Diatom Response to Global Warming in Lake Douhu, Southeast China

LI Jingjing¹, WANG Luo², CAO Qi³, Patrick RIOUAL ²,⁴, LEI Guoliang⁵,⁶, CAI Binggui⁵,⁶, ZHANG Jiaoyang¹, ZOU Yafei⁷, YAN Yao¹, WAN Xiaqiao¹ and XIAO Jule²,⁷

¹ China University of Geosciences (Beijing), Beijing 100083, China
² Institute of Geology and Geophysics, Chinese Academy of Sciences, Beijing 100029, China
³ School of Geographical Sciences, Fujian Normal University, Fuzhou 350007, China
⁴ CAS Center for Excellence in Life and Paleoenvironment, Beijing 100044, China
⁵ Key Laboratory of Humid Subtropical Eco-geographical Processes of the Ministry of Education, Fujian Normal University, Fuzhou 350007, China
⁶ Institute of Geography, Fujian Normal University, Fuzhou 350007, China
⁷ College of Earth and Planetary Sciences, University of Chinese Academy of Sciences, Beijing 100049, China

Abstract: A large number of lacustrine sedimentary records indicate that global warming is the main factor leading to significant changes in diatom communities in lakes of the northern hemisphere. However, due to the intensification of human activities since AD 1850, some scholars emphasized that the increasing lake trophic level may be the main reason for the changes in diatom communities. The debate is still going on. In order to avoid falling into the complex relationship between diatom changes and the seasonal cycle that characterizes lakes in middle and high latitudes, we chose a lake located at low latitude where the relationship between diatoms and temperature in this lake is not indirect but direct. The diatom record spans the past ca. 100 years and reveals that the abundance of *Aulacoseira granulata* increased from AD 1900 until 1985, and replaced the previously dominant *Aulacoseira ambigua*. These changes are in agreement with the increasing trend in global temperature. Since AD 1985, the percentages of the small-celled *Discostella stelligera* and benthic diatom *Navicula heimansioides* increase while *Aulacoseira granulata* decrease. This latest shift is caused by further global warming. We conclude that warming is the main factor leading to changing diatom communities in Lake Douhu.

Key words: diatom, global warming, recent decades, Lake Douhu, China

E-mail: wangluo@mail.iggcas.ac.cn

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In recent decades, diatom scientists have carried out detailed studies on diatom community changes in a large number of lakes in the northern hemisphere (Lotter and Bigler, 2000; Catalan et al., 2002; Perren et al., 2003, 2009; Rühland et al., 2003, 2008, 2010, 2015; Smol et al., 2005; Harris et al., 2006; Biger et al., 2007; Wang et al., 2008, 2012a, 2012b; Winder and Hunter, 2008; Winder et al., 2009; Douglas and Smol, 2010; Devlin and Finkelstein, 2011; Hobbs et al., 2011; Panizzo et al., 2013; Wischnewski et al., 2014; Yan et al., 2018). The research focuses on the changes of diatom community in the past 100 years (Perren et al., 2003, 2009; Gong et al., 2009; Tsugeki et al., 2010; Panizzo et al., 2013; Chen et al., 2014; Yang et al., 2017; Yan et al., 2018). The key issue of concern is what are the drivers for the changes that have taken place in diatom communities in the past 100 years? These lakes can be divided into two broad types: (1) lakes that have not been significantly affected by human activities (Perren et al., 2003, 2009; Chen et al., 2014; Yan et al., 2018), and (2) lakes that are clearly affected by human activities (Fenn et al., 2003; Hobbs et al., 2010; Hundey et al., 2014). The common characteristics of the first type of lakes is that the abundance of small and medium-sized planktonic diatoms (Cyclotella spp. sensu lato) increases greatly in the most recent past (Sorvari et al., 2002; Rühland et al., 2003; Jones and Birks, 2004; Solovieva et al., 2005; Antoniades et al., 2014). In some of these lakes the biodiversity of benthic diatoms has also significantly increased (Wischnewski et al., 2014, Yan et al., 2018). In the second type of lakes, characteristically the planktonic species, Asterionella formosa and Fragilaria crotonensis, increased significantly in the upper part of the sediment records (Wolfe et al., 2003; Saros et al., 2005, 2012; Bigler et al., 2007; Hobbs et al., 2010; Hyatt et al., 2011; Hadley et al., 2013; Hundey et al., 2014). Therefore, it is widely acknowledged that lacustrine diatom communities in the northern hemisphere have changed greatly in the past 100 years (Perren et al., 2003, 2009; Gong et al., 2009; Tsugeki et al., 2010; Panizzo et al., 2013; Chen et al., 2014; Yang et al., 2017; Yan et al., 2018). However, there are two completely different views on what are the driving factors. One view holds that global warming is the main factor (Sorvari et al., 2002; Perren et al., 2003, 2009; Salmaso, 2005; Rühland et al., 2008; Winder and Sommer, 2012; Chen et al., 2014; Yan et al., 2018), while the other view holds that increasing lake trophic level due to human activities is the main driving factor (Wolfe et al., 2003; Saros et al., 2005, 2012; Bigler et al., 2007; Hobbs et al., 2010; Hyatt et al., 2011; Hadley et al., 2013; Hundey et al., 2014).

On the above issues, a large number of studies have been published in recent years (Wolfe et al., 2003; Saros et al., 2005, 2012; Bigler et al., 2007; Thienepon et al., 2008, 2013; Hobbs et al., 2010; Guinder et al., 2010; Enache et al., 2011; Hobbs et al., 2011; Hyatt et al., 2011; Guilizzoni et al., 2012; Hawryshyn et al., 2012; Medeiros et al., 2012; Schmidt et al., 2012; Hadley et al., 2013; Jones et al., 2013; Panizzo et al., 2013; Wilson et al., 2013; Friel et al., 2014; Hundai et al., 2014; Michelutti et al., 2015). Rühland et al. (2015) conducted a detailed review of this literature, and clearly pointed out through the review that a large number of records show that recent global warming is the main factor leading to significant changes in diatom communities in lakes in the northern hemisphere. However, the debate has still not subsided because industrial activities have been intensifying in the past 100 years, and the abundances of some eutrophic diatoms have indeed increased in some lakes (Wolfe et al., 2003; Saros et al., 2005, 2012; Bigler et al., 2007; Hobbs et al., 2010; Hyatt et al., 2011; Hadley et al., 2013; Hundey et al., 2014).
One of the major problems with lake records from middle and high latitudes is that the climate signal on the diatom assemblages in these ecosystems is mostly indirect, as they are mediated by the effects of the strong seasonality of the climate on the physical characteristics of the water column (ice-cover, mixing, and stratification). In this study, we aim to investigate a subtropical lake system (no ice-cover and ice-free) where the composition of the diatom assemblage is more likely to be directly controlled by temperature, rather than indirectly controlled by temperature, and is dominated by species belonging to the planktonic genus *Aulacoseira*. Several investigations on the autoecology of species of *Aulacoseira*, in particular *Aulacoseira granulata* and *Aulacoseira ambigua* showed that these species directly respond to temperature (Reynolds, 1973; Shear et al., 1976; Reynolds and Reynolds, 1985; Siver and Kling, 1997; Wang et al., 2008; Zou et al., 2018). In this study, we will use the ecological preferences of *Aulacoseira* spp. to discuss the relationship between the changes in diatom community and global warming.

2 Regional Geological Backgrounds

Douhu Lake (25.78° N, 119.07° E, 953 m.a.s.l., Fig. 1) located in Fujian Province, southeast China, is of volcanic origin (Fig. 1). The bedrock of the lake basin is composed of Early Cretaceous quartzite-rhyolite and tuff. The soil types are mainly acidic and red soils derived from intermediate rocks. Douhu Lake is about 300 m long and 100 m wide, with a catchment area of ~0.1 km². The average water depth is ~1 m and the maximum depth is ~2.6 m. It has no natural inflows but there was an outflow on the southern margin (Fig. 1). It is mainly recharged by precipitation and groundwater. A small dam, ~2 m high, was constructed in AD 1973 on the southern shore of the lake to increase the amount of water retained in the lake basin. Currently, only one family lives within the lake basin and no road lead to the lake.
The climate type belongs to the subtropical monsoon climate. The annual average temperature is 19.5°C, the annual precipitation is about 1800 mm and is mostly concentrated in April to September, and the annual average relative humidity is 79% (Lin et al., 2003). Regionally, the vegetation is mainly composed of mixed coniferous and broad-leaved forest, bamboo forest, and shrub and swamp (Li et al., 2003), while the vegetation in the basin of Lake Douhu is mainly composed by grassland.

3 Methods and Results

3.1 Sediment cores and chronology

In 2016, a 72-cm-long sediment core (DH-2016) was retrieved from the central region of the lake using a UWITEC gravity corer at a water depth of 2.1 m. An age model for the upper 60 cm was developed using radiometric $^{210}$Pb, $^{137}$Cs (Fig. 2). The activities of $^{137}$Cs, $^{210}$Pb, and $^{226}$Ra were measured by gamma spectrometry using a low-background well-type germanium detector (EGPC...
100P-15R) at the Institute of Geology and Geophysics, Chinese Academy of Science, Beijing. The counting errors were less than 5 % and 3 % for $^{210}$Pb and $^{137}$Cs, respectively. Radiometric dates were calculated using the constant rate of supply (CRS) $^{210}$Pb dating model (Appleby and Oldfield, 1978; Appleby et al., 1986) and validated using the $^{137}$Cs stratigraphic record, notably the AD 1963 peak that corresponds with the maximum fallout from atmospheric testing of nuclear weapons (Appleby, 2001; Jha et al., 2003). Linear extrapolation was also used to extend the age model to the base of the core at ca. 1911 AD.

![Fig 2. DH-2016 short core $^{137}$Cs, $^{210}$Pb$_{ex}$ and rectified age model diagram.](image)

(a) Changes in the $^{137}$Cs concentration; (b) Changes in the $^{210}$Pb$_{ex}$ concentration; (c) The rectified age model based on the $^{210}$Pb and $^{137}$Cs CRS (Constant Rate of Supply) model.

### 3.2 Diatom analysis

Samples for diatom analysis were prepared following the methods of Battarbee et al. (2001). The samples were oxidized and cleaned, which involved heating approximately 0.05 g of dry sediment with HCl and subsequently with H$_2$O$_2$ to remove carbonates and organic material, respectively. The diatom concentration (valves per gram) of each sample was estimated by adding divinyl benzene microspheres to the cleaned suspensions (Battarbee and Kneen, 1982). Diatom slides were prepared by mounting with Naphrax (refractive Index = 1.7). Diatoms were identified under oil immersion with a phase-contrast light microscope at ×1000 magnification and identified to species level with principal reference to Krammer and Lange-Bertalot (1986-1991) although the taxonomic nomenclature was updated following online flora such as Diatoms of North America and Algaebase. A minimum of 1000 valves was counted for each sample.

106 diatom taxa were recorded in the studied sediment core from Douhu Lake included a few species reported for the first time from China (e.g. *Brevisira arenitii*, *Fragilaria longifusiformis*). Figure 3 shows the most common diatom taxa, expressed as percent relative abundances. Among them, planktonic diatom species include: *Aulacoseira granulata*, *Aulacoseira ambigua*, *Brevisira arenitii*, *Discostella stelligera*, *Fragilaria longifusiformis*. Benthic diatom species include: *Brachysira*
brebissonii, Brachysira liliana, Encyonema neogracile, Encyonema pergracile, Eunotia gallica, Eunotia minor, Frustulia saxonica, Sellaphora arvensis, Navicula heimansioides, Neidium promontorium, Stauroneis cf. madagascariensis, Tabellaria fenestrata. Planktonic diatoms largely dominate the assemblages (>80 % over the whole sequence).

Aulacoseira spp. are dominant throughout the sediment record (>50 %). We can notice that the abundance of A. granulata has increased slowly since AD 1900 in Lake Douhu (Fig. 3). It increased significantly from AD 1940 until it reached its peak in the mid-1980s (about AD 1985) and remained relatively high to AD 2011 when its abundance slightly decreased. At the same time, the abundance of another species, A. ambigua, continued to decrease from 40 % in AD 1900 to about 10 % in AD 2016. A. granulata increased gradually until AD 1985. After that, with increasing warming, the small-celled D. stelligera started to increase, especially from AD 2011, at the same time, N. heimansioides also abruptly increased. All these changes in diatom assemblage match with the result of the stratigraphically constrained zonation of the sequence that was established using CONISS analysis (Fig. 3).

Fig 3. Diatom assemblage changes in core DH-2016 during the last ~100 years.

Only the 15 most abundant taxa were selected (with an abundance of at least 2% and which also occurred in at least two samples) and are plotted in this simplified diagram.

3.3 Numerical analysis

Detrended correspondence analysis (DCA) was undertaken on a reduced dataset of diatom species (those with >1 % relative abundance in any one sample) to establish the magnitude of species turnover over the last century. Relative abundance data were square-root transformed in order to stabilize species variance and rare species were down-weighted. An axis 1 gradient length of 1.1 standard deviation (SD) units indicated that the linear ordination technique of principal components analysis (PCA) was appropriate for subsequent analysis (Leps and Smilauer, 2003). For PCA, only 15 taxa were included in the analysis as a more rigorous screening criterion was employed than for DCA (taxa were...
also deleted unless they occurred in two samples with an abundance of at least 2 %). Relative abundance data were not transformed. Ordination analyses were undertaken using Canoco version 5.0 (ter Braak and Smilauer, 2002).

PCA-axis 1 explains 94.5 % of the variation in diatom assemblages at Douhu Lake while Axis-2 explains only a minor amount of variation (3.8 %) (Fig. 4). A. granulata, F. longifusiformis and D. stelligera have positive species scores along axis 1 (0.99, 0.49 and 0.62) while A. ambigua and B. arentii have negative species scores of − 0.92 and − 0.95, respectively.

Fig 4. Results of principal component analysis (PCA) of the diatom data from core DH-2016.

The position of the arrow is determined by the regression coefficients of the standardized species data with the principal axes. The interpretation of the axes is based on the ecology of diatom species that are most strongly correlated with the axes; see text for explanation. (a) The ordination of main diatom species; (b) The ordination of core samples.

4 Discussions

Previous studies on diatom ecology have shown that many Aulacoseira species are meroplanktonic. Meroplanktonic organisms enter the plankton when mixing conditions are such that they can be suspended and maintained in the water column (Kilham, 1990). Aulacoseira species can adapt to low-light levels that cells experience in a well-mixed water column by increasing the amount of chlorophyll per cell and thus their light-harvesting capacity (Talling, 1957). These species also have resting stages that allow them to survive in the dark when they sink to the sediment surface at the lake bottom (Schelske et al., 1995). Aulacoseira species, such as A. ambigua and A. granulata, also appear to have rather high nutrient requirements (Kilham and Kilham, 1975). During periods of strong wind, the lake thermal stratification breaks down, causing nutrient concentrations to increase and therefore offering conditions for meroplanktonic diatoms to thrive in abundance (Wang et al., 2008, 2012a; Rühland et al. 2008, 2015).

The concentration of total phosphorus (TP) and total nitrogen (TN) is 0.024 and 0.480 mg/l respectively; the lake is strongly phosphorus limited (TN:TP mass ratio = 20). The concentration values for TP and TN indicate that this lake is an oligo- to mesotrophic lake, so in this lake nutrient availability is unlikely to be the main driving factor for the dominance of Aulacoseira spp.. Instead, strong turbulence in Lake Douhu is the main factor causing Aulacoseira spp. to become the dominant species. Turbulence is a ubiquitous hydrodynamic feature of all inland waters, but it is particularly prevalent in shallow lakes (Margalef, 1997). It is determined by wind velocity, and by the resulting turbulent kinetic-energy dissipation rate. The latter strongly depends on depth. In shallow lakes, the
turbulent kinetic-energy content and the turbulent shear forces are much higher, than those in stratified deep lakes (Tóth et al., 2011).

In many sediment records from deep lakes in the high latitudes of the northern hemisphere, the abundance of *Aulacoseira* spp. tends to decrease with global warming, but in Lake Douhu the overall abundance of *Aulacoseira* spp. increased until at least AD 1985. This is obviously different from the changes in lakes in the northern hemisphere. In many deep lakes in the high latitudes of the northern hemisphere, *Aulacoseira* spp. has gradually been replaced by small *Cyclotella* spp. (sensu lato) with the acceleration of global warming. The main reason for this phenomenon is that the duration of the ice-free period of these lakes is prolonged and the summer thermal stratification of these lakes is strengthened due to the increase in temperature. Although the abundance of *Aulacoseira* spp. in Douhu Lake has not decreased since AD 1900, the two species of *Aulacoseira* spp. have completely opposite trends. We think that this shift in species abundance is directly related to the increasing temperature.

Several studies suggested that that the effect of changing temperature on lake diatoms was indirect (Anderson, 2000; Battarbee et al., 2001), exerted by the control of environmental variables that were directly, or indirectly, related to temperature, such as light conditions in the water column (Reynolds, 1984; Maberly et al., 1994), the length of the ice-cover period (Smol, 1988; Lotter and Bigler, 2000; Rühland et al., 2008, 2015; Wang et al., 2012a), lake stratification/mixing mechanisms (Reynolds, 1984; Rühland et al., 2015), and nutrient concentrations (Anderson, 2000; Saros et al., 2003, 2014). Therefore, it has been assumed that in general diatoms are not sensitive to changes in water temperature (Anderson, 2000). However, several studies clearly show that some diatoms, especially among the species of the genus *Aulacoseira*, have marked temperature preference.

Zou et al. (2018) conducted a two-year monitoring program using sediment traps in Yunlong Lake, located in Yunnan in southern China, to study the seasonal changes in diatom assemblages. Diatom data indicate that water temperature was the strongest environmental variable determining the seasonal succession of diatom species in Yunlong Lake. In that lake, the abundance of *A. granulata* increased significantly with increasing water temperature during the warm season (May–November), but decreased significantly with the onset of the cold season. In England, a six-year seasonal diatom survey (1966–1971) on Crose Mere also showed that *A. granulata* was mainly abundant in summer and autumn (Reynolds, 1973).

In addition, the biogeographic distribution of *A. granulata* and its varieties from different latitudes provide evidence for the relatively thermophilic preference of this species. Previous investigations showed that this taxon is widely distributed in tropical and subtropical regions (Kilham and Kilham, 1975; Lewis, 1978; Kilham et al., 1986; Pilskahn and Johnson, 1991; Davies et al., 2002; Wang et al., 2008; Wang et al., 2012b; Nardelli et al., 2016). In addition, in many records from temperate lakes, their bloom periods were often concentrated in summer and autumn, when higher water temperature occurred (Reynolds, 1973; Shear et al., 1976; Reynolds and Reynolds, 1985; Pouličková, 1993). By contrast, in the arctic lakes where it is present *A. granulata* only became abundant in the most recent period when high temperatures are recorded (15–25 °C) (Simola et al., 1990). In summary, despite its wide latitudinal range, *A. granulata* appears to prefer relatively high water temperatures.

In contrast, *A. ambigua*, maintained an overall high relative abundance in Yunlong Lake over the two years, with its highest relative abundance during the cold season. In reservoirs of central China, *A.
*A. ambigua* was also reported to grow rapidly with the decline of temperature in early winter, to reach maximum abundance at a temperature of ~10°C in mid-December and to remain abundant until mid-February (Zhang et al., 2019). Outside China, many studies report that *A. ambigua* can be very abundant in temperate or high-latitude lakes (Holland, 1968; Dean et al., 1984; Bradbury, 1988; Siver and Kling, 1997; Kauppi et al., 2002; Poister et al., 2012).

More specifically, in studies in which both *A. granulata* and *A. ambigua* are reported, their difference in temperature preference is highlighted. For example, Shear et al. (1976) showed that in Rice Lake (USA), *A. granulata* (as *Melosira granulata*) only appeared in summer (~8%) while *A. ambigua* (as *Melosira ambigua*) was dominant for the rest of the year (representing ~80%). Similarly, Snitko et al. (2015) inferred from a large dataset of plankton samples collected in shallow lakes in the mountain-forest zone of the southern Urals (Russia) that *A. ambigua* is a stenothermal cryophilous species while *A. granulata* is a eurythermal thermobiont. All these results indicate that *A. ambigua* is able to grow in lower water temperatures, compared with *A. granulata*-related taxa.

*B. arentii*, the other planktonic species that is abundant at the start of the record follows the same trends as *A. ambigua*. *B. arentii* (previously called *Cylotella arentii* or *Melosira arentii* in the older studies) is commonly found in acid and dystrophic to mesotrophic lakes (Krammer and Lange-Bertalot, 1986–1991) and has also been found in shallow turbid lakes on the Falkland Islands (Flower, 2005). Low pH and high concentrations in dissolved organic carbon (DOC) characterize these waters (Vyverman et al., 1996; Fallu et al., 1999). No thermal preference has been reported for this species in the literature, yet from its biogeographical distribution, *B. arentii* appears to be associated with cool conditions as it is mainly found in the high latitudes of both Hemispheres from Canada (Fallu et al., 1999), northern Finland (Lange-Bertalot and Metzeltin, 1996) and northern Russia (Genkal and Chekryzheva, 2011) to Tasmania (John, 2018) and southern Argentina (Unkel et al., 2010).

By contrast with *B. arentii*, *F. longifusiformis* tends to increase gradually throughout the record. This species was originally described as *Synedra planktonica* from South Carolina (southeastern USA) by Hains and Sebring (1981) and has since been found in Connecticut, north eastern USA (Siver et al., 2005) and Brazil (Ludwig et al., 2015). Note that the similar form reported in large eutrophic rivers from Europe (Siver et al., 2006) is a different taxon as shown by Lange-Bertalot and Ulrich (2014). Besides its apparent preference for dilute, circumneutral waters in oligo- to mesotrophic ponds, lakes and reservoirs (Siver et al., 2005), we do not have autoecological data for *F. longifusiformis*. From its needle-like morphology and light silicification we can however surmise that this planktonic species is more competitive than chain-forming, heavy *Aulacoseira* species in thermally stratified waters due to a lower density and higher coefficient of form resistance to sinking (Reynolds, 2006).

PCA-axis 1 explains 94.5% of the variation in diatom assemblages at Douhu Lake while Axis-2 explains only a minor amount of variation (3.8%) (Fig. 4). *A. granulata, F. longifusiformis* and *D. stelligera* have positive species scores along axis 1 while *A. ambigua* and *B. arentii* have negative species scores of -0.92 and -0.95, respectively. From the autoecologies of the dominant diatoms we infer that the PCA-axis 1 represents a gradient of water temperature (Fig. 4), and that temperature is the main factor that drives the changes observed in the sediment record of Douhu Lake over the past 100 years.

Therefore, we infer that the trends in *A. granulata* and *A. ambigua* observed in the sediment record...
of Lake Douhu reflect directly the variations in temperature at the site. As local temperature increases in Lake Douhu with global warming (Fig. 5), *A. granulata* increased until AD 1980. After that, with further increasing warming, the small-celled *D. stelligera* started to increase.

Figure 5. Comparison between the diatom species responses to warming and the meteorological record.

The annual average air temperature record is from nearby Fuzhou Meteorological Station from AD 1951 to AD 2015.

From AD 1985, although the abundance of *A. ambigua* continued to decrease, the rise of *A. granulata* stopped and its abundance also started to decrease (Fig. 3). From this time on, the changes in diatom community are the same as those of lakes in the temperate and high latitudes of the northern hemisphere. The diatom data from Lake Douhu suggest that the wind decreased and the water stratification increased. In a similar way, the high-resolution sediment record of Huguang Maar Lake (HML) in south China already showed that the lower wind speed associated with the winter monsoon decrease observed since AD 1985 caused stronger stratification in that lake (Wang et al., 2008, 2012a). In the HML diatom record this is also translated by a decrease in the abundance of *Aulacoseira* and a simultaneous increase in *Discostella* spp. (Wang et al., 2008, 2012a).

In Lake Douhu, the shift from *Aulacoseira* to *Discostella* is not caused by the impact of human activity because, as seen earlier, the human presence around the lake was drastically reduced in the AD 1980s when most people of the village were relocated.

It is interesting to note that the benthic component of the assemblages changed very little throughout most of the sediment sequence. This suggests that the water chemistry of Douhu lake changed little and remained that of an acidic and oligotrophic lake. One noticeable change however, is the sharp rise in abundance of the epipelagic species *Navicula heimansioides* since AD 2005. This species is reported to be abundant in Lobelian lakes in Europe (Lange-Bertalot, 2001), which are characterized by clear water and oligotrophic conditions. Therefore, the expansion of this species that colonizes the surface of the sediment at the bottom of the lake suggests more transparent water. This is in agreement with the steady decline of *B. arenii*, which is a species associated with colored water. The more transparent

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water, as indicated by the increase of N. heimansioides is related to the weak mixing and strong stratification caused by global warming, as these conditions lead to much reduced resuspension of sediment from the lake bottom into the water column.

5 Conclusions

A. granulata and A. ambigua are dominant throughout the sediment record of Douhu Lake due to the high turbulence that prevails in this shallow lake. The two species of Aulacoseira spp. have completely opposite trends since AD 1900. The trends in A. granulata and A. ambigua observed in the sediment record of Lake Douhu reflect directly the variations in temperature at the site which match the increasing local temperature in Lake Douhu. We conclude that warming is the main factor leading to changes in diatom communities in Lake Douhu.

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Pb dates assuming a constant rate of supply of unsupported 


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**About the first author**

LI Jingjing, female; born in 1980 in Shenyang City, Liaoning Province; doctor; graduated from Liaoning Normal University; engineer of China University of Geosciences (Beijing). She is now interested in the study on micropaleontology, paleolimnology and global climate change. Email: lijingjing@cugb.edu.cn; phone: 010 – 82322527, 13810498923.
About the corresponding author

Wang Luo, male, born in 1968 in Lhasa City, Tibetan Autonomous Region; doctor, graduated from China University of Geosciences (Wuhan); associate professor of Institute of Geology and Geophysics, Chinese Academy of Sciences. He is now interested in the study on quaternary geology, micropaleontology, paleolimnology and global climate change. Email: wangluo@mail.iggcas.ac.cn; phone: 010–82998261, 15801425176.