Cyanobacterial blooms in Lake Atitlan, Guatemala

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A B S T R A C T

Lake Atitlan, one of the most important lakes not only in Central America but in the whole world, is facing serious problems with increasing water pollution. Over the last several decades, the uncontrolled nutrient input into the lake has lead to high P levels and low N:P ratios, initiating cyanobacterial blooms. The first bloom occurred in December of 2008, followed by more extensive bloom in October 2009. The blooms are formed by cyanobacteria from the rare planktic Lyngbya hieronymusii/birgei/robusta complex. Based on the species morphology, the Atitlan population corresponds to L. robusta and this is the first case of reported bloom of this species worldwide. Remote sensing images documented that at the maximum bloom development, 40% of the 137 km² of the lake area were covered by dense patches of Lyngbya, with the chlorophyll a concentration reaching over 100 μg L⁻¹. The only toxins detected in the 2009 bloom were trace levels of cylindrospermopsin and saxitoxin with 12 and 58 ng g⁻¹, respectively. The nitrogen fixation followed a pattern expected in non-heterocytous cyanobacteria, i.e., the nitrogenase activity was minimal during the day, while during the night the activity reached 2.2 nmol C₂H₄ μg Ch⁻¹ h⁻¹. Delta ¹⁵N of −0.86% was well in the range given for nitrogen fixing organisms. The cell C, N and P content was 36.7%, 5.9% and 0.9%, respectively, resulting in the molar ratio of 105:14:4:1. A well designed and executed lake monitoring program, strict control of nutrient input into the lake, and public education are the necessary prerequisites for potential prevention of even more severe blooms than the one from 2009.

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Introduction

Accelerated land use change and the resulting cultural eutrophication has become the primary water quality issue for most of the freshwater and coastal marine ecosystems in the world (Downing et al. 1999; Conley et al. 2009; Smith and Schindler 2009). Excessive input of nutrients, particularly phosphorus (P) and nitrogen (N), increases primary production, reduces water transparency, and often causes algal community shifts toward bloom-forming and cyanobacterial species that can be toxic (Suda et al. 1998; Funari and Testai 2008).

Lake Atitlan’s situation is a case in point. This lake, located in the highlands of Guatemala and described by many as one of the most beautiful lakes in the world (Huxley 1934), is presently facing a serious problem with increasing water pollution. Without remediation, this is almost certain to present a serious threat to local communities, who depend on the lake for their livelihood, as well as lead to the loss of Atitlan’s unique aesthetic status. Uncontrolled nutrient input into the lake has lead to high P levels, initiating cyanobacterial blooms.

In December 2008, the first extensive cyanobacterial bloom occurred. The news about the bloom made it into the national press and local residents were worried, but the lake authority appeared surprisingly unconcerned. A much larger bloom occurred in October 2009, and received intense media coverage both in Guatemala and abroad; unfortunately, the news articles were often highly inaccurate. This was partly because, despite its importance as the major reservoir of freshwater in Central America, little research is currently conducted at Lake Atitlan, and there is a shortage of reliable baseline data except for the phytoplankton monitoring by Dix (unpublished).

Our goals in this article are to: (1) summarize the limnologic history and phytoplankton changes of the lake, (2) describe the species complex forming the recent blooms, (3) provide data on nitrogen fixation of the cyanobacteria and interpret these in the context of water chemistry and N:P ratios.
Lake description and limnologic history

Lake Atitlán lies in the volcanic highlands of western Guatemala in a spectacular, steep-sided collapse caldera formed about 84,000 y BP (altitude 1555 m, maximum depth 341 m, mean depth 183 m, surface area 137 km^2, volume 24 km^3; Newhall 1987a). The first Maya settled the area circa 3500 BP. The land cover of the lake's watershed is about 46% forest, and 32% agriculture. The agricultural crops include largely subsistence corn and beans, as well as market crops such as onion, potato, and coffee, which are cultivated often on very steep, erodible slopes. The rest are urban areas, which are home to approximately 400,000 people, mainly Maya Indians.

Rapid development over recent decades has resulted in an increased agricultural runoff and erosion, as well as a substantial inflow of untreated wastewater from Panajachel, the largest municipality. In addition, there is a nutrient rich inflow from the Quisquab and San Francisco rivers, which drain highly disturbed watersheds.

One of the first descriptions of the lake was provided by Meek (1908), who focused on the ichthyology and suggested potential fish introductions. Meek brought phytoplankton samples to the US, where they were identified by Clark (1908). Further information comes from Juday (1915), who conducted limnological studies at four Central American Lakes, including Atitlán. Juday reported the littoral macrophyte species (Typha, Scirpus, Chara, and Potamogeton), noted small temperature differences between the surface and bottom, and high oxygen concentrations even at depth. His phytoplankton samples were dominated almost entirely by the diatom Melosira granulata with members of a few other genera such as “Gloeocapsa” and Zygnema, which occurred in the upper layers. Melosira also dominates the extremely large presence of diatom remains in the sediments (Newhall 1987b). Deevey (1957) visited the lake in 1950, documented its water quality (Table 1) and listed the Secchi disk depth of around 15 m. He pointed out that Lake Atitlán is a monomictic lake with water mixing freely in the dry season and stratified in the wet season, with the thermocline at about 50 m. Deevey calculated that the lake was extremely stable, and therefore a high quantity of work (i.e. wind) would be required to mix the entire volume of water to a uniform temperature, which was then quoted in several limnology textbooks (Hutchinson 1957; Wetzel 1983). More water chemistry data can be found in Brezonik and Fox (1974) who classified the lake as highly oligotrophic (Table 1). The first systematic and thorough lake survey was conducted during 1968–1970 by Weiss (1971). He obtained a time series of temperature measurements, expanding upon Deevey’s (1957) observations, and was able to specify the time period of lake stratification and mixing. He found that a well-defined metalimnion developed by late March and continued into early December. Complete mixing took place in mid-December and persisted into February. The mixing sequence happened in a narrow temperature range – the bottom water temperature stayed between 19.5 and 20 °C throughout the year and the surface water rarely exceeded 24 °C, further classifying it as a warm monomictic lake. During the stratification, the metalimnion extended to a depth of 60–120 m, with this depth varying at different lake locations, most probably because of currents. Weiss stated that the circulation mechanism of Lake Atitlán is primarily due to wind mixing associated with slightly cooler climate of November through February, which is in agreement with earlier observations of Deevey (1957). The Secchi depth ranged from a minimum of 8–10 m to maximum of 20 m (Fig. 1) during the rainy and dry season respectively. The phytoplankton was still dominated by Melosira (see also Juday 1915) and Closteriopsis, and its vertical distribution showed a tendency towards larger densities at lower depths. Weiss also measured the primary productivity by 14C method and obtained data ranging from 77.4 to 102.0 mg C m⁻² day – a range typical for oligotrophic lakes (Wetzel 1983).

Several fish species have been introduced (see the table in Labastille 1974). The introduction of largemouth bass (Micropterus salmoides, lobina negra) has had a large impact on local fish fauna and doubtless also contributed to the extinction of the Atitlán grebe, Podilymbus gigas (Hunter 1988). The perpetuated belief that the bass introduction also drastically changed the zooplankton community presents the Secchi depth in a dense part of the bloom in November 2009.
position has been contradicted by Newhall (1987a,b) who found a large similarity of zooplankton present in the sediment cores and in the water column. Newhall also pointed out an unusually rapid sedimentation rate of circa 0.5 cm yr⁻¹ caused apparently by large amounts of Quaternary pumice and ash on steep slopes and occasional torrential rains.

More recently the Universidad del Valle de Guatemala, UVG, with the support of various national and international organizations initiated the monitoring program. The results have been published in several reports (Castellanos et al. 2002; Dix et al. 2003; Castellanos and Dix 2009).

These reports provide a great deal of useful information on physical and chemical conditions, bacterial contamination and phytoplankton composition and densities (see below), unfortunately, due to the lack of proper water chemistry capabilities, the nutrient data are not very reliable and there is currently no regular monitoring of depth temperature profiles and mixing depths. Considering the profound impacts of the frequency of mixing depth on lake ecology and water quality, this needs to be remedied.

Cyanobacteria and cyanotoxins

Toxic and noxious cyanobacterial blooms are of high concern due to the increasing eutrophication of aquatic environments worldwide (Funari and Testai 2008). The most common cyanotoxins are hepatotoxins microcystins produced by several genera including Microcystis and planktic Anabaena (= Dolichospermum according to the modern classification; Wacklin et al. 2009). Microcystis is present at Lake Atitlan but has not yet reached bloom stages. Although Lyngbya, which bloomed in 2009, showed only traces of toxins (see later), it should be monitored because the majority of the local inhabitants use the lake's untreated water and resources. Exposure through the lake food sources may provide more potent routes for human intoxication. A strong candidate for cyanotoxin contamination might include the commercially important crab species or cangrejos (Potamocaricus guatemalensis), which are planktivorous filter-feeders.

Methods

Water analyses

Water samples for nutrient and chlorophyll analyses were collected into acid (HCl)-rinsed plastic bottles (surface water from replicated locations near San Pedro in March 2009 and from Pana-jachel, Lake center and San Pedro in November 2009) and stored on ice until processing. Water samples for NO₃⁻-N, NH₄⁻-N, and SRP were filtered through a 0.45 µm filter within an hour after sampling and frozen until analysis. Nitrogen species (NO₃⁻-N, NH₄⁻-N, and total N) were analyzed on the Lachat FIA 8000, using method # 10-107-04-1-B (cadmium column reduction), method # 10-107-06-1-F (indophenol), and a modified method # 10-115-01-4-F (persulphate digestion) for NO₃⁻-N, NH₄⁻-N and total N, respectively. SRP was analyzed by the ascorbic acid method of Murphy and Riley (1962). For chlorophyll a determination, a known volume of water was filtered through GF/C filter, the filter was kept refrigerated and analyzed spectrophotometrically in acetone extracts (APHA 1999).

Plankton

Beginning in 1976, water samples of known volume were collected in November at different depths, usually 5 and 10 m; and fixed, either in formalin to give a final concentration of 10% or in Lugol’s solution, final concentration 1%. Samples were concentrated by filtering and resuspended to a known volume for counting. Counts were made using Sedgewick Rafter and Palmer Maloney cells. Vertical 20 or 30 m plankton hauls were also made to permit a rapid qualitative evaluation of species present. The years included in the sampling were 1976, 1983, 1988, 1992, 1995 and 2001, followed by more frequent sampling in 2009.

Nitrogen fixation

The acetylene reduction technique (Stal 1988) was employed to estimate cyanobacterial nitrogen fixation by the reduction of acetylene to ethylene by nitrogenase. The cyanobacterial samples collected from 4 dense and 4 loose patches of Lyngbya were transferred to 40 ml test tubes with lids with a Teflon septum. Acetylene, freshly generated from calcium carbide, was injected into each bottle and the bottles were incubated outdoors floating in large tubs with water for several 3 h intervals (new set for each interval) (4–7 pm; 7–10 pm; 10 pm–1 am; 9–12 am). During the daylight hours, two sets of samples were employed, one exposed at natural light, one shaded by the cheesecloth, which lowered the solar radiation about seven-fold. At the end of the exposure, several ml of headspace was withdrawn with an airtight syringe (Alltech) and analyzed by gas chromatograph (Shimadzu 8 GC) with a flame ionization detector and a Porapak-T column at 80 °C. The results are reported as the nitrogenase activity in nmol C₂H₄ µg Ch⁻¹ h⁻¹. Controls with samples and no acetylene addition showed no endogenous ethylene production. Cyanobacteria enclosed in the bottles were kept for chlorophyll and biomass determination after terminating the exposure.

Isotope and cell nutrient analyses

Stable isotopes of N were measured by continuous flow isotope ratio mass spectrometry using a Europa ANCA elemental analyzer and a 20–20 isotope ratio mass spectrometer (PDZ Europa, Sandbach, UK). Dried samples containing approximately 5–7 µmol N were packaged in tin capsules (Elemental microanalysis, Manchester, MA). The samples were combusted at 1000 C in the elemental analyzer. The ratio of ¹⁵N/¹⁴N (R15) was measured for the sample (2 mg) and for an injection of standardized N₂ gas introduced into the mass spectrometer in each sample cycle ¹⁵N was calculated from:

\[ \delta^{15}N \text{ VAIR} = 1000 \times \left( \frac{R15 \text{ sample}}{R15 \text{ standard}} \right) \]

and expressed on “per mil” basis. Total P was measured spectrophotometrically using ascorbic acid reduction of phosphomolybdate complex after combustion and consequent acid digestion (McNamara and Hill 2000).

Cyanotoxins

Samples were collected on November 8th 2009 from four locations around the lake and freeze-dried. The following toxins were analyzed: anatoxin-a (AT) and microcystins LR, LA, YR and RR (liquid chromatography/tandem mass spectrometry (LC-MS/MS/MS) in Dr. Puschner’s lab at UC Davis, and LN tox (LT), dephosphomethylisoxazolin (DAT), anatoxins A (AT), cylindrospermopsin (CYN), and saxitoxins (STX) in Green Water Laboratories in Florida. ELISA (Abraxis) were utilized for quantitative detection of CYN and STX with the detection/quantification limit (as determined from kit sensitivity and dilution factors) of 10 ng g⁻¹ and 5 ng g⁻¹ respectively. Liquid chromatography/mass spectrometry/mass spectrometry (LC/MS/MS) were utilized for the determination of anatoxin, microcystins and LT and DAT. The [M+H]⁺ ion for LT (m/z 438.5) was fragmented and the product ions
Water results of the event of geological values that was considered to fix the Lyngbya−M. coregoni dominance. This was found in sites, consisting of 3-fold (Table 1). The old data can be trusted, then the concentration of SRP has increased about 3-fold (Table 1). It seems that the retention capacity of bottom sediments was exceeded during the last years. The SRP values were consistently lower during the last recorded bloom event (November 2009 data), apparently because the rapid growth of Lyngbya was responsible for rapid consuming the majority of available P. Both NO$_3$−N and NH$_4$−N concentrations are low. These lower concentrations of N relative to inorganic P correspond to the geological origin of the lake. N limitation accompanied by sufficient available P provides favorable conditions for cyanobacteria capable of fixing free N (Hendzel et al. 1994; Smith 1990). It gives cyanobacteria the competitive advantage over more desirable green algae.

Results and discussion

Water chemistry

The dataset (see the Table 1) is extremely limited, but even these limited data indicate that the lake has been recently changing from oligotrophic to mesotrophic, namely based on P and chlorophyll values. The SRP values are relatively uniform both spatially and temporally, ranging from 10 to 20 μg L$^{-1}$. This is not a range of values that are typical for an oligotrophic lake, and neither are the concentrations of TP ranging from 25 to 95 μg L$^{-1}$ (Table 1). If the old data can be trusted, then the concentration of SRP has increased about 3-fold (Table 1). It seems that the retention capacity of bottom sediments was exceeded during the last years. The SRP values were consistently lower during the last recorded bloom event (November 2009 data), apparently because the rapid growth of Lyngbya was responsible for rapid consuming the majority of available P. Both NO$_3$−N and NH$_4$−N concentrations are low. These lower concentrations of N relative to inorganic P correspond to the geological origin of the lake. N limitation accompanied by sufficient available P provides favorable conditions for cyanobacteria capable of fixing free N (Hendzel et al. 1994; Smith 1990). It gives cyanobacteria the competitive advantage over more desirable green algae.

Plankton

The phytoplankton analyses conducted periodically by M. Dix have revealed at least 40 genera of Pyrrophyt., Chryso-, Bacillari-, Chlorophytes and Cyanobacteria, of which the latter three represent 38%, 33%, and 23%, respectively (Dix et al. 2003, Dix in prep.). Both Bosmina longirostris and B. coregoni were encountered, which is intriguing considering that B. longirostris has been found to replace B. coregoni when lake productivity is increased (Hutchinson 1957). Microcystis was not mentioned by Weiss in 1967, but was recorded in 1976 in less than 10% of the total phytoplankton, while in 1983, 1988 and 1992 it increased to more than 50% of the total phytoplankton present (Dix et al. 2003). Overall, between 1968 and 2009, phytoplankton density increased almost 400x compared to values presented by Weiss (1971).

In 2009, plankton counts in March revealed dominance by Fragilaria cf. crotonensis in all sites sampled (between 47 and 77% of total, average 60%) and average numbers of plankton cells per L at 20 m of 12,331 (5771–27900) (Castellanos and Dix 2009). The genera considered to be indicators of oligotrophic to mesotrophic conditions, e.g., Dinobryon and Closteriopsis, are still present, although the density of Dinobryon has been reduced to less than 1% in samples from November 2001, and was hardly found at all in 2009 (Castellanos and Dix 2009). Similarly, in 2010 the plankton was dominated by Fragilaria, accompanied by small amounts of Dinobryon and also by Ceratium hirundinella and Aulacoseira spp. Thus the changes in phytoplankton evidently indicate the slow process of eutrophication over the last 33 years (Dix et al. 2003). From October to mid-November of 2009, the planktonic Lyngbya robusta dominated the plankton in the upper 10 meters. In mid-December, the dominance started shifting towards Aulacoseira, which dominated the plankton by January 2010.

Lyngbya blooms

The first recorded bloom started in December 2008, occurred only locally and the lake cleared by late January. The 2009 bloom started in October, apparently as a result of the upwelling of more nutrient rich water, and spread quite rapidly throughout the lake. At its maximum development, the sparse cyanobacteria were present

Fig. 2. Time course of the development of 2009 Lyngbya robusta bloom in Lake Atitlan. Red, orange, and yellow represent high, medium and low bloom density.
throughout the lake and dense patches covered some 40% of the lake surface (Fig. 2). The chlorophyll a concentration in these patches reached over 100 μg L$^{-1}$. The bloom eventually subsided and as of the end of December, the lake has been clear, although the solitary filaments of *Lyngbya* were still present in the upper 10 m in late February through April of 2010.

The dominant species of both 2008 and 2009 blooms was formed by cyanobacterium from the complex of planktic *Lyngbya*-species and identified as *L. robusta* (Fig. 3). Only three types (described as morphospecies) of the variable cyanobacterial genus *Lyngbya* (*L. hieronymusii, L. birgei, and L. robusta*) were found in the freshwater phytoplankton as in their main habitat (Komárek 2003; Komárek and Anagnostidis 2005). The main characters of the genus are relatively wide filaments (8–30 μm) composed of cylindrical inner trichomes with very short cells (several times shorter than wide), and a firm, relatively narrow gelatinous and colorless or yellowish sheath. The heterocytes, akinetes or any type of branching are lacking. In contrast to all other *Lyngbya* species, the cells of planktic morphospecies (including *L. robusta*) contain reversible gas vesicles, concentrated in fasciculated aerotopes, which can be irregularly distributed over the whole cell volume. However, the aerotopes are sometimes developed only in some part of the filament. Additional cytological investigations are in progress and phylogenetic status of planktic *Lyngbya* will be included in a special study.

There is hardly any information available on the ecology of the blooms of *L. robusta*. Planktic cyanobacterial species are known for their low light requirements (Reynolds et al. 1987). It is probable that the population resides in deeper parts of the lake and develops gas vesicles when the conditions of the lake change due to the upwelling. This would explain why no specimens of *L. robusta* were found in the upper zones of the lake (10 m and above) in March, 2009, after the first bloom (Dix, unpublished data).

### Cyanotoxins

The only toxins detected in the 2009 bloom were the CYN and STX with levels of 12 and 58 ng g$^{-1}$, respectively. To put the results into perspective: The very dense patches of *Lyngbya* in Atitlan contained about 50–100 mg of dry weight (DW) of *Lyngbya* per liter (based on the chlorophyll a being 0.42% of biomass dry weight; Rejmánková, unpublished data), which, assuming that all the toxin is released to the water, would result in the concentrations of: ~0.6 to 1.2 ng L$^{-1}$ of CYN and ~2.9 to 5.8 ng L$^{-1}$ of STX. The “non-patch” *Lyngbya* biomass was about 30–60 times lower, i.e., some 1–2 orders of magnitude less toxins. These concentrations are about 3 orders of magnitude lower than what the Brazilian Legislation recommends as the maximum concentration for potable water (3 and 15 μg L$^{-1}$ for saxitoxin equivalents and cylindrospermopsin, respectively [FUNASA 2004]). Detected values can be classified as “trace amounts”, i.e., the bloom of *Lyngbya* does not currently produce enough known toxins to represent a health risk in terms of drinking water. However, a potential accumulation along a trophic chain should be kept in mind and fish and crab tissue should be tested.

### Nitrogen fixation

During the day, nitrogenase activity was minimal, while during the night the activity reached 2.2 nmol C$_2$H$_4$ μg Ch$^{-1}$ h$^{-1}$ (Fig. 4). Similar diurnal changes of nitrogenase activity were reported by Elometri and Bel (2004) in marine periphytic species *Lyngbya majuscula*. In the trials run during the day, the samples from shaded environment exhibited consistently higher nitrogenase activity than samples exposed to the full light, 0.15 and 0.075 C$_2$H$_4$ μg Ch$^{-1}$ h$^{-1}$, respectively. No differences in nitrogenase activity were found between *Lyngbya* from dense and loose patches (data not shown). Delta $^{15}$N was found to be −0.86 (n = 4; SD = 0.03). This value fits well into the range of −2 to +2‰ given for nitrogen fixing organisms (Nadelhoffer and Fry 1994).

![Fig. 4](image_url)
Nutrient ratios

*Lynangea* C, N and P content was 36.7%, 5.9% and 0.9%, respectively, resulting in the molar ratio of 105:14:4:1. This is quite close to the Redfield ratio (106:16:1), which represents an average species-specific ratio for phytoplankton. According to Klausmeier et al. (2004) who focused on N:P, the ratio can range widely from 7.1 to 47.3, and it is determined by the ecological conditions under which the species grow. Specifically, the exponential growth selects low N:P ratios (5.2) while competitive equilibrium selects high N:P ratios (>36). Our ratio of 14.4 is relatively close to the value for the exponential growth which would agree with the timing of the sample collection, November 8, i.e., the exponential phase of the bloom formation (see Fig. 2). Note: although we assume that the bloom expansion was due to rapid growth of cyanobacteria in the surface layers, it is also possible that the bloom actually represented the accumulation from deeper layers rather than growth. Our 14.4 ratio can also indicate N limitation, considering the fact that the critical ratio marking the transition between N and P limitation lies in the range of 20–50 (Geider and La Roché 2002; Klausmeier et al. 2004). In any case, P content is much higher than 0.6% listed as a typical P content of cyanobacteria (Whitten and Potts 2000), which is in agreement with the increased P availability of the lake water.

High P availability is confirmed by the tissue analyses of littoral macrophytes. Both submersed (*Potamogeton* spp., *Hydrilla verticillata*) and emergent (*Schoenoplectus californicus*, *Typha domingensis*) species were found to have about 3 × higher tissue P compared to equivalent macrophytes from littoral/wetland environments from other Central American locations (Rejmánková 2005; Carpenter et al. submitted for publication). In addition, the N:P ratio (molar) was less than 4:1, indicating N limitation (Rejmánková 2005).

N-fixing cyanobacteria are dependent on the availability of P and they generally are more competitive than non-fixing planktonic species under conditions of low DIN:DIP ratios. As the blooms senesce, it is possible that the decay of the settling biomass will consume more oxygen, creating hypoxic conditions, which would then promote the release of DIP at the mud water interface. Thus, these blooms can be a serious contributor to the lakes internal P loading (Vahtera et al. 2007).

Bloom formation can be terminated by many factors such as nutrient limitation, mixing events, decreasing water temperature and possibly viral lysis (Vahtera et al. 2007). In our case, the most probable cause is temporal P limitation. In early November when the water samples were collected, the bloom was still in its “growing” phase and SRP values were already down to around 10 µg L⁻¹. Once the SRP levels drop to less than 7 µg L⁻¹, N-fixation becomes limited (Diaz et al. 2007). Apparently, the biomass of N-fixing cyanobacteria in the lake is closely dependent on the magnitude of P loading to the system. There were no cyanobacterial blooms when Devey and Weiss visited the lake in the 1950’s and 1970’s, which corresponds well with their measured SRP below the limit enabling N fixation. Identifying an appropriate range of SRP values, might be a target to aim for when trying to prevent the blooms.

Future prognosis

There is no doubt that without improved management, the cyanobacterial blooms will reappear and become increasingly severe. If nitrogen inputs increase, there is a serious danger of *Microcystis* blooms, which are known to produce toxins (Chorus and Bartram 1999) and are nearly impossible to control. *Microcystis* cf. *botryis* is a common species in the lake, this is why we talk about *Microcystis* rather than other cyanobacterial species. This would ultimately shift the beautiful blue waters of Lake Atitlán towards being more akin to the nearby green Lake Atitlán (~70 km in distance), which has extensive *Microcystis* blooms.

Many studies have concluded that managing P is critical to maintaining desirable water quality and ecosystem integrity (Schindler 2006; Schindler et al. 2008; but see Howarth and Paerl 2008; Conley et al. 2009). With relatively few exceptions, reductions in P inputs have led to successful recovery from eutrophication. This has been supported by decades of evidence indicating that the successful control of lake eutrophication involves reducing inputs of P to lake waters, regardless of whether the sources are external, such as sewage or land-use changes, or internal, by the recycling of phosphorus from sediments (Smith and Schindler 2009). While the control of eutrophication remains one of the greatest challenges to limnologists, perhaps a larger challenge is to educate policy makers and local residents, so that they understand the complexity of the ever increasing water quality problems that they face (Schindler 2006).

A well designed and executed lake monitoring program, strict control of nutrient input into the lake, and public education are the necessary prerequisites for potential prevention of even more severe blooms than the one that occurred in 2009. Lake monitoring is needed to provide data for the development of more mechanistic ecosystem models for the occurrence, persistence, and severity of bloom events. As evidenced by the research and management of other lakes such as Lake Tahoe, attacking the problem of eutrophication at the onset is the most cost effective way of slowing the process and preventing nearly irreversible damage to lake ecosystems.

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