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To bloom or not to bloom: contrasting responses of cyanobacteria to recent heat waves explained by critical thresholds of abiotic drivers

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Abstract Past heat waves are considered harbingers of future climate change. In this study, we have evaluated the effects of two recent Central European summer heat waves (2003 and 2006) on cyanobacterial blooms in a eutrophic, shallow lake. While a bloom of cyanobacteria developed in 2006, consistent with our expectations, cyanobacterial biomass surprisingly remained at a record-low during the entire summer of 2003. Critical thresholds of abiotic drivers extracted from the long-term (1993–2007) data set of the studied lake using classification tree analysis (CTA) proved suitable to explain these observations. We found that cyanobacterial blooms were especially favoured in 2006 because thermal stratification was critically intense (Schmidt stability >44 g cm cm^{-2}) and long-lasting (>3 weeks). Our results also suggest that some cyanobacterial species (*Anabaena* sp.) benefitted directly from the stable water column, whereas other species (*Planktothrix* sp.) took advantage of stratification-induced internal nutrient loading. In 2003, conditions were less favourable for cyanobacteria due to a spell of lower temperatures and stronger winds in mid-summer; as a result, the identified thresholds of thermal stratification were hardly ever reached. Overall, our study shows that extracting critical thresholds of environmental drivers from long-term records is a promising avenue for predicting ecosystem responses to future climate warming. Specifically, our results emphasize that not average temperature increase but changes in short-term meteorological variability will determine whether cyanobacteria will bloom more often in a warmer world.

Keywords Climate change · Cyanobacteria · Heat wave · Polymictic lake · Thermal stratification

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Introduction

Central Europe has recently experienced several extreme heat waves, most prominently the summer heat wave of 2003. Mean air temperature in the summer of that year exceeded the long-term average by around 3°C over a large part of Europe (Schär et al. 2004). Similarly, mean air temperatures in July 2006 were locally up to 5°C higher than on average (Struzewska and Kaminski 2008). Assessing the impacts of such extreme weather conditions on ecosystems is important, especially because summer heat waves are expected to occur more frequently in the future with climate change (Meehl and Tebaldi 2004; Schär and Jendritzky 2004). Aquatic ecosystems in Europe were strongly affected by the heat wave of 2003 (Jankowski

et al. 2006; Daufresne et al. 2007; Wilhelm and Adrian 2007). In particular, the incidence of harmful cyanobacterial blooms increased in some nutrient-rich water bodies (Paerl and Huisman 2008; Jöhnk et al. 2008). Terrestrial ecosystems were affected accordingly (e.g., Ciais et al. 2005).

Cyanobacteria pose a threat to water quality in many aquatic ecosystems (Huisman et al. 2005). This has led to intensive research on the factors that induce blooms of harmful cyanobacteria. As cyanobacterial species can differ quite substantially in terms of functional attributes (e.g., nitrogen fixation, buoyancy), it is difficult to determine the general conditions that promote blooms (Hyenstrand et al. 1998; Dokulil and Teubner 2000). However, it is well established that nutrient enrichment of water bodies (eutrophication) enhances the risk of cyanobacterial blooms (Huisman and Hulot 2005). High concentrations of total phosphorus (TP) and total nitrogen (TN) (Downing et al. 2001), as well as low supply ratios of nitrogen (N) to phosphorus (P) (Smith 1983) have been found to correlate with high cyanobacterial biomass in many systems.

More recently, scientists have turned their attention to the question of climate change as a potential catalyst for the extension and intensification of cyanobacterial blooms (De Senerpont Domis et al. 2007; Paerl and Huisman 2008). In addition to possible indirect effects, such as climate-induced nutrient enrichment, cyanobacteria are thought to be positively affected by rising water temperatures, as their high temperature optima for growth (e.g., around 28°C for the cyanobacterial species *Microcystis* sp.) give them a competitive advantage over other algae in warm water (Butterwick et al. 2005; Jöhnk et al. 2008). In eutrophic water bodies, buoyant cyanobacterial species are also known to benefit from the intensified and prolonged thermal stratification that often co-occurs with high water temperatures (Huisman et al. 2005). When the stability of the water column is high, their buoyancy enables them to float to the surface and out-compete other algae for light (Huisman et al. 2004).

Cyanobacterial blooms have been observed in Müggelsee, the nutrient-rich shallow lake studied here, during most summers since the start of a continuous monitoring program in 1979. The lake, located in north-eastern Germany, was affected by the Central European heat waves of 2003 and 2006. Physical conditions of the lake were similarly favourable for cyanobacterial blooms in both summers, with high water temperatures and relatively strong thermal stratification at times of anomalously hot weather. Nonetheless, cyanobacteria bloomed strongly only in the summer of 2006, whilst their biomass remained at a record low during all of 2003.

Wagner and Adrian (2009) recently used classification tree analysis (CTA) to identify the main environmental factors that determine the contribution of cyanobacteria to total phytoplankton biovolume in Müggelsee based on decadal records. They showed that high TP concentration was the best indicator of elevated cyanobacterial contribution, but that intensified and prolonged thermal stratification also promoted cyanobacterial dominance in this polymictic lake. Here we tested whether the critical thresholds of environmental factors determined by Wagner and Adrian (2009) could explain the surprisingly contrasting development of cyanobacteria during the hot summers of 2003 and 2006. We also used CTA to identify specific environmental factors that promote the dominant genera of cyanobacteria (*Aphanizomenon*, *Anabaena*, *Microcystis* and *Planktothrix*) and to characterise meteorological conditions that favour thermal stratification in the lake.

Methods

Study site and data basis

Müggelsee (52°26′N, 13°39′E) is a polymictic, shallow lake (mean depth 4.9 m, maximum depth 7.9 m) with a surface area of 7.3 km². An ongoing long-term sampling programme provides data on plankton, physical and chemical variables, with biweekly sampling in winter and weekly sampling in summer, beginning in 1979 (Driescher et al. 1993). Since the start of this sampling programme, the lake has experienced an increase in water temperature (around 0.5°C per decade in summer) and quasi-simultaneously a decrease in nutrient loading (Köhler et al. 2005; Huber et al. 2008). To restrict confounding effects of a change in trophic state and also due to missing data for TN prior to 1993, our analyses were restricted to 1993–2007, the eutrophic phase of the lake (as defined by Köhler et al. 2005). Intermittent thermal stratification during summer is common in this shallow lake, with consequent effects on water temperature, oxygen, internal nutrient load and phytoplankton development (Wilhelm and Adrian 2008).

Weekly profile measurements (0–5 m depth at 0.5 m intervals) of water temperature (°C) were used to calculate the Schmidt stability index (g cm cm^{-2}) according to Soranno (1997), which assesses the intensity of thermal stratification of the water column:

$$S_i = A_0^{-1} \sum_{s=0}^{z_{max}} (s - z*)(\rho_s - \rho*)A_s \Delta z \tag{1}$$

where A_0 is the surface area of the lake, A_s is the lake area at depth s; p_s is the density calculated from water temperature at depth s, $\rho*$ is the mean density; $z*$ is the depth

where mean density occurs, z_{max} is the maximum depth and Δz is the depth interval of 1 m.

We considered the lake to be thermally stratified when there was a >1°C difference in temperature between the surface water and water at a depth of 5 m. This criterion of stratification was taken from Wilhelm and Adrian (2008), who found that it best reflected the existence of a clearly distinguishable thermocline in Müggelsee. Using bathymetry data of the lake (Kozerski et al. 1999) and estimates of the thermocline depth (Wilhelm and Adrian 2008), we calculated that in up to 90% of the lake area (including areas of <5 m depth), the water column was indeed stratified when the chosen criterion of stratification was met. Despite the possibility of intermittent mixing, weekly measurements of water temperature are sufficient to assess the timing and duration of thermal stratification events in Müggelsee. Based on high-frequency data available from an automatic measurement station, Wagner and Adrian (2009) previously demonstrated that the duration of only one of six thermal stratification events lasting >1 week was misclassified in the period 2003–2006. Since cyanobacterial data were available only with a weekly time resolution, we were unable to investigate short-lived stratification events of <1 week duration, albeit possibly relevant for cyanobacterial species with high flotation velocities, such as *Microcystis* sp. (Ibelings et al. 1991).

Nutrient concentrations, TN (mg L^{-1}), TP (µg L^{-1}), dissolved inorganic N (DIN = $NO_3 + NH_4$, mg L^{-1}), soluble reactive P (SRP, µg L^{-1}), dissolved silicate (DSI, mg L^{-1}), molar ratios of N to P (TN:TP and NO_3:TP), and plankton abundance used in this study (see below) were determined from volumetrically weighted mixed samples. To construct a time-series of *epilimnetic* nutrient concentrations (subsequently denoted by subscript e), we only took into account the upper 3.5 m of the water column, corresponding to the average epilimnetic depth (Wilhelm and Adrian 2008), when the lake was stratified. Correspondingly, time-series of *hypolimnetic* nutrient concentrations (denoted by subscript h) were assembled by using data of the lower part of the water column (>3.5 m). In the absence of thermal stratification, all time-series contain data from the entire mixed water column.

Algal biovolumes (mm³ L^{-1}) were determined using standard limnological techniques based on microscope counts and individually measured cell volumes (Driescher et al. 1993). Data resolved to the phytoplankton species level were summed to yield biovolume time-series of total phytoplankton, total cyanobacteria, and the cyanobacterial genera *Aphanizomenon*, *Anabaena*, *Microcystis* and *Planktothrix*. These genera were dominant during the summer, contributing, on average, 65, 15, 10 and 5%, respectively, to total identified cyanobacterial biovolume in the summer of each year of the study period (1993–2007).

We used the available data on abundances (ind. L^{-1}) to construct time-series of the main zooplankton groups (cladocerans, daphnids, cyclopoid, calanoid and total copepods, bosminids, rotifers, and ciliates).

Mean weekly measurements of meteorological variables were provided by the nearby weather station Schöneiche (approx. 4 km to the northeast of Müggelsee) for 1993–2006. Weekly estimates of lake discharge (m³ s^{-1}) were available for 1993–2004. Summer was defined as the period from June to August.

Classification tree analysis

CTA is a nonparametric, recursive data-mining technique that produces a collection of rules, involving thresholds of key predictor variables, to best explain variability in a categorical response variable (for further details see Breiman et al. 1993; De'Ath and Fabricius 2000). These rules are hierarchically structured, yielding a list of predictor variables ordered according to explanatory power. When applying this method to data of cyanobacteria, Wagner and Adrian (2009) constructed categorical response variables that indicated whether the cyanobacterial contribution to total phytoplankton biovolume exceeded or fell below 10–80% (in steps of 10%). We focused on contribution classes 50 and 70% because these were found to be characteristic of bloom conditions. We adopted the classification rules identified by Wagner and Adrian (2009), including as key predictor variables TP$_e$, duration (S_d) and intensity (S_i) of thermal stratification (Table 1), to explore the reasons for the contrasting development of cyanobacteria in the summers of 2003 and 2006.

We assessed the predictive power of these rules by computing the proportion of cases in which cyanobacterial contribution was wrongly classified to lie below or above the chosen percentages (50 and 70%, respectively) for all weekly data collected between 1993 and 2007. We considered the classification rules appropriate for further analysis of the heat wave years 2003 and 2006 if these proportions were smaller than the proportions calculated based on a pre-defined null model. As our null model, we used the "go with the majority rule" by De'Ath and Fabricius (2000). Cyanobacterial contribution was predicted to always be smaller than the chosen percentage, in accordance with the majority of observations in the data set. The logic behind this approach was to accept only rules that produced fewer classification errors than a simple guessing rule (i.e., the null model). While the proportion of misclassifications for contribution class 50% was smaller than the null-model proportion (Table 1; 14 vs. 16%), this criterion was not fulfilled for contribution class 70% (17 vs. 10%). Thus, for further analysis we only used the subset of rules classifying cyanobacterial contribution smaller than

Table 1 Rules derived from classification tree analysis of Wagner and Adrian (2009) to predict cyanobacterial dominance in Müggelsee (defined as a cyanobacterial contribution to total phytoplankton biovolume of ≥50 and ≥70%, respectively); they comprise thresholds for epilimnetic total phosphorus concentrations (TP_e, µg L^{-1}), duration of thermal stratification (S_d, weeks), and intensity of stratification (Schmidt stability, S_i, g cm cm^{-2})

Cyanobacterial contribution	Symbol[a]	Rule	% Classification error[b]		
			Subset of rules	All rules	Null model[c]
<50%	▽	$TP_e < 70$	8 ($n = 510$)	14 ($n = 625$)	16 ($n = 625$)
	▼	$70 \leq TP_e \leq 215$ and $S_d \leq 3$			
≥50%	△	$TP_e > 215$	44 ($n = 115$)		
	▲	$70 \leq TP_e \leq 215$ and $S_d > 3$			
<70%	▽	$TP_e < 70$	5 ($n = 453$)	17 ($n = 564$)	10 ($n = 564$)
	▼	$70 \leq TP_e \leq 215$ and $S_i \leq 44$			
≥70%	△	$TP_e > 215$	66 ($n = 111$)		
	▲	$70 \leq TP_e \leq 215$ and $S_i > 44$			

[a] Symbols are for simplified reference in Fig. 3

[b] Percentage classification errors were calculated based on weekly data collected between 1993 and 2007

[c] For the null models, we assumed that cyanobacterial contribution was always <50% and <70%, respectively

Table 2 Rules resulting from classification tree analysis to predict the presence (contribution to total phytoplankton biovolume ≥10%) of cyanobacterial genera *Aphanizomenon*, *Anabaena*, *Microcystis* and *Planktothrix* in Müggelsee; they contain thresholds for total hypolimnetic phosphorus (TP_h, µg L^{-1}), total epilimnetic nitrogen (TN_e, mg L^{-1}), molar ratio of epilimnetic phosphorus to nitrogen ($TN_e:TP_e$), dissolved epilimnetic silicate (DSI_e, mg L^{-1}) and nitrogen (DIN_e, mg L^{-1}) and log-transformed abundances of rotifers (Rot, ind. L^{-1}), and copepods (Cope, ind. L^{-1}); For further abbreviations, see Table 1

Cyanobacterial genus	Class	Rule	% Classification error[a]		
			Subset of rules	All rules	Null model[b]
Aphanizomenon	Absent	$TP_h < 115$	10 ($n = 482$)	16 ($n = 637$)	24 ($n = 637$)
		$TP_h \geq 115$ and $TN_e < 1$			
	Present	$TP_h \geq 115$ and $TN_e \geq 1$	35 ($n = 155$)		
Anabaena	Absent	$S_i \leq 41.5$	3 ($n = 518$)	3 ($n = 529$)	4 ($n = 529$)
		$S_i > 41.5$ and $TN_e:TP_e > 27.5$			
	Present	$S_i > 41.5$ and $TN_e:TP_e \leq 27.5$	36 ($n = 11$)		
Microcystis	Absent	$TP_e < 251.5$	3 ($n = 606$)	3 ($n = 616$)	5 ($n = 616$)
		$TP_e \geq 251.5$ and $DSI_e < 6.6$			
		$TP_e \geq 251.5$ and $DSI_e \geq 6.6$ and $DIN_e \geq 0.22$			
	Present	$TP_e \geq 251.5$ and $DSI_e \geq 6.6$ and $DIN_e < 0.22$	10 ($n = 10$)		
Planktothrix	Absent	$TN_e:TP_e \geq 8.7$	3 ($n = 579$)	4 ($n = 596$)	5 ($n = 596$)
		$TN_e:TP_e < 8.7$ and Rot < 6.8			
		$TN_e:TP_e < 8.7$ and Rot ≥ 6.8 and Cope < 4.1			
	Present	$TN_e:TP_e < 8.7$ and Rot ≥ 6.8 and Cope ≥ 4.1	18 ($n = 17$)		

[a] Percentage classification errors were calculated based on weekly data collected between 1993 and 2007

[b] For the null models, we assumed that the specific cyanobacterial genus was always 'absent'

70%, which produced a classification error rate of a mere 5% (Table 1). One likely reason for the observed difference in classification power is the relatively rare occurrence of large blooms (cyanobacterial contribution >70%) as opposed to standard blooms (cyanobacterial contribution >50%) in the data set ($n = 56$ vs. $n = 100$; Table 1), thereby constraining the sample size upon which the 70% classification tree was constructed.

Since cyanobacterial species differ substantially in their environmental preferences, we ran additional CTAs to identify their specific promoting factors (Table 2). The dominant cyanobacterial genera were classified as 'present' or 'absent' when their contribution to total phytoplankton biovolume was <10 and ≥10%, respectively. Results on the most important predictor variables (leftmost variables in Table 2) were robust against setting the classification

Table 3 Rules resulting from classification tree analysis to predict the occurrence of thermal stratification in Müggelsee; they contain thresholds for incident radiation (IR, W m^{-2}), wind speed (WS, m s^{-1}), and air temperature (AT, °C)

Thermal stratification	Rule	% Classification error[a]		
		Subset of rules	All rules	Null model[b]
No	IR ≤ 173.9	10 ($n = 679$)	11 ($n = 728$)	14 ($n = 728$)
No	IR > 173.9 and WS > 3			
No	IR > 173.9 and WS ≤ 3 and AT ≤20.5			
Yes	IR > 173.9 and WS ≤ 3 and AT > 20.5	24 ($n = 49$)		

[a] Percentage classification errors were calculated based on mean weekly data collected between 1993 and 2006

[b] For the null model, we assumed that the lake was never stratified

limit alternatively to 2.5, 5, 7.5, 12.5 or 15% contribution to total phytoplankton biovolume [the only exception being when the classification limit was <7.5% for *Anabaena*; Electronic Supplementary Material (ESM) Table S1]. As potential predictor variables we used surface and mean water column temperature, intensity and duration of thermal stratification, lake discharge, epilimnetic and hypolimnetic nutrient concentrations and zooplankton abundances.

To identify the meteorological factors that determine the occurrence of thermal stratification in Müggelsee, CTA was again applied (Table 3). We used a categorical response variable indicating stratified or non-stratified conditions and included as predictor variables air temperature (°C), cloudiness (1–8), incident global radiation (W m^{-2}), wind speed (m s^{-1}) and relative humidity (%), which have been found previously to influence the thermal regime in Müggelsee (Wilhelm et al. 2006).

Classification trees were constructed using the Gini index as the splitting criterion, which is a common method for constructing classification trees (De'Ath and Fabricius 2000). Optimal tree size was chosen based on 100 cross-validation runs. Weekly data of the entire available time periods (1993–2006/2007) were considered, and predictive power was assessed using the same approach as for cyanobacterial classification rules. Error rates based on classification rules were always lower than error rates based on null models (Tables 2, 3), thereby validating the chosen rules. All computations were performed using MATLAB ver. 7.6.0 (The MathWorks, Natick, MA).

Results

Physical water conditions and contrasting development of cyanobacteria

The mean summer water temperature in 2003 and 2006 exceeded that in all other years (1993–2007), being around 1.6°C (2003) and 1.5°C (2006) higher than the long-term
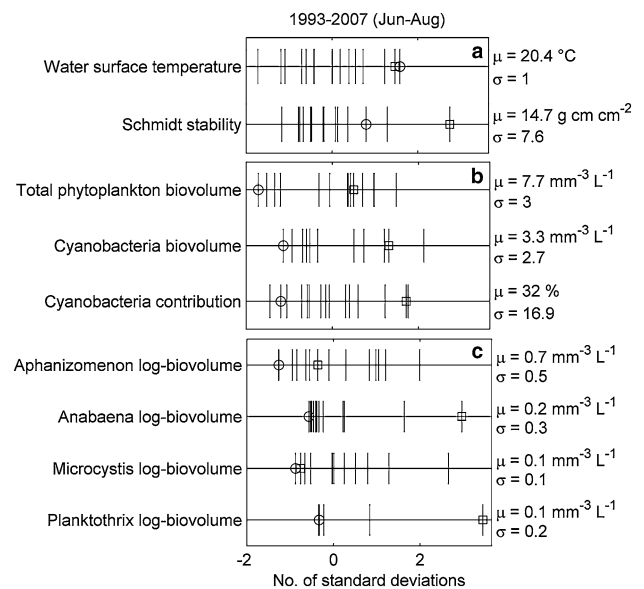

Fig. 1 Summer averages of selected variables of lake physics (**a**), aggregated phytoplankton (**b**) and cyanobacteria genera (**c**) in Müggelsee, Germany, for 1993–2007 (*vertical bars*), with special focus on the heat-wave years of 2003 (*open circles*) and 2006 (*open squares*). The averages were standardised by removing the long-term means (μ) and dividing by the long-term standard deviations (σ), both shown to the *right* of the figure. The value of Schmidt stability (thermal stratification intensity, S_i) intermediate to the values of 2003 and 2006 stems from 1994, which we did not include in our comparison of heat-wave summers because the mean water surface temperature was only 0.7 σ above μ

mean (μ) (Figs. 1a, 2a). Mean S_i (Schmidt stability) was especially strong in the summer of 2006 (2.7 standard deviations (σ) above μ), but was also relatively strong in 2003 (0.8 σ above μ; Fig. 1a).

Despite similarly favourable physical conditions during periods of hot weather, the development of cyanobacteria in the studied lake was strikingly different between years. In accordance with expectations, a bloom of cyanobacteria developed in the summer of 2006. Mean cyanobacterial biovolume as well as mean contribution to total phytoplankton biovolume was at the high end of values observed during the eutrophic phase of the lake (Figs. 1b, 2b).

In strong contrast, cyanobacterial biovolume, total phytoplankton biovolume and average cyanobacterial contribution were the lowest or second lowest on record in 2003 compared to all other years during the study period 1993–2007.

Environmental factors favouring cyanobacterial dominance

The thresholds of environmental factors identified by CTA were then used to investigate the surprising differences in the responses of cyanobacteria to the two heat waves. Except for five data points in 2003, the threshold-based rules correctly predicted cyanobacterial contribution to lie below or above the predefined limits (50 or 70%) in the two

summers (Fig. 3). The rules suggested that cyanobacteria were mostly inferior contributors to total phytoplankton (contribution <50%) in 2003, whereas dominance (contribution ≥50%) was predicted for most of the summer of 2006 (upward- vs. downward-facing triangles, Fig. 3a, b). Accordingly, cyanobacterial contribution was supposed to be <70% during much of the summer of 2003, but only rarely to reach this level in 2006 (Fig. 3c, d).

The most important predictor variable, TP_e, did not provide a clear explanation for the low contribution of cyanobacteria in 2003. TP_e concentrations below the lower critical threshold (<70 µg L^{-1}), i.e., very unfavourable for bloom formation, occurred in early summer of 2006, but never in 2003 (Figs. 2c, 3 white downward-facing triangles). After the breakup of thermal stratification at the end

Fig. 2 Weekly data from May (*M*) through November (*N*) during 2003 (*open circles, solid lines*) and 2006 (*open squares, dashed lines*) of water surface temperature (**a**), cyanobacterial biovolume (**b**), concentration of total epilimnetic phosphorus (TP_e) (**c**), Schmidt stability (**d**), concentration of total hypolimnetic phosphorus (TP_h) (**e**), molar ratio of epilimnetic nitrogen to phosphorus (TN_e:TP_e) (**f**). The weekly long-term means ±1 standard error (SE) of 1993–2007 are indicated in **a** by the *dotted line* and *shaded area*. Shading in **b** shows total phytoplankton biovolume (2003 *light grey shading*; 2006 *dark grey shading*). *Filled symbols* in **d** mark weeks in which the lake is considered to be thermally stratified. Thresholds contained in classification rules of Tables 1 and 2 are shown as *horizontal lines* in **c–f**
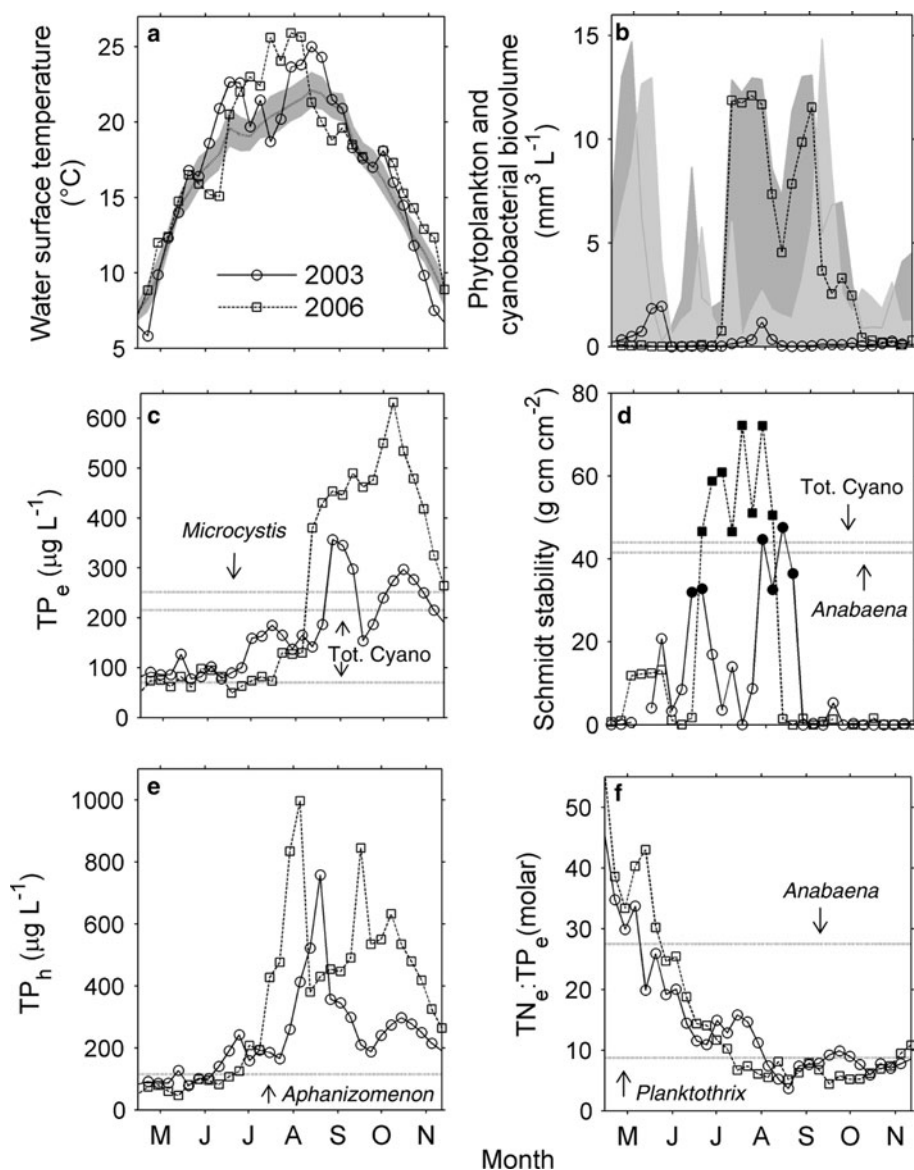
Fig. 3 Observed cyanobacterial contribution to total phytoplankton biovolume (*solid lines*) and rule-based predictions (*triangles*) for the summer of 2003 (*left column*) and 2006 (*right column*). Classification rules predict cyanobacterial contribution to be above (*upward-facing triangles*) or below (*downward-facing triangles*) the chosen percentages of 50% (**a**, **b**) and 70% (**c**, **d**), respectively (see legends in **a**, **c** and Table 1 for rules represented by *open* and *solid symbols*). Thresholds and units of total epilimnetic phosphorus concentration (TP_e), duration and intensity of thermal stratification (S_d and S_i, respectively) are shown in Fig. 2. Classification errors are marked with an *asterisk*. Predictions of cyanobacterial contribution >70% are not shown since average (1993–2007) error rates were extremely high in these cases (Table 1)
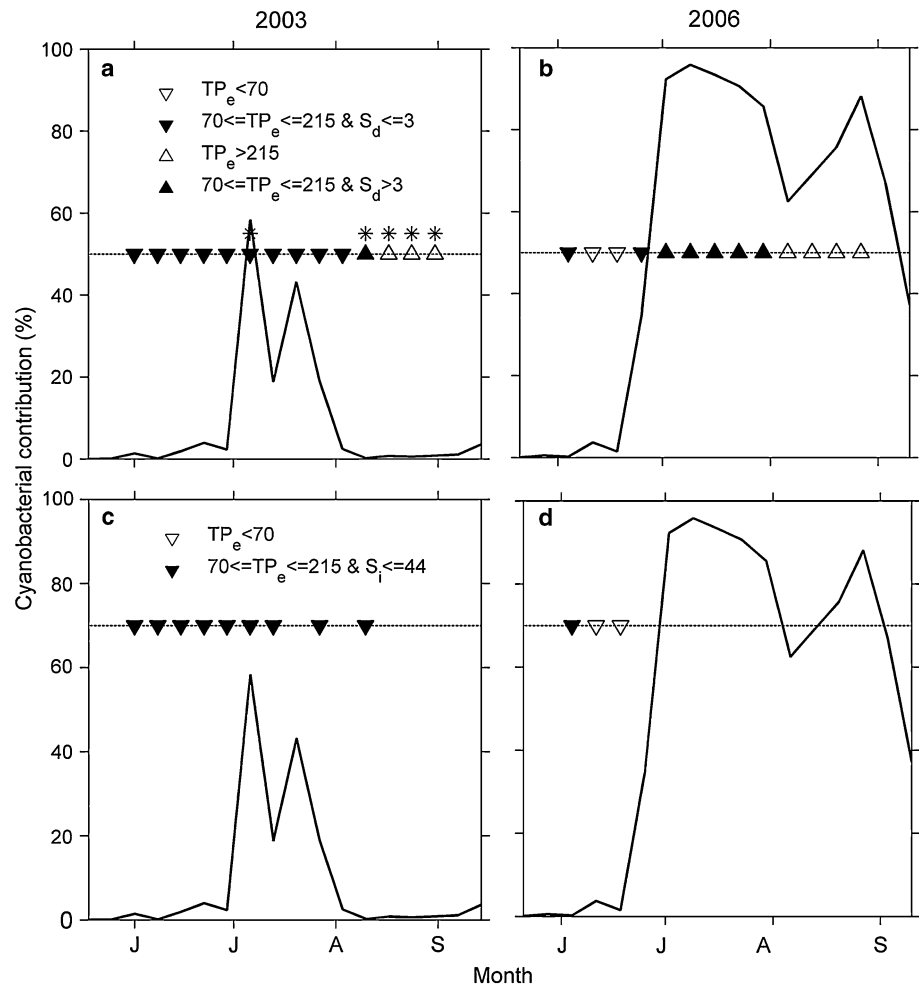
of summer (Fig. 2d), high TP_e concentrations (>215 μg L^{-1}) favoured cyanobacterial dominance in 2003 and 2006 (Figs. 2c, 3 white upward-facing triangles). Until August in both years, TP_e mostly stayed within the range of ≥70 and ≤215 μg L^{-1} (Figs. 2c, 3 black triangles), where the duration and intensity of thermal stratification is critical for the development of cyanobacterial dominance (Table 1).

During this period, differences in thermal stratification (S_i and S_d) largely explained differences in cyanobacterial contribution, in contrast to TP_e alone. In 2006, the mixing regime of the lake was extremely favourable for cyanobacteria, with 8 weeks of continuous thermal stratification (Figs. 2d, 3b, d). The critical thresholds of duration ($S_d >$ 3 weeks) and intensity ($S_i >$ 44 g cm cm^{-2}) were exceeded for an extended period of time. By contrast, intermittent mixing resulted in two much shorter periods of thermal stratification of only 2 and 4 weeks, respectively, in 2003. The insufficient duration ($S_d \leq$ 3 weeks) and intensity ($S_i \leq$ 44 g cm cm^{-2}) of thermal stratification apparently prevented cyanobacterial dominance in this year (Fig. 3a, c).

Cyanobacterial composition and genus-specific promoting factors

Since not all cyanobacterial species benefit from stratified conditions and species may differ in many other functional attributes, we also considered the composition of the cyanobacterial community in both years. Cyanobacteria were dominated by *Aphanizomenon* in 2003 (Fig. 4a), but its biovolume was extremely low compared to the long-term mean (Fig. 1c). In 2006, *Anabaena* and *Planktothrix* contributed most to cyanobacterial biovolume (Fig. 4b); their mean summer biovolumes reached more than 3 σ above μ (Fig. 1c). *Microcystis* biovolume remained low in both summers.

TP_h, S_i, TP_e and $TN_e:TP_e$ were identified as the most important predictor variables of *Aphanizomenon*, *Anabaena*, *Microcystis* and *Planktothrix* presence, respectively (Table 2). These genera were properly classified as 'absent' or 'present' at 84, 97, 97, and 96% of all data points considered (1993–2007) (Table 2). Also, the observed presence/absence patterns during the summers of

Fig. 4 Summer dynamics of the dominant cyanobacterial genera *Planktothrix*, *Microcystis*, *Anabaena*, and *Aphanizomenon* in 2003 (*left column*) and 2006 (*right column*). **a, b** Observed biovolumes, with residuals (*white areas*) mostly consisting of unidentified cyanobacterial cells. **c–j** Observed (*open symbols*) and predicted (*solid symbols*) presence of cyanobacterial genera. Genera are considered to be present when the contribution to total phytoplankton biovolume is $\geq 10\%$; predictions are based on classification rules of Table 2
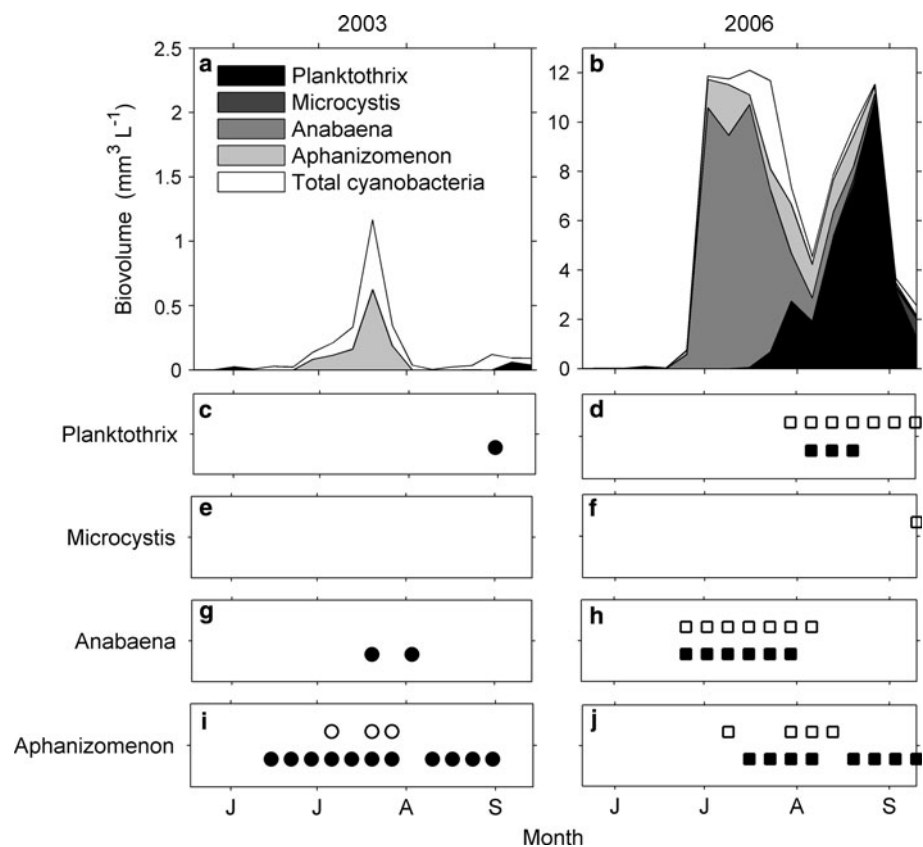
2003 and 2006 were correctly predicted with very few exceptions (Fig. 4c–j).

Identified predictor variables and their thresholds (Fig. 2; ESM Fig. S1) did not suggest any clear differences in environmental conditions favoured by either *Microcystis* or *Aphanizomenon* between 2003 and 2006 (Fig. 4e, f, i, j). In contrast, environmental conditions in 2006 were much more favourable for *Planktothrix* and *Anabaena* than those in 2003 (Fig. 4c, d, g, h).

While $TN_e:TP_e$ remained below the identified threshold (molar ratio <8.7), thereby promoting *Planktothrix*, for an extended period after the breakup of thermal stratification in 2006 (Fig. 2f), it did not constantly stay below the critical threshold in late summer and fall of 2003. The latter dynamics combined with unfavourable development of zooplankton (ESM Fig. S1) did not allow *Planktothrix* to develop significant biovolume in 2003 according to the classification rules.

The intensity of thermal stratification was much more in favour of *Anabaena* in 2006 than in 2003. Interestingly, the threshold of thermal stratification intensity ($S_i > 41.5$ g cm cm^{-2}) included in the classification rules for *Anabaena* (Table 2) almost coincided with the threshold identified for total cyanobacterial contribution (Fig. 2d). The classification rules also suggested that if $TN_e:TP_e$

had been smaller (molar ratio ≤ 27.5) in 2006, an even more extensive bloom of *Anabaena* could have developed.

Meteorological conditions influencing thermal stratification

Since thermal stratification was a critical predictor variable for total cyanobacteria and *Anabaena* contribution, we next examined potentially influential meteorological variables. CTA suggested that incident radiation, wind speed and air temperature were the main determinants of thermal stratification in Müggelsee (Table 3). Incident radiation of ≤ 173.9 W m^{-2} was generally a good indicator of non-stratified conditions, but it did not explain the mixing event in 2003 since it did not fall below this threshold before early fall (Fig. 5a). Mean wind speed of >3 m s^{-1} was associated with times of mixing. During the entire summer of 2006, wind speed remained ≤ 3 m s^{-1}. In contrast, wind speeds of >3 m s^{-1} were observed in mid-summer of 2003, exactly during the time period when intermittent mixing took place in the lake (Figs. 2d, 5b). At about the same time, air temperature also dropped below the critical threshold of 20.5°C, indicative of conditions that favoured mixing (Fig. 5c).
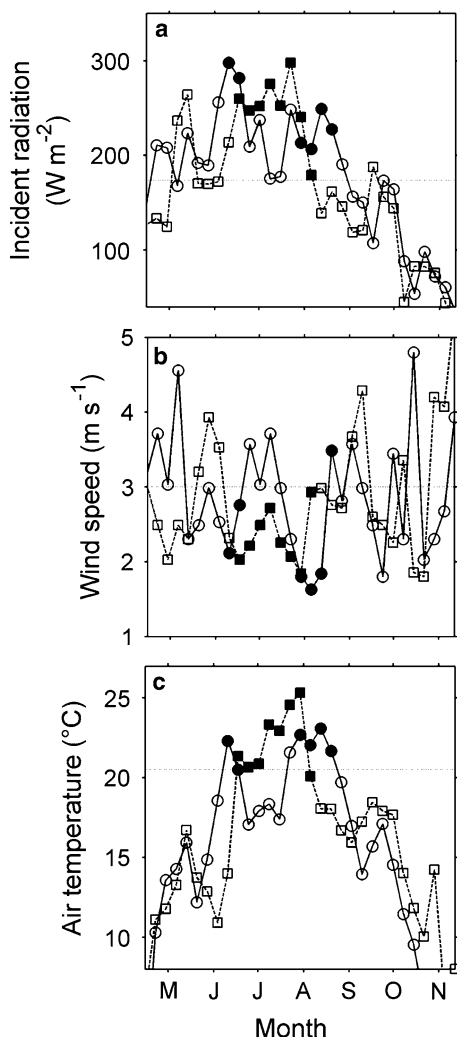
Fig. 5 Seasonal dynamics of incident radiation (**a**), wind speed (**b**), and air temperature (**c**) during 2003 and 2006. *Horizontal lines* mark thresholds from classification tree analysis (Table 3). Data for 2003 (*circles, solid line*) and 2006 (*squares, dashed line*) are shown. Weeks of thermal stratification are indicated by *filled symbols* (cf. Fig. 2d)

Discussion

In this study, we investigated the strikingly different development of cyanobacteria in Müggelsee during two recent heat waves, using critical thresholds of environmental drivers derived from CTA. The concentrations of nutrients, in particular TP, were generally the most important predictor variables of cyanobacterial dominance. However, differences in the intensity and duration of thermal stratification, related to differences in short-term weather variability, appeared to be the most obvious reason for the contrasting development of cyanobacteria during the two extreme summers. Similar to all data-mining techniques based on correlative relationships, CTA may miss existent causal links or may hint at causal links that do

not exist. Therefore, in the following sections, we address potential caveats of our analysis and compare our findings with known mechanisms of cyanobacterial bloom formation as published in the literature.

Direct and indirect effects of thermal stratification on cyanobacteria

Thermal stratification may favour cyanobacteria either directly by providing optimal buoyancy conditions or indirectly by facilitating nutrient release from the sediment. Considering competition for light between buoyant and non-buoyant algal species, Huisman et al. (2004) found that the vertical diffusive turbulence in the water column needs to remain below a critical limit in order to allow for the dominance of buoyant species. This finding corresponds well with our results on the importance of the *intensity* of thermal stratification for the dominance of *Anabaena*, comprising buoyant species known to be strongly favoured by low turbulence (Paerl 1988). Some cyanobacterial genera such as *Planktothrix*, adapted to very shallow water depths (<2.5 m), may also profit directly from thermal stratification because a shallow mixed-layer enables them to expand into deeper areas of the water body (Berger and Sweers 1988).

Whereas the results of Huisman et al. (2004) pertain to equilibrium conditions, the identified critical limit of the *duration* of thermal stratification suggests that the temporal dynamics of changes in turbulence are an additional important factor to consider under transient dynamics—at least in polymictic lakes where times of mixing and stratification alternate. The time-lag between the onset of thermal stratification and the establishment of cyanobacterial dominance may result from the time it takes for buoyant species to outcompete non-buoyant species and for nutrients to be released from the sediment and then to be exploited by cyanobacteria.

In fact, Wilhelm and Adrian (2008) demonstrated that the *duration* of stratification is the most important predictor for SRP concentrations in the hypolimnion during stratified conditions in Müggelsee. These authors also demonstrated that the increase in epilimnetic P during the onset of mixing is directly linked to the amount of P that has accumulated in the hypolimnion during the period of stratification. Cyanobacteria may benefit from sedimentary nutrient release either during stratification by migrating into the hypolimnion (albeit controversially discussed; see e.g., Bormans et al. 1999) or after stratification events when the released nutrients are mixed into the water column (Huisman et al. 2005). For example, the continuously low molar $TN_e:TP_e$ (<8.7), which favoured *Planktothrix* after the breakdown of thermal stratification in late summer of 2006, was most likely a result of the exceptionally

long-lasting thermal stratification event and correspondingly strong P release from the lake sediment in that year.

Two caveats regarding our findings on thermal stratification need mentioning. First, fast floating cyanobacterial genera, such as *Microcystis*, profit from thermal stratification at different time scales than slow floaters, such as *Planktothrix* (Bormans et al. 1999). The relatively long-lasting stratification events (>1 week) considered here may even have negative consequences on fast floaters, which are well adapted to regimes of intermittent mixing on hourly to daily time scales (Ibelings et al. 1991). This might explain why thermal stratification was not an important predictor variable in the CTA for *Microcystis*, while stratification at shorter scales than those considered here is known to provide these species with a competitive advantage (Jöhnk et al. 2008).

Second, the thresholds of thermal stratification intensity appeared in CTA for relatively strong dominance of cyanobacteria and *Anabaena*. Interestingly, water surface temperature was the most important predictor variable when lower contributions (<7.5%) of *Anabaena* to total phytoplankton biovolume were considered (ESM Table S1). It is thus conceivable that the direct effect of warm water outweighs the effect of thermal stratification at the initiation stage of the bloom.

N_2-fixing and non-N_2-fixing cyanobacteria

It is generally assumed that low ratios of N:P favour cyanobacterial growth (Smith 1983) because many cyanobacterial species possess the ability to fix N (Huisman et al. 2005). While this explanation is applicable to potentially N_2-fixing *Anabaena*, it cannot apply to the observed positive effects of low $TN_e:TP_e$ on non-N_2-fixing *Planktothrix*. Yet, other researchers have equally reported on the dominance of non-N_2-fixing cyanobacteria under low ratios of N:P (Fujimoto et al. 1997). In effect, Smith and Schindler (2009) have recently suggested that these ratios are imperfect predictors of cyanobacterial dominance because they represent the overall result of external nutrient inputs, N fixation and lake-internal recycling. Thus, our findings on the importance of $TN_e:TP_e$ for *Planktothrix* do not necessarily contradict the literature.

The unexplained surprises of summer 2003

While rules obtained from CTA showed that environmental conditions in 2003 were clearly less favourable for cyanobacteria than those in 2006, they did not provide a possible explanation for the exceptionally low summer biovolume of total phytoplankton in 2003 (Fig. 1b). It also remains unexplained why the cyanobacterial contribution was low despite high TP_e concentrations after the breakdown of

thermal stratification in August of 2003 (Figs. 2c, 3a). Here, we consider whether lake discharge and/or light conditions could have contributed to these surprising developments in 2003.

Climate change has been proposed to favour cyanobacterial blooms by affecting the hydrology of the watershed (Paerl and Huisman 2008). High discharge and strong nutrient load in winter and early spring followed by low discharge and weak flushing in summer is a particularly favourable condition for bloom development. In winter and spring, discharge rates of Müggelsee were significantly higher in 2003 than in 2006 (ESM Fig. S2a). In summer, discharge rates were below average in both years, but they were considerably lower in 2006. Thus, while discharge did not appear as an obvious reason for low biovolume of phytoplankton and cyanobacteria in 2003, low flushing in the summer may have additionally contributed to the bloom of cyanobacteria in 2006.

Due to the strong collinearity between light extinction and cyanobacterial biovolume in Müggelsee, we adopted the approach of Wagner and Adrian (2009) and did not include an index of light availability in our CTA. However, we cannot exclude that differences in light availability have contributed to the contrasting development of cyanobacteria in 2003 and 2006 (ESM Fig. S2b). The relatively low light intensity in the water column in late summer of 2006 might have reinforced the observed bloom of *Planktothrix*, which are known for their superior light-harvesting capabilities (Scheffer et al. 1997). Likewise, the relatively high light availability in late summer of 2003 might have contributed to suppressing growth of *Aphanizomenon* sp., which are considered 'shade species'—at least in comparison to other N-fixing cyanobacterial species, such as *Anabaena* sp. (De Nobel et al. 1998).

Generalisation to other lakes

We have presented data from only one shallow, polymictic lake of the temperate zone. At least one other study of a moderately deep (mean depth 18 m), hypertrophic lake in the Netherlands (Lake Nieuwe Meer) found that cyanobacteria were strongly promoted by the heat wave of 2003 (Jöhnk et al. 2008). Contrary to our findings, artificially-induced intermittent mixing with a 1- to 2-week periodicity was not sufficient in Lake Nieuwe Meer to suppress a bloom of *Microcystis* that occurred when the heat wave hit the lake in August. Interestingly, model predictions show that buoyant cyanobacteria outcompete other phytoplankton at a much lower intensity of thermal stratification in deep lakes than in shallow ones (Huisman et al. 2004). Thus, differences in lake depth might explain the contrasting observations. In addition, the different trophic states of the two lakes might play a role. Jöhnk et al. (2008)

reported extremely high mean summer concentrations of TP in Lake Nieuwe Meer in the range of approximately 400 μg L^{-1}. These concentrations largely exceed the threshold of approximately 252 μg L^{-1} TP$_e$ found in this study, above which the *Microcystis* contribution to total phytoplankton biovolume tended to be high in Müggelsee (Table 2, Fig. 2c). Furthermore, differences in lake size and food-web structure might have contributed to the contrasting response of Lake Nieuwe Meer to the heat wave of 2003.

Conclusions

Many studies have pointed to the increasing risk of cyanobacterial blooms with climate change. Accumulating evidence suggests that global warming indeed favours cyanobacteria (e.g., Paerl and Huisman 2008; Elliott 2010). However, the results of our study reveal that heat waves do not necessarily promote cyanobacterial blooms—not even in the same lake and when similarly high water temperatures occur.

At first glance, these conclusions may appear contrary to those of Wagner and Adrian (2009), who, based on the same data and type of analysis, concluded that "the incidence of cyanobacterial blooms will certainly increase in many lakes under future climate scenarios". In fact, we show that the critical thresholds of thermal stratification which Wagner and Adrian (2009) extracted from multi-decadal records are useful to explain observations in single extreme years. However, our results also indicate that if past heat waves are indeed harbingers of future climate warming, these critical thresholds will not necessarily be exceeded more often in a warmer world. By investigating short-term meteorological conditions, we determined that low wind speed may be more important than high air temperature in explaining stratified conditions in the studied lake. Hence, if wind patterns were to change in the future such that the critical intensity and duration of thermal stratification were not reached more often, the risk of cyanobacterial blooms would not increase despite warming. Wagner and Adrian (2009) base their conclusions on the assumption that thermal stratification will most likely intensify in a warmer world. We do not disagree in principle, but specify their conclusions by emphasizing the decisive role of short-term meteorological variability.

Hence, our results caution against concluding on climate change being a catalyst of cyanobacterial blooms solely based on summer averages of meteorological variables only. Any meaningful assessment of the future risk of cyanobacterial blooms in polymictic lakes requires detailed projections of short-term weather variability and a knowledge of critical environmental thresholds. Validating these

critical thresholds with other long-term records is an exciting prospect for further research that will ultimately improve our ability to foresee lake–ecosystem responses to climate change.

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