Wind induced algal migration manipulates sediment denitrification N-loss patterns in shallow Taihu Lake, China

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Abstract

Driven by winds, the distribution of algae is often noticeably patchy at kilometer scales in shallow lakes. The decomposition of the settled algal biomass may affect N biogeochemical cycles and thereby nitrogen (N) loss in sediments. In this study, we investigated sediment denitrification N-loss patterns along algal migration pathway in Taihu Lake, a shallow and eutrophic lake in China, and found that wind-induced algal migration in the overlying water manipulated the temporal and spatial patterns of denitrification N-loss in sediments. A N loss hotspot in sediments was created in the algae concentrated zone, where N loss was, however, temporarily inhibited during algal bloom seasons and generally exhibited a negative relationship with algal biomass. In the zone where algae have left, sediment N loss rate was relatively low and positively correlated with algal biomass. The decay of algal biomass generated organic carbon and created anoxia, favoring denitrification, while excessive algal biomass could deplete oxygen and inhibit nitrification, causing nitrate limitation for denitrification. Piecewise linear regression analysis indicated that algal biomass of *Chl-a* > 73.0 μg/L in the overlying water could inhibit denitrification N-loss in sediments. This study adds to our understanding of N biogeochemical cycles in shallow eutrophic lakes.

Keywords: denitrification, algal migration, nitrogen loss, sediment, shallow lake

1. Introduction

Human activities have greatly increased nitrogen (N) loading into the environment (Finlay et al., 2013; Horst et al., 2014; Paerl et al., 2011), with damaging effects including eutrophication and subsequent odoriferous algal blooms, water quality degradation and biodiversity reduction (Bianchi et al., 2010; Lewis Jr et al., 2011; Porter et al., 2013). In lakes, there are many nitrogen removal pathways, among which microbial nitrification (NF) and denitrification (DNF) in sediments play a key role in alleviating the negative impacts of excessive N by converting reactive N to gaseous forms and permanent removal them from lakes (Chen et al., 2012; Xia et al., 2016; Xia et al., 2009). In this process, NF is responsible for the oxidation of ammonium (NH_4^+-N) to nitrate (NO_3^--N), which is in turn a substrate for DNF (Gao et al., 2012; Kessler et al., 2013; Xia et al., 2016), and any perturbation on the coupled NF-DNF may alter N loss in the sediment (Gao et al., 2012; Kessler et al., 2013; Small et al., 2014). For instance, anoxia in permeable sediments inhibits NF and thereby breaks the coupled NF-DNF, leading to limited N loss in the hyporheic zone (Kessler et al., 2013; Kessler et al., 2012).

In algae dominated shallow lakes, the DNF-NF in sediments is mediated by the settling of algal biomass from the overlying water. Dissolved inorganic N in the overlying water is assimilated, converted to organic N, and sunk to bed sediments by algae. The degradation of organic N releases NH_4^+-N, which is subsequently oxidized to NO_3^--N through NF and eventually converted back to N_2 through DNF (Kuypers et al., 2018). Meanwhile, this deposition of algae-derived organic carbon results in oxygen consumption, and a transition towards anoxia, a requirement for heterotrophic denitrifying bacteria, and therefore DNF (Conley, 2012; Wang et al., 2016). Thus, sediment N loss, through DNF, is correlated with the accumulation of algal biomass in sediments (Chen et al., 2016). While anoxia/hypoxia favors DNF, it can also inhibit aerobic NF, causing nitrate limitation to DNF. Zhu et al. (2020) found that, when algal biomass was experimentally increased by a factor of 5 and 10, total sediment DNF rates were decreased by 32% and 79%, respectively. Such dense accumulations of algal biomass regularly occur in the shallow lakes, and are often caused by wind-driven algal redistribution (Marcé et al., 2010). This is because many bloom-forming algal species (e.g., *Microcystis* sp.) contain intracellular gas vesicles and are positively buoyant, making them prone to concentrate at the downwind shore (Cyr, 2017; Deng et al., 2016; George and Edwards, 1976). Cyr (2017) demonstrated that algal biomass was higher at the downwind sites than those at the upwind sites on windy days, and the magnitude of this difference increased linearly with increasing wind speed. Dense algal mats are also observed in the downwind northwestern bays following prevailing southeast winds in Taihu Lake, a eutrophic lake in China (Deng et al., 2016; Qin et al., 2010; Zhang et al., 2015). We hypothesize that, in shallow eutrophic lakes, (i) wind-driven algal migration in the overlying water manipulates DNF N-loss patterns in sediments; (ii) sediment DNF N-loss is relatively weak in the zone where algae have left, while it is strong but will be temporally inhibited during algal bloom seasons in the algae concentrated zone; (iii) there exists an algal biomass threshold, and sediment DNF N-loss rate increases beyond the threshold, after which the rate decreases as algal biomass further increases.

To test the hypothesis, we investigated DNF (N_2 gas production) along the algal migration pathway in Taihu Lake, and identity the impacts of algal biomass in the overlying water on sediment DNF N-loss. These rate measurements were combined with a genetic investigation targeted at the microbial pathways responsible for sediment NF and DNF. The objective of this study was to explore the impacts of wind-driven algal migration on sediment N biogeochemical cycling in a shallow and eutrophic lake.

2. Methods and materials

2.1. Study area

Taihu Lake, the 3rd largest freshwater lake (~2,400 km^2) in China. Taihu Lake has a mean depth of 1.9 m, a volume of 4.4 billion m^3 and a mean water retention time of 284 days (Qin et al., 2019). Taihu Lake is located in the Yangtze River delta (the lake center coordinates: 31°10′0″ N, 120° 9′0″ E), which is the most rapidly developing region of China (Figure 1A). The Taihu Basin accounts for only 0.4% of China’s land area, but contributes to 11% of its Gross Domestic Product (GDP) (Xu et al., 2010). Taihu Lake is a key drinking water, fishing and tourism resource for the region, but also serves as a depositional basin for urban, agricultural and industrial segments of the local economy. With recent increases in pollutant (N & P) loadings, Taihu Lake has experienced accelerated eutrophication and severe algal blooms in recent decades. These blooms have caused serious environmental, economic and societal problems, including a threat to drinking water supplies for ~10 million residents. In May 2007, a massive algal bloom overwhelmed the lake’s water treatment plants, leaving more than two million people without drinking water for a week (Paerl et al., 2011; Qin et al., 2019).

2.2. Field surveys

Field samplings were conducted along two hypothetical algal migration pathways from the lake center to two northwestern bays, Meiliang Bay and Gonghu Bay (Figure 1B), through which different amounts of algal biomass are transported. This will be beneficial to quantifying the relationship between algal biomass and DNF rate. There were 6 sampling sites in each corridor, from lake center to each bay, with a shared site at the lake center (11 sites in total), among which the shared site was used to represent lake center, and the site at the end of each corridor was used to represent lake bay, respectively. The distance between two neighboring sites was about 6 km. Six field surveys were conducted in Jan, Apr, Jun, Jul, Aug and Nov (algal bloom period: June-August) of 2018. On the sampling day, surface water (0–20 cm) and sediment were sampled in triplicate at each site using a stainless-steel bucket and an Ekman grab sampler, respectively. A water sample of 500 mL was preserved on ice for the analyses of chlorophyll a (*Chl-a*) and various N species, including total N (TN), NH_4^+-N, NO_3^--N and nitrite (NO_2^--N); after homogenized completely, a sediment sample of 50 g was frozen in liquid N for microbial analysis. Intact sediment cores (9 cm in diameter and 50 cm in height) were also carefully collected at each site in triplicate using a Jenkin corer for measuring sediment N loss rate as described in the following section. N species were analyzed using the Monitoring Analysis Method of Water and Waste Water (Ministry of Environmental Protection of China, 2002). Before the analyses of dissolved N species, water samples were filtered through Whatman GF/F membrane filters. *Chl-a* was determined using the hot ethanol method according to Pápista et al. (2002).

2.3. Sediment net N_2 flux measurements

Sediment net N_2 flux was measured using intact sediment cores (Figure S1) (Heiss et al., 2012). Immediately after collection, sediment cores were transported to the lab at Taihu Lake Laboratory Ecosystem Research Station. When algal accumulation occurs, light hardly reaches bed sediments under dense algal canopies (Thomsen et al., 2012), these sediment cores were therefore incubated in the dark in a water bath at the field temperature. Sediment cores were carefully sealed with a gas-tight rubber lid without air bubbles, and left to stand for 10 min to ensure equilibrium according to our preliminary experiments. Considering oxygen and substrates may change in the sealed system, potentially affecting the measured value, we collected samples in a short time to maintain DO above 2 mg/L. Water samples were collected every 5 min over a 20-min period and stored into a 12-mL pre-evacuated Exetainer® vial (839 W, Labco, UK) after adding 0.2 μL saturated $HgCl_2$ solution. Net DNF rates were calculated based on the linear rate of N_2 accumulation in the overlying water as a function of time. The concentration of dissolved N_2 was measured by the N_2/Ar method using a membrane inlet mass spectrometry system (Bay Instruments, Easton, MD, USA). These net N_2 flux measurements may represent the balance between N_2 fixation and DNF. However, sediment N fixation in these bays was estimated to be only 1.8% of sediment N loss via dentrification (Yao et al., 2018). We argue that these net N_2 flux measurements to be representative of potential DNF rates.

2.4. Microbial abundance analysis

The abundances of nitrifiers and denitrifiers in sediments were analysed using quantitative polymerase chain reaction method (qPCR). There are many functional genes involved in NF and DNF processes (Kuypers et al., 2018), of which *amoA*, *nirS*, *nirK* and *nosZ* were chosen as gene markers in this study. The *amoA* is a gene marker of ammonia-oxidizing bacteria, which are sensitive indicators of NF and play a more important role in the NF in Taihu Lake (Hou et al., 2015); *nirS*, *nirK* and *nosZ* are commonly used gene markers of denitrifiers, which encode nitric oxide reductase, nitrite reductase and nitrous oxide reductase, respectively (Hou et al., 2015; Li et al., 2019; Morales et al., 2010). Prior to analyses, sediment samples were stored at -80°C. DNA was extracted for qPCR amplification using a FastDNA Power-Max Soil DNA Isolation Kit (MP Biomedical, USA) according to the manufacturer's instructions. The detailed information for qPCR was presented in Text S1 in the supporting information.

2.5. Statistical analysis

Piecewise linear regression model was employed to investigate the impacts of algal biomass in the overlying water on sediment N loss. Piecewise linear regression can identify where the slope of a linear function changes and allow multiple linear models to be fitted to each distinct section (Turner et al., 2018; Zeng et al., 2019). To avoid the disturbances caused by temperature, data at the 11 sampling sites in July and August were used here, when water temperature showed no significant differences (Table S1). Piecewise linear regression analysis was conducted using MATLAB (MathWorks, USA). T-test was applied to test the differences between lake bay and the center using SPSS 22.0 (SPSS Inc., North Chicago, IL, USA). The level of statistical significance was set at $P < 0.05$.

3. Results

3.1. *Chl-a* and TN in the overlying water

In general, there was a remarkable increasing trend of algal biomass in the overlying water from the lake center to lake bays, especially during the algal accumulation season (Figure 2A). *Chl-a* increased from 8.7–15.6 μg/L in lake center to 22.7–56.3 μg/L in Meiliang Bay (M5) and 18.5–25.7 μg/L in Gonghu Bay (G5) during the non-algal bloom period (Nov-Apr), and increased from 13.5–18.1 μg/L in the lake center to 136.5–227.3 μg/L in Meiliang Bay (M5) and 54.9–112.2 μg/L in Gonghu Bay (G5) during the algal bloom period (Jun-Aug). Similarly, TN concentration in the bays was higher than in the lake center, especially during the algal bloom period. TN in Meiliang Bay (M5) and Gonghu Bay (S5) was 1.75–1.96 and 1.77–2.33 mg/L, respectively, during the non-algal bloom period. TN in these bay sites then reached maximal values of 3.83 and 2.34 mg/L during the algal bloom period, while TN in the lake center remained relatively consistent at 1.05–2.12 mg/L throughout the year (Figure 2B).

3.2. Sediment N loss rate

Net DNF rates in the lake bays was remarkably higher than at the lake center, and also showed different temporal patterns than trends at the lake center (Figure 3). In the lake bays, sediment N loss rate was higher during the non-algal bloom period than the algal bloom period, while, in the lake center, the rate was slightly lower during non-algal bloom period than the algal bloom period. Sediment N loss rate reached 2.22–2.51 and 1.11–1.26 mg/m^{2}h during the non-algal bloom period and decreased to 0.34–0.67 and 0.66–1.06 mg/m^{2}h during the algal bloom period in the Meiliang Bay and Gonghu Bay respectively. In contrast, sediment N loss rate in the lake center was 0.09 mg/m^{2}h during the non-algal bloom period and increased to a maximum of 0.42 mg/m^{2}h during the algal bloom period (Figure 3).

3.3. Relationship between N loss rate and algal biomass

Sediment N loss rate as a function of time showed an opposite pattern to algal biomass in the overlying water in Meiliang Bay and Gonghu Bay (Figure 4B), but a similar pattern with algal biomass in the lake center (Figure 4A). Correlation analysis indicated that sediment N loss rate exhibited a negative relationship with algal biomass in the overlying water in Meiliang Bay (r^2 = 0.41) and Gonghu Bay (r^2 = 0.66) (Figure 4D), but a positive relationship with algal biomass in the lake center (r^2 = 0.70) (Figure 4C). Piecewise linear regression analysis was further conducted, indicating that sediment N loss rate increased beyond a threshold of 73.0 μg/L, after which N loss rate decreased as algal biomass further increased (Figure 5).

3.4. Relationship between functional microbes and algal biomass

The abundances of nitrifiers and denitrifiers in sediments exhibited similar relationships with algal biomass in the overlying water (Figure 6). In both cases, the abundance remarkably increased at low levels of algal biomass and then gradually decreased as algal biomass further increased. The decreased microbe abundances mainly occur in algae concentrated lake bays.

4. Discussion

In lakes, wind can cause waves and subsequent advective movement of superficial water masses (Marce et al., 2007). When wind interacts with the lake surface, there is an energy transfer from the air towards the water, as mediated by wave-induced friction at the air-water interface. In shallow lakes, there is little space for wave energy to dissipate, and waves often have high turbulent kinetic-energy, initiating passive ‘migration’ of algal biomass (Wüest et al., 2000). The distribution of algae is noticeably patchy at kilometer scales in shallow eutrophic lakes, in part due to this factor (Deng et al., 2016; Huang et al., 2015). In Taihu Lake, there is a subtropical monsoon climate with prevailing southeast winds, continuously transporting algal biomass by this mechanism towards downwind, northwestern bays (Deng et al., 2016). Accordingly, we detected a remarkable increasing trend of algal biomass in the overlying water from the lake center to Meiliang and Gonghu Bay during the algal accumulation season (Jun-Aug) (Figure 2A).

By algae, dissolved inorganic N (NH_4^+-N and NO_3^--N) in the overlying water is assimilated, converted to organic N, and eventually sunk to lake bed sediments. This transport of algal biomass results in the re-location of large amounts of N together with fixed organic carbon to northwestern bays. In line with this, we observed significant increases in TN from the lake center to Meiliang Bay and Gonghu Bay (Figure 2B), and NO_3^--N and NH_4^+-N limitation in the overlying water during algal bloom period due to algae assimilation (Figure S2). The decomposition of this organic matter likely releases labile carbon substrates and consumes oxygen, creating favorable conditions for DNF in sediments. Low oxygen and availability of carbon result in converting algae concentrated zone into the hotspot of N loss by DNF. Due to frequent disturbances induced by winds, water column is difficult to be anoxia (Gao et al., 2017). We argue oxygen penetrated into sediments controls denitrification in sediments. Since the microelectrode needle is easily broken by hard stones in fields, we conducted incubation experiment to analyze responses of sediment oxygen profile to algal biomass, and found that the settlement of algal biomass can decrease oxygen penetration depth quickly in the surface sediment (Figure S3). In contrast, in the area where algae have left, sediment N loss was week due to the limited availability of necessary substrate, namely NO_3^--N and labile organic carbon. Thus, sediment N loss rates generally showed an increasing pattern from the lake center to the algae concentrated bays (Figure 3), and a similar temporal pattern with algal biomass in the lake center, where the rate was slightly lower during non-algal bloom period than the algal bloom period (Figure 4). Bernhardt (2013) outlined a paradigm where lakes need to be dirty (rich in nutrients) in order to support algal biomass at levels sufficient to fuel DNF for N removal. In shallow lakes, it is argued that wind-driven algal migration can effectively concentrate algal biomass into a ‘dirty zone’ where N removal might be maximized. Large amounts of N assimilated into the tissues of algal biomass were transported to this N removal region to be efficiently denitrified.

As a saying goes “A little wind kindles, much puts out the fire”. If algae accumulate into dense mats, the decay of excessive algal biomass can deplete oxygen and limit oxygen penetration into sediments, causing severe anoxia (Karim et al., 2002; Zhu et al., 2020). Sediment incubation experiment indicated surface sediment suffered a longer anoxia period after more algal biomass settled (Figure S3). In the field, severe anoxia in bed sediments may persist for the entire algal bloom season due to persistent wind-driven algal biomass inputs. This persistent anoxia can inhibit NF and cause NO_3^--N limitation on DNF, causing a break in coupled NF-DNF. We observed this to occur, and found that the effect was enhanced as algal biomass increased, suggesting that at high concentrations of algae, NO_3^--N likely limited DNF. This explains higher sediment N loss rate during the non-algal bloom period than the algal bloom period in lake bays. During the algal bloom season, nitrifiers and denitrifier abundances were relatively poor in the algae concentrated Meiliang Bay and Gonghu Bay (Figure 6). In the algae concentrated Meiliang Bay and Gonghu Bay, sediment N loss rates were negatively correlated with algal biomass (Figure 4D), and exhibited an opposite pattern with algal biomass as compared to the center of the lake (Figure 4B). The N loss rates in the lake bays were even lower in the hot summer than those in the cool winter, even lower than those in the algae-poor lake center (Figure 3). In sediments, direct DNF may also contribute to N loss, which is supposed to be enhanced by rich organic carbon and anoxia in the algae concentrated zone. Thus, we attributed the inhibited N loss to the breaking of the coupled NF-DNF. As anoxia receded post algal blooms, the coupled NF-DNF restarts, and the negative impacts of excessive algal biomass can weaken or disappear later, as seen in the increased N loss rate in the fall months (Figure 3). In contrast, in the lake center where algae have left, sediment N loss rates were positively correlated with algal biomass (Figure 4C) and showed a similar pattern with algal biomass (Figure 4A), suggesting that carbon availability may limit DNF under these conditions. Piecewise linear regression analysis indicated that, when algal biomass is over 70 μg/L, sediment N loss will be inhibited during algal bloom seasons in this study (Figure 5). Although the threshold may change in association with field conditions (temperature, turbulence intensity, etc.), it is possibly that, in portions of this eutrophic lake where wind-driven algal accumulations occur, water quality recovery is temporally prevented by the breaking of coupled NF-DNF, causing the redistribution of N removal amount over the whole year.

N biogeochemical cycles in lakes are complex, and many factors affect N loss in bed sediments, including zoobenthos and catchment features (Bonaglia et al., 2014; Nizzoli et al., 2018). In this study, we demonstrated that wind driven algal migration in the overlying water plays a key role in shaping sediment N loss patterns in shallow lakes. Algal migration created N loss hotspot in the algae concentrated zone. However, sediment N loss in this zone was inhibited during algal bloom seasons, and exhibited a negative relationship with algal biomass in the overlying water, which we associate with a broken link between NF and DNF. In the zone where algae have left, sediment N loss rates were relatively low and showed an increasing trend as algal biomass in the overlying water increased, suggesting an effective yet slow N removal process. By contrast, in deeper lakes, a larger fraction of algal biomass can be decomposed during the relatively long sinking time (Tammeorg et al., 2013). This may potentially result in algal blooms having a relatively smaller impact on sediment N processing in larger lakes, although it may also be that the associated impacts simply occur instead in the overlying water, a subject deserving of further study.

5. Conclusions

In this study, we investigated sediment DNF patterns along algal migration pathway in Taihu Lake, a shallow and eutrophic lake in China. The main findings are as follows:

(1) Wind driven algal migration in the overlying water manipulated DNF patterns in sediments in shallow lakes.

(2) A N loss hotspot in sediments was created in the algae concentrated zone, where N loss was, however, temporarily inhibited during algal bloom seasons and generally exhibited a

negative relationship with algal biomass.

(3) In the zone where algae have left, sediment N loss rate was relatively low and positively correlated with algal biomass.

(4) There is an algal biomass threshold. The sediment DNF rate increases beyond the threshold and decreases after the threshold.

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References

Bernhardt, E.S. 2013. Cleaner lakes are dirtier lakes. Science 342(6155), 205-206.

Bianchi, T.S., DiMarco, S., Cowan Jr, J., Hetland, R., Chapman, P., Day, J. and Allison, M. 2010. The science of hypoxia in the Northern Gulf of Mexico: a review. Sci Total Environ 408(7), 1471-1484.

Bonaglia, S., Nascimento, F.A., Bartoli, M., Klawonn, I. and Brüchert, V. 2014. Meiofauna increases bacterial denitrification in marine sediments. Nature Communications 5(1), 1-9.

Chen, X., Jiang, H., Sun, X., Zhu, Y. and Yang, L. 2016. Nitrification and denitrification by algae-attached and free-living microorganisms during a cyanobacterial bloom in Lake Taihu, a shallow Eutrophic Lake in China. Biogeochemistry 131(1-2), 135-146.

Chen, X., Yang, L., Xiao, L., Miao, A. and Xi, B. 2012. Nitrogen removal by denitrification during cyanobacterial bloom in Lake Taihu. J Freshwater Ecol 27(2), 243-258.

China, M.o.E.P.o. (2002) The monitoring analysis method of water and wastewater, China Environmental Science Press, Beijing.

Conley, D.J. 2012. Ecology: save the Baltic Sea. Nature 486(7404), 463-464.

Cyr, H. 2017. Winds and the distribution of nearshore phytoplankton in a stratified lake. Water Research 122, 114-127.

Deng, J., Chen, F., Liu, X., Peng, J. and Hu, W. 2016. Horizontal migration of algal patches associated with cyanobacterial blooms in an eutrophic shallow lake. Ecological Engineering 87, 185-193.

Finlay, J.C., Small, G.E. and Sterner, R.W. 2013. Human influences on nitrogen removal in lakes. Science 342(6155), 247-250.

Gao, H., Qian, X., Wu, H., Li, H., Pan, H., and Han, C. 2017. Combined effects of submerged macrophytes and aquatic animals on the restoration of a eutrophic water body-a case study of Gonghu Bay, Lake Taihu. Ecological Engineering 102, 15-23.

Gao, Y., Cornwell, J., Stoecker, D. and Owens, M. 2012. Effects of cyanobacterial-driven pH increases on sediment nutrient fluxes and coupled nitrification-denitrification in a shallow fresh water estuary. Biogeosciences 9(7), 2697-2710.

George, D.G. and Edwards, R.W. 1976. The Effect of Wind on the Distribution of Chlorophyll A and Crustacean Plankton in a Shallow Eutrophic Reservoir. Journal of Applied Ecology 13(3), 667.

Heiss, E.M., Fields, L. and Fulweiler, R.W. 2012. Directly measured net denitrification rates in offshore New England sediments. Continental Shelf Research 45, 78-86.

Horst, G.P., Sarnelle, O., White, J.D., Hamilton, S.K., Kaul, R.B. and Bressie, J.D. 2014. Nitrogen availability increases the toxin quota of a harmful cyanobacterium, Microcystis aeruginosa. Water research 54, 188-198.

Hou, J., Song, C., Cao, X. and Zhou, Y. Shifts between ammonia-oxidizing bacteria and archaea in?relation to nitrification potential across trophic gradients in?two large Chinese lakes (Lake Taihu and Lake Chaohu). Water Research 47(7), 2285-2296.

Hou, L., Yin, G., Liu, M., Zhou, J., Zheng, Y., Gao, J., Zong, H., Yang, Y., Gao, L. and Tong, C. 2015. Effects of sulfamethazine on denitrification and the associated N2O release in estuarine and coastal sediments. Environmental science & technology 49(1), 326-333.

Huang, C., Shi, K., Yang, H., Li, Y., Zhu, A.x., Sun, D., Xu, L., Zou, J. and Chen, X. 2015. Satellite observation of hourly dynamic characteristics of algae with Geostationary Ocean Color Imager (GOCI) data in Lake Taihu. Remote Sensing of Environment 159, 278-287.

Karim, M.R., Sekine, M. and Ukita, M. 2002. Simulation of eutrophication and associated occurrence of hypoxic and anoxic condition in a coastal bay in Japan. Marine Pollution Bulletin 45(1), 280-285.

Kessler, A.J., Glud, R.N., Cardenas, M.B. and Cook, P.L.M. 2013. Transport zonation limits coupled nitrification-denitrification in permeable sediments. Environmental Science & Technology 47(23), 13404-13411.

Kessler, A.J., Glud, R.N., Cardenas, M.B., Larsen, M., Bourke, M.F. and Cook, P.L. 2012. Quantifying denitrification in rippled permeable sands through combined flume experiments and modeling. Limnology and Oceanography 57(4), 1217-1232.

Kuypers, M.M., Marchant, H.K. and Kartal, B. 2018. The microbial nitrogen-cycling network. Nature Reviews Microbiology 16(5), 263.

Lewis Jr, W.M., Wurtsbaugh, W.A. and Paerl, H.W. 2011. Rationale for control of anthropogenic nitrogen and phosphorus to reduce eutrophication of inland waters. Environmental science & technology 45(24), 10300-10305.

Li, J., Wang, J.-T., Hu, H.-W., Cai, Z.-J., Lei, Y.-R., Li, W., Zhang, M.-Y., Li, Z.-M., Zhu, Y.-N. and Cui, L.-J. 2019. Changes of the denitrifying communities in a multi-stage free water surface constructed wetland. Science of the Total Environment 650, 1419-1425.

Marcé, R., FEIJOó, C., NAVARRO, E., ORDO?EZ, J., GOMà, J. and ARMENGOL, J. 2010. Interaction between wind-induced seiches and convective cooling governs algal distribution in a canyon-shaped reservoir. Freshwater Biol 52(7), 1336-1352.

Marce, R., Feijoo, C., Navarro, E., Ordonez, J., Goma, J. and Armengol, J. 2007. Interaction between wind-induced seiches and convective cooling governs algal distribution in a canyon-shaped reservoir. Freshwater Biology 52(7), 1336-1352.

Morales, S.E., Cosart, T. and Holben, W.E. 2010. Bacterial gene abundances as indicators of greenhouse gas emission in soils. The ISME Journal 4(6), 799-808.

Nizzoli, D., Bartoli, M., Azzoni, R., Longhi, D., Castaldelli, G. and Viaroli, P. 2018. Denitrification in a meromictic lake and its relevance to nitrogen flows within a moderately impacted forested catchment. Biogeochemistry 137(1), 143-161.

Paerl, H.W., Xu, H., McCarthy, M.J., Zhu, G., Qin, B., Li, Y. and Gardner, W.S. 2011. Controlling harmful cyanobacterial blooms in a hyper-eutrophic lake (Lake Taihu, China): the need for a dual nutrient (N & P) management strategy. water research 45(5), 1973-1983.

Pápista, É., Ács, É. and Böddi, B. 2002. Chlorophyll-a determination with ethanol – a critical test. Hydrobiologia 485(1), 191-198.

Porter, E.M., Bowman, W.D., Clark, C.M., Compton, J.E., Pardo, L.H. and Soong, J.L. 2013. Interactive effects of anthropogenic nitrogen enrichment and climate change on terrestrial and aquatic biodiversity. Biogeochemistry 114(1), 93-120.

Qin, B., Paerl, H.W., Brookes, J.D., Liu, J., Jeppesen, E., Zhu, G., Zhang, Y., Xu, H., Shi, K. and Deng, J. 2019. Why Lake Taihu continues to be plagued with cyanobacterial blooms through 10 years (2007–2017) efforts. Science Bulletin 64(6).

Qin, B., Zhu, G., Gao, G., Zhang, Y., Li, W., Paerl, H.W. and Carmichael, W.W. 2010. A Drinking Water Crisis in Lake Taihu, China: Linkage to Climatic Variability and Lake Management. Environ Manage 45(1), 105-112.

Small, G.E., Cotner, J.B., Finlay, J.C., Stark, R.A. and Sterner, R.W. 2014. Nitrogen transformations at the sediment–water interface across redox gradients in the Laurentian Great Lakes. Hydrobiologia 731(1), 95-108.

Tammeorg, O., Niemistö, J., Möls, T., Laugaste, R., Panksep, K. and Kangur, K. 2013. Wind-induced sediment resuspension as a potential factor sustaining eutrophication in large and shallow Lake Peipsi. Aquatic sciences 75(4), 559-570.

Thomsen, M. S., De Bettignies, T., Wernberg, T., Holmer, M., and Debeuf, B. 2012. Harmful algae are not harmful to everyone. Harmful Algae, 16, 74-80.

Turner, B.L., Brenes-Arguedas, T. and Condit, R. 2018. Pervasive phosphorus limitation of tree species but not communities in tropical forests. Nature 555(7696), 367-370.

Wang, H., Dai, M., Liu, J., Kao, S.J., Zhang, C., Cai, W.J., Wang, G., Qian, W., Zhao, M. and Sun, Z. 2016. Eutrophication-Driven Hypoxia in the East China Sea off the Changjiang Estuary. Environmental Science & Technology 50(5), 2255.

Wüest, A., Piepke, G. and Van Senden, D.C. 2000. Turbulent kinetic energy balance as a tool for estimating vertical diffusivity in wind-forced stratified waters. Limnology and Oceanography 45(6), 1388-1400.

Xia, X., Jia, Z., Liu, T., Zhang, S. and Zhang, L. 2016. Coupled nitrification-denitrification caused by suspended sediment (SPS) in rivers: importance of SPS size and composition. Environmental science & technology 51(1), 212-221.

Xia, X., Yang, Z. and Zhang, X. 2009. Effect of suspended-sediment concentration on nitrification in river water: importance of suspended sediment− water interface. Environmental science & technology 43(10), 3681-3687.

Xu, H., Paerl, H.W., Qin, B., Zhu, G. and Gaoa, G. 2010. Nitrogen and phosphorus inputs control phytoplankton growth in eutrophic Lake Taihu, China. Limnology and Oceanography 55(1), 420-432.

Yao, X., Zhang, L., Zhang, Y., Zhang, B., Zhao, Z., Zhang, Y., Li, M. and Jiang, X. 2018. Nitrogen fixation occurring in sediments: contribution to the nitrogen budget of Lake Taihu, China. Journal of Geophysical Research: Biogeosciences 123(9), 2661-2674.

Zeng, Z., Ziegler, A.D., Searchinger, T., Yang, L., Chen, A., Ju, K., Piao, S., Li, L.Z., Ciais, P. and Chen, D. 2019. A reversal in global terrestrial stilling and its implications for wind energy production. Nature Climate Change 9(12), 979-985.

Zhang, Y., Ma, R., Min, Z., Duan, H., Loiselle, S. and Xu, J. 2015. Fourteen-Year Record (2000–2013) of the Spatial and Temporal Dynamics of Floating Algae Blooms in Lake Chaohu, Observed from Time Series of MODIS Images. Remote Sensing 7(8), 10523-10542.

Zhu, L., Shi, W., Van Dam, B., Kong, L., Yu, J. and Qin, B. 2020. Algal Accumulation Decreases Sediment Nitrogen Removal by Uncoupling Nitrification-Denitrification in Shallow Eutrophic Lakes. Environmental Science & Technology 54(10), 6194-6201.

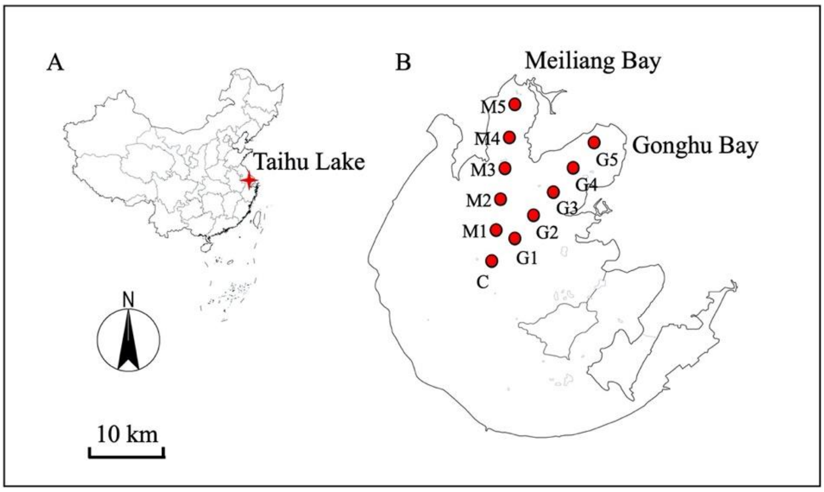

Figure 1. Map of Taihu Lake and locations of sampling sites in this study. Insert shows the location of Taihu in China.

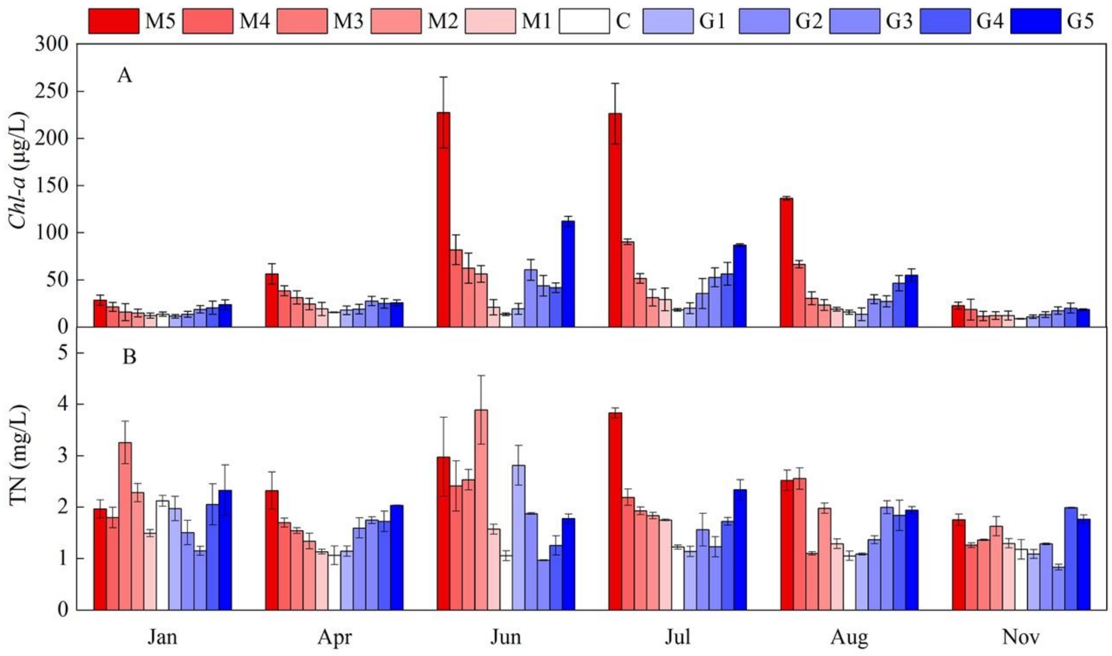

Figure 2. Temporal and spatial patterns of *Chl-a* and TN in the surface water along wind-driven algal migration pathway. (A) *Chl-a*; (B) TN. Error bars indicate standard deviations.

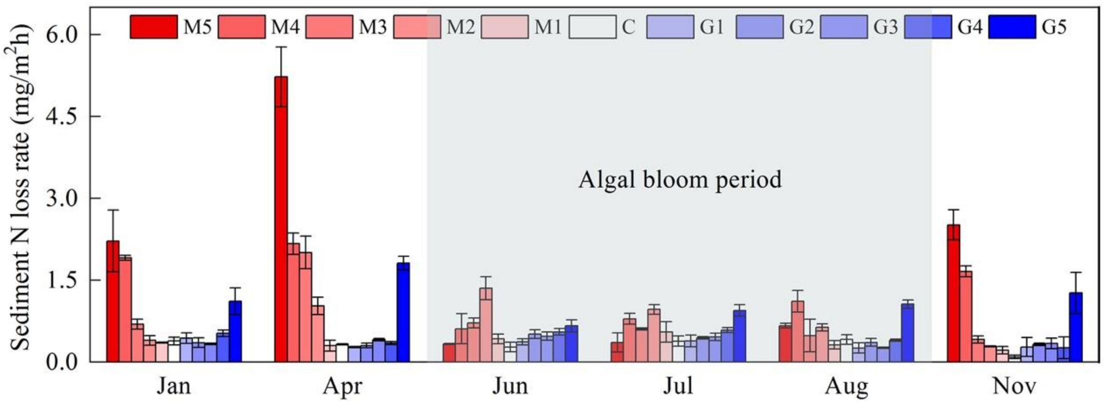

Figure 3. Temporal and spatial patterns of sediment N loss rate along algal migration pathway. Error bars indicate standard deviations.

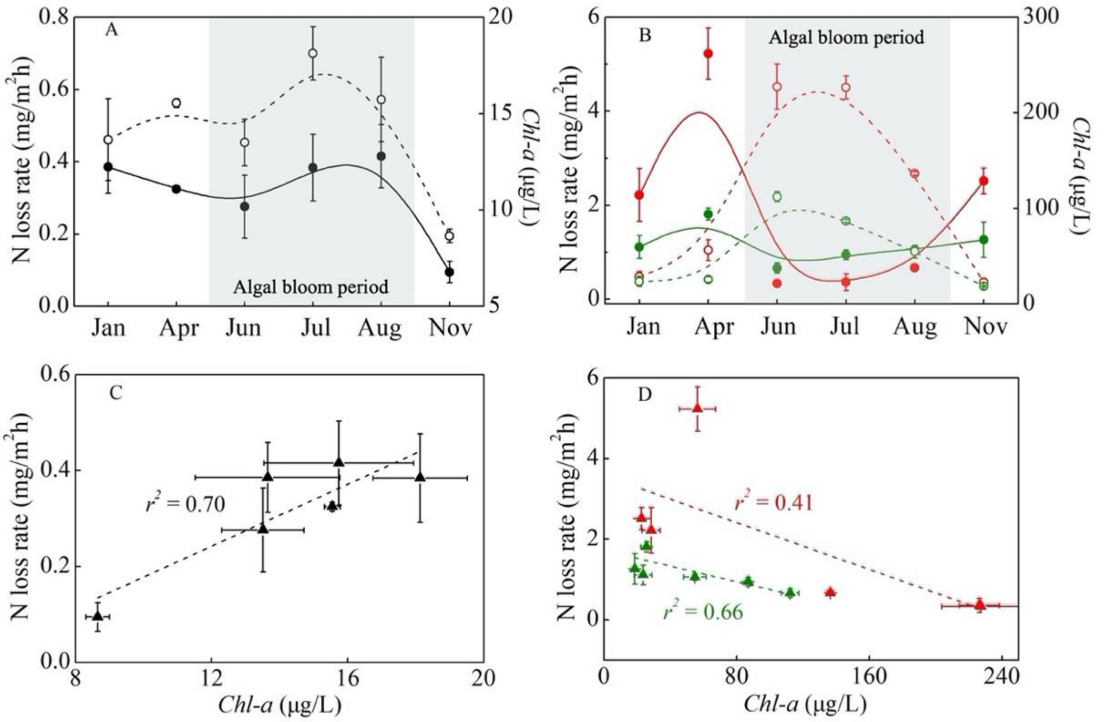

Figure 4. N loss pattern in bed sediments and its relationship with algal biomass in the overlying water. In figure 4A and 4B, the black, red and olive circles indicate lake center, Meiliang Bay and Gonghu Bay, respectively, of which solid circles indicate N loss rate and open circles indicate *Chl-a*. The lines were obtained using the B-spline model. In figure 4C and 4D, the black, red and olive triangles indicate lake center, Meiliang Bay and Gonghu Bay, respectively. Error bars indicate standard deviations.

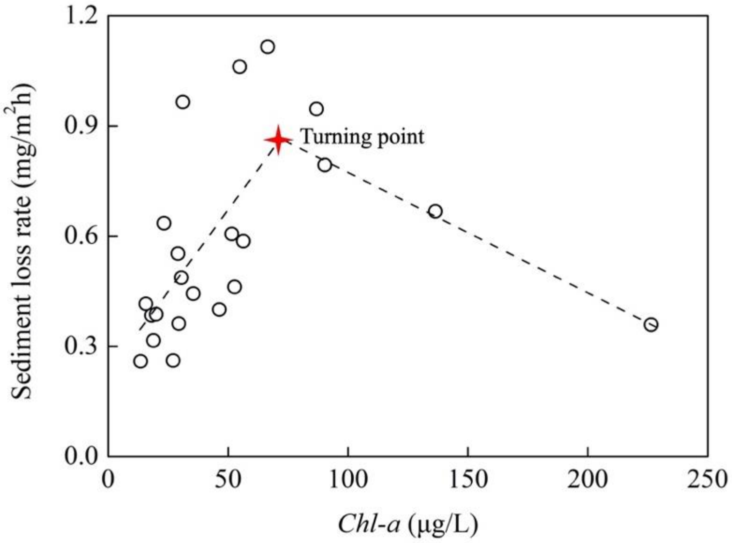

Figure 5. Changes of N loss rate in sediments as a function of algal biomass in the overlying water. To avoid the disturbances caused by temperature, data were from all of sampling sites in July and August, when water temperature showed no significant differences (Table S1).

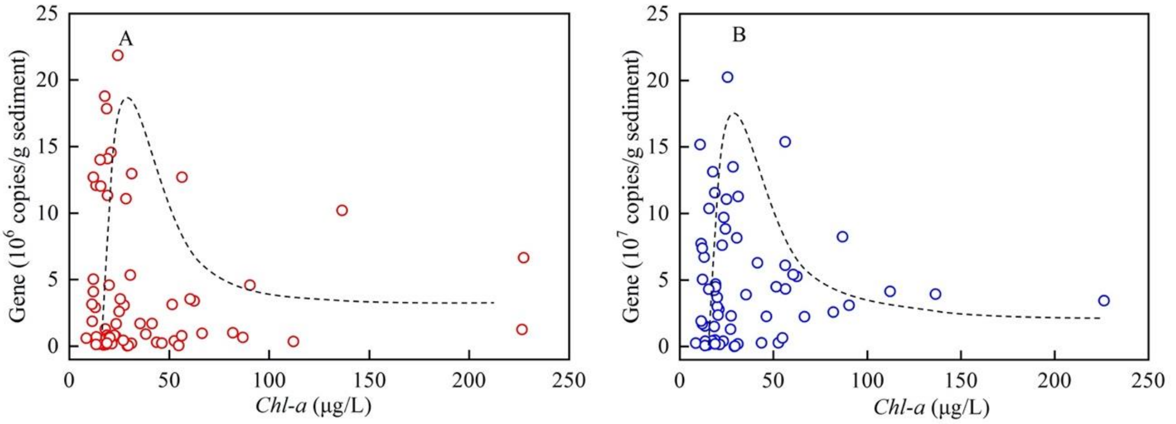

Figure 6. The relationship between nitrifier and denitrifier abundances in sediments and *Chl-a* in the overlying water. (A) Nitrifiers; (B) Denitrifiers. The abundance of nitrifiers was the sum of *amoA* and *arch-amoA*, and the abundance of denitrifiers was the sum of *nirS*, *nirK* and *nosZ* genes.