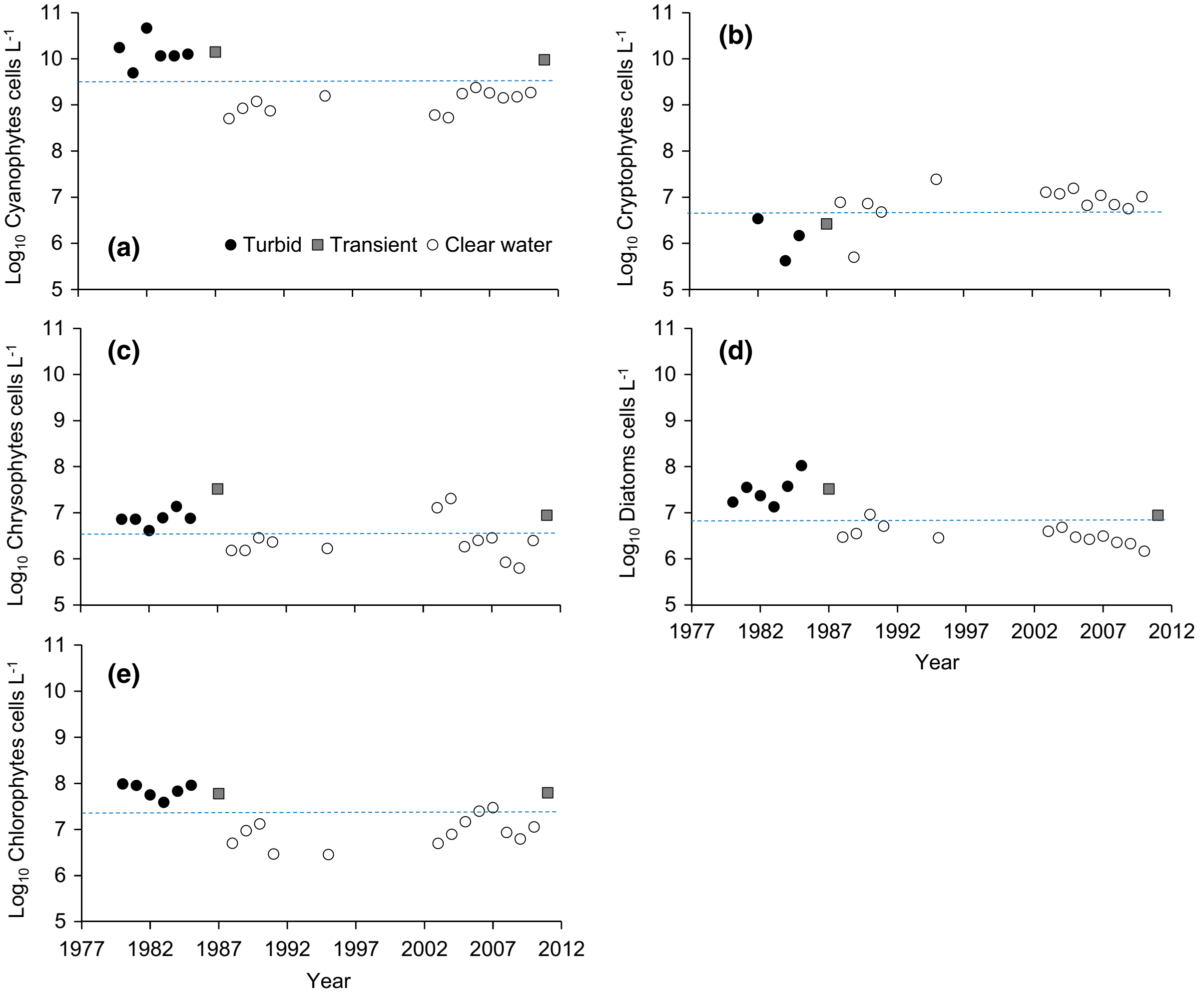

Fig. 3 Long-term dynamics of abundance of major algal groups in summer from 1980 to 2011 in Lake Krankesjön. **a** Cyanophytes; **b** Cryptophytes; **c** Chrysophytes; **d** Diatoms; **e** Chlorophytes. *Horizontal lines* are the average levels of algal abundances of the groups. Turbid (*filled circles*), transient (*gray squares*), and clear (*open circles*) water regimes were defined as in Fig. 2

likely reason for the differences in nutrient concentrations between clear and turbid regimes is nutrient utilization by primary producers. Likely nutrients became monopolized by the enormous biomass of macrophytes during the clear water regime, and that nutrients were made available for phytoplankton during the almost complete absence of macrophytes during the turbid regime (Hansson et al. 2010).

Regime shifts may be due to different mechanisms, such as a drastic impact on the system, or a stepwise change in external conditions (Scheffer and van Nes 2007). Moreover, a shift may not be triggered by a single factor or process, but rather by multiple stresses from both climatic and biotic variables (Hargeby et al. 2004; Scheffer et al. 2001). For the regime shift in Lake Krankesjön, the establishment and expansion of the submerged vegetation have likely been a major driving force (Blindow 1992; Blindow et al. 1993; Hargeby et al. 1994, 2007). Phosphorus is clearly another important factor triggering the local regime shift, since it affects phytoplankton growth potential, which is directly related to the turbidity of shallow lakes in many regions (Bayley and Prather 2003; Scheffer 2004). At the end of the study, there was a tendency for a shift toward a turbid state, which may have been a response to the increased TP levels in the

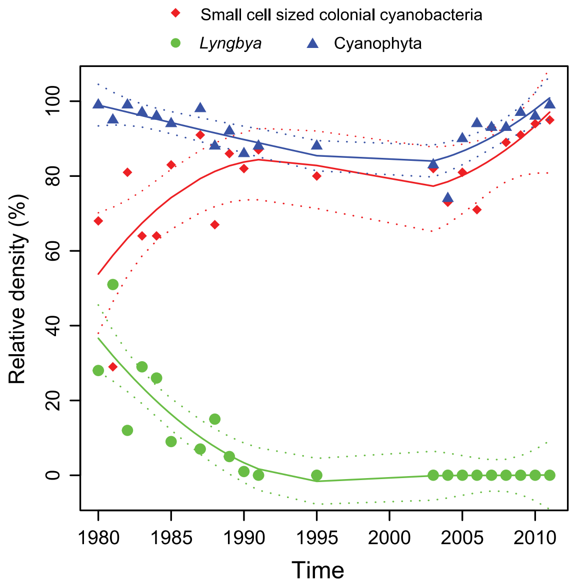

Fig. 4 The relative contribution (%) of abundant algal groups from 1980 to 2011 in Lake Krankesjön. Cyanophytes encompass both small cell-sized colonial cyanobacteria and *Lyngbya* taxa. *Solid lines* are LOWESS trend lines, which use locally weighted polynomial regression. *Dashed lines* are the 95 % confidence intervals

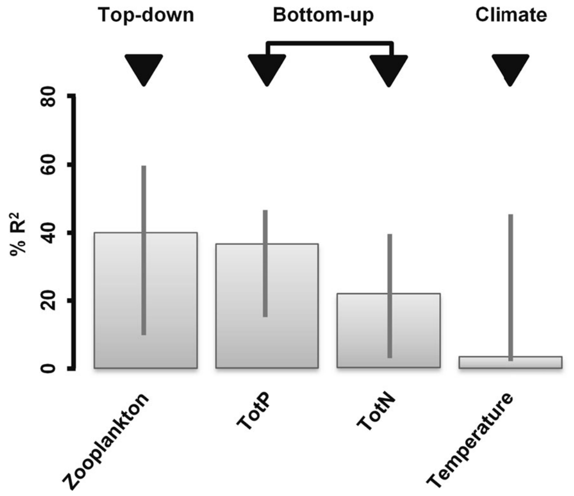

Fig. 5 Relative importance of local and climate factors on phytoplankton density. Relative importance metrics for the linear model are based on the method of LMG (R^2 partitioned by averaging over orders). *Bars* represent the confidence intervals of bootstrap measures of relative importance (1,000 samples)

preceding 5–7 years, which occurred without evident changes in chlorophyll or phytoplankton (see Fig. 2). This is in accordance with theory stating that gradual enrichment can cause the system to proceed along the clear water regime until the critical turbidity is reached at which macrophytes disappear, leading to a sudden jump into a turbid regime (Scheffer and van Nes 2007).

We found that phytoplankton density decreased, though community composition remained rather similar, with a dominance of cyanobacteria. Major summer interannual variations of different phytoplankton groups are typically related to two principal local forcing factors, namely the long-term variations in the nutrients and top-down effect from grazers (Fig. 5). These local forcing factors are closely related to regime shifts (van Donk and van de Bund 2002). *Lyngbya* increased in importance with TP in the 1980s, and this filamentous toxin-producing genus often shows remarkable invasive abilities in several types of aquatic ecosystems. Nutrient enrichment has been suggested as the major factor behind such invasions (Paerl and Fulton 2006), and accordingly, we here show that *Lyngbya* is losing its dominant position as water becomes clearer and less enriched in nutrients. The small-sized colonial cyanobacteria tended to dominate the cyanophyta and expressed a positive trend similar to the long-term variability in maximum water temperature, suggesting that warming may be a factor facilitating small-sized cyanobacteria (Vörös et al. 2009).

There was a significant positive relationship between phytoplankton density and zooplankton biomass. This suggests that top-down forces (predation) on zooplankton may not have been the major factor regulating the zooplankton community during the period investigated. Instead, zooplankton biomass was likely mainly regulated by food shortage, i.e., the abundance and availability of phytoplankton, and ultimately, by nutrient supply (Nicolle et al. 2011).

Our results also suggest that the water temperature effect on the phytoplankton community, at a time scale of 30 years, is subordinate to local, in-lake dynamics, but that it could be a potential driving factor behind changes in the phytoplankton assembly. The positive trend in the long-term dynamics of the maximum water temperature (July–August) in Lake Krankesjön follows regional summer climate warming (Moberg et al. 2003) and is also consistent with the increase in air temperatures in Europe (Auer et al. 2007) and on a worldwide basis (IPCC 2013).

In many shallow lakes, the proportion of cyanobacteria in phytoplankton communities has been shown to increase with temperature. For example, warmer lakes may not differ from cooler lakes in total phytoplankton biomass, but may show substantially higher cyanobacterial biomasses at a given nutrient concentration (Kosten et al. 2012). Simulated lake phytoplankton composition in a future warmer climate suggests that a future scenario with increased warming leads to a longer growing season for phytoplankton, slightly increased levels of total biomass, and a distinct shift in phytoplankton groups to favor nitrogen-fixing cyanobacteria at the expense of diatoms (Markensten et al. 2010). However, our results show that there were no significant relationship between percentage of total cyanophytes density and maximum water temperature, which indicated that local forces, such as nutrient competition between phytoplankton and macrophytes, may override climate change. Thus, in shallow lakes, which are not stratified, the indirect effects of increased temperatures may play a lesser role in shaping phytoplankton responses than in deep lakes, where increases in temperature may affect the phytoplankton community through increased stratification of the water column (Straile et al. 2003). However, the positive trend between the small cell-sized colonial cyanobacteria and maximum water temperature indicates a potential climate warming effect. This observation is strengthened by several studies showing that small-sized colonial cyanobacteria abundances were positively correlated with water temperature (Daufresne et al. 2009; Vörös et al. 2009).

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