

Diatom community succession in the recent history of a eutrophic Yunnan Plateau lake, Lake Dianchi, in subtropical China

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Abstract Fish introduction, eutrophication and disappearance of aquatic vegetation are important disturbances of aquatic ecosystems, especially in plateau lakes, which are generally considered to be very vulnerable. Fish were introduced to Lake Dianchi, a eutrophic plateau lake in southwest China, in the late 1950s and 1970s. After the introduction, invasive fish became the dominant species, and the total fish yield increased. Meanwhile, the trophic level of Lake Dianchi had a tendency to increase in the past decades because of the increases in human activities in the watershed area. In addition, the area of aquatic vegetation decreased from more than 90 to 1.8% of the lake area from the 1950s to 2000. This study investigated the effects of fish introduction, eutrophication and aquatic vegetation on the diatom community of Lake Dianchi by examining the changes of microfossil diatom assemblage and abundance. Results showed that the absolute abundance and diatom assemblages changed after fish were introduced. The endemic species, *Cyclotella rohomboideo-elliptica*, disappeared with the introduction of fish and increasing trophic levels after 1958. *Fragilaria crotonensis* entered into the lake with the introduction of fish and gradually thrived in the lake after 1958. Diatom species numbers also decreased

gradually from 21 to 9 from the past to present. Epiphytic diatoms disappeared with the decrease of aquatic vegetation after 1985. Our study indicated that eutrophication was the most important process determining diatom abundance, and fish introduction was a secondary process determining diatom abundance, while aquatic vegetation had a more important role in structuring the diatom community in this eutrophic plateau lake.

Keywords Lake Dianchi · Fish introduction · Eutrophication · Aquatic vegetation · Diatom microfossil

Introduction

The Yunnan Plateau, located in southwestern China, ranges from the highest elevation of 6,740 m in the northwest to the lowest of 76 m in the southeast, and its average elevation is about 2,000 m above sea level. It has a distinctive monsoon climate with an annual mean temperature of about 15°C and an annual mean precipitation of about 1,000 mm (Nanjing Institute of Geography and Limnology 1989). This unique combination of topographic complexity and favorable moisture conditions in the region supports an enormous richness of biological diversity and high degrees of endemism (Zhang 1999). The lakes in Yunnan Plateau are a Global 200 Priority Ecoregion of the Palearctic Lake Ecosystems (Olsen and Dinerstein 1998). Thus, lakes in Yunnan Plateau have attracted many zoologists, botanists, naturalists and collectors since the end of the nineteenth century (Ley et al. 1963; Yang et al. 2005a, b; Li et al. 2007; Cui et al. 2008). Nevertheless, most of them have received little rigorous scientific examination, particularly of the relationship between diatom communities and the environment.

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Lake Dianchi (24°51'N, 102°42'E) is a subtropical lake with a volume of $11.69 \times 10^8 \text{ m}^3$ and 297.9 km² surface area located in central Yunnan Province; it is a eutrophic freshwater lake. The maximum and average depths are 6.5 and 2.93 m, respectively (Nanjing Institute of Geography and Limnology 1989; Wang and Dou 1998). The average annual rainfall is about 1,000 mm. In general, the rainy season occurs from May to October and the dry season from November to April (Wang and Dou 1998). With the development of agriculture, industry and urbanization in the region, increasing sewage discharge has had an effect on the trophic status and aquatic macrophytes (Luo et al. 2006). Aquatic macrophytes decreased from 90 to 1.8% of the lake area from the 1950s to 1990s. The community structure has been simplex and has deteriorated drastically (Yu et al. 2000). Numbers of aquatic macrophytes decreased from more than 100 species to 22 species from the 1950s to 1997 (Ley et al. 1963; Yu et al. 2000). In Lake Dianchi, TN and TP increased from 1988 to 2000, ranging from 1.02 to 11.89 mg/l and 0.109 to 1.06 mg/l, respectively (Tuo 2002; Meng 1999). Increasing TN and TP concentrations have caused a rapid outburst of cyanobacteria bloom in Lake Dianchi (Nanjing Institute of Geography and Limnology 1989; Wei et al. 1994).

The introduction of exotic fish from the Yangtze River to the lakes of Yunnan-Guizhou Plateau has led to significant ecological consequences in the lake ecosystem. Invasion by fish in Lake Dianchi has been divided into two periods. First, Silver and bighead carp and other fish were introduced into Lake Dianchi in 1958. Second, *Neosalanx taihuensis* was introduced into Lake Dianchi in 1979 (Wang and Dou 1998).

Diatoms are an abundant, diverse and important component of algal assemblages in freshwater lakes. They comprise a large portion of total algal biomass over a broad spectrum of lake trophic status (Hall and Smol 1999). Because diatoms are an abundant, high-quality food source for herbivores, they may play an important role in the aquatic food-web structure and functioning (Round et al. 1990). Because of the large number of ecologically sensitive species, which conveniently leave a fossil record, diatoms are widely used in paleoecological studies (Stoermer and Smol 1999).

Long-term data about the components (i.e., diatom assemblages) of the ecosystem are not available for Lake Dianchi concerning the full time scale of exotic fish, trophic status and aquatic vegetation impacts. Fortunately, lakes accumulate vast amounts of ecological and chemical information in their deep-water sediments, which can be used to reconstruct past changes in lake ecosystems (Hall and Smol 1999). Diatoms are well preserved in most lake sediments and are useful bioindicators in applied lake ecosystems studies. The purposes of this research were to

describe diatom communities through sediments in Lake Dianchi and to discuss changes in diatom communities with the introduction of exotic fish, decreasing of aquatic macrophytes and increasing trophic status.

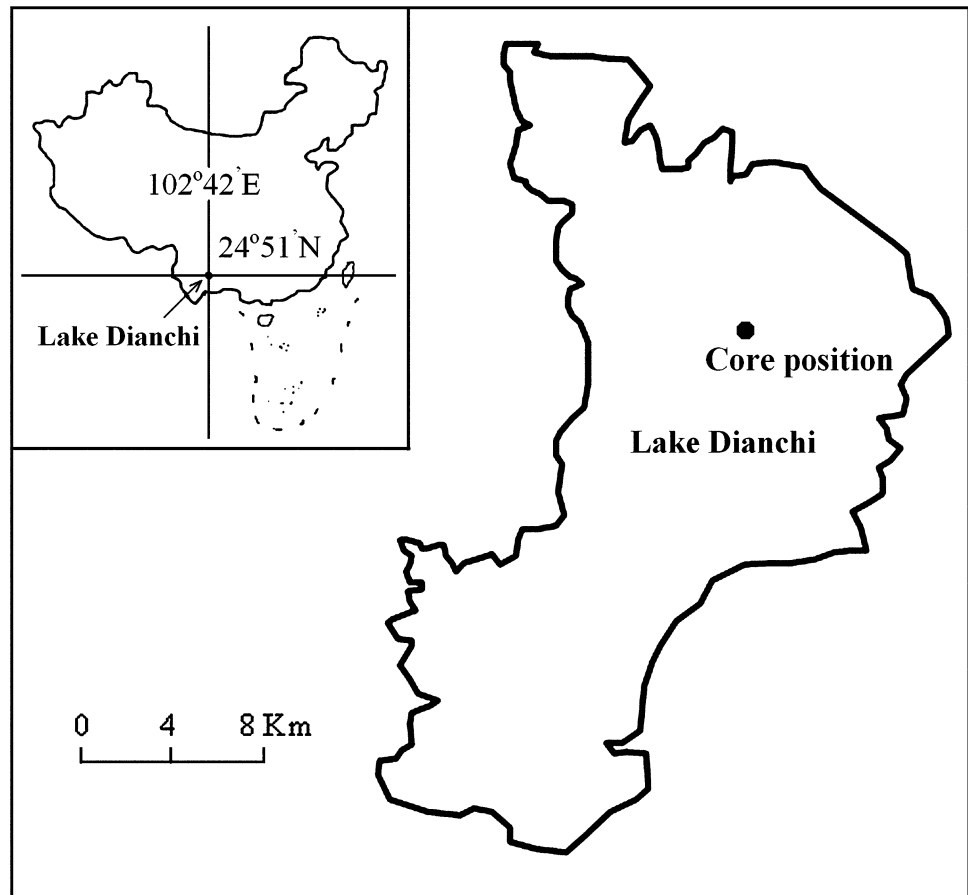
Materials and methods

A box core from a 6.0-m-deep site in the north basin was taken by a Kajak gravity corer in June 2007 (Fig. 1). The subsampled core was sectioned by extrusion in 1-cm intervals from 0 to 10 cm and 2-cm intervals from 10 to 44 cm. Core sections were refrigerated for further processing. Diatom samples (about 0.2 g) were treated using HCl and H₂O₂ (Battarbee 1986). Four replicate sub-samples were potentially available from each sample. Diatom valves were enumerated on each of two prepared slides from each sample, resulting in two replicate abundance estimates. Diatoms were identified using oil immersion at 1,000× magnification under the Olympus microscope (BX51). Identification was performed using manuals such as Krammer and Lange-Bertalot (1988, 1991), Rumrich et al. (2000), Zhu and Chen (2000) and Lange-Bertalot (2001). ²¹⁰Pb and ¹³⁷Cs dating was measured in the Nanjing Institute of Geography and Limnology, the Chinese Academy of Sciences. Dried sediments were analyzed for ²¹⁰Pb, ²²⁶Ra and ¹³⁷Cs by direct gamma spectrometry using the Ortec HPGe GWL series of well-type, coaxial, low background, intrinsic germanium detectors (Appleby et al. 1986). ²¹⁰Pb activity was determined via its direct gamma emissions at 46.5 keV and ²²⁶Ra via the 295.2 and 351.9 keV γ -rays emitted by its daughter isotope ²¹⁴Pb following 3-week storage in sealed containers to allow secular equilibration to be established. ¹³⁷Cs was measured by its emissions at 662.7 keV. Supported ²¹⁰Pb in each sample was assumed to be in equilibrium with in situ ²²⁶Ra. Unsupported ²¹⁰Pb activity at each depth was calculated by subtracting ²²⁶Ra activity from the total ²¹⁰Pb activity (Wu et al. 2004).

Results

Sediment chronology was established by the stratigraphic decay profile of unsupported ²¹⁰Pb activity and the constant rate of supply (CRS) model (Appleby and Oldfield 1978). The appearance and the peak of ¹³⁷Cs activity at 31- and 25-cm depths represent the year 1952, the date when ¹³⁷Cs fallout was first widely distributed, and 1963, the year of peak deposition in the northern hemisphere, respectively (Wu et al. 2007). The marker date for this peak agrees with the ²¹⁰Pb date for these samples. The ²¹⁰Pb dating data showed that the average deposition rate was 0.53 cm/year. There were 30 species from the core of

Fig. 1 Map of Lake Dianchi and the sample sites



Lake Dianchi. The diatom profile was divided into three zones by the absolute and relative abundance of the dominant species, *Aulacoseira granulata*, *Cyclostephanos dubius*, *Stephanodiscus minutulus*, *Cyclotella rohomboideo-elliptica*, *Thalassiosira bramaputrae*, *Fragilaria crotonensis*, *Fragilaria* aff. *venter*, *Fragilaria parasitica* and *Gyrosigma acuminatum*, and the absolute abundance of total diatoms, and the ^{210}Pb dating data (Fig. 2).

Zone 1: 12–0 cm, 1985–2007 A.D.

Zone 1 was characterized by predominant *C. dubius* whose relative abundance was more than 34%. The second dominant species was *A. granulata*, whose relative abundance ranged from 11.05 to 56.23%. The third species was *S. minutulus*, whose relative abundance ranged from 1.15 to 5.41%. Absolute abundance of total diatoms increased in this zone and ranged from 6.76×10^8 to 87.3×10^8 valves g^{-1} . *C. rohomboideo-elliptica* and *G. acuminatum* did not appear in the zone. Relative abundance of *F. aff. venter* ranged from 0 to 6.27%. *T. bramaputrae* disappeared gradually. *F. crotonensis*,

F. parasitica, *Cyclotella menghiniana*, *Cyclotella stelligera* and *Fragilaria breviatum* appeared in the zone, but their relative abundances were very low.

Zone 2: 26–10 cm, 1958–1985 A.D.

Zone 2 was dominated by *A. granulata*, whose relative abundance was more than 55%. The second dominant species was *C. dubius*, whose relative abundance ranged from 2.57 to 31.54%. The third species was *T. bramaputrae*, whose relative abundance was more than 8.5%. Absolute abundance of total diatoms increased in this zone and ranged from 1.94×10^8 to 6.39×10^8 valves g^{-1} . *S. minutulus*, *C. rohomboideo-elliptica*, *F. crotonensis*, *F. aff. venter*, *F. parasitica* and *G. acuminatum* appeared in the zone, but their relative abundances were low, and less than 2.05%. *Achnanthes* sp., *Amphora lybica*, *Cymbella minuta*, *Cymbella prostata*, *Gomphonema germanii*, *Navicula* sp., *Nitzschia palea*, *Nitzschia* sp., *Cyclotella krammeri*, *Cyclotella ocellate* and *Stephanodiscus hantzschia* appeared in the zone, but their relative abundances were very low, less than 0.5%.

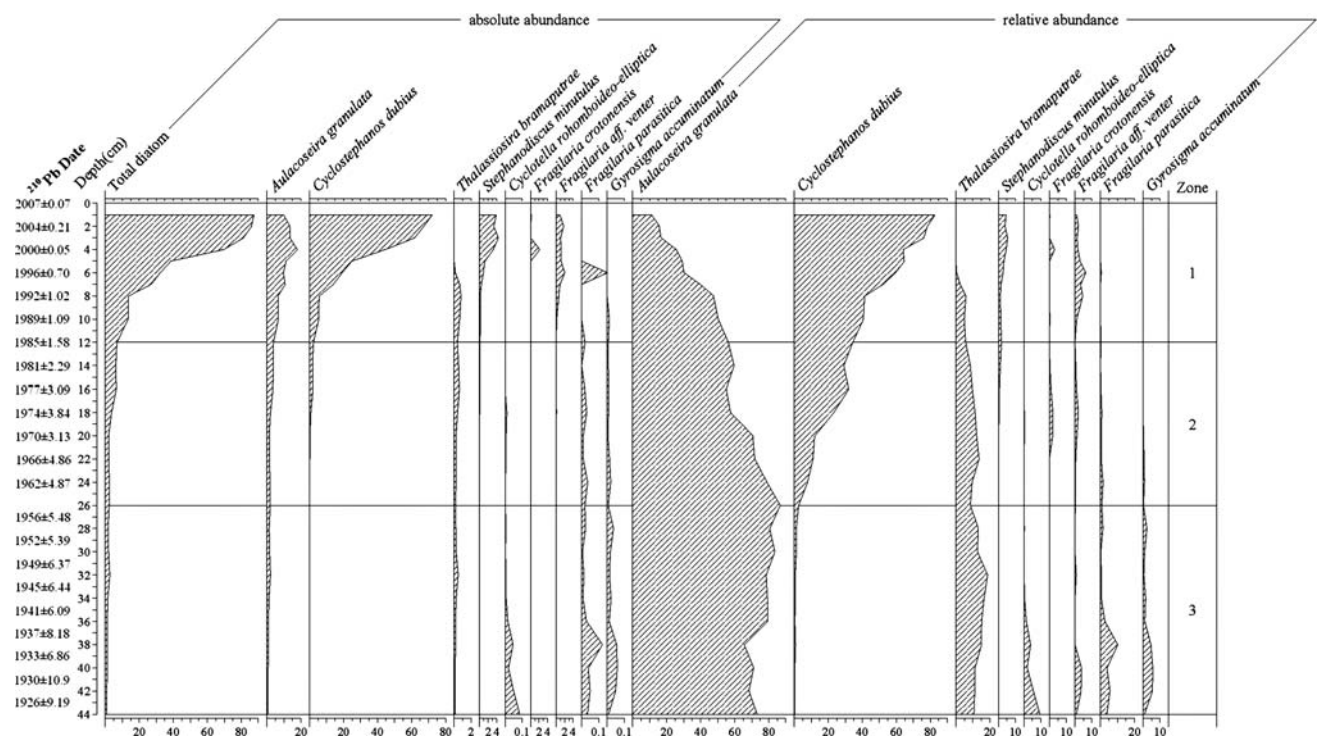


Fig. 2 Changes of absolute abundance ($\times 10^8$ valves g^{-1}) and relative abundance (%) of different dominant taxa at core and the ^{210}Pb dating data in Lake Dianchi

Zone 3: 44–26 cm, 1924–1958 A.D.

Zone 3 was characterized by *A. granulata*, whose relative abundance was more than 65.49%. *T. bramauptrae*, whose relative abundance ranged from 10.65 to 18.64%, was the second dominant species. The third species was *C. dubius*, whose relative abundance ranged from 0.28 to 1.24%. Absolute abundance of total diatoms ranged from 0.9×10^8 to 2.38×10^8 valves g^{-1} . Relative abundance of *C. rhomboideo-elliptica* ranged from 0.1 to 9.33%. Relative abundances of *F. aff. venter*, *F. parasitica* and *G. acuminatum* were more than 0.2%. *F. crotonensis* and *S. minutulus* did not appear in this zone. *Achnanthes* sp., *A. lybica*, *Cymbella ehrenbergi*, *Cymbella gracilis*, *Cocconeis* sp., *Hipponica* sp., *G. acuminatum*, *Navicula* sp., *Nitzschia* sp., *Cyclotella menhiniana*, *C. ocellate* and *C. stelligera* appeared in the zone, but their relative abundances were very low.

Discussion

Past studies indicated that *C. rhomboideo-elliptica* lives in dystrophic and mesotrophic environments (Ley et al. 1963; Li et al. 2007). *A. granulata* lives in mesotrophic to hypereutrophic, alkaline environments (Qi 1995). *S. minutulus* and *C. dubius* both are considered more eutrophic

taxa (Hall and Smol 1999; Reavie et al. 1995; Qi 1995; Edlund et al. 1995; Yang et al. 2005a, b). *C. dubius* and *S. minutulus* are also present in samples from lakes of the middle and lower Yangtze River (Yang et al. 2005a, b, 2008). Changes in the absolute and relative abundance of *A. granulata*, *C. rhomboideo-elliptica*, *S. minutulus* and *C. dubius* in this study suggest that the trophic state of Lake Dianchi has gradually increased over the past 83 years. The composition of fossil species indicates that Lake Dianchi experienced being mesotrophic before 1958, then being eutrophic from 1958–1985, moving to being hypereutrophic after 1985 and throughout the past 83 years; therefore, significant changes in diatom assemblages suggest that limnological conditions during that time have not been stable.

Before 1958, the absolute abundance of total diatoms changed very little, and diatom species were relatively abundant. *C. rhomboideo-elliptica*, which was endemic to the Yunnan Plateau in modern freshwater habitats, existed in the period (Qi 1995). The Dianchi flora and fauna had developed a relatively high degree of endemism before 1958. Endemism is reflected at all levels of the food web and is especially evident in fish. In this period, because anthropogenic impacts were low, diatoms and fish still held a high degree of endemism (Skuja 1937; Ley et al. 1963; Wang and Dou 1998). This indicates that limnological conditions were stable during that time. After 1958, exotic

fish, silver and bighead carp and other fish were introduced into the lake by human impacts (Wang and Dou 1998). In China, the disastrous impacts made by bighead and silver carp have been especially striking in many plateau lakes, where the continuous stocking of fingerlings has taken place on a wide scale since the late 1950s for increasing fish production (Xie and Chen 2001). The invaders have suppressed and in some instances eliminated the native or endemic species (Wang and Dou 1998; Li 2001). After 1958, *F. crotonensis* appeared in Lake Dianchi. The extent of taxa with widespread distributions may be related to human impact (Kociolek and Spaulding 2000). In this period, exotic fish from the Zhujiang and Yangtze River systems were introduced into the lake by humans. *F. crotonensis* was common in the Zhujiang and Yangtze River systems (Qi 1995), so it may have entered into the lake with the introduction of fish and gradually came to thrive in the lake. In this period the relative abundance of *C. dubius* gradually increased, and *A. granulata* and *C. rhomboideo-elliptica* gradually decreased. *C. rhomboideo-elliptica* disappeared gradually after 1974. The increasing relative abundance of *C. dubius* and appearance of *S. minutulus* were a signal that Lake Dianchi had the beginning and the acceleration of eutrophication. These changes may be related to increasing fish production in the lake (Ley et al. 1963; Nanjing Institute of Geography and Limnology 1989). Silver and bighead carp and other introduced fish can cause a significant decline in zooplankton abundance (Xie and Yang 2000). Grazing pressure of diatoms by zooplankton decreased, which made the total diatom abundance increase from 1.94×10^8 to 6.39×10^8 valves g^{-1} from 1958–1985.

Aquatic macrophytes decreased from 90 to 1.8% of the lake area after the 1990s (Yu et al. 2000; Yang et al. 2004a, b). Aquatic macrophytes play a key role in structuring food webs in shallow lakes and in maintaining water transparency by direct and indirect effects on phytoplankton growth (Scheffer et al. 1993; Jeppesen et al. 1998; Van Donk and Van de Bund 2002). Empirical studies undertaken in temperate and some subtropical areas have shown that water transparency is generally high in lakes with high macrophyte cover (Jeppesen et al. 1990; Canfield and Hoyer 1992). In the 1950s, the water transparency of Lake Dianchi was 2 m, whereas it was 0.37–0.48 m in 2000 (Zhu 2004). Decreasing water transparency has an effect on diatom communities. Diatom numbers decreased to nine species, and *C. dubius* became the predominant species after 1985.

Neosalanx taihuensis was largely introduced into the lake in 1979 and became predominant after 1986 (Wang and Dou 1998; Liu and Zhu 1994). After *N. taihuensis* entered the lake, it replaced endemic fish as the predominant fish taxa (Li 2003). The introduced fish, *N. taihuensis*,

has altered the food web. It has been suggested that the effects of zooplankton grazing and fish community structure on phytoplankton are stronger in eutrophic than in mesotrophic shallow lakes (Leibold 1989; Sarnelle 1993; Jeppesen et al. 2000). Schriver et al. (1995) observed in a mesocosm experiment that at increasing fish densities, phytoplankton shifted from small fast-growing species to cyanobacteria and dinoflagellates. With increasing production of *N. taihuensis* (2,319 tons in 1989), phytoplankton shifted from diatoms to Chlorophyta and cyanobacteria in Lake Dianchi (Wei et al. 1994; Luo et al. 2006; Zhang et al. 2006). The structure of the phytoplankton community is not only dependent on grazing pressure by herbivorous animals (the so-called top-down forces), but also is determined by nutrient conditions (the so-called bottom-up forces) (Shapiro 1980). With the development of agriculture, industry and urbanization in the region, increasing sewage discharge has had an effect on the trophic status (Li 2003; Wu et al. 2002). In Lake Dianchi, TN and TP showed substantial increases from 1988 to 2000, ranging from about 1.02 to 11.89 mg/l and 0.109 to 1.06 mg/l, respectively (Meng 1999; Tuo 2002; Mao et al. 2005). Increasing TN and TP concentrations have caused a rapid the outburst of cyanobacteria in Lake Dianchi (Nanjing Institute of Geography and Limnology 1989, Wei et al. 1994). The structure of diatom communities may change during cyanobacteria blooms, which may be due to shading by these blooms (Björk-Ramberg and Ånell 1985; Hansson 1992). *A. granulata* and cyanobacteria blooms grow in summer in Lake Dianchi, so maybe shading by cyanobacteria blooms results in an absolute and relative decrease in the abundance of *A. granulata* (Zhang et al. 2006). *C. dubius* mainly grows in the spring, and it can grow vastly in Lake Dianchi (Zhang et al. 2006). In this period, epiphytic diatoms (e.g., *Gomphonema*, *Gyrosigma* and *Cymbella*) disappeared entirely, which showed that aquatic macrophytes had mostly disappeared (Yang et al. 2004a, b). The results were consistent with the study of aquatic macrophytes in 2000 (Yu et al. 2000). In this period, the diatom number decreased to nine species, showing that Lake Dianchi was hypereutrophic after 1985. These changes in diatom communities implied that Lake Dianchi was a very sensitively poised system that was responsive to small changes in regional conditions as they affected nutrient loading in the lake as well as physical factors.

In conclusion, our study indicated that eutrophication and fish introduction were the most important processes determining diatom abundance, which increased from 1.94×10^8 to 87.3×10^8 valves g^{-1} during 1958–2007, while the number of diatom species decreased from 21 to 9 with the disappearance of aquatic vegetation, indicating that aquatic vegetation had a more important role in

structuring the diatom community in this eutropic plateau lake. It is very difficult, if not impossible, to separate these from each other, because the two overlap, and it is hard to tell whether one or both are affecting the diatom abundance and community. To understand the mechanisms underlying the changes in the structure of the diatom community in Lake Dianchi, Yunnan Plateau, more comprehensive studies are needed.

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