Population dynamics of harmful algal blooms in Lake Champlain: A tale of two phases

Edmund M. Hart[1,3,*], Nicholas J. Gotelli[1], Rebecca M. Gorney[2], Mary C. Watzin[2,4]

1. Department of Biology, University of Vermont, Burlington VT 05405
2. Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington VT 05405
3. Current address Department of Zoology, University of British Columbia Vancouver BC V6K 1S4
4. Current address College of Natural Resources, North Carolina State University, Raleigh, NC 27695-8001

* To whom correspondence should be addressed: ehart@zoology.ubc.ca

PeerJ PrePrints | https://peerj.com/preprints/75v1/ | v1 received: 4 Oct 2013, published: 4 Oct 2013, doi: 10.7287/peerj.preprints.75v1

Abstract

Understanding the dynamics of harmful algal blooms (HABs) in lakes can inform management strategies to reduce their economic and health impacts. Previous studies have analyzed spatially replicated samples from a single time or have fit phenomenological models to time series data. We fit mechanistic population models to test the effects of critical nutrient concentrations and the density of potential algal competitors on population growth parameters in HABs in Lake Champlain, U.S.A. We fit models to five years (2003-2006, 2008) of weekly cyanobacteria counts. Plankton dynamics exhibited two phases of population growth: an initial "bloom phase" of rapid population growth and a subsequent "post-bloom phase" of stochastic decline. Population growth rates in the bloom phase were strongly density dependent and increased with increasing TN:TP ratios. The post-bloom phase was largely stochastic and was not obviously related to nutrient concentrations. Because TN:TP was important only in the initial phase of population growth, correlative analyses of the relationship between cyanobacteria blooms and nutrient concentrations may be especially sensitive to when snapshot data are collected. Limiting nutrient inputs early in the season could be an effective management strategy for suppressing or reducing the bloom phase of cyanobacteria population growth.

Key words

Cyanobacteria, density dependence, population dynamics, time series, harmful algal blooms.

Introduction

Harmful algal blooms (HABs) of freshwater cyanobacteria are a potential threat to ecosystem function as well as human and animal health. Globally, the intensity and frequency of HABs has increased in recent years (Johnson et al. 2010). Colony-forming cyanobacteria (also known as blue-green algae) can grow to large population sizes and release toxins (Codd et al. 2005), creating HABs. The economic and human health impacts of HABs have led to extensive studies of cyanobacteria blooms; however, the mechanisms driving the bloom growth are still not well understood. Given that some species of cyanobacteria are N-fixing, which may give them a competitive advantage in low total nitrogen: total phosphorous ratio (TN:TP) environments (Smith 1983, Elser and Urabe 1999, Havens et al. 2003), many studies have measured correlations between HABs and nutrient concentrations (Stahl-Delbanco et al. 2003, Armitage and Fong 2004). Other studies have implicated water temperature (Chen et al. 2003), light availability and water turbidity (Scheffer et al. 1997), recruitment of resting algal stages from the sediment (Stahl-Delbanco et al. 2003), and standing algal biomass (Downing et al. 2001) as causative agents of HABs. Zooplankton can also alter the response of cyanobacteria to nutrient additions (Wang et al. 2010), suggesting that grazing zooplankton can mediate the responses of phytoplankton to nutrients (Elser and Urabe 1999, Elser et al. 2007). Other experiments have implicated competitive interactions with other algae, which may be mediated by nutrients or abiotic conditions (Brauer et al. 2012).

Many of these previous studies of HABs and nutrients have relied on one of three approaches: broad-scale snapshot surveys of algal communities and environmental covariates measured in many lakes (Downing et al. 2001, Kosten et al. 2012), small-scale experimental manipulations of nutrient concentrations (Armitage and Fong 2004), or long-term measurements

PeerJ PrePrints | https://peerj.com/preprints/75v1/ | v1 received: 4 Oct 2013, published: 4 Oct 2013, doi: 10.7287/peerj.preprints.75v1

of algal abundance within a single lake (McCarthy et al. 2009). The analyses have either examined static patterns of algal abundance in different sites (Downing et al. 2001) or have treated time series data as if they were not autocorrelated (Onderka 2007). Although these methods can demonstrate correlations between HABs and environmental variables such as nutrient concentrations, HABs are dynamic populations. To understand the role of nutrients and other environmental factors in controlling HABs, explicit population growth models (Royama 1992, Berryman 1999) should be fit to dynamic time series data (but see Brauer et al. 2012 for a dynamic modeling example).

We used a data set of weekly monitoring of cyanobacteria blooms, abiotic variables, and abundances of other algal taxa from several sites in Missisquoi Bay in Lake Champlain, Vermont, U.S.A., collected from 2003 to 2008 (excluding 2007 because no bloom occurred and therefore weekly monitoring was not conducted). We constructed 34 different population dynamic models to test multiple hypotheses about what factors control the growth of HABs. Using a time-series splitting approach (Berryman 1999), we found that algal blooms were best modeled by splitting the time series into a distinct "bloom phase" and "post-bloom phase." A two-phase growth model has been used in studies of zooplankton population dynamics (Drake and Griffen 2010), although initial dynamics are sometimes dismissed as "transient" effects. Because HABs are often transient events (Huppert et al. 2002), we focus on discovering what drives the initial phase of the HAB. Our two-stage population growth model revealed the importance of density dependence and nutrient ratios during the bloom phase of HABs in Lake Champlain.

Methods

Site description

Lake Champlain is a 170 km long lake with a maximum width of about 20 km, and a maximum depth of 122 m (average depth = 23 m) that creates the border between New York and Vermont (Appendix Figure A1). The shallow and highly eutrophic Missisquoi Bay drains to the south, into the main lake section of Lake Champlain, but the lake itself drains north into the Richelieu River, which eventually drains to the St. Lawrence. Potential toxin-producing cyanobacteria (*Microcystis*, *Anabaena*, and *Aphanizomenon* spp.) have always been present in shallow waters of Lake Champlain (Shambaugh et al. 1999), but abundance has increased in recent years. Samples are from a monitoring program designed to quickly provide information on potentially toxic blooms to public health officials (Appendix A).

Data structure

We used weekly sample data collected from nine different sites in Missisquoi Bay from 2003 to 2008 (excluding 2007 because weekly data were not collected). Settled counts of phytoplankton cells were identified to genus and total nitrogen (TN), total phosphorus (TP), and soluble reactive phosphorus (SRP) were measured for each sample. Because algal blooms are highly patchy in occurrence and can drift with wind and currents, we averaged data (cells/ml) that were collected at each time period from nine sites in Missisquoi Bay. The result was a 12 to 16-week time series for each year of averaged cell densities (Appendix Figure B1) and nutrient concentrations (Appendix Figure B3). Analysis was performed only on the dominant toxic genera: *Microcystis* in 2003, 2004, 2005, and 2008, and *Anabaena* in 2006.

Modeling framework

We fit mechanistic population growth models (Royama 1992, Berryman 1999) by assuming an *a priori* functional form for density dependence and using a linear generalization of the Ricker equation (Royama 1992) for the per capita growth rate, $r_t = \ln\left(\frac{N_{t+1}}{N_t}\right)$:

PeerJ PrePrints | https://peerj.com/preprints/75v1/ | v1 received: 4 Oct 2013, published: 4 Oct 2013, doi: 10.7287/peerj.preprints.75v1

$$r_t = r_0 - \mathrm{N}_{t-1}^{\theta}\mathrm{e}^{c} \qquad \text{eq. 1}$$

In this equation r_0 is the maximum intrinsic growth rate, e^c is the strength of density dependence, θ is the degree of non-linearity, and carrying capacity is estimated as $K = {r_0}/{\mathrm{e}^c}$ (Berryman 1999). We examined untransformed phase plots of the data and did not find evidence for non-linearity and therefore set $\theta = 1.0$, and tested hypotheses only about the effects of nutrients on r_0 and c (vertical and lateral perturbations *sensu* Royama 1992). Changes to r_0 were modeled as:

$$r_t = r_0 - N_{t-1}\mathrm{e}^{c} + f(E_{t-d}) \qquad \text{eq. 2}$$

where E is a nutrient or environmental variable measured at time lag d. Similarly, effects of nutrients on carrying capacity were modeled as:

$$r_t = r_0 - N_{t-1}\mathrm{e}^{(c + f(E_{t-d}))} \qquad \text{eq. 3}$$

We included effects of potentially competing algal species (S) as:

$$r_t = r_0 - N_{t-1}\mathrm{e}^{(c + f(S_{t-d}))} \qquad \text{eq. 4}$$

This basic but flexible modeling framework allowed us to describe the pattern of algal population dynamics and test a variety of hypotheses about the effects of nutrients and other species on population growth.

Data analysis

Our data was linear, non-stationary and exhibited a first order feedback (Appendix B). To account for non-stationarity we split each time series into two phases. We defined the initial portion of the time series up to and including the maximum population size reached as the "bloom phase" and the period for the remainder of the series after the population peak as the "post-bloom phase." The bloom phase included the first five weeks since the beginning of bloom formation from the years 2003, 2004, 2005, 2006, and 2008. The post-bloom phase included the remaining weeks of data from each series. This data splitting approach is recommended if investigators identify a separatrix between two different dynamical conditions (Berryman 1999). We tested the separatrix with a bootstrap analysis and it correctly predicted the two phases of our system 99% better than random split points (Appendix B, Figure B4). Because the split series were too short to analyze individually (n < 5 observations) we had too few degrees of freedom to make statistical tests within each year. Instead we aggregated data across years within each phase by calculating r_t and pairing it with N_{t-1} for each year in the series. Next we combined all the pairs of r_t and N_{t-1} from the bloom phase of each year in one data series and did the same for the post-bloom phase points (combined n = 19 for the bloom phase and n = 41 for the post-bloom phase). This aggregation method (Hsieh et al. 2008) assumes that the same underlying function can be fit to model growth rates measured for bloom trajectories in different years. We tested 34 models based on eqs. 2 - 4 (Appendix Table B1 for a full list) in each phase and ranked them by small sample size AIC (AIC_c), defined as: $AIC_c = AIC + 2J(J + 1)/n - J - 1$ where n is sample size and J is the number of parameters (Burnham and Anderson 2002). Using AICc weights (w_i), we calculated an evidence ratio to compare the relative fit of each model to the best-fit model. All models were fit in R 2.10 (R Core Development Team 2009) using the *lm()* for linear models *nls()* for non-linear models.

Results

The bloom phase and post-bloom phase portion of the cyanobacteria trajectories exhibited different population dynamics (Figure 1A). In the bloom phase, the best fitting model included negative density dependence and a positive effect of TN:TP on r_0, with a model R^2 of 0.76 (Table 1). The remaining best-fitting models for the bloom phase all included positive growth with density dependence, and usually a positive effect of N on growth rates, although only the best-fitting model included TN:TP (Table 1). In the best-fitting model of the bloom phase, a partial

PeerJ PrePrints | https://peerj.com/preprints/75v1/ | v1 received: 4 Oct 2013, published: 4 Oct 2013, doi: 10.7287/peerj.preprints.75v1

residual plot shows a strong positive relationship between growth rate and TN:TP (Figure 1B), even after accounting for density dependence. The post-bloom phase models all had a negative growth rate. Although the best-fitting model for the post-bloom phase included an effect of TN on density dependence, it had an R^2 of only 0.12 and low model weight (Table 1). With a ΔAICc of 1, this best-fitting model was not appreciably better than a null model that included only negative exponential growth ($R^2 = 0.04$). Based on these analyses, the best descriptor of algal blooms in Missisquoi bay is:

$$r_{t=}\begin{cases} r_0 - N_{t-1}\mathrm{e}^{c} + \beta_1 \frac{TN_t}{TP_t}, & t =< 5 \\ -r_0, & t > 5 \end{cases}$$

where t is time in weeks since the bloom began (t is therefore relative to the start of the bloom). The density of potentially competing algal species did not enter into any of the best-fitting models as a significant predictor of cyanobacteria blooms. To test whether cyanobacteria abundance was directly correlated with TN, TP or TN:TP, we regressed abundance against TN:TP and found no relationship overall, or within years or phases (Figure 2)

Discussion

HAB's in Lake Champlain were best described by a two-phase model with an early bloom phase and a late post-bloom phase (Figure 1A, Table 1). The bloom phase was characterized by strong negative density dependence (with a time lag of one week) and a positive effect of TN:TP on the exponential component of population growth rate (Figure 1B). Algal density increased rapidly during the bloom phase and reached a peak within four to five weeks. The post-bloom phase was more variable in length and was characterized by a slow, largely stochastic, reduction in density. Our results support previous studies suggesting that TN:TP is important in controlling cyanobacteria population dynamics (Smith 1983, Havens et al. 2003, McCarthy et al. 2009, Paerl

PeerJ PrePrints | https://peerj.com/preprints/75v1/ | v1 received: 4 Oct 2013, published: 4 Oct 2013, doi: 10.7287/peerj.preprints.75v1

et al. 2011), and that management strategies should look beyond controlling a single nutrient (Conley et al. 2009).

Although we found a positive effect of TN:TP on population growth rate, other studies have demonstrated a negative relationship between TN:TP ratios and cyanobacteria biomass (Kotak et al. 2000) or relative abundance (Havens et al. 2003). These studies, however spanned a much larger range of TN:TP ratios than ours (for example, 1-43, Lake Taihu; McCarthy et al. 2009) or measured TN:TP at a single time among a set of many lakes (1- 100, Smith 1983). During the five years of this Lake Champlain data series, the maximum TN:TP ratio was 16, well below the Redfield ratio suggesting that nitrogen is most often the limiting nutrient. Our positive results are similar to McCarthy et al. (2009), who found a positive relationship between TN:TP and relative abundance of cyanobacteria when TN:TP was below 29. The TN:TP hypothesis assumes a low TN:TP ratio is an advantage for N-fixing taxa such as *Anabaena* and *Aphanizomenon*, but in most years in the Lake Champlain data series, blooms in Missisquoi Bay were dominated by *Microcystis,* which cannot fix N. *Microcystis* is capable of dominating for several reasons: it is a superior competitor for dissolved N (Smith 1983), low TN:TP ratios support the recruitment of resting stages from the sediment (Stahl-Delbanco et al. 2003), and perhaps most importantly, *Microcystis* can regulate its buoyancy. Buoyance regulation allows *Microcystis* to monopolize light at the surface and take up nutrients from the sediment-water interface (Bormans et al. 1999). Other studies have also found that *Microcystis* has optimal growth conditions around an N:P ratio of 16 (Liu et al. 2011). The shallow average depth of Missisquoi Bay (less than 3 m), and hypoxic bottom conditions in mid-summer (Smith et al. 2011) provide an ideal environment for *Microcystis* to exploit dissolved N from the sediment-water interface.

PeerJ PrePrints | https://peerj.com/preprints/75v1/ | v1 received: 4 Oct 2013, published: 4 Oct 2013, doi: 10.7287/peerj.preprints.75v1

We found no evidence for effects of the abundance of other algal taxa on the population dynamics of cyanobacteria. We used taxonomic groups in this analysis, but the factors that favor specific groups are often cross-phyletic, so a functional or trait-based assessment may have been more effective (Kruk et al. 2011). Additionally, we could not incorporate direct effects of predators (i.e., *Daphnia*) into our models because zooplankton was not sampled as part of the monitoring program. There can be indirect facilitation of conditions that favor HABs via *Daphnia* grazing on competitors of cyanobacteria (Wang et al. 2010) or alterations in nutrient cycling following seasonal changes in the zooplankton community (Elser 1999). Cyanobacteria are only grazed by *Daphnia* in limited quantities because the colonial growth form inhibits ingestion (DeMott et al. 2001), poor nutritive value (Elser and Urabe 1999), and perhaps because of cyanotoxin production (Rohrlack et al. 1999). Once blooms have begun, experimental additions and deletions of *Daphnia* provides little evidence of control by grazers (Ghadouani et al. 2003).

The existence of two distinct phases of cyanobacteria blooms (Figure 1A) potentially complicates the interpretation of snapshot surveys of different lakes (e.g., Downing et al. 2001) because the results of such surveys will be highly dependent on when the samples were collected. In large-scale surveys (Kosten et al. 2012), the absolute magnitude of TN and TP were better predictors of cyanobacterial dominance than the TN:TP ratio, whereas in a detailed study of single lakes, the TN:TP ratio is important (Paerl et al. 2011). In our study, only the exponential component of growth during the bloom phase was related to TN:TP ratio. This result is consistent with other studies that have found *Microcystis* can maintain high growth rates at low N:P ratios (Marinho and Azevedo 2007). TN:TP ratios may be important at the initiation of blooms but they do not matter once the post-bloom phase begins, perhaps because nutrients are

PeerJ PrePrints | https://peerj.com/preprints/75v1/ | v1 received: 4 Oct 2013, published: 4 Oct 2013, doi: 10.7287/peerj.preprints.75v1

less important overall when cells begin to senesce. However, at high nutrient concentrations light may be a more important variable than nutrient ratio because it becomes a limiting factor that cyanobacteria are well-adapted to exploit (Brauer et al. 2012).

Algal blooms are dynamic, transient events, but with few exceptions (e.g. in Carpenter and Kitchell 1993) they have not been analyzed with population dynamics models. In Lake Champlain, we discovered two distinct phases of HABs, each controlled by a different population growth equation and different correlations with environmental variables. Although simple correlations of cyanobacteria abundance with nutrients are often weak, our results point to the importance of TN:TP ratios on population growth rates during the bloom phase. This further supports recent evidence that highlights the importance of nutrient ratios being a limiting factor for plants, not just single nutrients (Harpole et al. 2011). Once a bloom has occurred its decline appears largely stochastic, and mitigation through control of nutrients after initiation may not be effective. A management strategy of reducing all nutrient inputs early in the season could potentially suppress the initiation of the bloom phase of HABs or reduce the size of the bloom.

Acknowledgments

This work was funded by NOAA through the MERHAB program (Grant No. NA160P2788) & the US EPA through the Lake Champlain Basin Program. Thanks to Susan Fuller, the Complex Systems group, and the many scientists and volunteers of the Lake Champlain Basin Program for data collection and management.

PeerJ PrePrints | https://peerj.com/preprints/75v1/ | v1 received: 4 Oct 2013, published: 4 Oct 2013, doi: 10.7287/peerj.preprints.75v1

Literature Cited

Armitage, A. R., and P. Fong. 2004. Upward cascading effects of nutrients: shifts in a benthic microalgal community and a negative herbivore response. Oecologia 139:560–567.

Berryman, A. A. 1999. Principles of Population Dynamics and Their Application. Garland Science, London.

Bormans, M., B. S. Sherman, and I. T. Webster. 1999. Is buoyancy regulation in cyanobacteria an adaptation to exploit separation of light and nutrients? Marine And Freshwater Research 50:897–906.

Brauer, V., M. Stomp, and J. Huisman. 2012. The Nutrient-Load Hypothesis: Patterns of Resource Limitation and Community Structure Driven by Competition for Nutrients and Light. The American naturalist 179:721–740.

Carpenter, S. R., and J. F. Kitchell. 1993. The Trophic Cascade in Lakes. (S. R. Carpenter and J. F. Kitchell, Eds.) Ecosystems. Cambridge University Press, Cambridge.

Chen, Y. W., B. Q. Qin, K. Teubner, and M. T. Dokulil. 2003. Long-term dynamics of phytoplankton assemblages: *Microcystis*-domination in Lake Taihu, a large shallow lake in China. Journal of Plankton Research 25:445–453

Codd, G. A., L. F. Morrison, and J. S. Metcalf. 2005. Cyanobacterial toxins: risk management for health protection. Toxicology and Applied Pharmacology 203:264–272.

Conley, D. J., H. W. Paerl, R. W. Howarth, D. F. Boesch, S. P. Seitzinger, K. E. Havens, C. Lancelot, and G. E. Likens. 2009. Ecology. Controlling eutrophication: nitrogen and phosphorus. Science 323:1014–5.

PeerJ PrePrints | https://peerj.com/preprints/75v1/ | v1 received: 4 Oct 2013, published: 4 Oct 2013, doi: 10.7287/peerj.preprints.75v1

DeMott, W. R., R. D. Gulati, and E. Van Donk. 2001. *Daphnia* food limitation in three hypereutrophic Dutch lakes : Evidence for exclusion of large-bodied species by interfering filaments of cyanobacteria. Limonology And Oceanography 46:2054–2060.

Downing, J. A., S. B. Watson, and E. McCauley. 2001. Predicting Cyanobacteria dominance in lakes. Canadian Journal of Fisheries and Aquatic Sciences 58:1905–1908.

Drake, J. M., and B. D. Griffen. 2010. Early warning signals of extinction in deteriorating environments. Nature 467:456–459.

Elser, J. J., M. E. S. Bracken, E. E. Cleland, D. S. Gruner, W. S. Harpole, H. Hillebrand, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecology Letters 10:1135–1142

Elser, J. J., and J. Urabe. 1999. The stoichiometry of consumer-driven nutrient recycling: Theory, observations, and consequences. Ecology 80:735–751.

Ghadouani, A., B. Pinel-Alloul, and E. E. Prepas. 2003. Effects of experimentally induced cyanobacterial blooms on crustacean zooplankton communities. Freshwater Biology 48:363–381.

Harpole, W. S., J. T. Ngai, E. E. Cleland, E. W. Seabloom, E. T. Borer, M. E. S. Bracken, J. J. Elser, D. S. Gruner, H. Hillebrand, J. B. Shurin, and J. E. Smith. 2011. Nutrient co-limitation of primary producer communities. Ecology Letters 14:852–862.

Havens, K. E., R. T. James, T. L. East, and V. H. Smith. 2003. N : P ratios, light limitation, and cyanobacterial dominance in a subtropical lake impacted by non-point source nutrient pollution. Environmental Pollution 122:379–390.

PeerJ PrePrints | https://peerj.com/preprints/75v1/ | v1 received: 4 Oct 2013, published: 4 Oct 2013, doi: 10.7287/peerj.preprints.75v1

Hsieh, C. H., C. Anderson, and G. Sugihara. 2008. Extending Nonlinear analysis to short ecological time series. American Naturalist 171:71–80.

Huppert, A., B. Blasius, and L. Stone. 2002. A model of phytoplankton blooms. The American naturalist 159:156–171.

Johnson, P. T. J., A. R. Townsend, C. C. Cleveland, P. M. Glibert, R. W. Howarth, V. J. McKenzie, E. Rejmankova, and M. H. Ward. 2010. Linking environmental nutrient enrichment and disease emergence in humans and wildlife. Ecological Applications 20:16–29.

Kosten, S., V. L. M. Huszar, E. Becares, L. S. Costa, E. Donk, L.-A. Hansson, E. Jeppesen, C. Kruk, G. Lacerot, N. Mazzeo, L. Meester, B. Moss, M. Lürling, T. Nõges, S. Romo, and M. Scheffer. 2012. Warmer climates boost cyanobacterial dominance in shallow lakes. Global Change Biology 18:118–126.

Kotak, B., A. Lam, E. Prepas, and S. Hrudey. 2000. Role of chemical and physical variables in regulating microcystin-LR concentration in phytoplankton of eutrophic lakes. Canadian Journal of Fisheries and Aquatic Sciences 57:1584–1593.

Kruk, C., E. Peeters, E. H. Van Nes, L. Costa, and M. Scheffer. 2011. Phytoplankton community composition can be predicted best in terms of morphological groups. Limnology and Oceanography 56:110–118.

Liu, Y., L. Li, and R. Jia. 2011. The optimum resource ratio (N: P) for the growth of *Microcystis aeruginosa* with abundant nutrients. Procedia Environmental Sciences.

Marinho, M., and S. de O. e Azevedo. 2007. Influence of N/P ratio on competitive abilities for nitrogen and phosphorus by *Microcystis aeruginosa* and *Aulacoseira distans.* Aquatic ecology 41:525-533.

PeerJ PrePrints | https://peerj.com/preprints/75v1/ | v1 received: 4 Oct 2013, published: 4 Oct 2013, doi: 10.7287/peerj.preprints.75v1

McCarthy, M. J., R. T. James, Y. W. Chen, T. L. East, and W. S. Gardner. 2009. Nutrient ratios and phytoplankton community structure in the large, shallow, eutrophic, subtropical Lakes Okeechobee (Florida, USA) and Taihu (China). Limnology 10:215–227.

Onderka, M. 2007. Correlations between several environmental factors affecting the bloom events of cyanobacteria in Liptovska Mara reservoir (Slovakia) - A simple regression model. Ecological Modelling 209:412–416.

Paerl, H. W., N. S. Hall, and E. S. Calandrino. 2011. Controlling harmful cyanobacterial blooms in a world experiencing anthropogenic and climatic-induced change. The Science of the total environment 409:1739–45.

Rohrlack, T., E. Dittmann, M. Henning, T. Börner, and J.-G. Kohl. 1999. Role of microcystins in poisoning and food ingestion inhibition of *Daphnia galeata* caused by the cyanobacterium *Microcystis aeruginosa.* Applied and Environmental Microbiology 65:737–739.

Royama, T. 1992. Analytical Population Dynamics. Chapman and Hall, New York.

Scheffer, M., S. Rinaldi, A. Gragnani, L. R. Mur, and E. H. VanNes. 1997. On the dominance of filamentous cyanobacteria in shallow, turbid lakes. Ecology 78:272–282.

Shambaugh, A., A. Duchovnay, and A. McIntosh. 1999. A survey of Lake Champlain's Plankton. Lake Champlain in Transition: From Research Toward Restoration. American Geophysical Union, Washington.

Smith, L., M. Watzin, and G. Druschel. 2011. Relating sediment phosphorus mobility to seasonal and diel redox fluctuations at the sediment—Water interface in a eutrophic freshwater lake. Limnology and Oceanography 56:2251–2264.

Smith, V. H. 1983. Low Nitrogen to Phosphorus rations favor dominance by blue-green algae in lake phytoplankton. Science 221:669–671.

Stahl-Delbanco, A., L. A. Hansson, and M. Gyllstrom. 2003. Recruitment of resting stages may induce blooms of Microcystis at low N : P ratios. Journal of Plankton Research 25:1099–1106.

Wang, X. D., B. Q. Qin, G. Gao, and H. W. Paerl. 2010. Nutrient enrichment and selective predation by zooplankton promote *Microcystis* (Cyanobacteria) bloom formation. Journal of Plankton Research 32:457–470.

Table 1

Phase	*Model*	*AICc*	*ΔAICc*	*Evidence Ratio*	R^2
Bloom	$r_t = r_0 - N_{t-1}e^c + \beta_1 TN_t{:}TP_t$	42.4	0	-	0.76
	$r_t = r_0 - N_{t-1}e^c$	46.5	4.1	9	0.65
	$r_t = r_0 - N_{t-1}e^c + \beta_1 TN_t$	48	5.6	20	0.68
	$r_t = r_0 - N_{t-1}e^c + \beta_1 TN_{t-1}$	48.4	6	20	0.67
	$r_t = r_0 - N_{t-1}e^c + \beta_1 SRP_{t-1}$	48.6	6.2	30	0.67
Decline	$r_t = -r_0 - N_{t-1}e^{(c-\beta_1 TN_t)}$	90.7	0	-	0.12
	$r_t = -r_0$	91.7	1	1.75	-
	$r_t = -r_0 - N_{t-1}e^c$	91.8	1.1	1.75	0.04
	$r_t = -r_0 - N_{t-1}e^c + \beta_1 TN_t$	92.8	2.1	2.8	0.08
	$r_t = -r_0 + \beta_1 TN_t$	93.1	2.4	3.5	0.02

Table 1. The top five models for bloom phase dynamics and post-bloom phase dynamics of cyanobacteria in Lake Champlain, with the best-fitting models listed first for each phase. Models were assessed based on small sample size AIC (AICc). Model parameters are as follows: r_o is the maximum per-capita growth rate, *c* is the strength of density dependence, *TN* is total nitrogen, *TP* is total phosphorus, and *SRP* is soluble reactive phosphorus. Evidence ratios are calculated as the AICc weight of the best fitting model divided by the *ith* model as ranked by ΔAICc (w_1/w_i). Evidence ratios in excess of 10 are usually interpreted as strong evidence favoring a particular model (Burnham and Anderson 2000).

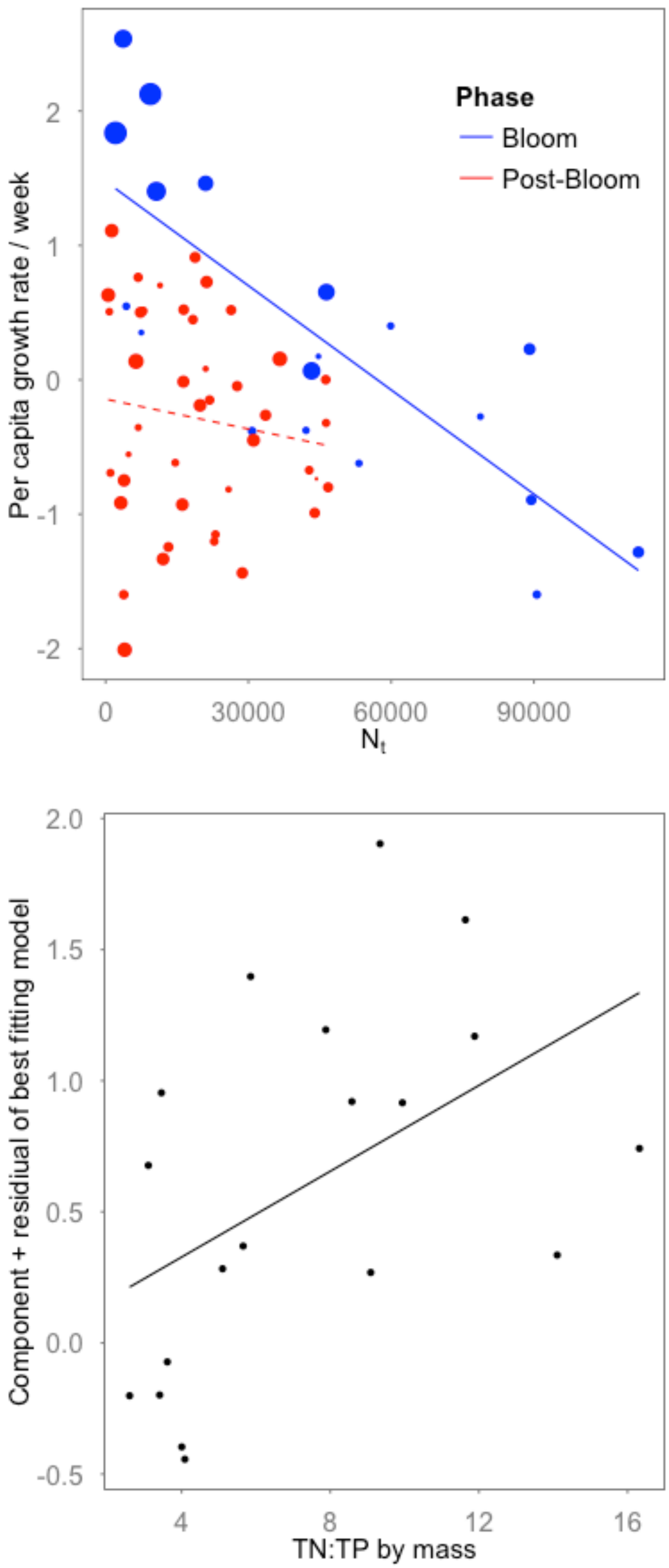
PeerJ PrePrints | https://peerj.com/preprints/75v1/ | v1 received: 4 Oct 2013, published: 4 Oct 2013, doi: 10.7287/peerj.preprints.75v1

Figure 1. (A). Phase plot of population growth of growth rate (r_0) versus population size at the previous time step (N_{t-1}). The size of each symbol is proportional to the TN:TP ratio. Blue points represent the bloom phase, and the solid blue line is the best-fitting density dependent model (linear regression, df = 14 ,R^2=0.76, p = 0). Red points represent the post-bloom phase, and the dashed red line is a simple, non-significant density dependent model (linear regression, df = 38, R^2=0.04, p = 0.339). The slope of zero with a negative intercept indicates a simple exponential decline with no effect of density-dependence. (B) A plot of partial-residuals vs. the TN:TP ratio for the best-fitting model of plankton dynamics during the bloom phase. The positive correlation demonstrates that population growth rate increases with increasing TN:TP ratios even after taking density dependence into account.

Figure 2 A plot of cyanobacteria abundance vs. nutrients separated by phase [bloom (open) and post-bloom (closed) points] and by year (colour). Neither nutrients nor nutrient ratios could explain a significant portion of the variance in abundance.

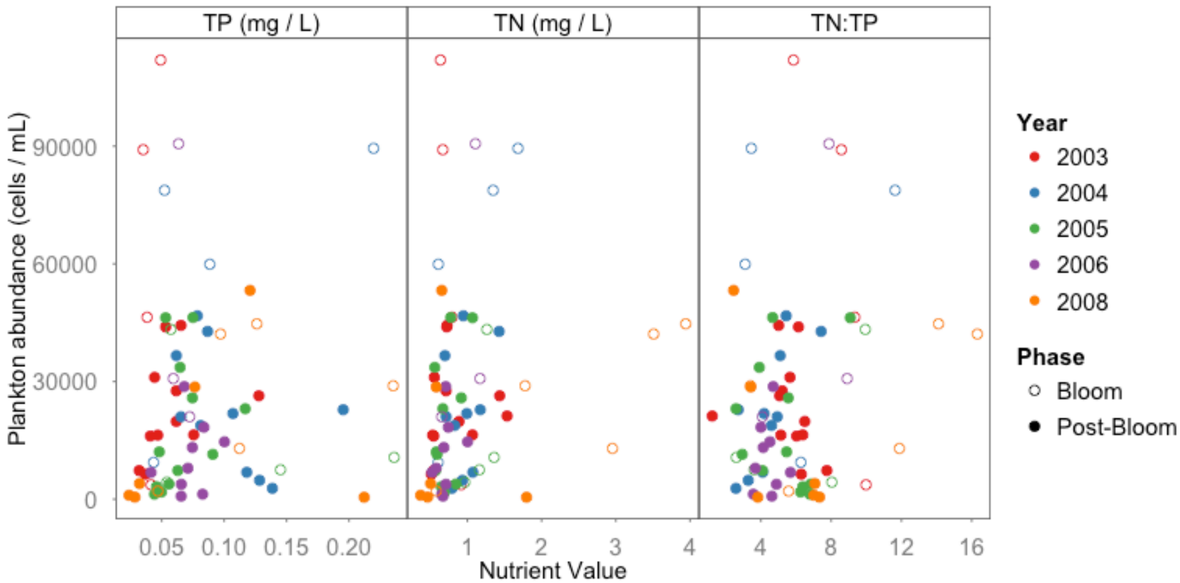
PeerJ PrePrints | https://peerj.com/preprints/75v1/ | v1 received: 4 Oct 2013, published: 4 Oct 2013, doi: 10.7287/peerj.preprints.75v1

Figure 1



PeerJ PrePrints | https://peerj.com/preprints/75v1/ | v1 received: 4 Oct 2013, published: 4 Oct 2013, doi: 10.7287/peerj.preprints.75v1

Figure 2



PeerJ PrePrints | https://peerj.com/preprints/75v1/ | v1 received: 4 Oct 2013, published: 4 Oct 2013, doi: 10.7287/peerj.preprints.75v1