![DiVA logo](http://www.diva-portal.org)
This is the published version of a paper published in *Biogeochemistry*.

CrossMark

Climate-driven changes in energy and mass inputs systematically alter nutrient concentration and stoichiometry in deep and shallow regions of Lake Champlain

Peter D. F. Isles · Yaoyang Xu · Jason D. Stockwell · Andrew W. Schroth

Abstract Concentrations of nitrogen (N) and phosphorus (P) in lakes may be differentially impacted by climate-driven changes in nutrient loading and by direct impacts of temperature and wind speed on internal nutrient cycling. Such changes may result in systematic shifts in lake N:P under future climate warming. We used 21 years of monitoring data to compare long-term and intra-annual trends in total N (TN), total P (TP) and TN:TP at 15 sites in Lake Champlain to concurrent measurements of watershed nutrient inputs and meteorological drivers. TN:TP declined sharply lake-wide, particularly in the past decade, yet the drivers of this trend varied based on site depth. In deep sites, declines were driven by changes in watershed loading of dissolved P and N and (in some cases) by decreases in hypolimnetic dissolved oxygen. In shallow sites, declines in TN:TP were primarily driven by long-term increases in temperature and decreases in wind speed, and exhibited systematic seasonal variability in TN:TP due to the timing of sediment P loading, N removal processes, and external nutrient inputs. We developed a conceptual model to explain the observed trends, and suggest that while climate drivers have affected nutrient dynamics in shallow and deep sites differently, both deep and shallow sites are likely to experience further declines in N:P and increases in cyanobacteria dominance if recent climate trends continue.

Responsible Editor: Jennifer Leah Tank.

P. D. F. Isles · Y. Xu · J. D. Stockwell
Rubenstein Ecosystem Science Laboratory, University of Vermont, Burlington, VT, USA

P. D. F. Isles · J. D. Stockwell
Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT, USA

P. D. F. Isles · Y. Xu · A. W. Schroth
Vermont EPSCoR, University of Vermont, Burlington, VT, USA

A. W. Schroth
Department of Geology, University of Vermont, Burlington, VT, USA

Present Address:
P. D. F. Isles (✉)
Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden
e-mail: peter.isles@umu.se

Introduction

Nitrogen (N) and phosphorus (P) are the primary nutrients limiting phytoplankton production in lakes (Guildford and Hecky 2000). The ratio of N to P (N:P) is often cited as an important factor determining phytoplankton community composition and the likelihood of cyanobacteria blooms (Smith 1983; Guildford and Hecky 2000), although other studies suggest the absolute concentrations (Downing et al. 2001; Brauer et al. 2012) or forms of N and P (Blomqvist et al. 1994; Reynolds and Davies 2001; Hessen 2013) are more important determinants of community structure, and cyanobacteria dominance can be a cause as well as a consequence of changes in N:P (Xie et al. 2003; Cottingham et al. 2015). Changing patterns of temperature and precipitation are expected to alter patterns of nutrient delivery from lake catchments (Jeppesen et al. 2009; Leavitt et al. 2009; Jones et al. 2011) and internal cycling of nutrients (Grantz et al. 2014). Therefore, N and P may respond differently to climate change, resulting in changing lake N:P ratios and corresponding shifts in biological communities (Elser et al. 2000).

Climate change may affect lake N:P indirectly through changes in mass fluxes of water and nutrients to lakes mediated by lake catchments, or directly through changes in fluxes of energy to lakes (air temperature, wind, or solar radiation) (Leavitt et al. 2009; Blenckner 2005). Recent studies suggest that external loads of P have already increased in some lakes as a result of changing climate patterns, despite reductions in anthropogenic inputs (Jeppesen et al. 2009). Substantial changes in N and P loading (Andersen et al. 2006) and in water inputs and flushing rates (Jones et al. 2011) are likely with future climate warming. Changes to tributary nutrient loading may be manifest in changes in the loads of nutrient inputs (Jeppesen et al. 2009) or in the timing of these inputs (Pierson et al. 2013). The form of nutrients delivered to lakes may also be affected by changing climate (Vanni et al. 2001). Many climate models predict an increase in storm intensity under warming scenarios (Guilbert et al. 2015). Higher energy storms are expected to lead to increased transport of particulate nutrients, while the effects on dissolved nutrient transport are less clear (Sharpley et al. 2008). Because P transport is frequently dominated by the particulate fraction while most N is transported in dissolved form,

stronger storms may result in changing N:P of river loads (Rosenberg and Schroth 2017). Climate-driven changes in N and P loading are likely to interact with changes in land use and land management practices, potentially resulting in further changes to lake N:P (Michalak et al. 2013).

Internal processing of nutrients and N:P ratios can be influenced by changes in temperature, wind mixing, and solar radiation (energy fluxes), which impact both physical and biological processes. Deep and shallow lakes may respond differently to these drivers. Deep temperate lakes are generally expected to experience longer periods of summer stratification under warmer climates (Wagner and Adrian 2009; Williamson et al. 2009; Foley et al. 2011). Longer periods of stratification may lead to hypolimnetic oxygen depletion and increased P release from sediments (Soranno et al. 1997; Jankowski et al. 2006). In shallow polymictic lakes, nutrient processing may exhibit complex responses to climate drivers. Warmer sediment temperatures are likely to boost sediment respiration rates and lower oxygen concentrations near the sediment–water-interface in shallow lakes. Lower oxygen concentrations may lead to enhanced release of P adsorbed to reducible Fe oxyhydroxides (Davison 1993; Hupfer and Lewandowski 2008; Smith et al. 2011). Lower oxygen concentrations may also affect nitrogen cycling, leading to increased denitrification or inhibition of nitrification and increased fluxes of ammonium to the water column (McCarthy et al. 2016). However, nutrient release processes are likely to be mediated by site depth, trophic state, sediment composition, and the frequency of lake mixing (Jöhnk et al. 2008; Kosten et al. 2011). In addition to changes in nutrient supply rates, biological processes are also likely to directly respond to changes in energy fluxes, which may result in changes in water column nutrient concentrations (Cottingham et al. 2015). Higher temperatures may increase phytoplankton growth rates (Butterwick et al. 2005), and increased water column stability resulting from increased temperature is likely to increase cyanobacteria dominance by relieving light limitation (Huisman et al. 2004; Paerl and Huisman 2008). Increased cyanobacteria dominance may increase water column N and P concentrations, particularly in shallow sites where phytoplankton can access sediment nutrients. Projections of future

trends in wind speed are uncertain (Pryor et al. 2009, Pryor and Barthelmie 2010), and may either compound or mitigate these effects.

The impacts of changing climate and land use on lake N:P are difficult to resolve due to the multiple factors influencing lake N and P concentrations. Several large lakes have experienced increases in the ratio of dissolved inorganic nitrogen to TP over the period from 1970–2010 as a result of decreases in anthropogenic P loading and climate-mediated changes in water residence time (Finlay et al. 2013). In contrast, TN:TP has declined over the same period in Lake Erie (Scavia et al. 2014) and Lake Winnipeg (Schindler et al. 2012) as a result of changes in precipitation, temperature, agricultural practices. Smaller, shallow northern European lakes have experienced falling N concentrations in recent decades as a result of decreasing N deposition and increasing temperature (Weyhenmeyer et al. 2007). Decoupling the effects of climate and land use on lake function requires comprehensive datasets capable of resolving multiple explanatory variables over long timescales.

In this study, we compared decadal and intra-annual trends in TN, TP, and TN:TP to inputs of dissolved and particulate nutrients from tributaries, and to meteorological drivers which may influence internal nutrient cycling, at 15 long-term monitoring sites in Lake Champlain from 1992 to 2012. We focused on contrasts between deep dimictic and shallow polymictic sites, and examined trends in other variables (water temperature, dissolved oxygen, and cyanobacteria abundance) to explain or corroborate trends in N and P. The monitoring sites spanned a wide range of depths and trophic conditions (VT DEC and NY DEC 2014). Additionally, the lake has several distinct basins with limited exchange of water, making the long-term dataset useful to compare trends across a range of conditions while retaining the consistency of a single, standardized dataset. Lake Champlain is also notable for its large ratio of watershed area to lake area (19:1), making it an ideal site for studying the interacting effects of climate and watershed loading on lake processes. Our objectives were to: (1) determine whether lake N and P concentrations and stoichiometry have changed over the 21-year monitoring period, (2) mechanistically interpret long-term trends in lake nutrient dynamics as a function of changes in inputs to the system, (3) identify characteristic seasonal patterns of nutrient concentration and stoichiometry in shallow and deep sites and their connection to meteorological drivers, and (4) develop a broadly applicable conceptual model based on our results to explain the drivers of nutrient behavior across diverse lake environments and project the response of these environments to climate-driven changes in energy and mass fluxes.

Methods

Site description

Lake Champlain is a large natural lake located between the Adirondack Mountains in New York, the Green Mountains in Vermont, and the St. Lawrence valley in Quebec (Fig. 1). Lake Champlain is 193 km long and 19 km wide at its widest point, with a maximum depth of 122 m and an average depth of 20 m. Lake Champlain contains five major basins separated by human-made and natural barriers, and different regions of the lake experience a wide range of trophic conditions (Xu et al. 2015b). N-fixing and non N-fixing cyanobacteria blooms have increased in recent years (Levine et al. 2012; Smeltzer et al. 2012; Watzin et al. 2012).

Data sources

Epilimnetic TP, epilimnetic TN, bottom water dissolved oxygen (DO), and bottom water temperature data were collected approximately fortnightly during the ice-free period (April–November) from 1992 to 2012. Data were obtained from the Lake Champlain Long Term Monitoring Program (http://www.watershedmanagement.vt.gov/lakes/htm/lp_longterm.htm) for all 15 lake monitoring sites (VT DEC and NY DEC 2014), which ranged in depth from 4 to 100 m (Supplementary Table 1). Phytoplankton cell count data from 63-µm plankton net vertical plankton samples were obtained from the Vermont Department of Environmental Conservation by request. Tributary nutrient loads (daily and annual) for TN, TP, and DP from each of the 18 monitored tributaries to the lake for 1992–2012 were estimated by Medalie (2013). TN:TP in the lake and tributaries are expressed as $TN:TP_{lake}$ and $TN:TP_{river}$ to avoid ambiguity. Meteorological data were obtained from Weather Underground for the Burlington International
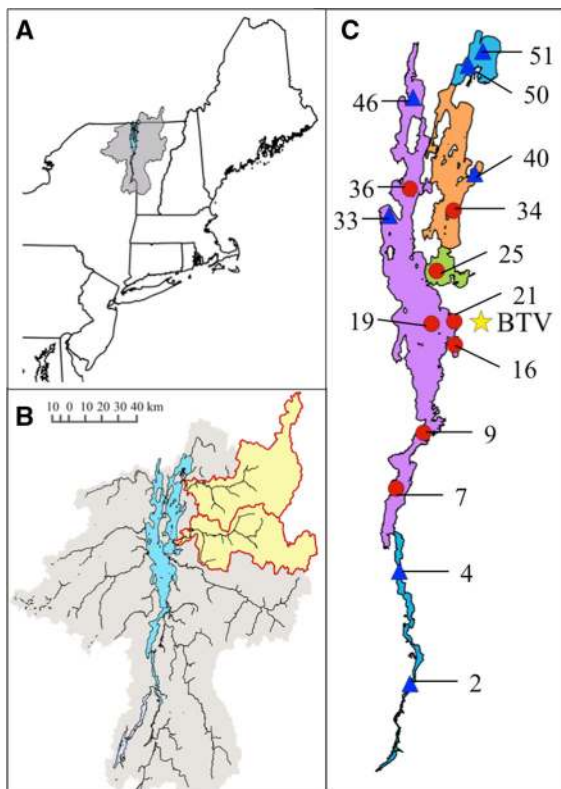
Fig. 1 a Location of the Lake Champlain basin in the northeastern United States. **b** Lake Champlain catchment, showing all monitored tributaries. Two catchments where detailed river–lake comparisons are carried out are highlighted. C: Locations of the shallow (*triangles*) and deep (*circles*) long-term monitoring sites in the lake, with station identification numbers from the Long Term Monitoring Program. The five major lake basins are shown in different *colors*; *clockwise from top right* they are Missisquoi Bay, Northeast Arm, Malletts Bay, Main Lake, and South Lake. Burlington Airport (BTV), where weather data were collected, is marked with a *star*. (Color figure online)

Airport from 1 January 1992 through 31 December 2012 (http://www.wunderground.com/history/airport/KBTV/). River discharge (Q) data were acquired from USGS gage stations for the nine largest tributaries to Lake Champlain (USGS gage stations 04275500, 04276500, 04271500, 04292500, 04294000, 04282500, 04280000, 04273500, and 04290500). Together, the gaged area of these stations covered 60.3% of the area of the Lake Champlain Basin.

Statistical methods

Lake TN and TP data were aggregated into shallow (<15 m) and deep (≥15 m) sites for analysis of long-term and within-year trends. The 15-m threshold was

based on visual inspection of plots of surface and bottom water temperature by Julian date (Supplemental Fig. 2); 15 m was the threshold above which monitoring sites within the lake tended to exhibit stable stratification during the summer growing season, and below which sites were polymictic. We note that similar thresholds are likely to be shallower in smaller lakes less exposed to wind mixing and seiche activity. Data from three sites where data collection began in 2001 (Missisquoi Bay Central, Shelburne Bay, Otter Creek Segment) were omitted for analysis of long-term trends, but included for analysis of within-year trends. Sites within the same lake basin (Fig. 1; Supplementary Table 1) are likely to experience similar water masses, so should not be considered truly independent; however, substantial differences may still exist within basins, particularly in the large Main Lake basin, due to the influence of different riverine inputs and site depths (Smeltzer et al. 2012).

Segmented regression was used to fit linear models with breakpoints to nutrient data against date or Julian date using the R package "segmented" (Muggeo 2003, 2008) for sites where Davies' test was significant ($\alpha = 0.01$) (Davies 2002). Slopes of TN and TP during the main growing season (July and August), when cyanobacteria blooms tend to occur in Lake Champlain (Watzin et al. 2012), were used to investigate within-year trends in nutrients. N and P dynamics in the spring and fall are expected to be strongly influenced by watershed inputs, whereas nutrient dynamics during the summer are expected to be primarily influenced by internal processes (sediment nutrient transformation and biological uptake; Rosenberg and Schroth 2017; Isles et al. 2015; Giles et al. 2016). Where Davies' test was not significant, slopes were determined with least-squares regression. All nutrient ratios are molar ratios, and all regressions of N:P data were conducted on $\log_{10}$-transformed N:P. Log transformations are appropriate when calculating statistical metrics on data presented in the form of ratios because (1) log ratios respond symmetrically to changes in concentrations of N or P, and (2) the slopes of similar proportional changes in nutrient concentration are comparable in log-transformed data regardless of trophic status (Keene 1995; Hillebrand et al. 2013). Plots of data were presented with untransformed axis labels to allow easier interpretation of the data.

Long-term changes in annual river loads of TN, TP, TN:TP and DN:DP were also analyzed using least-

squares regression and segmented regression. Because trends in annual loads did not match trends in lake nutrient concentrations (see Results), average annual concentrations of river nutrients were calculated as the total annual load divided by the total annual discharge, and were compared to lake nutrient concentrations. Further analyses were conducted for two sites representative of shallow and deep bays with major tributary inputs (Missisquoi Bay station 50 and Malletts Bay station 25, respectively; Fig. 1), where direct comparisons of lake and tributary nutrient concentrations were possible. For these sites, regressions were conducted of DN_{river} and DP_{river} of tributary nutrient inputs against TN_{lake} and TP_{lake}. Log($TN:TP_{river}$) and log($DN:DP_{river}$) were both compared to log($TN:TP_{lake}$) of the receiving bays, to determine whether epilimnetic nutrient concentrations reflected dissolved or total external nutrient loads. DN_{river} for these regressions was estimated as $0.85 \times TN_{river}$, based on the mean (0.867) and median (0.891) ratios of $DN:TN_{river}$ measured in the two tributaries where DN_{river} data were available (Missisquoi and Winooski Rivers; Supplemental Fig. 1). Similar regressions were also conducted for the aggregate annual loads of all monitored tributaries against nutrient concentrations at the central Main Lake station.

Long-term trends were determined for air temperature and wind speed using averages for the lake monitoring season (April–November), and long-term trends in aggregate tributary discharge were determined using annual averages. In addition, monthly changes in meteorological drivers, river discharge, and lake nutrients from 1992 to 2012 were estimated using least-square regressions against time for each variable subsetted by each month. The slopes of the resulting regression lines were used to estimate the total change for each month from 1992 to 2012. All regressions were evaluated for statistical significance at $\alpha = 0.05$.

To test the combined influence of external inputs and climate drivers, stepwise multiple regression model selection (forward and backward) was used to identify the best models to explain TN_{lake} and TP_{lake} in the representative deep and shallow bay. Separate regression models were evaluated for lake nutrients measured in spring (April–June), summer (July–August), fall (September–October), and annual (monitoring season). Because of the potential importance of lagged effects of winter and spring discharge on summer nutrient concentrations (Stumpf et al. 2012), tributary nutrient concentrations and discharge for seasonal models were calculated as cumulative values for the calendar year through the season being modeled (e.g. summer TN_{lake} is compared to TN_{river} loads from January to August).

In deep lake sites which displayed stable thermal stratification each summer, quantile regression was used to test for significant trends in the maxima of bottom water temperature and minima of bottom water DO over time (Cade and Noon 2003). Quantile regression analyses were conducted using the R package "quantreg" (Koenker 2015). The upper end of the temperature distribution was modeled as the 80th percentile, while the lower end of the DO distribution was modeled as the 20th percentile. Models using more extreme quantiles were heavily influenced by outliers and provided poor fits to the data. Quantile regression was also used to evaluate trends in peak cyanobacteria abundance (cells mL^{-1}) for the three most abundant genera (*Anabaena*, *Aphanizomenon*, and *Microcystis*). A tau of 0.9 was used for these models, and regressions were conducted on log (n + 1) transformed abundance data to correct for heteroscedasticity (Ives 2015).

Results and discussion

Long-term trends in lake and tributary nutrient concentrations

TN_{lake} and TP_{lake} had opposite trajectories over the study period (Fig. 2). TN_{lake} decreased significantly in both deep and shallow sites ($p < 0.0001$) at an average annual rate of 3.5 µg L^{-1} year^{-1} (deep and shallow sites; Fig. 2). In deep sites TN_{lake} declined steadily over time, whereas in shallow sites it remained constant for the first decade but then declined following 2002 (although there were substantial differences among sites; Supplemental Fig. 3). Long-term declines in TN_{lake} were greatest in May–July in shallow sites, and in July–August in deep sites (Fig. 3). In contrast to TN_{lake}, TP_{lake} increased significantly lakewide ($p < 0.0001$) at average annual rates of 0.30 µg L^{-1} year^{-1} (shallow sites) and 0.20 µg L^{-1} year^{-1} (deep sites; Fig. 2). Increases in TP_{lake} were greatest in June and October in shallow sites, and in
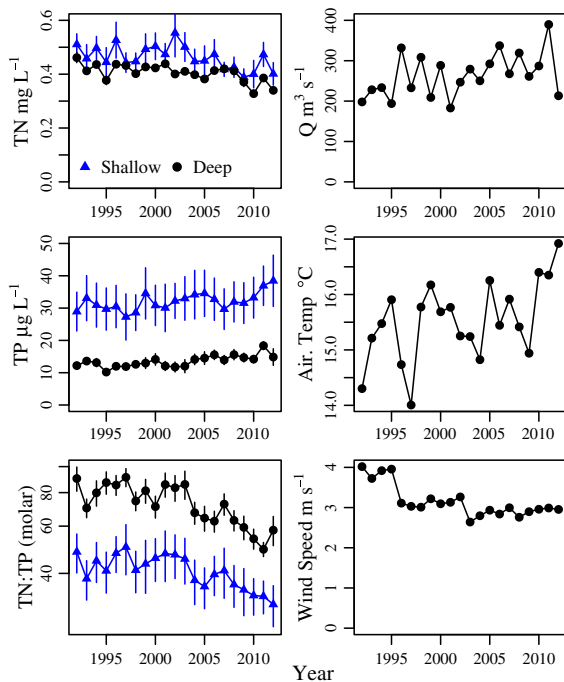
Fig. 2 Long-term trends in TN (mg L^{-1}), TP (μg L^{-1}), log$_{10}$(TN:TP) (molar), daily discharge from all tributaries (m^3 s^{-1}, annual average), air temperature (°C, April–November average) and wind speed (m s^{-1}, April–November average) in Lake Champlain

Fig. 3 Average changes from 1992 to 2014 for each month in: lake TN (mg L^{-1}), TP (μg L^{-1}), and log$_{10}$(TN:TP) (molar), aggregate daily discharge rates from the nine largest tributaries to the lake (log scale, cubic meters per second), and air temperature and wind speed from the Burlington airport. Significant changes are marked with an *asterisk* (p < 0.05)

September in deep sites (Fig. 3). As a result of both decreasing TN$_{lake}$ and increasing TP$_{lake}$, TN:TP$_{lake}$ decreased sharply throughout Lake Champlain (Fig. 2). In shallow sites, TN:TP$_{lake}$ decreased most dramatically in spring and fall, while in deep sites the largest decreases were in summer. The time-series of TN:TP$_{lake}$ had significant breakpoints in 2002–2003 for deep sites within the main lake basin (α < 0.01; Supplemental Fig. 3), with minor increases preceding the breakpoints, and sharp declines following. Collectively, the data indicate that while large scale declines in TN:TP were evident across Lake Champlain over the monitoring period, the environmental drivers responsible for these declines likely differed between deep and shallow monitoring stations.

Long-term trends in external loads of TN$_{river}$ and TP$_{river}$ to the lake did not match trends in TN$_{lake}$ and TP$_{lake}$. Aggregate annual loads of TN$_{river}$ from all tributaries increased over time, in contrast to the decrease in TN$_{lake}$ (Supplemental Fig. 4). Similarly, annual TP$_{river}$ loads did not change over the monitoring period, in contrast to the lake-wide increases in
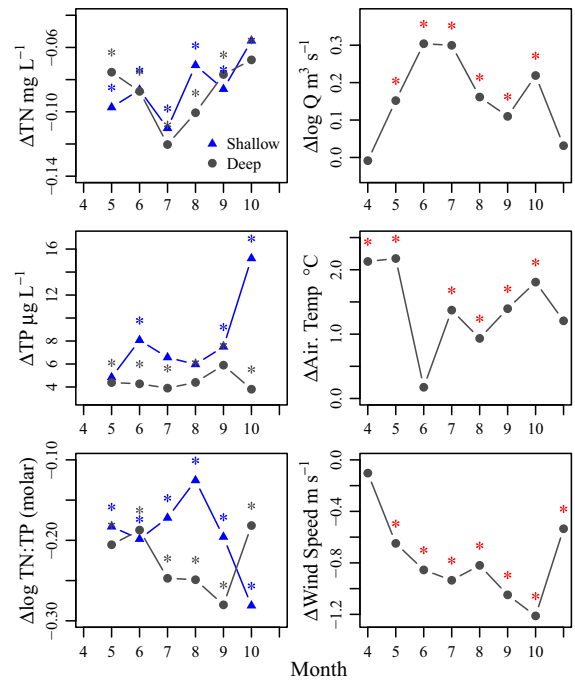
TP$_{lake}$. Annual TN:TP$_{river}$ was constant through time, in contrast to the sharp decline in TN:TP$_{lake}$. The fraction of external loads which most closely matched the trajectory of TN:TP$_{lake}$ was the ratio of dissolved nutrients (DN:DP$_{river}$). Because TP$_{river}$ loads were dominated by the particulate fraction (74% on average; Medalie [2013]) and most TN$_{river}$ was delivered in dissolved form (85%; Supplemental Fig. 1), DN:DP$_{river}$ was much higher than TN:TP$_{river}$. A significant breakpoint was evident in the time series of DN:DP$_{river}$ in 2002, similar to the breakpoints in TN:TP$_{lake}$ for sites in the main lake basin (Supplemental Figs. 3, 4). DN:DP$_{river}$ increased slightly before this breakpoint, and declined sharply following. Annual TN:TP$_{lake}$ of the deep, central Main Lake station was significantly correlated with aggregate annual DN:DP$_{river}$ (p = 0.00733, R^2 = 0.322), but was not correlated with aggregate annual TN:TP$_{river}$. These results suggest that dissolved riverine nutrient inputs had more influence on TN:TP$_{lake}$ than total riverine nutrient inputs in the main lake basin and that

changes to their ratio in river water were driving the observed trends over the monitoring period in deeper areas of Lake Champlain.

Because annual *loads* of nutrient inputs failed to explain trends in lake nutrients, particularly the decline in TN_{lake}, we also calculated average annual *concentrations* of total and dissolved nutrient inputs and compared them to in-lake total nutrient concentrations. Trends in nutrient loads to the lake over the monitoring period were primarily controlled by changes in precipitation and tributary discharge (Medalie 2013). However, average TN_{river} and TP_{river} concentrations were strongly affected by changing land management over this period (Ghebremichael et al. 2010). As a result, although TN_{river} loads from rivers draining forested catchments increased over time as a result of increasing precipitation, average TN_{river} concentrations declined as a result of decreased atmospheric N deposition (Canham et al. 2012) and changes in nutrient management (Medalie 2013). The declines in TN_{river} concentrations matched the observed declines in TN_{lake}.

To further investigate the role of external inputs, dissolved and total river nutrient concentrations were directly compared to lake nutrients in one deep and one shallow bay, each with large tributary inputs (stations 25 and 50; Fig. 1). For the deep bay, average annual concentrations of DN_{river} declined over time, and were highly significant predictors of TN_{lake} ($p = 0.00015$, $R^2 = 0.51$). Furthermore, TN_{lake} was distributed close to the 1:1 line (Fig. 4). Similarly, the concentration of DP_{river} was a highly significant predictor of TP_{lake} in the deep bay ($p = 0.0023$, $R^2 = 0.39$), and the regression line was very close to the 1:1 line (Fig. 4), while the concentration of TP_{river} was uncorrelated with TP_{lake}. Annual $\log(TN:TP_{lake})$ of the deep bay was not significantly correlated with annual $\log(TN:TP_{river})$ from its major tributary ($p = 0.23$, $R^2 = 0.071$), but was strongly positively correlated with $\log(DN:DP_{river})$ ($p < 0.0001$, $R^2 = 0.64$), and the regression line was close to the 1:1 line (Fig. 4). All results support the previous contention that dissolved nutrient concentrations of tributary inputs are important determinants of TN_{lake}, TP_{lake} and $TN:TP_{lake}$ in deep monitoring stations across Lake Champlain.

Relationships between tributary and lake nutrient concentrations were weaker for the shallow bay. The concentration of DN_{river} was not a significant predictor
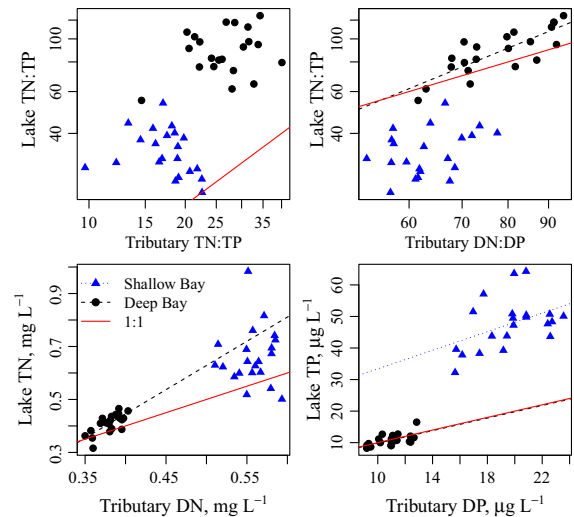

Fig. 4 Comparison of tributary and lake nutrient ratios and concentrations in a selected deep (Malletts) and shallow (Missisquoi) bay, each with a major tributary input. *Points* represent annual averages of lake and tributary nutrients for 1992–2012. *Regression lines* (*dotted* and *dashed*) are only shown for significant regressions. *Solid red line* represents 1:1. (Color figure online)

of TN_{lake} ($p = 0.95$, $R^2 = 0$). TN_{lake} was usually higher than DN_{river} in the shallow site, suggesting that another source of N contributed to TN_{lake}. Particulate N_{river} inputs may be available to the water column after mineralization in the sediments. Previous work in the bay suggests that benthic N fluxes are important sources of ammonium to the lake water column during the growing season (McCarthy et al. 2016). N-fixation may also contribute to higher TN_{lake} at this site relative to DN_{river}, although the evidence for this is unclear. The plankton community at the shallow site is usually dominated by a mix of diatoms, diazotrophs and non N-fixing cyanobacteria. Previous field assays, however, have found little evidence of N-fixation even when diazotrophs were present (McCarthy et al. 2013). DP_{river} was a significant predictor of TP_{lake} in the shallow bay ($p = 0.045$, $R^2 = 0.15$). However, average annual concentrations of TP_{lake} were roughly twice the average annual concentrations of DP_{river} (Fig. 4) and much of the variance was unexplained, suggesting that another major source of P contributed to TP_{lake} in shallow sites. Annual $TN:TP_{lake}$ in the shallow bay was not significantly correlated with either $TN:TP_{river}$ or $DN:DP_{river}$ from its tributary (Fig. 4). We note that, while the deep and shallow bays were similar in their surface areas and the size of their

watersheds, the river feeding the shallow bay had substantially higher average concentrations of both N and P (Fig. 4); this difference in loading may have contributed to differences in internal nutrient processing between the two sites independent of depth effects by predisposing the shallow site to greater cyanobacteria dominance (Brauer et al. 2012). Collectively, however, the weak relationship of annual nutrient inputs with lake nutrient concentrations in the shallow bay suggests that internal nutrient transformations were more important determinants of year-to-year variation in N and P than external inputs.

Within-year trends in lake and tributary nutrient concentrations

Shallow polymictic sites had substantial and predictable variability in nutrient concentrations over the course of the monitoring season that can be attributed to internal nutrient processing (Fig. 5, Supplemental Fig. 5). Most shallow sites experienced seasonal declines in TN_{lake} from spring through summer, and these declines were largest in the shallowest sites (Supplemental Figs. 5, 6). Sites with higher spring TN_{lake} had steeper seasonal declines (Missisquoi Bay; stations 50, 51), which may be the result of higher denitrification rates at sites with higher nitrate concentrations (David et al. 2006; Kolzau et al. 2014; McCarthy et al. 2016). By contrast, TN_{lake} in the shallow site with lowest spring TN_{lake} tended to increase over the monitoring season (St. Albans Bay; station 40). Phytoplankton communities in this site are

usually dominated by N-fixing cyanobacteria (Watzin et al. 2012), suggesting that increases in TN_{lake} could be the result of higher N-fixation rates at sites with N deficiencies. However, release of sediment N or inputs of N from un-gaged streams during the summer could also contribute to the observed increases.

TP_{lake} increased in all shallow sites during the summer when tributary inputs were low, suggesting that sediment P loading fueled summer increases in TP_{lake} (Supplemental Fig. 5). The rate at which TP_{lake} increased was strongly negatively correlated with $\log_{10}$ depth ($p = 0.00089$, Supplemental Fig. 6). The negative correlation was likely driven by increased sediment nutrient release at shallower sites coupled with reduced dilution of sediment-derived nutrients in shallow water columns. The central role of sediment P loading has been established in Missisquoi Bay (Smith et al. 2011; Isles et al. 2015; Giles et al. 2016). The combination of declining TN_{lake} and increasing TP_{lake} drove seasonal declines of $TN:TP_{lake}$, which was high in spring following snowmelt but then decreased throughout the growing season until early autumn. In the shallowest sites, seasonal declines frequently resulted in $TN:TP_{lake}$ that approached the Redfield ratio and potential N limitation late in the summer, before $TN:TP_{lake}$ increased again following breakpoints in late August or September (Fig. 5). In Missisquoi Bay, water column N limitation has previously been observed during late summer, consistent with the results presented here (McCarthy et al. 2013).

In contrast to shallow sites, deep sites had remarkably consistent TN_{lake}, TP_{lake}, and $TN:TP_{lake}$ over the course of the monitoring season (Fig. 5, Supplemental Fig. 5), with only slight increases or decreases and no significant breakpoints. The generally consistent TN_{lake} and TP_{lake} concentrations throughout the stratified period, in combination with the strong correlations with DN_{river} and DP_{river} described above, suggest that external nutrients (which are delivered primarily in the spring) are efficiently recycled in the epilimnion of deep sites through the stratified period. Slight seasonal losses of TN_{lake} and TP_{lake} were evident at most deep sites (Supplemental Fig. 5) which can be attributed to the sedimentation of planktonic biomass (Finlay et al. 2013).

The only deep site which did not have consistent $TN:TP_{lake}$ throughout the monitoring season was the Northeast Arm (Station 34), which experienced large
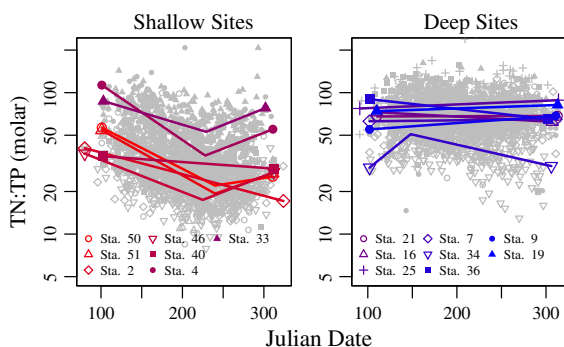

Fig. 5 TN:TP plotted against Julian date at the 15 monitoring sites showing seasonal trends and significant breakpoints if present, separated into shallow sites (<15 m) and deep sites (≥15 m). Sites are *colored* by depth, with *red* representing the shallowest sites, and *blue* the deepest. (Color figure online)

increases in TP_{lake} late in the summer (Fig. 5, Supplemental Fig. 5). Unlike deep sites in the Main Lake basin, the Northeast Arm basin frequently experienced hypolimnetic hypoxia in late summer and early fall (Supplemental Fig. 7). The late season increases in TP_{lake} at this site were consistent with sediment P release driven by hypoxia (Nürnberg and Peters 1984; Foley et al. 2011), although advection of P from adjacent eutrophic bays may also have contributed. Oxygen profile data are only available after 2006, but for this period minimum bottom DO concentrations decreased consistently in all deep, stratified sites, while bottom water temperatures increased (Supplemental Fig. 7). Increased hypolimnetic DO depletion likely contributed to observed long-term increases in TP_{lake} at station 34 in recent years, and may have contributed marginally to internal P loading in other deep basins. The large long-term increases in TP in all deep sites in September, just before the breakdown of thermal stratification (Fig. 3), is consistent with a widespread increase in late season internal loading across deep sections of Lake Champlain.

Long-term trends in meteorological variables influencing internal loading

The timing and magnitude of external nutrient inputs and the factors that promote internal nutrient transformations were likely influenced by long-term trends in meteorological forcing. From 1992 to 2012, aggregate annual river discharge from the 9 largest tributaries increased, and average discharge increased for each month of the growing season (May–October) (Fig. 2, 3). Increases in $\log_{10}$ discharge were largest in June and July (Fig. 3). Air temperature increased over the same time period (Fig. 2) with the highest increases in April and May (Fig. 3), and wind speed declined (Fig. 2) in each month except April, with the greatest decreases in September and October (Fig. 3). The trends in climatic variables (increased temperature and discharge, and decreased wind speed) are generally expected to contribute to increased nutrient concentrations, water column stability, and cyanobacteria bloom development (Paerl et al. 2011).

To examine the combined impacts of external nutrient loads and meteorological conditions, multiple regression models were selected for TN_{lake} and TP_{lake} as functions of nutrient loads and meteorological

drivers in the representative deep (station 25) and shallow (station 50) bays where direct comparisons to external loads were possible. The models revealed that lake nutrients in the deep and shallow bay were controlled by different meteorological variables, and different factors were important in different seasons (Table 1). TN_{lake} in the deep site was strongly influenced by TN_{river} concentrations during summer and fall and on an annual basis. In addition to the influence of external loading, high temperatures during the summer and high wind speeds during the fall were associated with low TN_{lake}, although in the absence of a clear mechanism we interpret the result of fall wind speed cautiously. In the shallow site, high spring TN_{lake} appeared to be associated with wet springs with dilute river nutrient concentrations; however, this model explained only 33% of the variation in TN_{lake} and no significant models for TN_{lake} were found in the shallow site during other seasons. In general, the multiple regression models suggest that TN_{river} concentrations remained the strongest explanatory variable for TN_{lake} in the deep site, but the drivers of TN_{lake} in the shallow site could not be resolved.

The lack of a strong model for TN_{lake} in the shallow site suggests that N dynamics were driven by unmeasured factors. N transformations in both the sediment and the water column of Missisquoi Bay are highly dynamic, and vary both spatially and seasonally (McCarthy et al. 2013, 2016). Denitrification in lake sediments is NO_3^- limited, and strongest in spring and in shallow sites near riverine inputs. Sediment NH_4^+ fluxes to the water column are sometimes high, particularly in early summer, and are stimulated by periods of bottom water DO depletion (McCarthy et al. 2016). In the water column, N can cycle rapidly to satisfy the demands of phytoplankton growth, with an average residence time of just 13 days during the summer (McCarthy et al. 2013). The rapid N transformations in both the sediments and the water column are mediated by biological processes, particularly the accumulation of phytoplankton biomass, and are difficult to model using TN data collected and aggregated at coarse temporal resolution.

TP_{lake} in the deep site was most strongly influenced by discharge, DP_{river} concentrations, and wind speed (Table 1), with discharge the most important predictor of TP_{lake} in spring and on an annual basis. The importance of discharge may reflect high

Table 1 Best models explaining variation in TN_{lake} (top) and TP_{lake} (bottom) in different seasons as a function of both external inputs and atmospheric variables for a representative deep bay (Malletts Bay) and shallow bay (Missisquoi Bay)

TN_{lake} (mg L^{-1})	Best model	R^2 (adjusted)	p
Deep bay (annual)	**1.201** TN_{river} − 0.01136 $AirTemp$ − 0.03591	0.5403	**0.00036**
Deep bay (spring)	0.8311 TN_{river} − 0.0276	0.1287	0.06135
Deep bay (summer)	**1.164** TN_{river} − **0.0237** $AirTemp$ + 0.288	0.677	**<0.0001**
Deep bay (fall)	**1.594** TN_{river} − **0.0327** $WindSpeed$ − 0.3447	0.4103	**0.00334**
Shallow bay (annual)	*No model*	–	–
Shallow bay (spring)	**−2.382** TN_{river} + 0.395 $Discharge$ + 2.155	0.3295	**0.0106**
Shallow bay (summer)	*No model*	–	–
Shallow bay (fall)	*No model*	–	–

TP_{lake} (µg L^{-1})	Best model	R^2 (adjusted)	p
Deep bay (annual)	**5.716** $Discharge$ + 0.5983 $AirTemp$ − 5.788	0.5688	**0.00020**
Deep bay (spring)	**12.45** $Discharge$ + 0.6093 $AirTemp$ − 7.724	0.5621	**0.00023**
Deep bay (summer)	**0.9592** DP_{river} − **1.5179** $WindSpeed$ + 3.468	0.5609	**0.00023**
Deep bay (fall)	**1.1611** DP_{river} − 0.4417 $AirTemp$ − **1.0773** $WindSpeed$ + 4.444	0.7743	**<0.00001**
Shallow bay (annual)	**1.65597** DP_{river} − 0.1255 TP_{river} + 22.19	0.2777	**0.0207**
Shallow bay (spring)	*No model*	–	–
Shallow bay (summer)	**5.161** DP_{river} − 0.1752 TP_{river} − **11.223** $WindSpeed$ − 37.69 $Discharge$ + 4.189	0.6584	**0.00021**
Shallow bay (fall)	1.864 DP_{river} − 0.1635 TP_{river} + 14.02 $Discharge$ + 12.55	0.2436	0.05225

Initial models for TN_{lake} and TP_{lake} were: $TN_{lake} = f(TN_{river} + AirTemperature + WindSpeed + Discharge)$, and $TP_{lake} = f(TP_{river} + DP_{river} + AirTemperature + WindSpeed + Discharge)$. Models with the lowest AIC were chosen using stepwise multiple regression model selection (forward and backward). "No model" indicates that the best model selected excluded all variables. Significant coefficients are shown in bold ($\alpha = 0.05$)

concentrations of suspended sediment and associated P during periods of high discharge in spring. In summer and fall in the deep bay, TP_{lake} was positively influenced by DP_{river} concentrations and negatively influenced by wind speed. Again, the drivers of TP_{lake} in the shallow bay were more difficult to resolve for most seasons. For the summer and annual models, TP_{lake} was strongly positively influenced by DP_{river} concentrations. In the summer, when cyanobacteria blooms are common in shallow areas of the lake, TP_{lake} was also very strongly negatively influenced by wind speed, and was higher in years with lower discharge; this model explained 65% of the variance in summer TP_{lake}. Although DP_{river} was frequently an important predictor for TP_{lake}, TP_{river} concentration was not a significant predictor in any model at either shallow or deep sites. In those tests where TP_{river} was selected in the best model, the coefficients were always negative. Collectively, the multiple regression analysis indicated that the primary driver of TP_{lake} concentrations in deep areas was DP_{river}, but the primary drivers of TP_{lake} in shallow areas were associated with calm, dry conditions, in addition to DP_{river}, during the summer bloom period.

## Conceptual model of nutrient cycling in deep and shallow sites

Our results suggest that Lake Champlain has experienced relatively dramatic changes in the magnitude and seasonality of energy (air temperature, wind speed) and mass inputs (discharge, N, and P) over recent decades, driven both by climate changes and anthropogenic activities. These environmental dynamics have produced systematic changes in lake nutrient concentrations and ratios which were mediated by watershed processes and lake depth. We present a conceptual model that synthesizes these observations and proposes mechanisms by which TN_{lake} and TP_{lake} are likely to respond to ongoing

climate change (Fig. 6). Considering the diverse range of hydrodynamic, biogeochemical and ecological environments that span the 15 sites of the Lake Champlain monitoring network (Xu et al. 2015a, b), our conceptual framework should be broadly applicable to a wide array of lakes which experience similar climate-driven changes in energy and mass fluxes, although the relative importance of different drivers may vary among lakes. Our conceptual model does not address several important factors that may impact TN_{lake} and TP_{lake}, including changes in ice cover (Schroth et al. 2015), lagged effects of off-season climate drivers on summer production (Pierson et al. 2013), invasive species introductions (Smeltzer et al. 2012), and impacts on trophic cascades

(Carvalho and Kirika 2003; Winder and Schindler 2004), all of which warrant further study. However, the strong and spatially consistent trends that we have discussed and the high amount of variance explained by external loads and climate drivers (Table 1) suggest that our model accounts for much of the observed variation in $TN:TP_{lake}$ in Lake Champlain. Our conceptual model is therefore useful for understanding and projecting the impacts of climate change on the diverse environments of Lake Champlain and similar systems elsewhere, with implications for pollution mitigation strategies under climate change.

In shallow polymictic sites (Fig. 6, panel A), both dissolved and particulate nutrients are delivered to the lake from external sources, primarily in the spring.

Fig. 6 Conceptual model of external influences on TN:TP in shallow and deep lake sites (*top*) showing intra-annual drivers of nutrient variability (*middle*) and possible responses to changing climate (*bottom*). **a** Response of shallow sites to dissolved and particulate nutrient inputs. **b** Response of deep sites to dissolved and particulate nutrient inputs. **c** Intra-annual patterns of TN:TP in shallow lakes related to tributary inputs and temperature. **d** Seasonal depletion of hypolimnetic oxygen in deep sites leading to late-season sediment P loading. **e** Potential effects of climate change on TN:TP in shallow sites. **f** Potential effect of climate change on deep sites. See text for a more detailed description of model
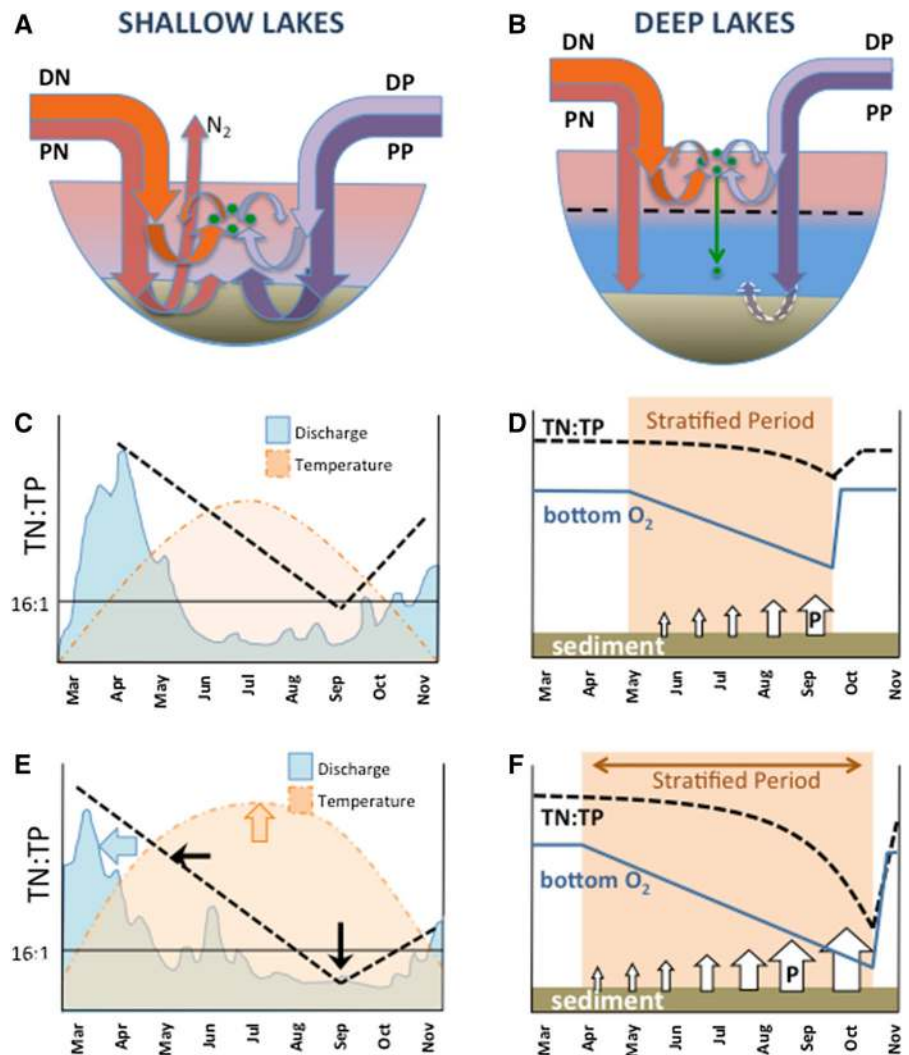
Particulate nutrients quickly settle to the sediments, resulting in spring nutrient ratios similar to DN:DP$_{river}$ of tributary inputs. Because most N is delivered in dissolved form, whereas most P is delivered in particulate form (Supplemental Fig. 1), initial TN:TP$_{lake}$ is high (Fig. 6, panel C). However, following the spring freshet, sedimentation and denitrification gradually reduce TN$_{lake}$ (although specific forms of N, particularly NH$_4^+$, may increase if bottom water oxygen becomes low, and TN$_{lake}$ may increase during bloom development as a result of increased cyanobacteria biomass and nutrient storage; McCarthy et al. 2016; Cottingham et al. 2015). At the same time, warm temperatures and increased sediment oxygen demand promote the release of sediment P to the water column and increase TP$_{lake}$. The combination of these processes results in declining TN:TP$_{lake}$ throughout the dry, warm period, frequently resulting in TN:TP$_{lake}$ approaching the Redfield ratio late in the summer (Fig. 6, panel C). TN:TP$_{lake}$ then rises again in the autumn with declining temperatures and increased tributary N inputs. In future warming scenarios, when spring discharge and N loading peak earlier due to earlier snowmelt, TN$_{lake}$ in shallow sites is likely to peak earlier in the season (Grantz et al. 2014; Guilbert et al. 2014). At the same time, earlier onset of warm temperatures is likely to result in earlier onset of internal P loading and warmer temperatures conducive to cyanobacteria growth earlier in the season, resulting in increased TP$_{lake}$ (Nürnberg and LaZerte 2015). Given the strong effect of wind speed on summer TP concentrations in the shallow bay (Table 1), changes in mean wind speed may also have a large impact on nutrient concentrations and summer blooms. Decreasing wind speed may result in a more stable water column, leading to increased cyanobacteria growth due to release from light limitation (Huisman et al. 2004), as well as increased PO$_4^{3-}$ and NH$_4^+$ loading resulting from more frequent depletion of oxygen at the sediment water interface (Giles et al. 2016; McCarthy et al. 2016). The effects of wind are likely to be strongly impacted by site-specific mixing regimes and basin morphology. When taken together, earlier declines in TN$_{lake}$ and longer periods of internal P loading are likely to result in earlier declines in TN:TP$_{lake}$ and lower average TN:TP$_{lake}$ with future climate warming (Fig. 6, panel E). Declines in TN:TP$_{lake}$ in shallow sites of Lake Champlain over the monitoring period have been strongest in the

spring and fall (Fig. 3), which may reflect a lengthening summer bloom season over the past two decades, suggesting that these processes are already occurring.

In deep lake sites, which remain stratified during the summer growing season, dissolved nutrients from tributary inputs are delivered primarily in the spring, and are efficiently recycled in the epilimnion throughout the stratified period, with slight losses of both N and P due to sedimentation of plankton. Particulate nutrients from tributary inputs are deposited in nearshore areas or settle to the benthos, and are generally unavailable to planktonic production, unless hypolimnetic oxygen depletion promotes the release of sediment P late in the stratified period (Fig. 6, panel B). On a within-season basis, such a scenario results in generally consistent TN:TP$_{lake}$ resembling DN:DP$_{river}$ throughout the growing season. TN:TP$_{lake}$ may decline in late summer or early autumn as bottom water DO decreases and sediment P loading increases (Nürnberg 1984; Foley et al. 2011) (Fig. 6, panel D); these effects are likely to be stronger in shallower and more eutrophic stratified basins with high sediment concentrations of labile P. Increases in sediment NH$_4^+$ release are also expected if bottom water anoxia increases (McCarthy et al. 2016). However, NH$_4^+$ fluxes are likely to be balanced by denitrification and sediments will likely remain net N sinks (David et al. 2006). In deep lake sites, future changes are likely to be influenced primarily by changes in the dissolved nutrient concentrations of tributary inputs (Fig. 4), and secondarily by increases in bottom water temperature, decreases in hypolimnetic DO, and subsequent increases in sediment P release. Dissolved nutrient inputs are likely to change in the future due to changes in precipitation regimes (Guilbert et al. 2014), phenology of catchment processes (Bernal et al. 2012), and anthropogenic activities (Michalak et al. 2013). Furthermore, future climate warming may lead to longer stratified periods and more frequent incidence of hypolimnetic anoxia. Increased anoxia may result in increased sediment P release and declines in TN:TP$_{lake}$ late in the summer in deep sites (Fig. 6, panel F), particularly if high external dissolved nutrient concentrations coupled with increased water temperatures continue to support increasing epilimnetic production throughout the early summer (Foley et al. 2011).

The long-term declines in TN:TP throughout Lake Champlain, in combination with increased water

temperature, have likely contributed to the observed increases in cyanobacteria over the monitoring period, and particularly to increases in N-fixing cyanobacteria (Supplemental Fig. 7; Smith 1983; Butterwick et al. 2005; Paerl and Huisman 2008). The effect of low N:P ratios on the development of cyanobacteria blooms may be particularly important during bloom initiation (Isles et al. 2015). Once blooms are underway, eutrophic bays are frequently limited by light (Brauer et al. 2012; McCarthy et al. 2013), and TN and TP concentrations in shallow sites may be controlled by phytoplankton dynamics. However, the occurrence of N-limiting conditions at the beginning of the growth period may enable cyanobacteria to outcompete other phytoplankton groups and establish dominance. In our conceptual model (Fig. 6), all of the observed climatic trends during the monitoring period (increased temperature, decreased wind speeds, increased discharge; Fig. 2) are consistent with the increased development of N-limiting conditions. Local climate projections suggest that these trends are likely to continue, at least with respect to temperature and precipitation (Guilbert et al. 2014). While the declines in N:P in Lake Champlain contrast with observations in some large lakes where point-source pollution controls resulted in large declines in P loading over the historical period (Finlay et al. 2013), the declines are similar to recent trends in large lakes heavily influenced by non-point-source agricultural pollution (Schindler et al. 2012; Scavia et al. 2014; Nürnberg and LaZerte 2015), where synergistic effects of climate warming and diffuse nutrient loading have resulted in increases of both external and internal loading.

We expect that the processes identified in our conceptual model are relevant in a wide variety of lakes, but that the relative importance of different processes is likely to vary with the watershed to lake area ratio, water residence time, trophic status, lake depth, and mixing regime. Shallow polymictic lakes frequently show seasonal patterns of N:P similar to those depicted here (Søndergaard et al. 2005; Nõges et al. 2008; Grantz et al. 2014; Kolzau et al. 2014), but the strength of seasonal variation may be partly dependent on the magnitude of watershed inputs at different times throughout the year and the DN:DP of those inputs. In some regions, summer precipitation is expected to increase with climate change, and substantial water inputs during summer may partially counteract the effects of in-lake processes on N:P

(Grantz et al. 2014). Deep stratified lakes with longer residence times than Lake Champlain are unlikely to have such strong year-to-year correlations between dissolved nutrient inputs and lake nutrients because of stronger hysteresis, and because as residence time increases, internal processes mediating N:P will likely be more important.

Our analysis suggests several broadly applicable insights for lake managers dealing with eutrophication and climate change. For deep mono- or dimictic systems, management actions should emphasize controlling dissolved nutrient inputs. In most deep areas of Lake Champlain, where TN_{lake} has declined substantially (Fig. 2), external inputs of dissolved P are particularly important. The importance of tributary dissolved nutrient concentrations (rather than loads) for deep lake sites suggests that management actions may be able to achieve targets for lake water quality despite the increase in nutrient loads expected with projected increases in precipitation (Jeppesen et al. 2009; Jeppesen et al. 2010). The current management regime for the Lake Champlain Basin, implemented in a new Total Maximum Daily Load (TMDL) plan (U.S. Environmental Protection Agency 2016), regulates loads of total P; our analysis suggests that annual average concentration of dissolved P would likely be a more effective target. Some best management practices that reduce particulate P and TP loads may increase dissolved loads, resulting in failure to meet lake water quality goals. Recent increases in DP loading in the western basin of Lake Erie have been attributed to the adoption of low-till and tile-drainage agricultural practices starting in 2002 (Jarvie et al. 2017). The decline in $DN:DP_{river}$ and $TN:TP_{lake}$ in Lake Champlain also began in 2002 (Supplemental Figs. 3, 4), suggesting that simultaneous adoption of similar agricultural management practices may be partially responsible for the observed trends. Control of external dissolved nutrients is particularly important given the potential for increased late-season anoxia and sediment P release in deep basins such as the Northeast Arm (Fig. 1, station 34). Reducing epilimnetic nutrient concentrations early in the season will reduce production in surface waters, thereby reducing sedimentation of algal carbon to the hypolimnion and subsequent oxygen depletion (Foley et al. 2011).

In shallow polymictic basins where particulate N and P are available to the water column through

internal loading, lake recovery is likely to be difficult, and managers should target particulate as well as dissolved nutrient fractions. Because the majority of P is delivered in particulate form, efforts to control erosion and sediment transport should be emphasized in catchments feeding shallow lakes, as well as efforts to control dissolved nutrient loads. Climate change is predicted increase the incidence of the strongest storm events in many areas (Guilbert et al. 2014), leading to corresponding increases in particulate phase nutrient transport. In other eutrophic shallow lakes, and in highly eutrophic shallow sites such as Missisquoi Bay where sediment P stores are high, external inputs of N are also likely to be important for sustaining high cyanobacteria biomass (Paerl et al. 2016). Missisquoi Bay is frequently dominated by non N-fixing *Microcystis* species, which thrive when reduced N compounds, particularly NH_4^+ and urea, are available (Blomqvist et al. 1994; Donald et al. 2011). Increased fluxes of reduced N from fertilizers is not observable in the TN_{river} data, but may have contributed to increased fertilization of cyanobacteria blooms. Given the increasing recognition of the importance of dual nutrient management strategies in eutrophic lakes (Paerl et al. 2011) and the need to better understand the role of these reactive N species on bloom development, we recommend increasing the collection of data on dissolved N species in both Lake Champlain and its tributaries, particularly in areas where agriculture is most intensive and cyanobacteria blooms are most common. If N limited conditions become more widespread in the future, as seems likely from this conceptual model, the need for a dual N + P management strategy to mitigate cyanobacteria blooms is likely to increase in the future.

References

Andersen HE, Kronvang B, Larsen SE et al (2006) Climate-change impacts on hydrology and nutrients in a Danish lowland river basin. Sci Total Environ 365:223–237. doi:10.1016/j.scitotenv.2006.02.036

Blenckner T (2005) A conceptual model of climate-related effects on lake ecosystems. Hydrobiologia 533:1–14

Bernal S, Hedin LO, Likens GE et al (2012) Complex response of the forest nitrogen cycle to climate change. Proc Natl Acad Sci USA 109:3406–3411. doi:10.1073/pnas.1121448109

Blomqvist P, Pettersson A, Hyenstrand P (1994) Ammonium-nitrogen: a key regulatory factor causing dominance of non-nitrogen-fixing cyanobacteria in aquatic systems. Arch Hydrobiol 132:141–164

Brauer VS, Stomp M, Huisman J (2012) The nutrient-load hypothesis: patterns of resource limitation and community structure driven by competition for nutrients and light. Am Nat 179:721–740. doi:10.1086/665650

Butterwick C, Heaney SI, Talling JF (2005) Diversity in the influence of temperature on the growth rates of freshwater algae, and its ecological relevance. Freshw Biol 50:291–300. doi:10.1111/j.1365-2427.2004.01317.x

Cade BS, Noon BR (2003) A gentle introduction to quantile regression for ecologists. Front Ecol Environ 1:412–420

Canham CD, Pace ML, Weathers KC et al (2012) Nitrogen deposition and lake nitrogen concentrations: a regional analysis of terrestrial controls and aquatic linkages. Ecosphere 3:art66. doi:10.1890/ES12-00090.1

Carvalho L, Kirika A (2003) Changes in shallow lake functioning: response to climate change and nutrient reduction. Hydrobiologia 506(1–3):789–796

Cottingham KL, Ewing HA, Greer ML et al (2015) Cyanobacteria as biological drivers of lake nitrogen and phosphorus cycling. Ecosphere 6:art 1. doi:10.1890/ES14-00174.1

David MB, Wall LG, Royer TV et al (2006) Denitrification and the nitrogen budget of a reservoir in an agricultural landscape. Ecol Appl 16:2177–2190

Davies RB (2002) Hypothesis testing when a nuisance parameter is present only under the alternative: linear model case. Biometrika 89:484–489

Davison W (1993) Iron and manganese in lakes. Earth Sci Rev 34:119–163. doi:10.1016/0012-8252(93)90029-7

Donald DB, Bogard MJ, Finlay K, Leavitt PR (2011) Comparative effects of urea, ammonium, and nitrate on phytoplankton abundance, community composition, and toxicity in hypereutrophic freshwaters. Limnol Oceanogr 56:2161–2175

Downing JA, Watson SB, Mccauley E (2001) Predicting cyanobacteria dominance in lakes. Can J Fish Aquat Sci 58:1905–1908

Elser JJ, Fagan WF, Denno RF et al (2000) Nutritional constraints in terrestrial and freshwater food webs. Nature 408:578–580. doi:10.1038/35046058

Finlay JC, Small GE, Sterner RW (2013) Human influences on nitrogen removal in lakes. Science 342:247–250. doi:10.1126/science.1242575

Foley B, Jones ID, Maberly SC, Rippey B (2011) Long-term changes in oxygen depletion in a small temperate lake: effects of climate change and eutrophication. Freshw Biol 57:278–289. doi:10.1111/j.1365-2427.2011.02662.x

Ghebremichael LT, Veith TL, Watzin MC (2010) Determination of critical source areas for phosphorus loss: lake Champlain basin, Vermont. Trans ASABE 53:1595–1604

Giles CD, Isles PDF, Manley T et al (2016) The mobility of phosphorus, iron, and manganese through the sediment–water continuum of a shallow eutrophic freshwater lake under stratified and mixed water-column conditions. Biogeochemistry 127:15–34. doi:10.1007/s10533-015-0144-x

Grantz EM, Haggard BE, Scott JT (2014) Stoichiometric imbalance in rates of nitrogen and phosphorus retention, storage, and recycling can perpetuate nitrogen deficiency in highly-productive reservoirs. Limnol Oceanogr 59:2203–2216. doi:10.4319/lo.2014.59.6.2203

Guilbert J, Beckage B, Winter JM et al (2014) Impacts of projected climate change over the lake champlain basin in vermont. J Appl Meteorol Climatol 53:1861–1975. doi:10.1175/JAMC-D-13-0338.1

Guilbert J, Betts AK, Rizzo DM et al (2015) Characterization of increased persistence and intensity of precipitation in the northeastern United States. Geophys Res Lett. doi:10.1002/(ISSN)1944-8007

Guildford SJ, Hecky RE (2000) Total nitrogen, total phosphorus, and nutrient limitation in lakes and oceans: Is there a common relationship? Limnol Oceanogr 45:1213–1223. doi:10.4319/lo.2000.45.6.1213

Hessen DO (2013) Inorganic nitrogen deposition and its impacts on N:P-ratios and lake productivity. Water 5:327–341. doi:10.3390/w5020327

Hillebrand H, Steinert G, Boersma M et al (2013) Goldman revisited: faster-growing phytoplankton has lower N:P and lower stoichiometric flexibility. Limnol Oceanogr 58:2076–2088. doi:10.4319/lo.2013.58.6.2076

Huisman J, Sharples J, Stroom JM et al (2004) Changes in turbulent mixing shift competition for light between phytoplankton species. Ecology 85:2960–2970

Hupfer M, Lewandowski J (2008) Oxygen controls the phosphorus release from lake sediments—a long-lasting paradigm in limnology. Int Rev Hydrobiol 93:415–432. doi:10.1002/iroh.200711054

Isles PDF, Giles CD, Gearhart TA et al (2015) Dynamic internal drivers of a historically severe cyanobacteria bloom in Lake Champlain revealed through comprehensive monitoring. J Great Lakes Res 43:818–829. doi:10.1016/j.jglr.2015.06.006

Ives AR (2015) For testing the significance of regression coefficients, go ahead and log-transform count data. Methods Ecol Evol 6:828–835. doi:10.1111/2041-210X.12386

Jankowski T, Livingstone DM, Bührer H (2006) Consequences of the 2003 European heat wave for lake temperature profiles, thermal stability, and hypolimnetic oxygen depletion: implications for a warmer world. Limnol Oceanogr 51:815–819

Jarvie HP, Johnson LT, Sharpley AN, Smith DR, Baker DB, Bruulsema TW, Confesor R (2017) Increased soluble phosphorus loads to Lake Erie: unintended consequences of conservation practices? J Environ Qual 46:123–132. doi:10.2134/jeq2016.07.0248

Jeppesen E, Kronvang B, Meerhoff M et al (2009) Climate change effects on runoff, catchment phosphorus loading and lake ecological state, and potential adaptations. J Environ Qual 38:1930. doi:10.2134/jeq2008.0113

Jeppesen E, Kronvang B, Olesen JE et al (2010) Climate change effects on nitrogen loading from cultivated catchments in Europe: implications for nitrogen retention, ecological state of lakes and adaptation. Hydrobiologia 663:1–21. doi:10.1007/s10750-010-0547-6

Jöhnk KD, Huisman J, Sharples J et al (2008) Summer heatwaves promote blooms of harmful cyanobacteria. Glob Change Biol 14:495–512. doi:10.1111/j.1365-2486.2007.01510.x

Jones ID, Page T, Alex Elliott J et al (2011) Increases in lake phytoplankton biomass caused by future climate-driven changes to seasonal river flow. Glob Change Biol 17:1809–1820. doi:10.1111/j.1365-2486.2010.02332.x

Keene OH (1995) The log transformation is special. Stat Med 14:811–819

Koenker R (2015) quantreg: Quantile regression. R package version 5.18. http://CRAN.R-project.org/package=quantreg

Kolzau S, Wiedner C, Rücker J et al (2014) Seasonal patterns of nitrogen and phosphorus limitation in four german lakes and the predictability of limitation status from ambient nutrient concentrations. PLoS ONE 9:e96065. doi:10.1371/journal.pone.0096065.s003

Kosten S, Jeppesen E, Huszar VL et al (2011) Ambiguous climate impacts on competition between submerged macrophytes and phytoplankton in shallow lakes. Freshw Biol 56:1540–1553

Leavitt PR, Fritz SC, Anderson NJ et al (2009) Paleolimnological evidence of the effects on lakes of energy and mass transfer from climate and humans. Limnol Oceanogr 54:2330–2348

Levine SN, Lini A, Ostrofsky ML et al (2012) The eutrophication of Lake Champlain's northeastern arm: Insights from paleolimnological analyses. J Great Lakes Res 38:35–48. doi:10.1016/j.jglr.2011.07.007

McCarthy MJ, Gardener WS, Lehmann MF et al (2013) Implications of water column ammonium uptake and regeneration for the nitrogen budget in temperate, eutrophic Missisquoi Bay, Lake Champlain (Canada/USA). Hydrobiologia 718:173–188. doi:10.1007/s10750-013-1614-6

McCarthy MJ, Gardner WS, Lehmann MF et al (2016) Benthic nitrogen regeneration, fixation, and denitrification in a temperate, eutrophic lake: Effects on the nitrogen budget and cyanobacteria blooms. Limnol Oceanogr. doi:10.1002/lno.10306

Medalie L (2013) Concentration, flux, and the analysis of trends of total and dissolved phosphorus, total nitrogen, and chloride in 18 tributaries to Lake Champlain, Vermont and New York, 1990–2011. US Geological Survey, pp 1–39

Michalak A, Anderson E, Beletsky D et al (2013) Record-setting algal bloom in Lake Erie caused by agricultural and meteorological trends consistent with expected future conditions. Proc Natl Acad Sci 110:6448–6452

Muggeo VMR (2003) Estimating regression models with unknown break-points. Statistics Med 22:3055–3071

Muggeo VMR (2008) segmented: an R package to fit regression models with broken-line relationships. R News 8: 20–25. http://cran.r-project.org/doc/Rnews/

Nõges T, Laugaste R, Noges P et al (2008) Critical N:P ratio for cyanobacteria and N$_2$-fixing species in the large shallow temperate lakes Peipsi and Võrtsjärv, North-East Europe. Hydrobiologia 599:77–86

Nürnberg GK (1984) The prediction of internal phosphorus load in lakes with anoxic hypolimnia. Limnol Oceanogr 29:111–124

Nürnberg GK, LaZerte BD (2015) More than 20 years of estimated internal phosphorus loading in the polymictic, eutrophic Lake Winnipeg, Manitoba. J Great Lakes Res 42:18–27. doi:10.1016/j.jglr.2015.11.003

Nürnberg GK, Peters RH (1984) The importance of internal phosphorus load to the eutrophication of lakes with anoxic hypolimnia. Verh Int Ver Limnol 22:190–194

Paerl HW, Huisman J (2008) CLIMATE: blooms like it hot. Science 320:57–58. doi:10.1126/science.1155398

Paerl HW, Hall NS, Calandrino ES (2011) Controlling harmful cyanobacterial blooms in a world experiencing anthropogenic and climatic-induced change. Sci Tot Environ 409:1739–1745. doi:10.1016/j.scitotenv.2011.02.001

Paerl HW, Scott JT, McCarthy MJ et al (2016) It takes two to tango: When and where dual nutrient (N & P) reductions are needed to protect lakes and downstream ecosystems. Environ Sci Technol 50:10805–10813. doi:10.1021/acs.est.6b02575

Pierson DC, Samal NR, Owens EM, Schneiderman EM, Zion MS (2013) Changes in the timing of snowmelt and the seasonality of nutrient loading: can models simulate the impacts on freshwater trophic status? Hydrol Process 27:3083–3093

Pryor SC, Barthelmie RJ (2010) Climate impacts on wind energy: a review. Renew Sustain Energy Rev 14:430–437

Pryor SC, Barthelmie RJ, Young DT et al (2009) Wind speed trends over the contiguous United States. J Geophys Res 114:D14105

Reynolds C, Davies P (2001) Sources and bioavailability of phosphorous fractions in freshwaters: a British perspective. Biol Rev 76:27–64

Rosenberg BD, Schroth AW (2017) Coupling of reactive riverine phosphorus and iron species during hot transport moments: impacts of land cover and seasonality. Biogeochemistry. doi:10.1007/s10533-016-0290-9

Scavia D, Allan JD, Arend KK et al (2014) Assessing and addressing the re-eutrophication of Lake Erie: Central basin hypoxia. J Great Lakes Res 40:226–246. doi:10.1016/j.jglr.2014.02.004

Schindler DW, Hecky RE, McCullough GK (2012) The rapid eutrophication of Lake Winnipeg: greening under global change. J Great Lakes Res 38:6–13. doi:10.1016/j.jglr.2012.04.003

Schroth AW, Giles CD, Isles PDF et al (2015) Dynamic coupling of iron, manganese, and phosphorus behavior in water and sediment of shallow ice-covered eutrophic lakes. Environ Sci Technol. doi:10.1021/acs.est.5b02057

Sharpley AN, Kleinman PJA, Heathwaite AL et al (2008) Phosphorus loss from an agricultural watershed as a function of storm size. J Environ Qual 37:362. doi:10.2134/jeq2007.0366

Smeltzer E, Shambaugh AD, Stangel P (2012) Environmental change in Lake Champlain revealed by long-term monitoring. J Great Lakes Res 38:6–18. doi:10.1016/j.jglr.2012.01.002

Smith VH (1983) Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science 221:669–671. doi:10.1126/science.221.4611.669

Smith L, Watzin MC, Druschel G (2011) Relating sediment phosphorus mobility to seasonal and diel redox fluctuations at the sediment-water interface in a eutrophic freshwater lake. Limnol Oceanogr 56:2251–2264. doi:10.4319/lo.2011.56.6.2251

Søndergaard M, Jensen JP, Jeppesen E (2005) Seasonal response of nutrients to reduced phosphorus loading in 12 Danish lakes. Freshw Biol 50:1605–1615

Soranno PA, Carpenter SR, Lathrop RC (1997) Internal phosphorus loading in Lake Mendota: response to external loads and weather. Can J Fish Aquat Sci 54:1883–1893

Stumpf RP, Wynne TT, Baker DB, Fahnenstiel GL (2012) Interannual variability of cyanobacterial blooms in Lake Erie. PLoS ONE 7:e42444. doi:10.1371/journal.pone.0042444.t004

U.S. Environmental Protection Agency (2016) Phosphorus TMDLs for Vermont Segments of Lake Champlain. https://www.epa.gov/tmdl/lake-champlain-phosphorus-tmdl-commitment-clean-water

Vt, DEC (Vermont Department of Environmental Conservation) and NY DEC (New York Department of Environmental Conservation) (2014) Lake Champlain long-term water quality and biological monitoring program–Program description. Grand Isle, Vermont. http://www.watershedmanagement.vt.gov/lakes/htm/lp_longterm.htm

Vanni MJ, Renwick WH, Headworth JL et al (2001) Dissolved and particulate nutrient flux from three adjacent agricultural watersheds: a five-year study. Biogeochemistry 54:85–114

Wagner C, Adrian R (2009) Cyanobacteria dominance: quantifying the effects of climate change. Limnol Oceanogr 54:2460

Watzin M, Fuller S, Gorney R, Caron J (2012) Monitoring and evaluation of cyanobacteria in Lake Champlain – 2011. Lake Champlain Basin ProgR Tech Rep 71:1–80

Weyhenmeyer GA, Jeppesen E, Adrian R et al (2007) Nitrate-depleted conditions on the increase in shallow northern European lakes. Limnol Oceanogr 52:1346–1353

Williamson CE, Saros JE, Vincent WF, Smol JP (2009) Lakes and reservoirs as sentinels, integrators, and regulators of climate change. Limnol Oceanogr 54:2273–2282

Winder M, Schindler DE (2004) Climatic effects on the phenology of lake processes. Glob Change Biol 10:1844–1856. doi:10.1111/j.1365-2486.2004.00849.x

Xie L, Xie P, Li S et al (2003) The low TN:TP ratio, a cause or a result of *Microcystis* blooms? Water Res 37:2073–2080

Xu Y, Schroth AW, Isles PDF, Rizzo DM (2015a) Quantile regression improves models of lake eutrophication with implications for ecosystem-specific management. Freshw Biol 60:1841–1853. doi:10.1111/fwb.12615

Xu Y, Schroth AW, Rizzo DM (2015b) Developing a 21st century framework for lake-specific eutrophication assessment using quantile regression. Limnol Oceanogr 13:237–249. doi:10.1002/lom3.10021