RESEARCH ARTICLE

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

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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 twentieth 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

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),

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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 systems (Scheffer 1998). At the same time, climate warming has increased the occurrence of extreme hydrologic events (e.g., droughts) at regional and global scales (Dai 2011; IPCC 2013), augmenting the decline of water level and ecological health (Lake 2011). In comparison, nutrient fertilization usually enhances phytoplankton production at the expense of benthic taxa such as diatoms (Vadeboncoeur et al. 2003). In principle, changes in lake level and nutrient influx could drive algal abundance and community composition in different directions in shallow lakes that are subject to multiple stressors. Furthermore, there may exist strong interactions between nutrient dynamics and hydrologic fluctuation, as prolonged water retention time due to impoundment can lead to an increased level of nutrients (Maavara et al. 2015) and accelerate eutrophication in shallow lakes (Chen et al. 2013). To date, little is known of how such hydrologic fluctuations in shallow lakes may interact with eutrophication in regulating the abundance and composition of primary producers over time.

In many lakes, analysis of sedimentary records can provide a reliable temporal perspective on limnological responses to anthropogenic disturbances and climate change (Adrian et al. 2009; Battarbee 2010; Smol 2010). Fossil pigments and diatoms are two widely used paleolimnological indicators of algal abundance and community composition (Leavitt and Hodgson 2001; Stoermer and Smol 2001). For example, sediment pigments have recorded the independent effects of both nutrient fertilization and climate (Hall and Leavitt 1999; Leavitt et al. 2006; Bunting et al. 2007), as have fossil diatom assemblages (Smol et al. 2005; Rühland et al. 2008). Diatoms from shallow lakes were found to be sensitive to lake-level changes through their response to habitat quantity and quality (Brugam et al. 1998), while shifts in the vertical zonation of algae with lake depth have

been identified from fossil pigments (Cuddington and Leavitt 1999; McGowan et al. 2005; Hambright et al. 2008). Therefore, 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.

Materials and methods

Study site

Yilong Lake, located in southeast part of Yunnan Province, southwest China (Fig. 1), is a large (~ 34 km^2) 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 2300 h/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%.
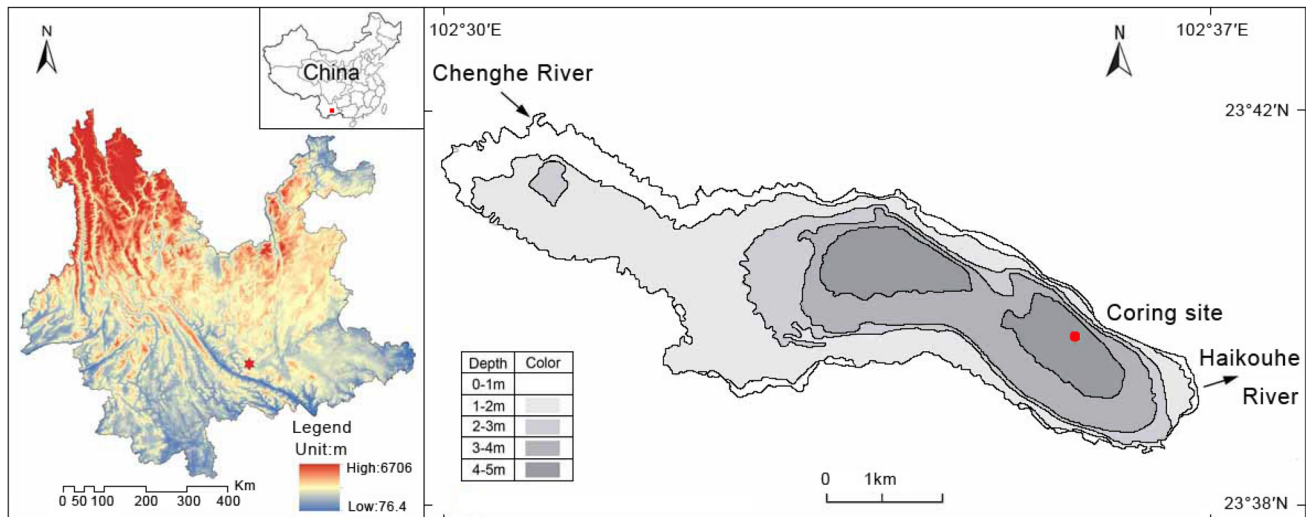
Fig. 1 Site map (left) showing the location of Yilong Lake and lake morphometry (right)

Table 1 Summary of key limnological features of Yilong Lake

Variable	Value
Altitude (m)[a]	1413.4
Lake surface area (km²) [a]	34.0
Catchment area (km²) [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 and Li (2010)

[b]Data were collected in the summer of 2013 from the current study

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 and 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).

Sample collection and sediment dating

A 34-cm sediment core was collected from Yilong Lake in July 2013 from the deep basin (23º39′53″N, 102º36′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

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. Meterological data are from the National Climate Center (http://cmdp.ncc.cma.gov.cn/cn/index.htm); Population data were collected from the ECSCA (2005); TP, TN, Chl-*a*, transparency, water level and volume data were collected from previous studies (Ley et al. 1963; Chou and Xia 1998; Whitmore et al. 1997; Shi and Sun 2005; Yang and Li 2010; Wei and Tang 2014)
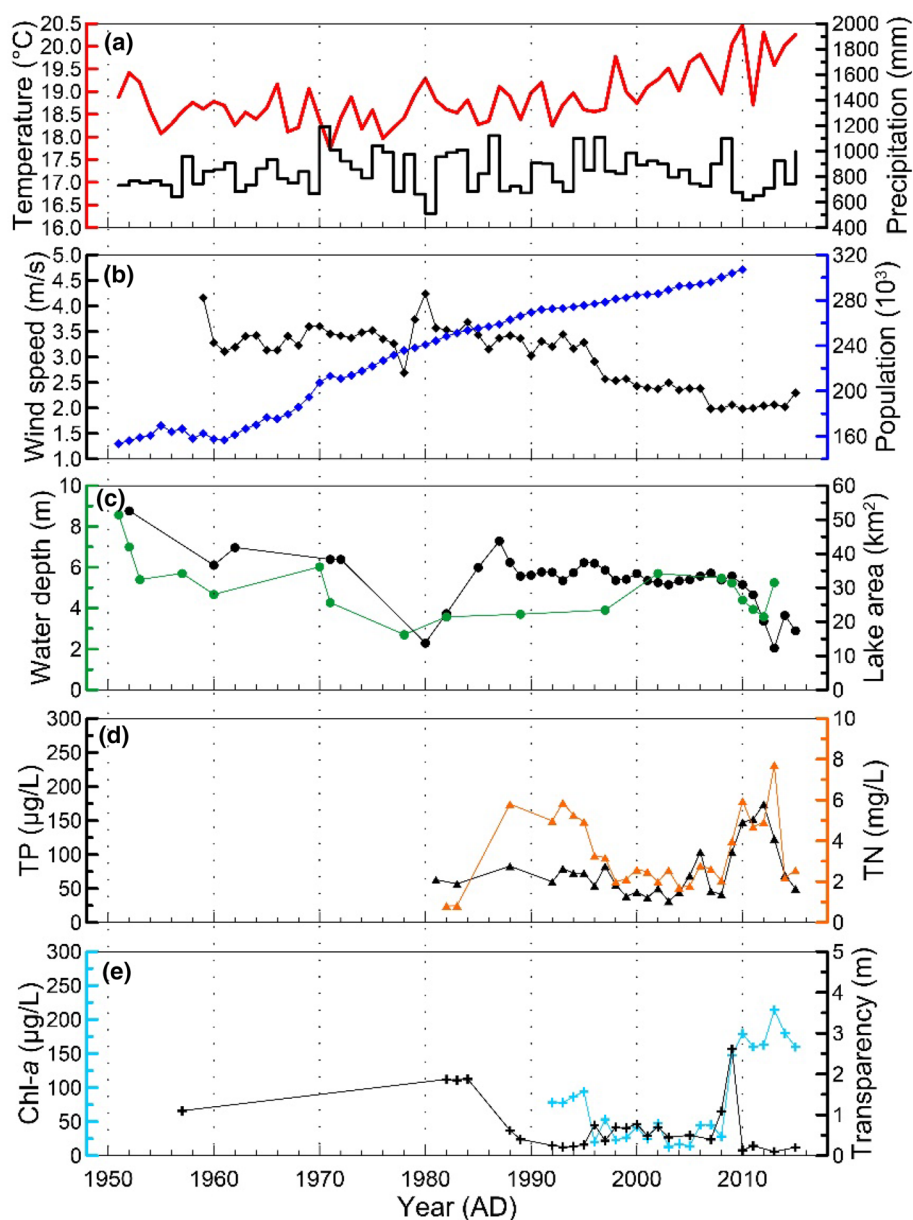
pigment analyses within 24 h. The remaining sediments were freeze-dried and stored in the dark for subsequent analyses.

Sediment chronology was estimated based on ^{210}Pb activities in sediment core samples. Around 3–5 g of freeze-dried sediments were used for measuring the radio-activities of ^{210}Pb and ^{137}Cs 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 using the stratigraphic profile of unsupported ^{210}Pb activities (Appleby 2001).

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

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 (*Pediastrum simplex*)		89.23	
1992	180.47[c]	4.00[c]	193.21[c]	Cyanobacteria (*Aphanizomenon flosaquae*)	93.41[c]	82.95	27.3[e]
1993			50.88[d]	Chlorophyta (*Pediastrum simplex*)		73.84	
1997	19.76[e]	0.21[e]	21.78[e]	Cyanobacteria (*Microcystis aeruginosa*)	90.75[e]	38.28	40.0[e]
2008	82.30[f]	1.31[f]	88.51[f]	Cyanobacteria (*Microcystis aeruginosa*)	92.98[f]	49.65	60.0[e]
2010			317.20[e]	Cyanobacteria (*Cylindrospermopsis raciborskii*)	99.00	40.33	< 10.0[e]
2015	244.65	0.59	248.14	Cyanobacteria (*Aphanizomenon flosaquae*)	98.59	51.20	

Data were collected from [a]Ley et al. (1963)

[b]Jin et al. (1995)

[c]Wang (1997)

[d]Wang and Dou (1998)

[e]Zhao (2013)

[f]Zhang et al. (2009)

dispersed with 10 ml of 0.05 mol/l $(NaPO_3)_6$ 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 ($\delta^{13}C$ and $\delta^{15}N$) 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 $< \pm 0.1$‰ for isotopic data and $< \pm 1\%$ for elemental data, respectively.

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 (LOI_{550}) 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).

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 1000× 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).

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 assemblagesP. Pigment CA 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, $\delta^{13}C$, $\delta^{15}N$, 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

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***
$\delta^{13}C$ (‰)	0.094	0.419***	− 0.022	− 0.017
$\delta^{15}N$ (‰)	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 (℃)	–	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**

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

Significance codes for P level: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$

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* and *rioja*.

Results

Archived data

Meteorological data generally show a warming trajectory with marked variation in precipitation during the last 6 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 2 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 6 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 6 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 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 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-1990 s (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 8.41×10^6 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).

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
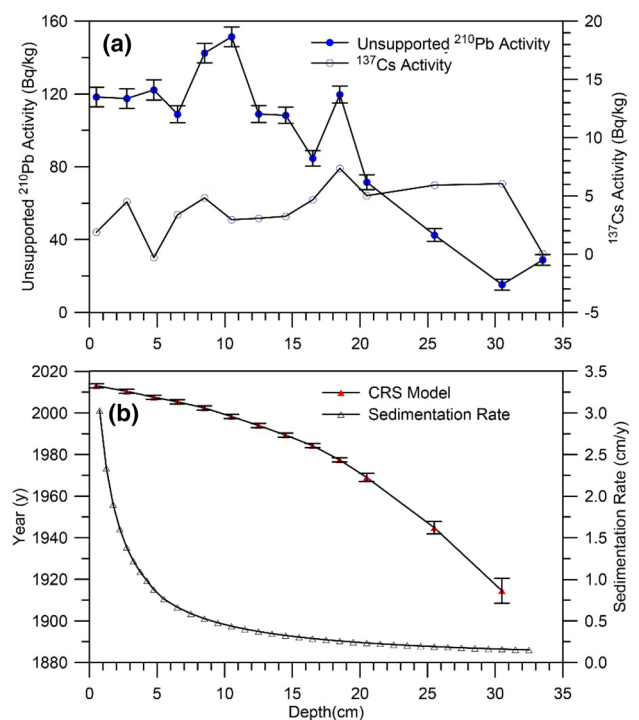

Fig. 3 Depth profiles showing the ^{210}Pb and ^{137}Cs radioactivities (**a**) and the CRS age model and sedimentation rate (**b**) for Yilong Lake

no obvious peak (Fig. 3a), reflecting a possible combination of sediment mixing and post-deposition mobility (e.g., Wieland et al. 1993; Sommerfield and Nittrouer 1999). Overall, radio-isotope profiles and CRS calculations suggest a recent acceleration in the rate of sediment accumulation (Fig. 3b).

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 ± 1.4 µm, with the clay (< 2 µm) and sand (> 63 µm) 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 twentieth 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 (LOI_{550}) 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 $\delta^{15}N$ signal of bulk sediments remained stable around the near-atmospheric value (~ 0‰) until the mid-1960 s, at which time it increased dramatically up to a maximum value of ~ 4.5‰ in surface sediments. Correspondingly, the bulk sediment $\delta^{13}C$ signal declined from around − 14‰ to nearly − 16‰ over the twentieth 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 ($r = -0.92$, $P < 0.001$).

Pigment variations

Analysis of sedimentary pigments suggested a progressive increase in autotrophic production during the twentieth 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 twentieth 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 ~ 8 cm), as identified by the CONISS results (Fig. 5a).
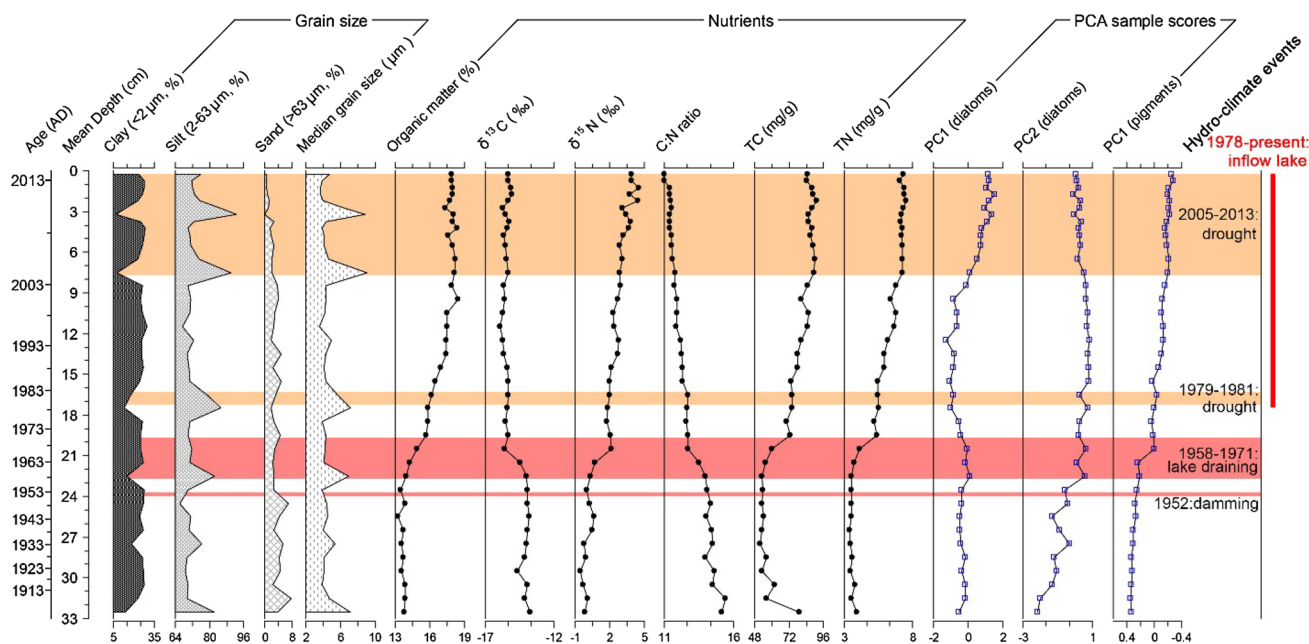

Fig. 4 Sedimentary profile showing the proxies of grain sizes, nutrient concentrations and isotopes, as well as the diatom and pigment PCA site scores, for Yilong Lake
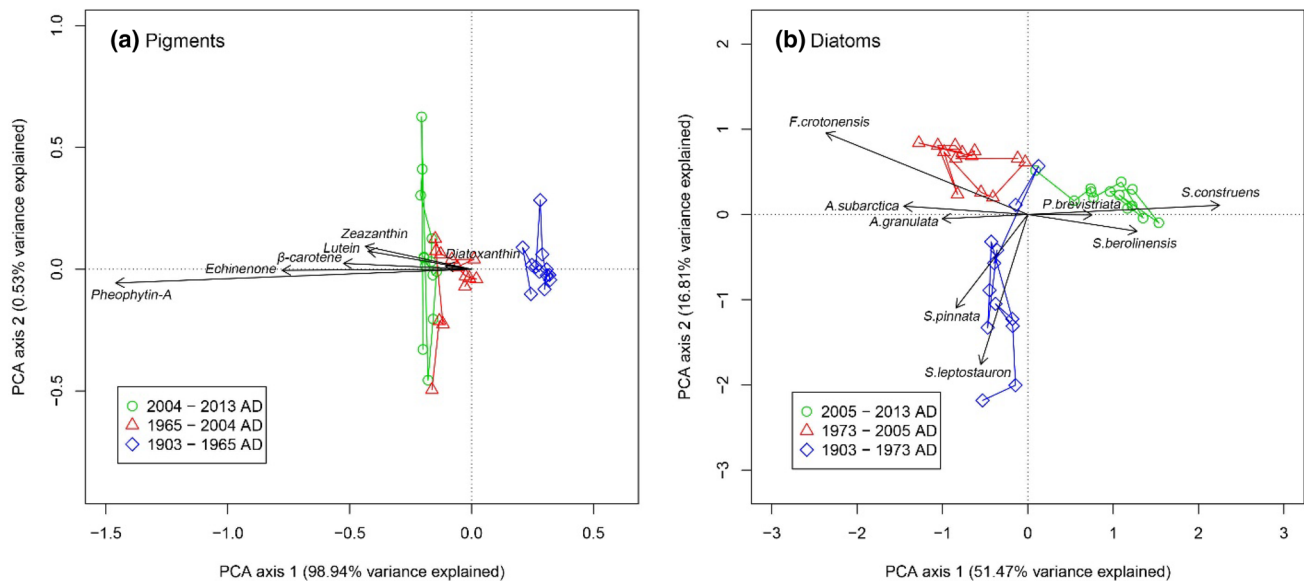
Fig. 5 Stratigraphic profiles showing the temporal changes in pigment concentrations (ng/g OM) for total algae and major components (**a**; Z:PD, the zeaxanthin:planktonic diatoxanthin ratio) and the compositional change of common diatoms (> 2% relative abundance in at least one sample; **b** with the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

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.

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

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 twentieth century (Fig. 5b). For example, *Staurosira construens* (a range of 4.2–51.0%), *S. berolinensis* (6.5–44.6%) and *Achnanthidium 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.

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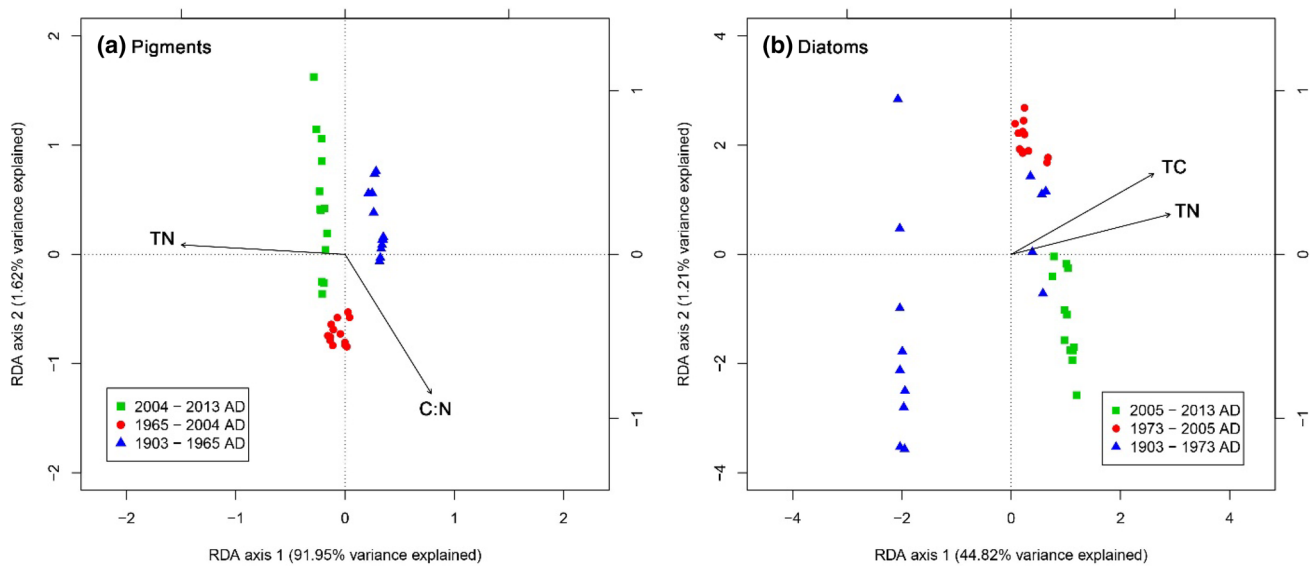
Fig. 7 Biplots of redundancy analysis showing the selected significant drivers for pigment concentrations (**a**) and diatom assemblages (**b**) during 1903–2013 AD in Yilong Lake

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 6 decades and accounted for ≥ 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).
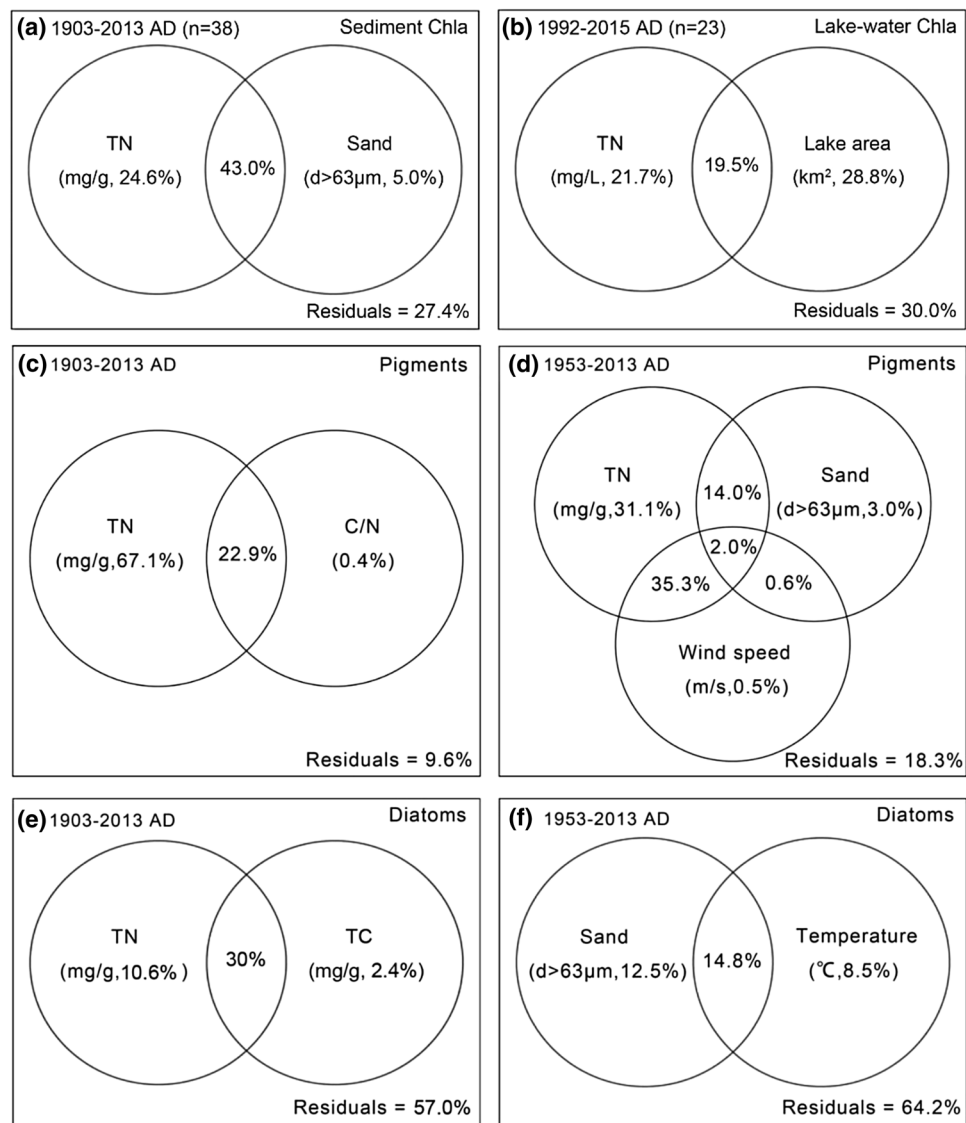
The variance partitioning results further showed that lake-water TN concentration, but not TP, was a significant diver, accounting for 21.7% of the change in water-column Chl-*a* for the monitoring period of 1992–2015 (Fig. 8b). Furthermore, hydrologic fluctuation inferred from changes in lake area independently 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).

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

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

(a) 1903-2013 AD (n=38)   Sediment Chla
TN (mg/g, 24.6%)   43.0%   Sand (d>63μm, 5.0%)
Residuals = 27.4%

(b) 1992-2015 AD (n=23)   Lake-water Chla
TN (mg/L, 21.7%)   19.5%   Lake area (km², 28.8%)
Residuals = 30.0%

(c) 1903-2013 AD   Pigments
TN (mg/g, 67.1%)   22.9%   C/N (0.4%)
Residuals = 9.6%

(d) 1953-2013 AD   Pigments
TN (mg/g, 31.1%)   14.0%   Sand (d>63μm, 3.0%)
2.0%
35.3%   0.6%
Wind speed (m/s, 0.5%)
Residuals = 18.3%

(e) 1903-2013 AD   Diatoms
TN (mg/g, 10.6%)   30%   TC (mg/g, 2.4%)
Residuals = 57.0%

(f) 1953-2013 AD   Diatoms
Sand (d>63μm, 12.5%)   14.8%   Temperature (℃, 8.5%)
Residuals = 64.2%

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 twentieth century, although effects of hydrologic fluctuations appear to have been more pronounced in the past 2 decades.

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 δ^{13}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 δ^{15}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 δ^{15}N prior to the mid-1960 s 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. 2004; 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).

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 6 decades (Figs. 2a, 4). Lake regulation can often amplify the nutrient effect and promote algae production by concentrating nutrients (Serruya and Pollingher 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 2 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 2 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 ~ 2.3 m with a loss of ~ 0.67 billion m[3] 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; 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).

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 twentieth century, when sedimentary $\delta^{15}N$ was low and characteristic of fixed N_2 from diazotrophic cyanobacteria, and disproportionately high P influx occurred with agricultural development in 1960s (ECSCA 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 2 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; Table 2). Meanwhile, the benthic diatom percentage rose sharply as water column depth declined during the last 2 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 overiding 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.

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.

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