1   **ABSTRACT**

2   Mixing regime and CO_2 availability may control cyanobacterial blooms in polymictic lakes, but

3   the underlying mechanisms still remain unclear. We integrated detailed results from a natural

4   experiment comprising an average-wet year (2011) and one with heat waves (2012), a long-term

5   meteorological dataset (1960–2010), historical phosphorus concentrations and sedimentary

6   pigment records, to determine the mechanistic controls of cyanobacterial blooms in a eutrophic

7   polymictic lake. Intense warming in 2012 was associated with: 1) increased stability of the water

8   column with buoyancy frequencies exceeding 40 cph at the surface, 2) high phytoplankton

9   biomass in spring (up to 125 mg WW L^{-1}), 3) reduced downward transport of heat and 4)

10   depleted epilimnetic CO_2 concentrations. CO_2 depletion was maintained by intense uptake by

11   phytoplankton (influx up to 30 mmol m^{-2} d^{-1}) in combination with reduced, internal and external,

12   carbon inputs during dry, stratified periods. These synergistic effects triggered bloom of buoyant

13   cyanobacteria (up to 300 mg WW L^{-1}) in the hot year. Complementary evidence from

14   polynomial regression modelling using historical data and pigment record revealed that warming

15   explains 78% of the observed trends in cyanobacterial biomass, whereas historical phosphorus

16   concentration only 10% thereof. Together the results from the natural experiment and the long-

17   term record indicate that effects of hotter and drier climate are likely to increase water column

18   stratification and decrease CO_2 availability in eutrophic polymictic lakes. This combination will

19   catalyze blooms of buoyant cyanobacteria.

20

21   Keywords: harmful blooms, carbon dioxide, climate warming, eutrophication, buoyant

22   cyanobacteria.

1 INTRODUCTION

Harmful cyanobacterial blooms are of increasing concern globally, raising questions about the controls on their development (Ho & 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 & 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 & 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 & Maberly, 1998; Posch et al., 2012) particularly when alkalinity is high (Caraco & 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

47   of how these interacting factors impact cyanobacteria in nutrient-rich polymictic lakes (Kosten et

48   al., 2012), where the water column mixes on a daily to weekly basis, and where the impacts of

49   future climate, with changes in both temperature and rainfall, could affect physico-chemical

50   conditions in potentially different ways.

51

52   Across the globe heat waves have become increasingly frequent as a consequence of

53   climate change (Karl & Trenberth, 2003). The short-term responses of lakes to these events may

54   provide specific insights into the longer-term effects of climate warming on the functioning of

55   lake ecosystems (Havens et al., 2016). In polymictic lakes, strong stratification may develop

56   during years with heat waves (Bartosiewicz et al., 2015). Periods of exceptionally hot weather

57   can be interrupted by windy and/or rainy days when relatively deep mixing and/or high runoff

58   supplies pulses of nutrients and carbon to lakes. Buoyant cyanobacteria may benefit from

59   stratification and intermittent mixing by making the most efficient use of the unsteady supply of

60   resources (Huber et al., 2012). Correlative evidence indicates that the combined effects of

61   warmer temperatures, thermal stratification and nutrient loading can modulate the abundance of

62   cyanobacteria in shallow lakes, but the interactive mechanisms behind these effects remain

63   unclear (Kosten et al., 2012).

64

65   Natural experiments comparing average and heat-wave years (e.g., Jankowski et al.,

66   2006; Bartosiewicz et al., 2016) provide qualitative constraints on the potential links between

67   climatic effects and the proliferation of cyanobacteria in lakes (Jöhnk et al., 2008). However, the

68   integration of studies spanning interannual to interdecadal timescales and using multiple proxies

69   provides more robust information on potential mechanisms. Recent survey of sedimentary

70   pigment records and meteorological data for 83 lakes shows that cyanobacterial abundance is

71   controlled by nutrient and temperature effects, with the former explaining three times more of

72   the observed variation than the latter (Tarnau et al., 2015). However, among the 83 lakes taken

73   into consideration, only a few were shallow (6 lakes < 9 m deep). The functioning of shallow,

74   polymictic lakes differs greatly from larger and deeper water bodies, and thus further

75   investigation is required to determine the global applicability of these relationships. In this

76   context, it is important to underline that small and shallow lakes represent approximately half of

77   the global lentic area (Verpoorter et al., 2014), and that the impact of warming air temperatures

78   on the physical structure and phytoplankton of these ecosystems may be more immediate than in

79   larger and deeper lakes.

80

81   This study aimed to provide insight into the synergistic effects of limnological conditions

82   related to atmospheric warming, including reduced precipitation, enhanced water column

83   stability, increased surface-water temperature and CO_2 depletion, which together catalyze

84   cyanobacterial blooms. This was done by: 1) comparing measures of stratification, nutrient

85   regimes, CO_2 concentrations, and phytoplankton community in a shallow eutrophic, polymictic

86   lake over two years, one of which presented heat-wave conditions; and 2) integrating records of

87   sedimentary pigments with meteorological data and historical P and CO_2 concentrations.

88

89   **2 METHODS**

90   **2.1 Study site and regional climate**

91   Lake St. Augustin (46º 42'N, 71º 22'W) is a small (0.63 km^2) and shallow (average depth of 3.5

92   m) lake located on the outskirts of Quebec City (Figure 1). In the past two centuries, the lake has

93   been exposed to the effects of intensified farming and urbanization (Deshpande et al., 2014) and

94   became eutrophic by the mid-twentieth century. Currently, the lake is still classified as eutrophic

4

95   to hypereutrophic, with total phosphorus concentrations (TP) between 20-160 μg L^{-1} and

96   summertime chlorophyll-a (Chl-a) concentrations between 20 and 60 μg L^{-1}.

97

98   **2.2 Interannual meteorology and physicochemistry**

99   In 2011 and 2012, the lake was sampled at bi-weekly to monthly intervals throughout the entire

100   open-water season (3 May – 13 October 2011, 22 April – 18 October 2012). During these two

101   years, meteorological data were obtained from an Environment Canada weather station located

102   1.5 km from the lake (*http://climate.weather.gc.ca/*).

103

104   Water column profiles of temperature, conductivity, pH and dissolved oxygen (DO) were

105   measured with a 600R multi-parametric probe (Yellow Spring Instruments). In addition, a

106   thermistor chain (Onset Tidbit v2; accuracy 0.2°C, resolution 0.2°C, response time of 5 min) was

107   installed to measure water temperature from June to October 2012 in the pelagic zone of the lake

108   (10 m inshore from the regular sampling station, Figure 1), with loggers deployed at 10 depths

109   (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-minute intervals. The

110   dynamics of the diurnal mixed layer were evaluated using equations developed by Imberger

111   (1985), and the surface energy budget was computed following MacIntyre et al. (2002). We

112   computed buoyancy frequency $N = (g/\rho \ d\rho/dz)^{1/2}$ where g is gravity, ρ is density, and z is depth.

113   Salinity (S) was computed as a function of specific lake water conductance (550-650 μS cm^{-1}),

114   by multiplying by a factor 0.8, as an estimate for the typical range between 0.6 and 0.9

115   (Pawlowicz 2008). Density was computed from temperature and salinity of 0.48 g kg^{-1} (Chen &

116   Millero, 1977; MacIntyre, et al., 2018). As meteorological data were not collected on site, we

117   computed a heat budget for the lake based on measured temperatures and bathymetric data and

118   compared it with that obtained from the meteorological data. We sequentially reduced winds

119   until the two budgets matched, and obtained congruence for wind speeds that were 70% of those

120   recorded at the weather station. Lake number (L_N) was computed following Imberger and

121   Patterson (1990) using the reduced wind speeds.

122

123   On each sampling date, discrete surface and near-bottom water samples taken at the

124   deepest point of the lake were filtered through cellulose acetate filters (0.2-µm pore size) for the

125   analyses of soluble reactive phosphorus (SRP, duplicates, detection limit, DL, of 0.5 µg L^{-1}) and

126   nitrogen (N-NO_3^-, DL of 0.01 mg L^{-1}) using standard methods (Stainton et al., 1977). Total

127   phosphorus and nitrogen analyses were carried out on unfiltered water samples following

128   Stainton et al. (1977). Surface-water samples (100–500 ml, in duplicates) were also filtered

129   through GF/F glass fiber filters (0.7-µm pore size) for the determination of Chl-*a* concentration

130   by UV−Vis spectrophotometry after extraction of pigments in ethanol (Winterman & De Mots,

131   1965). The CO_2 concentrations (in triplicates) were assessed by equilibrating 2.0 L of water with

132   20 ml of air. After equilibration, the headspace was sampled into He-purged, pre-evacuated

133   Exetainers (Labco Limited, UK), and the collected gas was analyzed as described in Laurion et

134   al. (2010). The CO_2 fluxes were measured with a floating chamber (circular, 23.4 L), made of 10

135   mm thick PVC plastic with floaters distributed evenly on the sidewall, extending 4 cm into the

136   water, which was equipped with an infra-red gas analyzer (EGM-4, PP-Systems), and deployed 2

137   m away from the boat during each sampling for up to 20 minutes during the day (10-14h) and

138   every 6h over 24h period in July 2012.

139

140   **2.3 Phytoplankton**

141   For phytoplankton analyses, 1L water samples were collected from 0 to 5 meters at 1 m

142   intervals, integrated by taking subsamples from each depth, preserved with Lugol's iodine

6

143 solution (5% final concentration) and analyzed following Utermohl (1958) using an inverted

144 microscope (Zeiss Axiovert 2000). The threshold for defining bloom was taken at 10^4 cell per

145 ml. The biovolumes were calculated following Hillebrand et al. (1999).

146

147 **2.4 Sedimentary pigments**

148 A single sediment core was retrieved in January 2011 using an open-barrel corer deployed at the

149 deepest point of the lake, close to the main sampling station (Figure 1). The core was sub-

150 sectioned at 0.5-cm intervals between 0 and 20 cm and sediment samples (6 to 7 g) were

151 collected for pigment analysis were frozen and freeze-dried for 48 h, then stored at -20°C until

152 further processing. A description of the sediment lithology and a ^{210}Pb and ^{137}Cs-based age

153 model, validated with ^{14}C accelerator mass spectrometry (AMS) measurements, is provided in

154 Deshpande et al. (2014). After extraction of approximately 0.2 g of dried sediment in 90%

155 acetone and subsequent filtration of the extract, pigments were quantified by high performance

156 liquid chromatography, and analyzed according to Zapata et al. (2000). All pigment

157 concentrations are reported in *micrograms per gram of sediment* organic matter [µg (g OM) $^{-1}$].

158 Chlorophyll-a (Chl-a : Pheophytin >0.5; Chl-a : Pyropheophytin >2.0) and ß-carotene (stable)

159 were used as a general biomarkers of phytoplankton biomass, and zeaxanthin, echinenone and

160 canthaxanthin as a quantitative proxy of cyanobacterial biomass (total cyanobacterial pigments).

161 Zeaxanthin is also present in some rhodophytes and chlorophytes but in concentrations that are

162 ten times lower than those reported for cyanobacteria (i.e., *Aphanizomenon gracile*, Schlüter et

163 al. 2006). Furthermore, as blooms in Lake St-Agustin consist interchangeably of cyanobacteria,

164 dinophytes or diatoms (Bouchard-Valentine, 2004), we considered that change in zeaxanthin is

165 most likely associated with cyanobacterial biomass. A long-term (~400 years) pigment record

166   from this core was previously reported by Deshpande et al. (2014), while in the current study, we

167   focused on the last 50 years (~1960 to 2010). This higher resolution data set (with 20 dates

168   obtained over the 50-year period) was related to climate change indices and historical total

169   phosphorus concentrations (TP). Data on past changes in TP for Lake St. Augustin were taken

170   from various sources (available from http://www.lacsaintaugustin.com/), but all measurements

171   were done using the same colorimetric method (Table S1). Past summertime CO_2 concentrations

172   in surface waters were calculated using total alkalinity and pH values following approach by

173   Millero et al. (2002). These data were available for 12 individual years between 1968 and 2010.

174

175   **2.5 Statistical analyses**

176   The data collected in 2011 and 2012 were compared using a Welch t-test (hereafter referred to as

177   t-test), which accounts for unequal sampling frequency. For the polynomial regression analysis

178   historical meteorological and P data were treated as independent and sedimentary pigment

179   concentrations as depended variables. Temperatures (summer and winter) were averaged only for

180   those years for which also sediment ages were available. For the analysis of snowfall versus

181   sedimentary data, precipitation rates were averaged over the preceding winter. The historical

182   phosphorus concentration (TP) record had lower temporal resolution than either the climate or

183   sedimentary datasets, thus we limited the regression analysis only to years with available TP

184   data. Correlations between sedimentary pigment concentrations, climatic conditions and

185   phosphorus in Lake St. Augustin were also analyzed using sequential t-test followed by an

186   ANOVA to reveal significant changes in temporal trends. The relationship between

187   concentrations of specific pigments and P, surface air temperature and precipitation were

188 analyzed using a multiple polynomial regression model. All statistical analyses were performed

189 with XLStat (2016).

190

191 **3 RESULTS**

192 **3.1 Climate change and eutrophication in Lake Saint Augustin**

193 During the period covered by this study (1960 to 2010), the average air temperatures near

194 the lake increased in winter and summer (Figure 2). The warming, however, was not linear. A

195 sequential t-test followed by an ANOVA revealed a significant difference in warming trends

196 between 1960-1990 and 1990-2010, with a faster increase during the latter period (Figure S1).

197 Although there was no evident change in the overall amount of summertime rainfall, annual

198 snowfall decreased significantly in the watershed of the lake during the last 50 years (Figure 2).

199

200 The first recorded TP concentrations from 1967 (values between 50 and 460 µg L^{-1},

201 average 220 µg L^{-1}) indicated severe phosphorus pollution. Later records indicate a decrease in

202 TP to ca. 20 µg L^{-1} between 1975 and 1983, an increase after 1983, and relatively high

203 concentrations (> 25 µg L^{-1}) persisting over the last three decades. These trends are well in range

204 with previous estimates based on diatom fossils (Pienitz et al. 2006). No significant overall trend

205 in the TP dataset was detected ($p > 0.05$).

206

207 **3.2 Meteorological conditions during an average and a heat-wave year**

208 The weather over Lake St. Augustin in May 2012 was hotter and drier in comparison to the

209 previous year (Figure 3). For example, the average air temperature in May was in the upper 3%

210 of the respective temperature distribution since 1945. Similarly, average temperatures in July and

211 August were in the upper 5% of respective distributions. In fact, the heat wave in August 2012

212 made this month the warmest August in Quebec since 1945.

213

214   The average and maximum air temperatures for the summer were 16.2°C and 33°C in

215 2012, respectively, as opposed to 15.3°C and 30°C in 2011 (Table 1). Rain events were less

216 frequent during that period in 2012, and daily rainfall was lower than in 2011 (3.6 and 4.2 mm, t-

217 test, p = 0.001). Unusually long dry periods (> 7 days) in July 2012 resulted in a low daily

218 precipitation mean of 2.6 mm. The intensity of rain events was, however, greater in 2012 than in

219 2011. Change in cumulative precipitation resulted in an increase of water retention time from

220 188 days in 2011 to 223 days in 2012 (for calculation details see Bergeron et al., 2002).

221 Although in 2012, the average wind speed at the meteorological station was lower than in 2011

222 (3.3 compared to 3.6 m s^{-1}), the frequency analysis did not reveal significant differences in

223 energy on diurnal time scales (Figure 3).

224

225 **3.3 Stratification dynamics and biogeochemistry**

226   The surface waters in Lake St. Augustin were warmer in 2012 than in 2011 (21°C

227 compared to 17°C, p = 0.05, t-test, Figure 4). In contrast, bottom waters remained colder during

228 2012 (18°C compared to 19°C). Detailed temperature profiling revealed that the temperature

229 difference between surface and bottom waters reached 9.5°C during the heat wave between 17

230 and 21 June when air temperatures exceeded 30°C (Figure 4). The situation was similar during

231 heat waves in July when temperature differences also regularly exceeded 5°C indicating strong

232 stratification.

233   Temperatures exceeded 25°C in surface waters four times in the summer of 2012, times

234 which corresponded to the heat waves (Figures 4 and 5). A critical component of the warming

10

235   was a decrease in wind speeds at night below the instrument threshold. Daytime winds varied

236   during these periods, but were often less than 4 m s^{-1} and sometimes dropped to 2 m s^{-1}. These

237   lower values contrast to winds speeds of up to 6 m s^{-1} when heat waves were not occurring. The

238   Lake number (L_N), an index of the extent of upwelling and downwelling of the thermocline, that

239   is, the degree of tilting and the potential for mixing across it from breaking internal waves

240   (Imberger & Patterson, 1990; MacIntyre et al., 2009), had values approaching 1 during daytime

241   over these warm periods as opposed to values dropping an order of magnitude lower at other

242   times (Figures 4 & 5). In response, the diurnal thermocline downwelled at the sampling site,

243   which implies upwelling at the other end of the lake. The extent of downwelling was less during

244   the warm periods (Figure 5). With the decrease in wind speeds at night and related increase in

245   L_N, the diurnal thermocline upwelled. Values of buoyancy frequency near the surface in the day

246   were high enough during periods of heating to suppress near-surface mixing regardless of the

247   mixing expected with low values of L_N (MacIntyre et al., 2018), and also increased in the lower

248   water column during both day and night further indicating reduced mixing across the

249   thermocline. Due to the low winds at night, and concomitantly decreased losses of heat by

250   conduction and evaporation, nocturnal heat losses reached only up to -200 W m^{-2}, as opposed to -

251   300 -500 W m^{-2} on windier nights (data not shown). Hence, mixed layer deepening at night was

252   suppressed (Figure 5, lower panel), much of the heat was retained, and stratification intensified.

253

254   During stormy conditions that started on 5 August 2012 (in the midst of a bloom),

255   minimum values of L_N reached 10^{-3}, which, if such conditions persisted, implies complete

256   mixing (Figure 5) that would lead to changes in phytoplankton community. Indeed, the mixed

257   layer did reach the lake bottom, but the lake re-stratified rapidly once the winds ceased. This

258   rapid re-stratification implies that the water in the lower water column upwelled at the upwind

259   end of the lake, but full mixing did not occur. The estimates of turbulent mixing immediately

260   below the mixing layer were of order 10^{-6} to 10^{-5} m^2 s^{-1}, indicating that mixing across the

261   thermocline was not effective (Figure S2). Full water column mixing did occur, though,

262   following a sustained event with low L_N at the beginning of September.

263

264   The biogeochemistry of the lake differed markedly between the two years, with the

265   temperature and oxygen concentrations indicating greater isolation of the lower water column in

266   the warmer summer (Figure 6). Near-surface waters were more oxygenated and bottom waters

267   were more oxygen-depleted in 2012 compared to 2011 (11.7 vs 10.4 mg L^{-1} at the surface and

268   2.7 vs 4.7 mg L^{-1} at the bottom, respectively). During most of summer 2011, CO_2 levels were

269   above saturation in surface waters (relative to atmospheric equilibrium), and increased after

270   rainfall (R = 0.6, p = 0.04). In contrast, surface waters in 2012 were depleted in CO_2 between

271   May and August (by down to -5 µM below saturation). Diurnal analyses of the CO_2 saturation

272   levels in mid-July revealed that even at night, CO_2 levels at the surface remained low (< 2 µM,

273   Figure S3). This persistent CO_2 depletion ended after three days of continuous rain in mid-

274   September, during which the mixed layer deepened (Figure 6 E, F). Consistent with higher

275   surface water concentrations, CO_2 fluxes were on average higher in 2011 than in 2012 (8.7

276   and -2.5 mmol m^{-2} d^{-1}, p=0.037, Wilcoxon test, Figure 6 G, H). Except for a brief period of high

277   CO_2 efflux recorded during complete overturn after the summer with heat waves, when CO_2

278   emission reached 78 mmol m^{-2} d^{-1}, the CO_2 uptake by surface lake waters was more persistent

279   and higher in 2012 than in 2011, with maximum influx rates of -30 mmol m^{-2} d^{-1} during heat

280   waves in the second half of July.

281

282   The TP and TN concentrations remained high over the entire study period (2011-2012),

283   indicating eutrophic conditions in the lake. Yet in 2012, summer TP and TN concentrations were

284   higher than in 2011 (72 vs 45 µg P L^{-1} and 420 vs 370 µg N L^{-1}). In contrast, concentrations of

285   inorganic nutrients were lower in surface waters in 2012 than in 2011 (3.5 vs 5.0 µg L^{-1} for SRP,

286   and 100 vs 150 µg L^{-1} for N-NO$_3^-$).

287

288   **3.4 Phytoplankton**

289   Throughout most of the productive season in 2011, dinophytes dominated the phytoplankton

290   biomass, starting from June when their biomass reached 96 mg wet weight L^{-1} (mg WW L^{-1};

291   Figure 7 A, C), corresponding to 15 µg Chl-a L^{-1} (data not shown). In the second half of June,

292   the total phytoplankton biomass decreased to 30 mg WW L^{-1} and consisted of a mixture of

293   dinophytes, cyanophytes and diatoms. Later that year, diatoms became increasingly abundant

294   showing a maximum of 401 mg WW L^{-1} in the first week of September (Figure 7 A, C).

295

296   Seasonal patterns in phytoplankton biomass were different in 2012 (Figure 7 B). The

297   phytoplankton was dominated by cryptophytes and diatoms early in the season (May), and

298   dinophytes in May and June, with the total phytoplankton biomass reaching a maximum of 125

299   mg WW L^{-1}. Buoyant cyanobacteria (*Dolichospermum* sp. and *Aphanizomenon* sp.) were first

300   evident around 5 July and dominated the phytoplankton community between 20 July and 15

301   August when they formed a dense surface bloom ($> 20 \times 10^3$ cells ml^{-1} or up to 300 mg WW

302   L^{-1}). Results of the partial least square regression analysis (PLS) revealed that cyanobacterial

303   biomass can be predicted ($R^2 = 0.70$, n = 30, p=0.0001) using stratification strength (difference

304   between surface and bottom T; Variable Importance in the Projection, VIP = 1.9), pH values

305   (VIP = 1.7) as well as interactions between rainfall and pH (VIP = 1.4) and pH and bottom O$_2$

13

306 (VIP= 1.35). Including the interaction between SRP and N-NO$_3$ improved these predictions by

307 additional 8% (VIP = 1.4 R^2=0.78, p = 0.0001).

308

309 **3.5 Sedimentary pigment record and historical data**

310 Temperatures and snowfalls observed in the vicinity of Lake St. Agustin during the last fifty

311 years correlated with sedimentary pigments (Figure 8; p < 0.05, n = 20). For instance, the Chl-*a*

312 and ß-carotene concentration in surface sediments increased proportionally with summer

313 temperatures (R = 0.71 and R = 0.59, respectively, p = 0.0001). The concentration of zeaxanthin

314 (a proxy for cyanobacteria in Lake St. Augustin) and of total cyanobacterial pigments (sum of

315 zeaxanthin, canthaxanthin and echinenone) were also correlated with summer temperatures (R =

316 0.78, and 0.69, respectively, p < 0.0001). Noteworthy, canthaxanthin alone showed a negative

317 relationship to temperatures (R = -0.41, p = 0.1). Decreasing snowfall also influenced

318 phytoplankton biomass and community structure, as indicated by increase in Chl-a, ß-carotene

319 and zeaxanthin concentrations over the last two decades. In contrast to climatic parameters, the

320 historical TP concentrations (1967-2010; Figure 9) did not correlate with changes in Chl-*a,* ß-

321 carotene or zeaxanthin (n = 14, p > 0.3).

322

323   Changes in zeaxanthin were not linear over time. Consistent with the climate trend

324 analysis, a sequential t-test followed by an ANOVA showed significant differences with regards

325 to trends in the concentration of these pigments before and after 1990 (p < 0.001; Figure 9).

326 Zeaxanthin decreased between 1965 and 1990, and subsequently showed a positive trend

327 between 1990 and 2011. The historical TP dataset did not reveal any trends over the past 50

328 years (p > 0.7). In contrast to historical TP concentrations, past pH values and CO$_2$

329 concentrations in surface waters indicate an alkalinization (from an average of pH = 8.3 between

330   1968 and 1998 to pH = 8.8 between 1998 and 2010) and the associated decrease of summertime

331   CO_2 concentrations (from 25.5 ± 11.9 µM between 1968 and 1998 to 9.3 ± 6.7 µM between 1998

332   and 2010; R = -0.58, n=12 p=0.02, Figure 9). Historical surface water CO_2 concentrations

333   correlated to air temperatures recorded over the lake (R = -0.78, p=0.003), and because the

334   temperature record is more complete, the latter dataset was used in all subsequent analyses.

335

336   The multiple polynomial regression model, considering both climatic parameters (T,

337   precipitation) and phosphorus concentrations, indicates that most of the variability in

338   sedimentary zeaxanthin ($R^2 = 0.75$, n= 18, p=0.001) can be explained by changes in summer and

339   winter air temperatures, with an improvement by 15% after including the historical TP data.

340   Overall, the accumulation of zeaxanthin in the sediments of Lac Saint Augustin, can be well

341   predicted ($R^2 = 0.9$, n=14 p = 0.001) using these three variables. The accumulation of

342   cyanobacterial pigments can also be predicted using polynomial regression based on climate

343   characteristics only ($R^2 = 0.78$, p=0.001). Including historical TP concentrations results in further

344   improvement of the model prediction by 10% (R^2=0.88, p=0.001, n=14).

345

346   **4 DISCUSSION**

347   Effects of meteorological forcing on cyanobacteria in the lake were either direct through

348   increased surface temperatures (Johnk et al., 2007), or indirect through the modulating control on

349   the duration and strength of water column stratification, residence time, pH and nutrients.

350   Particularly an interactive effect of enhanced stratification and increasing pH (associated to

351   lower CO_2 levels) appears as an important catalyzer of cyanobacterial blooms. Our data indicate

352   that heat waves and long-term warming affect functioning of polymictic lake ecosystem along

353   the same axis. Correlative analyses of the sedimentary pigment record, historical TP and pH

354   (CO_2 concentrations), and associated meteorological time series, as well as results from a natural

355   experiment comparing years with contrasting meteorology indicate that warming and pH control

356   the abundance of buoyant cyanobacteria. On the other hand, our work does not provide support

357   for the existence of any specific P concentration threshold that may act to trigger blooms of

358   cyanobacteria, suggesting that nutrients were sufficient already five decades ago to support

359   persistent summertime blooms. While our results, show that effects of temperature are

360   interacting with those of alkalinity (CO_2 depletion) when nighttime winds are low and

361   stratification is strong (Visser et al., 2016) to stimulate cyanobacteria, high frequency monitoring

362   of hydrodynamics and phytoplankton (Marcé et al., 2016) coupled to models (e.g., Recknagel et

363   al., 2013) may help to gain further insight into the mechanism of bloom formation.

364

365   **4.1 Warming-related effects on the water column physicochemistry**

366   Heat waves had a strong effect on the stratification of Lake St. Augustin. The surface was

367   warmer and the bottom colder in 2012 than in 2011. The enhanced temperature gradient during

368   heat waves impeded exchanges between the upper and lower water column as shown also in

369   other lakes (Shatwell et al., 2016). The detailed data in Lake St. Augustin indicate how the

370   mixing dynamics changed during heat waves such that conditions favored cyanobacteria. During

371   typical weather conditions, winds are moderate over the lake, with maxima between 4 m s^{-1} and 6

372   m s^{-1}. L_N drops below 1, implying the thermocline up and downwells and mixing occurs on a

373   daily basis (Yeates & Imberger, 2003). On nights when winds remained high, heat losses were

374   elevated up to -500 W m^{-2} and stratification was reduced, as expected with classic polymixis.

375   During heat waves, winds and L_N were lower in the day (between 1 and 5), and fetch was

376   reduced as winds were across rather than along the lake. Thus, while thermocline still tilted, the

16

377   magnitude of this movement was less, and reduced downward mixing of heat contributed to

378   greater and more persistent stratification (buoyancy frequencies increased above 40 cph).

379

380   Although air temperatures increased during heat waves, the co-varying decrease in wind

381   speeds and associated reduction in latent heat fluxes, the major heat loss term for the lake, were

382   the critical determinants of warming and stratification. In fact, the incoming heat from sensible

383   heat during heat waves was small (<20 W m^{-2} as compared to between -40 W m^{-2} and -100 W

384   m^{-2} during windier conditions). With decreased heat losses at night under low winds, more of the

385   heat which accumulated in the day was retained contributing to more stable stratification.

386

387   Enhanced stratification associated with heat waves resulted in the deoxygenation of bottom

388   waters. The lake has accumulated large quantities of P in its sediments over the last 50 years, and

389   currently experiences release of this legacy P when oxygen is depleted (Galvez-Cloutier et al.,

390   2012). However, because of the ineffective exchange between the bottom and surface (euphotic)

391   layers of the lake during the summer 2012, this surplus bioavailable P likely remained in the

392   lower water column where it was accessible for migrating phytoplankton i.e., buoyant

393   cyanobacteria, but not for other species.

394

395   While alkalinity and CO_2 levels appear to play an important role in shaping the

396   phytoplankton community structure (Maileht et al., 2013), their effect may be particularly

397   important in controlling cyanobacteria (Dam et al., 2018). In the near future many lakes around

398   the globe will stratify more strongly (Woolway and Merchant 2019) and, with their sediments

399   remaining colder throughout the summer (Bartosiewicz et al., 2019), less carbon will be release

400   into the upper layers of the water column. These conditions are likely to favor bloom-forming

401   cyanobacteria (Marcus et al 1983) in the thinner and warmer epilimnion. The persistent diurnal

402   CO_2 depletion, increasing alkalinity as well as very high rates of CO_2 uptake during the bloom

403   indicate that buoyant cyanobacteria benefitted from their ability to concentrate carbon around

404   their cells and migrated to optimize usage of atmospheric CO_2. In fact, measured CO_2 uptake

405   rates were higher than expected from estimated values of the gas transfer coefficient (MacIntyre

406   e al., 2010, Tedford et al., 2013, data not shown,) thus further supporting biologically enhanced

407   CO_2 influx. Some previous experimental work suggested that cyanobacteria may outcompete

408   other phytoplankton if CO_2 availability is low and alkalinity high (Caraco & Miller 1998). Our

409   results (using data from both natural experiment that compared two years and historical records

410   that spanned over the last five decades) provide observational support for this positive

411   interaction.

412

413   Here we argue that, in addition to exploiting of bicarbonates and using a highly effective C

414   concentrating mechanism buoyant cyanobacteria gain an ecological advantage when heatwave-

415   enhanced stratification allows them to more readily use atmospheric CO_2. Shallow polymictic

416   lakes have traditionally been assumed to mix on a daily to weekly basis so that filamentous

417   cyanobacteria could not use their buoyancy regulation to gain much of an advantage. Yet, here

418   we demonstrate that during heat waves, and more frequently under future climate, lakes that

419   mixed often will mix less and become a better habitat for buoyant cyanobacteria.

420

421   **4.2 Decadal warming effects on the phytoplankton community**

422   Historical records provide additional evidence for the link between climate change and

423   cyanobacterial blooms than our two-year limnological study. The 38% increase in zeaxanthin

424   between 1990 and 2012 (and in total cyanobacterial pigments), relative to the long-term average,

425   indicates potential recent proliferation of cyanobacteria. This increase coincides with accelerated

426   warming, increasing pH and decreasing summertime CO_2 levels. The regression analyses reveal

427   that while the climate variables have high explanatory power in relation to cyanobacterial

428   pigments, the P concentrations were comparatively less useful in that regard for this eutrophic

429   lake. The counterintuitive decrease in the sedimentary canthaxanthin may have been associated

430   to lower contribution from this pigment in the total produced carotenoids under moderate levels

431   of warming (Halfen & Francis 1972, Klodawska et al., 2019). The potential effects and

432   interaction of ambient temperature and related environmental conditions (alkalinity) on cell-

433   specific pigment production in cyanobacteria require further study.

434

435   Our results differ from previous findings indicating that nutrients rather than temperature

436   control cyanobacterial blooms in lakes (Rigosi et al., 2014). Although we have studied only one

437   specific lake, we propose that for lakes with a history of high nutrient loading and the efficient

438   recycling of nutrients (Kilham & Kilham, 1990), continued nutrient input is not a key

439   determinant of the frequency of harmful cyanobacterial blooms. In fact, many of the earlier

440   observations pointing towards nutrient supply as the key determinant of cyanobacterial blooms

441   are from lakes deeper than 10 m that develop blooms once stably stratified. Our data imply that

442   these results are not necessarily pertinent to polymictic lakes with continuously high nutrient

443   supply and support previous observations (Kosten et al., 2012) with a more mechanistic

444   explanation. On the other hand, many shallow lakes host abundant macrophytes that may, under

445   specific conditions, suppress cyanobacteria (Chang et al., 2012). The impact of climate change

446   on macrophytes (Li et al., 2017) as well as the impact of macrophytes on water column

447 stratification under warming (Vilas et al., 2017) and thus on the competitive abilities of buoyant

448 cyanobacteria also requires further investigation.

449

4.3 Conclusion

451 Our results suggest that the synergy between warming and water column stratification is

452 the key factor catalyzing cyanobacterial blooms in eutrophic polymictic lake. The effects of

453 meteorological forcing on cyanobacteria blooms are both direct and indirect as they moderate

454 temperature and precipitation as well as the related duration and strength of stratification. While

455 persistent stratification and phytoplankton activity leads to elevated pH and enables CO_2 to

456 remain undersaturated such that cyanobacteria had an advantage over other phytoplankton, our

457 data imply that this effect can trigger cyanobacterial blooms only when acting in combination

458 with lower nighttime winds and concomitant rapid warming of surface waters. Blooms of

459 buoyant cyanobacteria will occur more frequently in polymictic lakes as climate warms and as

460 these waters stratify more strongly. Harmful phytoplankton blooms under such conditions will

461 have profound consequences for the biogeochemistry and aquatic food webs and hence for the

462 functioning of aquatic ecosystems.

468

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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 $\mu g\ L^{-1}$	TP^B $\mu g\ L^{-1}$	SRP $\mu g\ L^{-1}$	TN $\mu g\ L^{-1}$	$N\text{-}NO_3^-$ $mg\ L^{-1}$	Chl-a $\mu g\ L^{-1}$	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

CAPTIONS

Figure 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.

Figure 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.

Figure 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.

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

Figure 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.

Figure 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).

Figure 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).

Figure 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).

Figure 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.

SUPPLEMENTARY CAPTIONS

689 **Figure S1**. Changes in monthly average temperatures over Lake St. Augustin winter and summer
690 months for the period between 1955 and 1990 (white circles) and from 1990 to 2010 (black
691 circles). The p-values indicate results of an ANCOVA when a significant difference in the slope
692 or elevation (August) was observed between period 1953-1989 and 1989-2010.

693 **Figure S2.** Preliminary estimation of the coefficient of eddy diffusivity (K_z) calculated using the
694 heat budget method of Jassby and Powell (1975) with the thermistor data Gaussian-filtered for a
695 3-d period to avoid contamination of the heat budgets by internal wave motions. The heat budget
696 method is a 1D approach that allows to estimate K_z only whenever the lake is gaining heat and
697 lateral advection is minor (MacIntyre, Clark, Jellison, & Fram, 2009a).

698 **Figure S3** Diurnal changes in the CO_2 fluxes at the water-air interface during the cyanobacterial
699 bloom (July 2012) in lake St-Augustin.
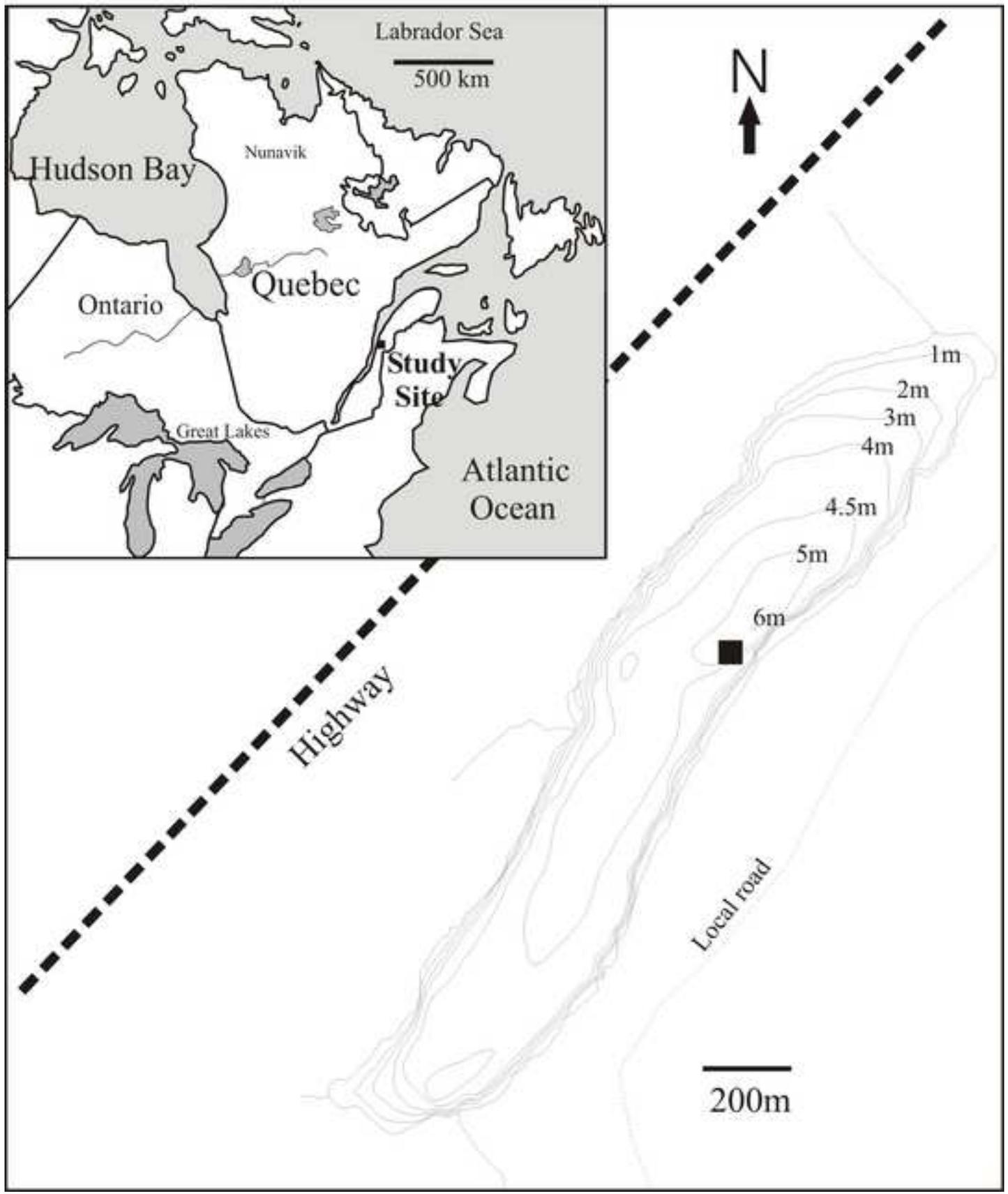
Figure 2
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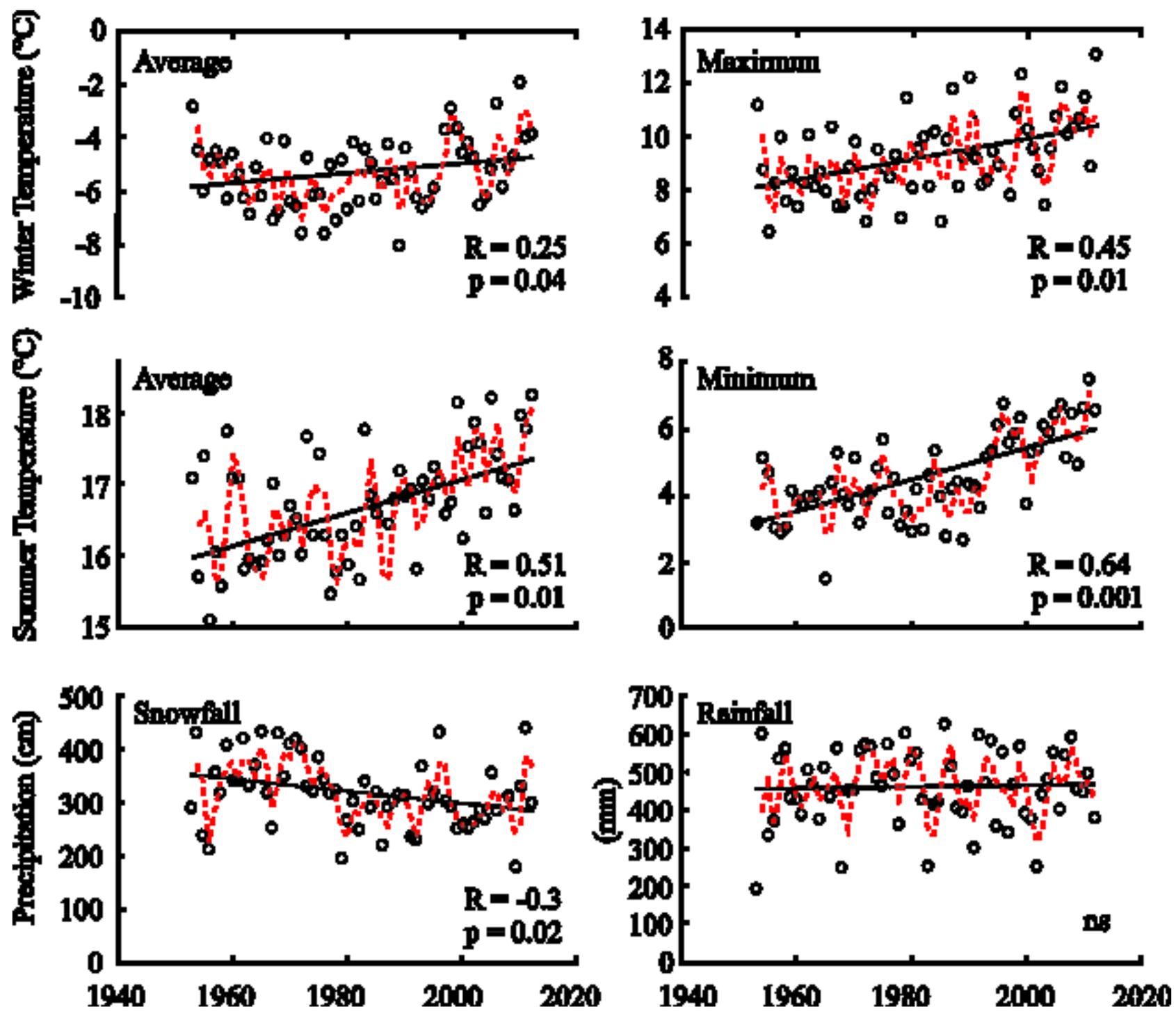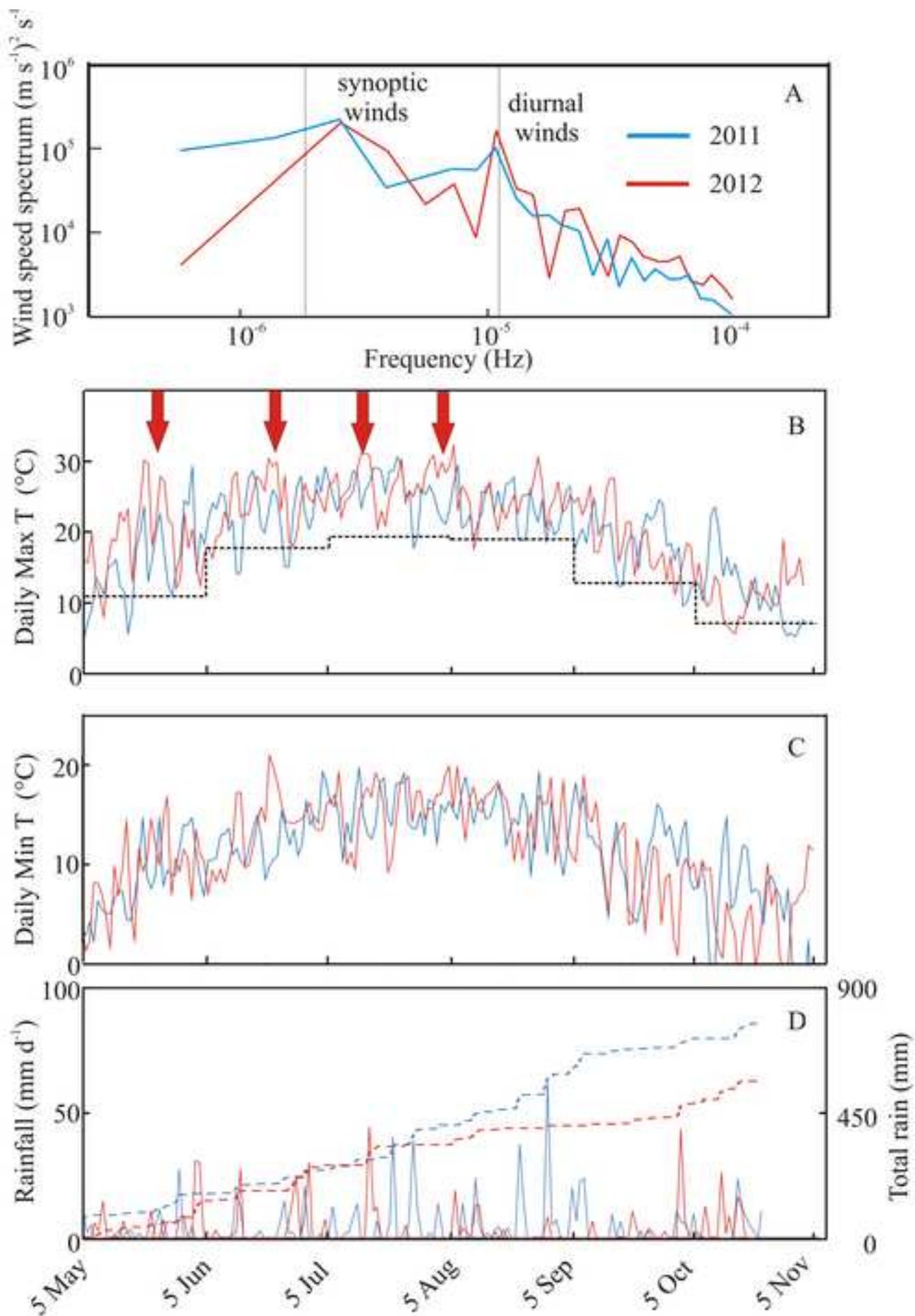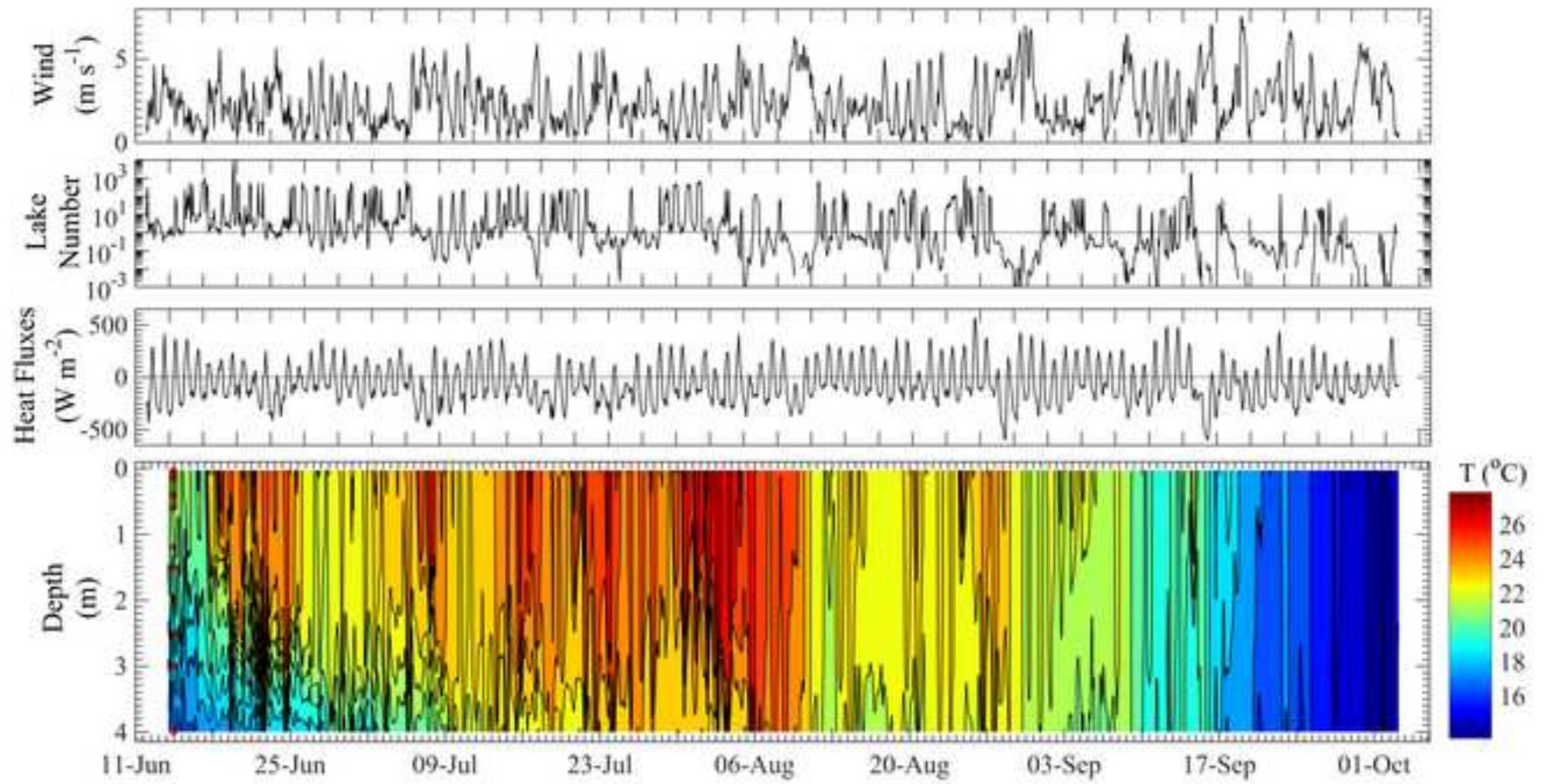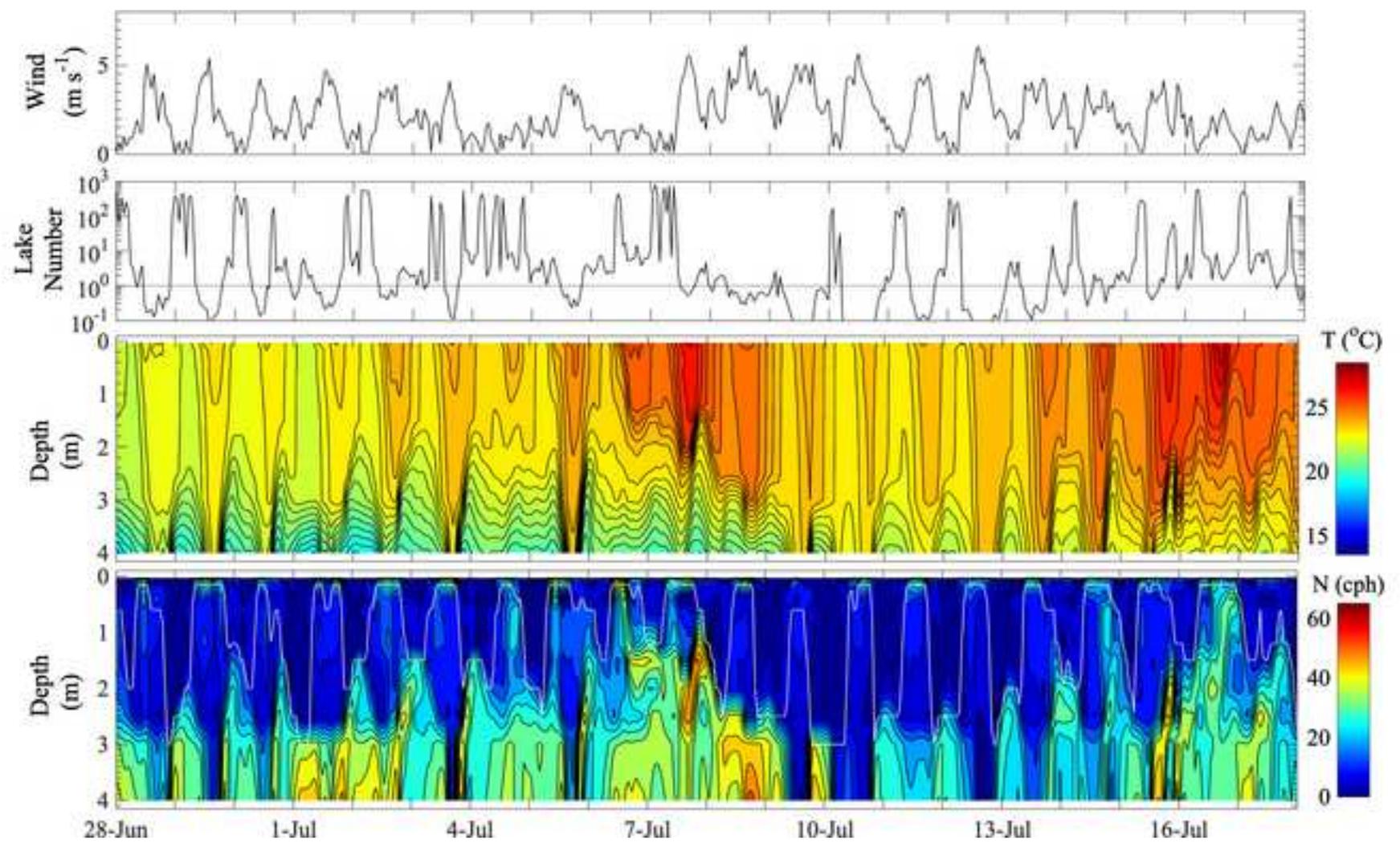
Figure 6
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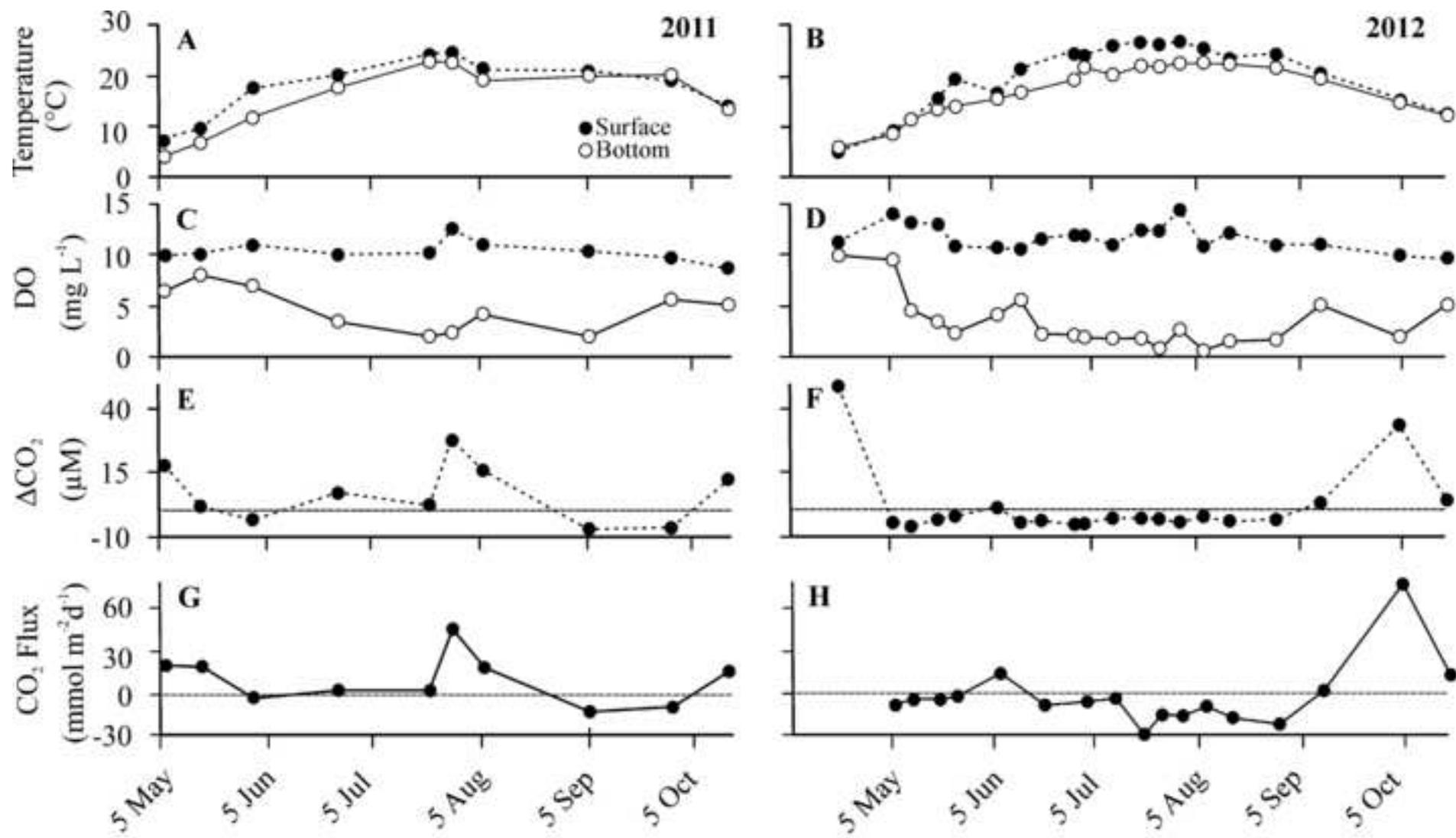
Figure 7
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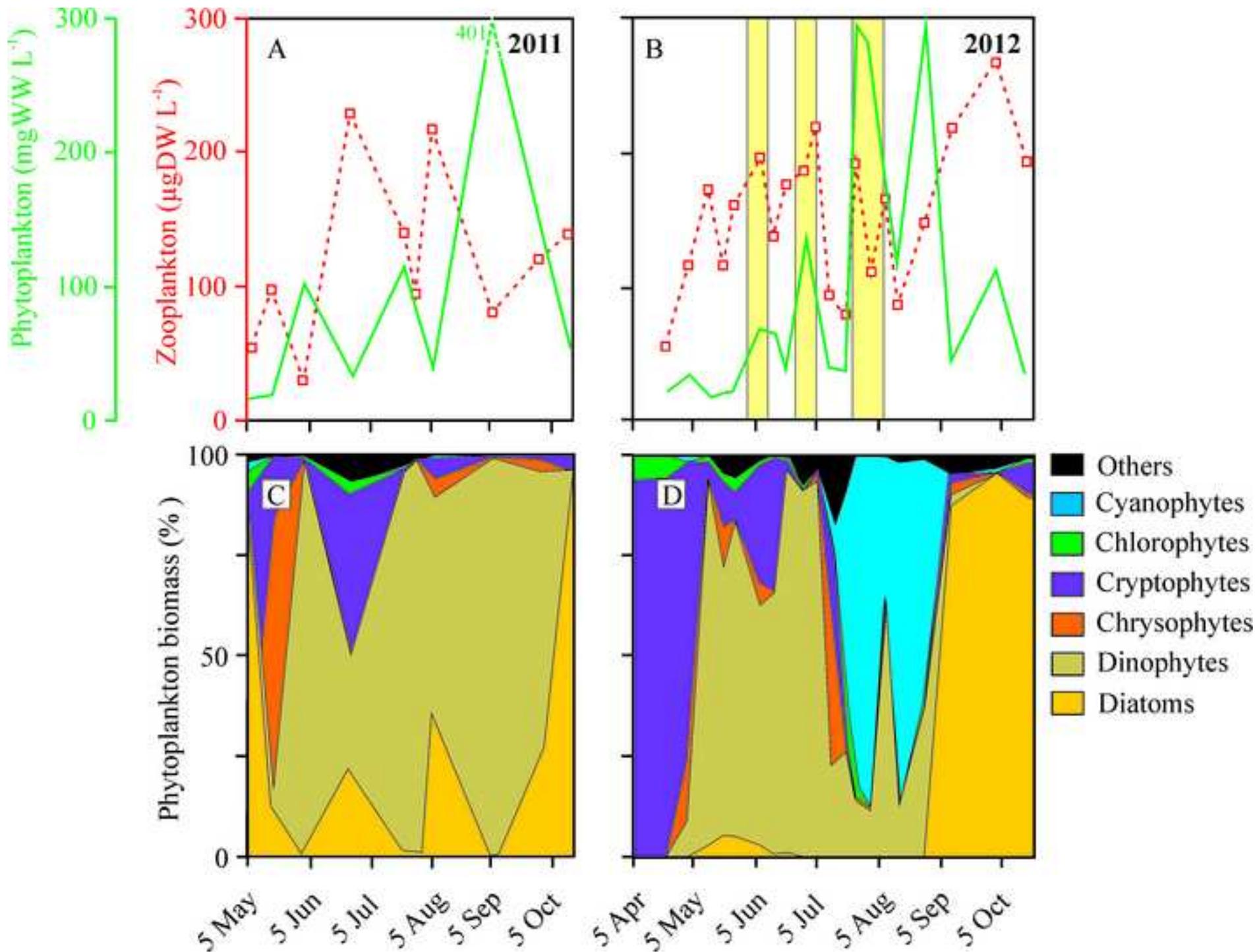
Figure 8
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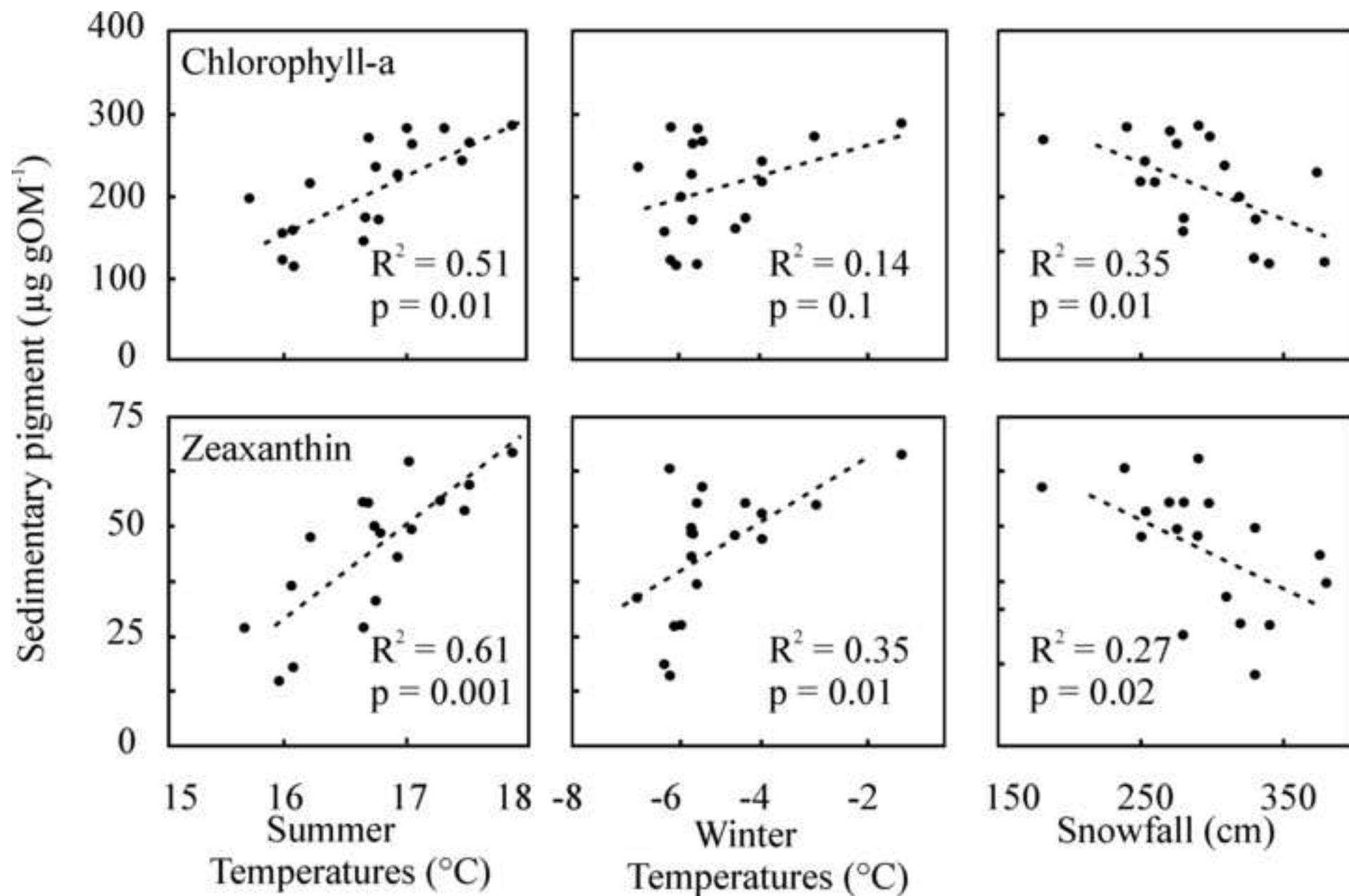
Figure 8

Figure 9
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Fig S1

Fig S2

Fig S3

Table S1