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Effects of climate change and episodic heat events on cyanobacteria in a eutrophic polymictic lake

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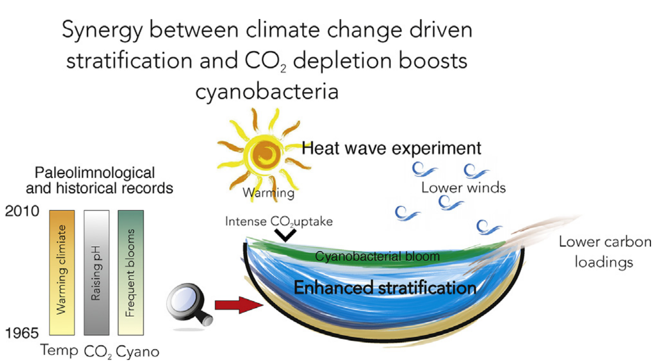
HIGHLIGHTS

- Enhanced stratification along with reduced wind speed during summers with heat waves, as compared to a more average year, lead to intensified warming of surface waters in a shallow polymictic eutrophic lake.
- Surface warming fosters development of high phytoplankton biomass, which, under reduced carbon inputs, is conducive to persistent CO_2 depletion in the epilimnion.
- Buoyant cyanobacteria produce massive blooms when warm surface waters of strongly stratified shallow eutrophic lake become CO_2 depleted.
- In polymictic lakes, synergistic mechanisms may catalyze cyanobacterial blooms once a certain threshold in warming is reached, carbon inputs are reduced and the water column is sufficiently stable to allow epilimnetic CO_2 depletion.
- This effect was responsible for proliferation of cyanobacteria in the lake over the last decades and will likely result in more frequent blooms in the future.

GRAPHICAL ABSTRACT



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ABSTRACT

Mixing regime and CO_2 availability may control cyanobacterial blooms in polymictic lakes, but the underlying mechanisms still remain unclear. We integrated detailed results from a natural experiment comprising an average-wet year (2011) and one with heat waves (2012), a long-term meteorological dataset (1960–2010), historical phosphorus concentrations and sedimentary pigment records, to determine the mechanistic controls of cyanobacterial blooms in a eutrophic polymictic lake. Intense warming in 2012 was associated with: 1) increased stability of the water column with buoyancy frequencies exceeding 40 cph at the surface, 2) high phytoplankton

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biomass in spring (up to 125 mg WW L^{-1}), 3) reduced downward transport of heat and 4) depleted epilimnetic CO_2 concentrations. CO_2 depletion was maintained by intense uptake by phytoplankton (influx up to 30 mmol m^{-2} d^{-1}) in combination with reduced, internal and external, carbon inputs during dry, stratified periods. These synergistic effects triggered bloom of buoyant cyanobacteria (up to 300 mg WW L^{-1}) in the hot year. Complementary evidence from polynomial regression modelling using historical data and pigment record revealed that warming explains 78% of the observed trends in cyanobacterial biomass, whereas historical phosphorus concentration only 10% thereof. Together the results from the natural experiment and the long-term record indicate that effects of hotter and drier climate are likely to increase water column stratification and decrease CO_2 availability in eutrophic polymictic lakes. This combination will catalyze blooms of buoyant cyanobacteria.

1. Introduction

Harmful cyanobacterial blooms are of increasing concern globally, raising questions about the controls on their development (Ho and Michalak, 2015). Increasing surface air temperatures, the immediate consequence of climate change, reduce the duration of ice cover and, with a longer and warmer season, lake surface temperature and stratification also increase (Dibike et al., 2011). In eutrophic lakes, such conditions stimulate phytoplankton growth and harmful blooms (Kraemer et al., 2017). Buoyant, bloom-forming cyanobacteria, for example, have an ecological advantage during warm stratified periods because they are capable to quickly optimize their vertical position in the water column (Ganf and Oliver, 1982). Indirect effects of climate change, such as altered precipitation patterns, catchment hydrology and reduced winds (Karnauskas et al., 2018), can also influence phytoplankton and favour cyanobacteria through effects on water clarity, retention times and mixing (Reichwaldt and Ghadouani, 2012).

It is well established that changes in nutrient concentration and stoichiometry, for example decreasing nitrogen (N) to phosphorus (P) ratios, can shift phytoplankton communities toward a greater contribution from cyanobacteria (Paerl et al., 2011). Numerous examples indicate that N limitation in stratified lakes may favour diazotrophic cyanobacteria (e.g., Gobler et al., 2016). With respect to carbon (C), cyanobacteria that are capable of efficiently exploit bicarbonates can also use CO_2 at lower concentrations than other phytoplankton species (Ibelings and Maberly, 1998; Posch et al., 2012) particularly when alkalinity is high (Caraco and Miller, 1998). Buoyant cyanobacteria can also actively move to the air-water interface to efficiently exploit atmospheric CO_2. Combined and interlinked effects of enhanced stratification and changes in nutrient ratios have led to the proliferation of cyanobacteria in stratified lakes globally (de Senerpont Domis et al., 2007). There is, however, relatively little mechanistic understanding of how these interacting factors impact cyanobacteria in nutrient-rich polymictic lakes (Kosten et al., 2012), where the water column mixes on a daily to weekly basis, and where the impacts of future climate, with changes in both temperature and rainfall, could affect physicochemical conditions in potentially different ways.

Across the globe heat waves have become increasingly frequent as a consequence of climate change (Karl and Trenberth, 2003). The short-term responses of lakes to these events may provide specific insights into the longer-term effects of climate warming on the functioning of lake ecosystems (Havens et al., 2016). In polymictic lakes, strong stratification may develop during years with heat waves (Bartosiewicz et al., 2015). Periods of exceptionally hot weather can be interrupted by windy and/or rainy days when relatively deep mixing and/or high runoff supplies pulses of nutrients and carbon. Buoyant cyanobacteria may benefit from stratification and intermittent mixing by making the most efficient use of the unsteady supply of resources (Huber et al., 2012). Correlative evidence indicates that the combined effects of warmer temperatures, thermal stratification and nutrient loading can modulate the abundance of cyanobacteria in shallow lakes, but the interactive mechanisms behind these effects remain unclear (Kosten et al., 2012).

Natural experiments comparing average and heat-wave years (e.g., Jankowski et al., 2006; Bartosiewicz et al., 2016) provide qualitative constraints on the potential links between climatic effects and the proliferation of cyanobacteria in lakes (Johnk et al., 2008). However, the integration of studies spanning interannual to interdecadal timescales and using multiple proxies provides more robust information on potential mechanisms. Recent survey of sedimentary pigment records and meteorological data for 83 lakes shows that cyanobacterial abundance is controlled by nutrient and temperature effects, with the former explaining three times more of the observed variation than the latter (Tarnau et al., 2015). However, among the 83 lakes taken into consideration, only a few were shallow (6 lakes <9 m deep). The functioning of shallow, polymictic lakes differs greatly from larger and deeper water bodies, and thus further investigation is required to determine the global applicability of these relationships. In this context, it is important to underline that small and shallow lakes represent approximately half of the global lentic area (Verpoorter et al., 2014), and that the impact of warming air temperatures on the physical structure and phytoplankton of these ecosystems may be more immediate than in larger and deeper lakes.

This study aimed to provide insight into the synergistic effects of limnological conditions related to atmospheric warming, including reduced precipitation, enhanced water column stability, increased surface-water temperature and CO_2 depletion, which together catalyze cyanobacterial blooms. This was done by: 1) comparing measures of stratification, nutrient regimes, CO_2 concentrations, and phytoplankton community in a shallow eutrophic, polymictic lake over two years, one of which presented heat-wave conditions; and 2) integrating records of sedimentary pigments with meteorological data and historical P and CO_2 concentrations.

2. Methods

2.1. Study site and regional climate

Lake St. Augustin (46° 42′N, 71° 22′W) is a small (0.63 km^2) and shallow (average depth of 3.5 m) lake located on the outskirts of Quebec City (Fig. 1). In the past two centuries, the lake has been exposed to the effects of intensified farming and urbanization (Deshpande et al., 2014) and became eutrophic by the mid-twentieth century. Currently, the lake is still classified as eutrophic to hypereutrophic, with total phosphorus concentrations (TP) between 20 and 160 μg L^{-1} and summertime chlorophyll-a (Chl-a) concentrations between 20 and 60 μg L^{-1}.

2.2. Interannual meteorology and physicochemistry

In 2011 and 2012, the lake was sampled at bi-weekly to monthly intervals throughout the entire open-water season (3 May – 13 October 2011, 22 April – 18 October 2012). During these two years, meteorological data were obtained from an Environment Canada weather station located 1.5 km from the lake (http://climate.weather.gc.ca/).

Water column profiles of temperature, conductivity, pH and dissolved oxygen (DO) were measured with a 600R multi-parametric probe (Yellow Spring Instruments). In addition, a thermistor chain (Onset Tidbit v2; accuracy 0.2 °C, resolution 0.2 °C, response time of 5 min) was installed to measure water temperature from June to October 2012 in the pelagic zone of the lake (10 m inshore from the regular sampling station, Fig. 1), with loggers deployed at 10 depths (0, 0.2, 0.4, 0.8, 1.2, 2.0, 2.5, 3.0, 3.5 and 4.0 m), and recording at 4-min intervals. The dynamics of the diurnal mixed layer were evaluated using equations developed by Imberger (1985), and the surface energy budget was computed following MacIntyre et al. (2002). We computed buoyancy frequency $N = (g/\rho\ d\rho/dz)^{1/2}$ where g is gravity, ρ is density, and z is depth. Salinity (S) was computed as a function of specific lake water conductance (550–650 μS cm^{-1}), by multiplying by a factor 0.8, as an estimate for the typical range between 0.6 and 0.9 (Pawlowicz, 2008). Density was computed from temperature and salinity of 0.48 g kg^{-1} (Chen and Millero, 1977; MacIntyre et al., 2018). As meteorological data were not collected on site, we computed a heat budget for the lake based on measured temperatures and bathymetric data and compared it with that obtained from the meteorological data. We sequentially reduced winds until the two budgets matched, and obtained congruence for wind speeds that were 70% of those recorded at the weather station. Lake number (L_N) was computed following Imberger and Patterson (1990) using the reduced wind speeds.

On each sampling date, discrete surface and near-bottom water samples taken at the deepest point of the lake were filtered through cellulose acetate filters (0.2-μm pore size) for the analyses of soluble reactive phosphorus (SRP, duplicates, detection limit, DL, of 0.5 μg L^{-1}) and nitrogen (N-NO_3^-, DL of 0.01 mg L^{-1}) using standard methods (Stainton et al., 1977). Total phosphorus and nitrogen analyses were carried out on unfiltered water samples following Stainton et al. (1977). Surface-water samples (100–500 ml, in duplicates) were also filtered through GF/F glass fiber filters (0.7-μm pore size) for the determination of Chl-*a* concentration by UV–Vis spectrophotometry after extraction of pigments in ethanol (Winterman and de Mots, 1965). The CO_2 concentrations (in triplicates) were assessed by equilibrating 2.0 L of water with 20 ml of air. After equilibration, the headspace was sampled into He-purged, pre-evacuated Exetainers (Labco Limited, UK), and the collected gas was analyzed as described in Laurion et al. (2010). The CO_2 fluxes were measured with a floating chamber (circular, 23.4 L), made of 10 mm thick PVC plastic with floaters distributed evenly on the side-wall, extending 4 cm into the water, which was equipped with an infrared gas analyzer (EGM-4, PP-Systems), and deployed 2 m away from the boat during each sampling for up to 20 min during the day (10-14 h) and every 6 h over a 24 h period in July 2012.

2.3. Phytoplankton

For phytoplankton analyses, 1 L water samples were collected from 0 to 5 m at 1 m intervals, integrated by taking subsamples from each depth, preserved with Lugol's iodine solution (5% final concentration) and analyzed following Utermöhl (1958) using an inverted microscope (Zeiss Axiovert 2000). The threshold for defining a bloom was taken at

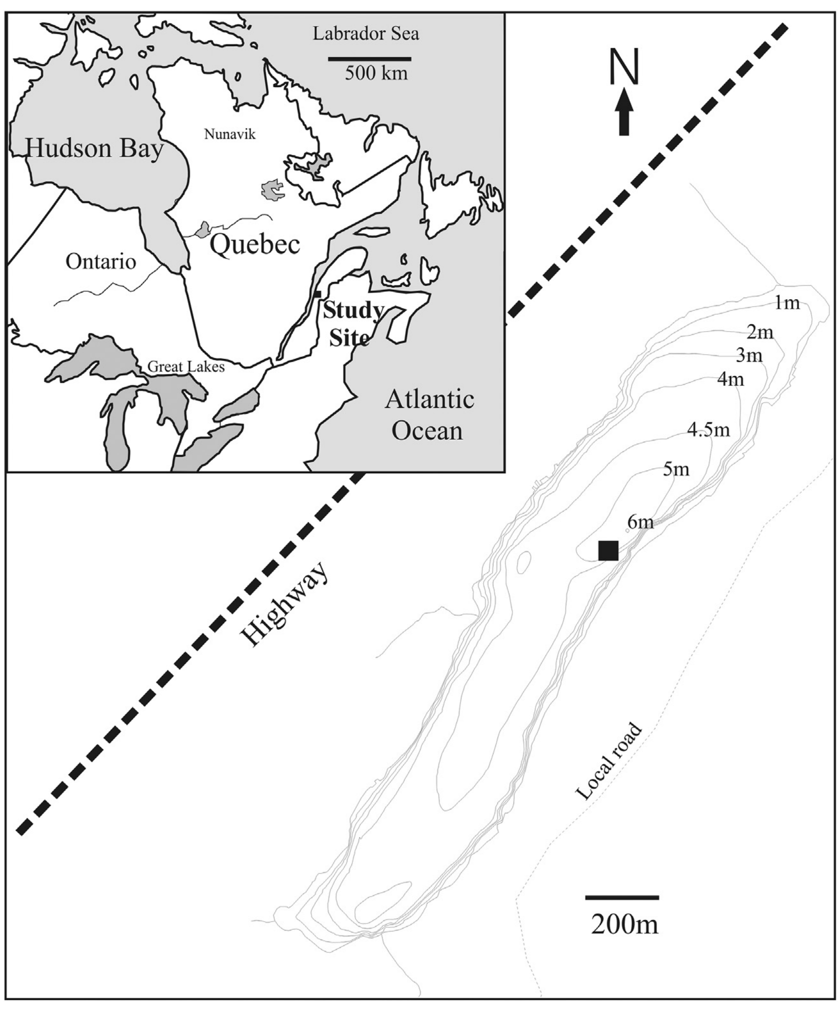

Fig. 1. Bathymetric map of Lake St. Augustin with inset indicating the location of this study site and black square indicating location of the sampling station on the lake. Thermistor chain was deployed 10 m inshore from the station where the water column was only 4.5 m deep.

10^4 cells per mL. The biovolumes were calculated following Hillebrand et al. (1999).

2.4. Sedimentary pigments

A single sediment core was retrieved in January 2011 using an open-barrel corer deployed at the deepest point of the lake, close to the main sampling station (Fig. 1). The core was sub-sectioned at 0.5-cm intervals between 0 and 20 cm and sediment samples (6 to 7 g) were collected for pigment analysis were frozen and freeze-dried for 48 h, then stored at −20 °C until further processing. A description of the sediment lithology and a ^{210}Pb and ^{137}Cs-based age model, validated with ^{14}C accelerator mass spectrometry (AMS) measurements, is provided in Deshpande et al. (2014). After extraction of approximately 0.2 g of dried sediment in 90% acetone and subsequent filtration of the extract, pigments were quantified by high performance liquid chromatography, and analyzed according to Zapata et al. (2000). All pigment concentrations are reported in *micrograms per gram of sediment* organic matter [μg(gOM)$^{-1}$]. Chlorophyll-a (Chl-a: Pheophytin >0.5; Chl-a: Pyropheophytin >2.0) and β-carotene (stable) were used as a general biomarkers of phytoplankton biomass, and zeaxanthin, echinenone and canthaxanthin as a quantitative proxy of cyanobacterial biomass (total cyanobacterial pigments). Zeaxanthin is also present in some rhodophytes and chlorophytes but in concentrations that are ten times lower than those reported for cyanobacteria (i.e., *Aphanizomenon gracile*, Schlüter et al., 2006). Furthermore, as blooms in Lake St-Augustin consist interchangeably of cyanobacteria, dinophytes or diatoms (Bouchard-Valentine, 2004), we considered that change in zeaxanthin is most likely associated with cyanobacterial biomass. A long-term (~400 years) pigment record from this core was previously reported by Deshpande et al. (2014), while in the current study, we focused on the last 50 years (~1960 to 2010). This higher resolution data set (with 20 dates obtained over the 50-year period) was related to climate change indices and historical TP concentrations. Data on past changes in TP for Lake St. Augustin were taken from various sources (available from http://www.lacsaintaugustin.com/), but all measurements were done using the same colorimetric method (Table S1). Past summertime CO_2 concentrations in surface waters were calculated using water temperature, total alkalinity and pH values following approach by Millero et al. (2002). These data were available for 12 individual years between 1968 and 2010.

2.5. Statistical analyses

The data collected in 2011 and 2012 were compared using a Welch t-test (hereafter referred to as t-test), which accounts for unequal sampling frequency. For the polynomial regression analysis historical meteorological and TP data were treated as independent and sedimentary pigment concentrations as depended variables. Temperatures (summer and winter) were averaged only for those years for which also sediment ages were available. For the analysis of snowfall versus sedimentary data, precipitation rates were averaged over the preceding winter. The historical TP record had lower temporal resolution than either the climate or sedimentary datasets, thus we limited the regression analysis

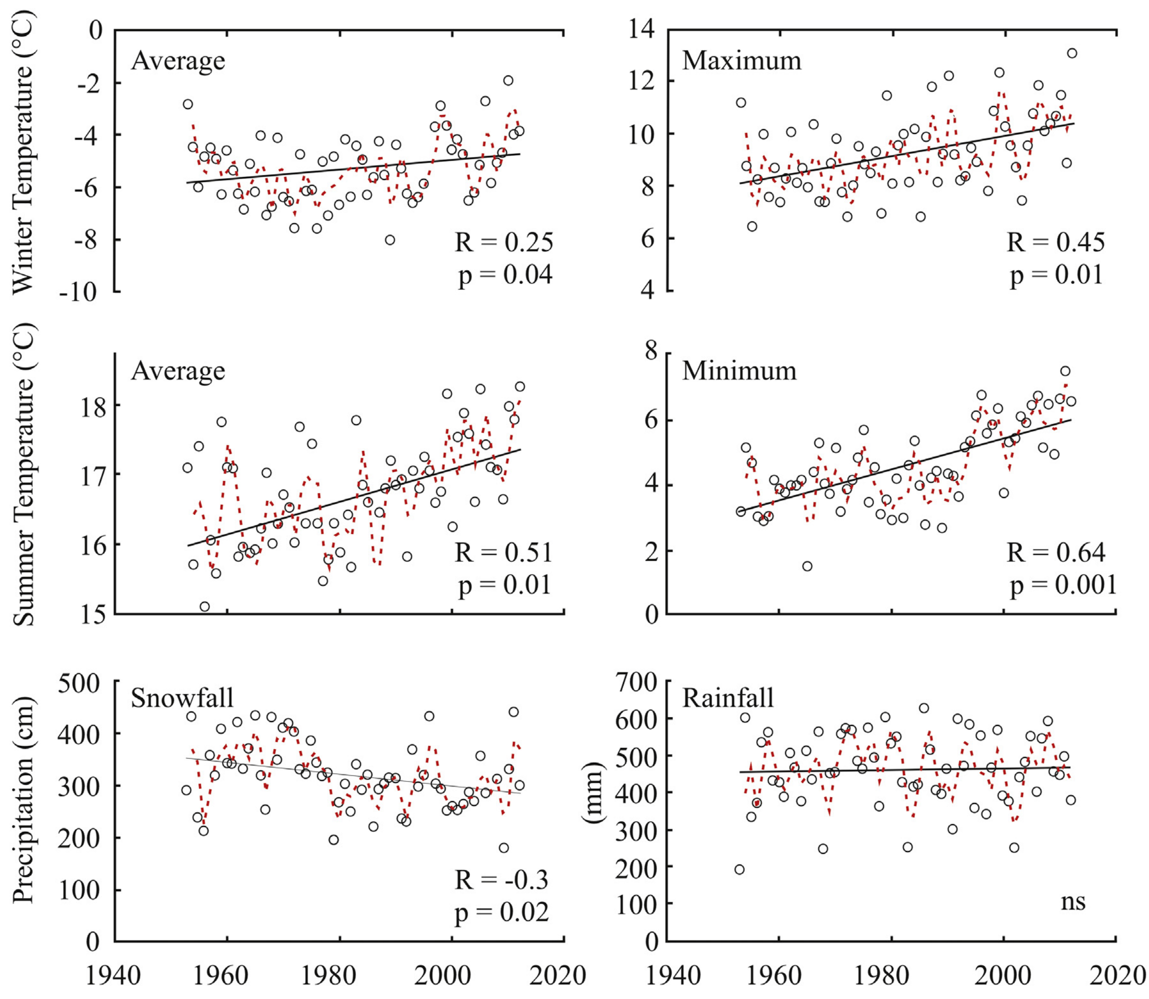

Fig. 2. Regional signatures of climate change including trends in the average, maximum (winter) and minimum (summer) temperatures, as well as the cumulated annual snowfall and rainfall over Lake St. Augustin between 1950 and 2010.

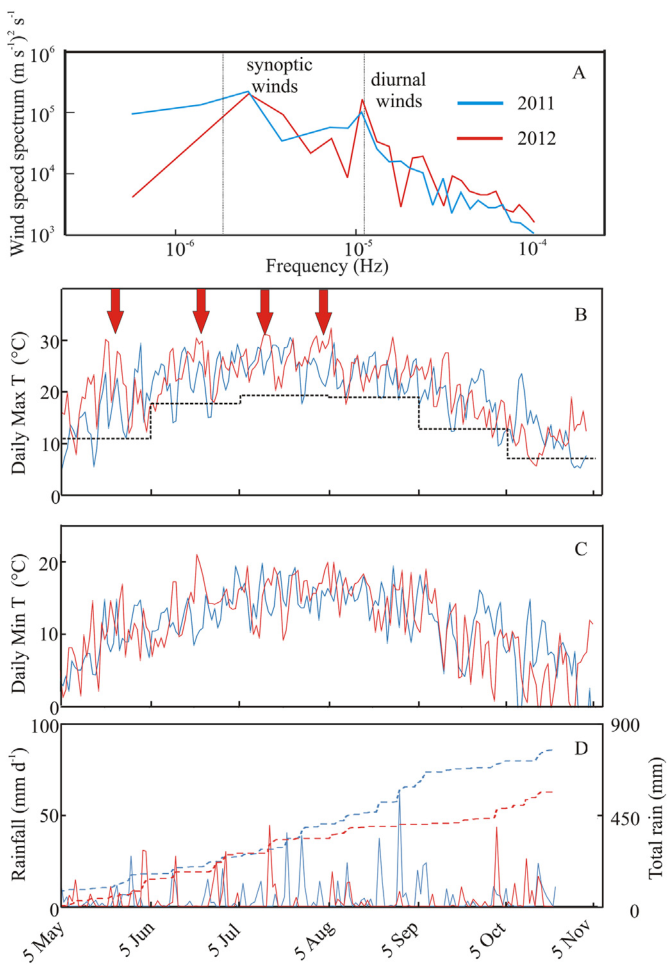

Fig. 3. Wind speed spectra (hourly winds in 2011 and at 8 min intervals in 2012), daytime maximum and nighttime minimum temperatures, as well as daily and total rainfall at Lake St. Augustin during an average (blue) and a heat-wave year (red). Red arrows indicate heat events, dotted black line indicates long-term average monthly temperatures. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

only to years with available TP data. Correlations between sedimentary pigment concentrations, climatic conditions and phosphorus in Lake St. Augustin were also analyzed using sequential t-test followed by an ANOVA to reveal significant changes in temporal trends. The relationship between concentrations of specific pigments and TP, surface air temperature and precipitation were analyzed using a multiple polynomial regression model. All statistical analyses were performed with XLStat 2016.

3. Results

3.1. Climate change and eutrophication in Lake Saint Augustin

During the period covered by this study (1960 to 2010), the average air temperatures near the lake increased in winter and summer (Fig. 2). The warming, however, was not linear. A sequential *t*-test followed by an ANOVA revealed a significant difference in warming trends between 1960 and 1990 in relation to that between 1990 and 2010, with a faster increase during the latter period (Fig. S1). Although there was no evident change in the overall amount of summertime rainfall, annual snowfall decreased significantly in the watershed of the lake during the last 50 years (Fig. 2).

The first recorded TP concentrations from 1967 (values between 50 and 460 μg L^{-1}, average 220 μg L^{-1}) indicated severe phosphorus pollution. Later records indicate a decrease in TP to ca. 20 μg L^{-1} between 1975 and 1983, an increase after 1983, and relatively high concentrations (>25 μg L^{-1}) persisting over the last three decades. These trends are well in range with previous estimates based on diatom fossils (Pienitz et al., 2006). No significant overall trend in the TP dataset was detected ($p > 0.05$).

3.2. Meteorological conditions during an average and a heat-wave year

The weather over Lake St. Augustin in May 2012 was hotter and drier in comparison to the previous year (Fig. 3). For example, the average air temperature in May was in the upper 3% of the respective temperature distribution since 1945. Similarly, average temperatures in July and August were in the upper 5% of respective distributions. In fact, the heat wave in August 2012 made this month the warmest August in Quebec since 1945.

The average and maximum air temperatures for the summer were 16.2 °C and 33 °C in 2012, respectively, as opposed to 15.3 °C and 30 °C in 2011 (Table 1). Rain events were less frequent during that period in 2012, and daily rainfall was lower than in 2011 (3.6 and 4.2 mm, t-test, $p = 0.001$). Unusually long dry periods (>7 days) in July 2012 resulted in a low daily precipitation mean of 2.6 mm. The intensity of rain events was, however, greater in 2012 than in 2011. Change in cumulative precipitation resulted in an increase of water retention time from 188 days in 2011 to 223 days in 2012 (for calculation details see Bergeron et al., 2002). Although in 2012, the average wind speed at the meteorological station was lower than in 2011 (3.3 compared to 3.6 m s^{-1}), the frequency analysis did not reveal significant differences in energy on diurnal time scales (Fig. 3).

3.3. Stratification dynamics and biogeochemistry

The surface waters in Lake St. Augustin were warmer in 2012 than in 2011 (21 °C compared to 17 °C, $p = 0.05$, t-test, Fig. 4). In contrast, bottom waters remained colder during 2012 (18 °C compared to 19 °C). Detailed temperature profiling revealed that the temperature difference between surface and bottom waters reached 9.5 °C during the heat wave between 17 and 21 June when air temperatures exceeded 30 °C (Fig. 4). The situation was similar during heat waves in July when temperature differences also regularly exceeded 5 °C indicating strong stratification.

Temperatures exceeded 25 °C in surface waters four times in the summer of 2012, times which corresponded to the heat waves (Figs. 4 and 5). A critical component of the warming was a decrease in wind speeds at night below the instrument threshold. Daytime winds varied during these periods, but were often <4 m s^{-1} and sometimes dropped to 2 m s^{-1}. These lower values contrast to winds speeds of up to 6 m s^{-1}

Table 1
Wind speed, rainfall and limnological characteristics of Lake St-Augustin during the natural experiment comparing two years (2011 and 2012). Water temperature (T), dissolved oxygen (O_2) and total phosphorus (TP) are given both for surface (S) and bottom waters (B). Nutrients and Chl-a concentrations as well as total phytoplankton abundance (Biomass) were measured in duplicates on ten sampling dates in 2011 and twenty sampling dates in 2012 (total of 60 values for each parameter); CO_2 concentrations were measured in triplicates ($n = 90$).

Var. Unit	Wind m s^{-1}	Rain mm	T^S °C	T^B °C	O_2^S mg L^{-1}	O_2^B mg L^{-1}	TP^S μg L^{-1}	TP^B μg L^{-1}	SRP μg L^{-1}	TN μg L^{-1}	N-NO_3^- mg L^{-1}	Chl-a μg L^{-1}	Biomass mg L^{-1}	pH	CO_2 μmol
2011	3.3	590	17	19	10.4	4.7	45	95	5.0	370	150	14	99	8.4	6.8
2012	3.6	810	21	18	11.7	2.7	72	89	3.5	420	100	21	110	8.6	−0.98

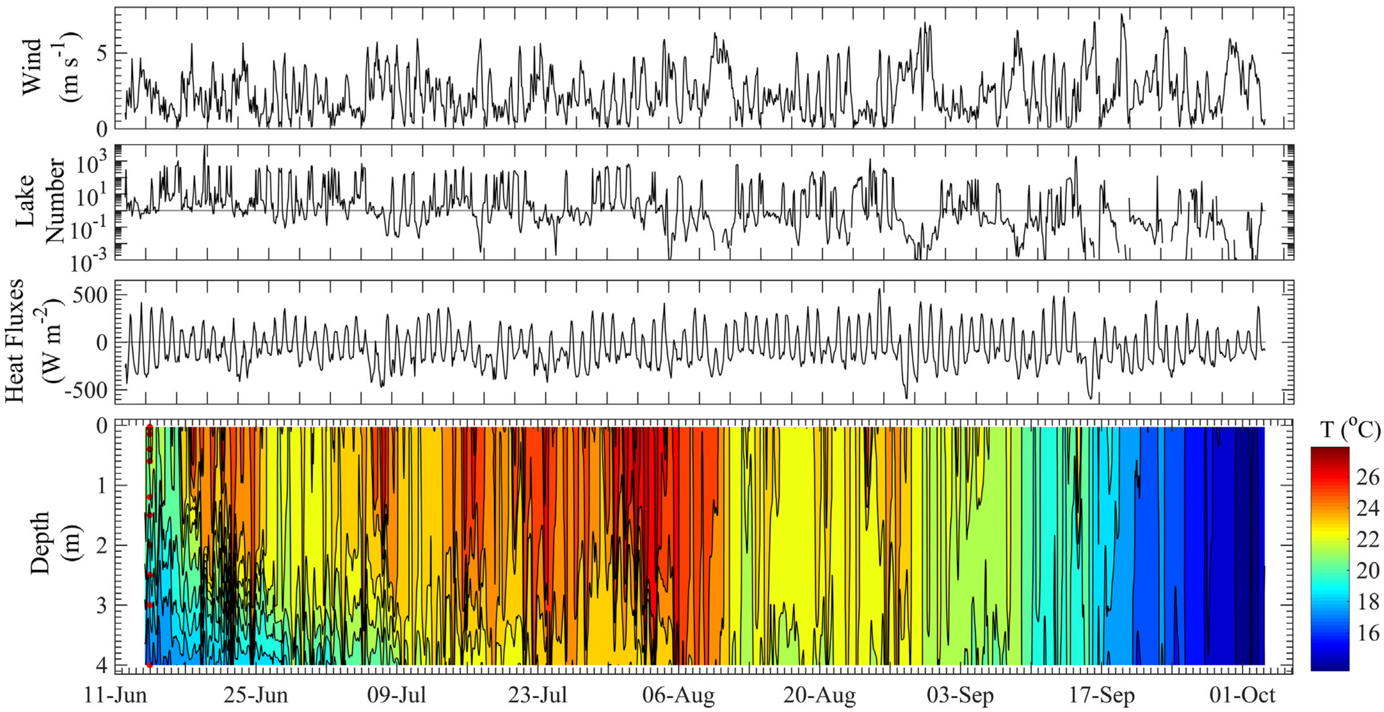

Fig. 4. Two hourly averaged wind speeds, Lake Numbers and heat fluxes along with temperature structure in Lake St. Augustin during summer of 2012.

when heat waves were not occurring. The Lake number (L_N), an index of the extent of upwelling and downwelling of the thermocline, that is, the degree of tilting and the potential for mixing across it from breaking internal waves (Imberger and Patterson, 1990; MacIntyre et al., 2009), had values approaching 1 during daytime over these warm periods as opposed to values dropping an order of magnitude lower at other times (Figs. 4 & 5). In response, the diurnal thermocline downwelled at the sampling site, which implies upwelling at the other end of the

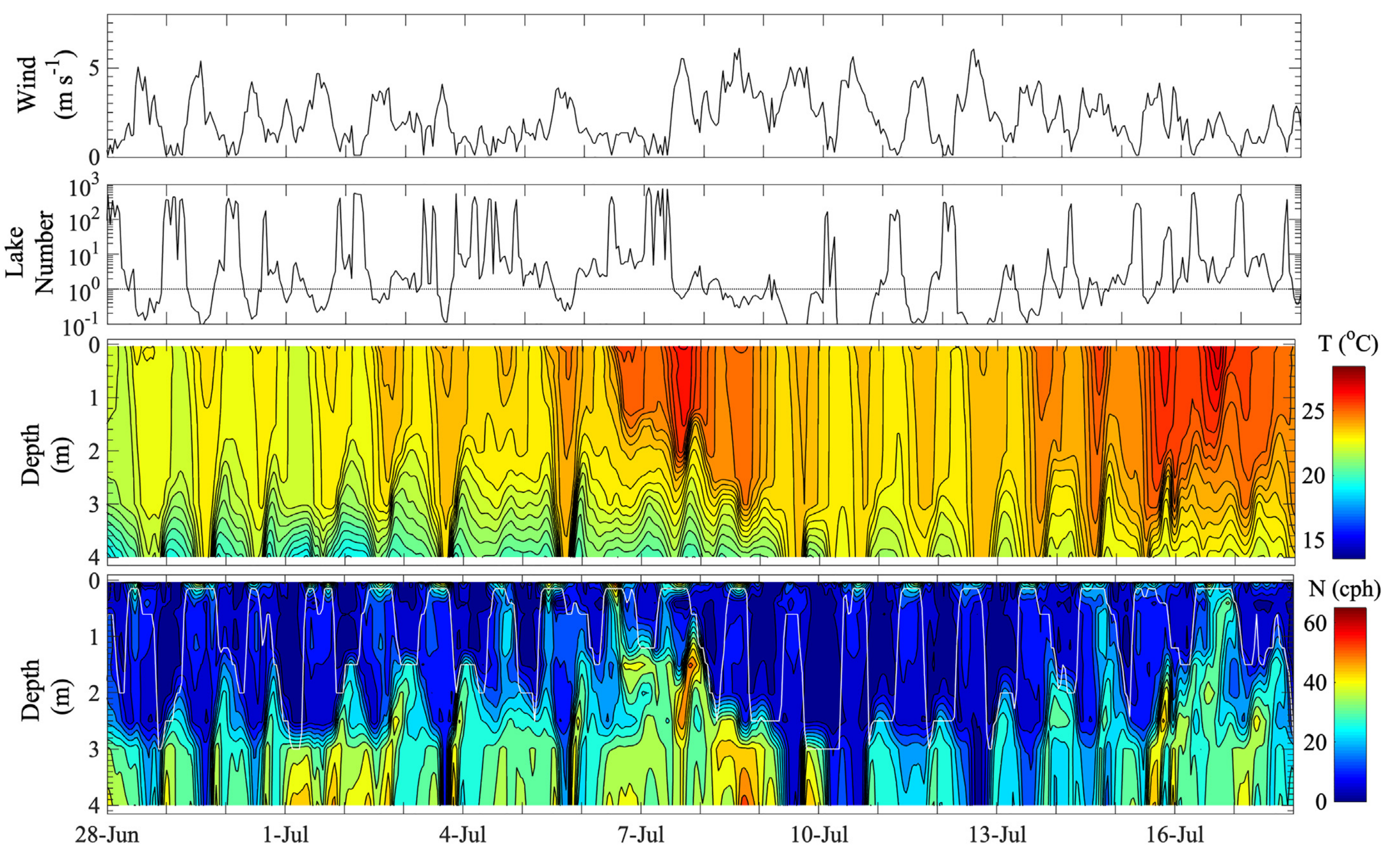

Fig. 5. Hourly averaged wind speeds, Lake Numbers, temperature and buoyancy frequencies (N) as well as mixed layer depths during the period with heat waves in 2012. Near surface N exceeded 20 cph on days with heat gain, and on days with greatest heat gain N exceeded 40 cph.

lake. The extent of downwelling was less during the warm periods (Fig. 5). With the decrease in wind speeds at night and related increase in L_N, the diurnal thermocline upwelled. Values of buoyancy frequency near the surface in the day were high enough during periods of heating to suppress near-surface mixing regardless of the mixing expected with low values of L_N (MacIntyre et al., 2018), and also increased in the lower water column during both day and night further indicating reduced mixing across the thermocline. Due to the low winds at night, and concomitantly decreased losses of heat by conduction and evaporation, nocturnal heat losses reached only up to -200 W m^{-2}, as opposed to -300 -500 W m^{-2} on windier nights (data not shown). Hence, mixed layer deepening at night was suppressed (Fig. 5, lower panel), much of the heat was retained, and stratification intensified.

During stormy conditions that started on 5 August 2012 (in the midst of a bloom), minimum values of L_N reached 10^{-3}, which, if such conditions persisted, implies complete mixing (Fig. 5) that would lead to changes in phytoplankton community. Indeed, the mixed layer did reach the lake bottom, but the lake re-stratified rapidly once the winds ceased. This rapid re-stratification implies that the water in the lower water column upwelled at the upwind end of the lake, but full mixing did not occur. The estimates of turbulent mixing immediately below the mixing layer were of order 10^{-6} to 10^{-5} m^2 s^{-1}, indicating that mixing across the thermocline was not effective (Fig. S2). Full water column mixing did occur, though, following a sustained event with low L_N at the beginning of September.

The biogeochemistry of the lake differed markedly between the two years, with the temperature and oxygen concentrations indicating greater isolation of the lower water column in the warmer summer (Fig. 6). Near-surface waters were better oxygenated and bottom waters were more oxygen-depleted in 2012 compared to 2011 (11.7 vs 10.4 mg L^{-1} at the surface and 2.7 vs 4.7 mg L^{-1} at the bottom, respectively). During most of summer 2011, CO_2 levels were above saturation in surface waters (relative to atmospheric equilibrium), and increased after rainfall ($R = 0.6$, $p = 0.04$). In contrast, surface waters in 2012 were depleted in CO_2 between May and August (by down to -5 μM below saturation). Diurnal analyses of the CO_2 saturation levels in mid-July revealed that even at night, CO_2 levels at the surface remained low (<2 μM, Fig. S3). This persistent CO_2 depletion ended after three days of continuous rain in mid-September, during which the mixed layer deepened (Fig. 6 E, F). Consistent with higher surface water concentrations, CO_2 fluxes were on average higher in 2011 than in 2012 (8.7 and -2.5 mmol m^{-2} d^{-1}, $p = 0.037$, Wilcoxon test, Fig. 6 G, H). Except f6or a brief period of high CO_2 efflux recorded during complete overturn after the summer with heat waves, when CO_2 emission reached 78 mmol $m^{-2}d^{-1}$, the CO_2 uptake by surface lake waters was more persistent and higher in 2012 than in 2011, with maximum influx rates of -30 mmol $m^{-2}d^{-1}$ during heat waves in the second half of July.

The TP and TN concentrations remained high over the entire study period (2011–2012), indicating eutrophic conditions in the lake. Yet in 2012, summer TP and TN concentrations were higher than in 2011 (72 vs 45 μg PL^{-1} and 420 vs 370 μg N L^{-1}). In contrast, concentrations of inorganic nutrients were lower in surface waters in 2012 than in 2011 (3.5 vs 5.0 μg L^{-1} for SRP, and 100 vs 150 μg L^{-1} for N-NO_3^-).

3.4. Phytoplankton

Throughout most of the productive season in 2011, dinophytes dominated the phytoplankton biomass, starting from June when their biomass reached 96 mg wet weight L^{-1} (mg WW L^{-1}; Fig. 7 A, C), corresponding to 15 μg Chl-a L^{-1} (data not shown). In the second half of June, the total phytoplankton biomass decreased to 30 mgWW L^{-1} and consisted of a mixture of dinophytes, cyanophytes and diatoms. Later that year, diatoms became increasingly abundant showing a maximum of 401 mgWW L^{-1} in the first week of September (Fig. 7 A, C).

Seasonal patterns in phytoplankton biomass were different in 2012 (Fig. 7 B). The phytoplankton was dominated by cryptophytes and diatoms early in the season (May), and dinophytes in May and June, with the total phytoplankton biomass reaching a maximum of 125 mg WW L^{-1}. Buoyant cyanobacteria (*Dolichospermum* sp. and *Aphanizomenon* sp.) were first evident around 5 July and dominated the phytoplankton community between 20 July and 15 August when they formed a dense surface bloom (>20×10^3 cells ml $^{-1}$ or up to 300 mg WW L^{-1}). Results of the partial least square regression analysis (PLS) revealed that cyanobacterial biomass can be predicted ($R^2 = 0.70$, $n = 30$, $p =$

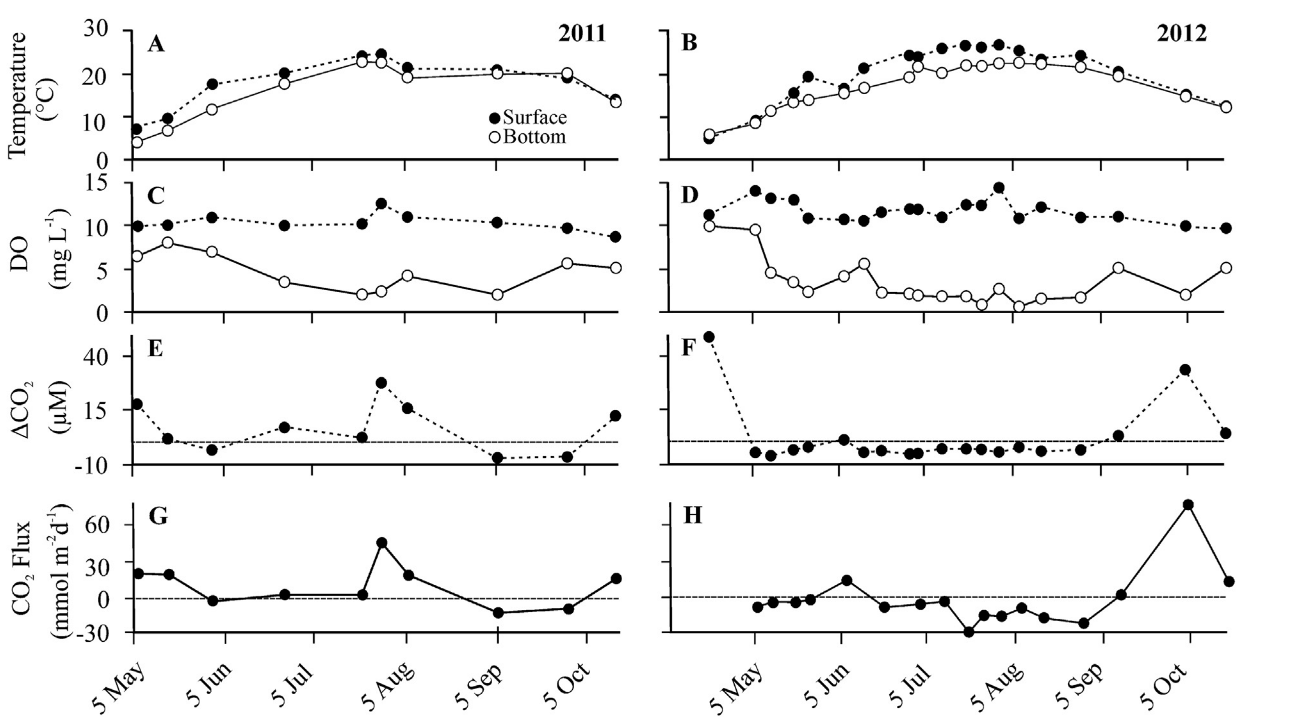

Fig. 6. Seasonal changes in daytime surface and bottom water temperatures, dissolved oxygen (DO), carbon dioxide departure from saturation levels (CO_2, triplicate measurements) and fluxes at the water-atmosphere interface in Lake St. Augustin during 2011 (left panels) and 2012 (right panels).

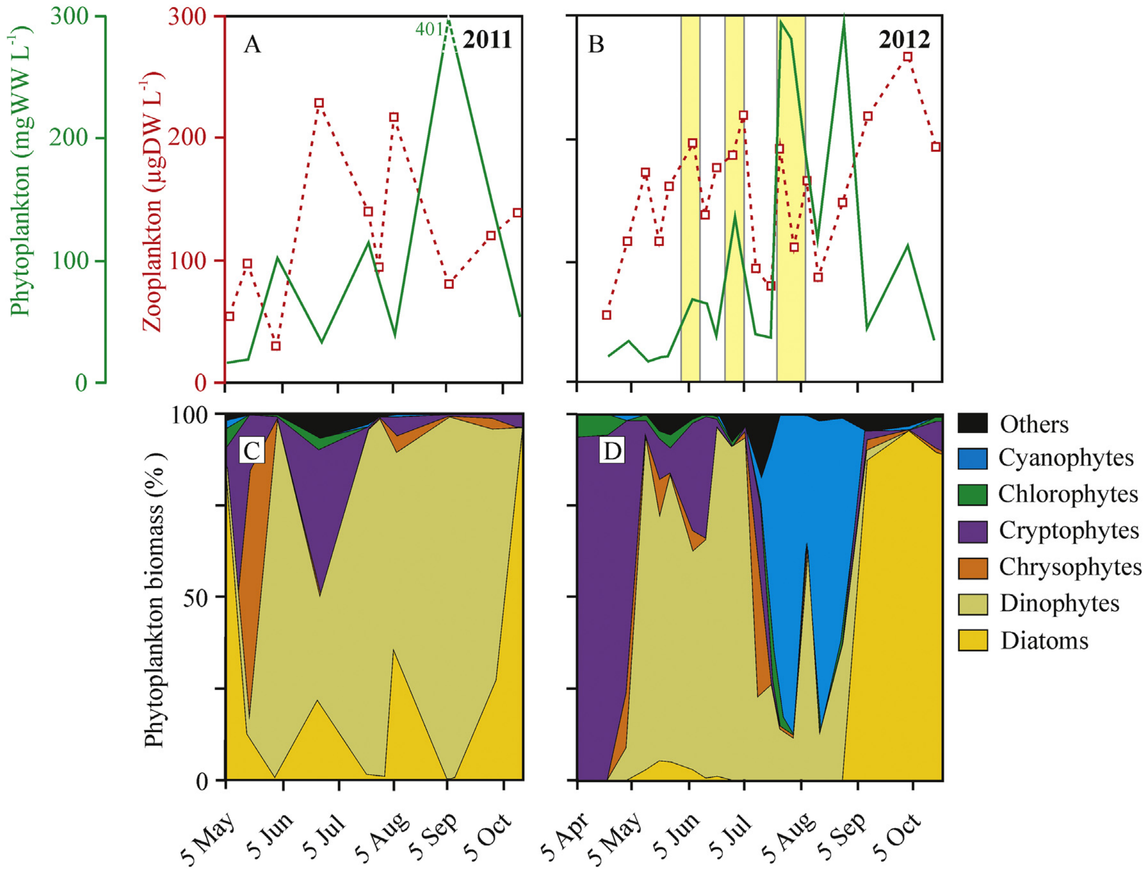

Fig. 7. Seasonal changes in the plankton biomass, including phytoplankton (as wet weight) and zooplankton (as dry weight), as well as the relative contribution of seven main taxonomic groups to the overall phytoplankton biovolume in Lake St. Augustin during an average wet (2011, left panels) and hot summer (2012, right panels). Yellow-shaded indicate major heat events in 2012 (upper panel). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

0.0001) using stratification strength (difference between surface and bottom T; Variable Importance in the Projection, VIP = 1.9), pH values (VIP = 1.7) as well as interactions between rainfall and pH (VIP = 1.4) and pH and bottom O_2 (VIP = 1.35). Including the interaction between SRP and N-NO_3 improved these predictions by additional 8% (VIP = 1.4, $R^2 = 0.78$, p = 0.0001).

3.5. Sedimentary pigment record and historical data

Temperatures and snowfalls observed in the vicinity of Lake St. Agustin during the last fifty years correlated with sedimentary pigments (Fig. 8; $p < 0.05$, $n = 20$). For instance, the Chl-*a* and β-carotene concentration in surface sediments increased proportionally with summer temperatures ($R = 0.71$ and $R = 0.59$, respectively, p = 0.0001). The concentration of zeaxanthin (a proxy for cyanobacteria in Lake St. Augustin) and of total cyanobacterial pigments (sum of zeaxanthin, canthaxanthin and echinenone) were also correlated with summer temperatures ($R = 0.78$, and 0.69, respectively, $p < 0.0001$). Noteworthy, canthaxanthin alone showed a negative relationship to temperatures ($R = -0.41$, $p = 0.1$). Decreasing snowfall also influenced phytoplankton biomass and community structure, as indicated by increase in Chl-a, ß-carotene and zeaxanthin concentrations over the last two decades. In contrast to climatic parameters, the historical TP concentrations (1967–2010; Fig. 9) did not correlate with changes in Chl-*a*, ß-carotene or zeaxanthin ($n = 14$, $p > 0.3$).

Changes in zeaxanthin were not linear over time. Consistent with the climate analysis, a sequential *t*-test followed by an ANOVA showed significant differences with regards to trends in the concentration of these pigments before and after 1990 ($p < 0.001$; Fig. 9). Zeaxanthin decreased between 1965 and 1990, and subsequently showed a positive trend between 1990 and 2011. The historical TP dataset did not reveal any trends over the past 50 years ($p > 0.7$). In contrast to insignificant trend in historical TP concentrations, pH values in surface waters indicate ongoing alkalinization (increase from an average of pH = 8.3 between 1968 and 1998 to pH = 8.8 between 1998 and 2010) and associated decrease of summertime CO_2 levels (from 25.5 ± 11.9 µM between 1968 and 1998 to 9.3 ± 6.7 µM between 1998 and 2010; $R = -0.58$, $n = 12$ $p = 0.02$, Fig. 9). Historical surface water CO_2 concentrations correlated to air temperatures recorded over the lake ($R = -0.78$, $p = 0.003$), and because the temperature record is more complete, the latter dataset was used in all subsequent analyses.

The multiple polynomial regression model, considering both climatic parameters (T, precipitation) and phosphorus concentrations, indicates that most of the variability in sedimentary zeaxanthin ($R^2 = 0.75$, $n = 18$, $p = 0.001$) can be explained by changes in summer and winter air temperatures, with an improvement by 15% after including the historical TP data. Overall, the accumulation of zeaxanthin in the sediments of Lac Saint Augustin, can be well predicted ($R^2 = 0.9$, $n = 14$ p = 0.001) using these three variables. The accumulation of cyanobacterial pigments can also be predicted using polynomial regression based on climate characteristics only ($R^2 = 0.78$, p = 0.001). Including historical TP concentrations results in further improvement of the model prediction by 10% ($R^2 = 0.88$, p = 0.001, n = 14).

4. Discussion

Effects of meteorological forcing on cyanobacteria in the lake were either direct through increased surface temperatures (Johnk et al.,

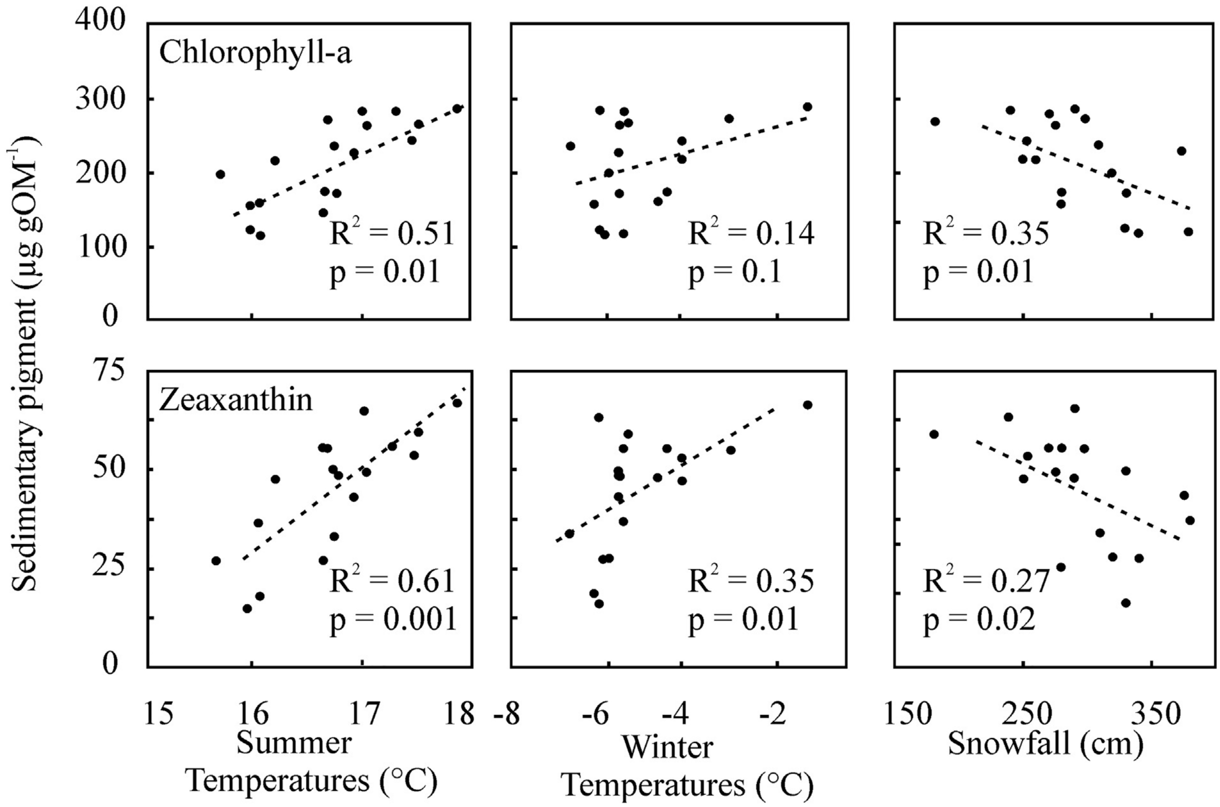

Fig. 8. Correlations between concentrations of selected pigments in the sediments of Lake St. Augustin and climate indices (average summer and winter temperature, cumulated annual snowfall).

2008), or indirect through the modulating control on the duration and strength of water column stratification, residence time, pH and nutrients. Particularly an interactive effect of enhanced stratification and increasing pH (associated to lower CO_2 levels) appears as an important catalyzer of cyanobacterial blooms. Our data indicate that heat waves and long-term warming affect functioning of polymictic lake ecosystem along the same axis. Correlative analyses of the sedimentary pigment record, historical TP and pH (CO_2 concentrations), and associated meteorological time series, as well as results from a natural experiment comparing years with contrasting meteorology indicate that warming and pH control the abundance of buoyant cyanobacteria. On the other hand, our work does not provide support for the existence of any specific P concentration threshold that may act to trigger blooms of cyanobacteria, suggesting that nutrients were sufficient already five decades ago to support persistent summertime blooms. While our results, show that effects of temperature are interacting with those of alkalinity (CO_2 depletion) when nighttime winds are low and stratification is strong (Visser et al., 2016) to stimulate cyanobacteria, high frequency monitoring of hydrodynamics and phytoplankton (Marcé et al., 2016) coupled to models (e.g., Recknagel et al., 2013) may help to gain further insight into the mechanism of bloom formation.

4.1. Warming-related effects on the water column physicochemistry

Heat waves had a strong effect on the stratification of Lake St. Augustin. The surface was warmer and the bottom colder in 2012 than in 2011. The enhanced temperature gradient during heat waves impeded exchanges between the upper and lower water column as shown also in other lakes (Shatwell et al., 2016). The detailed data in Lake St. Augustin indicate how the mixing dynamics changed during heat waves such that conditions favored cyanobacteria. During typical weather conditions, winds are moderate over the lake, with maxima between 4 m s^{-1} and 6 m s^{-1}. L_N drops below 1, implying the thermocline up and downwells and mixing occurs on a daily basis (Yeates and Imberger, 2003). On nights when winds remained high, heat losses were elevated up to −500 W m^{-2} and stratification was reduced, as expected with classic polymixis. During heat waves, winds and L_N were lower in the day (between 1 and 5), and fetch was reduced as winds were across rather than along the lake. Thus, while thermocline still tilted, the magnitude of this movement was less, and reduced downward mixing of heat contributed to greater and more persistent stratification (buoyancy frequencies increased above 40 cph).

Although air temperatures increased during heat waves, the covarying decrease in wind speeds and associated reduction in latent heat fluxes, the major heat loss term for the lake, were the critical determinants of warming and stratification. In fact, the incoming heat from sensible heat during heat waves was small (<20 W m^{-2} as compared to between −40 W m^{-2} and −100 W m^{-2} during windier conditions). With decreased heat losses at night under low winds, more of the heat which accumulated in the day was retained contributing to more stable stratification.

Enhanced stratification associated with heat waves resulted in the deoxygenation of bottom waters. The lake has accumulated large quantities of P in its sediments over the last 50 years, and currently experiences release of this legacy P when oxygen is depleted (Galvez-Cloutier et al., 2012). However, because of the ineffective exchange between the bottom and surface (euphotic) layers of the lake during the summer 2012, this surplus bioavailable P likely remained in the lower water column where it was accessible only for migrating phytoplankton i.e., buoyant cyanobacteria.

While alkalinity and CO_2 levels appear to play an important role in shaping the phytoplankton community structure (Maileht et al., 2013), their effect may be particularly important in controlling cyanobacteria (Van Dam et al., 2018). In the near future many lakes around the globe will stratify more strongly (Woolway and Merchant, 2019) and, with their sediments remaining colder throughout the

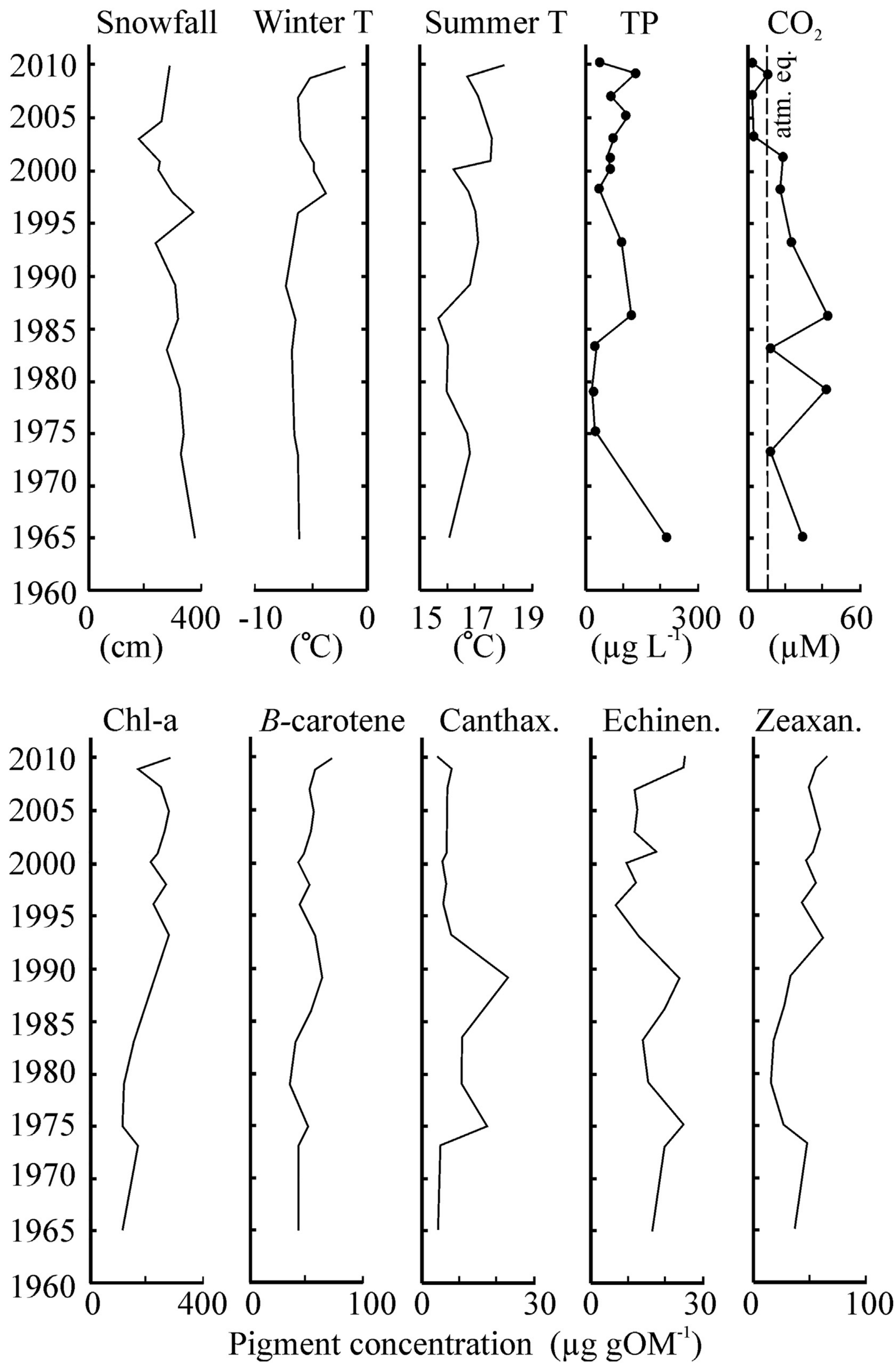

Fig. 9. Sedimentary pigment profiles (redrawn at higher temporal resolution following Deshpande et al., 2014), historical meteorological conditions and total phosphorus concentrations in Lake St. Augustin between 1960 and 2010.

summer (Bartosiewicz et al., 2019), less carbon will be release into the upper layers of the water column. These conditions are likely to favour bloom-forming cyanobacteria (Marcus et al., 1983) in the thinner and warmer epilimnion. The persistent diurnal CO_2 depletion, increasing alkalinity as well as very high rates of CO_2 uptake during the bloom indicate that buoyant cyanobacteria benefitted from their ability to concentrate carbon around their cells and migrated to optimize usage of atmospheric CO_2. In fact, measured CO_2 uptake rates were higher than expected from estimated values of the gas transfer coefficient (MacIntyre et al., 2010, Tedford et al., 2014, data not shown,) thus further supporting biologically enhanced CO_2 influx. Some previous experimental work suggested that cyanobacteria may outcompete other phytoplankton if CO_2 availability is low and alkalinity high (Caraco and Miller, 1998). Our results (using data from both natural experiment that compared two years and historical records that spanned over the last five decades) provide observational support for this positive interaction.

Here we argue that, in addition to exploiting of bicarbonates and using a highly effective C concentrating mechanism buoyant cyanobacteria gain an ecological advantage when heatwave-enhanced stratification allows them to more readily use atmospheric CO_2. Shallow polymictic lakes have traditionally been assumed to mix on a daily to weekly basis so that filamentous cyanobacteria could not use their buoyancy regulation to gain much of an advantage. Yet, here we demonstrate that during heat waves, and more frequently under future climate, lakes that mixed often will mix less and become a better habitat for buoyant cyanobacteria.

4.2. Decadal warming effects on the phytoplankton community

Historical records provide additional evidence for the link between climate change and cyanobacterial blooms. The 38% increase in zeaxanthin between 1990 and 2012 (and in total cyanobacterial pigments), relative to the long-term average, indicates potential recent proliferation of cyanobacteria. This increase coincides with accelerated warming, increasing pH and decreasing summertime CO_2 levels. The regression analyses reveal that while the climate variables have high explanatory power in relation to cyanobacterial pigments, the P concentrations are comparatively less useful in that regard for this eutrophic lake. The counterintuitive decrease in the sedimentary canthaxanthin may have been associated to lower contribution from this pigment to the total produced carotenoids under moderate levels of warming (Halfen and Francis, 1972; Kłodawska et al., 2019). The potential effects and interaction of ambient temperature and related environmental conditions (alkalinity) on cell-specific pigment production in cyanobacteria require further study.

Our results differ from some previous findings indicating that nutrients rather than temperature control cyanobacterial blooms in lakes (Rigosi et al., 2014). Although we have studied only one lake, we propose that for waters with a history of high loading and the efficient recycling of nutrients (Kilham and Kilham, 1990), continued input is not a key determinant of the frequency of harmful cyanobacterial blooms. In fact, many of the earlier observations pointing toward nutrient supply as the key determinant of cyanobacterial blooms are from lakes deeper than 10 m that develop blooms once stably stratified. Our data imply that these results are not necessarily pertinent to polymictic lakes with continuously high nutrient supply and support previous observations (Kosten et al., 2012) with a more mechanistic explanation. On the other hand, many shallow lakes host abundant macrophytes that might suppress cyanobacteria (Chang et al., 2012). The impact of climate change on macrophytes (Li et al., 2017) as well as the impact of macrophytes on water column stratification under warming (Vilas et al., 2018) and thus on the competitive abilities of buoyant cyanobacteria and other phytoplankton also requires further investigation.

4.3. Conclusion

Our results suggest that the synergy between warming and water column stratification is the key factor catalyzing cyanobacterial blooms in eutrophic polymictic lake. The effects of meteorological forcing on cyanobacteria blooms are both direct and indirect as they moderate temperature and precipitation as well as the related duration and strength of stratification. While persistent stratification and phytoplankton activity leads to elevated pH and enables CO_2 to remain undersaturated such that cyanobacteria had an advantage over other phytoplankton, our data imply that this effect can trigger cyanobacterial blooms only when acting in combination with lower nighttime winds and concomitant rapid warming of surface waters. Blooms of buoyant cyanobacteria will occur more frequently in polymictic lakes as climate warms and as these waters stratify more strongly. Harmful phytoplankton blooms under such conditions will have profound consequences for the biogeochemistry and food webs and hence for the functioning of aquatic ecosystems.

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