Controlling harmful cyanobacterial blooms in a hyper-eutrophic lake (Lake Taihu, China): The need for a dual nutrient (N & P) management strategy

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Abstract
Harmful cyanobacterial blooms, reflecting advanced eutrophication, are spreading globally and threaten the sustainability of freshwater ecosystems. Increasingly, non-nitrogen (N₂)-fixing cyanobacteria (e.g., Microcystis) dominate such blooms, indicating that both excessive nitrogen (N) and phosphorus (P) loads may be responsible for their proliferation. Traditionally, watershed nutrient management efforts to control these blooms have focused on reducing P inputs. However, N loading has increased dramatically in many watersheds, promoting blooms of non-N₂ fixers, and altering lake nutrient budgets and cycling characteristics. We examined this proliferating water quality problem in Lake Taihu, China’s 3rd largest freshwater lake. This shallow, hyper-eutrophic lake has changed from bloom-free to bloom-plagued conditions over the past 3 decades. Toxic Microcystis spp. blooms threaten the use of the lake for drinking water, fisheries and recreational purposes. Nutrient addition bioassays indicated that the lake shifts from P limitation in winter–spring to N limitation in cyanobacteria-dominated summer and fall months. Combined N and P additions led to maximum stimulation of growth. Despite summer N limitation and P availability, non-N₂ fixing blooms prevailed. Nitrogen cycling studies, combined with N input estimates, indicate that Microcystis thrives on both newly supplied and previously-loaded N sources to maintain its dominance. Denitrification did not relieve the lake of excessive N inputs. Results point to the need to reduce both N and P inputs for long-term eutrophication and cyanobacterial bloom control in this hyper-eutrophic system.

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1. Introduction
Harmful (toxic, food web-disrupting) cyanobacterial blooms (CyanoHABs) are a troubling indicator of advanced eutrophication. These blooms are increasing worldwide and represent a serious threat to drinking water supplies, and the ecological and economic sustainability of our largest freshwater ecosystems (Reynolds, 1987; Paerl, 1988; Carmichael,
algal bloom potentials (Schindler, 1977). However, nutrient reductions have slowed eutrophication rates and reduced treatments have been implemented widely since the 1960s. These a volume of 4.4 billion m$^3$ (Pu and Yan, 1998; Qin et al., 2007, (Likens, 1972) and CyanoHAB bloom formation (Paerl, 1988, a central role in the control of freshwater primary production problem. The answer to this question is of immense ecological and economic importance, because it dictates the strategies and costs involved in mitigating this serious water quality problem.

Phosphorus has been implicated traditionally as having a central role in the control of freshwater primary production (Likens, 1972) and CyanoHAB bloom formation (Paerl, 1988, 2008). This conclusion is particularly relevant to nutrient (N$_2$) fixing CyanoHABs, since they may satisfy their own N requirements (Smith, 1983, 1990). As a result, P input restrictions have been implemented widely since the 1960s. These reductions have slowed eutrophication rates and reduced algal bloom potentials (Schindler, 1977). However, nutrient loading dynamics have changed considerably since the 1960s. Agricultural, urban and industrial sources have accelerated rapidly (Vitousek et al., 1997; Galloway and Cowling, 2002). These sources are treated more effectively for removal of P than N before being discharged, leading to higher N than P loading to already nutrient-stressed water bodies (Paerl, 1997; Rabalais, 2002; Boyer et al., 2004). Excessive N loads have promoted non-N$_2$ fixing CyanoHABs, including expanding blooms of the toxin producing, colonial, surface-dwelling (buoyant) cya

A severely impacted large lake system is Taihu (meaning "great lake" in Mandarin), with an area of 2338 km$^2$ and a volume of 4.4 billion m$^3$ (Pu and Yan, 1998; Qin et al., 2007, 2010). This shallow (mean depth 1.9 m) polymictic lake is located in the Yangtze River delta; the most rapidly developing region in China (Fig. 1). Approximately 40 million people live within the Taihu watershed. The Taihu Basin accounts for only 0.4% of China’s land area, but the region accounts for 11% of its Gross Domestic Product (Qin et al., 2007). The lake is a key drinking water, fishing and tourism resource for the region. However, it also serves as a waste repository for urban, agricultural and industrial segments of the local economy (Guo, 2007; Qin et al., 2007). Consequently, Taihu has experienced accelerated eutrophication over the past 3 decades (Qin et al., 2007, 2010). During this period, it has changed from a mesotrophic, diatom-dominated lake to hyper-eutrophic, cyanobacteria-dominated systems. Microcystis blooms now occurring regularly throughout much of the lake (Chen et al., 2003a,b) (Fig. 1). These blooms have caused environmental, economic and societal problems, including a threat to potable water supplies for approximately 10 million consumers (Guo, 2007).

Fig. 1 – Upper: Satellite (MODIS) image of Lake Taihu, the nearby cities of Wuxi (N), Souzhou (E), and Shanghai (E), near the mouth of the Yangtze River on 7 June, 2007, when a massive cyanobacterial (Microcystis spp.) bloom that covered almost the entire lake (image courtesy NASA). Lower: Photograph of a Microcystis bloom on the north side of the lake on 24 October, 2009 (photograph by H. Paerl).

Microcystis and other non-N-fixing cyanobacteria are effective competitors for reduced N forms, especially ammonium (NH$_4^+$) (Kappers, 1980; Blömquist et al., 1994), which is rapidly regenerated in the water column and sediments of these shallow systems. Cyanobacteria capable of N$_2$ fixation can also assimilate NH$_4^+$ when available. For example, Shelburne Pond in Vermont was dominated by N$_2$ fixers, but characterized by low rates of N fixation (~9% of total N uptake) and NO$_x$ uptake (~5%), but high acquisition rates of NH$_4^+$ (82–98%) in summer (Ferber et al., 2004). Thus, the presence of N$_2$ fixers does not ensure that N$_2$ fixation is a significant N source; regenerated NH$_4^+$ may be a key N source for sustaining blooms, even among N$_2$ fixing groups.

Although Microcystis blooms dominate, heterocystous, filamentous genera capable of N$_2$ fixation (Anabaena, Aphanizomenon) are also present in the water column and as over-wintering cells in the sediments of Taihu. The N$_2$ fixing genera increase in numeric importance toward the lake center, i.e., away from shoreline locations, although they remain sub-dominant to Microcystis (Chen et al., 2003a,b). While N$_2$ fixation rates have not been measured in the lake, these observations
suggest that N$_2$ fixing conditions may increase from the lake’s shorelines to its open waters, as hypothesized by McCarthy et al. (2007). These observations also suggest that nutrient availability and limitations may vary spatially in the lake. Temporal differences may also be important because watershed N and P inputs exhibit seasonal patterns (Qin et al., 2007, 2010; Xu et al., 2010).

The fact that both N$_2$ fixing and non-N$_2$ fixing cyanohABs coexist in hyper-eutrophic Taihu has raised questions as to whether N, P or both N and P inputs should be reduced to control blooms. Based on research in other lakes, primary production and bloom formation may be controlled by both N and P inputs, either contemporaneously or sequentially, with different individual nutrients being limiting at different times of the year (Dodds et al., 1989; Elser et al., 2007; Havens et al., 2001; Kronvang et al., 2005; Jeppesen et al., 2007; North et al., 2007; Lewis and Wurtsbaugh, 2008; Özkan et al., 2009; Xu et al., 2010). These findings have been challenged recently, based on the premise that lake eutrophication cannot be controlled by reducing N inputs (Schindler et al., 2008). This conclusion relies on the observation that many systems exhibiting advanced eutrophication also contain significant N$_2$ fixing cyanohAB populations, and the assumption that N fixed by these populations can meet ecosystem N requirements. However, diverse studies show that only a fraction, usually far less than 50% of ecosystem-level N demands, is met by N$_2$ fixation (Howarth et al., 1988; Paerl, 1990; Lewis and Wurtsbaugh, 2008). In fact, a recent re-examination of Schindler et al.’s (2008) data on P-fertilized Lake 227 indicates that N$_2$ fixation does not meet ecosystem N demands (Scott and McCarthy, 2010). In other cases, N$_2$ fixation rates are very low and supply little new N, even when N fixing cyanobacteria are dominant (Ferber et al., 2004). Furthermore, factors in addition to stoichiometric N:P ratios (Smith, 1983, 1990) control this energy-demanding process in aquatic ecosystems (Howarth et al., 1988; Paerl, 1990; Forbes et al., 2008). Reversing eutrophication and reducing CyanohABs in a range of lakes have required either reduction of only P (Schindler, 1977) or both N and P inputs (Kronvang et al., 2005; Jeppesen et al., 2007). Hence, nutrient reduction strategies appear system-specific.

We examined effects of individual and combined N and P additions on phytoplankton growth (based on chlorophyll a concentrations) in Taihu, using short-term (up to 6 days) nutrient addition bioassays incubated under natural light and temperature conditions. These bioassays provide a rapid assessment of nutrient limitation characteristics, i.e., immediate growth responses, rather than predicting long-term phytoplankton succession patterns (Paerl and Bowles, 1987; Piehler et al., 2009). We also evaluated NH$_3$ regeneration and potential uptake rates within the context of dominance by non-N$_2$ fixing cyanohABs.

2. Methods and materials

2.1. Location and field sites

Lake Taihu is located approximately 150 km west of Shanghai; with the lake center coordinates at 31°10'0"N, 120°9'0"E. The Taihu drainage basin is 36,500 km$^2$ (Fig. 2). The lake has more than 30 input sources, ranging from rivers to small streams and man-made drainage canals. Water exits the southeastern corner of Lake Taihu via the Taipu River, which drains through Shanghai into the East China Sea (Figs. 1 and 2).

Field monitoring and bioassay water collection sites were located in one of the northern bays, Meiliang Bay (Inner Bay, Outer Bay), and the lake proper (Main Lake) (Fig. 2). Other lake sites sampled included the least bloom-impacted eastern regions of the lake (ELT stations) (Fig. 2). Meiliang Bay was chosen as a focal point because it is the site of recurring and intensifying Microcystis spp. blooms (Chen et al., 2003a,b; Qin et al., 2007). Meiliang Bay receives freshwater inputs from the Liangxi and Zhihu Gang rivers, which drain untreated wastewater from factories, residential and agricultural areas. The named rivers in Fig. 2 contribute more than 85% of the lake’s freshwater inflow.

2.2. Nutrient inputs to Lake Taihu

Data were obtained from the Taihu Basin Authority, Ministry of Water Resources, China, for 30 primary tributaries from 2000 to 2005, including monthly flow discharge and TN and TP concentrations, to estimate N and P loads discharged to the lake (Fig. 2). These tributaries with 30 monitoring stations accounted for approximately 85% of the total runoff input to the lake (Qin et al., 2007). TN or TP load for each month was calculated by the following formula:

$$F_i = 2.592 \sum_{j=1}^{30} C_{ij} Q_{ij}$$

where $F_i$ is TN or TP load for ith month (i = 1–12) in metric tons, $C_{ij}$ is the TN or TP concentration for ith month and jth tributary (j = 1–30) in mg/L, $Q_{ij}$ is the flow discharge for ith month and jth tributary (j = 1–30) in m$^3$/s. 2.592 is the factor for converting g/s to ton/mo. Spring, summer, autumn and winter in this paper represent March–May, June–August, September–November, and December–February, respectively.

We estimated historic changes in atmospheric N loads to the lake based on data derived from regional atmospheric deposition models (Lelieveld and Dentener, 2000) and direct measurements (Zhai et al., 2009).

2.3. Lake environmental measurements

Monthly samples for nutrients, chlorophyll a, and phytoplankton identification and enumeration were collected at the Meiliang Bay and Main Lake locations (Fig. 2). Water samples for nutrient addition bioassays were collected at the Inner Bay location. For logistical reasons, the bioassays were incubated at a lake location near the Taihu Laboratory for Lake Ecosystem Research (TLLER), Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences (Fig. 2).

Monthly physical, chemical, and biological parameters, including surface water temperature, dissolved oxygen, pH, and electrical conductivity, were measured using a Yellow Springs Instruments (YSI) 6600 multi-sensor sonde. Integrated water samples were taken using a 2-m long, 0.1-m wide plastic tube with a 1-way valve.
2.4. Nutrient analyses

Water samples were analyzed for total nitrogen (TN), total dissolved nitrogen (TDN), dissolved inorganic nitrogen (DIN; ammonium (NH₄⁺) + nitrate (NO₃⁻)) + nitrite (NO₂⁻)), total phosphorus (TP), total dissolved phosphorus (TDP), and dissolved inorganic phosphorus (DIP). DIP was determined using the molybdenum blue method (APHA, 1995). NH₄⁺ was determined using the indophenol blue method, and NO₃⁻ and NO₂⁻ with the cadmium reduction method (APHA, 1995). TP, TDP, TN, and TDN were determined using a combined persulphate digestion (Ebina et al., 1983), followed by spectrophotometric analysis as for DIP and NO₃⁻. Particulate nitrogen (PN) was obtained by subtracting TDN from TN, and particulate phosphorus (PP) by subtracting TDP from TP. Analytical errors were determined as the average % coefficients of variation of triplicates. Average errors for PP and PN were 6.3% and 5% respectively.

2.5. Biological measurements

Phytoplankton samples were preserved with Lugol’s iodine solution (2% final conc.) and settled for 48 h. Phytoplankton species were identified and counted according to Hu et al. (1980). Chlorophyll a (Chl a) concentrations were determined spectrophotometrically, following extraction in 90% hot ethanol (Papista et al., 2002).

2.6. Nutrient limitation bioassay experiments

In situ nutrient addition bioassays were performed seasonally in 2008–2009 on “inner bay” water (Fig. 2) to examine nutrient limitation of the natural phytoplankton community. Water samples were collected from 0.2 m below the surface using 0.01 N HCl-washed and then lake water-rinsed 20 L polyethylene carboys. Water was screened through 200 μm mesh to remove large zooplankton and dispensed into acid (0.01 HCl) and then lake water washed 1-L polyethylene Cubitainers (Hedwin Co.). Cubitainers are chemically inert, unbreakable and transparent (80% PAR transmittance). The methodology and deployment for Cubitainer bioassays followed Paerl and Bowles (1987). At the start of each experiment (T₀), water samples were analyzed for Chl a and nutrients. Three treatments were conducted, in addition to a control (no nutrient additions): (1) N addition (+ N) (2) P addition (+ P) (3) N and P addition (+ NP).
Nitrogen was added as KNO₃, reflecting the dominant form of inorganic N in Taihu. NH₄Cl was also used as an N source in summer 2009 to compare phytoplankton growth responses to different N forms. Phosphorus was added as K₂HPO₄·3H₂O. The final concentration of N was 2.00 mg N/L, and the final concentration of P was 0.50 mg P/L. These concentrations approximated the values of these nutrient forms in the lake during maximum discharge periods (Pu and Yan, 1998; Qin et al., 2007).

All treatments were conducted in triplicate. Following nutrient additions, Cubitainers were incubated in situ near the surface for 4 or 6 days by placing them in a floating frame suspended off a pier at TLLER (Fig. 2). This approach provided natural light, temperature and surface wave action conditions. One layer of neutral density screening was placed over the frame to prevent photoinhibition during the incubations. Following deployment, Cubitainers were subsampled at 2–3 d intervals for Chl a and nutrient concentrations.

2.7 Water column NH₄⁺ regeneration and potential uptake rates

Water column NH₄⁺ regeneration and potential uptake rates in Taihu, as described in McCarthy et al. (2007), were conducted to provide insights into consequences of unmitigated N discharges into Taihu. Previously published water column N cycling rates were determined in late summer 2002 from four sites in northern Taihu (McCarthy et al., 2007). The N and P addition bioassays described in the present study were conducted on water collected at sites corresponding to “inner bay” and “main lake” in McCarthy et al. (2007). Water column NH₄⁺ recycling rates also were determined at the main lake station and four sites in East Lake Taihu (ELT) in January 2004 and all northern Taihu and ELT locations in May 2004 (Fig. 2). The ELT sites were located in the southeastern portion of the lake, near the outflow of the lake into the Taipu River. Methodological details are provided in McCarthy et al. (2007).

Briefly, water samples were amended with saturating levels of ¹⁵NH₄⁺ and incubated at ambient temperature and light for ~24 h. Total NH₄⁺ concentration and isotope ratios were determined using high performance liquid chromatography (HPLC; Gardner et al., 1995), and regeneration and potential uptake rates were calculated using the isotope dilution technique (Blackburn, 1979; Caperon et al., 1979). Since Lake Taihu is shallow and well-mixed, rates were extrapolated to the whole water column to estimate a total internal N load from water column recycling processes.

2.8 Statistical analyses

Differences in the growth responses between various treatments were analyzed by one-way ANOVA. Post Hoc Multiple Comparisons of treatment means were performed by Tukey’s least significant difference procedure. Untransformed data in all cases satisfied assumptions of normality and homoscedasticity. Statistical analysis was performed using the SPSS 13.0 statistical package for personal computers, and the level of significance used was at p < 0.05 for all tests.

3. Results and discussion

3.1 Nutrient inputs and concentrations

Seasonal and annual surface water TN and TP loads to Taihu during 2000–2005 indicate that the lake received high amounts of N and P on a year-round basis, with N loads being higher, relative to P, in the winter (Fig. 3). Ratios (by weight) of TN to TP loading range from ~22 to over 25, indicating relatively N enriched conditions on an annual basis. Lowest N:P loading ratios occur in summertime, whereas highest ratios occur in winter–spring.

The Taihu basin has, over the past 3 decades, experienced dramatic increases in population and urbanization (Qin et al., 2007; Guo, 2007). The high N:P loading reflects the combined effects of population growth, changes in land use, including increasing agricultural, and urban and rural wastewater discharge. These changes and the emphasis of P over N control in wastewater treatment (Wang and Wang, 2009) have led to increases in N:P loading from cities. In addition, reflecting a worldwide pattern (Galloway and Cowling, 2002), chemical N fertilizer use has increased in agricultural regions.
of the Taihu watershed, leading to N relative to P enrichment. Lastly, atmospheric deposition, which is enriched in N relative to P (Zhai et al., 2009), is an increasing source of N, accounting for approximately 30% of the external N loading to the lake. Atmospheric N inputs are estimated to have undergone a 25-fold increase over the past 150 years, and this trend has accelerated during the past 3 decades (Lelieveld and Dentener, 2000) (Supplementary material 1: S-1).

Recent increases in TN and TP loading can be seen as trends in TN and TP concentrations in the lake (mid-lake location) (Fig. 4). Increases were evident between the mid 1980s and 2000, a period of rapid population growth and urbanization in the Taihu watershed (Qin et al., 2007; Guo, 2007). They may have leveled off since the early 2000, possibly a result of persistent droughts (Qin et al., 2007, 2010), diversion of sewage from the cities of Wuxi and Suzhou to waterways draining to the East China Sea, and usage of the Wangyuu River canal, which exchanges water between Taihu and the Yangtze River. The decreases TN loading may have resulted from a reduction in pollutant input from the watershed in 1998. However, at the end of 1998, a pollutant emission reduction movement (the so called “zero point action”) launched by the government throughout the entire watershed, did not persist over time.

Both TN and TP, as well as DIN and DIP concentrations, showed strong seasonal variation in Taihu. Maximum TN and DIN values occurred in winter and spring, whereas minimum values were observed in summer and autumn during the 2-yr period (Fig. 5). In contrast, TP and DIP values showed an inverse pattern, with winter having low values and summer high values. DIN patterns closely tracked TN over time (Fig. 5). Overall, TN values were higher in Meiliang Bay than in the lake proper, reflecting large external loads and elevated internal loading.

3.2. Nutrient addition bioassays

The in situ nutrient addition bioassays showed stimulation of algal biomass production (as Chl a) in response to individual and combined N and P additions, indicating that nutrient enrichment enhanced algal growth and bloom potentials. Nutrient limitation showed strong repeated seasonal patterns in 2008 and 2009, although different degrees of algal biomass stimulation were observed between the two years (Fig. 6). P limitation prevailed in winter and spring, while N limitation occurred in summer and fall. In most instances, algal growth responses to N and P additions exceeded those observed with

![Fig. 4](image_url) Annual average TN and TP concentrations, as mg/L of each element, in Lake Taihu. Data are from the Main Lake station.

![Fig. 5](image_url) Patterns of TN, DIN, TP and DIP, as mg/L of each element, at Inner Bay and Main Lake locations during 2008-2009.
N and P alone (Fig. 6). This “synergistic” N and P effect was most pronounced in summer and fall, when algal growth rates, and hence nutrient demands, were highest.

Nutrient limitation patterns followed inverse concentration patterns of dissolved inorganic N (DIN) and P (DIP). DIN concentrations were high during winter and spring, reflecting high N inputs, while DIP concentrations were at their lowest levels (Fig. 5). As a result, DIP proved to be the limiting nutrient at this time. Then, DIN decreased rapidly as growth and bloom conditions improved in late spring and summer with increased light levels and temperatures. In contrast, DIP concentrations remained quite high and actually increased during summer bloom periods. The summer DIP increases may relate to elevated pH conditions (due to photosynthetic CO₂ demand by blooms), which can enhance DIP release from the sediments (Andersen, 1975; Xu et al., 2010). Further, *Microcystis* can store P during sedimentary phases and assimilate N in larger proportion to P during bloom phases (Ahn et al., 2002). This uneven nutrient assimilation pattern can lead to decreases in N:P and enhance N limitation. It appears that DIN availability during this period determines the magnitudes and duration of booms.

The availability of iron (Fe), a nutrient required for photosynthetic growth and N₂ fixation, may have played an additional role in controlling phytoplankton production. However, when Fe (as EDTA-chelated and non-chelated Fe⁴⁺) was added alone and in combination with N and P to Inner Bay and open lake water samples during summer 2009, no significant stimulatory (or inhibitory) effects of Fe were observed (not shown).

Parallel microscopic determinations of phytoplankton biomass agreed with chlorophyll a results (Xu et al., 2010), confirming that Chl a was a good indicator of phytoplankton biomass response in the bioassays. Additional total particulate organic carbon measurements made on the bioassays confirmed that Chl a responses reflected true increases in phytoplankton biomass.

*Microcystis* spp. remained the dominant bloom-forming cyanobacteria during the summer-fall bloom periods of both years, despite chronic N limitation. These N limited periods should have provided optimal conditions for N₂ fixing genera (i.e., *Anabaena*, *Aphanizomenon*) to become dominant (Smith, 1983, 1990; Schindler et al., 2008), but this situation did not develop, even though DIP remained plentiful (Figs. 4 and 5). Possible explanations for this result include; (1) superior ability of *Microcystis* spp. to compete for NH₄⁺ (Kappers, 1980) and watercolumn regeneration (Blomqvist et al., 1994), and (2) mutually-beneficial bacterial—cyanobacterial interactions in the “phycosphere” of *Microcystis* spp. colonies, which can enhance nutrient cycling and growth of “host” *Microcystis* populations (Paerl and Pinckney, 1996).

Bioassays illustrated that *Microcystis* spp. competed for DIN effectively, especially for NH₄⁺. Per amount of N added, ammonium stimulated significantly more algal biomass formation than nitrate (Fig. 7). The extent to which natural *Microcystis* populations dominated the absolute uptake of NH₄⁺ was not determined, but phytoplankton biomass was dominated (>80%) by *Microcystis* in bioassays. This mechanism helps explain the persistence of *Microcystis* during periods of low DIN concentrations. In addition, *Microcystis’* ability to...
adjust its vertical position by buoyancy compensation (Reynolds, 1987) may enable exploitation of the entire water column, taking advantage of regenerated as well as externally-supplied (atmospheric, surface runoff) N sources.

The results indicate that inputs of both nutrients should be reduced to control bloom formation and magnitude. Algal biomass production may be controlled by P availability in the spring, while N availability may determine the magnitude, spatial extent and duration of the bloom during summer-fall when the bloom potential is highest. Nutrient co-limitation was observed during all periods; i.e., combined enrichment with N and P led to higher magnitudes of biomass formation than either N or P alone. This result suggests that N and P supplies are closely balanced with regard to the requirements for supporting and promoting eutrophication and bloom formation.

3.3. Water column NH$_4^+$ regeneration and potential uptake

Water column NH$_4^+$ regeneration and potential uptake rates showed seasonal and spatial differences (S-1). In January, light uptake rates were significantly lower ($p < 0.01$; ANOVA) than those in September (main lake) and May (main lake and ELT sites). In northern Taihu, only the inner bay had a seasonal difference in regeneration rates, although the difference was large (0.89 µmol N/L h in May versus 0.19 µmol N/L h in September). In ELT, uptake and regeneration rates were lower than the Meiliang Bay sites, but this pattern was expected since ELT is dominated by submerged aquatic vegetation (SAV) rather than phytoplankton.

To scale regeneration rates and to compare with external loads, sites were first regrouped based on location within the lake. Lake Taihu has a surface area of 2338 km$^2$, but Meiliang Bay and ELT account for only 100 and 131 km$^2$, respectively, of the total surface area. The outer bay site was located at the interface between Meiliang Bay and the main lake and is 15–20 km from river discharges. Thus, this site was grouped with the main lake station. After regrouping the sampling sites, volumetric regeneration rates (see S-1) were converted to areal rates using water depth and extrapolated based on surface area of the appropriate lake region.

Extrapolated water column NH$_4^+$ regeneration rates suggest that $3.77 \times 10^7$ kg N/yr are regenerated as NH$_4^+$ in Meiliang Bay, where the most severe Microcystis blooms occur. Despite actual regeneration rates being an order of magnitude lower in the main lake than Meiliang Bay, the large surface area of the central basin results in $6.57 \times 10^7$ kg N/yr regenerated as NH$_4^+$. As expected, ELT plays a minor role in total N recycling in the water column (0.13 \times 10^7$ kg N/yr). The sum of these annual regeneration estimates is about 400% of total estimated N loading to the lake ($2.5 \times 10^7$ kg N/yr; James et al., 2009). However, these estimates include only N regenerated as NH$_4^+$. No estimates of the NH$_4^+$ proportion of the total N load are known, but the proportion is presumably small relative to oxidized (i.e., NO$_3^-$) and organic N forms. Internal N cycling is important for the maintenance and species succession of cyanobacteria blooms in Taihu, especially as it pertains to Microcystis spp. (McCarthy et al., 2007). Atmospheric deposition is a significant additional source of bioavailable N in the lake (Zhai et al., 2009) (S-2). For example, NH$_4^+$ and NO$_3^-$ concentrations of a rainwater sample collected in May 2004 were 370 and 146 µM, respectively (McCarthy and Gardner, unpublished data).

Direct denitrification measurements in Meiliang Bay and the main lake in late summer 2002 (McCarthy et al., 2007) and Meiliang Bay, the main lake, and ELT from January to May 2004 (McCarthy and Gardner, unpublished data) were extrapolated to estimate a lake-wide denitrification rate. This rate ranged from 7360 kg N/km$^2$ per year when estimated by net N$_2$ flux to 26,700 kg N/km$^2$ per year when estimated using $^{15}$NO$_3^-$ addition assays. Both estimates were obtained from continuous-flow incubations of intact sediment cores. Rates from $^{15}$NO$_3^-$ additions should be qualified as potential rates, whereas rates from net N$_2$ flux would include any N$_2$ fixing activities, which were not significant in sediments of this lake (McCarthy et al., 2007). Therefore, net N$_2$ flux represents the best estimate of denitrification and accounts for 66.2% of external N loading. This N loss via denitrification would not account for the N recycled in the water column. In late summer, Meiliang Bay and main lake sediments are an N source to the water column (McCarthy et al., 2007). Sediments also are an N source in ELT and the main lake in January and May (McCarthy and Gardner, unpublished data). However, sediments in Meiliang Bay were a strong N sink in January and May. These patterns suggest that late summer cyanobacteria blooms rely, in part, on nutrients released from sediments (McCarthy et al., 2007).

Depth averaged water column NH$_4^+$ regeneration rates for the shallow water column imply that water column regeneration supplies a greater amount of N (5-fold more on an areal basis) than sediments for cyanobacterial assimilation in the summer (McCarthy et al., 2007).

In addition to the importance that total N loads play in determining rates of eutrophication, the supply rates and ratios of various N forms help structure microalgal communities mediating freshwater primary production (Paerl, 1988; McCarthy et al., 2007, 2009). For example, the ratio of NH$_4^+$ to oxidized N was related to the proportion of cyanobacteria comprising the total phytoplankton community of Lake Okeechobee, FL, USA (McCarthy et al., 2009). While non-N$_2$ fixing cyanobacteria, such as Microcystis, compete effectively for reduced N (Blomqvist et al., 1994), N$_2$ fixing cyanobacteria also assimilate ammonium preferentially if it is available (Ferber et al., 2004). Ammonium and other reduced N forms, such as dissolved free amino acids, are more available than oxidized N forms (nitrate and nitrite) to bacteria (Vallino et al., 1996) and cyanobacteria because less energy is required to incorporate and assimilate the former (Syrett, 1981; Gardner et al., 2004; Flores and Herrero, 2005).

These issues were not addressed in recent studies suggesting that eutrophication cannot be controlled by reducing N inputs (e.g., Schindler et al., 2008; Wang and Wang, 2009). The assumption that N$_2$ fixing genera will replace non-N$_2$ fixing genera like Microcystis when N is limiting and P is sufficient could not be confirmed in Taihu. Furthermore, our observation that Taihu does not fit the proposed “P only” management paradigm of Schindler et al. (2008) is not unique. Numerous other lakes, reservoirs, rivers and fjords worldwide exhibit N and P co-limitation, either simultaneously or in
seasonally-shifting patterns (Dodds et al., 1989; Elser et al., 2007; Forbes et al., 2008; Scott et al., 2008; North et al., 2007; Lewis and Wurtsbaugh, 2008; Conley et al., 2009; Xu et al., 2010; Abell et al., 2010).

4. Conclusions

Nutrient loading analyses, nutrient addition bioassays and nutrient cycling studies provide the basis for recommending that N control be included, along with the previously prescribed P control (Chen et al., 2003a,b; Wang and Wang, 2009), as a nutrient management strategy for Taihu. Denitrification rates, while high relative to other lakes, are lower than estimates of N loading and therefore would not mitigate high N loads. Also, late summer cyanobacterial blooms are maintained primarily by water column N regeneration. Recycling produces NH4 available to non-N-fixing cyanobacterial blooms (Microcystis), regardless of the N form discharged into the lake.

The fact that Microcystis spp. were not replaced by N2 fixing cyanobacterial bloom species during N limited, but P sufficient summer periods is evidence that predictions of succession from non-N2 to N2 fixing taxa based on N:P stoichiometry (Smith, 1990; Schindler et al., 2008) may not apply to hyper-eutrophic lakes. Excess inputs of both N and P, combined with internal cycling of these nutrients, may overwhelm the ability of a single nutrient to control increasing eutrophication and bloom intensification in Lake Taihu and other large lakes experiencing such blooms (e.g., Lake Erie, Lake Okeechobee, Lake Victoria).

P input reductions are an important component of eutrophication management in large lakes and reservoirs. However, failure to control N inputs may result in continued serious eutrophication problems caused by non-N2 fixing cyanobacterial blooms.

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Appendix. Supplementary data

Supplementary data related to this article can be found online at doi:10.1016/j.watres.2010.09.018

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