**QUEEN'S
UNIVERSITY
BELFAST**

Hydrological fluctuations modulate phototrophic responses to nutrient fertilization in a large and shallow lake of Southwest China

Hu, K., Chen, G., Gregory-Eaves, I., Huang, L., Chen, X., Liu, Y., & Leavitt, P. R. (2019). Hydrological fluctuations modulate phototrophic responses to nutrient fertilization in a large and shallow lake of Southwest China. *Aquatic Sciences*, 81(2), [37]. <https://doi.org/10.1007/s00027-019-0633-4>

Published in:
Aquatic Sciences

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
[Link to publication record in Queen's University Belfast Research Portal](#)

Publisher rights

© Springer Nature Switzerland AG 2019. This work is made available online in accordance with the publisher's policies. Please refer to any applicable terms of use of the publisher.

General rights

Copyright for the publications made accessible via the Queen's University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The Research Portal is Queen's institutional repository that provides access to Queen's research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact openaccess@qub.ac.uk.

Hydrological fluctuations modulate phototrophic responses to nutrient fertilization in a large and shallow lake of Southwest China

Kui Hu¹, Guangjie Chen^{1,*}, Irene Gregory-Eaves², Linpei Huang¹, Xiaolin Chen¹, Yuanyuan Liu, Peter R. Leavitt^{3,4}

¹Yunnan Key Laboratory of Plateau Geographical Processes and Environment Change, School of Tourism and Geography, Yunnan Normal University, Kunming 650500, China

²Department of Biology, McGill University, Montreal, Quebec H3A 1B1, Canada

³Institute of Environmental Change and Society, University of Regina, 3737 Wascana Parkway, Regina, SK S4S 0A2, Canada

⁴Institute for Global Food Security, Queen's University Belfast, Belfast, County Antrim, United Kingdom

*Email: guangjiechen@gmail.com, Tel: (+86) 13658805128

Abstract

Lake nutrient budgets and hydrology are being altered by human activities and climate change, yet little is known of how fertilization and hydrologic mechanisms interact to structure assemblages of primary producers. Here, we present sediment records from a large shallow lake in Southwest China to separate the relative importance of nutrients and hydrological fluctuation in regulating the abundance and composition of primary producers during the 20th century, with a focus on their differential effects on diatoms and cyanobacteria. Shifts in sedimentary particle-size distribution were consistent with the documented events of hydrological regulation during ~1953-1971 and subsequent changes in water level associated with severe droughts. Nutrient enrichment since ~1965 resulted in a significant increase in the abundance of total phototrophs (pheophytin *a*, β -carotene) as inferred from pigment analyses, with stronger responses of cyanobacteria (echinenone, zeaxanthin) over siliceous algae (diatoxanthin). Fossil diatom assemblages revealed a pronounced replacement of benthic taxa by eutrophic and planktonic species (e.g., *Fragilaria crotonensis*) since ~1973, but we observed a significant increase of small benthic *Fragilaria sensu lato* taxa following ~2005, which generally corresponded with a moderate increase in fossil pigments. Although eutrophication was the paramount predictor of changes in phototrophs during the last century, variation in lake hydrology due to climate and water management also modulated phototroph abundances and, more recently, diatom assemblages. Specifically, our sediment evidence suggests that hydrological fluctuation has overridden fertilization by nutrients in structuring diatom composition, leading to a heterogeneous response of cyanobacteria and diatoms to external forcing of this shallow lake.

Keywords: Yilong Lake; pigments; diatoms; eutrophication; water regulation; extreme drought

1. Introduction

Lake phytoplankton and phytobenthos are known to be sensitive to environmental fluctuations such as climate change (Carvalho and Kirika, 2003) and nutrient fertilization (Jeppesen et al., 2005; Schindler, 2006). However, the relative importance of individual environmental controls may vary among basins, depending on algal identity and lake characteristics. For example, global warming can enhance phytoplankton production as temperature can directly affect algal photosynthesis and growth rate (Reynolds, 2006; Jöhnk et al., 2008). Prokaryotes, such as cyanobacteria, can be selectively promoted because their optimum growth rates occur at higher temperatures than do those of diatoms and other eukaryotic algae (Paerl and Huisman, 2008). Recent studies show that nutrient enrichment can also lead to a disproportional increase in the production of harmful algae when compared to other phytoplankton (Taranu et al., 2015), reflecting their competitive ability at high nutrient concentration (Tilman, 1987; Sterner and Elser, 2002). Furthermore, increased water-column stability due to atmospheric warming can enhance the production of harmful filamentous cyanobacteria in deep lakes (Huisman et al., 2005; Posch et al., 2012). However, nutrient fertilization can overwhelm climate control of algal production in shallow lakes (Taranu et al., 2012). Therefore, algal identity and lake typology should be considered in evaluating the strength of lake warming and eutrophication in driving primary producers (Vogt et al., 2018).

Shallow lakes are vulnerable to changes in climate and water influx due to their low volume and short water residence time when compared to deep lakes (Scheffer, 1998; Søndergaard et al., 2003). During the last few decades, anthropogenic regulation of water fluxes has been identified as a significant stressor for freshwaters in populous areas (Yang and Lu, 2014), with a decline in lake water levels often stimulating algal production and favoring phytobenthos in shallow

1
2
3
4 65 systems (Scheffer, 1998). At the same time, climate warming has increased the occurrence of
5
6 66 extreme hydrologic events (e.g., droughts) at regional and global scales (Dai, 2011; IPCC,
7
8
9 67 2013), augmenting the decline of water level and ecological health (Lake, 2011). In comparison,
10
11 68 nutrient fertilization usually enhances phytoplankton production at the expense of benthic taxa
12
13
14 69 such as diatoms (Vadeboncoeur et al., 2003). In principle, changes in lake level and nutrient
15
16 70 influx could drive algal abundance and community composition in different directions in
17
18
19 71 shallow lakes that are subject to multiple stressors. Furthermore, there may exist strong
20
21 72 interactions between nutrient dynamics and hydrologic fluctuation, as prolonged water retention
22
23
24 73 time due to impoundment can lead to an increased level of nutrients (Maavara et al., 2015) and
25
26 74 accelerate eutrophication in shallow lakes (Chen et al., 2013). To date, little is known of how
27
28
29 75 such hydrologic fluctuations in shallow lakes may interact with eutrophication in regulating the
30
31 76 abundance and composition of primary producers over time.

32
33 77 In many lakes, analysis of sedimentary records can provide a reliable temporal perspective
34
35
36 78 on limnological responses to anthropogenic disturbances and climate change (Adrian et al.,
37
38
39 79 2009; Battarbee, 2010; Smol, 2010). Fossil pigments and diatoms are two widely used
40
41 80 paleolimnological indicators of algal abundance and community composition (Leavitt and
42
43
44 81 Hodgson, 2001; Stoermer and Smol, 2001). For example, sediment pigments have recorded the
45
46 82 independent effects of both nutrient fertilization and climate (Hall and Leavitt, 1999; Leavitt et
47
48
49 83 al., 2006; Bunting et al., 2007), as have fossil diatom assemblages (Smol et al., 2005; Rühland
50
51 84 et al., 2008). Diatoms from shallow lakes were found to be sensitive to lake-level changes
52
53
54 85 through their response to habitat quantity and quality (Brugam et al., 1998), while shifts in the
55
56 86 vertical zonation of algae with lake depth have been identified from fossil pigments
57
58 87 (Cuddington and Leavitt, 1999; McGowan et al., 2005; Hambright et al., 2008). Therefore,
59
60
61
62
63
64
65

sediment studies in shallow lakes can be applied to quantify the relative importance of multiple stressors in driving algal community structure and abundance over time.

We conducted sediment analyses to evaluate the long-term concordance between algal abundance and diatom assemblage composition in response to multiple stressors in Yilong Lake, southwest China. This large and shallow lake has undergone significant catchment development, hydrological regulation and extreme droughts since the 1950s (Cui and Zhai, 2006). Modern survey data also show a shift in phytoplankton density from predominately diatoms to mainly cyanobacteria during the last few decades (Zhao, 2013). Consequently, we predicted that both nutrient enrichment and variation in lake morphology could significantly enhance the production of phytoplankton over time, particularly that of cyanobacteria, while the intensification of water level changes may modulate the role of nutrients in altering the community structure of diatoms (i.e. an increase of phytobenthos). Combining sediment records with modern survey data, we first identified the temporal trajectories of phototrophic community composition, and then by applying multivariate statistics, we identified the relative importance of environmental factors which influenced phototrophs over different time intervals. Overall, this study provided evidence on dual effects of nutrients and hydrologic fluctuations on primary producer assemblages, with fertilization accelerating the growth of cyanobacteria-rich phytoplankton, while climate warming and hydrological management increased benthic diatoms over the last few decades.

2. Material and methods

2.1 Study site

Yilong Lake, located in southeast part of Yunnan Province, southwest China (Fig. 1), is a

large (~34 km²) shallow system with a maximum and average water depth of ~3.7 m and 2.9 m, respectively (Table 1). Yilong Lake is currently hyper-eutrophic with elevated concentrations of total phosphorus (TP; ~120 µg/L), total nitrogen (TN; ~7.7 mg/L) and Chlorophyll-a (Chl-a; ~215 µg/L). The catchment is strongly influenced by Indian monsoons and experiences a mean annual precipitation is 928.3 mm, a mean annual air temperature of ~18 °C (Fig. 2) and an average insolation of 2,300 hours/year (Meteorology station of Mengzi County; <http://cmdp.ncc.cma.gov.cn/cn/index.htm>). Bedrock within the Yilong watershed is characterized by limestone and sandstone due to its Karst geology. The catchment vegetation is composed mainly of Yunnan pine (*Pinus yunnanensis*) and mixed deciduous species, with a forest cover of ~34.2%.

Currently, Yilong Lake is a semi-closed system, with a hydrological residence time of ~2.4 years (Li et al., 2015). However, Yilong Lake has been modified by both anthropogenic and climate forcing since the 1950s (Fig. 2). The main inflow of Yilong Lake is the Chenghe River, located at the northwest of the basin, which flows through the largest town within the catchment, Shiping (Fig.1). Lake area dynamics derived from monitoring data (Jin, 1995) and Landsat satellite imagery (Wu et al., 2016) document a consistent pattern of pronounced shrinking and reduced depth during 1952-1982 and 2009-2013 (Fig. 2). For example, dredging and damming of the outflowing Haikou River for electricity generation led to a decline in lake level by ~2 m from 1952 (maximum depth ~7.0 m) to 1953 (~5.0 m), and a further drop of 0.7 m in 1960 (Yang and Li, 2010). Lake area further reduced in 1971 with the construction of an underground tunnel for lake reclamation, which lead to a decline in maximum depth from 6.0 m in 1970 to 4.3 m in late 1971 (Fig. 2), before the tunnel was abandoned in 1978 (Cui and Zhai, 2006). With extremely low precipitation, the maximum water depth in Yilong Lake had declined further to < 1 m in

spring of 1981, and then fluctuated between 3.6-5.5 m due to climatic and anthropogenic effects, including a period of extreme drought during 2008-2012 (Zhao, 2013).

With agricultural expansion and catchment development starting in ~1955, non-point source pollution has become the dominant source of nutrient loading to the lake, despite the substantial input of urban effluent (Zhao, 2013; Zhao et al., 2013). By 2007, annual TP and TN influx from farmland surface runoff accounted for 59% and 52% of total nutrient inputs, respectively (Wang and Wang, 2008). Furthermore, farming of fish within cages was initiated in 1985 and experienced an accelerating growth until 1997 (Shi and Sun, 2005), after which this practice was officially forbidden in Yilong Lake. During its period of operation, cage farming extensively harvested aquatic vegetation within the lake to feed herbivorous grass carp (*Ctenopharyngodon idellus*) (Chou and Xia, 1998), resulting in a rapid loss of macrophyte coverage from 95.0% in 1982 to 27.3% in 1992 (Table 2).

2.2 Sample collection and sediment dating

A 34-cm sediment core was collected from Yilong Lake in July 2013 from the deep basin (23°39'53"N, 102°36'15"E) using a Renberg gravity corer (Fig. 1). The sediment core was sectioned immediately at 0.5-cm intervals for the top 5 cm and at 1-cm intervals for depths below 5 cm. Samples were kept dark and frozen until subsampling for pigment analyses within 24 h. The remaining sediments were freeze-dried and stored in the dark for subsequent analyses.

Sediment chronology was estimated based on ²¹⁰Pb activities in sediment core samples. Around 3-5 g of freeze-dried sediments were used for measuring the radio-activities of ²¹⁰Pb and ¹³⁷Cs in each sample using a Canberra well-detector gamma spectrometer (GCW 3023). The sediment chronology sequence was established with the constant rate of supply (CRS) model

1
2
3
4 157 using the stratigraphic profile of unsupported ^{210}Pb activities (Appleby, 2001).
5
6

7 158
8
9 159 2.3 Sediment physical and geochemical analyses
10

11 Grain-size distribution of sediment samples was determined using a Mastersizer 2000 laser
12 analyzer (Malvern Instruments Limited, Malvern, UK). Briefly, ~0.3 g freeze-dried and
13
14 161 disaggregated sediment from each sample was pre-treated with 10-20 ml of 10% H_2O_2 to remove
15
16 162 organic matter and then heated in 10 ml of 10% aqueous HCl to remove carbonates. Thereafter,
17
18 163 ~100 ml of deionized water was added and the sample solution was kept for 24 h to remove
19
20 164 acidic ions. The sample residue was dispersed with 10 ml of 0.05 mol/L $(\text{NaPO}_3)_6$ on an
21
22 165 ultrasonic vibrator for 10 min prior instrumental analysis.
23
24 166
25

26
27
28 167 Organic matter (OM) content was estimated for bulk sediments using the method of loss-on-
29
30 168 ignition (% LOI₅₅₀) at 550 °C following the standard method (Heiri et al., 2001). Stable carbon
31
32 169 (C) and nitrogen (N) isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were conducted following the standard
33
34 170 methods of Meyer (2001). Briefly, ~10 mg of homogenized, dried bulk sediment was combusted
35
36 171 in a tin capsule at 960 °C in a FLASH 2000 elemental analyzer linked to a continuous isotope
37
38 172 ratio flow mass spectrometer (MAT-253, Thermo Scientific, USA). C and N isotope ratios are
39
40 173 expressed as per mil (‰) relative to Vienna Pee Dee Belemnite (VPDB) and atmospheric N_2
41
42 174 (AIR), respectively. Relative contents of C and N (% dry mass) and the mass ratio of carbon to
43
44 175 nitrogen (C:N) were also measured. The analytical precision was $< \pm 0.1\%$ for isotopic data and
45
46 176 $< \pm 1\%$ for elemental data, respectively.
47
48
49
50
51
52

53 177
54
55 178 2.4 Pigment analyses
56

57
58 179 All pigments were measured following procedures described in Saulnier-Talbot et al. (2014)
59
60
61
62
63
64
65

using high performance liquid chromatography (HPLC) at the Gregory-Eaves Lab of McGill University, Canada. Briefly, sediments were freeze-dried and pigments were extracted in acetone (at -20 °C for 24 h) before the extract solution was centrifuged and the supernatant filtered through a PTFE (0.2-µm pore) filter and placed in vials for pigment analysis. The analysis was conducted using a Waters HPLC system (model 600/626) equipped with a Waters Photodiode Array (model 2996) and a Waters 2475 Multi-wavelength fluorescence detector. The HPLC was calibrated previously using external standards from DHI (Denmark). Individual compounds were tentatively identified using a combination of chromatographic position (polarity) and spectral characteristics relative to authentic samples. Pigment concentrations were expressed as ng pigment/g organic matter, determined by mass loss on ignition at 550 °C (LOI₅₅₀) for 1 h. Cyanobacteria were represented by the carotenoid zeaxanthin and echinenone, while algal groups included compounds ubiquitous in phototrophs (chlorophyll-*a*, β -carotene, pheophytin-*a*), chlorophytes (lutein), cryptophytes (alloxanthin), and mainly diatoms (diatoxanthin). As Yilong Lake is a large system with documented hydrological fluctuations, we used the mass ratio of Chl-*a*:pheophytin to evaluate historical changes in pigment preservation and the importance of benthic phototrophs (Cuddington and Leavitt, 1999; Leavitt and Hodgson, 2001).

2.5 Diatom analysis

Fossil diatoms were prepared for enumeration following the standard methods of Battarbee et al. (2001). Briefly, hydrochloric acid (10%) was added for the removal of carbonates before processing, while 30% hydrogen peroxide was added at ~80 °C to remove organic material. A portion of the digested slurry was dried on cover slips and mounted with Naphrax[®]. Diatom identification and enumeration were performed under oil immersion at 1,000× magnification

using a Leica DM 2500 microscope with phase contrast. A minimum of 400 valves was counted for each sample. Diatom taxonomy mainly followed Krammer and Lange-Bertalot (1986-1991). The community data were expressed as percent abundance of the total diatom sum in each sample. Diatom species were categorized into planktonic and benthic groups following their habitat preferences based on previous studies (e.g., Round et al., 2007).

2.6 Numerical methods

The major zones for the biostratigraphy were identified through the analyses of constrained incremental sum of squares (CONISS), while a broken-stick model was used to test for the significance of each break. We conducted ordination analyses to define the historical trajectories of pigment and diatom changes. Preliminary investigation with Detrended Correspondence Analysis (DCA) of pigment and diatom assemblages revealed short gradient lengths of 0.68 and 1.76 SD, respectively, indicating that pigments and diatom taxa responded in a linear fashion to environmental gradients (ter Braak and Prentice, 1988). Subsequently, Principal Components Analysis (PCA) was applied to extract the major direction of variation in both the diatom species compositions and fossil pigment assemblages. Pigment PCA used only the most chemically-stable pigments as suggested by Leavitt and Hodgson (2001) and Moorhouse et al. (2014). Redundancy Analysis (RDA) was performed subsequently to explore the relationship between biological data and nine environmental predictor variables (Hall and Leavitt, 1999; ter Braak and Šmilauer, 2002). Specifically, these environmental variables included grain size components, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C:N ratio, total carbon and total nitrogen measured from bulk sediments (Table 3). Monte Carlo analysis with 999 permutations was used to test the significance of each predictor variable in partial RDA. Only variables with a P-value <0.05 were retained for the minimum

adequate model (ter Braak and Šmilauer, 2002). In addition, environmental variables with a variation inflation factor (VIF) of > 20 were excluded due to their strong co-linearity with other variables.

Multiple regression with forward selection and variation partitioning analysis were used to identify a minimum subset of significant explanatory variables for the time window of ~1903-2013 (ter Braak and Šmilauer, 2002). We also performed RDA and variation partitioning analyses for the time window of ~1953-2013, the period with the most complete meteorological and catchment data, including air temperature, precipitation, wind speed, and catchment population. Finally, we conducted a third variation partitioning exercise for lake-water Chl-*a* for the monitoring period 1992-2015 using six environmental variables (temperature, precipitation, wind speed, TP, TN and lake area) to predict recent changes in water quality. In all cases, we transformed environmental predictor time series for normalization and square-root transformed diatom relative abundance data with rare species down-weighted (Lepš and Šmilauer, 2003). All the data analyses were performed using the R packages *vegan* (Oksanen et al., 2015) and *rioja* (Juggins, 2015).

3. Results

3.1 Archived data

Meteorological data generally show a warming trajectory with marked variation in precipitation during the last six decades. The annual mean temperature shows a warming trend, increasing from an average ($\pm$ SD) of 18.5 ± 0.3 °C during 1951-1990 to a mean of 19.2 ± 0.6 °C for the last two decades (Fig. 2a). The annual precipitation displays no clear trend since 1951, but shows reduced values (< 600 mm) during the intervals of 1961-1962, 1979-1980, 1987-1989,

2004-2005 and 2010-2012. Annual wind speed (Fig. 2b) is relatively stable during 1951-1995 (3.4 ± 0.3 m/s), but declines to 2.3 ± 0.3 m/s by 2010. Lake level and surface area both decrease over the last six decades, with abrupt drops in the mid-1950s, late-1970s and during 2009-2013 (Fig. 2c). Meanwhile, the total catchment population doubles during the last six decades (Fig. 2b).

Variables related to lake primary production and water quality indicate a substantial increase in primary producer abundance over the historical record (Fig. 2). The lake-water concentrations of TN, TP and Chl-*a* have experienced a rapid increase concomitant with a decline in transparency from > 2 m to < 1 m during 1985-1997 (Fig. 2e) and a rapid loss of submerged aquatic vegetation (Table 2). For example, the mean concentration of measured total phosphorus (TP) and total nitrogen (TN) show an undulating pattern since late 1980s, but a clear tendency to nutrient enrichment during ~2009-2012 (Fig. 2d). From the mid-1980s to the mid-1990s, TP and TN levels are elevated with a mean ($\pm$ SD) of 75.2 ± 21.2 $\mu\text{g/L}$ and 5.0 ± 0.6 mg/L , respectively. Nutrient content is relatively stable during the 2000s (TP = 54.0 $\mu\text{g/L}$, TN = 1.8 mg/L), before increasing after ~2009 (Fig. 2d). In general TP and TN increase at similar rates ($r = 0.68$, $p < 0.001$, $n = 21$), with a N:P mass ratio consistently above 20 (or molar ratio of 44) since 1988 (Table 2).

Monitoring data show that Chl-*a* values are relatively high in the mid-1990s (ca. 100 $\mu\text{g/L}$), decline to minima (< 50 $\mu\text{g/L}$) for 15 years, then increase to historical maxima (> 150 $\mu\text{g/L}$) after ~2010 (Fig. 2e). At the sample time, measured phytoplankton density increase gradually from 8.41×10^6 cells/L in 1957 to 193.21×10^6 cells/L in 1992, and thereafter from $< 100 \times 10^6$ cells/L during 1993-2008 to $> 200 \times 10^6$ cells/L after 2008 (Table 2). During this period, phytoplankton community composition gradually shifts from predominantly Bacillariophyta in 1957 to Chlorophyta in 1988 and 1993, and, more recently, to Cyanobacteria (Table 2). Consistent with

the fluctuation in nutrients and phytoplankton, water transparency decreases from > 1.8 m during the early 1980s to < 1 m in 2007 and then shows a swift drop from > 1 m in 2008-2009 to ~0.2 m since 2010 (Fig. 2e).

3.2 Sediment chronology

The unsupported ^{210}Pb radioactivity profile declined with increasing core depth between 10 and ~30 cm (Fig. 3a), suggesting that the ^{210}Pb -based CRS model was applicable in constructing the chronological profile. Sediment samples above the ~7 cm depth showed a uniform ^{210}Pb activity, possibly reflecting sediment mixing or variation in sediment focusing due to changes in basin morphology (Fig. 2c). In lakes where mixing has occurred, the ^{210}Pb dates covering 10-year accumulation, as is the case for this sediment core (Fig. 3b), often provide a maximum error of less than 2 years (Appleby, 2001). Increased autochthonous production which would dilute the atmospheric ^{210}Pb fallout may also cause a decrease in its activity as observed in surface sediments above ~7 cm (Fig. 3a). The depth profile of ^{137}Cs showed no obvious peak (Fig. 3a), reflecting a possible combination of sediment mixing and post-deposition mobility (e.g., Wieland et al., 1993; Sommerfield and Nitttrouer, 1999). Overall, radio-isotope profiles and CRS calculations suggest a recent acceleration in the rate of sediment accumulation (Fig. 3b).

3.3 History of lake environmental change

Grain size data showed modest changes over the length of the core (Fig. 4), with a decline in sand particles and the occurrence of abrupt fluctuations in median grain size during the last century. For example, the median size varied around a mean (± 1 SD) of $4.8 \pm 1.4 \mu\text{m}$, with the clay (< $2 \mu\text{m}$) and sand (> $63 \mu\text{m}$) components varying in the range of 7.2-30.0% (mean = 25.8%)

and 0.03-7.7% (mean = 1.7%), respectively. Both the silt composition and median grain size spiked around the depths of 23.5, 17.5, 7.5 and 3.25 cm (Fig. 4).

Stable sedimentary TN content in the early 20th century (3.6 ± 0.2 mg/g) gave way to an increase since ~1970, with a recent mean of 6.7 ± 0.8 mg/g (Fig. 4). The concentrations of both total carbon (TC) and organic matter (LOI₅₅₀) displayed similar trajectories suggesting that lake production increased after the late-1960s. The mass ratio of C/N in bulk sediments declined from historical values of ~16 to modern ratios of ~11, consistent with an increasing input of organic matter derived from algae.

The $\delta^{15}\text{N}$ signal of bulk sediments remained stable around the near-atmospheric value (~0‰) until the mid-1960s, at which time it increased dramatically up to a maximum value of ~4.5‰ in surface sediments. Correspondingly, the bulk sediment $\delta^{13}\text{C}$ signal declined from around -14‰ to nearly -16‰ over the 20th century, with a marked decline after ~1960. These relatively enriched values are characteristic of lakes with high carbonate content in sediments (Jarvis et al., 2006), and were correlated inversely with the total algal abundance as measured by the total phototroph biomarker, β -carotene ($r = -0.92$, $P < 0.001$).

3.4 Pigment variations

Analysis of sedimentary pigments suggested a progressive increase in autotrophic production during the 20th century with a particularly marked upturn starting in the mid-1960s for most of the major taxonomic groups (Fig. 5a). The concentrations of many pigment biomarkers were low and stable prior to the mid 20th century (zone I), including chemically-stable (pheophytin-*a*, β -carotene) and labile (Chl-*a*) indices of total phototrophic abundance, as well as pigments from bloom-forming cyanobacteria (zeaxanthin, echinenone). During ~1965-

2004 (zone II), all pigment components increased significantly (Fig. 5a), with a greater than three-fold increase in concentrations of ubiquitous biomarkers of total phototrophic abundance (β -carotene, pheophytin-*a*) and bloom-forming chlorophytes (lutein) and cyanobacteria (zeaxanthin, echinenone). Fossil pigment concentrations were also generally higher after ~2004 (zone III, above ~8cm), as identified by the CONISS results (Fig. 5a). During this later interval, the ratio of chlorophyll-*a*/pheophytin-*a* increased markedly, suggesting that preservation conditions have been relatively constant throughout the core except for zone III (Fig. 5a). Overall, historical changes in concentrations of the major pigments were highly correlated with increased content of TN, including compounds from total algae (i.e. Chl-*a*; $r = 0.900$, $P < 0.001$, $n = 37$), cyanobacteria (i.e. zeaxanthin; $r = 0.918$, $P < 0.001$) and diatoms (diatoxanthin; $r = 0.864$, $P < 0.001$).

The Principal Components Analysis (PCA) results further revealed only one significant axis for algal abundance data, which accounted for 98.9% of the variation in biomarker assemblages (Fig. 6a). PCA axis 1 showed a significant relationship with TN ($r = 0.903$, $P < 0.001$) during the last century. In addition, this axis was correlated significantly with sand content ($r = 0.226$, $P < 0.01$) over the last century, as well as measured air temperature ($r = 0.313$, $P < 0.001$) and wind speed ($r = 0.406$, $P < 0.01$) during ~1953-2013.

3.5 Diatom compositional changes

A total of 62 diatom taxa were identified in sediment samples, including 23 taxa with a maximum abundance of $\geq 1\%$, 16 of which occurred with a relative abundance of $\geq 2\%$ in at least one sample. Diatom assemblages were composed mainly of benthic species with strong variations amongst taxa over the 20th century (Fig. 5b). For example, *Staurosira construens* (a

range of 4.2-51.0%), *S. berolinensis* (6.5-44.6%) and *Achnantheidium minutissimum* (0-12.1%) all exhibited wide variation in relative abundance. Benthic diatoms were generally predominant (> 50% relative abundance) across the core except in the depths of 17.5-9.5 cm (~1978-2000), at which time planktonic and tychoplanktonic diatoms became more important within the assemblage (~50-80% of total frustules). Planktonic diatoms mainly included *Fragilaria crotonensis* (1.2-52.4%), while tychoplanktonic taxa were composed of *Aulacoseira subarctica* (1.6-25.1%), *A. granulata* (0.7-14.7%), and *A. ambigua* (1.0-8.2%).

Similar to the pigment changes, diatom assemblages were characterized by two significant shifts (Fig. 5b). During the period of ~1903-1973 (zone I), the community was composed of both benthic taxa, such as *S. berolinensis* (mean = 17.7%) and *S. construens* (16.8%), and several planktonic taxa such as *F. crotonensis* (15.1%) and *A. subarctica* (13.2%). After ~1973 (zone II), there was a significant community shift towards more eutrophic taxa and an associated decrease in small benthic *Fragilaria sensu lato* taxa, coupled with an increase in *F. crotonensis* to over 30% and the disappearance of *S. leptostauron*. After ~2005 (zone III), the community was characterized by the replacement of planktonic taxa such as *F. crotonensis* and *Aulacoseira* spp. (< 10%) by small benthic taxa such as *S. construens* and *S. berolinensis* (mean = 40.8% and 28.3%, respectively).

Principal components analysis (PCA) of diatom data showed that the first two PCA axes were statistically significant based on the broken-stick model, accounting for 51.5% and 16.8% of the total variance, respectively (Fig. 6b). Planktonic species (such as *F. crotonensis*, *A. subarctica*, *A. granulata*) were strongly associated with the left side of axis 1, with several benthic species such as *S. construens* and *S. berolinensis* sitting at the opposite end of this axis. PC axis 1 further showed a significant correlation with the proportion of benthic diatoms ($r =$

0.953, $P < 0.001$), as well as the sand component ($r = 0.571$, $P < 0.001$) and TN ($r = 0.548$, $P < 0.001$). In contrast, benthic taxa such as *S. pinnata* and *S. leptostauron* were more abundant during the period of 1903-1973 (zone I) and were strongly associated with PCA axis 2, which itself displayed a significant correlation with TN ($r = 0.606$, $P < 0.001$). Only PCA axis 1 showed a significant relationship between diatom composition and air temperature ($r = 0.658$, $P < 0.001$) during the ~1953-2013 interval.

3.6 Identifying limnological drivers for algal changes

The Redundancy Analysis (RDA) suggested that nutrient and hydrological parameters played independent roles in shaping the temporal changes in primary producer assemblages of Yilong Lake (Fig. 7). The measured physio-chemical variables collectively accounted for the majority of the changes in pigments (i.e. $> 90\%$), but less than half of the historical variation in diatom assemblages (Table 3). Specifically, nutrients (i.e. TN) were found to be the most significant forces in driving the changes of both pigments and diatoms since ~1903. The nutrient-associated RDA axis 1 accounted for 92.0% of the total variance for pigment data but smaller amount for diatom data (42.3%; Fig. 7). Over a shorter time window of ~1953-2013 (Table 3), nutrient variables remained as the predominant factor in driving pigment changes ($> 90\%$) but structured diatom assemblages to a much lesser degree ($< 15\%$). In contrast, the grain-size proxies played an insignificant role in driving both indicators over the last century; however, the sand content was identified as a significant factor over the last six decades and accounted for $\geq 20\%$ of the total variance for both pigments and diatoms. Temperature also displayed a significant impact on both algal indicators since ~1953 (28.8% and 23.3%, respectively), but wind speed was found to be a major driver only for pigments (38.4%; Table 3).

The variance partitioning results further showed that lake-water TN concentration, but not TP, was a significant driver, accounting for 21.7% of the change in water-column Chl-*a* for the monitoring period of 1992-2015 (Fig. 8b). Furthermore, hydrologic fluctuation inferred from changes in lake area independently explained 28.8% of the total variance in lake-water Chl-*a*, with a high proportion shared with nutrients (19.5%) over the monitoring period. Likewise, sediment TN alone explained 24.6% of the total variance in sedimentary Chl-*a*, while the variation of sediment sand content alone accounted for 5.0% of the total variance in Chl-*a* with a strong interaction with nutrients (43.0%) during the last century (Fig. 8a).

Over the whole core, sedimentary TN collectively accounted for a large proportion of the total variance for both algal pigments and diatom assemblages (i.e. 90.0% and 40.6%, respectively; Fig. 8c, e). However, the nutrient effect was found to be insignificant for diatom assemblages during ~1953-2013 (Fig. 8f), whereas it accounted for the majority of the total variance in phototrophic abundance over the same time window (82.4%; Fig. 8d). In comparison, the relative importance of hydrological fluctuation (as inferred from sand content) for diatom assemblages increased from 4.7% (Table 3) over the core to 27.3% during ~1953-2013 (Fig. 8f), the period when temperature was also found to be a significant driver (8.5%) and interacted moderately with hydrological fluctuation (14.8%; Fig. 8f). From ~1953, both wind speed and hydrological fluctuation showed a strong influence on algal production, but mostly through its interaction with nutrients such as TN (i.e. 35.3% and 14.0%, respectively; Fig. 8d).

4. Discussion

Our multi-proxy sedimentary records revealed a clear trajectory of phototrophic changes in response to a combination of nutrient enrichment and hydrologic fluctuation in Yilong Lake

during the last century. The sedimentary record of fossil pigments showed a dramatic increase concomitant with nutrient enrichment, while more recent changes in production appear to correspond to declining water level and wind speed. Meanwhile, the sediment records of grain size (e.g. sand content and median size) documented the role of hydrological regulation and extreme droughts on lake levels, which affected algal production and diatom assemblages over time. Diatom community composition showed two significant shifts during the past century; with a gradual replacement of oligotrophic taxa by eutrophic species since ~1973, and a distinct increase in small benthic *Fragilaria sensu lato* taxa in after ~2005. In general, diatom community composition was structured mainly by nutrient enrichment over the 20th century, although effects of hydrologic fluctuations appear to have been more pronounced in the past two decades.

4.1 Lake eutrophication and phototrophic responses

Our sedimentary records of lake eutrophication were highly consistent with patterns recorded from monitoring data for Yilong Lake. As the human population in the catchment began to increase in the 1960s, sediment TN values steadily increased, with a concomitant decrease in bulk sediment C/N ratios and $\delta^{13}\text{C}$ values after the 1960s (Fig. 4), patterns that are consistent with increased input of nutrients and autochthonous C sources (Meyers and Ishiwatari, 1993). For example, an annual input of 341 and 40 tons of TN and TP was estimated for the early 1990s (Chou and Xia, 1998). The archival data showed that the content of lake-water nutrients and Chl-*a* generally increased concurrent with a decline in lake-water transparency during 1985-1997 and 2009-2013 (Fig. 2). The decline of the bulk sediment carbon isotopic signal, coupled with an increase in cyanobacteria, suggested a shift of carbon source and transfer towards a planktonic

pathway typical of eutrophic subtropical (Xu et al., 2014) and temperate lakes (McGowan et al., 2005). The rise in $\delta^{15}\text{N}$ is also consistent with the release of isotopically-enriched pollutants arising from urban (Leavitt et al., 2006) and agricultural sources (Bunting et al., 2007), while the depletion of $\delta^{15}\text{N}$ prior to the mid-1960s may be linked with deposition of atmospheric nitrogen (Kang et al., 2019) and/or a paramount importance in fixed nitrogen within the lake (Hayes et al., 2019).

Concentrations of fossils from total algae and major algal components increased dramatically from ~1965 in a pattern similar to that observed in other lakes impacted by agriculture (Bunting et al., 2007; Moorhouse et al., 2014) and urbanization (Leavitt et al., 2006). Similar long-term increases in primary producer abundance as a result of intensified catchment development have been recorded in other lakes within this study region (Wu et al., 2002; Shi and Sun, 2005), as well as those from eastern China (Xu et al., 2014; Deng et al., 2016). Furthermore, these changes are generally consistent with a 100-fold increase in the cell density of monitored lake-water phytoplankton during the last few decades (Table 2). Similarly, monitoring programs within Yilong Lake reveal that the dominant phytoplankton by cell density gradually shifted from Bacillariophyta in 1957 to positively-buoyant (and more easily sampled) Cyanobacteria since 1997. The moderate concentration for cyanobacterial pigments, such as zeaxanthin, prior to ~1965 was consistent with the presence of cyanobacterial blooms of *Microcystis aeruginosa* in 1957 (Ley et al., 1963).

Nutrient input also led to significant shifts in the diatom community, although effects of fertilization appear to have declined in the last decade. For example, the period of ~1973-1998 was characterized by a rapid enrichment in TN and the predominance of *F. crotonensis*, a planktonic species often found in nutrient-enriched lakes (Bennion et al., 2009; Hu et al., 2012).

This taxon declined during the period of 1998-2008, when lake-water nutrients and algal production were lower (Fig. 2), and there existed a moderate drop in sediment pigment concentrations (e.g. zeaxanthin and lutein). Since ~1998, the abundance of small benthic *Fragilaria sensu lato* taxa increased significantly at the expense of planktonic diatoms in Yilong Lake, suggesting a decreasing role of nutrients in driving diatom community reorganization over the last decade. Finally, from the late 2000s, analyses of monitoring and sediment data suggest that cyanobacterial abundance has increased relative to that of diatoms. Similarly, increasing dominance of cyanobacteria has been well recorded in regional studies of temperate lakes under nutrient-enriched conditions (Taranu et al., 2015).

4.2 Hydrological and climatic impacts on algae

Analyses of sediment grain size distribution, together with archival environmental data, provide evidence for that hydrologic fluctuations served as a significant driver of phototrophic community change. Specifically, the hydrologic fluctuation inferred from changes in sediment sand content explained a large proportion of the variance in sediment Chl-*a* pigments, while variation in lake area (another hydrological proxy) was a strong predictor of changes in lake-water Chl-*a* concentration (Fig. 8). A moderate decrease of sediment sand content starting from the 1950s corresponds to the documented history of hydrological regulation and decreased water levels (Cui and Zhai, 2006). Lake regulation often decreases the natural variation of water level and lake turbulence (Menking, 1997; Digerfeldt et al., 2000), resulting in a gradual decrease in the sand component over time (Wang et al., 2019). Similarly, the spikes in median grain size were synchronous with several major events of extreme drought over the last six decades (Figs. 2a and 4). Lake regulation can often amplify the nutrient effect and promote algae production by

concentrating nutrients (Serruya and Pollinger, 1977; Peršić et al., 2007), enhancing nutrient retention (Maavara et al., 2015) and reducing water turnover (Posch et al., 2012). Accordingly, our results showed a pronounced increase in the content of sediment nutrient and pigment concentrations starting from ~1953 (Fig. 4), as well as a significant interaction between hydrologic fluctuation and nutrients (Fig. 8) at this time. These patterns are consistent with earlier studies of other hydrologically-managed and drought-sensitive shallow lakes based on monitoring data (Yang and Lu, 2014) and sediment records (Chen et al., 2011).

Previous surveys show that phototrophic response to nutrient concentrations within lakes can be modulated by both warming (Vogt et al. 2018) and extreme climate (Anderson, 2000; Berthon et al., 2014). Recent warming during the last two decades has been identified as an important factor regulating diatom compositional shift in this study region (Chen et al., 2014a), as well as in many parts of the world (Winder and Hunter, 2008; Finkel et al., 2009; Rühland et al., 2015). The stability of water column can be further enhanced by a falling wind speed (i.e. < 3 m/s) during the last two decades, which often favors the bloom of buoyant cyanobacteria such as *Microcystis* in eutrophic shallow lakes (Zhang et al., 2012). The most recent drought, occurring during 2009-2012, reduced lake levels by ~2.3m with a loss of ~0.67 billion m³ of water (Wang et al., 2014). Meanwhile, the shift from planktonic diatoms to small benthic *Fragilaria sensu lato* taxa indicated the expansion of littoral taxa. This can result from warming-associated hydrodynamic change (i.e. increased evaporation; Byllaardt and Cyr, 2011), and the loss of lake volume which was caused by severe droughts and possibly amplified by elevated water use due to an increased population size (Fig. 2 and Table 2).

In 2010, the dominant Cyanobacteria (*Microcystis*) was replaced by *Cylindrospermopsis raciborskii* (Table 2), a species that can tolerate varying N:P ratios (Barica et al., 1980) as well as

extreme droughts (Marc et al., 2000). Similarly, there was a clear loss of *Aulacoseira* spp. during the last decade, a taxon which had been consistently subdominant in diatom assemblages over much of the core (Fig. 5b). *Aulacoseira* taxa have a high siliceous content and are known to proliferate in frequently-mixed waters that favor resuspension of these heavy taxa (Reynolds, 1987; Chen et al., 2011). This trend was synchronous with the recent decrease of wind speed, that was widely observed across China and linked with the weakening east Asian monsoon (Xu et al., 2006). Therefore, changes in lake level and thermal stability may favor specific algae in the context of regional warming (Wagner and Adrian, 2009; Romo et al., 2013).

4.3 Heterogeneity in algal responses to multiple stressors

Despite pigment and diatom data exhibiting generally coherent shifts during the past century (Fig. 4a, b), there exist key differences in the importance of nutrient supply to the apparent production of individual photosynthetic groups. For example, the strong relationship between sediment TN and cyanobacteria pigments agrees with the demonstrated ability of lake-water TN to predict cyanobacteria abundance in temperate regions (Beaulieu et al., 2014) and the positive response of primary producers to N influx (Leavitt et al., 2006; Bunting et al. 2007). N supply to Yilong Lake may have limited algal growth early in the 20th century, when sedimentary $\delta^{15}\text{N}$ was low and characteristic of fixed N_2 from diazotrophic cyanobacteria, and disproportionately high P influx occurred with agricultural development in 1960s (Shiping Yearbook, 2005), leading to a low N:P mass ratio of 12.9-14.4 (Fig. 2). Thereafter, this shallow system was characterized by a consistently high N:P mass ratio (i.e. > 40) for the past two decades (Table 2), suggesting that the content of P, coupled with increasing N influx, may have impacted algal production through changing N:P ratio (Li et al., 2015). Later on, a rapid decrease

of N:P mass ratio from > 80 to < 50 corresponded to a shift of dominant Cyanobacteria from heterocystous diazotroph *Aphanizomenon flosaquae* in 1992 to non-nitrogen fixing *Microcystis aeruginosa* in 1997 and 2008, respectively (Table 2). This pattern suggests that non-nitrogen fixers can bloom with varying N:P ratios when there is sufficient P supply, as is found in other large shallow lakes (Xie et al., 2003; Xu et al. 2010; Hayes et al., 2019).

Our comparative study highlights the increasing effects of hydrologic fluctuations and regional climate variability on variation in phototrophs over the last few decades. Noticeably, an increase in the lake-water Chl-*a* concentration and its sediment pigment is strongly linked with hydrologic fluctuations over time (Fig. 8a, b). Even though the increased ratio of chlorophyll-*a*/pheophytin-*a* (Fig. 5a) suggested an incomplete pigment degradation and preservation in sediments during 2004-2013, the major pigment components generally display an increasing trend of Chl-*a* and cyanobacteria concentrations that are comparable with lake-water surveys (Fig. 2e and Table 2). Meanwhile, the benthic diatom percentage rose sharply as water column depth declined during the last two decades, despite the concurrent decline in macrophyte coverage (Table 2). The rapid rise in the cyanobacteria (zeaxanthin) pigments also suggests that there was an increase in the growth of cyanobacteria at the expense of other algae as observed in other shallow lakes (McGowan et al., 2005). Previous studies show that hydrologic fluctuation could serve as a key driver of algae in nutrient-enriched shallow lakes through increasing benthic production (Vadeboncoeur et al., 2003), or even overriding nutrients in structuring diatom composition (Liu et al., 2017). More recently, water level drops may have exposed more benthic habitats (e.g. mud and rocks) favoring small *Fragilaria sensu lato* taxa as is found in neighboring shallow lakes (Liu et al., 2017; Kang et al., 2019). The diatom compositional change is also broadly consistent with the finding that lake depth could play a significant role in

affecting biotic responses to climate change in polymictic lakes (Chen et al., 2014b). Therefore, the role of nutrients was relatively truncated in driving diatom composition with hydrologic modulation and warming climate, leading to a heterogeneous pattern in the algal changes.

5. Conclusion

Our lake sediment records reveal a predominant effect of nutrient enrichment on phototrophic abundance in this shallow lake, as well as an increasing role of hydrological variability during the past few decades. Although fossil pigments appear to record a history of continuous fertilization, the replacement of eutrophic diatom species by small benthic taxa also suggests that anthropogenic water regulation, extreme droughts and warming have an influence on species composition. Such an interaction between nutrient and hydrological stressors is increasingly recognized (Vogt et al. 2018) and should be fully considered for reliable interpretation of paleoecological indicators and long-term ecosystem changes in shallow lakes. Finally, this study highlights the necessity of using multiple indicators for tracking primary production and phototrophic changes in shallow lakes. In particular, biological proxies (e.g. diatoms and pigments) have been increasingly and successfully applied in sediment-based studies to infer the temporal change of ecosystem structure in shallow systems, but they are often applied singularly without a full consideration of the differences in their sensitivity to multiple stressors for data interpretation which is evidenced in this work.

Acknowledgements

This work was supported by the National Key Research and Development Program of China [grant number 2017YFA0605202], National Natural Science Foundation of China [grant number

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

41171048, U1133601], and Ministry of Education of China [grant number 213034A]. PRL and
IGE were supported by the Canada Research Chair program. We are grateful to Huibin Lu and
Haibin Shi for their field work assistance, as well as Jiaoyuan Wang, Jianshuang Tao and
Wengang Kang for their constructive comments. Constructive comments provided by two
anonymous reviewers and editor are appreciated.

References

- Adrian R, O'Reilly CM, Zagarese H, Baines SB, Hessen DO, Keller W, Livingstone DM, Sommaruga R, Straile D, Donk EV, Weyhenmeyer GA, Winder M (2009) Lakes as sentinels of climate change. *Limnol Oceanogr* 54:2283-2297.
- Anderson JN (2000) Miniview: Diatoms, temperature and climatic change. *Eur J Phycol* 35:307-314.
- Appleby PG (2001) Chronostratigraphic techniques in recent sediments. In: Tracking environmental change using lake sediments. Volume 1: Basin analysis, coring and chronological techniques, (eds Smol JP, Birks HJB, Last WM) vol 1. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 171-203.
- Barica J, Kling HJ, Gibson J (1980) Experimental Manipulation of Algal Bloom Composition by Nitrogen Addition. *Can J Fish Aquat Sci* 37:1175-1183.
- Battarbee RW, Jones VJ, Flower RJ, Cameron NG, Bennion H (2001) Diatoms. In: Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial, Algal, and Siliceous Indicators (eds Smol JP, Birks HJB, Last WM) vol 3. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 155-201.
- Battarbee RW (2010) Foreword. In: Global Change Impacts on Mountain Lakes (eds Eggermont H, Kernan M, Martens K). *Hydrobiologia* 648:1-2.
- Beaulieu M, Pick F, Palmer M, Watson S, Winter J, Zurawell R, Gregory-Eaves I, Prairie Y (2014) Comparing predictive cyanobacterial models from temperate regions. *Can J Fish Aquat Sci* 71:1830-1839.
- Bennion H, Rawcliffe R, Clarke G, Clarke SJ, Davidson TA, Rose C, Rose N, Sayer CD, Turner S (2009) Using novel palaeolimnological techniques to define lake conservation objectives. Final Report to Natural England. <http://discovery.ucl.ac.uk/id/eprint/399621>.

- Berthon V, Alric B, Rimet F, Perga M-E (2014) Sensitivity and responses of diatoms to climate warming in lakes heavily influenced by humans. *Freshwater Biol* 59:1755-1767.
- Brugam RB, McKeever K, Kolesa L (1998) A diatom-inferred water depth reconstruction for an Upper Peninsula, Michigan, lake. *J Paleolimnol* 20:267-276.
- Bunting L, Leavitt PR, Gibson CE, McGee EJ (2007) Degradation of water quality in Lough Neagh, Northern Ireland, by diffuse nitrogen flux from a phosphorus-rich catchment. *Limnol Oceanogr* 52:354-369.
- Byllaardt JV, Cyr H (2011) Does a warmer lake mean smaller benthic algae? Evidence against the importance of temperature-size relationships in natural systems. *Oikos* 120:162-169.
- Carvalho L, Kirika A (2003) Changes in shallow lake functioning: response to climate change and nutrient reduction. *Hydrobiologia* 506-509:789-796.
- Chen C, Zhao L, Zhu C, Wang J, Jiang J, Yang S (2014a) Response of diatom community in Lugu Lake (Yunnan–Guizhou Plateau, China) to climate change over the past century. *J Paleolimnol* 51:357-373.
- Chen G, Selbie DT, Griffiths K, Sweetman JN, Botrel M, Taranu ZE, Knops S, Bondy J, Michelutti N, Smol JP, Gregory-Eaves I (2014b) Proximity to ice fields and lake depth as modulators of paleoclimate records: a regional study from southwest Yukon, Canada. *J Paleolimnol* 52:185-200.
- Chen X, Yang X, Dong X, Liu E (2013) Environmental changes in Chaohu Lake (southeast, China) since the mid 20th century: The interactive impacts of nutrients, hydrology and climate. *Limnologica* 43:10-17.
- Chen X, Yang X, Dong X, Liu Q (2011) Nutrient dynamics linked to hydrological condition and anthropogenic nutrient loading in Chaohu Lake (southeast China). *Hydrobiologia* 661:223-234.

- Chou G, Xia F (1998) Enhancing Environmental Management Promotes Water Quality in Yilong Lake. *Yunnan Environ Sci* 17:54-56.
- Cuddington K, Leavitt PR (1999) An individual-based model of pigment flux in lakes: implications for organic biogeochemistry and paleoecology. *Can J Fish Aquat Sci* 56:1964-1977.
- Cui B, Zhai H (2006) Characteristics of wetland functional degradation and its ecological water requirement for restoration in Yilong Lake of Yunnan Plateau. *Chinese Sci Bull* 51:127-135.
- Dai A (2011) Drought under global warming: a review. *Wiley Interdisciplinary Reviews: Clim Change* 2:45-65.
- Deng J, Qin B, Sarvala J, Salmaso N, Zhu G, Ventelä A-M, Zhang Y, Gao G, Nurminen L, Kirkkala T, Tarvainen M, Vuorio K (2016) Phytoplankton assemblages respond differently to climate warming and eutrophication: A case study from Pyhäjärvi and Taihu. *J Great Lakes Res* 42:386-396.
- Digerfeldt G, Olsson S, Sandgren P (2000) Reconstruction of lake-level changes in lake Xinias, central Greece, during the last 40 000 years. *Palaeogeogr Palaeoclimatol Palaeoecol* 158:65-82.
- Finkel ZV, Vaillancourt CJ, Irwin AJ, Reavie ED, Smol JP (2009) Environmental control of diatom community size structure varies across aquatic ecosystems. *Proc R Soc B* 276:1627-1634.
- Hall RI, Leavitt PR (1999) Effects of agriculture, urbanization, and climate on water quality in the northern Great Plains. *Limnol Oceanogr* 44:739-756.
- Hambright KD, Zohary T, Eckert W, Schwartz SS, Schelske CL, Laird KR, Leavitt PR (2008) Exploitation and destabilization of a warm, freshwater ecosystem through engineered hydrological change. *Ecol Appl* 18:1591-1603.

Hayes, NM, A Patoine, HA Haig, GL Simpson, VJ Swarbrick, E Wiik, PR Leavitt (2019) Spatial and temporal variation in nitrogen fixation and its importance to phytoplankton in phosphorus-rich lakes. *Freshwater Biol* 64: 269-283.

Heiri O, Lotter F, Lemcke G (2001) Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *J Paleolimnol* 25:101-110.

Hu Z, Li Y, Li S (2012) Spatial and temporal distributions of diatom communities and their relationships with environmental factors in Lake Erhai. *J Lake Sci* 24:400-408.

Huisman J, Matthijs HCP, Visser PM (2005) *Harmful Cyanobacteria*. Springer-Verlag GmbH, 3:1-23.

IPCC (2013) Synthesis Report. Contribution of Working Groups I , II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Jarvis IAN, Gale AS, Jenkyns HC, Pearce MA (2006) Secular variation in Late Cretaceous carbon isotopes: a new $\delta^{13}\text{C}$ carbonate reference curve for the Cenomanian-Campanian (99.6-70.6 Ma). *Geol Mag* 143:561-608.

Jeppesen E, Søndergaard M, Jensen JP, Havens KE, Anneville O, Carvalho L, Coveney M, Deneke R, Dokulil MT, Foy B, Gerdeaux D, Hampton SE, Hilt S, Kangur K, Köhler J, Lammens E, Lauridsen TL, Manca M, Miracle M, Moss B, Nöges P, Persson G, Phillips G, Portielje R, Romo S, Schelske CL, Straile D, Tatrai I, Willén E, Winder M (2005) Lake responses to reduced nutrient loading-an analysis of contemporary long-term data from 35 case studies. *Freshwater Biol* 50:1747-1771.

Jin XC (1995) *China Lake Environment (Volume 3)*. Haiyang Publishers, China, pp 263-273.

Jöhnk KD, Huisman JEF, Sharples J, Sommeijer BEN, Visser PM, Stroom JM (2008) Summer heatwaves promote blooms of harmful cyanobacteria. *Global Change Biol* 14:495-512.

Juggins S (2015) rioja: Analysis of Quaternary Science Data (R package version 2.0-6. CRAN. R-project.org/Package = rioja).

Kang W, Chen G, Wang J, Huang L, Wang L, Li R, Hu K, Liu Y, Tao J, Blais JM, Smol JP (2019) Assessing the impact of long-term changes in climate and atmospheric deposition on a shallow alpine lake from southeast Tibet. *Sci Total Environ* 650:713-724.

Krammer K, Lange-Bertalot H (1986-1991) Bacillariophyceae 1-4. In: *Susswasserflora von Mitteleuropa*, Band 1-4 (eds Ettl H, Gerloff J, Heynig H, Mollenhauer D). Gustav Fischer Verlag, Jena, Germany.

Lake SP (2011) *Drought and Aquatic Ecosystems Effects and Responses*. A John Wiley and Sons, Ltd., Publication.

Leavitt PR, Hodgson DA (2001) Sedimentary pigments. In: *Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial, Algal, and Siliceous Indicators* (eds Smol JP, Birks HJB, Last WM) vol 3. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 295-325.

Leavitt PR, Brock CS, Ebel C, Patoine A (2006) Landscape-scale effects of urban nitrogen on a chain of freshwater lakes in central North America. *Limnol Oceanogr* 51:2262-2277.

Lepš J, Šmilauer P (2003) *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press, Cambridge, UK.

Ley S, Yu M, Li K, Tseng C, Chen C, Kao P, Huang F (1963) Limnological Survey of the lakes of Yunnan Plateau. *Oceanol ET Limnol Sinica* 5:87-114.

Li Y, Liu Y, Zhao L, Hastings A, Guo H (2015) Exploring change of internal nutrients cycling in a shallow lake: A dynamic nutrient driven phytoplankton model. *Ecol Model* 313:137-148.

- Liu Y, Chen G, Hu K, Shi H, Huang L, Chen X, Lu H, Zhao S, Chen L (2017) Biological responses to recent eutrophication and hydrologic changes in Xingyun Lake, southwest China. *J Paleolimnol* 57:343-60.
- Maavara T, Parsons CT, Ridenour C, Stojanovic S, Durr HH, Powley HR, Van Cappellen P (2015) Global phosphorus retention by river damming. *Proc Natl Acad Sci USA* 112:15603–15608.
- Marc B, Falcão D, Marinho M, Pagano M, Moura A (2000) Occurrence of *Cylindrospermopsis* (Cyanobacteria) in 39 Brazilian tropical reservoirs during the 1998 drought. *Aquatic Microbial Ecol* 23:13-27.
- McGowan S, Leavitt PR, Hall RI, Anderson NJ, Jeppesen E, Odgaard BV (2005) Controls of algal abundance and community composition during ecosystem state change. *Ecology* 86:2200-2211.
- Menking KM (1997) Climate signals in clay mineralogy and grain-size variations in Owens Lake core OI-92, eastern California. *Special Paper of the Geol. Soc Am* 317:25-36.
- Meyer TJ (2001) Sediment organic matter. In: *Tracking Environmental Change Using Lake Sediments. Volume 2: Physical and geochemical methods* (eds Smol JP, Birks HJB, Last WM) vol 3. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 239-269.
- Meyers PA, Ishiwatari R (1993) Lacustrine organic geochemistry - an overview of indicators of organic matter sources and diagenesis in lake sediments. *Org Geochem* 20:867-900.
- Moorhouse HL, McGowan S, Jones MD, Barker P, Leavitt PR, Brayshaw SA, Haworth EY (2014) Contrasting effects of nutrients and climate on algal communities in two lakes in the Windermere catchment since the late 19th century. *Freshwater Biol* 59:2605-2620.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Min-Chin PBR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H (2015) *vegan: Community Ecology Package* (R package version 2.0-6. CRAN. [R-project.org/Package = vegan](http://R-project.org/Package=vegan)).

Paerl H, Huisman J (2008) Blooms like it hot. *Science* 320:57-58.

Peršić V, Horvatić J, Has-Schön E, Bogut I (2007) Changes in N and P limitation induced by water level fluctuations in Nature Park Kopački Rit (Croatia): nutrient enrichment bioassay. *Aquat. Ecology* 43:27-36.

Posch T, Köster O, Salcher MM, Pernthaler J (2012) Harmful filamentous cyanobacteria favoured by reduced water turnover with lake warming. *Nature Climate Change* 2:809-813.

R Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.

Reynolds CS (1987) The response of phytoplankton communities to changing lake environments. *Swiss J Hydrol* 49:220-236.

Reynolds CS (2006) *Ecology of Phytoplankton (Ecology, Biodiversity and Conservation)*. Cambridge University Press, Cambridge, UK.

Romo S, Soria JM, Campo FFD, Benkaddour YO, Barón-Sola Á (2013) Water residence time and the dynamics of toxic cyanobacteria. *Freshwater Biol* 58:513-522.

Round F, Crawford R, Man D (2007) *The diatoms biology and morphology of the genera*. Cambridge University Press, Cambridge, UK.

Rühland K, Paterson AM, Smol JP (2008) Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes. *Global Change Biol* 14:2740-2754.

Rühland KM, Paterson AM, Smol JP (2015) Lake diatom responses to warming: reviewing the evidence. *J Paleolimnol* 54:1-35.

Saulnier-Talbot É, Gregory-Eaves I, Simpson KG, Efitre J, Nowlan TE, Taranu ZE, Chapman LJ (2014) Small Changes in Climate Can Profoundly Alter the Dynamics and Ecosystem Services of Tropical Crater Lakes. *Plos One* 9:e86561.

Scheffer MS, Hosper SH, Meijer ML, Moss B, Jeppesen E (1993) Alternative equilibria in shallow lakes. *Trends Ecol Evol* 8:275-279.

Scheffer M (1998) *Ecology of Shallow Lakes*. London, UK: Chapman and Hall

Schindler DW (2006) Recent advances in the understanding and management of eutrophication. *Limnol Oceanogr* 51:356-363.

Serruya C, Pollinger U (1977) Lowering of water level and algal biomass in Lake Kinneret. *Hydrobiologia* 54:73-80.

Shi L, Sun Q (2005) Brief Talk on Effect of Aquatic Plant Purifying Water body of Yilong Lake. *Yunnan Environ Sci* 24:40-42.

Shiping Yearbook (2005) *Shiping Year Book* (County Condification Committee). Yunnan Peoples's Publishing Press, pp 56-67, 169-173.

Smol JP, Wolfe AP, Birks HJ, Douglas MS, Jones VJ, Korhola A, Pienitz R, Rühland K, Sorvari S, Antoniades D, Brooks SJ, Fallu MA, Hughes M, Keatley BE, Laing TE, Michelutti N, Nazarova L, Nyman M, Paterson AM, Perren B, Quinlan R, Rautio M, Saulnier-Talbot E, Siitonen S, Solovieva N, Weckstrom J (2005) Climate-driven regime shifts in the biological communities of arctic lakes. *Proc Natl Acad Sci USA* 102:4397-4402.

Smol JP (2010) The power of the past: using sediments to track the effects of multiple stressors on lake ecosystems. *Freshwater Biol* 55:43-59.

Sommerfield C, Nitttrouer C (1999) Modern

accumulation rates and a sediment budget for the Eel shelf: a flood-dominated depositional environment. *Mar Geol* 154:227-241.

Søndergaard M, Jensen JP, Jeppesen E (2003) Role of sediment and internal loading of phosphorus in shallow lakes. *Hydrobiologia* 506:135-145.

Sterner R, Elser JJ (2002) *Ecological Stoichiometry: The Biology of Elements From Molecules to The Biosphere*. Princeton University Press, pp 439.

Stoermer EF, Smol JP (2001) *The Diatoms: Applications for the environmental and earth science*. Cambridge: Cambridge University Press. Cambridge: Cambridge University Press.

Taranu ZE, Zurawell RW, Pick F, Gregory-Eaves I (2012) Predicting cyanobacterial dynamics in the face of global change: the importance of scale and environmental context. *Global Change Biol* 18:3477-3490.

Taranu ZE, Gregory-Eaves I, Leavitt PR, Bunting L, Buchaca T, Catalan J, Domaizon I, Guilizzoni P, Lami A, McGowan S, Moorhouse H, Morabito G, Pick FR, Stevenson MA, Thompson PL, Vinebrooke RD (2015) Acceleration of cyanobacterial dominance in north temperate-subarctic lakes during the Anthropocene. *Ecol Lett* 18:375-384.

ter Braak CJF, Prentice IC (1988) A theory of gradient analysis. *Adv Ecol Res* 18:271-313.

ter Braak CJF, Šmilauer P (2002) *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination [Version 4.5]*. Microcomputer Power, Ithaca, NY.

Tilman D (1987) Resource competition and community structure. *Monographs in Population Biology*. Princeton University Press 17:1-296.

- 776 Vadeboncoeur Y, Jeppesen E, Zanden MJV, Schierup HH, Christoffersen K, Lodge DM (2003)
- 777 From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in
- 778 lakes. *Limnol Oceanogr* 48:1408-141.
- 779 Vogt RJ, Sharma S, Leavitt PR (2018) Direct and interactive effects of climate, meteorology,
- 780 river hydrology, and lake characteristics on water quality in productive lakes of the Canadian
- 781 Prairies. *Can J Fish Aquat Sci* 75:47-59.
- 782 Wagner C, Adrian R (2009) Cyanobacteria dominance: Quantifying the effects of climate chang.
- 783 *Limnol Oceanogr* 54:2460-2468.
- 784 Wang H, Yang Z, Wang L, Liu Y, Song Y, Gao J (2014) The application of TVDI in drought
- 785 monitoring over Yunnan province during 2009 to 2010. *J. Yunnan University (Sci.)* 36:59-65.
- 786 Wang J, Chen G, Kang W, Hu K, Wang L (2019) Impoundment intensity determines temporal
- 787 patterns of hydrological fluctuation, carbon cycling and algal succession in a dammed lake of
- 788 Southwest China. *Water Res* 148:162-75.
- 789 Wang W, Wang L (2008) Current situation of agricultural non-point source pollution and Control
- 790 Countermeasures in Yilong lake. *Yunnan Agricultural Science and Technology*, pp 139-141.
- 791 Wang Z (1997) Survey of zooplankton and fish productivity in Yilong Lake, Yunnan. *J. Fisheries*
- 792 *China* 402-407.
- 793 Wieland E, Santschi P, Höhener P, Sturm M (1993) Scavenging of Chernobyl ^{137}Cs and natural
- 794 ^{210}Pb in Lake Sempach, Switzerland. *Geochimica Et Cosmochimica Acta* 57:2959-2979.
- 795 Winder M, Hunter DA (2008) Temporal organization of phytoplankton communities linked to
- 796 physical forcing. *Oecologia* 156:179-192.
- 797 Wu F, Zheng M, Hu G (2016) The Estimation of Vegetation Coverage of Yanshan County in
- 798 Yunnan by Remote Sensing Based on OLI Data. *Environ Sci Survey* 36:5-7.

- Wu J, Jiang X, Xia W, Pan H, Yin Y (2002) Climate and Primary Productivity over the last 500 years of the Chenghai Lake, Yunnan. *Mar Geol Quaternary Geol* 22:95-98.
- Xie L, Xie P, Li S, Tang H, Liu H (2003) The low TN:TP ratio, a cause or a result of *Microcystis* blooms? *Water Res* 37:2073-2080.
- Xu H, Paerl H, Qin B, Zhu G, Gao G (2010) Nitrogen and phosphorus inputs control phytoplankton growth in eutrophic lake Taihu, China. *Limnol Oceanogr* 55:420-432.
- Xu J, Wen Z, Ke Z, Zhang M, Zhang M, Guo N, Hansson LA, Xie P (2014) Contrasting energy pathways at the community level as a consequence of regime shifts. *Oecologia* 175:231-241.
- Xu M, Chang CP, Fu CB, Qi Y, Robock A, Robinson D, Zhang HM (2006) Steady decline of east Asian monsoon winds, 1969-2000: Evidence from direct ground measurements of wind speed. *J Geophys Res* 111: 1-8.
- Yang L, Li H, (2010) *Wetlands of Yunnan*. China Forestry Publishing House, pp 94-101.
- Yang X, Lu X (2014) Drastic change in China's lakes and reservoirs over the past decades. *Sci Rep* 4:6041.
- Zhang J, Wang Z, Song Z, Xie Z, Li L, Song L (2012) Bioaccumulation of microcystins in two freshwater gastropods from a cyanobacteria-bloom plateau lake, Lake Dianchi. *Environ Pollut* 164:227-34.
- Zhang Y, zhang E, Liu M (2009) Spectral absorption properties of chromophoric dissolved organic matter and particulate matter in Yunnan Plateau lakes. *J Lake Sci* 21:255-263.
- Zhao L (2013) The regime shifts and inversion of catastrophic driving factors in the ecosystems of Yilong Lake, Yunnan. Dissertation, University of Chinese Academy of Science.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

820 Zhao L, Li Y, Zou R, He B, Zhu X, Liu Y, Wang J, Zhu Y (2013) A three-dimensional water
821 quality modeling approach for exploring the eutrophication responses to load reduction scenarios
822 in Lake Yilong (China). Environ Pollut 177:13-21.

Table 1 Summary of key limnological features of Yilong Lake

Variable	Value
Altitude (m) ^a	1,413.4
Lake surface area (km ²) ^a	34.0
Catchment area (km ²) ^a	326.0
Average water depth (m) ^a	2.9
Max. water depth (m) ^a	3.7
Chlorophyll (µg/l) ^b	214.3
Transparency (m) ^b	0.1
TN (mg/l) ^b	7.7
TP (µg/l) ^b	123.3
pH ^b	8.8

^a Data are from Yang & Li (2010).

^b Data were collected in the summer of 2013 from the current study.

Table 2 Monitored changes of algae abundance, lake-water N:P mass ratio and macrophyte coverage over time in Yilong Lake

Year	Cyanobacteria (10 ⁶ cell/l)	Diatoms (10 ⁶ cell/l)	Phytoplankton (10 ⁶ cell/l)	Dominant algae	Cyanobacteria (%)	N:P ratio (by mass)	Macrophyte coverage (%)
1957			8.41 ^a	Bacillariophyta (except episodic cyanobacteria bloom in Aug.)			
1982						14.39	95.0 ^d
1988			46.00 ^b	Chlorophyta (<i>Pediastrum simplex</i>)		89.23	
1992	180.47 ^c	4.00 ^c	193.21 ^c	Cyanobacteria (<i>Aphanizomenon flosaquae</i>)	93.41 ^c	82.95	27.3 ^e
1993			50.88 ^d	Chlorophyta (<i>Pediastrum simplex</i>)		73.84	
1997	19.76 ^e	0.21 ^e	21.78 ^e	Cyanobacteria (<i>Microcystis aeruginosa</i>)	90.75 ^e	38.28	40.0 ^e
2008	82.30 ^f	1.31 ^f	88.51 ^f	Cyanobacteria (<i>Microcystis aeruginosa</i>)	92.98 ^f	49.65	60.0 ^e
2010			317.20 ^e	Cyanobacteria (<i>Cylindrospermopsis raciborskii</i>)	99.00	40.33	<10.0 ^e
2015	244.65	0.59	248.14	Cyanobacteria (<i>Aphanizomenon flosaquae</i>)	98.59	51.20	

Data were collected from ^aLey et al. (1963); ^bJin et al. (1995); ^cWang (1997); ^dWang & Dou (1998); ^eZhao (2013); ^fZhang et al. (2009)

Table 3 Summary of individual RDAs for key environmental variables in accounting for the variance (adjusted R^2) in the algal production and diatom PC1 score during the periods of ~1903-2013 and ~1953-2013, respectively

Environmental Variable	Pigments		Diatom PC1	
	1903-2013	1953-2013	1903-2013	1953-2013
Median grain size (μm)	-0.027	-0.034	-0.023	-0.024
Clay (%)	-0.027	-0.033	-0.022	-0.019
Silt (%)	-0.024	-0.016	-0.016	0.007
Sand (%)	0.034	0.197 **	0.047	0.273 ***
$\delta^{13}\text{C}$ (‰)	0.094	0.419 ***	-0.022	-0.017
$\delta^{15}\text{N}$ (‰)	0.217 **	0.783 ***	0.038	0.224 ***
C/N ratio	0.233 **	0.846 ***	0.034	0.189 ***
TC (mg/g)	0.786 ***	0.796 ***	0.324 ***	0.103 *
TN (mg/g)	0.900 ***	0.824 ***	0.406 ***	0.159 ***
Population	-	0.822 ***	-	0.121 **
Temperature ($^{\circ}\text{C}$)	-	0.288 ***	-	0.233 ***
Precipitation (mm)	-	-0.020	-	0.044
Wind speed (m/s)	-	0.384 ***	-	-0.009
All variables	0.914 ***	0.912 ***	0.270 ***	0.136 **

Significance codes for P -level: '***', $P < 0.001$; '**', $P < 0.01$; '*', $P < 0.05$.

Note: An adjusted R^2 near 0 indicates that the environmental variable does not explain more of the variation of the biotic assemblages change than random normal variable would do; Negative adjusted R^2 indicates that the explanatory variables perform similarly as random normal variables would.

Figure captions

Fig. 1 Site map (left) showing the location of Yilong Lake and lake morphometry (right).

Fig. 2 Time series of archived data showing the changes in annual mean temperature and precipitation (a), catchment population and wind speed (b), calculated water depth and lake area (c), nutrient variables total phosphorus and total nitrogen (d), Chl-*a* and transparency (e) for Yilong Lake, respectively. Meteorological data are from the National Climate Center (<http://cmdp.ncc.cma.gov.cn/cn/index.htm>); Population data were collected from the Shipping Yearbook (2005); TP, TN, Chl-*a*, transparency, water level and volume data were collected from previous studies (Chou and Xia, 1998; Ley et al., 1963; Li, 2009; Shi and Sun, 2005; Wei and Tang, 2014; Whitmore et al., 1997; Yang and Li, 2010).

Fig. 3 Depth profiles showing the ^{210}Pb and ^{137}Cs radioactivities (a) and the CRS age model and sedimentation rate (b) for Yilong Lake.

Fig. 4 Sedimentary profile showing the proxies of grain sizes, nutrient concentrations and isotopes, as well as the diatom and pigment PCA site scores, for Yilong Lake.

Fig. 5 Stratigraphic profiles showing the temporal changes in pigment concentrations (ng/g OM) for total algae and major components (a; Z:PD, the zeaxanthin:planktonic diatoxanthin ratio) and the compositional change of common diatoms (>2% relative abundance in at least one sample; b) with the CONISS clusters at Yilong Lake. Colors denote the documented hydrological (green) and extreme climate events (light blue), respectively, as detailed in Fig. 4.

Fig. 6 PCA biplots showing the first two axes for pigments (a) and diatom assemblages (b) in Yilong Lake during 1903-2013 AD.

Fig. 7 Biplots of redundancy analysis showing the selected significant drivers for pigment concentrations (a) and diatom assemblages (b) during 1903-2013 AD in Yilong Lake.

24 **Fig. 8** Results of variation partitioning and forward selection showing the minimum adequate
25 models for sediment (a) and lake-water Chl-*a* (b), pigments and diatoms in Yilong Lake during
26 the time windows of 1903-2013 (c and d), and 1953-2013 (e and f), respectively.

27 **Fig. 1**

28

29 **Fig. 2**

30

31 **Fig. 3**

32

33 **Fig. 4**

34

37 **Fig. 6**

38

39 **Fig. 7**

40

**Hydrological fluctuations modulate phototrophic responses to nutrient fertilization in a
large and shallow lake of Southwest China**

Kui Hu¹, Guangjie Chen^{1,*}, Irene Gregory-Eaves², Linpei Huang¹, Xiaolin Chen¹, Yuanyuan Liu,
Peter R. Leavitt^{3,4}

¹Yunnan Key Laboratory of Plateau Geographical Processes and Environment Change, School of
Tourism and Geography, Yunnan Normal University, Kunming 650500, China

²Department of Biology, McGill University, Montreal, Quebec H3A 1B1, Canada

³Institute of Environmental Change and Society, University of Regina, 3737 Wascana Parkway,
Regina, SK S4S 0A2, Canada

⁴Institute for Global Food Security, Queen's University Belfast, Belfast, County Antrim, United
Kingdom

*Email: guangjiechen@gmail.com, Tel: (+86) 13658805128

Abstract

Lake nutrient budgets and hydrology are being altered by human activities and climate change, yet little is known of how fertilization and hydrologic mechanisms interact to structure assemblages of primary producers. Here, we present sediment records from a large shallow lake in Southwest China to separate the relative importance of nutrients and hydrological fluctuation in regulating the abundance and composition of primary producers during the 20th century, with a focus on their differential effects on diatoms and cyanobacteria. Shifts in sedimentary particle-size distribution were consistent with the documented events of hydrological regulation during ~1953-1971 and subsequent changes in water level associated with severe droughts. Nutrient enrichment since ~1965 resulted in a significant increase in the abundance of total phototrophs (pheophytin *a*, β -carotene) as inferred from pigment analyses, with stronger responses of cyanobacteria (echinenone, zeaxanthin) over siliceous algae (diatoxanthin). Fossil diatom assemblages revealed a pronounced replacement of benthic taxa by eutrophic and planktonic species (e.g., *Fragilaria crotonensis*) since ~1973, but we observed a significant increase of small benthic *Fragilaria* *sensu lato* taxa following ~2005, which generally corresponded with a moderate increase in fossil pigments. Although eutrophication was the paramount predictor of changes in phototrophs during the last century, variation in lake hydrology due to climate and water management also modulated phototroph abundances and, more recently, diatom assemblages. Specifically, our sediment evidence suggests that hydrological fluctuation has overridden fertilization by nutrients in structuring diatom composition, leading to a heterogeneous response of cyanobacteria and diatoms to external forcing of this shallow lake.

Keywords: Yilong Lake; pigments; diatoms; eutrophication; water regulation; extreme drought

删除的内容: tease out

带格式的: 字体:斜体

删除的内容: human hydrological

删除的内容: s

1. Introduction

Lake phytoplankton and phytobenthos are known to be sensitive to environmental fluctuations such as climate change (Carvalho and Kirika, 2003) and nutrient fertilization (Jeppesen et al., 2005; Schindler, 2006). However, the relative importance of individual environmental controls may vary among basins, depending on algal identity and lake characteristics. For example, global warming can enhance phytoplankton production as temperature can directly affect algal photosynthesis and growth rate (Reynolds, 2006; Jöhnk et al., 2008). Prokaryotes, such as cyanobacteria, can be selectively promoted because their optimum growth rates occur at higher temperatures than do those of diatoms and other eukaryotic algae (Paerl and Huisman, 2008). Recent studies show that nutrient enrichment can also lead to a disproportional increase in the production of harmful algae when compared to other phytoplankton (Taranu et al., 2015), reflecting their competitive ability at high nutrient concentration (Tilman, 1987; Sterner and Elser, 2002). Furthermore, increased water-column stability due to atmospheric warming can enhance the production of harmful filamentous cyanobacteria in deep lakes (Huisman et al., 2005; Posch et al., 2012). However, nutrient fertilization can overwhelm climate control of algal production in shallow lakes (Taranu et al., 2012). Therefore, algal identity and lake typology should be considered in evaluating the strength of lake warming and eutrophication in driving primary producers (Vogt et al., 2018).

Shallow lakes are vulnerable to changes in climate and water influx due to their low volume and short water residence time when compared to deep lakes (Scheffer, 1998; Søndergaard et al., 2003). During the last few decades, anthropogenic regulation of water fluxes has been identified as a significant stressor for freshwaters in populous areas (Yang and Lu, 2014), with a decline in lake water levels often stimulating algal production and favoring phytobenthos in shallow

删除的内容: high

1
2
3 69 systems (Scheffer, 1998). At the same time, climate warming has increased the occurrence of
4
5 70 extreme hydrologic events (e.g., droughts) at regional and global scales (Dai, 2011; IPCC,
6
7 71 2013), augmenting the decline of water level and ecological health (Lake, 2011). In comparison,
8
9 72 nutrient fertilization usually enhances phytoplankton production at the expense of benthic taxa
10
11 73 such as diatoms (Vadeboncoeur et al., 2003). In principle, changes in lake level and nutrient
12
13 74 influx could drive algal abundance and community composition in different directions in
14
15 75 shallow lakes that are subject to multiple stressors. Furthermore, there may exist strong
16
17 76 interactions between nutrient dynamics and hydrologic fluctuation, as prolonged water retention
18
19 77 time due to impoundment can lead to an increased level of nutrients (Maavara et al., 2015) and
20
21 78 accelerate eutrophication in shallow lakes (Chen et al., 2013). To date, little is known of how
22
23 79 such hydrologic fluctuations in shallow lakes may interact with eutrophication in regulating the
24
25 80 abundance and composition of primary producers over time.

24 81 In many lakes, analysis of sedimentary records can provide a reliable temporal perspective
25
26 82 on limnological responses to anthropogenic disturbances and climate change (Adrian et al.,
27
28 83 2009; Battarbee, 2010; Smol, 2010). Fossil pigments and diatoms are two widely used
29
30 84 paleolimnological indicators of algal abundance and community composition (Leavitt and
31
32 85 Hodgson, 2001; Stoermer and Smol, 2001). For example, sediment pigments have recorded the
33
34 86 independent effects of both nutrient fertilization and climate (Hall and Leavitt, 1999; Leavitt et
35
36 87 al., 2006; Bunting et al., 2007), as have fossil diatom assemblages (Smol et al., 2005; Rühland
37
38 88 et al., 2008). Diatoms from shallow lakes were found to be sensitive to lake-level changes
39
40 89 through their response to habitat quantity and quality (Brugam et al., 1998), while shifts in the
41
42 90 vertical zonation of algae with lake depth have been identified from fossil pigments
43
44 91 (Cuddington and Leavitt, 1999; McGowan et al., 2005; Hambright et al., 2008). Therefore,
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

sediment studies in shallow lakes can be applied to quantify the relative importance of multiple stressors in driving algal community structure and abundance over time.

We conducted sediment analyses to evaluate the long-term concordance between algal abundance and diatom assemblage composition in response to multiple stressors in Yilong Lake, southwest China. This large and shallow lake has undergone significant catchment development, hydrological regulation and extreme droughts since the 1950s (Cui and Zhai, 2006). Modern survey data also show a shift in phytoplankton density from predominately diatoms to mainly cyanobacteria during the last few decades (Zhao, 2013). Consequently, we predicted that both nutrient enrichment and variation in lake morphology could significantly enhance the production of phytoplankton over time, particularly that of cyanobacteria, while the intensification of water level changes may modulate the role of nutrients in altering the community structure of diatoms (i.e. an increase of phytobenthos). Combining sediment records with modern survey data, we first identified the temporal trajectories of phototrophic community composition, and then by applying multivariate statistics, we identified the relative importance of environmental factors which influenced phototrophs over different time intervals. Overall, this study provided evidence on dual effects of nutrients and hydrologic fluctuations on primary producer assemblages, with fertilization accelerating the growth of cyanobacteria-rich phytoplankton, while climate warming and hydrological management increased benthic diatoms over the last few decades.

2. Material and methods

2.1 Study site

Yilong Lake, located in southeast part of Yunnan Province, southwest China (Fig. 1), is a

1
2
3 115 large (~34 km²) shallow system with a maximum and average water depth of ~3.7 m and 2.9 m,
4
5 116 respectively (Table 1). Yilong Lake is currently hyper-eutrophic with elevated concentrations of
6
7 117 total phosphorus (TP; ~120 µg/L), total nitrogen (TN; ~7.7 mg/L) and Chlorophyll-a (Chl-a;
8
9 118 ~215 µg/L). The catchment is strongly influenced by Indian monsoons and experiences a mean
10
11 119 annual precipitation is 928.3 mm, a mean annual air temperature of ~18 °C (Fig. 2) and an
12
13 120 average insolation of 2,300 hours/year (Meteorology station of Mengzi County;
14
15 121 <http://cmdp.ncc.cma.gov.cn/cn/index.htm>). Bedrock within the Yilong watershed is characterized
16
17 122 by limestone and sandstone due to its Karst geology. The catchment vegetation is composed
18
19 123 mainly of Yunnan pine (*Pinus yunnanensis*) and mixed deciduous species, with a forest cover of
20
21 124 ~34.2%.

22
23 125 Currently, Yilong Lake is a semi-closed system, with a hydrological residence time of ~2.4
24
25 126 years (Li et al., 2015). However, Yilong Lake has been modified by both anthropogenic and
26
27 127 climate forcing since the 1950s (Fig. 2). The main inflow of Yilong Lake is the Chenghe River,
28
29 128 located at the northwest of the basin, which flows through the largest town within the catchment,
30
31 129 Shiping (Fig.1). Lake area dynamics derived from monitoring data (Jin, 1995) and Landsat
32
33 130 satellite imagery (Wu et al., 2016) document a consistent pattern of pronounced shrinking and
34
35 131 reduced depth during 1952-1982 and 2009-2013 (Fig. 2). For example, dredging and damming of
36
37 132 the outflowing Haikou River for electricity generation led to a decline in lake level by ~2 m from
38
39 133 1952 (maximum depth ~7.0 m) to 1953 (~5.0 m), and a further drop of 0.7 m in 1960 (Yang and
40
41 134 Li, 2010). Lake area further reduced in 1971 with the construction of an underground tunnel for
42
43 135 lake reclamation, which lead to a decline in maximum depth from 6.0 m in 1970 to 4.3 m in late
44
45 136 1971 (Fig. 2), before the tunnel was abandoned in 1978 (Cui and Zhai, 2006). With extremely
46
47 137 low precipitation, the maximum water depth in Yilong Lake had declined further to < 1 m in
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

删除的内容: and depth

删除的内容: was

1
2
3 140 spring of 1981, and then fluctuated between 3.6-5.5 m due to climatic and anthropogenic effects,
4
5 141 including a period of extreme drought during 2008-2012 (Zhao, 2013).

6 142 With agricultural expansion and catchment development starting in ~1955, non-point source
7
8 143 pollution has become the dominant source of nutrient loading to the lake, despite the substantial
9
10 144 input of urban effluent (Zhao, 2013; Zhao et al., 2013). By 2007, annual TP and TN influx from
11
12 145 farmland surface runoff accounted for 59% and 52% of total nutrient inputs, respectively (Wang
13
14 146 and Wang, 2008). Furthermore, farming of fish within cages was initiated in 1985 and
15 147 experienced an accelerating growth until 1997 (Shi and Sun, 2005), after which this practice was
16
17 148 officially forbidden in Yilong Lake. During its period of operation, cage farming extensively
18
19 149 harvested aquatic vegetation within the lake to feed herbivorous grass carp (*Ctenopharyngodon*
20
21 150 *idellus*) (Chou and Xia, 1998), resulting in a rapid loss of macrophyte coverage from 95.0% in
22 151 1982 to 27.3% in 1992 (Table 2).
23
24 152
25

26 153 2.2 Sample collection and sediment dating

27
28 154 A 34-cm sediment core was collected from Yilong Lake in July 2013 from the deep basin
29
30 155 (23°39'53"N, 102°36'15"E) using a Renberg gravity corer (Fig. 1). The sediment core was
31 156 sectioned immediately at 0.5-cm intervals for the top 5 cm and at 1-cm intervals for depths
32
33 157 below 5 cm. Samples were kept dark and frozen until subsampling for pigment analyses within
34
35 158 24 h. The remaining sediments were freeze-dried and stored in the dark for subsequent analyses.

36
37 159 Sediment chronology was estimated based on ²¹⁰Pb activities in sediment core samples.
38
39 160 Around 3-5 g of freeze-dried sediments were used for measuring the radio-activities of ²¹⁰Pb and
40 161 ¹³⁷Cs in each sample using a Canberra well-detector gamma spectrometer (GCW 3023). The
41
42 162 sediment chronology sequence was established with the constant rate of supply (CRS) model
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

删除的内容: of

删除的内容: analysis of

using the stratigraphic profile of unsupported ^{210}Pb activities (Appleby, 2001).

2.3 Sediment physical and geochemical analyses

Grain-size distribution of sediment samples was determined using a Mastersizer 2000 laser analyzer (Malvern Instruments Limited, Malvern, UK). Briefly, ~0.3 g freeze-dried and disaggregated sediment from each sample was pre-treated with 10-20 ml of 10% H_2O_2 to remove organic matter and then heated in 10 ml of 10% aqueous HCl to remove carbonates. Thereafter, ~100 ml of deionized water was added and the sample solution was kept for 24 h to remove acidic ions. The sample residue was dispersed with 10 ml of 0.05 mol/L $(\text{NaPO}_3)_6$ on an ultrasonic vibrator for 10 min prior instrumental analysis.

Organic matter (OM) content was estimated for bulk sediments using the method of loss-on-ignition (% LOI_{550}) at 550 °C following the standard method (Heiri et al., 2001). Stable carbon (C) and nitrogen (N) isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were conducted following the standard methods of Meyer (2001). Briefly, ~10 mg of homogenized, dried bulk sediment was combusted in a tin capsule at 960 °C in a FLASH 2000 elemental analyzer linked to a continuous isotope ratio flow mass spectrometer (MAT-253, Thermo Scientific, USA). C and N isotope ratios are expressed as per mil (‰) relative to Vienna Pee Dee Belemnite (VPDB) and atmospheric N_2 (AIR), respectively. Relative contents of C and N (% dry mass) and the mass ratio of carbon to nitrogen (C:N) were also measured. The analytical precision was $< \pm 0.1\text{‰}$ for isotopic data and $< \pm 1\%$ for elemental data, respectively.

2.4 Pigment analyses

All pigments were measured following procedures described in Saulnier-Talbot et al. (2014)

using high performance liquid chromatography (HPLC) at the Gregory-Eaves Lab of McGill University, Canada. Briefly, sediments were freeze-dried and pigments were extracted in acetone (at -20 °C for 24 h) before the extract solution was centrifuged and the supernatant filtered through a PTFE (0.2-µm pore) filter and placed in vials for pigment analysis. The analysis was conducted using a Waters HPLC system (model 600/626) equipped with a Waters Photodiode Array (model 2996) and a Waters 2475 Multi-wavelength fluorescence detector. The HPLC was calibrated previously using external standards from DHI (Denmark). Individual compounds were tentatively identified using a combination of chromatographic position (polarity) and spectral characteristics relative to authentic samples. Pigment concentrations were expressed as ng pigment/g organic matter, determined by mass loss on ignition at 550 °C (LOI₅₅₀) for 1 h. Cyanobacteria were represented by the carotenoid zeaxanthin and echinenone, while algal groups included compounds ubiquitous in phototrophs (chlorophyll-*a*, β-carotene, pheophytin-*a*), chlorophytes (lutein), cryptophytes (alloxanthin), and mainly diatoms (diatoxanthin). As Yilong Lake is a large system with documented hydrological fluctuations, we used the mass ratio of Chl-*a*:pheophytin to evaluate historical changes in pigment preservation and the importance of benthic phototrophs (Cuddington and Leavitt, 1999; Leavitt and Hodgson, 2001).

2.5 Diatom analysis

Fossil diatoms were prepared for enumeration following the standard methods of Battarbee et al. (2001). Briefly, hydrochloric acid (10%) was added for the removal of carbonates before processing, while 30% hydrogen peroxide was added at ~80 °C to remove organic material. A portion of the digested slurry was dried on cover slips and mounted with Naphrax[®]. Diatom identification and enumeration were performed under oil immersion at 1,000× magnification

1
2
3 211 using a Leica DM 2500 microscope with phase contrast. A minimum of 400 valves was counted
4
5 212 for each sample. Diatom taxonomy mainly followed Krammer and Lange-Bertalot (1986-1991).
6
7 213 The community data were expressed as percent abundance of the total diatom sum in each
8
9 214 sample. Diatom species were categorized into planktonic and benthic groups following their
10
11 215 habitat preferences based on previous studies (e.g., Round et al., 2007).
12
13 216

13 217 2.6 Numerical methods

15 218 The major zones for the biostratigraphy were identified through the analyses of constrained
16
17 219 incremental sum of squares (CONISS), while a broken-stick model was used to test for the
18
19 220 significance of each break. We conducted ordination analyses to define the historical trajectories
20
21 221 of pigment and diatom changes. Preliminary investigation with Detrended Correspondence
22
23 222 Analysis (DCA) of pigment and diatom assemblages revealed short gradient lengths of 0.68 and
24
25 223 1.76 SD, respectively, indicating that pigments and diatom taxa responded in a linear fashion to
26
27 224 environmental gradients (ter Braak and Prentice, 1988). Subsequently, Principal Components
28
29 225 Analysis (PCA) was applied to extract the major direction of variation in both the diatom species
30
31 226 compositions and fossil pigment assemblages. Pigment PCA used only the most chemically-
32
33 227 stable pigments as suggested by Leavitt and Hodgson (2001) and Moorhouse et al. (2014).
34
35 228 Redundancy Analysis (RDA) was performed subsequently to explore the relationship between
36
37 229 biological data and nine environmental predictor variables (Hall and Leavitt, 1999; ter Braak and
38
39 230 Šmilauer, 2002). Specifically, these environmental variables included grain size components,
40
41 231 $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C:N ratio, total carbon and total nitrogen measured from bulk sediments (Table 3).
42
43 232 Monte Carlo analysis with 999 permutations was used to test the significance of each predictor
44
45 233 variable in partial RDA. Only variables with a P-value <0.05 were retained for the minimum
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

adequate model (ter Braak and Šmilauer, 2002). In addition, environmental variables with a variation inflation factor (VIF) of > 20 were excluded due to their strong co-linearity with other variables.

Multiple regression with forward selection and variation partitioning analysis were used to identify a minimum subset of significant explanatory variables for the time window of ~1903-2013 (ter Braak and Šmilauer, 2002). We also performed RDA and variation partitioning analyses for the time window of ~1953-2013, the period with the most complete meteorological and catchment data, including air temperature, precipitation, wind speed, and catchment population. Finally, we conducted a third variation partitioning exercise for lake-water Chl-*a* for the monitoring period 1992-2015 using six environmental variables (temperature, precipitation, wind speed, TP, TN and lake area) to predict recent changes in water quality. In all cases, we transformed environmental predictor time series for normalization and square-root transformed diatom relative abundance data with rare species down-weighted (Lepš and Šmilauer, 2003). All the data analyses were performed using the R packages *vegan* (Oksanen et al., 2015) and *rioja* (Juggins, 2015).

3. Results

3.1 Archived data

Meteorological data generally show a warming trajectory with marked variation in precipitation during the last six decades. The annual mean temperature shows a warming trend, increasing from an average ($\pm$ SD) of 18.5 ± 0.3 °C during 1951-1990 to a mean of 19.2 ± 0.6 °C for the last two decades (Fig. 2a). The annual precipitation displays no clear trend since 1951, but shows reduced values (< 600 mm) during the intervals of 1961-1962, 1979-1980, 1987-1989,

- 删除的内容: ed
- 删除的内容: ($\pm$ SD)
- 删除的内容: ed
- 删除的内容: n
- 删除的内容: increasing
- 删除的内容: with a mean of 19.2 ± 0.6 °C for the last two decades, but was is relatively stable
- 删除的内容: with an average of 18.5 ± 0.3 °C
- 删除的内容: ed
- 删除的内容: ed

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

2004-2005 and 2010-2012. Annual wind speed (Fig. 2b) is relatively stable during 1951-1995 (3.4 ± 0.3 m/s), but declines to 2.3 ± 0.3 m/s by 2010. Lake level and surface area both decrease over the last six decades, with abrupt drops in the mid-1950s, late-1970s and during 2009-2013 (Fig. 2c). Meanwhile, the total catchment population doubles during the last six decades (Fig. 2b).

Variables related to lake primary production and water quality indicate a substantial increase in primary producer abundance over the historical record (Fig. 2). The lake-water concentrations of TN, TP and Chl-*a* have experienced a rapid increase concomitant with a decline in transparency from > 2 m to < 1 m during 1985-1997 (Fig. 2e) and a rapid loss of submerged aquatic vegetation (Table 2). For example, the mean concentration of measured total phosphorus (TP) and total nitrogen (TN) show an undulating pattern since late 1980s, but a clear tendency to nutrient enrichment during ~2009-2012 (Fig. 2d). From the mid-1980s to the mid-1990s, TP and TN levels are elevated with a mean (± SD) of 75.2 ± 21.2 µg/L and 5.0 ± 0.6 mg/L, respectively. Nutrient content is relatively stable during the 2000s (TP = 54.0 µg/L, TN = 1.8 mg/L), before increasing after ~2009 (Fig. 2d). In general TP and TN increase at similar rates ($r = 0.68$, $p < 0.001$, $n = 21$), with a N:P mass ratio consistently above 20 (or molar ratio of 44) since 1988 (Table 2).

Monitoring data show that Chl-*a* values are relatively high in the mid-1990s (ca. 100 µg/L), decline to minima (< 50 µg/L) for 15 years, then increase to historical maxima (> 150 µg/L) after ~2010 (Fig. 2e). At the sample time, measured phytoplankton density increase gradually from 8.41×10⁶ cells/L in 1957 to 193.21×10⁶ cells/L in 1992, and thereafter from < 100×10⁶ cells/L during 1993-2008 to > 200×10⁶ cells/L after 2008 (Table 2). During this period, phytoplankton community composition gradually shifts from predominantly Bacillariophyta in 1957 to Chlorophyta in 1988 and 1993, and, more recently, to Cyanobacteria (Table 2). Consistent with

- 删除的内容: wa
- 删除的内容: d
- 删除的内容: d
- 删除的内容: ed
- 删除的内容: d
- 删除的内容: s
- 删除的内容: were
- 删除的内容: was
- 删除的内容: d
- 删除的内容: suggests
- 删除的内容: were
- 删除的内容: d
- 删除的内容: d
- 删除的内容: s
- 删除的内容: ed

1
2
3 306 the fluctuation in nutrients and phytoplankton, water transparency decreases~~s~~ from > 1.8 m during
4 307 the early 1980s to < 1 m in 2007 and then show~~s~~ a swift drop from > 1 m in 2008-2009 to ~0.2 m
5 308 since 2010 (Fig. 2e).
6
7
8 309
9

删除的内容: d

删除的内容: ed

10 310 3.2 Sediment chronology

11
12 311 The unsupported ^{210}Pb radioactivity profile declined with increasing core depth between 10
13 312 and ~30 cm (Fig. 3a), suggesting that the ^{210}Pb -based CRS model was applicable in constructing
14 313 the chronological profile. Sediment samples above the ~7 cm depth showed a uniform ^{210}Pb
15 314 activity, possibly reflecting sediment mixing or variation in sediment focusing due to changes in
16 315 basin morphology (Fig. 2c). In lakes where mixing has occurred, the ^{210}Pb dates covering 10-
17 316 year accumulation, as is the case for this sediment core (Fig. 3b), often provide a maximum error
18 317 of less than 2 years (Appleby, 2001). Increased autochthonous production which would dilute the
19 318 atmospheric ^{210}Pb fallout may also cause a decrease in its activity as observed in surface
20 319 sediments above ~7 cm (Fig. 3a). The depth profile of ^{137}Cs showed no obvious peak (Fig. 3a),
21 320 reflecting a possible combination of sediment mixing and post-deposition mobility (e.g., Wieland
22 321 et al., 1993; Sommerfield and Nittrouer, 1999). Overall, radio-isotope profiles and CRS
23 322 calculations suggest a recent acceleration in the rate of sediment accumulation (Fig. 3b).
24
25
26
27
28
29
30
31
32

33 323 34 35 324 3.3 History of lake environmental change

36
37 325 Grain size data showed modest changes over the length of the core (Fig. 4), with a decline in
38 326 sand particles and the occurrence of abrupt fluctuations in median grain size during the last
39 327 century. For example, the median size varied around a mean (± 1 SD) of $4.8 \pm 1.4 \mu\text{m}$, with the
40 328 clay ($< 2 \mu\text{m}$) and sand ($> 63 \mu\text{m}$) components varying in the range of 7.2-30.0% (mean = 25.8%)
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

and 0.03-7.7% (mean = 1.7%), respectively. Both the silt composition and median grain size spiked around the depths of 23.5, 17.5, 7.5 and 3.25 cm (Fig. 4).

Stable sedimentary TN content in the early 20th century (3.6 ± 0.2 mg/g) gave way to an increase since ~1970, with a recent mean of 6.7 ± 0.8 mg/g (Fig. 4). The concentrations of both total carbon (TC) and organic matter (LOI₅₅₀) displayed similar trajectories suggesting that lake production increased after the late-1960s. The mass ratio of C/N in bulk sediments declined from historical values of ~16 to modern ratios of ~11, consistent with an increasing input of organic matter derived from algae.

The $\delta^{15}\text{N}$ signal of bulk sediments remained stable around the near-atmospheric value (~0‰) until the mid-1960s, at which time it increased dramatically up to a maximum value of ~4.5‰ in surface sediments. Correspondingly, the bulk sediment $\delta^{13}\text{C}$ signal declined from around -14‰ to nearly -16‰ over the 20th century, with a marked decline after ~1960. These relatively enriched values are characteristic of lakes with high carbonate content in sediments (Jarvis et al., 2006), and were correlated inversely with the total algal abundance as measured by the total phototroph biomarker, β -carotene ($r = -0.92$, $P < 0.001$).

3.4 Pigment variations

Analysis of sedimentary pigments suggested a progressive increase in autotrophic production during the 20th century with a particularly marked upturn starting in the mid-1960s for most of the major taxonomic groups (Fig. 5a). The concentrations of many pigment biomarkers were low and stable prior to the mid 20th century (zone I), including chemically-stable (pheophytin-*a*, β -carotene) and labile (Chl-*a*) indices of total phototrophic abundance, as well as pigments from bloom-forming cyanobacteria (zeaxanthin, echinenone). During ~1965-

2004 (zone II), all pigment components increased significantly (Fig. 5a), with a greater than three-fold increase in concentrations of ubiquitous biomarkers of total phototrophic abundance (β -carotene, pheophytin-*a*) and bloom-forming chlorophytes (lutein) and cyanobacteria (zeaxanthin, echinenone). Fossil pigment concentrations were also generally higher after ~2004 (zone III, above ~8cm), as identified by the CONISS results (Fig. 5a). During this later interval, the ratio of chlorophyll-*a*/pheophytin-*a* increased markedly, suggesting that preservation conditions have been relatively constant throughout the core except for zone III (Fig. 5a). Overall, historical changes in concentrations of the major pigments were highly correlated with increased content of TN, including compounds from total algae (i.e. Chl-*a*; $r = 0.900$, $P < 0.001$, $n = 37$), cyanobacteria (i.e. zeaxanthin; $r = 0.918$, $P < 0.001$) and diatoms (diatoxanthin; $r = 0.864$, $P < 0.001$).

The Principal Components Analysis (PCA) results further revealed only one significant axis for algal abundance data, which accounted for 98.9% of the variation in biomarker assemblages (Fig. 6a). PCA axis 1 showed a significant relationship with TN ($r = 0.903$, $P < 0.001$) during the last century. In addition, this axis was correlated significantly with sand content ($r = 0.226$, $P < 0.01$) over the last century, as well as measured air temperature ($r = 0.313$, $P < 0.001$) and wind speed ($r = 0.406$, $P < 0.01$) during ~1953-2013.

3.5 Diatom compositional changes

A total of 62 diatom taxa were identified in sediment samples, including 23 taxa with a maximum abundance of $\geq 1\%$, 16 of which occurred with a relative abundance of $\geq 2\%$ in at least one sample. Diatom assemblages were composed mainly of benthic species with strong variations amongst taxa over the 20th century (Fig. 5b). For example, *Staurosira construens* (a

1
2
3 377 range of 4.2-51.0%), *S. berolinensis* (6.5-44.6%) and *Achnanthisidium minutissimum* (0-12.1%) all
4 378 exhibited wide variation in relative abundance. Benthic diatoms were generally **predominant** (>
5 379 50% relative abundance) across the core except in the depths of 17.5-9.5 cm (~1978-2000), at
6 380 which time planktonic and tychoplanktonic diatoms became more important within the
7
8 381 assemblage (~50-80% of total frustules). Planktonic diatoms mainly included *Fragilaria*
9
10 382 *crotonensis* (1.2-52.4%), while tychoplanktonic taxa were composed of *Aulacoseira subarctica*
11
12 383 (1.6-25.1%), *A. granulata* (0.7-14.7%), and *A. ambigua* (1.0-8.2%).
13
14

删除的内容: a

删除的内容: paramount

15 384 Similar to the pigment changes, diatom assemblages were characterized by two significant
16
17 385 shifts (Fig. 5b). During the period of ~1903-1973 (zone I), the community was composed of
18
19 386 both benthic taxa, such as *S. berolinensis* (mean = 17.7%) and *S. construens* (16.8%), and several
20
21 387 planktonic taxa such as *F. crotonensis* (15.1%) and *A. subarctica* (13.2%). After ~1973 (zone II),
22
23 388 there was a significant community shift towards more eutrophic taxa and an associated decrease
24 389 in small benthic *Fragilaria sensu lato* taxa, coupled with an increase in *F. crotonensis* to over 30%
25
26 390 and the disappearance of *S. leptostauron*. After ~2005 (zone III), the community was
27
28 391 characterized by the replacement of planktonic taxa such as *F. crotonensis* and *Aulacoseira* spp.
29
30 392 (< 10%) by small benthic taxa such as *S. construens* and *S. berolinensis* (mean = 40.8% and
31 393 28.3%, respectively).
32

带格式的: 字体:斜体

33 394 Principal components analysis (PCA) of diatom data showed that the first two PCA axes
34
35 395 were statistically significant based on the broken-stick model, accounting for 51.5% and 16.8%
36
37 396 of the total variance, respectively (Fig. 6b). Planktonic species (such as *F. crotonensis*, *A.*
38
39 397 *subarctica*, *A. granulata*) were strongly associated with the left side of axis 1, with several
40
41 398 benthic species such as *S. construens* and *S. berolinensis* sitting at the opposite end of this axis.
42 399 PC axis 1 further showed a significant correlation with the proportion of benthic diatoms ($r =$
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

0.953, $P < 0.001$), as well as the sand component ($r = 0.571$, $P < 0.001$) and TN ($r = 0.548$, $P < 0.001$). In contrast, benthic taxa such as *S. pinnata* and *S. leptostauron* were more abundant during the period of 1903-1973 (zone I) and were strongly associated with PCA axis 2, which itself displayed a significant correlation with TN ($r = 0.606$, $P < 0.001$). Only PCA axis 1 showed a significant relationship between diatom composition and air temperature ($r = 0.658$, $P < 0.001$) during the ~1953-2013 interval.

3.6 Identifying limnological drivers for algal changes

The Redundancy Analysis (RDA) suggested that nutrient and hydrological parameters played independent roles in shaping the temporal changes in primary producer assemblages of Yilong Lake (Fig. 7). The measured physio-chemical variables collectively accounted for the majority of the changes in pigments (i.e. $> 90\%$), but less than half of the historical variation in diatom assemblages (Table 3). Specifically, nutrients (i.e. TN) were found to be the most significant forces in driving the changes of both pigments and diatoms since ~1903. The nutrient-associated RDA axis 1 accounted for 92.0% of the total variance for pigment data but smaller amount for diatom data (42.3%; Fig. 7). Over a shorter time window of ~1953-2013 (Table 3), nutrient variables remained as the predominant factor in driving pigment changes ($> 90\%$) but structured diatom assemblages to a much lesser degree ($< 15\%$). In contrast, the grain-size proxies played an insignificant role in driving both indicators over the last century; however, the sand content was identified as a significant factor over the last six decades and accounted for $\geq 20\%$ of the total variance for both pigments and diatoms. Temperature also displayed a significant impact on both algal indicators since ~1953 (28.8% and 23.3%, respectively), but wind speed was found to be a major driver only for pigments (38.4%; Table 3).

The variance partitioning results further showed that lake-water TN concentration, but not TP, was a significant driver, accounting for 21.7% of the change in water-column Chl-*a* for the monitoring period of 1992-2015 (Fig. 8b). Furthermore, hydrologic fluctuation inferred from changes in lake area independently explained 28.8% of the total variance in lake-water Chl-*a*, with a high proportion shared with nutrients (19.5%) over the monitoring period. Likewise, sediment TN alone explained 24.6% of the total variance in sedimentary Chl-*a*, while the variation of sediment sand content alone accounted for 5.0% of the total variance in Chl-*a* with a strong interaction with nutrients (43.0%) during the last century (Fig. 8a).

删除的内容: identified as a significant driver in

Over the whole core, sedimentary TN collectively accounted for a large proportion of the total variance for both algal pigments and diatom assemblages (i.e. 90.0% and 40.6%, respectively; Fig. 8c, e). However, the nutrient effect was found to be insignificant for diatom assemblages during ~1953-2013 (Fig. 8f), whereas it accounted for the majority of the total variance in phototrophic abundance over the same time window (82.4%; Fig. 8d). In comparison, the relative importance of hydrological fluctuation (as inferred from sand content) for diatom assemblages increased from 4.7% (Table 3) over the core to 27.3% during ~1953-2013 (Fig. 8f), the period when temperature was also found to be a significant driver (8.5%) and interacted moderately with hydrological fluctuation (14.8%; Fig. 8f). From ~1953, both wind speed and hydrological fluctuation showed a strong influence on algal production, but mostly through its interaction with nutrients such as TN (i.e. 35.3% and 14.0%, respectively; Fig. 8d).

删除的内容: impact

4. Discussion

Our multi-proxy sedimentary records revealed a clear trajectory of phototrophic changes in response to a combination of nutrient enrichment and hydrologic fluctuation in Yilong Lake

1
2
3 450 during the last century. The sedimentary record of fossil pigments showed a dramatic increase
4
5 451 concomitant with nutrient enrichment, while more recent changes in production appear to
6
7 452 correspond to declining water level and wind speed. Meanwhile, the sediment records of grain
8
9 453 size (e.g. sand content and median size) documented the role of hydrological regulation and
10
11 454 extreme droughts on lake levels, which affected algal production and diatom assemblages over
12
13 455 time. Diatom community composition showed two significant shifts during the past century; with
14
15 456 a gradual replacement of oligotrophic taxa by eutrophic species since ~1973, and a distinct
16
17 457 increase in small benthic *Fragilaria sensu lato* taxa in after ~2005. In general, diatom
18
19 458 community composition was structured mainly by nutrient enrichment over the 20th century,
20
21 459 although effects of hydrologic fluctuations appear to have been more pronounced in the past two
22
23 460 decades.

带格式的: 字体:斜体

24 462 4.1 Lake eutrophication and phototrophic responses

25
26 463 Our sedimentary records of lake eutrophication were highly consistent with patterns
27
28 464 recorded from monitoring data for Yilong Lake. As the human population in the catchment began
29
30 465 to increase in the 1960s, sediment TN values steadily increased, with a concomitant decrease in
31
32 466 bulk sediment C/N ratios and $\delta^{13}\text{C}$ values after the 1960s (Fig. 4), patterns that are consistent
33
34 467 with increased input of nutrients and autochthonous C sources (Meyers and Ishiwatari, 1993).
35
36 468 For example, an annual input of 341 and 40 tons of TN and TP was estimated for the early 1990s
37
38 469 (Chou and Xia, 1998). The archival data showed that the content of lake-water nutrients and Chl-
39
40 470 *a* generally increased concurrent with a decline in lake-water transparency during 1985-1997 and
41
42 471 2009-2013 (Fig. 2). The decline of the bulk sediment carbon isotopic signal, coupled with an
43
44 472 increase in cyanobacteria, suggested a shift of carbon source and transfer towards a planktonic

删除的内容: change

删除的内容: shift

1
2
3 475 pathway typical of eutrophic subtropical (Xu et al., 2014) and temperate lakes (McGowan et al.,
4
5 476 2005). The rise in $\delta^{15}\text{N}$ is also consistent with the release of isotopically-enriched pollutants
6
7 477 arising from urban (Leavitt et al., 2006) and agricultural sources (Bunting et al., 2007), while the
8 478 depletion of $\delta^{15}\text{N}$ prior to the mid-1960s may be linked with deposition of atmospheric nitrogen
9
10 479 (Kang et al., 2019) and/or a paramount importance in fixed nitrogen within the lake (Hayes et al.,
11
12 480 2019).

13 481 Concentrations of fossils from total algae and major algal components increased
14
15 482 dramatically from ~1965 in a pattern similar to that observed in other lakes impacted by
16
17 483 agriculture (Bunting et al., 2007; Moorhouse et al., 2014) and urbanization (Leavitt et al., 2006).
18
19 484 Similar long-term increases in primary producer abundance as a result of intensified catchment
20
21 485 development have been recorded in other lakes within this study region (Wu et al., 2002; Shi and
22
23 486 Sun, 2005), as well as those from eastern China (Xu et al., 2014; Deng et al., 2016). Furthermore,
24 487 these changes are generally consistent with a 100-fold increase in the cell density of monitored
25
26 488 lake-water phytoplankton during the last few decades (Table 2). Similarly, monitoring programs
27
28 489 within Yilong Lake reveal that the dominant phytoplankton by cell density gradually shifted from
29
30 490 Bacillariophyta in 1957 to positively-buoyant (and more easily sampled) Cyanobacteria since
31 491 1997. The moderate concentration for cyanobacterial pigments, such as zeaxanthin, prior to
32
33 492 ~1965 was consistent with the presence of cyanobacterial blooms of *Microcystis aeruginosa* in
34
35 493 1957 (Ley et al., 1963).

36
37 494 Nutrient input also led to significant shifts in the diatom community, although effects of
38
39 495 fertilization appear to have declined in the last decade. For example, the period of ~1973-1998
40 496 was characterized by a rapid enrichment in TN and the predominance of *F. crotonensis*, a
41
42 497 planktonic species often found in nutrient-enriched lakes (Bennion et al., 2009; Hu et al., 2012).
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

删除的内容: has

1
2
3 499 This taxon declined during the period of 1998-2008, when lake-water nutrients and algal
4
5 500 production were lower (Fig. 2), and there existed a moderate drop in sediment pigment
6
7 501 concentrations (e.g. zeaxanthin and lutein). Since ~1998, the abundance of small benthic
8
9 502 *Fragilaria sensu lato* taxa increased significantly at the expense of planktonic diatoms in Yilong
10 503 Lake, suggesting a decreasing role of nutrients in driving diatom community reorganization over
11
12 504 the last decade. Finally, from the late 2000s, analyses of monitoring and sediment data suggest
13
14 505 that cyanobacterial abundance has increased relative to that of diatoms. Similarly, increasing
15 506 dominance of cyanobacteria has been well recorded in regional studies of temperate lakes under
16
17 507 nutrient-enriched conditions (Taranu et al., 2015).

20 21 509 4.2 Hydrological and climatic impacts on algae

22 510 Analyses of sediment grain size distribution, together with archival environmental data,
23
24 511 provide evidence for that hydrologic fluctuations served as a significant driver of phototrophic
25
26 512 community change. Specifically, the hydrologic fluctuation inferred from changes in sediment
27
28 513 sand content explained a large proportion of the variance in sediment Chl-*a* pigments, while
29
30 514 variation in lake area (another hydrological proxy) was a strong predictor of changes in lake-
31 515 water Chl-*a* concentration (Fig. 8). A moderate decrease of sediment sand content starting from
32
33 516 the 1950s corresponds to the documented history of hydrological regulation and decreased water
34
35 517 levels (Cui and Zhai, 2006). Lake regulation often decreases the natural variation of water level
36
37 518 and lake turbulence (Menking, 1997; Digerfeldt et al., 2000), resulting in a gradual decrease in
38
39 519 the sand component over time (Wang et al., 2019). Similarly, the spikes in median grain size
40 520 were synchronous with several major events of extreme drought over the last six decades (Figs.
41
42 521 2a and 4). Lake regulation can often amplify the nutrient effect and promote algae production by

带格式的: 字体:斜体

1
2
3 522 concentrating nutrients (Serruya and Pollinger, 1977; Peršić et al., 2007), enhancing nutrient
4
5 523 retention (Maavara et al., 2015) and reducing water turnover (Posch et al., 2012). Accordingly,
6
7 524 our results showed a pronounced increase in the content of sediment nutrient and pigment
8
9 525 concentrations starting from ~1953 (Fig. 4), as well as a significant interaction between
10
11 526 hydrologic fluctuation and nutrients (Fig. 8) at this time. These patterns are consistent with
12
13 527 earlier studies of other hydrologically-managed and drought-sensitive shallow lakes based on
14
15 528 monitoring data (Yang and Lu, 2014) and sediment records (Chen et al., 2011).

15 529 Previous surveys show that phototrophic response to nutrient concentrations within lakes can
16
17 530 be modulated by both warming (Vogt et al. 2018) and extreme climate (Anderson, 2000; Berthon
18
19 531 et al., 2014). Recent warming during the last two decades has been identified as an important
20
21 532 factor regulating diatom compositional shift in this study region (Chen et al., 2014a), as well as
22
23 533 in many parts of the world (Winder and Hunter, 2008; Finkel et al., 2009; Rühland et al., 2015).
24
25 534 The stability of water column can be further enhanced by a falling wind speed (i.e. < 3 m/s)
26
27 535 during the last two decades, which often favors the bloom of buoyant cyanobacteria such as
28
29 536 *Microcystis* in eutrophic shallow lakes (Zhang et al., 2012). The most recent drought, occurring
30
31 537 during 2009-2012, reduced lake levels by ~2.3m with a loss of ~0.67 billion m³ of water (Wang
32
33 538 et al., 2014). Meanwhile, the shift from planktonic diatoms to small benthic *Fragilaria sensu lato*
34
35 539 taxa indicated the expansion of littoral taxa. This can result from warming-associated
36
37 540 hydrodynamic change (i.e. increased evaporation; Byllaardt and Cyr, 2011), and the loss of lake
38
39 541 volume which was caused by severe droughts and possibly amplified by elevated water use due
40
41 542 to an increased population size (Fig. 2 and Table 2).

40 543 In 2010, the dominant Cyanobacteria (*Microcystis*) was replaced by *Cylindrospermopsis*
41
42 544 *raciborskii* (Table 2), a species that can tolerate varying N:P ratios (Barica et al., 1980) as well as
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1
2
3 545 extreme droughts (Marc et al., 2000). Similarly, there was a clear loss of *Aulacoseira* spp. during
4
5 546 the last decade, a taxon which had been consistently subdominant in diatom assemblages over
6
7 547 much of the core (Fig. 5b). *Aulacoseira* taxa have a high siliceous content and are known to
8
9 548 proliferate in frequently-mixed waters that favor resuspension of these heavy taxa (Reynolds,
10 549 1987; Chen et al., 2011). This trend was synchronous with the recent decrease of wind speed,
11
12 550 that was widely observed across China and linked with the weakening east Asian monsoon (Xu
13
14 551 et al., 2006). Therefore, changes in lake level and thermal stability may favor specific algae in
15 552 the context of regional warming (Wagner and Adrian, 2009; Romo et al., 2013).

删除的内容: dense

17 553 18 19 554 4.3 Heterogeneity in algal responses to multiple stressors

20
21 555 Despite pigment and diatom data exhibiting generally coherent shifts during the past
22
23 556 century (Fig. 4a, b), there exist key differences in the importance of nutrient supply to the
24 557 apparent production of individual photosynthetic groups. For example, the strong relationship
25
26 558 between sediment TN and cyanobacteria pigments agrees with the demonstrated ability of lake-
27
28 559 water TN to predict cyanobacteria abundance in temperate regions (Beaulieu et al., 2014) and the
29
30 560 positive response of primary producers to N influx (Leavitt et al., 2006; Bunting et al. 2007). N
31 561 supply to Yilong Lake may have limited algal growth early in the 20th century, when sedimentary
32
33 562 $\delta^{15}\text{N}$ was low and characteristic of fixed N_2 from diazotrophic cyanobacteria, and
34
35 563 disproportionately high P influx occurred with agricultural development in 1960s (Shiping
36
37 564 Yearbook, 2005), leading to a low N:P mass ratio of 12.9-14.4 (Fig. 2). Thereafter, this shallow
38
39 565 system was characterized by a consistently high N:P mass ratio (i.e. > 40) for the past two
40 566 decades (Table 2), suggesting that the content of P, coupled with increasing N influx, may have
41
42 567 impacted algal production through changing N:P ratio (Li et al., 2015). Later on, a rapid decrease
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1
2
3 569 of N:P mass ratio from > 80 to < 50 corresponded to a shift of dominant Cyanobacteria from
4
5 570 heterocystous diazotroph *Aphanizomenon flosaquae* in 1992 to non-nitrogen fixing *Microcystis*
6
7 571 *aeruginosa* in 1997 and 2008, respectively (Table 2). This pattern suggests that non-nitrogen
8
9 572 fixers can bloom with varying N:P ratios when there is sufficient P supply, as is found in other
10
11 573 large shallow lakes (Xie et al., 2003; Xu et al. 2010; Hayes et al., 2019).

删除的内容: the

12 574 Our comparative study highlights the increasing effects of hydrologic fluctuations and
13
14 575 regional climate variability on variation in phototrophs over the last few decades. Noticeably, an
15
16 576 increase in the lake-water Chl-*a* concentration and its sediment pigment is strongly linked with
17
18 577 hydrologic fluctuations over time (Fig. 8a, b). Even though the increased ratio of chlorophyll-
19
20 578 *a*/pheophytin-*a* (Fig. 5a) suggested an incomplete pigment degradation and preservation in
21
22 579 sediments during 2004-2013, the major pigment components generally display an increasing
23
24 580 trend of Chl-*a* and cyanobacteria concentrations that are comparable with lake-water surveys
25
26 581 (Fig. 2e and Table 2). Meanwhile, the benthic diatom percentage rose sharply as water column
27
28 582 depth declined during the last two decades, despite the concurrent decline in macrophyte
29
30 583 coverage (Table 2). The rapid rise in the cyanobacteria (zeaxanthin) pigments also suggests that
31
32 584 there was an increase in the growth of cyanobacteria at the expense of other algae as observed in
33
34 585 other shallow lakes (McGowan et al., 2005). Previous studies show that hydrologic fluctuation
35
36 586 could serve as a key driver of algae in nutrient-enriched shallow lakes through increasing benthic
37
38 587 production (Vadeboncoeur et al., 2003), or even overriding nutrients in structuring diatom
39
40 588 composition (Liu et al., 2017). More recently, water level drops may have exposed more benthic
41
42 589 habitats (e.g. mud and rocks) favoring small *Fragilaria sensu lato* taxa as is found in
43
44 590 neighboring shallow lakes (Liu et al., 2017; Kang et al., 2019). The diatom compositional change
45
46 591 is also broadly consistent with the finding that lake depth could play a significant role in
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

删除的内容: impact

删除的内容: of

删除的内容: s

删除的内容: or

带格式的: 字体:斜体

1
2
3 597 affecting biotic responses to climate change in polymictic lakes (Chen et al., 2014b). Therefore,
4
5 598 the role of nutrients was relatively truncated in driving diatom composition with hydrologic
6
7 599 modulation and warming climate, leading to a heterogeneous pattern in the algal changes.
8
9 600

10 601 **5. Conclusion**

11 602 Our lake sediment records reveal a ~~predominant~~ effect of nutrient enrichment on
12
13 603 phototrophic abundance in this shallow lake, as well as an increasing role of hydrological
14
15 604 variability during the past few decades. Although fossil pigments appear to record a history of
16
17 605 continuous fertilization, the replacement of eutrophic diatom species by small benthic taxa also
18
19 606 suggests that anthropogenic water regulation, extreme droughts and warming have an influence
20
21 607 on species composition. Such an interaction between nutrient and hydrological stressors is
22
23 608 increasingly recognized (Vogt et al. 2018) and should be fully considered for reliable
24
25 609 interpretation of paleoecological indicators and long-term ecosystem changes in shallow lakes.
26 610 Finally, this study highlights the necessity of using multiple indicators for tracking primary
27
28 611 production and phototrophic changes in shallow lakes. In particular, biological proxies (e.g.
29
30 612 diatoms and pigments) have been increasingly and successfully applied in sediment-based
31
32 613 studies to infer the temporal change of ecosystem structure in shallow systems, but they are often
33
34 614 applied singularly without a full consideration of the differences in their sensitivity to multiple
35 615 stressors for data interpretation which is evidenced in this work.

36 37 616 38 617 Acknowledgements

39
40 618 This work was supported by the National Key Research and Development Program of China
41
42 619 [grant number 2017YFA0605202], National Natural Science Foundation of China [grant number

删除的内容: paramount

带格式的: 左对齐

1
2
3 621 41171048, U1133601], and Ministry of Education of China [grant number 213034A]. PRL and
4
5 622 IGE were supported by the Canada Research Chair program. We are grateful to Huibin Lu and
6
7 623 Haibin Shi for their field work assistance, as well as Jiaoyuan Wang, Jianshuang Tao and
8
9 624 Wengang Kang for their constructive comments. Constructive comments provided by two
10 625 anonymous reviewers and editor are appreciated.

删除的内容:

删除的内容:

References

- Adrian R, O'Reilly CM, Zagarese H, Baines SB, Hessen DO, Keller W, Livingstone DM, Sommaruga R, Straile D, Donk EV, Weyhenmeyer GA, Winder M (2009) Lakes as sentinels of climate change. *Limnol Oceanogr* 54:2283-2297.
- Anderson JN (2000) Miniview: Diatoms, temperature and climatic change. *Eur J Phycol* 35:307-314.
- Appleby PG (2001) Chronostratigraphic techniques in recent sediments. In: Tracking environmental change using lake sediments. Volume 1: Basin analysis, coring and chronological techniques, (eds Smol JP, Birks HJB, Last WM) vol 1. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 171-203.
- Barica J, Kling HJ, Gibson J (1980) Experimental Manipulation of Algal Bloom Composition by Nitrogen Addition. *Can J Fish Aquat Sci* 37:1175-1183.
- Battarbee RW, Jones VJ, Flower RJ, Cameron NG, Bennion H (2001) Diatoms. In: Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial, Algal, and Siliceous Indicators (eds Smol JP, Birks HJB, Last WM) vol 3. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 155-201.
- Battarbee RW (2010) Foreword. In: Global Change Impacts on Mountain Lakes (eds Eggermont H, Kernan M, Martens K). *Hydrobiologia* 648:1-2.
- Beaulieu M, Pick F, Palmer M, Watson S, Winter J, Zurawell R, Gregory-Eaves I, Prairie Y (2014) Comparing predictive cyanobacterial models from temperate regions. *Can J Fish Aquat Sci* 71:1830-1839.
- Bennion H, Rawcliffe R, Clarke G, Clarke SJ, Davidson TA, Rose C, Rose N, Sayer CD, Turner S (2009) Using novel palaeolimnological techniques to define lake conservation objectives. Final Report to Natural England. <http://discovery.ucl.ac.uk/id/eprint/399621>.

1
2
3 651 Berthon V, Alric B, Rimet F, Perga M-E (2014) Sensitivity and responses of diatoms to climate
4
5 652 warming in lakes heavily influenced by humans. *Freshwater Biol* 59:1755-1767.
6
7 653 Brugam RB, McKeever K, Kolesa L (1998) A diatom-inferred water depth reconstruction for an
8 654 Upper Peninsula, Michigan, lake. *J Paleolimnol* 20:267-276.
9
10 655 Bunting L, Leavitt PR, Gibson CE, McGee EJ (2007) Degradation of water quality in Lough
11
12 656 Neagh, Northern Ireland, by diffuse nitrogen flux from a phosphorus-rich catchment. *Limnol*
13
14 657 *Oceanogr* 52:354-369.
15 658 Byllaardt JV, Cyr H (2011) Does a warmer lake mean smaller benthic algae? Evidence against
16
17 659 the importance of temperature-size relationships in natural systems. *Oikos* 120:162-169.
18
19 660 Carvalho L, Kirika A (2003) Changes in shallow lake functioning: response to climate change
20
21 661 and nutrient reduction. *Hydrobiologia* 506-509:789-796.
22 662 Chen C, Zhao L, Zhu C, Wang J, Jiang J, Yang S (2014a) Response of diatom community in
23
24 663 Lugu Lake (Yunnan-Guizhou Plateau, China) to climate change over the past century. *J*
25
26 664 *Paleolimnol* 51:357-373.
27
28 665 Chen G, Selbie DT, Griffiths K, Sweetman JN, Botrel M, Taranu ZE, Knops S, Bondy J,
29
30 666 Michelutti N, Smol JP, Gregory-Eaves I (2014b) Proximity to ice fields and lake depth as
31 667 modulators of paleoclimate records: a regional study from southwest Yukon, Canada. *J*
32
33 668 *Paleolimnol* 52:185-200.
34
35 669 Chen X, Yang X, Dong X, Liu E (2013) Environmental changes in Chaohu Lake (southeast,
36
37 670 China) since the mid 20th century: The interactive impacts of nutrients, hydrology and climate.
38
39 671 *Limnologica* 43:10-17.
40 672 Chen X, Yang X, Dong X, Liu Q (2011) Nutrient dynamics linked to hydrological condition and
41
42 673 anthropogenic nutrient loading in Chaohu Lake (southeast China). *Hydrobiologia* 661:223-234.
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1
2
3 674 Chou G, Xia F (1998) Enhancing Environmental Management Promotes Water Quality in Yilong
4
5 675 Lake. Yunnan Environ Sci 17:54-56.
6
6 676 Cuddington K, Leavitt PR (1999) An individual-based model of pigment flux in lakes:
7
8 677 implications for organic biogeochemistry and paleoecology. Can J Fish Aquat Sci 56:1964-1977.
9
10 678 Cui B, Zhai H (2006) Characteristics of wetland functional degradation and its ecological water
11
12 679 requirement for restoration in Yilong Lake of Yunnan Plateau. Chinese Sci Bull 51:127-135.
13
13 680 Dai A (2011) Drought under global warming: a review. Wiley Interdisciplinary Reviews: Clim
14
15 681 Change 2:45-65.
16
17 682 Deng J, Qin B, Sarvala J, Salmaso N, Zhu G, Ventelä A-M, Zhang Y, Gao G, Nurminen L,
18
19 683 Kirkkala T, Tarvainen M, Vuorio K (2016) Phytoplankton assemblages respond differently to
20
21 684 climate warming and eutrophication: A case study from Pyhäjärvi and Taihu. J Great Lakes Res
22
23 685 42:386-396.
24 686 Digerfeldt G, Olsson S, Sandgren P (2000) Reconstruction of lake-level changes in lake Xinias,
25
26 687 central Greece, during the last 40 000 years. Palaeogeogr Palaeoclimatol Palaeoecol 158:65-82.
27
28 688 Finkel ZV, Vaillancourt CJ, Irwin AJ, Reavie ED, Smol JP (2009) Environmental control of
29
30 689 diatom community size structure varies across aquatic ecosystems. Proc R Soc B 276:1627-1634.
31 690 Hall RI, Leavitt PR (1999) Effects of agriculture, urbanization, and climate on water quality in
32
33 691 the northern Great Plains. Limnol Oceanogr 44:739-756.
34
35 692 Hambright KD, Zohary T, Eckert W, Schwartz SS, Schelske CL, Laird KR, Leavitt PR (2008)
36
37 693 Exploitation and destabilization of a warm, freshwater ecosystem through engineered
38
39 694 hydrological change. Ecol Appl 18:1591-1603.

1
2
3 695 Hayes, NM, A Patoine, HA Haig, GL Simpson, VJ Swarbrick, E Wiik, PR Leavitt (2019) Spatial
4
5 696 and temporal variation in nitrogen fixation and its importance to phytoplankton in phosphorus-
6
6 697 rich lakes. *Freshwater Biol* 64: 269-283.
7
8 698 Heiri O, Lotter F, Lemcke G (2001) Loss on ignition as a method for estimating organic and
9
10 699 carbonate content in sediments: reproducibility and comparability of results. *J Paleolimnol*
11
12 700 25:101-110.
13
14 701 Hu Z, Li Y, Li S (2012) Spatial and temporal distributions of diatom communities and their
15 702 relationships with environmental factors in Lake Erhai. *J Lake Sci* 24:400-408.
16
17 703 Huisman J, Matthijs HCP, Visser PM (2005) *Harmful Cyanobacteria*. Springer-Verlag GmbH,
18
19 704 3:1-23.
20
21 705 IPCC (2013) Synthesis Report. Contribution of Working Groups I , II and III to the Fourth
22
23 706 Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva,
24
25 707 Switzerland.
26 708 Jarvis IAN, Gale AS, Jenkyns HC, Pearce MA (2006) Secular variation in Late Cretaceous
27
28 709 carbon isotopes: a new $\delta^{13}\text{C}$ carbonate reference curve for the Cenomanian-Campanian (99.6-
29
30 710 70.6 Ma). *Geol Mag* 143:561-608.
31
32 711 Jeppesen E, Søndergaard M, Jensen JP, Havens KE, Anneville O, Carvalho L, Coveney M,
33
34 712 Deneke R, Dokulil MT, Foy B, Gerdeaux D, Hampton SE, Hilt S, Kangur K, Köhler J, Lammens
35 713 E, Lauridsen TL, Manca M, Miracle M, Moss B, Nöges P, Persson G, Phillips G, Portielje R,
36
37 714 Romo S, Schelske CL, Straile D, Tatrai I, Willén E, Winder M (2005) Lake responses to reduced
38
39 715 nutrient loading-an analysis of contemporary long-term data from 35 case studies. *Freshwater*
40
41 716 *Biol* 50:1747-1771.Jin XC (1995) *China Lake Environment* (Volume 3). Haiyang Publishers,
42 717 China, pp 263-273.
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1
2
3 718 Jöhnk KD, Huisman JEF, Sharples J, Sommeijer BEN, Visser PM, Stroom JM (2008) Summer
4
5 719 heatwaves promote blooms of harmful cyanobacteria. *Global Change Biol* 14:495-512.
6
7 720 Juggins S (2015) rioja: Analysis of Quaternary Science Data (R package version 2.0-6. CRAN.
8 721 R-project.org/Package = rioja).
9
10 722 Kang W, Chen G, Wang J, Huang L, Wang L, Li R, Hu K, Liu Y, Tao J, Blais JM, Smol JP
11
12 723 (2019) Assessing the impact of long-term changes in climate and atmospheric deposition on a
13
14 724 shallow alpine lake from southeast Tibet. *Sci Total Environ* 650:713-724.
15 725 Krammer K, Lange-Bertalot H (1986-1991) Bacillariophyceae 1-4. In: *Susswasserflora von*
16
17 726 *Mitteleuropa*, Band 1-4 (eds Ettl H, Gerloff J, Heynig H, Mollenhauer D). Gustav Fischer Verlag,
18
19 727 Jena, Germany.
20
21 728 Lake SP (2011) *Drought and Aquatic Ecosystems Effects and Responses*. A John Wiley and
22
23 729 Sons, Ltd., Publication.
24 730 Leavitt PR, Hodgson DA (2001) Sedimentary pigments. In: *Tracking Environmental Change*
25
26 731 *Using Lake Sediments. Volume 3: Terrestrial, Algal, and Siliceous Indicators* (eds Smol JP, Birks
27
28 732 HJB, Last WM) vol 3. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 295-325.
29
30 733 Leavitt PR, Brock CS, Ebel C, Patoine A (2006) Landscape-scale effects of urban nitrogen on a
31
32 734 chain of freshwater lakes in central North America. *Limnol Oceanogr* 51:2262-2277. Lepš J,
33 735 Šmilauer P (2003) *Multivariate analysis of ecological data using CANOCO*. Cambridge
34
35 736 University Press, Cambridge, UK.
36
37 737 Ley S, Yu M, Li K, Tseng C, Chen C, Kao P, Huang F (1963) Limnological Survey of the lakes
38
39 738 of Yunnan Plateau. *Oceanol ET Limnol Sinica* 5:87-114.
40 739 Li Y, Liu Y, Zhao L, Hastings A, Guo H (2015) Exploring change of internal nutrients cycling in
41
42 740 a shallow lake: A dynamic nutrient driven phytoplankton model. *Ecol Model* 313:137-148.
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1
2
3 741 Liu Y, Chen G, Hu K, Shi H, Huang L, Chen X, Lu H, Zhao S, Chen L (2017) Biological
4
5 742 responses to recent eutrophication and hydrologic changes in Xingyun Lake, southwest China. J
6
7 743 Paleolimnol 57:343-60.
8 744 Maavara T, Parsons CT, Ridenour C, Stojanovic S, Durr HH, Powley HR, Van Cappellen P
9
10 745 (2015) Global phosphorus retention by river damming. Proc Natl Acad Sci USA 112:15603–
11
12 746 15608.
13
14 747 Marc B, Falcão D, Marinho M, Pagano M, Moura A (2000) Occurrence of *Cylindrospermopsis*
15 748 (Cyanobacteria) in 39 Brazilian tropical reservoirs during the 1998 drought. Aquatic Microbial
16
17 749 Ecol 23:13-27.
18
19 750 McGowan S, Leavitt PR, Hall RI, Anderson NJ, Jeppesen E, Odgaard BV (2005) Controls of
20
21 751 algal abundance and community composition during ecosystem state change. Ecology 86:2200-
22 752 2211. Menking KM (1997) Climate signals in clay mineralogy and grain-size variations in Owens
23
24 753 Lake core OI-92, eastern California. Special Paper of the Geol. Soc Am 317:25-36.
25
26 754 Meyer TJ (2001) Sediment organic matter. In: Tracking Environmental Change Using Lake
27
28 755 Sediments. Volume 2: Physical and geochemical methods (eds Smol JP, Birks HJB, Last WM)
29
30 756 vol 3. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 239-269.
31 757 Meyers PA, Ishiwatari R (1993) Lacustrine organic geochemistry - an overview of indicators of
32
33 758 organic matter sources and diagenesis in lake sediments. Org Geochem 20:867-900.
34
35 759 Moorhouse HL, McGowan S, Jones MD, Barker P, Leavitt PR, Brayshaw SA, Haworth EY
36
37 760 (2014) Contrasting effects of nutrients and climate on algal communities in two lakes in the
38
39 761 Windermere catchment since the late 19th century. Freshwater Biol 59:2605-2620.

1
2
3 762 Oksanen J, Blanchet FG, Kindt R, Legendre P, Min-Chin PBR, O'Hara RB, Simpson GL,
4 763 Solymos P, Henry M, Stevens H (2015) vegan: Community Ecology Package (R package version
5
6 764 2.0-6. CRAN. R-project.org/Package = vegan).
7
8 765 Paerl H, Huisman J (2008) Blooms like it hot. Science 320:57-58.
9
10 766 Peršić V, Horvatić J, Has-Schön E, Bogut I (2007) Changes in N and P limitation induced by
11
12 767 water level fluctuations in Nature Park Kopački Rit (Croatia): nutrient enrichment bioassay.
13
14 768 Aquat. Ecology 43:27-36.
15 769 Posch T, Köster O, Salcher MM, Pernthaler J (2012) Harmful filamentous cyanobacteria
16
17 770 favoured by reduced water turnover with lake warming. Nature Climate Change 2:809-813.
18
19 771 R Team (2013) R: a language and environment for statistical computing. R Foundation for
20
21 772 Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
22 773 Reynolds CS (1987) The response of phytoplankton communities to changing lake
23
24 774 environments. Swiss J Hydrol 49:220-236.
25
26 775 Reynolds CS (2006) Ecology of Phytoplankton (Ecology, Biodiversity and Conservation).
27
28 776 Cambridge University Press, Cambridge, UK.
29
30 777 Romo S, Soria JM, Campo FFD, Benkaddour YO, Barón-Sola Á (2013) Water residence time
31 778 and the dynamics of toxic cyanobacteria. Freshwater Biol 58:513-522.
32
33 779 Round F, Crawford R, Man D (2007) The diatoms biology and morphology of the genera.
34
35 780 Cambridge University Press, Cambridge, UK.
36
37 781 Rühland K, Paterson AM, Smol JP (2008) Hemispheric-scale patterns of climate-related shifts in
38 782 planktonic diatoms from North American and European lakes. Global Change Biol 14:2740-
39
40 783 2754.
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1
2
3 784 Rühland KM, Paterson AM, Smol JP (2015) Lake diatom responses to warming: reviewing the
4
5 785 evidence. *J Paleolimnol* 54:1-35.
6 786 Saulnier-Talbot É, Gregory-Eaves I, Simpson KG, Efitre J, Nowlan TE, Taranu ZE, Chapman LJ
7
8 787 (2014) Small Changes in Climate Can Profoundly Alter the Dynamics and Ecosystem Services
9
10 788 of Tropical Crater Lakes. *Plos One* 9:e86561.
11
12 789 Scheffer MS, Hosper SH, Meijer ML, Moss B, Jeppesen E (1993) Alternative equilibria in
13
14 790 shallow lakes. *Trends Ecol Evol* 8:275-279.
15 791 Scheffer M (1998) *Ecology of Shallow Lakes*. London, UK: Chapman and Hall
16
17 792 Schindler DW (2006) Recent advances in the understanding and management of eutrophication.
18
19 793 *Limnol Oceanogr* 51:356-363.
20
21 794 Serruya C, Pollinger U (1977) Lowering of water level and algal biomass in Lake Kinneret.
22 795 *Hydrobiologia* 54:73-80.
23
24 796 Shi L, Sun Q (2005) Brief Talk on Effect of Aquatic Plant Purifying Water body of Yilong Lake.
25
26 797 *Yunnan Environ Sci* 24:40-42.
27
28 798 Shiping Yearbook (2005) Shiping Year Book (County Condification Committee). Yunnan
29
30 799 Peoples's Publishing Press, pp 56-67, 169-173.
31 800 Smol JP, Wolfe AP, Birks HJ, Douglas MS, Jones VJ, Korhola A, Pienitz R, Rühland K, Sorvari
32
33 801 S, Antoniades D, Brooks SJ, Fallu MA, Hughes M, Keatley BE, Laing TE, Michelutti N,
34
35 802 Nazarova L, Nyman M, Paterson AM, Perren B, Quinlan R, Rautio M, Saulnier-Talbot E,
36
37 803 Siitonen S, Solovieva N, Weckstrom J (2005) Climate-driven regime shifts in the biological
38
39 804 communities of arctic lakes. *Proc Natl Acad Sci USA* 102:4397-4402.
40 805 Smol JP (2010) The power of the past: using sediments to track the effects of multiple stressors
41
42 806 on lake ecosystems. *Freshwater Biol* 55:43-59. Sommerfield C, Nittroer C (1999) Modern
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1
2
3 807 accumulation rates and a sediment budget for the Eel shelf: a flood-dominated depositional
4
5 808 environment. *Mar Geol* 154:227-241.
6 809 Søndergaard M, Jensen JP, Jeppesen E (2003) Role of sediment and internal loading of
7
8 810 phosphorus in shallow lakes. *Hydrobiologia* 506:135-145.
9
10 811 Sterner R, Elser JJ (2002) *Ecological Stoichiometry: The Biology of Elements From Molecules*
11
12 812 *to The Biosphere*. Princeton University Press, pp 439.
13
14 813 Stoermer EF, Smol JP (2001) *The Diatoms: Applications for the environmental and earth science*.
15 814 Cambridge: Cambridge University Press. Cambridge: Cambridge University Press.
16
17 815 Taranu ZE, Zurawell RW, Pick F, Gregory-Eaves I (2012) Predicting cyanobacterial dynamics in
18
19 816 the face of global change: the importance of scale and environmental context. *Global Change*
20
21 817 *Biol* 18:3477-3490.
22 818 Taranu ZE, Gregory-Eaves I, Leavitt PR, Bunting L, Buchaca T, Catalan J, Domaizon I,
23
24 819 Guilizzoni P, Lami A, McGowan S, Moorhouse H, Morabito G, Pick FR, Stevenson MA,
25
26 820 Thompson PL, Vinebrooke RD (2015) Acceleration of cyanobacterial dominance in north
27
28 821 temperate-subarctic lakes during the Anthropocene. *Ecol Lett* 18:375-384.
29
30 822 ter Braak CJF, Prentice IC (1988) A theory of gradient analysis. *Adv Ecol Res* 18:271-313.
31 823 ter Braak CJF, Šmilauer P (2002) *CANOCO Reference Manual and CanoDraw for Windows*
32
33 824 *User's Guide: Software for Canonical Community Ordination [Version 4.5]*. Microcomputer
34
35 825 Power, Ithaca, NY.
36
37 826 Tilman D (1987) Resource competition and community structure. *Monographs in Population*
38
39 827 *Biology*. Princeton University Press 17:1-296.

1
2
3 828 Vadeboncoeur Y, Jeppesen E, Zanden MJV, Schierup HH, Christoffersen K, Lodge DM (2003)
4
5 829 From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in
6 830 lakes. *Limnol Oceanogr* 48:1408-141.
7
8 831 Vogt RJ, Sharma S, Leavitt PR (2018) Direct and interactive effects of climate, meteorology,
9
10 832 river hydrology, and lake characteristics on water quality in productive lakes of the Canadian
11
12 833 Prairies. *Can J Fish Aquat Sci* 75:47-59.
13
14 834 Wagner C, Adrian R (2009) Cyanobacteria dominance: Quantifying the effects of climate chang.
15 835 *Limnol Oceanogr* 54:2460-2468.
16
17 836 Wang H, Yang Z, Wang L, Liu Y, Song Y, Gao J (2014) The application of TVDI in drought
18
19 837 monitoring over Yunnan province during 2009 to 2010. *J. Yunnan University (Sci.)* 36:59-65.
20
21 838 Wang J, Chen G, Kang W, Hu K, Wang L (2019) Impoundment intensity determines temporal
22 839 patterns of hydrological fluctuation, carbon cycling and algal succession in a dammed lake of
23
24 840 Southwest China. *Water Res* 148:162-75.
25
26 841 Wang W, Wang L (2008) Current situation of agricultural non-point source pollution and Control
27
28 842 Countermeasures in Yilong lake. *Yunnan Agricultural Science and Technology*, pp 139-141.
29
30 843 Wang Z (1997) Survey of zooplankton and fish productivity in Yilong Lake, Yunnan. *J. Fisheries*
31 844 *China* 402-407.
32
33 845 Wieland E, Santschi P, Höhener P, Sturm M (1993) Scavenging of Chernobyl ¹³⁷Cs and natural
34
35 846 ²¹⁰Pb in Lake Sempach, Switzerland. *Geochimica Et Cosmochimica Acta* 57:2959-2979.
36
37 847 Winder M, Hunter DA (2008) Temporal organization of phytoplankton communities linked to
38
39 848 physical forcing. *Oecologia* 156:179-192.
40 849 Wu F, Zheng M, Hu G (2016) The Estimation of Vegetation Coverage of Yanshan County in
41
42 850 Yunnan by Remote Sensing Based on OLI Data. *Environ Sci Survey* 36:5-7.
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1
2
3 851 Wu J, Jiang X, Xia W, Pan H, Yin Y (2002) Climate and Primary Productivity over the last 500
4
5 852 years of the Chenghai Lake, Yunnan. *Mar Geol Quaternary Geol* 22:95-98.
6
7 853 Xie L, Xie P, Li S, Tang H, Liu H (2003) The low TN:TP ratio, a cause or a result of *Microcystis*
8 854 blooms? *Water Res* 37:2073-2080.
9
10 855 Xu H, Paerl H, Qin B, Zhu G, Gao G (2010) Nitrogen and phosphorus inputs control
11
12 856 phytoplankton growth in eutrophic lake Taihu, China. *Limnol Oceanogr* 55:420-432.
13
14 857 Xu J, Wen Z, Ke Z, Zhang M, Zhang M, Guo N, Hansson LA, Xie P (2014) Contrasting energy
15 858 pathways at the community level as a consequence of regime shifts. *Oecologia* 175:231-241.
16
17 859 Xu M, Chang CP, Fu CB, Qi Y, Robock A, Robinson D, Zhang HM (2006) Steady decline of east
18
19 860 Asian monsoon winds, 1969-2000: Evidence from direct ground measurements of wind speed. *J*
20
21 861 *Geophys Res* 111: 1-8.
22
23 862 Yang L, Li H, (2010) *Wetlands of Yunnan*. China Forestry Publishing House, pp 94-101.
24 863 Yang X, Lu X (2014) Drastic change in China's lakes and reservoirs over the past decades. *Sci*
25
26 864 *Rep* 4:6041.
27
28 865 Zhang J, Wang Z, Song Z, Xie Z, Li L, Song L (2012) Bioaccumulation of microcystins in two
29
30 866 freshwater gastropods from a cyanobacteria-bloom plateau lake, Lake Dianchi. *Environ Pollut*
31 867 164:227-34.
32
33 868 Zhang Y, Zhang E, Liu M (2009) Spectral absorption properties of chromophoric dissolved
34
35 869 organic matter and particulate matter in Yunnan Plateau lakes. *J Lake Sci* 21:255-263.
36
37 870 Zhao L (2013) The regime shifts and inversion of catastrophic driving factors in the ecosystems
38
39 871 of Yilong Lake, Yunnan. Dissertation, University of Chinese Academy of Science.

1
2
3 872 Zhao L, Li Y, Zou R, He B, Zhu X, Liu Y, Wang J, Zhu Y (2013) A three-dimensional water
4
5 873 quality modeling approach for exploring the eutrophication responses to load reduction scenarios
6 874 in Lake Yilong (China). Environ Pollut 177:13-21.
7
8
9

1

2

3 875

4

5

6

7

8

9

10

11

12

13

14

15

16

17

18

19 876

20 877

21

22 878

23

24

25

26

27

28

29

30

31

32

33

34

35

36

37

38

39

40

41

42

43

44

45

46

47

48

49

50

51

52

53

54

55

56

57

58

59

60

61

62

63

64

65

Table 1

Summary of key limnological features of Yilong Lake

Variable	Value
Altitude (m) ^a	1,413.4
Lake surface area (km ²) ^a	34.0
Catchment area (km ²) ^a	326.0
Average water depth (m) ^a	2.9
Max. water depth (m) ^a	3.7
Chlorophyll (µg/l) ^b	214.3
Transparency (m) ^b	0.1
TN (mg/l) ^b	7.7
TP (µg/l) ^b	123.3
pH ^b	8.8

^a Data are from Yang & Li (2010).

^b Data were collected in the summer of 2013 from the current study.

14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

879 **Table 2** Monitored changes of algae abundance, lake-water N:P mass ratio and macrophyte coverage over time in Yilong Lake

Year	Cyanobacteria (10 ⁶ cell/l)	Diatoms (10 ⁶ cell/l)	Phytoplankton (10 ⁶ cell/l)	Dominant algae	Cyanobacteria (%)	N:P ratio (by mass)	Macrophyte coverage (%)
1957			8.41 ^a	Bacillariophyta (except episodic cyanobacteria bloom in Aug.)			
1982						14.39	95.0 ^d
1988			46.00 ^b	Chlorophyta (<i>Pediastrum simplex</i>)		89.23	
1992	180.47 ^c	4.00 ^c	193.21 ^c	Cyanobacteria (<i>Aphanizomenon flosaquae</i>)	93.41 ^c	82.95	27.3 ^e
1993			50.88 ^d	Chlorophyta (<i>Pediastrum simplex</i>)		73.84	
1997	19.76 ^e	0.21 ^e	21.78 ^e	Cyanobacteria (<i>Microcystis aeruginosa</i>)	90.75 ^e	38.28	40.0 ^e
2008	82.30 ^f	1.31 ^f	88.51 ^f	Cyanobacteria (<i>Microcystis aeruginosa</i>)	92.98 ^f	49.65	60.0 ^e
2010			317.20 ^e	Cyanobacteria (<i>Cylindrospermopsis raciborskii</i>)	99.00	40.33	<10.0 ^e
2015	244.65	0.59	248.14	Cyanobacteria (<i>Aphanizomenon flosaquae</i>)	98.59	51.20	

880 Data were collected from ^aLey et al. (1963); ^bJin et al. (1995); ^cWang (1997); ^dWang & Dou (1998); ^eZhao (2013); ^fZhang et al. (2009)

Table 3 Summary of individual RDAs for key environmental variables in accounting for the variance (adjusted R^2) in the algal production and diatom PC1 score during the periods of ~1903-2013 and ~1953-2013, respectively

Environmental Variable	Pigments		Diatom PC1	
	1903-2013	1953-2013	1903-2013	1953-2013
Median grain size (μm)	-0.027	-0.034	-0.023	-0.024
Clay (%)	-0.027	-0.033	-0.022	-0.019
Silt (%)	-0.024	-0.016	-0.016	0.007
Sand (%)	0.034	0.197 **	0.047	0.273 ***
$\delta^{13}\text{C}$ (‰)	0.094	0.419 ***	-0.022	-0.017
$\delta^{15}\text{N}$ (‰)	0.217 **	0.783 ***	0.038	0.224 ***
C/N ratio	0.233 **	0.846 ***	0.034	0.189 ***
TC (mg/g)	0.786 ***	0.796 ***	0.324 ***	0.103 *
TN (mg/g)	0.900 ***	0.824 ***	0.406 ***	0.159 ***
Population	-	0.822 ***	-	0.121 **
Temperature ($^{\circ}\text{C}$)	-	0.288 ***	-	0.233 ***
Precipitation (mm)	-	-0.020	-	0.044
Wind speed (m/s)	-	0.384 ***	-	-0.009
All variables	0.914 ***	0.912 ***	0.270 ***	0.136 **

Significance codes for P -level: '***', $P < 0.001$; '**', $P < 0.01$; '*', $P < 0.05$.

Note: An adjusted R^2 near 0 indicates that the environmental variable does not explain more of the variation of the biotic assemblages change than random normal variable would do; Negative adjusted R^2 indicates that the explanatory variables perform similarly as random normal variables would.