

Importance of climate change-physical forcing on the increase of cyanobacterial blooms in a small, stratified lake

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ABSTRACT

The community structure of planktonic cyanobacteria was studied in a dimictic lake in which recurrent summer surface algal blooms have frequently occurred since the beginning of this millennium. In eutrophic-hypereutrophic lakes, epilimnetic cyanobacterial blooms are promoted by increased ambient temperatures and water column thermal stability, which favour the vertical migration of buoyancy-regulating cyanobacteria. Here we propose that intensified external energy (wind) that alters thermocline stability could explain the occurrence of heavy blooms in the surface of lakes with low external nutrient loading. Specifically, we hypothesized that: i) in small stratified lakes with low external nutrient sources, cyanobacterial growth primarily occurs near the lake bottom, where phosphorus is more abundant and light is available; ii) we additionally hypothesized that turbulence induced by strong winds increases the amplitude and energy of metalimnetic internal waves and entrains meta- and hypolimnetic water, rich in nutrients and cyanobacteria, into the epilimnion. The study was done in a small lake (45 Ha, maximum and mean depth 7.2 m and 4.3 m, respectively) with mean epilimnetic dissolved phosphorus concentrations $\approx 4 \mu\text{g L}^{-1}$ and chlorophyll $\alpha \approx 8 \mu\text{g L}^{-1}$. Vertical temperature profiles during the open season were continuously registered using thermistors. Weekly vertical profiles of light transmission, phytoplankton distribution and water chemistry were also taken. On one occasion, these variables were measured throughout a continuous 24 h cycle. Results demonstrated that summer cyanobacterial blooms were dominated by *Plankthotrix* spp., which began their cycle in late spring at the bottom of the lake, and grew to form dense metalimnetic biomass peaks. Time series analysis of isotherms and the Lake number indicated that internal metalimnetic waves (seiches) were present through the summer. During the diel sampling cycle, we found that medium to strong westerly wind gust events (~ 5 to $> 12 \text{ m s}^{-1}$) induced large amplitude internal waves (mainly V2H1 mode) that vertically displaced the isotherms by more than 3.5 m. During this event the top of the metalimnetic algal peak was entrained through the epilimnion, bringing metalimnetic *Plankthotrix* spp. to the lake surface, modified the deep metalimnion and hypolimnion concentrations of dissolved oxygen, and caused an up-surge in phosphorus. We conclude that algal and nutrient upwelling linked to intermittent deep mixing events, play an important role in supporting summer cyanobacterial blooms in lake Bromont.

Key words: Cyanobacteria blooms; deep chlorophyll maximum; oscillatoriales; turbulence; entrainment.

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INTRODUCTION

Climate change has major physical, chemical, and biological effects on aquatic ecosystems. Globally averaged air and ocean temperatures have both undisputably increased since 1850, and this trend has accelerated towards the end of the last century. The period from 1983 to 2012 was likely the warmest 30-year period of the last 800 years (IPCC high confidence; Pachauri and Meyer 2014).

In Northern Hemisphere, the greatest seasonal increase in air temperature has occurred in the winter, while summer heat waves occur more frequently, are both more intense and becoming longer in duration (Solomon *et al.*, 2007). The consequences of such changes on the thermal regime in lakes have already been reported, including shorter periods of ice-cover, changes in water column density, and the earlier onset and longer duration of stratification (De Stasio *et al.*, 1996; Peeters *et al.*, 2002;

Stainsby *et al.*, 2011). In addition, increasing precipitation is modifying watershed hydrology, intensifying runoff, and likely increasing nutrient loading (Parry *et al.*, 2007). These changes have major implications for phytoplankton biomass and community structure. Phytoplankton communities are expected to undergo changes in species composition that generally favor cyanobacterial (CYAN) growth, particularly the harmful species (Pearl and Huisman, 2008; Pomati *et al.*, 2012).

CYAN blooms have occurred for centuries, in both marine and freshwater systems (Fogg *et al.*, 1973). Since the 1950s, CYAN blooms have increased worldwide in biomass, frequency and duration (Hallegraeff, 1993). This phenomenon has traditionally been attributed to anthropogenic perturbations, particularly phosphorus (P) enrichment (Schindler, 1974). Lake eutrophication has decreased in the last 20-30 yrs, at least in western countries (Pomati *et al.*, 2012), and eutrophied lakes have in

many cases recovered, or are recovering after reduction or elimination of nutrient sources (Edmondson and Leman, 1981; Ruggiu *et al.*, 1998; Jeppesen *et al.*, 2005; Ibelings *et al.*, 2007). In some cases, increases in temperature may offset the effects of oligotrophication by promoting the expansion of some forms of CYAN (Kosten *et al.*, 2012). Further, in many cases the increase in CYAN is mainly due to increased growth of metalimnetic species. For instance, the relative abundance of *Plankthotrix* has increased in both alpine and Scandinavian lakes (Feuillade and Druart, 1994; Buergi and Stadelmann, 2000; Jacquet *et al.*, 2005; Halstvedt *et al.*, 2007).

Growing evidence suggests that variables related to climate, such as temperature and water-column stability, could explain additional or greater variation in CYAN abundance than nutrients (Soranno *et al.*, 1996; Kosten *et al.*, 2012). Kosten *et al.* (2012) found that the relative contribution of CYAN to total phytoplankton biomass increased with temperature across 143 lakes of varying trophic conditions along a latitudinal gradient from Northern Europe to Southern South America. Warming may lower the nutrient concentration thresholds at which CYAN blooms can be initiated and sustained (Weyhenmeyer, 2001; Nöges *et al.*, 2003). Now it is clear that warming waters can have an additive effect on CYAN dominance in lakes, and augment the intensity and occurrence of blooms (Mooij *et al.*, 2005; Jöhnk *et al.*, 2008; Paerl and Huisman, 2009). The question is, what is the ultimate cause: climate, nutrients, or both? This question is difficult to answer because we have limited knowledge on the synergistic effects of nutrient loading and climate change in supporting CYAN.

Increased intensity and frequency of wind and gusts linked to climate change may have large implications for lake stability dynamics. Climate change could modify the action of the wind on lake turbulence. Even small changes in convective-, and wind-driven mixing can have large implications for the internal transport and availability of nutrients in lake photic zones (Catalan and Fee, 1994). Accordingly, the ongoing warming of surface waters and changing water-column stability may be the primary drivers of CYAN abundance, particularly in stratified lakes (Jöhnk *et al.*, 2008; Taranu *et al.*, 2012). Increased frequency of episodic events (strong winds and storms) linked to climate change generates strong shear flow and turbulence through internal wave dynamics in stratified lakes (Imberberg, 1994). Though the study of physical processes in lakes began nearly a century ago (Wedderburn, 1913), the role of wind forcing on lake processes is rarely studied (Mortimer, 1974; Imberger, 1980; Imboden *et al.*, 1983, among others). The importance of physical forcing to biological processes in lakes has gained increasing recognition in the last three decades (Reynolds, 1994; Oftrovsky *et al.*, 1996; Evans *et al.*, 2008; Marcé

et al., 2007). But, these studies were done in large-medium size lakes or reservoirs. Recent evidence suggests that these effects have potentially large implications for CYAN dynamics in small lakes (Pannard *et al.*, 2011).

Given the widespread warming trend in aquatic habitats worldwide, our research aim was to understand how changes in physical forcing related to warming may induce heavy surface CYAN blooms in small lakes. We were especially interested in the role that CYAN living in the deepest part of the water column may play in supporting summer surface blooms. Our hypothesis were:

H1. In stratified lakes with low external nutrient sources, CYAN growth occurs in the deep part of the lakes where P is more abundant, given sufficient light availability. This hypothesis is supported both by existing empirical data on deep phytoplankton maxima, and by models of maximum algal growth in relation to vertical light and nutrient availability (Fee, 1976; Klausmeier and Litchman, 2001).

H2. To explain why cyanobacteria growing below the thermocline cause surface blooms, we predicted that changing climate, including warming but also, increased wind-driven mixing, and heavy rainfall events, can enhance lake turbulence.

H2-1. Turbulence increases the amplitude and energy of metalimnetic internal waves (seiches) and reduces the stability of the thermocline.

H2-2. Internal waves of high amplitude entrain metalimnetic water, rich in nutrients and organisms (CYAN), into the epilimnion, thereby causing surface CYAN blooms.

The hypotheses were tested in a small, stratified lake that experiences frequent and random summer CYAN blooms, despite low external P-loading.

METHODS

Study site

The study was done in Lake Bromont, located in the SE of Canada (45°16'N, 72°40'W). The surface area of the lake is 45 ha and its drainage area 2 410 ha; the volume $2 \times 10^6 \text{ m}^3$ and, mean and maximum depth are 4.5 m and 7.2 m, respectively (Fig. 1).

The lake is set in a central plain surrounded by mountains and isolated hills extending eastward (Fig. 1). The main axis of the lake is in the East-West direction and the lake opens in the direction of dominant westerly winds, which are funnelled to the Eastern end of the lake. The recent study of Pannard *et al.* (2011) found persistent internal wave activities linked to the dominant winds. The spectral analysis of the isotherms has shown that the second (V2H1) mode waves dominated over the first mode (V1H1), which occurs only during larger wind events (Pannard *et al.*, 2011). In the V2H1 mode the epilimnion and hypolimnion oscillate in the opposite direction con-

secutively, thereby squeezing and broadening the metalimnion vertically. The V2H1 mode, in resonance with diurnal winds, is the primary cause of the large amplitude of the second mode (Münnich *et al.*, 1992)

The lake has four permanent inflowing streams and one outflow. Until 1990, agriculture was the main activity in the largest (60%) and second largest (16%) sub-watersheds, respectively located to the South and North of the lake. Loading of P from the south stream represented 80 to 90% of riverine total phosphorus (TP) inputs. Presently, farmland in the watershed is mainly composed of pasture (Pannard *et al.*, 2011). Since the early 1990s, efforts to protect the lake have increased, culminating in the recent formation of the *Watershed Conservation Action Lac Bromont* association.

Meteorological data

Wind speed and direction, plus precipitation data, were collected from a weather station installed on a raft on the lake (Fig. 1). Here, reported wind velocities are averages of observations made at 15 min. intervals, and wind gust speeds are the averaged maximum speed across intervals. Pannard *et al.* (2011), found a good relation between wind velocity and the surface current velocities measured in the lake.

Physical, chemical and biological data

Sampling was done in the ice-free season (April-May to October) of 2010, at the deepest part of the lake (Fig 1). *In situ* water temperature was continuously registered with 3 strings of moored Hobo Pro temperature loggers, at 50 cm intervals between 1 and 3 m, then every 25 cm from 3 to 6.75 m. The calibrated thermistors (accuracy $\pm 0.2^\circ\text{C}$ between 0°C and 50°C) recorded measurements every 10 min. Light transmission, chemical and biological variables were sampled weekly at the deepest part of the lake. Photosynthetic Active Radiation (PAR) profiles were measured *in situ* at 25 cm intervals using a submersible spherical sensor (Li-193) and the incident light reaching the lake surface was recorded with an air sensor (Li-190) (LICOR-Environment, Lincoln, NE, USA). To characterize the oxycline we measured dissolved oxygen (DO) at 0.5 m depth intervals with a YSI 6920 sonde (YSI Environmental, San Diego, CA, USA). The vertical structure of phytoplankton was measured at every centimetre *in situ* with a FluoroProbe (Biological Biophysical Engineering BBE Moldaenke GmbH, Kiel-Kronshagen, Germany). The FluoroProbe distinguished four taxonomic groups (Beutler *et al.*, 2002). The accuracy of CYAN biomass estimated by the fluoroprobe was validated by identifying, counting and measuring the species sampled at discrete

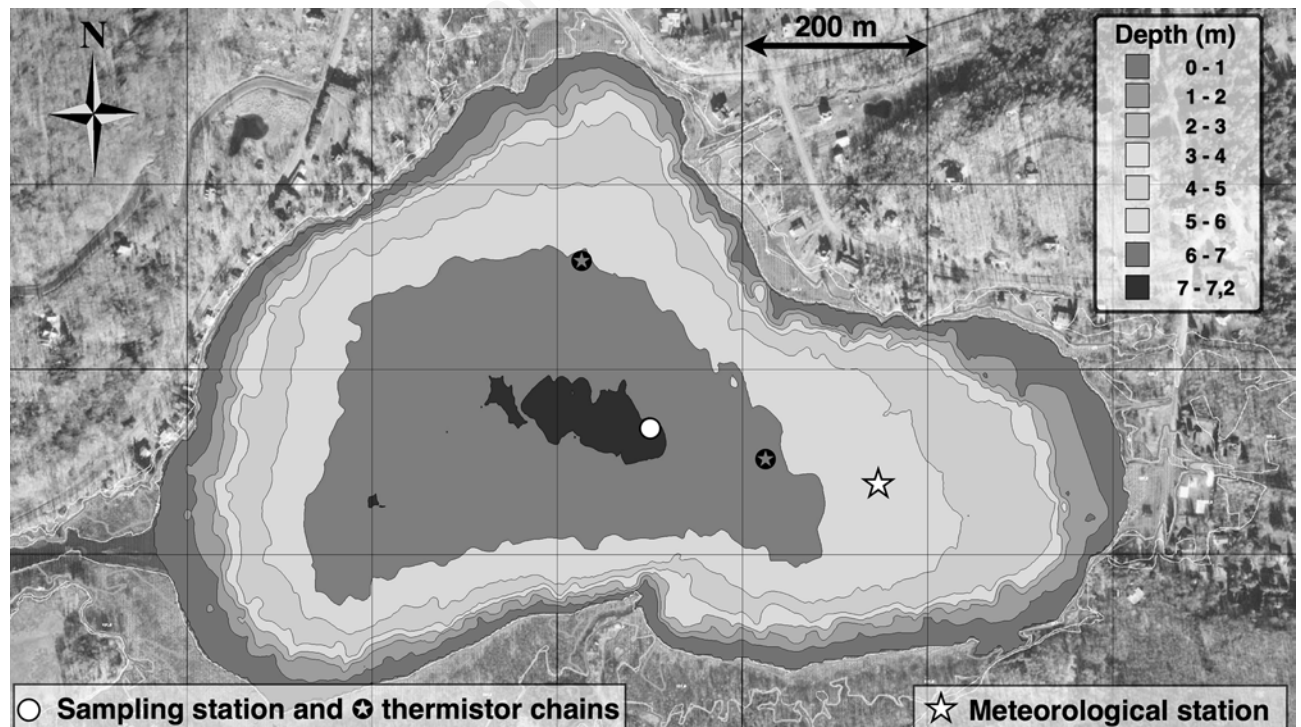


Fig. 1. Bathymetric map of lake Bromont. The white dot marks the sampling station, the star shows the placement of the meteorological station, and the circle with the star shows the location of the thermistor chains.

depths (see below), with an inverted microscope, using the Utermöhl technique. The spatio-temporal distribution of CYAN was estimated in each 0.5 m strata of the epi-, meta-, and hypolimnion from fluoroprobe-derived concentrations of chlorophyll a (Chla).

Discrete water samples were collected with a van Dorn bottle (37 cm length) in the middle of each thermal strata in the epilimnion and metalimnion, and at 0.5 m above the sediment layer in the hypolimnion. Water for chemical and biological analyses was collected in clear acid washed bottles, and dark detergent washed bottles, respectively. Immediately after sampling, samples were collected for total dissolved P (DP) by filtration across acid washed polycarbonate nucleopore filters (0.45 μm) and Chla by filtering suspended materials onto GF/F filters. Phytoplankton samples were preserved with lugol solution. All samples were kept cool when travelling from the lake to the Laboratory. Nutrient samples were analyzed within 24 h of collection, and Chla was frozen at minus 80°C until analysis.

Dissolved (DP) and total P (TP) were digested in an autoclave at 150 atm with persulfate solution (Menzel and Corwin, 1965) and determined using the molybdenum blue colorimetric method (Murphy and Riley, 1962, modified by Stainton *et al.*, 1974). Chla was extracted with hot ethanol (Nusch, 1980) and measured, before and after acidification, by spectrophotometry (Sartory and Großbehaar, 1984). The spatial-temporal distribution of CYAN biomass for individual strata was estimated from the concentration of Chla measured by the fluoroprobe profiles. Total FluoroProbe's Chla estimates and spectrophotometric concentrations of Chla were highly correlated ($r^2=0.94$; $n=19$; Pannard *et al.*, 2015).

We used sediment peepers (Hesslein, 1976) to measure P-fluxes from the sediments following the modified method of Carignan (1984). Peepers were deployed, for 2-4 weeks, at the central station of the lake by divers. We measured DP with the same methods as in the water column, except that samples were not filtered and digested, since samples collected by the peepers were already in inorganic form. Fluxes from the sediments were estimated following Carignan and Lean (1991).

Wind mixing calculations

Lake Number, L_N , was calculated on a daily basis from the continuous *in situ* temperature record (see below) following methods of Imberger and Patterson (1989). $L_N < 1$ indicates a fully mixed water column; a value very close to 1 indicates that there is upwelling of hypolimnetic waters; and a L_N between 1 to 12 is characteristic of internal waves $L_N > 12$, indicates calm and stable stratification (Robertson and Imberger, 1994). See Pannard *et al.* (2001) for more details.

The amount of P entrained in the epilimnion from the

metalimnion when the thermocline deepened 1m d^{-1} (Soranno *et al.*, 1997) was calculated by the volume of water transported (estimated from bathymetric data), multiplied by the average P-concentration at the thermocline depth (Kamarainen *et al.*, 2009).

RESULTS AND DISCUSSION

Local climate change

Mean air temperature near lake Bromont for this millennium was $\sim 1^\circ\text{C}$ higher than in the previous 50 yrs (mean temperature from 1948 to 1999 = 5.95°C , and from 2000 to 2014 = 6.98°C). In the last 15 years, minimum temperatures rose more ($+5^\circ\text{C}$) than maximum ($+^\circ\text{C}$) values. The trend over the past 15 years is consistent with the global trend, for which the last decade was the hottest of the entire 160-year temperature record (Pachauri and Meyer, 2014). Additionally, the frequencies of storms associated to gust events have undergone noticeable changes (*data not shown*).

Thermal structure

Summertime mean (± 1 SD) epi-, meta-, and hypolimnetic temperatures were $23 \pm 2.5^\circ\text{C}$, $17 \pm 3.2^\circ\text{C}$ and $12 \pm 0.91^\circ\text{C}$, respectively (Tab. 1). From mid July to the end of August, a *heat wave* raised epilimnetic water temperatures to up to 29.33°C from July 7th to 16th (Fig. 2a). In the metalimnion, temperature oscillated as a function of the amplitude of internal waves. Stratification in 2010 lasted 175 days (Tab. 1). Within the 5 years study, the length of the stratification augmented half a month between 2007-2008 and 2009-2010.

Lake Bromont became thermally stratified almost immediately following ice melt (Fig. 2a). In 2010, ice melt occurred the 1st week of April, three weeks earlier than in previous study years (in preparation), but stratification remained weak until the end of April. The thermal structure of the lake was characterized by a relatively shallow mixed layer (2-3 m) a thicker metalimnion (3-4 m) and a thin hypolimnion (1-1.5 m) (Fig. 2a). Thicker metalimnia are common in small lakes (LaZerte, 1998).

Small diurnal changes in surface water temperature were registered in the lake. Internal metalimnetic waves (seiches) were present almost through the whole summer, as indicated by L_N values between 1 and 12 from the end of May to mid-September (see below, Fig. 3a). Temperature shifts within the metalimnion were more frequent than in the epilimnion, a phenomenon that has been observed in the lake in 2007 (Pannard *et al.*, 2011). Dominant westerly winds had diurnal periodicity, and surface current velocity was proportional with the wind speed (Pannard *et al.*, 2011). Following wind events > 5 m/sec, large amplitude internal waves were observed in the metalimnion after winds subsided. Gust wind events > 15 m sec in early

May and late August strongly modified the vertical thermal structure of the lake, and caused an upwelling of hypolimnetic waters (Figs. 2a, 3a).

Oxygen and phosphorus structure

Phosphorus concentrations [P] (Tab. 1) and oxygen concentrations [O₂] (Fig. 2b) in Lakes Bromont were strongly stratified, though chemical stratification was temporally perturbed by winds that induced high amplitude internal waves. Dissolved oxygen concentrations were closely related to vertical thermal stability. Following ice melt, the whole water column was super-saturated with O₂ but O₂ diminished in the lower metalimnion to <25% saturation following the onset of stratification. A hypo-anoxic period (O₂ <5% saturation) began at the lake bottom in spring and progressively expanded upward in the metalimnion, reaching 3 m above the lake bottom in August (Fig. 2b). The length of the anoxic period was 126 days (Tab. 1).

During anoxic periods, sediments release P to the water column and augment internal P loads (Nürnberg, 1984). Internal loading (4273 kg during summer; Tab. 1) was extremely high, and represented the main input of P in lake Bromont since external P-loads are relatively low (222 kg in 2010; Tab. 1). Such a high quantity of internal P loading is expected, due to the intensity and long duration of anoxia.

It is well established that sedimentary P loading plays an important role in overall shallow lake nutrient dynamics following reductions in external loading (Søndergaard *et al.*, 2003; Jacquet *et al.*, 2005), as was the case for lake Bromont. The spatio-temporal distribution of P (Table 1) showed a decreasing gradient from the epi- to hypolimnion. Mean [DP] ranged from 4±2 µg L⁻¹ in the epilimnion, to 7±3 µg L⁻¹ in the meta-, and 11±14 µg L⁻¹ in the hypolimnion, while mean [TP] ranged from 18±8 µg L⁻¹ in the epilimnion, to 51±31 µg L⁻¹ in the meta-, and 102±95 µg L⁻¹ in the hypolimnion (Tab. 1). Sedimentary P release likely responded to temperature increases, in ad-

dition to anoxia, since a 1-2°C increase in hypolimnetic temperature could intensify the release of P from 9% to 57% (George *et al.*, 2004).

Cyanobacterial structure

The algal biomass was generally low in the epilimnion of lake Bromont. Mean epilimnetic [Chl] was 8±4.3 µg L⁻¹, but increasing with depth, as meta- and hypolimnetic means were 13±14.0 µg L⁻¹, and 24±24.8 µg L⁻¹, respectively (Tab. 1). Concentrations ranged greatly, from 2-18 µg L⁻¹, 2-82 µg L⁻¹, and 4-150 µg L⁻¹, in the epi-, meta- and hypolimnion respectively, with the greatest range in the meta- and hypolimnion.

From late spring onward, phytoplankton community composition was dominated by CYAN, which represented more than 80% of the total community during the whole summer. The dominant species was *Planthotrix* spp. (formerly *Oscillatoria*). Two *Planthotrix* species were present in the meta- and hypolimnion: *P. agardhii* (Gomont) Anagnostides & Komárek, and *P. rubescens* Gomont. Since the counting was on fixed lugol's samples, we could not ascertain the species, but the color of the *Planthotrix* blooms was always very green. It is known that these two *Planthotrix* species had similar depth distribution in some lakes (Halstvedt *et al.*, 2007). Furthermore, it has recently been reported that the horizontal transfer of genes, involved in the synthesis of the photosynthetic pigments, occurs between red and green strains of this genus, including *P. agardhii* and *P. rubescens* strains (Tooming-Klunderud *et al.*, 2013).

Other relatively abundant CYAN were, *Dolichospermum spiroides* (Klebahn) L. Wacklin, L. Hoffman & J. Komárek, *Dolichospermum flosoquae* P. Wacklin, L. Hoffman & J. Komárek, *Dolichospermum solitaria* (Klebahn), *Aphanizomenon gracile* (Lemmerm.), *Aphanizomenon flexuosum* (Kom. Et Kováčik), *Aphanizomenon flosoquae* Ralfs ex Bornet & Flahault. Relative abundances of each of these species vary spatially or/and temporally through

Tab. 1. Mean and standard deviation of environmental conditions during the open season at Lake Bromont. Air temperature (T) was registered on the lake weather platform, while water temperature, dissolved phosphorus (DP), total phosphorus (TP), and chlorophyll (Chl) were measured independently in each thermal strata. Other data include the duration of lake stratification, duration of bottom - anoxia, and masses of external and internal phosphorus loading.

	Open season	Epilimnion	Metalimnion	Hypolimnion
T _{air} (°C)	20±4.2			
T _{water} (°C)		23±2.5	17±3.2	12±0.9
DP (µg L ⁻¹)		4±2	7±3	11±14
TP (µg L ⁻¹)		18±8	51±31	102±95
Chl (µg L ⁻¹)		8±4.3	13±14	24±25
Stratification (days)	127			
Anoxia (days)	126			
TP Loading - external (kg)	222			
TP Loading - internal (kg)	4273			

the open season, since they occupy different niches among the epi-, meta-, and hypolimnion (Jourdain, 2010; Cabal Gomez, 2014). *D. flosaquae* was dominant in the littoral zone, and caused spring blooms in the lake (Figure 3b, end May). *A. gracile* and *A. flexuosum* were present in the epi- and upper metalimnion; their distribution was modulated by internal waves that affected their light exposure and nu-

trient availability at the epi-metalimnion boundary (Litchman, 1998; MacIntyre *et al.*, 1999; Jourdain, 2010; Pannard, *et al.*, 2011; Cabal Gomez, 2014).

Plankthothrix spp. started to grow at the bottom of the lake around the summer solstice, when the euphotic zone was more than 6 m (see below). It persisted and grew in the meta- and hypolimnion for the whole summer, forming a

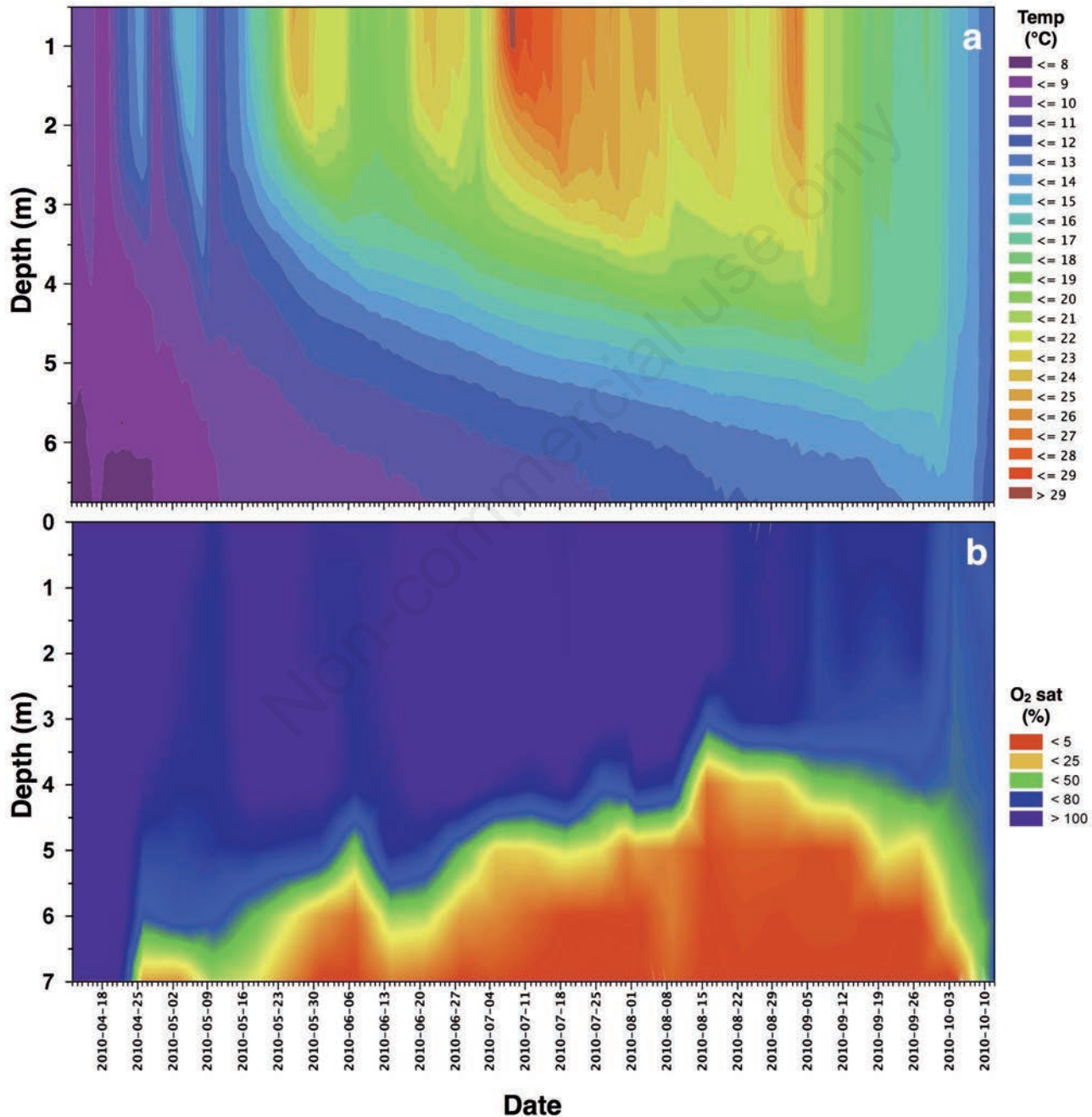


Fig. 2. Temporal changes in vertical (a) temperature based on continuous *in situ* measurements, and (b) weekly measurements of dissolved oxygen saturation.

very thick Deep Chlorophyll Maximum (DCM) (Fig. 4c). Maximum biomass occurred in the lake in spring and early summer, at 6-7 m depth, and persisted until the middle of July with concentrations reaching $200 \mu\text{g L}^{-1}$ (6 m, July 5th). The CYAN peak expanded vertically up to 4 m until the beginning of August, then shifted upward to depths of 3-4 m, following increased surface wind speed (Fig. 4 a,b) that induced mixing of epi- and metalimnetic waters, and decreased epilimnetic temperatures (Figs. 2a, 3a). At the beginning of September, strong wind gusts deepened the

epilimnion to below 5m, causing the DCM to disappear and CYAN to be uniformly distributed throughout the epilimnion (Figs. 2a, 4 a,c). The total biomass measured in the meta- and hypolimnion DCM was around 1900 kg in 2010 and was highly correlated to hypolimnetic TP ($r = 0.92$; $P = 0.0262$).

The diminution of *Planthothrix* spp. during fall entrainment could be explained by growth-limiting dilution of DP-concentrations (Walsby and Schanz, 2002), or by competition with *A. flosaquae*, which became very abun-

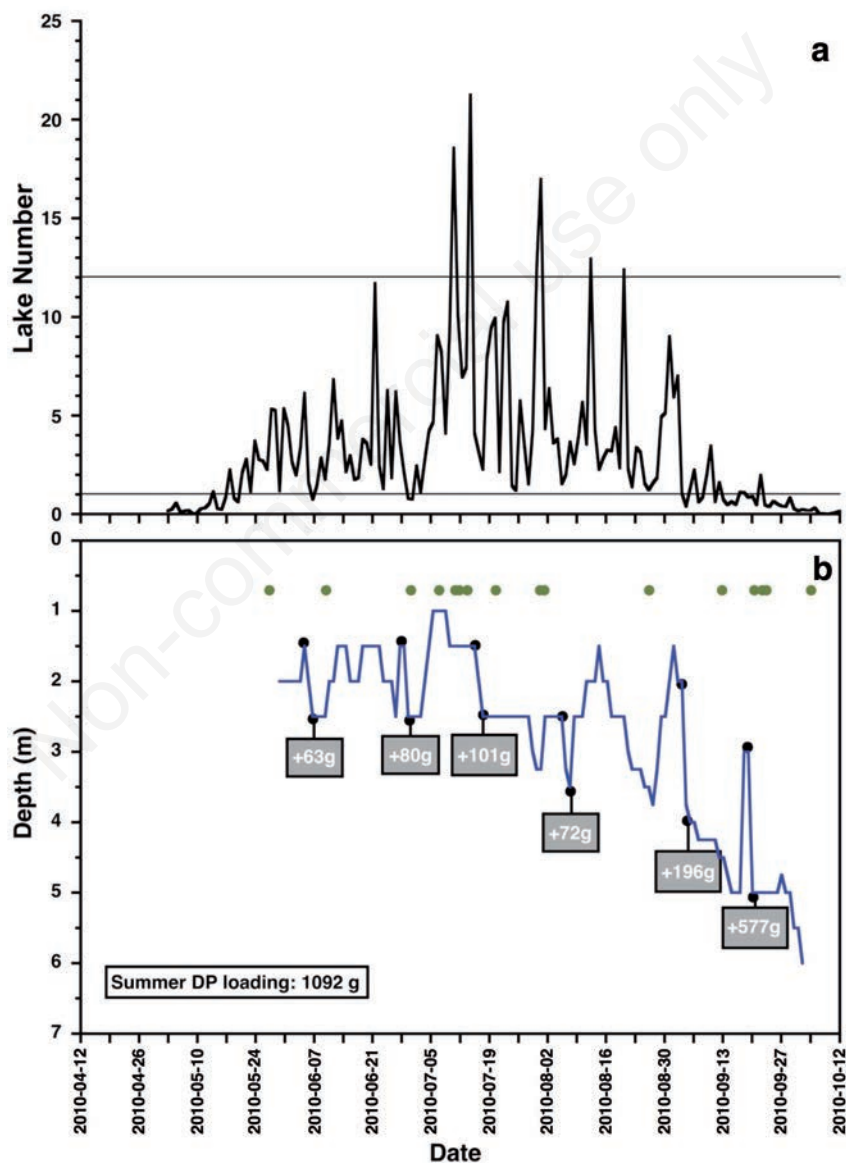


Fig. 3. a) L_N calculated from *in situ* thermistors. b) Epilimnetic dissolved phosphorus entrainment. The continuous line shows the thermocline depth, grey boxes show the amount of phosphorus entrained following individual thermocline deepening events, and the white box is the sum of each event during the study period. The green dots in the top show the days with surface blooms; black dots denote daily thermocline variation when changes exceeded 1 m in depth.

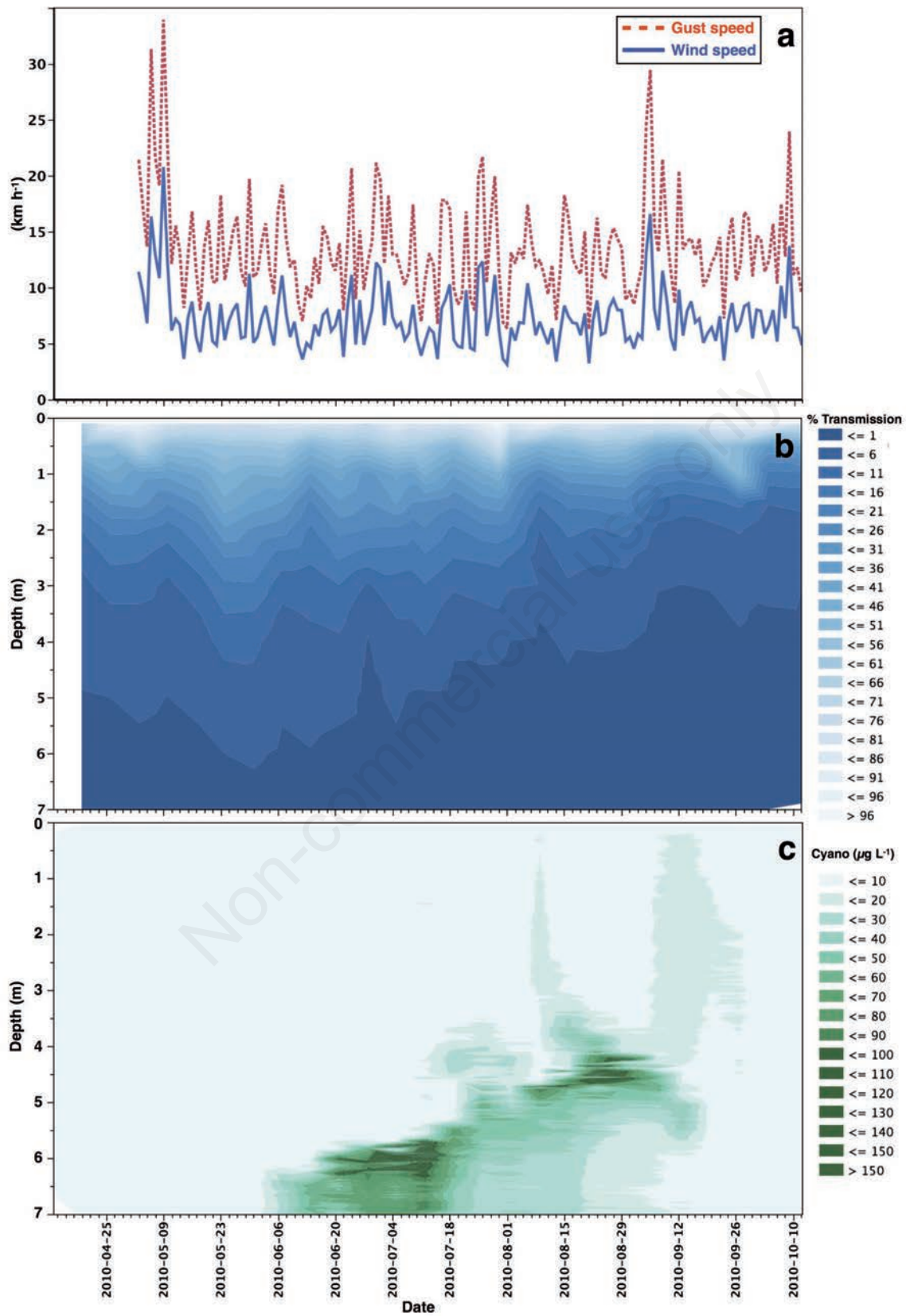


Fig. 4. a) Wind and gust speed measured at the lake meteorological station. b) Spatio-temporal distribution of the % of photosynthetic active radiation transmitted in the lake. c) Spatio-temporal distribution of the cyanobacterial biomass measured *in situ*.

dant in the fall overturn. Growth of *A. flosaquae* began in the metalimnion in August, persisting in the water column until the onset of ice-cover, with frequent *A. flosaquae* surface blooms throughout this period (*data non presented*). The late spring and summer metalimnetic growth of both, *P. agardhii* and *P. rubescens*, is well documented across different continents, mainly in deep subalpine European lakes and in small lakes and reservoirs (Klemer, 1976; Konopka, 1982; Ramón and Moyá, 1984; Ruggiu and Mosello, 1984; Micheletti *et al.*, 1998; Salmaso, 2000; Jacquet *et al.*, 2005; Kangro *et al.*, 2005; Halstvedt *et al.*, 2007). In lake Bromont, the growth and persistence of *Planthotrix* spp. in the meta- and hypolimnion may be linked to ideal physical and chemical conditions that favour the growth of these species; namely low temperatures, sufficient light availability, and high nutrient supply (Van Liere and Mur, 1979; Feuillade, 1994). In lake Bromont, mean summer temperatures were around 17°C in the metalimnion and around 12°C in the hypolimnion (Tab. 1), while irradiance was variable, changing in relation to internal waves and selfshading (Fig. 4b). Elevated bottom-water P-concentrations were sustained by sedimentary loading of DP, which supported *P. agardhii* and *A. flosaquae* dominance in the DCM. Low summertime epilimnetic DP-concentrations limited CYAN growth in surface waters during stratification (Tab. 1).

Light climate

Light transmission was influenced by internal wave dynamics through self-shading. In the spring, between 2 to 8 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, reach 6.5-7m, and these light conditions supported the onset and growth of CYAN between 7 and 6 m (see below, Fig. 4 b,c). At the beginning of July, mixing and upwelling of hypo-metalimnetic waters (Figs. 3b, 4 b,c) caused increased CYAN growth and its vertical expansion above the 6 m depth, which in turn caused a reduction in light penetration depth that lasted the entire month (Figs. 2a, 3 a,b, 4 a,b). Two more important changes in light transmission linked to CYAN growth occurred between the end of July to the beginning of September, when periods of strong metalimnion mixing alternated with stable stratification and the DCM peak was shallower (Figs. 3a, 4 b,c). Following strong winds at the beginning of September, the DCM disappeared for the rest of the month when the mixed layer depth deepened to below 4.5 m, and DCM algae were distributed throughout the water column in parallel to an increase in light penetration and a huge upsurge of DP (Fig. 4 a,b). In combination, these effects supported surface algal growth that lowered light transmission and caused the disappearance of CYAN in the deep waters (Fig. 4 b,c).

Bloom occurrence and physical forcing

In lake Bromont, summer surface blooms have occurred almost every year since 2006, at variable frequency

and intensity (*e.g.*, few and small in biomass in 2007, but frequent, intense and long lasting in 2010 to 2011 (Cabal Gomes, 2014). Summer blooms in lake Bromont were formed by *Planthotrix* spp., the dominants species present in the DCM metalimnetic peak. These blooms were associated with the upsurge of metalimnetic waters (Fig. 3b), which were responsible for the delivery of 1 kg of DP, and 8 kg of TP and 7 kg of particulate phosphorus (PP) to the epilimnetic layer. Here, PP consisted mainly of algal-P contained in bloom-forming *Planthotrix*.

We used diurnal sampling over a 36-h period between the 9th and 10th of July, to elucidate the bloom dynamics of CYAN during an intense bloom period. Diel sampling coincided with the onset of a heat wave that caused a surface to bottom lake temperature gradient of almost 20°C, during which time [Chla] at the DCM peak reached >150 $\mu\text{g L}^{-1}$. The cycle started at sunrise on July 9th, when an intense surface *Planthotrix* spp. bloom was present. The [Chla] at the DCM peak at 6.0 m was 75 $\mu\text{g L}^{-1}$ and a secondary smaller peak (23 $\mu\text{g L}^{-1}$) was present at 4.5 m (Fig. 6a). At sunrise, the gust speed was very low, <4 m s^{-1} , but increased to around 6 m s^{-1} from 9 a.m. to 5 p.m. Consequently, internal wave oscillations increased, but the disturbance of the DCM was probably compensated by algal primary production. The algal biomass at the DCM peak increased from 5 a.m. to 8 p.m. (Fig. 6a).

In the evening of the 9th of July, two storms were registered, the first at 6 p.m., which was accompanied by strong SW winds, with gust velocities up to 13 m s^{-1} (Fig. 5a), not strong winds were associated with the second. Three hours after the occurrence of these strong winds, the amplitude of metalimnetic internal wave oscillations increased (Figs. 5 a,c), with the 2 and 5.75 m isotherms in phase, and a 2°C isotherm deflection occurring at the epi-metalimnetic boundary. Within this period, the 4 m isotherm was out of phase (the second vertical wave mode, V2H1, dominated during the cycle), causing larger amplitude oscillations that in turn generated temperature fluctuations of up to 3.25°C (Fig. 5c). The enhanced metalimnetic turbulence disrupted the CYAN-DCM peak. It swept the algae at the surface and subsurface of the peak upward into the epilimnion and biomass decreased at the DCM at the peak, and a huge bloom was observed again in the sunrise samplings of the 10th July (Figs. 5c, 6a).

It is known that in lakes with a thick metalimnion, wind events can alter patterns of internal waves, causing brief occurrence of the V1H1 mode, followed by the dominance of the V2H1 mode (Münich *et al.*, 1992; Pannard *et al.*, 2011). In Lake Bromont, Pannard *et al.* (2011) observed changes in thermal structure when surface current velocity exceeded 10 cm s^{-1} , since surface currents were strongly dependent on the speed of westerly winds above the lake surface. Consistent with our findings, Pannard *et al.*, (2011) also observed large temperature fluctuations

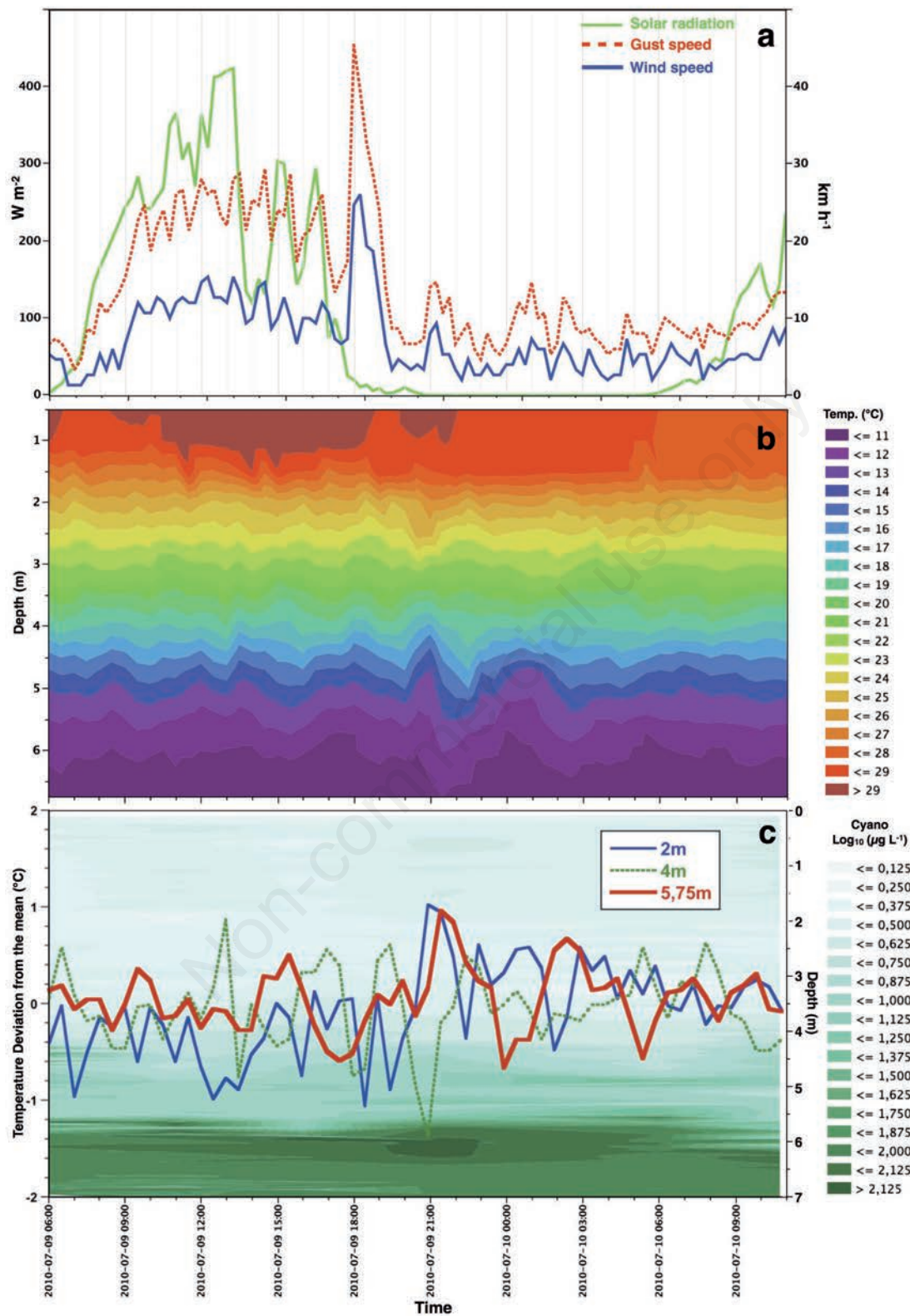


Fig. 5. Hourly physical and algal biomass data during the 24 h cycle (9 July at sunrise to 10 July at 10 a.m.). a) Incident photosynthetic active radiation ($W m^{-2}$) measured at the lake meteorological station, wind speed ($km h^{-1}$) and the gust speed ($km h^{-1}$). b) Hourly vertical profiles of temperature measured by *in situ* thermistor chains. c) Temperature deviations from the daily mean at three depths; 5.75 m (deeper metalimnion), 4 m (mid-metalimnion), and 2 m (meta-epilimnion boundary). In the background of the figure, changes in cyanobacterial biomass over 5 h time intervals are shown.

that coincided with maximum amplitudes at 4.5 m depth in lake Bromont. It has been reported that winds in excess of 10 m s^{-1} cause the rates of dissipation of turbulent kinetic energy to be high (MacIntyre and Jellison, 2001). Kinetic energy introduced to the lake by wind is transferred to metalimnetic waves, and may cause vertical displacement of suspended biomass, periodic variation in light intensity, and redistribution of dissolved substances (Münnich *et al.*, 1992).

Samplings on July 9th showed that algal biomass at the deep peak increased around 20% between 10 a.m and 3 p.m., and increased by 50% by 8 p.m. (Fig. 6a). At 8 p.m. sampling the DCM peak had widened almost 0.5 m (Fig. 6a), and the light reaching 6m depth decreased. The apparent contradiction in the above mentioned increase in algal biomass at the DCM in spite the decrease in PAR light transmission could be explained by internal wave displacement of phytoplankton through a vertical light gradient (Holloway and Denman, 1989). In our study, with an amplitude of internal waves as high as 3.5 m, the algae at the lower layers of the metalimnion were exposed to light intensities between 1% to 36% and hence, photosynthesis could be stimulated. In our lake, Pannard *et al.* (2011) demonstrated that metalimnetic photosynthetic productivity fluctuated between $\pm 20\%$ to 25%. Similar results were found by Evans *et al.* (2011), who compared primary production incubation results from fixed *versus* moving depths (simulating internal waves of 0.5^{-1} m amplitude). Both studies found that primary production responses differed in relation to incoming irradiance, and that rates were lower still when cloud cover occurred. In our study, the lower incoming PAR irradiance on the 10th of July (170 W m^{-2}) compared to the 9th (300 W m^{-2}) (Fig. 5a) may help explain the relative lack of algal deep peak recovery, which was 4 times lower on the 10th, relative to algal biomass on the 9th of July (Fig. 6a). In lake Bromont, the large amplitude of internal waves in the metalimnion, driven by strong wind events, not only altered the biomass of the CYAN-DCM, but also the physical and chemical characteristics in the lower part of the meta- and hypolimnion. Nutrient enrichment in the water column has previously been linked to internal waves (Ostrovsky *et al.*, 1996; MacIntyre and Jellison, 2001). In line with these studies, Pannard *et al.* (2011) showed for 2007 in lake Bromont that the vertical excursion of the metalimnion enhanced phosphorus concentrations and may have enhanced algal biomass. Increased nutrient concentrations (DP, ammonia) related to the amplitude of oscillations were also measured (*data non reported*). However, to our knowledge, what has not been reported in past studies is the variation in DO observed over the course of the diel sampling cycle. During this cycle, the deep metalimnion (6.5 m and 5.5 m) was initially anoxic at 10 a.m. on July 9th, but reached up to 60% saturation by midnight on July 10th. Fourfold increase in DO at 5.5 m

depth on July 9th from 8 pm to midnight were linked to the storm at 6 p.m. that, as mentioned before, induced larger amplitude oscillations after 9 pm (Figs. 6b, 5 b,c). The diurnal increase in amplitude of the oscillations from 9 a.m. to 5 p.m. together with daytime algal photosynthesis, could explain the increase in DO from 10 a.m. to 8 p.m. On July 10th DO in morning sampling was lower ($< 2 \text{ mg L}^{-1}$) below a depth of 6 m, as was the recovery of the algal DCM biomass peak, possibly due to the fact that the PAR irradiance on July 10th was almost half of that on the 9th.

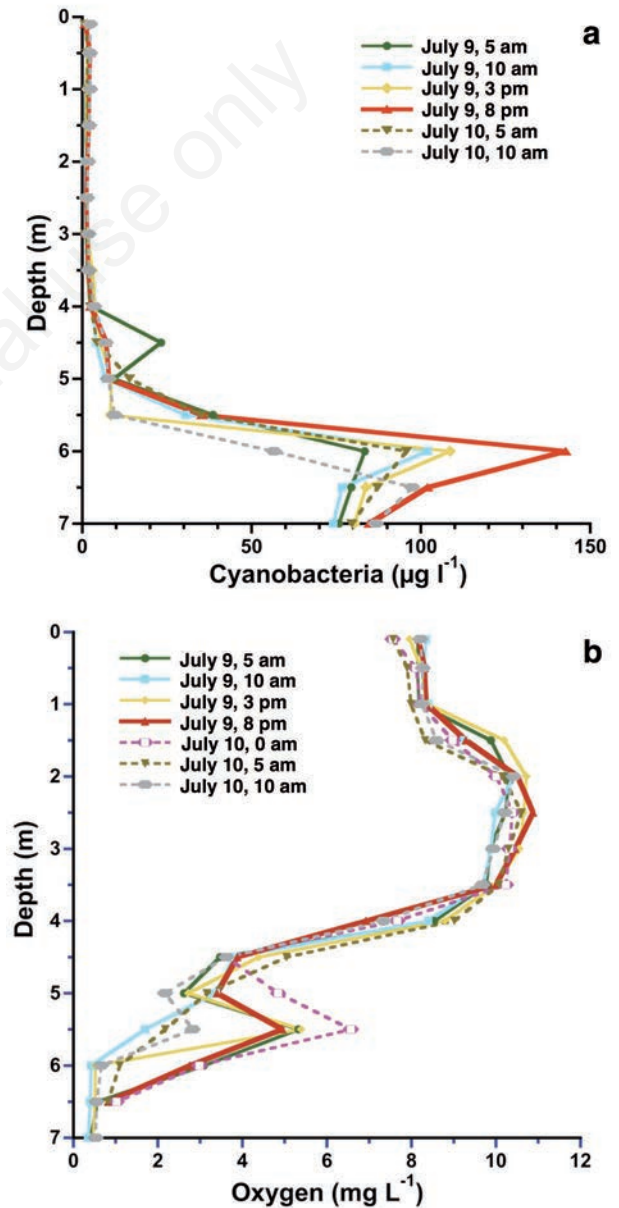


Fig. 6. Water column profiles during the cycle, including (a) cyanobacterial biomass, and (b) concentration of dissolved oxygen.

CONCLUSIONS

In summary, in small and stratified lake Bromont, despite low external nutrient inputs during the ice-free season, cyanobacteria dominated the phytoplankton community, growing abundantly in the meta- and hypolimnion as a result of plentiful internally supplied P, low ambient light, and low temperatures. These environmental conditions were ideal for the meta- and hypolimnetic growth and community dominance of both *P. rubescens* and *P. agardii*. The maximum biomass of cyanobacteria, up to 150 µg Chl *a* L⁻¹, was measured between 7 to 6.5 m, at the limit of, or below the photic zone. The L_N indicated metalimnetic internal waves commonly caused the DCM algae to oscillate vertically with the waves, and to be exposed to varying light intensities, thereby enabling photosynthesis even when deep waters receive very little light. After strong wind events, the amplitude of the internal wave oscillation increased and the DCM peak was disrupted, causing blooms to appear at the surface of the lake 12 h after the strong wind event. Not only did the large internal wave oscillations affect nutrient and DCM algal dynamics, but they also affected DO at 6.5 to 4.5 m depths.

Because changes in lake Bromont local temperatures over the past 50 years are consistent with the global trend (Pachauri and Meyer, 2014), from our results, we predict that atmospheric warming and boosted wind speeds, linked to increased storm frequency and intensity, will together rise the frequency and intensity of cyanobacterial blooms. In particular, *Planthotrix* blooms may become more prevalent in small (surface area lower than 1 km²) lakes with characteristics similar to lake Bromont, which may number up to 300 * 10⁶, and may collectively represent 43.3% of the total global lake surface area (Downing *et al.* 2006).

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