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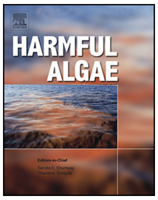

Delineation of the role of nutrient variability and dreissenids (Mollusca, Bivalvia) on phytoplankton dynamics in the Bay of Quinte, Ontario, Canada

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ABSTRACT

The Bay of Quinte, a Z-shaped embayment at the northeastern end of Lake Ontario, has a long history of eutrophication problems primarily manifested as spatially extensive algal blooms and predominance of toxic cyanobacteria. The purpose of this study was to identify the structural changes of the phytoplankton community induced by two environmental alterations: point-source phosphorus (P) loading reduction in the late 1970s and establishment of dreissenid mussels in the mid-1990s. A combination of statistical techniques was used to draw inference about compositional shifts of the phytoplankton assemblage, the consistency of the seasonal succession patterns along with the mechanisms underlying the algal biovolume variability in the Bay of Quinte over the past three decades. Based on a number of diversity and similarity indices, the algal assemblages in the upper and middle segments of the Bay are distinctly different from those typically residing in the outer segments. Our analysis also identified significant differences among the phytoplankton communities, representing the pre- and post-P control as well as the pre- and post-dreissenid invasion periods. Recent shifts in phytoplankton community composition were mainly associated with increased frequency of occurrence of toxin-producing *Microcystis* outbreaks and reduced biovolume of N_2 fixers, such as *Aphanizomenon* and *Anabaena*. Bayesian hierarchical models were developed to elucidate the importance of different abiotic factors (light attenuation, water temperature, phosphorus, and ammonium) on total cyanobacteria, *Microcystis*, *Aphanizomenon*, and *Anabaena* relative biovolume. Our modelling exercise suggests that there is significant spatial heterogeneity with respect to the role of the factors examined, and thus total phosphorus alone cannot always explain the year-to-year variability of cyanobacteria succession patterns in the system. The lessons learned from the present analysis will be helpful to the water quality criteria setting process and could influence the management decisions in order to delist the system as an Area of Concern.

1. Introduction

The Great Lakes have historically been subject to “cultural eutrophication”, primarily manifested as nuisance algal blooms, low water clarity, toxin-producing cyanobacteria dominance, and hypoxia (Mills et al., 2003; Dove, 2009; Winter et al., 2012). With the realization of broader ecosystem impairments, the Great Lakes Water Quality Agreements (GLWQA) between Canada and United States ignited major management actions in the early 1970s, aiming to reduce point source nutrient loading (Mills et al., 2003). Generally, the restoration efforts were successful in controlling external nutrient loading, initiating a “re-oligotrophication” process in many sites of the Great Lakes area (Mills et al., 2003; Dove, 2009). In Lake Ontario, phosphorus loading was reduced by approximately 50% and the total phosphorus (TP) concentration levels declined from 20–25 $\mu g\ TP\ L^{-1}$ in the early 1970s to

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10 μg TP L^{-1} in 1986 (Dove, 2009; Mills et al., 2003). Conditions of increased water clarity and significantly reduced plankton productivity have gradually prevailed in the system (Dove, 2009). In fact, emerging evidence suggests that Lake Ontario experiences an "offshore desertification", whereby the low ambient phosphorus levels undermine pelagic ecosystem integrity (Dove, 2009).

Despite the improvement of offshore water quality conditions, six near shore locations in Lake Ontario remain designated as Areas of Concern (AOC) with severe environmental degradation and impaired beneficial uses, i.e., they are characterized by distinct depression of their physical, chemical, and biological integrity (Dove, 2009; Gudimov et al., 2011; Nicholls and Carney, 2011). The invasion of zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena rostriformis bugensis*) has been identified as one of the main culprits for the persistence of eutrophication problems after the mid-1990s, as the timing of the colonization of mussels coincided with elevated nearshore TP levels and frequent cyanobacteria blooms (Vanderploeg et al., 2001; Nicholls and Carney, 2011). Dreissenid mussels, exotic invasive species native in the Ponto-Caspian basin, were introduced through ballast water from ocean vessels in the 1990s and rapidly proliferated over the inshore zones in the Great Lakes (Higgins and Vander Zanden, 2010). The ecological impacts of dreissenids on freshwater ecosystems are wide-ranging, including the increased water clarity as a result of their filtration of suspended solids (James et al., 1997; Makarewicz et al., 1999), which in turn creates favourable light environment for submerged macrophytes (Fahnenstiel et al., 1995), decreased plankton biomass (Johengen et al., 1994), altered nutrient levels and forms (soluble/particulate, organic/inorganic, nitrogen to phosphorus ratios) through their excretion (Fahnenstiel et al., 1995; Heath et al., 1995; Bykova et al., 2006), and increased benthic productivity (Higgins and Vander Zanden, 2010). Less clear evidence exists about the effects of dreissenid invasion on the phytoplankton compositional patterns, and even less so about the relative competitive capacity of cyanobacteria (Kirsch and Dzialowski, 2012). For example, increasing trends of *Microcystis aeruginosa* were observed in Saginaw Bay and Lake Erie after the colonization of dreissenids (Vanderploeg et al., 2001), while the relative abundance of *M. aeruginosa* has declined in the Hudson River (Caraco et al., 1997; Smith et al., 1998). N_2-fixing cyanobacteria, such as *Aphanizomenon* spp. and *Anabaena* spp., appear to have benefited by the presence of dreissenids in eutrophic Oneida Lake (Horgan and Mills, 1997), whereas the biomass of *Anabaena* spp. was 4.6 times lower in Southern Michigan lakes that have experienced dreissenid invasion (Knoll et al., 2008). Potential mechanisms for the various responses of different cyanobacteria species to dreissenid-related environmental shifts are not fully understood, and therefore a handful of hypotheses have been proposed to explain the contradictory empirical evidence, such as the selective filtration by dreissenids (Vanderploeg et al., 2001), inhibitory effects on filtration by toxin producing strains of cyanobacteria (Baker et al., 1998), and different response patterns to increased light intensity (Nicholls et al., 2002).

The Bay of Quinte, a Z-shaped embayment at the northeastern end of Lake Ontario with a long history of eutrophication, characterized by frequent and spatially extensive algal blooms, and predominance of toxic cyanobacteria (Nicholls et al., 2002). Because of these water quality problems, the Bay of Quinte was one of the 43 degraded sites around the Great Lakes designated by the International Joint Commission as an Area of Concern (AOC) in 1986. Reduction of phosphorus in detergents along with upgrades at local waste water treatment plants resulted in substantial decline of point-source loadings during the 1970s, prompting a significant decrease of nutrient concentration and phytoplankton biomass levels (Minns et al., 2011). Nonetheless, recognizing the continuing water quality problems, there are recent attempts to shed light on the ecological implications of the establishment of invasive zebra and quagga mussels in the mid-1990s, comparing with the effects of the substantial ($\approx$50%) reduction in the point-source phosphorus loading into the upper segments during the winter of 1977–1978 (Nicholls et al., 2002; Nicholls and Carney, 2011). Total phosphorus concentrations in the post-dreissenid period have shown significant within-year variability, characterized by relatively low spring and fall levels, 10–15 μg TP L^{-1}, and high summer concentrations, $>$50 μg TP L^{-1} (Munawar et al., 2011). This pattern may stem from the sediment diagenesis processes and biological nutrient regeneration (Kim et al., 2013). Existing empirical evidence suggests that the presence of dreissenid mussels in the system may have induced both physical and chemical changes that could ultimately be characterized as an ecosystem regime shift (deYoung et al., 2008). For example, the significant increase of the light penetration has stimulated growth of submerged macrophytes and rapid proliferation of existing shallow water macrophyte beds into deeper water (Leisti et al., 2006). The arrival of dreissenid mussels has coincided with both desirable (e.g., *Aphanizomenon* spp. and *Oscillatoria* spp. decline) and undesirable (e.g., *Microcystis* spp. increase) changes in the phytoplankton community composition. These shifts of the algal assemblage could directly stem from the feeding selectivity of dreissenids or indirectly from the improvements in the water column transparency, although the role of the feedback loop associated with the mussel's nutrient recycling activity should not be ruled out (Bierman et al., 2005; Arhonditsis et al., 2016). The post-dreissenid increase of the cyanophyte *Microcystis* spp. has profound ramifications for the aesthetics and other beneficial uses in the Bay, through the formation of "scums" on the water surface (Jacoby et al., 2000) as well as the fact that some strains of *Microcystis* spp. are toxin producers (Brittain et al., 2000), e.g., one of the most common species, *M. aeruginosa*, is a producer of the hepatotoxin microcystin-LR (Repavich et al., 1990; Watson et al., 2008).

The main objective of the present study is to identify the structural changes of the phytoplankton community in the Bay of Quinte induced by two environmental alterations: point-source phosphorus (P) loading reduction in the late 1970s and establishment of dreissenid mussels in the mid-1990s. A combination of statistical techniques are used to draw inference about compositional shifts of the phytoplankton assemblage, the consistency of the seasonal succession patterns along with the mechanisms underlying the algal biovolume variability in the Bay of Quinte over the past three decades. Diversity and similarity indices are also used to delineate the longitudinal structural features of the algal assemblages in the Bay. Furthermore, Bayesian hierarchical models attempt to elucidate the importance of different abiotic factors (light attenuation, water temperature, phosphorus, and ammonium) on the total cyanobacteria, *Microcystis* spp., *Aphanizomenon* spp., and *Anabaena* spp. relative abundance. Recognizing that the elimination of harmful algal blooms represents one of the major challenges of eutrophication management in the area, our modelling exercise is designed to offer insights into the dynamics of the local phytoplankton community and ultimately assist with the establishment of suitable delisting criteria of the Bay of Quinte as an Area of Concern.

2. Methods

2.1. Data description

Phytoplankton and water chemistry data for the present study were obtained from a long-term monitoring program, the Project Quinte. This program was launched in 1972 as a multi-year study of the abiotic and biotic system characteristics in response to phosphorus reduction from municipal water treatment plants (Johnson and Hurley, 1986). This sampling program focuses on information related to physical (temperature, oxygen, pH, conductivity, light attenuation, Secchi disc depth), chemical (total phosphorus, soluble reactive phosphorus, dissolved inorganic and organic carbon, total Kjeldahl nitrogen, nitrate, nitrite, ammonium/ammonia and silica) properties as well as on the study of phytoplankton and zooplankton community structure in the Bay of Quinte (Nicholls et al., 2002). Phytoplankton samples were collected from nine (9) open water locations within the Bay of Quinte; Upper Bay (Trenton, Belleville), Middle Bay (Napanee, Upper Hay Bay, Hay Bay, Picton), and Lower Bay (Glenora, Conway, Lennox). The present study however, focused only on data from Belleville, Napanee, Hay Bay, and Conway due to their consistent sampling records (Fig. 1). Phytoplankton data were available for 39 years (1973–2011) from Belleville, 19 years (1973–1977, 1989, 1990, 1999–2009, 2011) from Napanee, 23 years (1973–1978, 1986–1990, 2000–2011) from Hay Bay, and 21 years (1973–1978, 1986–1990, 2000–2009) from Conway. Phytoplankton samples were collected as composites from the euphotic zone on bi-weekly basis during the growing season (May to October). Detailed description of the methods for phytoplankton sampling and analyses are provided in Nicholls and Carney (1979) and Nicholls et al. (1986).

Additional long-term data were also available from the Great Lakes Intake Program. This monitoring program began as early as 1966 at 17 municipal treatment plants throughout the Great Lakes. Weekly untreated samples from intake pipes were collected by water treatment plant staff and analyzed at the Ontario Ministry of Environment and Climate Change. Intake pipes from the local water treatment plant at Belleville were located 490 m offshore at a depth of 5 m (Winter et al., 2012). Phytoplankton samples were collected, identified to genus (or species) level and enumerated as total monthly values of biovolume units ($\mu m^3\,mL^{-1}$). The phytoplankton biovolume data were available throughout the year from 1985 to 2011, which allowed us to examine the shifts in the seasonal dynamics of the algal community. More detailed sample collection, preservation, and enumeration methods were described in Winter et al. (2012). Several water chemistry variables were also collected by the Great Lakes Intake Program more consistently than Project Quinte data. Surface water temperature and light attenuation coefficients were regularly sampled starting from 1973, while the majority of water chemistry data was only available after the late 1980s.

To elucidate the potential causal linkages between phytoplankton and abiotic conditions, the physical/chemical variables were linearly interpolated and were then matched with the sampling date of the algal samples. First, the water chemistry and biological data from the Bay of Quinte were classified into three study periods; before P control (1973–1977), before (1978–1994) and after (1995–2011) the dreissenid invasion (Nicholls and Carney, 2011). Summary statistics for all the limnological variables were calculated for each period. Phytoplankton biovolume and biomass data were grouped into classes and genera to illustrate the structural changes induced by the two environmental perturbations examined. Quantile logistic regression models were developed at 5%, 25%, 50%, 75% and 95% of the total algal biovolume data (Watson et al., 1992; see also our Supporting Information Section).

Microcystin concentrations were also monitored by the Bay of Quinte Harmful Algal Bloom (BQHABs) Initiative and Environment Canada since 2003 (Watson et al., 2011). Samples collected from various locations within the bay (i.e., beaches, offshore open water, near shore, downstream of wastewater treatment plant, and rivers) were analyzed for total microcystins/nodularins (Watson et al., 2011). Toxin concentrations were determined using an enzyme-linked immuno-sorbent assay (ELISA) and protein phosphatase inhibition assay (PPIA) (Watson et al., 2007). In this study, a *post-hoc* exercise examined the likelihood of raw water microcystin levels to exceed the Ontario Drinking Water Standard of 1.5 $\mu g\,L^{-1}$, as well as two other threshold values (1.0 and 0.5 $\mu g\,L^{-1}$), for different TP concentrations. Our statistical model postulated that the violation of a toxin threshold resembles a Bernoulli process, meaning that the collected samples represent a sequence of independent identically distributed Bernoulli trials. Simply put, each time we collect a sample, the likelihood of exceedance of a toxin threshold (or not) is independent from previous or subsequent samples. Importantly, the violation probability of a certain level of the toxin can be determined by a series of potentially important covariates, such as the nutrient concentrations, temperature, light, conductivity. In this study, the relationship between the probability of exceedance of a specific microcystin threshold and the corresponding TP concentrations was modelled using logistic regression (Mahmood et al., 2014).

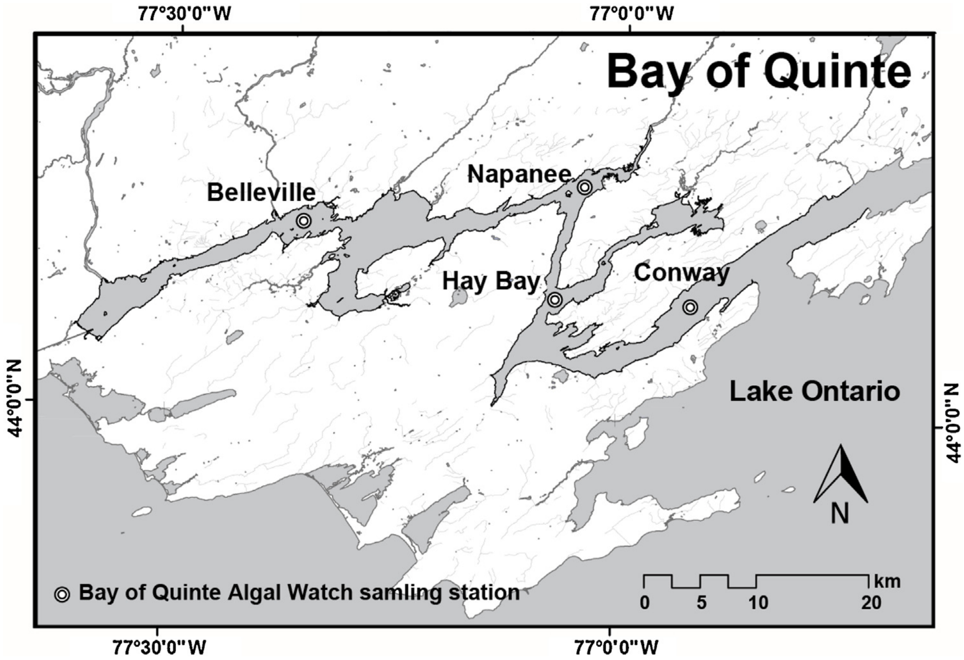

Fig. 1. Map of the Bay of Quinte and sampling locations of the Algae Watch sampling program.

$$\begin{aligned}\mathrm{Microcystin}_i|\mathrm{p}_i(\beta_0,\beta_1,\mathrm{TP}_i) &\sim \mathrm{Bernoulli}(\mathrm{p}_i)\\ \log\mathrm{it}(\mathrm{p}_i) &= \beta_0+\beta_1\cdot\mathrm{TP}_i\\ \beta_0,\beta_1 &\sim N(0,10000)\end{aligned}$$

where, $\mathrm{Microcystin}_i$ denotes the exceedance or not of a certain microcystin threshold (1 or 0) in the ith sample; TP_i is corresponding total phosphorus concentration; and β_0 and β_1 are the regression coefficients which were assigned flat (or diffuse) normal prior distributions with mean 0 and variance 10000 or $N(0, 10000)$.

2.2. Ecological diversity

Quantitative assessment of the phytoplankton community structure driven by the environmental changes in the Bay of Quinte was also carried out using ecological indices (i.e., Groth and Roelfs, 1987; Tsirtsis and Karydis, 1998; Zargaran et al., 2011). Specifically, four types of indices were used to shed light on the spatiotemporal variability of the local algal assemblages; diversity indices that express the species richness and variety of the community (Pielou, 1975), evenness indices that focus on the equitability of species abundance in the community (Washington, 1984), dominance indices that emphasize the role of the most important species (McNaughton, 1967), and similarity indices that indicate both compositional overlap and species abundance differences in time and/or space. Tsirtsis and Karydis (1998) and Arhonditsis et al. (2003) provided a thorough evaluation of various ecological indices in regard to their ability to characterize the eutrophication signature on phytoplankton community structure. Based on their recommendations, the taxonomic richness (number of genera), Gleason's diversity index, $D=\frac{S}{\ln N}$ (Ludwig and Reynolds, 1988), Evenness index, $E1=\frac{-\sum_{i=1}^{S}\frac{n_i}{n}\times\ln\frac{n_i}{n}}{\ln S}$ (Pielou, 1975), and McNaughton's dominance index, $\delta=\frac{n_1+n_2}{n}$ (McNaughton, 1967) were selected. In the previous formulations, S represents the number of genera in the sample, N represents the total biovolume (biomass in $\mathrm{mm}^3\,\mathrm{L}^{-1}$) in the sample, and n_i denotes the biovolume of genus i in the sample.

Three similarity indices were used to estimate the longitudinal phytoplankton community resemblance from Upper to Lower Bay of Quinte; namely, the similarities between Belleville and Napanee (B–N), Napanee and Hay Bay (N–HB), Hay Bay and Conway (HB–C) were evaluated. The three indices were selected based on the different weights assigned to the pair-wise differences between the abundant (Pandeya's index), distinct (Ellenberg's index), and common (Bray–Curtis' index) genera of the locations compared. The formulations of the three similarity indices used were as follows:

$$\text{Pandeya's index}\,SI_{\mathrm{PA}}=\frac{\sum_{\mathrm{T}}(x_i+y_i)}{\sum_i(x_i+y_i)+\sum_{\mathrm{T}}|x_i-y_i|}$$

$$\text{Ellenberg's index}\,SI_{\mathrm{EL}}=\frac{\sum_{\mathrm{T}}(x_i+y_i)}{2\sum_{\mathrm{U}}x_i+2\sum_{\mathrm{V}}y_i+\sum_{\mathrm{T}}(x_i+y_i)}$$

$$\text{Bray–Curtis' index}\,SI_{\mathrm{BC}}=\frac{\sum_i|x_i-y_i|}{\sum_i(x_i+y_i)}$$

where, x_i and y_i are biovolume of the ith phytoplankton genera in the two comparing sites, T denotes the subset of genera occurring in both samples compared, U and V represent the subset of genera that only occur in one (U) or the other (V) sampling site. Pandeya's index evaluates the total biovolume of the common genera over the two compared locations relative to their corresponding (absolute) deviation plus the total biovolume of all the genera observed in the two locations. Likewise, Ellenberg's index considers the total biovolume of the common genera over the two compared locations standardised by the total biovolume of both common and site-specific genera. Thus, lower values of the two indices suggest phytoplankton assemblages that differ with respect to their structure. By contrast, the Bray–Curtis' index considers the sum of all the genus-specific (absolute) differences between the compared sites relative to the total biovolume of all the genera observed, and therefore higher values are indicative of distinctly different algal assemblages (Arhonditsis et al., 2003).

2.3. Bayesian hierarchical modelling

To delineate the role of different abiotic factors on the spatiotemporal variability of the phytoplankton assemblage, we opted for a Bayesian hierarchical exercise that has two distinguishing features: first, the data were classified according to the time period (before or after the invasion of dreissenids) and location collected; and the model itself had its own hierarchical configuration, with the parameters of the location-specific regressions at the first level, controlled by the hyper-parameters of a second (upper) level model. With the hierarchical model structure, significant sources of variability (dreissenid invasion, sampling location) can be explicitly accommodated, while overcoming problems of insufficient group-specific data by "borrowing strength" from well-studied modelled units (Zhang and Arhonditis, 2009; Cheng et al., 2010). This strategy is particularly useful for the Bay of Quinte, as the data are inconsistently collected over time among sampling locations and the unique morphology of the Bay could conceivably generate spatially distinct patterns within the system.

Total phosphorus (*TP*), ammonium (*NH*$_4$), light attenuation coefficient (K_{ext}), and surface water temperature (*Temp*) were selected as explanatory variables to predict the relative composition (%) of the phytoplankton community to total cyanobacteria, *Anabaena*, *Aphanizomenon*, and *Microcystis*. Location-specific coefficients for three variables (*TP*, *NH*$_4$, K_{ext}) were also considered, while a spatially-constant coefficient was introduced for the surface water temperature. We also emulated the influence of the dreissenids on the cyanobacteria relative biovolume levels as an abrupt shift in the average system-wide conditions; hence, two spatially-constant intercepts for the pre- and post-invasion periods were considered. The mathematical notation for the hierarchical model is summarized as follows:

$$\begin{gathered}
CYAN_{measij}\sim N(CYAN_{predij},\psi^2)\\
CYAN_{predij}=\beta_{0t}+\beta_{TP_j}\log(TP_{ij})+\beta_{NH_{4j}}\log(NH_{4ij})+\beta_{K_{extj}}K_{extij}+\beta_{temp}(Temp_{ij}-20)\\
\beta_{0_t}\sim N(\beta_{0_g},\tau_{0g}^2)\beta_{TP_j}\sim N(\beta_{TP_g},\tau_{TPj}^2)\beta_{NH_{4j}}\sim N(\beta_{NH_{4g}},\tau_{NH4j}^2)\beta_{K_{extj}}\sim N(\beta_{K_{extg}},\tau_{Kextj}^2)\\
\beta_{0_g}\sim N(\mu_0,\tau_0^2)\beta_{TP_g}\sim N(\mu_{TP},\tau_{gTP}^2)\beta_{NH4g}\sim N(\mu_{NH4},\tau_{gNH4}^2)\beta_{K_{ext}g}\sim N(\mu_{Kext},\tau_{gKext}^2)\\
\mu_0\sim N(0,10000)\mu_{TP}\sim N(0,10000)\mu_{NH_4}\sim N(0,10000)\mu_{Kext}\sim N(0,10000)\\
\tau_{0g}^{-2}\sim G(0.001,0.001)\tau_{TPj}^{-2}\sim G(0.001,0.001)\tau_{NH_4j}^{-2}\sim G(0.001,0.001)\tau_{Kextj}^{-2}\sim G(0.001,0.001)\\
\tau_0^{-2}\sim G(0.001,0.001)\tau_{gTP}^{-2}\sim G(0.001,0.001)\tau_{gNH4}^{-2}\sim G(0.001,0.001)\tau_{gKext}^{-2}\sim G(0.001,0.001)\\
\beta_{temp}\sim N(0,10000)\psi^{-2}\sim G(0.001,0.001)\\
i=1,\ldots.,n\quad j=1,\ldots.,4\quad t=1\,or\,2(before\,and\,after\,1995)
\end{gathered}$$

where, $CYAN_{measij}$ represents the measured (arcsine square root transformed) relative cyanobacteria biovolume in the sample i collected from location j (Belleville, Napanee, Hay Bay, and Conway); $CYAN_{predij}$ and ψ^2 represent the predicted concentrations and model error variance, respectively; β_{TPj}, β_{NH4j}, and β_{Kextj} are the location-specific regression coefficients related to the role of total phosphorus, ammonium, and light attenuation; the location-specific coefficients are treated as draws from normal distributions with global means (β_{TPg}, β_{NH4g}, and β_{Kextg}) and location-specific variances ($\tau_{TPj}{}^2$, $\tau_{NH4j}{}^2$, and $\tau_{Kextj}{}^2$), respectively; β_{temp} is spatially constant regression coefficient for temperature; β_{0t} are the two spatially-constant intercepts for the pre- and post-invasion periods that are derived from normal distribution with a global mean β_{0g} and variance $\tau_{0g}{}^2$; μ_0, μ_{TP}, μ_{NH4}, μ_{Kext} and $\tau_{0g}{}^2$, $\tau_{gTP}{}^2$, $\tau_{gNH4}{}^2$, $\tau_{gKext}{}^2$ are the mean and variance of the hyper parameters, respectively; $N(0, 10000)$ is the normal distribution with mean 0 and variance 10000, and $G(0.001, 0.001)$ is the gamma distribution with shape and scale parameters of 0.001. These prior distributions are considered "non-informative" or vague. Finally, we note that the three covariates were standardized prior to the analysis, and thus the posterior estimates of the intercepts reflect the relative cyanobacteria abundance in the Bay of Quinte at 20 °C, when total phosphorus, ammonium, and light attenuation are set equal to their average levels.

3. Results

The temporal trends of water quality in the four locations of the Bay of Quinte (Belleville, Napanee, Hay Bay, and Conway) are shown in Table 1 and Fig. 1 in the Supporting Information (or Fig. S1). The prevailing water quality conditions have improved over the three time periods, with increased water clarity (decreased light attenuation coefficient values), decreased total phosphorus and ammonium concentrations. No distinct changes were observed in the average surface water temperature among the three time periods, while the soluble reactive phosphorus levels decreased in Belleville but remained fairly stable in Napanee and even increased in Hay Bay; especially from the mid-1990s until the early 2000s (Fig. S1c). The oxidized forms of inorganic nitrogen (nitrate + nitrite) have not demonstrated a statistically significant change between the last two periods (i.e., before and after dreissenid invasion). The sampling station at Conway was the only exception, where there is a statistically significant increase of the recent nitrate/nitrite concentrations. Further, a water quality gradient was evident among the three locations in the upper/middle segments of the Bay of Quinte and the outer sampling site with lower TP levels and higher water clarity at Conway, likely due to its deeper bathymetry and frequent exchanges with Lake Ontario. Likewise, intake water quality data from the Belleville water treatment plant are also indicative of dramatic changes in water chemistry between the pre- and post-dreissenid invasion periods (Fig. S2). In particular, we highlight the distinct increase of the SRP:TP ratio, reflecting both a statistically significant SRP increase and a TP decrease after the colonization of the system by dreissenids (Fig. S2). Interestingly, this increase of the SRP:TP ratio was more pronounced in Hay Bay but less so in the main stem of the upper Bay of Quinte (Table 1). Total phytoplankton biovolume was significantly reduced throughout the Bay of Quinte during the growing (May to October) season; the observed patterns are indicative of a decrease of the algal biovolume levels between

Table 1

Summary statistics (mean and standard deviation values in parentheses) of the abiotic conditions and phytoplankton (including four diversity indices) in the Bay of Quinte. Values are summarized in three periods: pre-P control (1973–1977), post-P control and pre- (1980–1994) dreissenid invasion, and post- (1995–2011) dreissenid invasion.

	Abiotic conditions							Phytoplankton				
	Temp (°C)	K_{ext} (m^{-1})	TP ($\mu g\,L^{-1}$)	SRP ($\mu g\,L^{-1}$)	NH_4 ($\mu g\,L^{-1}$)	NO_3–NO_2 ($\mu g\,L^{-1}$)	DO ($mg\,L^{-1}$)	Biovolume ($mm^3\,L^{-1}$)	Taxonomic richness	Gleason's D	Evenness E1	McNaughton's δ
Belleville												
1973–1977	18.9	1.95	78.1	11.6	65.6	11.1	N/A	13.05	33.48	3.61	0.43	0.73
	(3.85)	(0.54)	(28.5)	(9.33)	(62.1)	(6.52)		(9.08)	(14.54)	(1.54)	(0.14)	(0.14)
1978–1994	19.1	1.48*	43.9*	6.23*	77.8	45.9*	9.35	7.35*	40.14*	4.67*	0.50*	0.65*
	(3.98)	(0.42)	(16.5)	(6.76)	(44.8)	(63.9)	(1.21)	(6.05)	(16.13)	(1.74)	(0.13)	(0.15)
1995–2011	19.6	1.06*	33.8*	3.80*	42.9*	55.3	9.19	4.68*	57.98*	7.31*	0.44*	0.68*
	(4.68)	(0.33)	(14.7)	(4.27)	(42.2)	(137.0)	(1.14)	(4.69)	(24.08)	(3.01)	(0.17)	(0.17)
Napanee												
1973–1977	19.0	1.92	70.1	9.35	79.4	10.1	N/A	11.3	32.81	3.60	0.51	0.65
	(3.9)	(0.51)	(22.9)	(7.03)	(105.2)	(8.6)		(7.36)	(13.53)	(1.43)	(0.13)	(0.15)
1978–1994	19.3	1.51*	41.9*	4.95*	63.2	46.4*	9.71	8.29	62.38*	7.09*	0.48	0.62
	(4.1)	(0.43)	(1.46)	(8.12)	(56.3)	(55.2)	(0.91)	(5.08)	(15.36)	(1.79)	(0.1)	(0.14)
1995–2011	19.6	0.91*	31.3*	4.08	34.4*	50.5	9.40*	3.61*	64.44	8.34	0.43	0.67
	(4.81)	(0.21)	(13.3)	(4.34)	(28.6)	(136.9)	(1.06)	(3.40)	(19.64)	(2.38)	(0.15)	(0.18)
Hay Bay												
1973–1977	18.4	1.43	54.5	N/A	54.4	19.5	N/A	8.80	33.18	3.74	0.55	0.60
	(2.4)	(0.39)	(18.8)		(42.0)	(19.3)		(5.83)	(13.21)	(1.44)	(0.11)	(0.15)
1978–1994	18.6	1.23*	31.2*	2.13	88.6*	65.0*	9.90	6.99*	41.68	4.87*	0.52	0.62
	(3.2)	(0.38)	(12.8)	(2.59)	(67.8)	(71.2)	(0.75)	(5.49)	(20.51)	(2.23)	(0.14)	(0.15)
1995–2011	19.1	0.77*	31.4*	3.92*	36.5*	55.0	9.60*	3.86*	69.56*	8.68*	0.43*	0.65
	(3.3)	(0.24)	(11.7)	(5.21)	(30.9)	(98.8)	(0.64)	(2.28)	(18.02)	(2.2)	(0.11)	(0.14)
Conway												
1973–1977	16.0	0.63	21.6	4.39	39.4	59.1	N/A	2.34	28.59	3.80	0.56	0.62
	(3.88)	(0.14)	(6.56)	(3.06)	(0.03)	(46.5)		(2.02)	(12.87)	(1.66)	(0.12)	(0.15)
1978–1994	16.2	0.56*	16.9*	2.62	40.4	151.3*	10.4	2.42	40.28*	5.48*	0.58	0.55
	(4.34)	(0.15)	(5.34)	(2.74)	(23.2)	(76.4)	(1.20)	(3.01)	(20.84)	(2.48)	(0.17)	(0.2)
1995–2009	17.0*	0.37*	11.7*	1.86*	18.9*	218.1*	9.92*	0.59*	52.77*	8.58*	0.55	0.55
	(4.63)	(0.12)	(2.93)	(1.59)	(10.4)	(70.9)	(1.29)	(0.53)	(13.38)	(1.87)	(0.11)	(0.15)

Abbreviations of abiotic conditions denote surface water temperature (Temp), light attenuation coefficient (Kext), total phosphorus (TP), soluble reactive phosphate (SRP), ammonium (NH_4) and nitrate–nitrite concentration (NO_3–NO_2), dissolved oxygen concentration (DO).

* Denote statistically significant differences ($p < 0.01$) of the paired t-test comparisons between 1973–1977 vs 1978–1994 and 1978–1994 vs 1995–2011.

pre-P control and post-dreissenid periods by 64%, 68%, 56%, and 75% in Belleville, Napanee, Hay Bay, and Conway, respectively (Table 1). Importantly, while the algal biovolume decline was nearly monotonic over the three time periods, the invasion of dreissenids appears to have accelerated these declining trends; especially, in Napanee and Conway (>55%). Decline in total algal biovolume was relatively constant (approximately 40%) during the two environmental perturbations in Belleville.

The establishment of dreissenids induced distinct changes in the seasonal phytoplankton community succession patterns. With year-round algal biovolume data from Belleville intake water, the spring bloom practically disappeared after the invasion of dreissenids (Fig. 2), which was originally dominated by genera from the classes of Bacillariophyceae (*Synedra* spp., *Stephanodiscus* spp., *Aulacoseira* spp.) and Chrysophyceae (*Dynobryon* spp.). Additional effects include the replacement of N_2-fixing genera, such as *Anabaena* spp. and *Aphanizomenon* spp., by the non-N_2 fixer *Microcystis* spp. in the summer phytoplankton assemblage. Considerable longitudinal variability characterizes the phytoplankton community composition, mainly separating the upper/middle Bay of Quinte (Belleville, Napanee, and Hay Bay) from the most distinctive algal assemblages in Conway. Generally, *Aulacoseira* spp. has been the predominant genus throughout the study period and in all locations of the Bay of Quinte except from Conway (Table 2). The relative contribution of *Aulacoseira* spp. to the total algal biovolume during the pre-P control period was on average 46% in Belleville, 26% in Napanee, and 24% in Hay Bay. Following the invasion of dreissenids, this chain-forming, centric diatom increased in the system in terms of its relative biovolume and accounts for 40–50% of the total algal biomass in the upper/middle Bay of Quinte. The relative contribution of *Stephanodiscus* spp. to the total algal biovolume, one of the other predominant diatom genera, gradually decreased over time, with the highest percentage contribution (17%) recorded during the pre-P control period, followed by a decline during the post-P control/pre-dreissenid period (11%) and the lowest (4%) after the mussel establishment. Of the cyanophytes, *Anabaena* spp. and *Aphanizomenon* spp. have been two major residents of the algal assemblage in the Bay of Quinte. In the upper/middle area, *Anabaena* spp. has been consistently present, while *Aphanizomenon* spp. was one of the predominant cyanophytes in Hay Bay. Interestingly, *Anabaena* spp. biovolume increased (in relative terms) after the phosphorus reduction in nearly all sampling locations, but dramatically decreased after the dreissenid invasion. Likewise, *Aphanizomenon* spp. nearly disappeared after the dreissenid establishment in Hay Bay (Table 2). The non-N_2 fixing and potentially toxin-producing cyanobacterium, *Microcystis* spp., has been recently increasing its presence at the upper segments of the embayment, with the highest relative biovolume recorded in Hay Bay (14%).

The spatiotemporal patterns of the phytoplankton community structure were also analyzed using diversity and similarity indices (Table 1, Fig. 3). Taxonomic richness (number of genera) and Gleason's index were the most sensitive to systematic changes in the Bay of Quinte over the last 40 years, demonstrating dramatic increases in all sampling locations after 2000. On the other hand, the post-dreissenid period was also characterized by reduced Evenness (E1) and somewhat increased McNaughton's dominance (δ) values (Table 1). Remarkable similarity exists among the phytoplankton assemblages of the three sampling locations in the upper/middle segments, whereas the algal community composition was distinctly different in the outer embayment (Fig. 3). All similarity indices indicated the clear deviation of the phytoplankton assemblage in Conway, characterized by the lowest values of Paydeya's and Ellenberg's indices, and the highest value of Bray–Curtis' index. This spatially distinctive phytoplankton community pattern was also evident with the average percentage composition (Table 2). Conway has relatively high percentage of *Cryptomonas* spp. and *Fragilaria* spp. compared with the other three studied

Table 2

Summary statistics (mean and standard deviation values in parentheses) of phytoplankton composition in the Bay of Quinte. Six major taxonomic groups were presented in average percentage composition of total algal biovolume during the three periods: pre-P control (1973–1977), post-P control and pre- (1980–1994) dreissenid invasion, and post- (1995–2011) dreissenid invasion.

	Aulacoseira spp.	*Stephanodiscus* spp.	*Microcystis* spp.	*Anabaena* spp.	*Aphanizomenon* spp.	*Cryptomonas* spp.	*Fragilaria* spp.
	(%)	(%)	(%)	(%)	(%)	(%)	(%)
Belleville							
1973–1977	45.8	16.7	0.7	7.8	4.2	3.5	0.7
	(27.2)	(18.0)	(1.1)	(10.6)	(3.8)	(3.1)	(1.4)
1978–1994	37.3	10.9	1.1	12.9[*]	8.0[*]	4.2	4.4[*]
	(21.7)	(14.3)	(1.7)	(11.9)	(9.5)	(7.1)	(6.8)
1995–2011	51.9[*]	4.6[*]	3.4[*]	5.9[*]	0.9[*]	4.5	2.6[*]
	(24.8)	(5.9)	(7.0)	(12.1)	(1.5)	(6.4)	(4.9)
Napanee							
1973–1977	26.1	15.4	1.1	17.2	7.2	6.2	1.7
	(20.9)	(18.2)	(1.1)	(18.6)	(5.5)	(9.7)	(4.6)
1978–1994	34.6	11.0	1.0	13.2	8.3	5.1	4.8
	(26.6)	(13.2)	(1.1)	(14.4)	(9.5)	(5.7)	(7.1)
1995-2011	41.0	7.6	6.3[*]	5.8	1.0	6.1	4.6
	(26.3)	(13.8)	(8.9)	(10.5)	(1.8)	(9.4)	(8.9)
Hay Bay							
1973–1977	24.0	13.4	0.8	13.2	7.7	6.3	2.1
	(20.1)	(11.9)	(1.2)	(14.1)	(6.0)	(6.3)	(2.8)
1978–1994	23.5	13.7	0.9	13.5	7.5	8.0	5.5
	(24.7)	(16.6)	(1.2)	(20.1)	(7.2)	(8.2)	(9.3)
1995–2011	36.0[*]	3.9[*]	13.9[*]	7.7	1.7[*]	7.8	5.7
	(21.6)	(11.0)	(13.6)	(12.4)	(1.9)	(8.4)	(6.7)
Conway							
1973–1977	17.1	9.8	1.5	8.1	3.4	14.3	3.8
	(21.8)	(14.9)	(4.3)	(9.7)	(5.5)	(13.5)	(4.4)
1978–1994	12.9	13.2	0.2	7.7	0.8[*]	8.6[*]	10.3[*]
	(17.0)	(22.9)	(0.6)	(12.9)	(2.2)	(7.4)	(7.7)
1995–2009	15.3	5.9	6.9[*]	2.3	0.4	13.3[*]	12.5
	(21.1)	(11)	(12.3)	(3.6)	(0.8)	(11.4)	(14.9)

[*] Denote statistically significant differences ($p < 0.01$) of the paired t-test comparisons between 1973–1977 vs 1978–1994 and 1978–1994 vs 1995–2011.

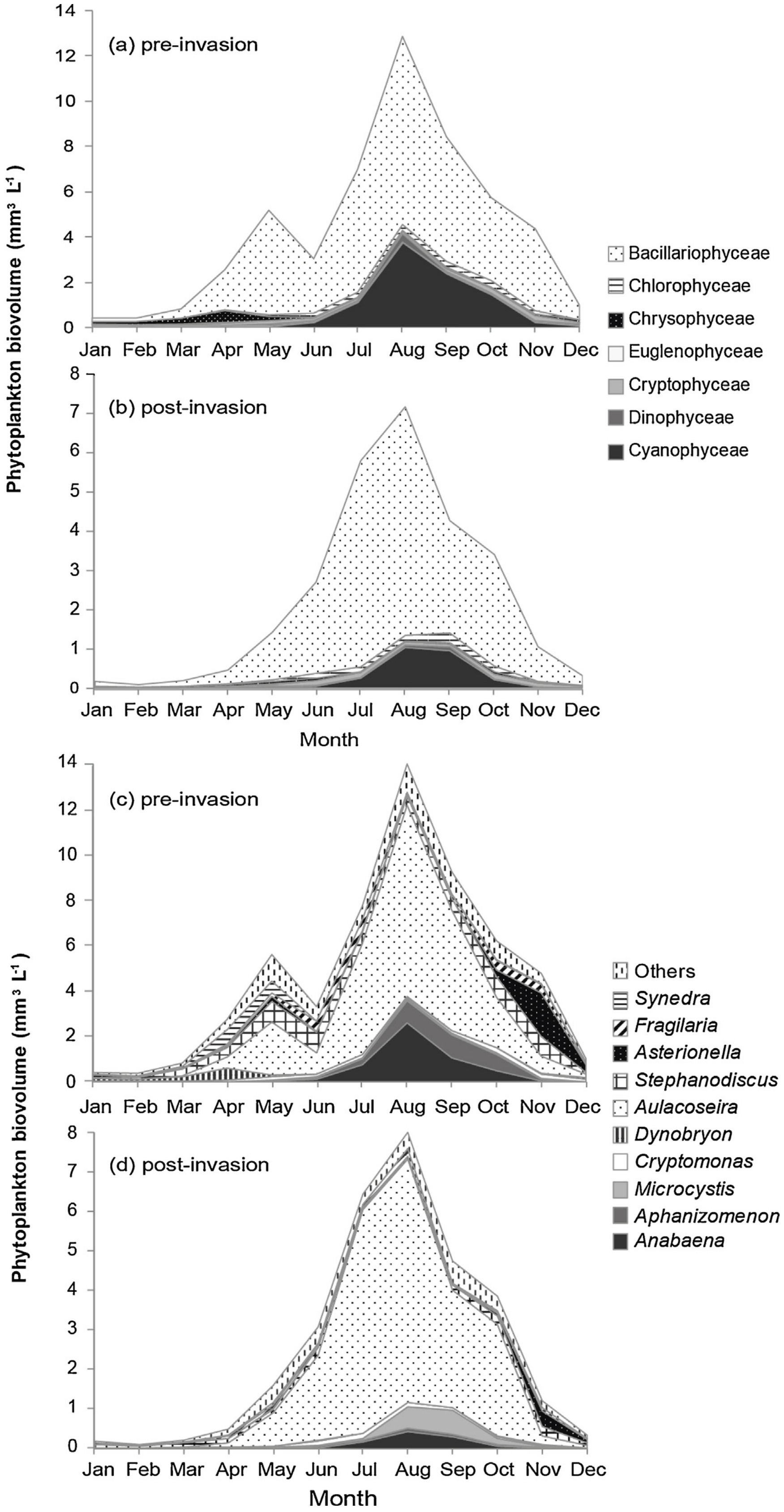

Fig. 2. Seasonal phytoplankton succession patterns in the Bay of Quinte during the (a, c) pre- and (b, d) post-dreissenid invasion periods at the intake of the Belleville Water Treatment Plant. Phytoplankton were categorized by class (a, b) and genera (c, d) in the upper and lower panels, respectively.

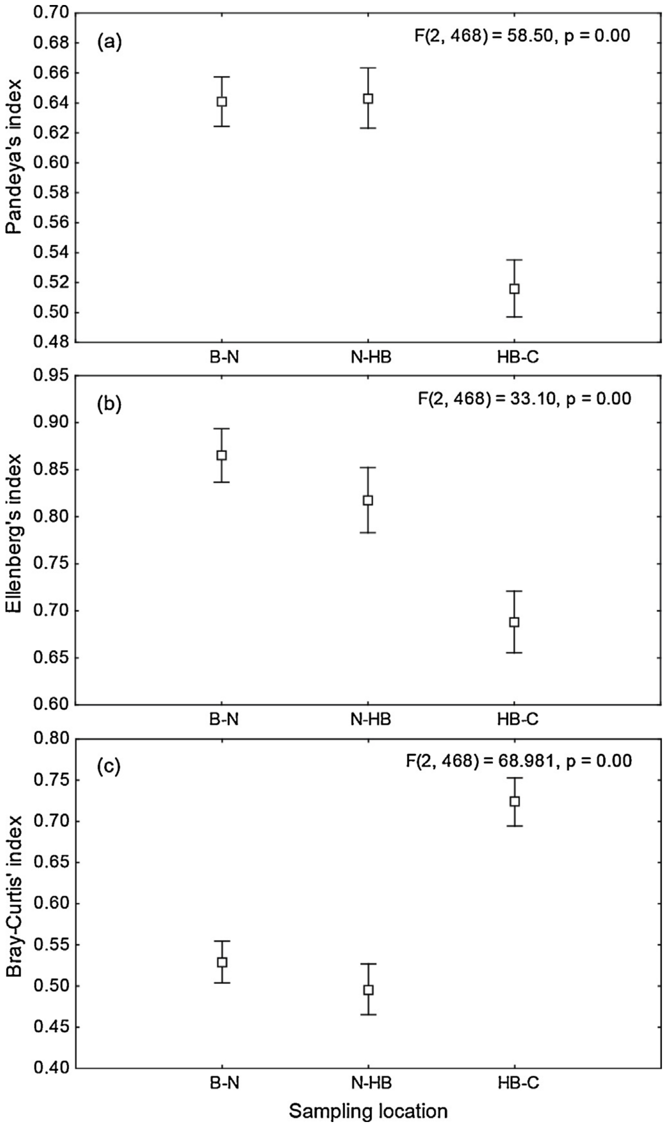

Fig. 3. Comparison of phytoplankton community structure among the four sampling locations, based on three similarity indices: B–N (Belleville–Napanee), N–HB (Napanee–Hay Bay), HB–C (Hay Bay–Conway).

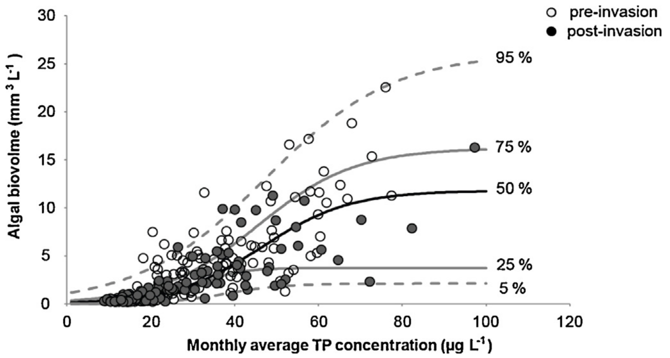

Fig. 4. Scatter plots of total algal biovolume against TP concentrations in the Bay of Quinte along with 0.95, 0.75, 0.50, 0.25, and 0.05 quantile regression estimates.

locations. More than 80% of the common genera with upstream locations are considered minor in terms of their biovolume in Conway, further reducing the corresponding values of Pandeya's and Ellenberg's indices. Finally, somewhat lower values of Ellenberg's index were realized when comparing the phytoplankton assemblages between Napanee and Hay Bay, which likely reflects the greater weight assigned to the biovolume of the non-common species with the formula of the latter index.

To shed light on the ecological mechanisms that predominantly shape the phytoplankton community structure in the Bay of Quinte, we examined the strength/nature of the relationships between phytoplankton community and abiotic conditions, such as TP, PO_4, NH_4, NO_3, surface water temperature, and light attenuation coefficient. We first plotted monthly total phytoplankton biovolume data against the corresponding TP concentrations using quantile regression, which provided evidence that TP variability is indeed one of the factors that predominantly modulate phytoplankton dynamics (Fig. 4). Quantile regression estimates were all statistically significant (Table S1), indicative of a strongly positive, non-linear algal biovolume-TP relationship, characterized by a steep increase once the level of 40 μg TP L^{-1} is exceeded. However, when the data points are classified into two subsets, representing the pre- (open circle) and post- (filled circle) establishment periods of dreissenid mussels, it can be easily seen that the upper quantile models are primarily driven by data from the pre-dreissenid (and/or pre-P control) period, and therefore these relationships may not be fully applicable in the current state of Bay of Quinte. The confounding effect of dreissenids has masked the apparent response of class or even individual phytoplankton genera to nutrient variability (Fig. 5). *Aphanizomenon* spp. was the most profound examples of the latter assertion, being suppressed even under nutrient rich conditions after the mussel invasion (Fig. 5e and f). Contrasting response was found for *Microcystis* with high biovolume ($>500\ \mu m^3\ mL^{-1}$) experienced only during the post-dreissenid period (Fig. 5g and h). Apart from the TP ambient levels, there were also positive relationships between the biomass of total cyanobacteria or the three most abundant genera (*Anabaena* spp., *Aphanizomenon* spp., *Microcystis* spp.) with surface water temperature and light attenuation coefficient, whereas the relationships were less clear with NH_4 and NO_3–NO_2 (Figs. S3–S6). In a similar manner, there was a nearly monotonic decrease of the Gleason's index values with ambient phosphorus and light attenuation, which was distinctly steeper below critical threshold values of 40 $\mu g\ L^{-1}$ and 1.0–1.5 m^{-1}, respectively, in the upper/middle Bay (Fig. S7; see also Table 1).

Bayesian hierarchical modelling was used to examine the relative importance of each of the four abiotic factors on the relative (percentage) biovolume of total cyanobacteria, and individual cyanobacteria genera (*Microcystis* spp., *Anabaena* spp., and *Aphanizomenon* spp.) (Table 3; see also posterior results in Table S2). The positive signature of ambient TP variability was consistently evident with all models developed, although the strength of the corresponding parameter posteriors demonstrated both group- and site-specific variability. The role of NH_4 varied longitudinally, with positive signatures found in the upper Bay (especially in Belleville) and mainly negative ones in the middle (Hay Bay) and lower (Conway) segments. In particular, there was a strongly negative association between NH_4 and non-N_2fixing *Microcystis* in Napanee and Hay Bay. It should be noted that the negative signs stem from the adopted temporal resolution of the study (data from individual samplings with no time averaging) and also reflect the ability of *Microcystis* to promptly respond to nutrient variability, increase their biovolume and, consequently, decrease the contemporaneous nutrient levels; especially those in shortest supply (Arhonditsis et al., 2007a,b). Interestingly, *Microcystis* was characterized by a distinctly negative relationship with the light attenuation coefficient throughout the embayment. The effects of temperature on the relative biovolume of cyanobacteria were weakly positive, except from *Anabaena* spp. which was characterized by a strongly positive relationship. Finally, based on our model configuration, the posterior estimates of the intercepts

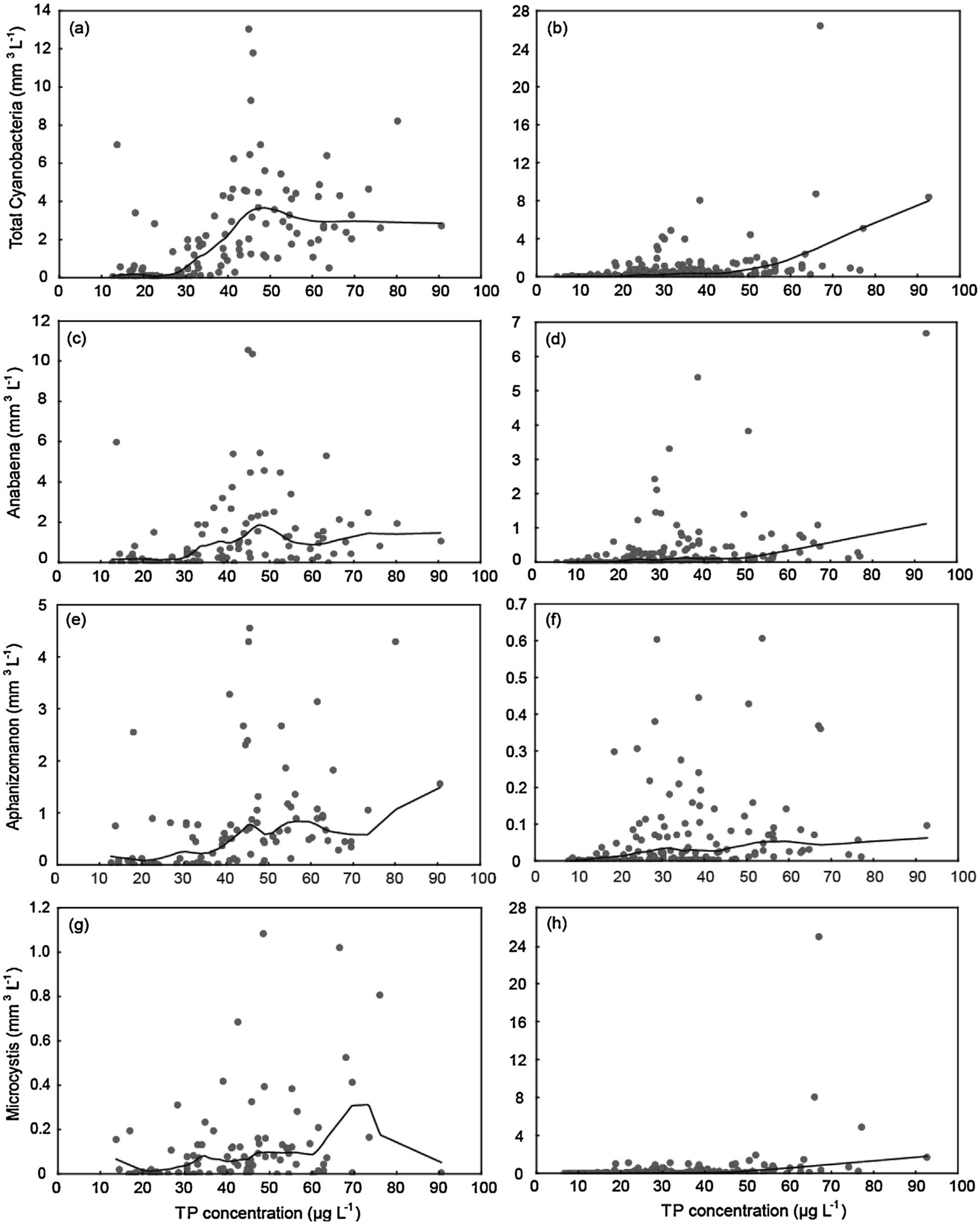

Fig. 5. Scatter plots of cyanobacteria biomass against TP concentrations ($\mu g\ L^{-1}$) in the Bay of Quinte. (a and b) Total cyanobacteria, (c and d) *Anabaena*, (e and f) *Aphanizomenon*, and (g and h) *Microcystis*. Left and right panels represent the pre- and post-dreissenid invasion periods, respectively. The solid lines represent LOWESS (locally weighted scatter plot smoothing) fit; a non-parametric method that combines polynomial regression models in a *k*-nearest-neighbor-based meta-model, thereby providing a clearer picture of the overall shape of the relationship between two variables.

reinforce our earlier assertion that the relative biovolume of total cyanobacteria has on average declined after the invasion of dreissenids. The same pattern holds true for *Anabaena* spp. and *Aphanizomenon* spp., whereas *Microcystis* spp. demonstrated a distinct increase in regard to its relative contribution to the algal assemblages typically experienced in the Bay of Quinte.

Our Bayesian hierarchical models can also be used to make predictions about the relative cyanobacteria biovolume at different TP levels before and after the colonization of dreissenid mussels (Fig. 6). For example, prior to the invasion of dreissenids, the expected relative biovolume for total cyanobacteria was 24.6% at 40 μg TP L^{-1} and has declined down to 16.9% in the post-invasion era (Fig. 6a and b). An alternative way to read the same predictive distribution is that the level of relative cyanobacteria biovolume exceeded 10% of the time is 28% in the post-dreissenid period compared with a 40% level prior to their establishment in the system. The same decreasing trend was evident with the predictive distributions of the two N_2-fixing cyanobacteria, *Anabaena* and *Aphanizomenon*, i.e., mean probability values that declined from 9.8% and 4.3% (Fig. 6c and e) to 4.9% and 1.2% at 40 μg TP L^{-1} (Fig. 6d and f), respectively. By contrast, the mean expected percentage contribution of *Microcystis* increased from 1.4% to 4.5% between

Table 3
Importance of the abiotic factors used to predict total cyanobacteria and three major genera relative to the total phytoplankton biovolume. Relative importance of the abiotic factors was classified into five levels, as depicted by the different arrow thickness, while upward and downward directions denote positive or negative relationships, respectively. Numerical ranges used to characterize the strength of each relationship are provided in Table S3.

Location	Variables	Cyanobacteria group			
		Total cyanobacteria	*Microcystis*	*Anabaena*	*Aphanizomenon*
Belleville	*TP*	↑	↑	↑	↑
	NH₄	↑	↑	↑	↑
	Light attenuation	↑	↓	↑	↑
Napanee	*TP*	↑	↑	↑	↑
	NH₄	↑	↓	↓	↓
	Light attenuation	↓	↓	↓	↑
Hay Bay	*TP*	↑	↑	↑	↑
	NH₄	↓	↓	↓	↓
	Light attenuation	↑	↓	↑	↑
Conway	*TP*	↑	↑	↓	↑
	NH₄	↓	↓	↑	↑
	Light attenuation	↓	↓	↑	↑
	Temperature	↑	↑	↑	↑
		pre post	pre post	pre post	pre post
	Intercept	↑ ↑	↑ ↑	↑ ↑	↑ ↑

pre- and post-dreissenid invasion period (Fig. 6g and h). Interestingly, our Bernoulli-logistic regression model indicated that TP concentrations alone fails to predict many exceedances of the three microcystin (1.5, 1.0, and 0.5 $\mu g\ L^{-1}$) levels considered (Fig. 7), and thus more comprehensive modelling needs to be in place in order to reliably predict microcystin violations.

4. Discussion

The paradigm of phosphorus as the primary regulatory factor of the severity of eutrophication problems, traced back as far as Neumann's description from 1919 (Lewis and Wurtsbaugh, 2008), has profoundly shaped the restoration actions in the Laurentian Great Lakes. Centered on the control of external nutrient loading, the mitigation efforts in the late 1970s were rapidly effective as significant declines in ambient nutrient levels, primary productivity and phytoplankton abundance, improved water clarity, and reduced frequency of harmful algal blooms (Schindler and Vallentyne, 2008; Dove, 2009). The establishment of dreissenid mussels in the early 1990s, however, has induced profound alterations in the biogeochemical cycles, the phytoplankton community structure along with the broader trophodynamics, and ultimately the overall functioning of the nearshore zone (Coleman and Williams, 2002; Hecky et al., 2004; Kim et al., 2013). In this regard, we presented a retrospective analysis that aims to shed light on the variability of the abiotic environment triggered from two seminal events (point-source P loading reduction and invasion of dreissenid mussels) as well as their direct and indirect effects on the quantitative/qualitative characteristics of the phytoplankton community in the Bay of Quinte AOC, Lake Ontario.

4.1. What is the level of improvement of the abiotic conditions in the Bay of Quinte?

Daily annual average total phosphorus loads to the Bay of Quinte between 1973 and 1977 from six municipal sewage treatment plants bordering the Bay of Quinte were 157 $kg\ day^{-1}$ and were reduced to 68 $kg\ day^{-1}$ for 1978 to 1986. Smaller declines occurred over the ensuing two decades, so that by the early 2000s the average point source loading rate to the Bay has been varying between 8.6 and 22.3 $kg\ day^{-1}$ (Munawar et al., 2011). Adopting the concept of net loading (=$\text{Flows}_{\text{exogenous}} \times [\text{TP}_{\text{exogenous}} - \text{TP}_{\text{Bay of Quinte}}]$), Kim et al. (2013) showed that although the point source load discharges still have a positive sign, their actual contribution (i.e., absolute magnitude) has been significantly reduced. Following the exogenous phosphorus reduction, the ambient TP levels have dramatically decreased and the established delisting criterion of a seasonal (May–September) average of 30 $\mu g\ TP\ L^{-1}$, based on samples collected from the entire upper Bay, was occasionally realized during the 2000s (Munawar et al., 2011). Nonetheless, Zhang et al. (2013) pointed out that the coarse spatiotemporal resolution of the existing TP target neither

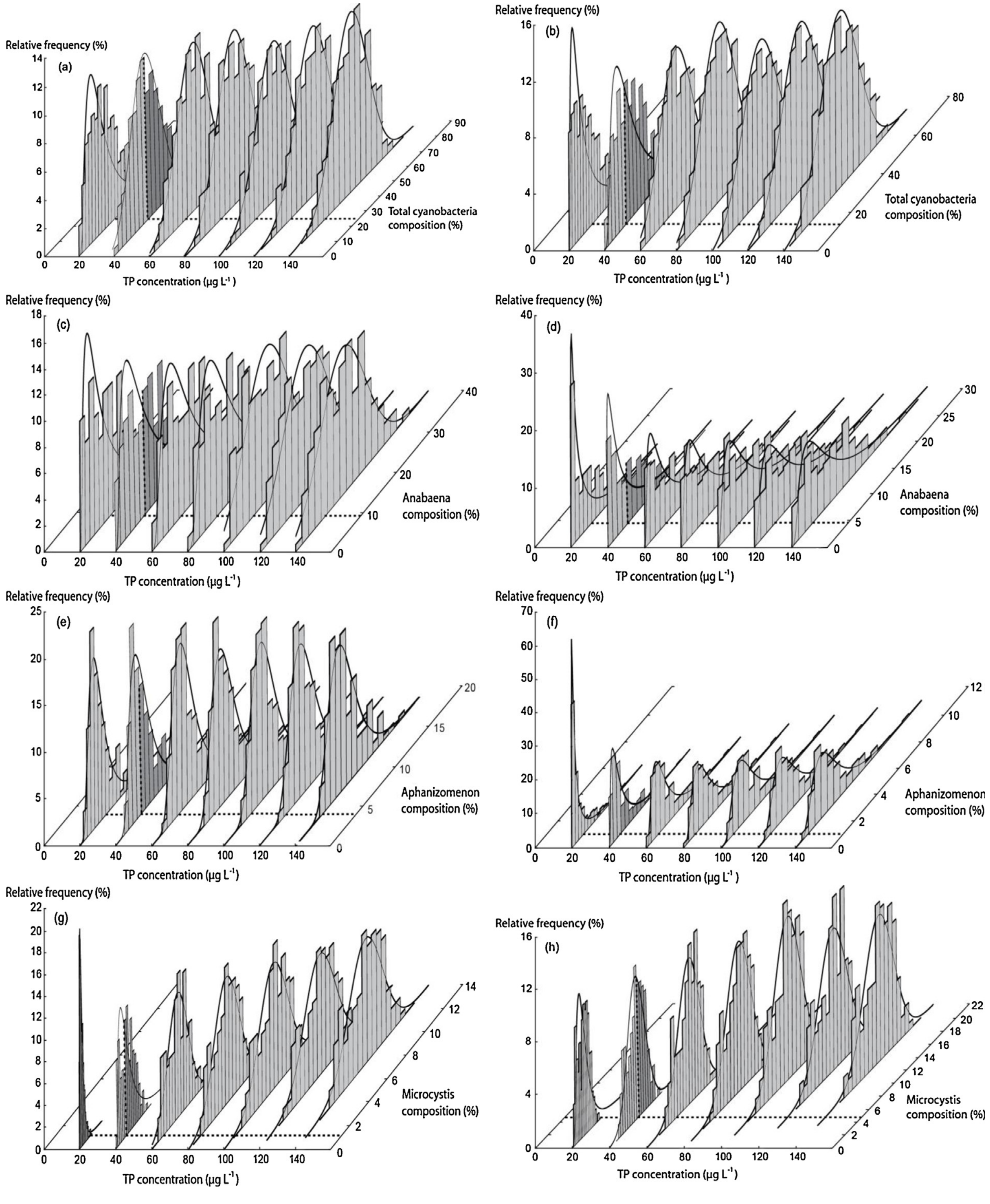

Fig. 6. Posterior predictive distributions of phytoplankton composition at different ambient TP levels. Left and right panels present the relative abundance (%) during the pre- and post-dreissenid invasion periods of: (a and b) total cyanobacteria, (c and d) *Anabaena*, (e and f) *Aphanizomenon*, and (g and h) *Microcystis*, respectively. Shaded areas represent the probability mass above the median (upper 50%) of the distributions corresponding to 40 μg TP L^{-1}.The latter value represents the TP criterion, proposed by Kim et al. (2013), which should not be exceeded more than 10-15% of the samples collected from the upper Bay of Quinte during the growing season.

reflects the intra-annual variability in the upper Bay nor is representative of the water quality conditions in nearshore areas of high public exposure (e.g., beaches). Namely, the seasonal TP variability in the euphotic zone is typically characterized by low spring and autumn levels (10–15 μg TP L^{-1}) and relatively high end-of-summer/early-autumn concentrations (45–50 μg TP L^{-1}). The latter pattern was attributed to the complex interplay among macrophytes, dreissenids, and sediment diagenesis that appears to modulate the nutrient recycling in the present state of the Bay of Quinte (Kim et al., 2013). In particular, Arhonditsis et al. (2016) projected that the sediments (resuspension and diffusion from the sediments to water column minus particle settling) act as a net source of phosphorus in the upper segments of the Bay (57.9–70.4 kg day^{-1}). In the same area, dreissenids subtract approximately

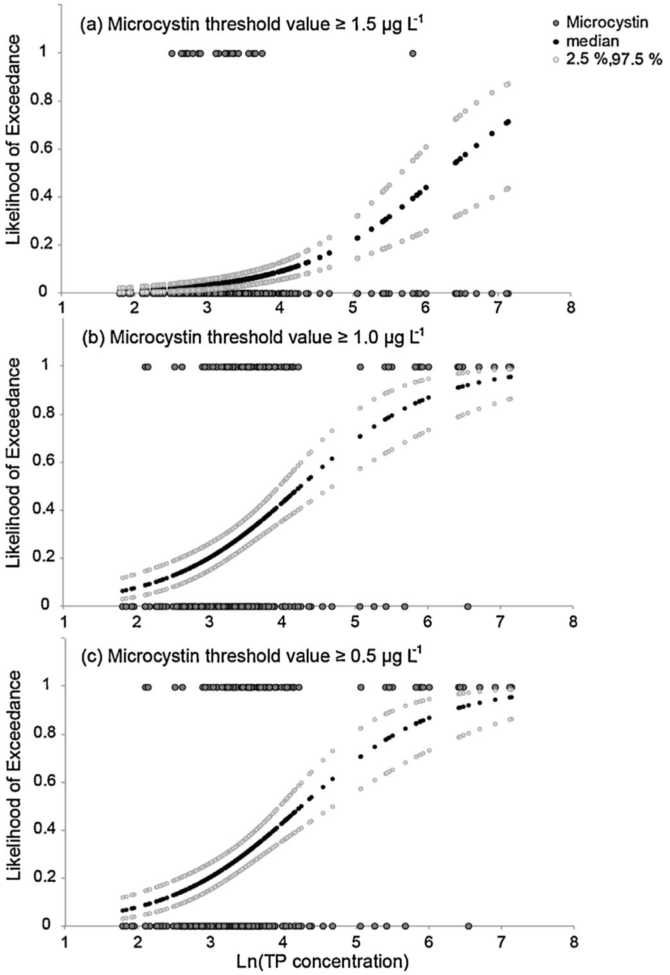

Fig. 7. Likelihood of exceedance of critical microcystin concentrations as a function of TP levels in the Bay of Quinte. The logistic regression coefficients corresponding to threshold values of 1.5, 1.0, and 0.5 μg L^{-1}were: (i) β_0 = -6.410 ± 0.853 and β_1 = 1.029 ± 0.193, (ii) β_0 = −4.700 ± 0.669 and β_1 = 0.812 ± 0.167, (iii) β_0 = −4.644 ± 0.701 and β_1 = 1.098 ± 0.193.

65.9–112 kg day^{-1} from the water column (particle filtration minus respiration) and subsequently deposit 62.4–105 kg day^{-1} via their excretion and particle rejection. Further, the submerged macrophytes could conceivably provide a major pathway (10–42.3 kg day^{-1}) for the rapid transport of the nutrients assimilated from the sediments into the water column through the decomposition of dead plant tissues; especially since macrophytes demonstrate luxury uptake and thus tend to accumulate nutrients in concentrations higher than their physiological requirements (Arhonditsis et al., 2016).

Along the same line of reasoning, we also found an increase of the fraction of dissolved phase inorganic phosphorus relative to total phosphorus between the pre- and post-dreissenid periods in all four sampling locations in the Bay of Quinte, particularly from the mid-1990s until the early 2000s (Fig. S1c). One of the plausible explanations for this trend could have been the nature of the watershed loading due to factors associated with demographic changes, altered agricultural practices (e.g., conservation tillage), and animal density. However, Arhonditsis et al. (2016) showed that the SRP:TP ratios in all the major tributaries in the Bay of Quinte area have not been following a clear increasing trend, counter to what has been reported elsewhere (e.g., Lake Erie). Thus, it stands to reason that the primary driving factor is the ability of dreissenid mussels to filter significant amount of particulate matter relative to what they actually ingest (Walz, 1978), and thus a large proportion is excreted in soluble form or released in particulate form as either feces or pseudofeces. Given also that a significant portion of the latter particulate material is subsequently remineralized by the community of detritivores and decomposers, it is plausible to hypothesize that dreissenids mediate the nutrient cycling and may have significantly modulated the dynamics (and relative fractionation) of nearshore nutrient concentrations in the Bay of Quinte (Hecky et al., 2004; Dove, 2009). Because soluble reactive phosphorus directly stimulates the primary production, the latter pattern highlights the importance of dreissenid mussels in shaping the nature of the recent algal assemblages in the Bay of Quinte; especially, if we also consider the significant improvement in the water column illumination (reduced light attenuation in Table 1).

The oxidized fraction of dissolved inorganic nitrogen concentration has been increasing since the late 1970s, with the highest values observed in the lower Bay of Quinte. Except from Wilton Creek (upstream of Hay Bay), there is no obvious change in the nitrogen loading from any of the major tributaries in the area (Minns et al., 2004). Nitrate/nitrite concentrations have been increasing at an exponential rate for almost four decades in other nearshore areas in Lake Ontario, e.g., Hamilton Harbour (Gudimov et al., 2011), but evidently this accumulation of nitrate is a more general pattern in the Great Lakes, as similar increasing trends with substantial decline of the summer NO_3 drawdown have been reported in Lakes Erie, Superior, and Ontario (Finlay et al., 2007; Dove, 2009; Bridgeman et al., 2012; Winter et al., 2012). In this regard, Finlay et al. (2007) asserted that NO_3 accumulation in Lake Superior is almost entirely derived from nitrification occurring within the system, whereas others have suggested that it could also be associated with the external loading trends, e.g., atmospheric deposition (North et al., 2012; Winter et al., 2012). In the Bay of Quinte, alongside with the increasing NO_3 trend, a statistically significant NH_4 decrease was found in all four sites (i.e., 35–58% decline between pre- and post-dreissenid invasion) likely stemming from the point source loading control, although it could also be perceived as evidence of increased nitrification rates in the system. In any event, counter to the upward trend of the SRP levels, it is interesting to note that there is no empirical support of an increase in the ambient NH_4 levels in the water column due to the excretion of dreissenid mussels (Arnott and Vanni, 1996; Ozersky et al., 2013). Given also that the dissolved inorganic nitrogen concentrations are lying at moderately low levels over fairly prolonged periods of the seasonal cycle, the likelihood of nitrogen to be one of the underlying drivers of the phytoplankton dynamics in the Bay of Quinte cannot be ruled out.

4.2. What is the signature of the abiotic environment on the phytoplankton community structure?

Depending on the location examined, our study showed that the total phytoplankton biovolume during the growing season (May to October) was reduced by up to 45% after the P control and by an additional 25–80% after the dreissenid invasion relative to the 1973–1977 levels. In a similar attempt to evaluate the apparent effects of the two environmental alterations on the phytoplankton of the Bay of Quinte, Nicholls et al. (2002) delineated five major response categories into which phytoplankton variables (classes, genera) can be classified (see their Table 4 in Nicholls et al., 2002). Although some of our findings deviate from the predictions of this classification scheme, the most distinct change of the seasonal succession patterns was the declining trend of the genera that typically dominated the spring algal assemblages, such as *Synedra* spp., *Fragilaria* spp., *Stephanodiscus* spp., and *Aulacoseira* spp. (Nicholls and Carney, 2011). This dramatic diatom decrease apparently reflects a negative net growth-minus-losses balance after the establishment of dreissenid mussels in the Bay of Quinte, which provides a window of opportunity for other algal species to exploit the available resources in late spring/early summer (Rockwell et al., 2005; Barbiero et al., 2006). Counter to Nicholls et al.'s (2002) assertions, the growth habit (long multi-cellular trichomes) of the two major *Aulacoseira* species (*A. granulata* and *A. ambigua*) did not allow them to escape the efficient removal from the water by dreissenids, and therefore their decline (not their relative contribution to the total phytoplankton biovolume) was fairly similar (≈26%) to the one brought about by P mitigation strategies (≈23%). By contrast, *Stephanodiscus* spp. demonstrated a monotonic pattern, experiencing a decline greater than 90% during the two environmental changes. Interestingly, *Fragilaria* spp. biovolume remained fairly stable after the P control but subsequently declined by nearly 30% after the invasion of dreissenids.

Species of the genus *Dinobryon* were originally hypothesized to thrive under conditions of phosphorus limitation owing to their motility and hence their ability to migrate and exploit deeper waters with higher P concentrations (Nicholls et al., 2002). Nonetheless, the Bay of Quinte dataset does not support this prediction, as this assemblage of (predominantly chemoautotrophic/phagotrophic) species underwent a nearly monotonic decrease (≈50%) over the 40-year time span examined. The same pattern holds true for species of the genera *Cryptomonas* and *Rhodomonas*, which on average experienced a decline by 35% after the P control, accompanied by an additional 20% decline after the invasion of dreissenids. Given the high nutritional value of the latter functional group, the implications of this declining trend could be profound for the broader food web functioning (Perhar et al., 2012). Generally, the invasion of exotic species is considered a major disturbance of the food web (Madenjian et al., 2002; Mills et al., 2003) that can alter biogeochemical cycles and habitat structure (Hall and Mills, 2000), and may reduce the native diversity (Holeck et al., 2004; Barbiero et al., 2006). Kirsch and Dzialowski (2012) presented inconclusive results about the species diversity after the dreissenid invasion in three Kansas reservoirs, asserting that zebra mussels potentially influence the native biotic communities. The magnitude of the structural shifts is environment-dependent and may vary depending on the trophic state and/or resident phytoplankton assemblages of individual systems (Kirsch and Dzialowski, 2012). Our dataset provides phytoplankton taxonomy down to the genus level and therefore we were not able to unequivocally delineate the biodiversity patterns after the two environmental alterations in the Bay of Quinte. We did show that, however, the post-dreissenid period was characterized by increased number of genera of the phytoplankton assemblages along with reduced Evenness (E1) and somewhat increased McNaughton's dominance (δ) values.

Consistent with Nicholls et al.'s (2002) conceptualization, the total cyanobacteria biovolume has declined in response to both P control and dreissenid colonization, and this pattern became more pronounced after the latter environmental perturbation. Notably, the Bay of Quinte also experienced a dramatic decline in *Oscillatoria* and *Lyngbya* species, which was attributed to the increased illumination of the water column brought about by the dreissenid filtration of particulate matter rather than by their direct grazing pressure (Nicholls et al., 2002). Characterized by superior kinetics under low light regimes, it has been hypothesized that several of these species likely lose their competitive advantage under supra-optimal light conditions and may even undergo cell lysis (Meffert, 1989; Mur and Schreurs, 1995). In a similar manner, the N_2-fixing *Anabaena* spp. and *Aphanizomenon* spp. have been an important component of the cyanobacteria assemblages typically residing in the Bay of Quinte, but their biovolume has dramatically declined during the post-dreissenid period. Similar *Aphanizomenon* declines have also been reported in the western basin of Lake Erie (Makarewicz et al., 1999) and Saginaw Bay (Higgins and Vander Zanden, 2010). Our hierarchical modelling exercise identified phosphorus and light variability as important factors that modulate the relative contribution of the two genera to the total algal biovolume, whereas the signature of ammonium was fairly weak. The causal linkage between relative algal biovolume and light was originally considered to account for the stimulatory effects of light on phytoplankton growth. However, counterintuitive positive signs were found for the regression coefficient linking light attenuation with phytoplankton biovolume (e.g., see the *Anabaena* and *Aphanizomenon* models). In a strict causal sense, this implies an opposite direction path in that higher/lower algal biovolume lead to higher/lower attenuation coefficient values. On the other hand, nitrogen availability is often neglected as an underlying driver of the algal succession patterns in the Great Lakes (Kim et al., 2014). In this particular case though, given that NH_4 concentrations lie well below the saturation levels during the post-dreissenid period, it would have been reasonable to assume that the prevailing conditions render competitive advantage to the N_2-fixing residents of the phytoplankton community. The weak linkage between NH_4 and relative biovolume, however, can have two plausible explanations: (i) the active dreissenid filtration is a major confounding factor that does not allow this relationship to manifest itself in our data, and (ii) the likelihood of a relative competitive advantage for N_2-fixers is low, because the increasing NO_3 pool may alleviate the nitrogen limitation to eukaryotic phytoplankton or other non-N_2-fixing cyanobacteria (Blomqvist et al., 1994).

4.3. *Assessing the risk of* Microcystis *blooms and toxin production*

Similar to the patterns observed in western Lake Erie and Saginaw Bay (Lavrentyev et al., 1995; Budd et al., 2001; Vanderploeg et al., 2001), the chroococcoid *Microcystis* was the main genus to increase after the establishment of zebra mussels. Both empirical and modelling work has provided evidence that the associated mechanism may involve selective filtration by dreissenids, whereby more palatable food items are depleted from the water column, while *Microcystis*is rejected and subsequently accumulates in the absence of competition for light and nutrients (Vanderploeg et al., 2001). It is also hypothesized that the documented selective rejection of loosely consolidated pseudofeces of aggregated colonies of *Microcystis* may solely involve toxic strains, because non-toxic strains can be actively consumed by dreissenids in laboratory studies (Baker et al., 1998; Vanderploeg et al., 2001). In the same context, Bierman et al. (2005) and Fishman et al. (2009) postulated three additional conditions that could potentially magnify the proliferation of *Microcystis*: (i) enhanced sediment-water phosphorus fluxes; (ii) increased light availability due to the particle removal from the water column; and (iii) high dreissenid mussel density along with predominance of adults relative to young-of-year mussels in their colonies. Regarding the first condition, there is abundant evidence that the internal nutrient recycling represents a major feedback loop into the system that can fuel excessive *Microcystis* growth towards the end of the summer/early fall; especially with the recent variations of the SRP:TP ratio. Of equal importance could also be the episodic summer precipitation events that subsidize with nutrients the nearshore areas in a relative short time span (Bridgeman et al., 2012). Notably, the relatively stronger signature of NH_4 variability in Napanee and Hay Bay suggests that nitrogen competition may be one of the factors that control the likelihood of *Microcystis* blooms. Along the same line of reasoning, evidence in support of the second condition is the negative relationship between light attenuation and *Microcystis* relative biovolume in Napanee and Hay Bay, i.e., improved illumination of the water column may trigger their higher (relative) contribution to the total algal biovolume (see also following discussion).

Existing empirical evidence suggests that there is considerable spatiotemporal variability in the dreissenid mussel density, distribution patterns, and their size groups in the Bay of Quinte (Dermott and Bonnell, 2011). For example, relative to the quagga mussel-dominated lower Bay, characterized by a stable silty-sand substrate on which they can survive and grow, zebra mussels are more abundant in the shallower upper part of the system. The density of the zebra mussel population in the latter location can be variable, while the frequent exposure to waves and storms generally favours the predominance of smaller mussels less than 5 mm in length (Dermott and Bonnell, 2011). The selective predatory pressure of round goby (*Neogobius melanostomus*) that favours smaller mussels (<8 mm) may suppress their dominance and makes the prediction of distribution pattern very difficult. On the other hand, there is evidence of a clear transition from smaller young mussels to larger adults toward the end of the growing season. The latter trend may suggest seasonal variability with respect to the filtering pressure on the algal assemblage as well as the nutrient fluxes mediated by dreissenid activity.

Microcystis outbreaks occur in an episodic manner with a nearly exponential increase of the density/biovolume in time and rapid proliferation in space (Vanderploeg et al., 2001; Nicholls et al., 2002; Fishman et al., 2009). Except from a few isolated events, both absolute and relative values of *Microcystis* biovolume are relatively low in the Bay of Quinte. For this reason, our hierarchical modelling exercise primary depicts the typically prevailing interplay between *Microcystis* biovolume and the abiotic conditions in the system, and thus may not necessarily provide a forecasting tool of the actual magnitude of nuisance blooms. Even more challenging is the establishment of predictive linkages with toxin, because the mechanisms associated with toxin production are complex and not all *Microcystis* species produce toxins (Kotak et al., 2000; Vanderploeg et al., 2001). There are several studies that suggest a positive relationship between nitrogen concentration and toxin-producing *Microcystis* strains (Murphy et al., 2003) or microcystin production (Orr and Jones, 1998). In particular, urea is hypothesized to be an energetically favourable form of nitrogen and therefore a predominant stimulant of *Microcystis* blooms (Finlay et al., 2010). On the other hand, Makarewicz et al. (2009) indicated that TP concentrations explained 70% of the microcystin variability in embayments, rivers, creeks, ponds, nearshore, and offshore sites of Lake Ontario, while other potentially reliable predictors include the concentration of micronutrients, UV radiation stress, chlorophyll a and Secchi disc depth (Orr and Jones, 1998; Lyck, 2004; Makarewicz et al., 2009; Yuan et al., 2014). The capacity of dreissenids to modulate the elemental ratios (i.e., tendency to lower inorganic N/P) in the water column may also contribute to the emergence of *Microcystis* blooms (Bykova et al., 2006), although our analysis does not render support to this hypothesis (Fig. S1e). Further, empirical evidence from the system is indicative of a weak correlation between chlorophyll a and cyanobacterial toxin concentrations (Watson et al., 2011), while our empirical modelling with total phosphorus as the sole predictor fails to capture many violations of threshold values of microcystin concentration (see Fig. 7).

5. Conclusions

This study attempted to delineate the structural shifts of the phytoplankton community induced by two environmental alterations: point-source phosphorus (P) loading reduction in the late1970s and establishment of dreissenid mussels in the mid-1990s. A number of diversity and similarity indices indicated that the structural features of the algal assemblages in the upper and middle segments appear to be distinctly different from those typically residing in the outer segments of the Bay. Our analysis also identified significant differences among the phytoplankton communities, corresponding to pre- and post-P control as well as pre- and post-dreissenid invasion periods. Recent shifts in phytoplankton community composition were mainly the distinct decline of diatom biovolume of the spring assemblage, occurrence of toxin-producing *Microcystis* spp. outbreaks, and reduced biovolume of N_2-fixers *Aphanizomenon* spp. and *Anabaena* spp. Our analysis suggests that there is significant longitudinal heterogeneity with respect to the role of the factors shaping cyanobacteria dynamics, and thus total phosphorus alone cannot always explain the year-to-year variability of the algal assemblage. Dissolved inorganic nitrogen falls well below saturation levels for phytoplankton growth over a long period of time, and therefore the role of nitrogen warrants consideration for the design of the on-going best management practices.

In a system like the Bay of Quinte, where the severity of eutrophication phenomena is driven by both external and internal factors, there will inevitably be some uncertainty in the overall assessment of its water quality status. A rigorous analysis of decision problems in water quality management requires specification of pragmatic delisting criteria that are framed upon the appropriate spatiotemporal resolution and explicitly accommodate the natural system variability; a number of realistic management actions, including any constraints on their use; predictive models formulated in terms of quantities relevant to management targets; objective functions that effectively balance between environmental concerns and socioeconomic values; and a monitoring program to follow system evolution and responses to management. Consistent with our recent work (Kim et al., 2013; Zhang et al., 2013), we favour a shift in the focus of the Bay of Quinte Remedial Action Plan from coarser resolution metrics (seasonal or spatial averages) to the evaluation of the occurrence frequency of extreme states (i.e., exceedance of maximum allowable nutrient or total phytoplankton biomass levels, toxic algal blooms). Recognizing that it is practically impossible to eliminate these extreme events in the foreseeable future, the comprehensive investigation of the underlying drivers and effective communication of the actual trends to the end-users (stakeholders and public) should be essential steps of the local management efforts. Viewed from this context, the lessons learned from the present analysis are relevant to the water quality criteria setting and modelling process and could influence the management decisions that need to be made in order to delist the system as an Area of Concern.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.hal.2016.02.005.

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DELINEATION OF THE ROLE OF NUTRIENT VARIABILITY AND DREISSENIDS (MOLLUSCA, BIVALVIA) ON PHYTOPLANKTON DYNAMICS IN THE BAY OF QUINTE, ONTARIO, CANADA

(Supporting Information)

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Table S1: Summary statistics for the quantile regression models, $Algal biovolume = \theta_1 \cdot \exp(\theta_2 + \theta_3 \cdot TP) / (1 + \exp(\theta_2 + \theta_3 \cdot TP))$, developed to connect total algal biovolume with monthly average TP concentration (μg L^{-1}) at the intake of the Belleville water treatment plant.

	Coefficient	**t**	**P (>|t|)**
5th quantile			
θ_1	2118	2.26	0.00012
θ_2	-5.36	-11.12	0
θ_3	141.9	3.93	0
25th quantile			
θ_1	3744.6	5.23	0
θ_2	-6.1	-7.67	0
θ_3	199.9	4.70	0
50th quantile			
θ_1	11801.3	3.92	0.00012
θ_2	-4.4	-15.63	0
θ_3	95.0	6.84	0
75th quantile			
θ_1	16211.3	4.87	0
θ_2	-3.9	-11.82	0
θ_3	85.9	5.52	0
95th quantile			
θ_1	26136.1	3.61	0.00037
θ_2	-3.1	-8.63	0
θ_3	65.7	3.49	0.00058

Table S2: Posterior parameter statistics of the hierarchical models developed to predict the relative abundance of total cyanobacteria, *Anabaena*, *Aphanizomenon*, and *Microcystis* at four sampling locations (Belleville, Napanee, Hay Bay, Conway) in the Bay of Quinte. Values in parentheses represent the posterior standard deviations.

	Total cyanobacteria				*Anabaena*				*Aphanizomenon*				*Microcystis*			
	Belleville	Napanee	Hay Bay	Conway	Belleville	Napanee	Hay Bay	Conway	Belleville	Napanee	Hay Bay	Conway	Belleville	Napanee	Hay Bay	Conway
β_{TP}	0.100 (0.031)	0.196 (0.042)	0.254 (0.068)	0.067 (0.053)	0.034 (0.023)	0.048 (0.031)	0.091 (0.051)	-0.021 (0.04)	0.032 (0.015)	0.023 (0.02)	0.092 (0.033)	0.011 (0.026)	0.076 (0.02)	0.148 (0.027)	0.17 (0.044)	0.083 (0.034)
β_{NH_4}	0.050 (0.016)	0.003 (0.031)	-0.010 (0.041)	-0.003 (0.034)	0.02 (0.012)	-0.001 (0.023)	-0.006 (0.03)	0.000 (0.025)	0.02 (0.007)	-0.012 (0.015)	-0.007 (0.019)	0.002 (0.016)	0.007 (0.01)	-0.03 (0.02)	-0.04 (0.026)	-0.012 (0.021)
$\beta_{K_{ext}}$	0.051 (0.026)	-0.089 (0.049)	0.009 (0.075)	-0.043 (0.062)	0.054 (0.019)	-0.013 (0.036)	0.08 (0.056)	0.02 (0.047)	0.04 (0.012)	0.037 (0.023)	0.059 (0.036)	0.000 (0.03)	-0.012 (0.017)	-0.056 (0.031)	-0.113 (0.049)	-0.078 (0.04)
β_{temp}	0.021(0.003)				0.183 (0.479)				0.002 (0.001)				0.008 (0.002)			
$\beta 0_g$	0.314(0.472)				0.035 (0.133)				0.088 (0.483)				0.086 (0.473)			
β_{TP_g}	0.148(0.148)				0.002 (0.132)				0.036 (0.128)				0.115 (0.132)			
$\beta_{NH_{4g}}$	0.008(0.135)				0.036 (0.133)				-0.001 (0.132)				-0.021 (0.133)			
$\beta_{K_{ext_g}}$	-0.016(0.142)				0.183 (0.479)				0.034 (0.128)				-0.063 (0.134)			
$\beta 0_1$	0.394(0.030)				0.254 (0.022)				0.151 (0.014)				0.046 (0.019)			
$\beta 0_2$	0.293(0.017)				0.149 (0.013)				0.046 (0.008)				0.148 (0.011)			
$g\sigma_{TP}$	5.997 (310.9)	1.119 (7.702)	2.262 (58.87)	1.163 (9.745)	5.141 (262.8)	1.047 (7.098)	1.845 (41.1)	1.092 (9.589)	5.366 (280)	1.041 (6.979)	1.753 (35.77)	1.05 (9.762)	5.994 (317.8)	1.065 (7.418)	1.816 (39.42)	1.065 (9.625)
$g\sigma_{NH_4}$	1.624 (23.74)	1.181 (17.32)	1.109 (7.200)	1.146 (13.61)	1.589 (22.98)	1.179 (17.85)	1.083 (6.814)	1.148 (14.48)	1.584 (22.98)	1.171 (17.46)	1.072 (6.616)	1.154 (15.12)	1.592 (23.11)	1.169 (17.15)	1.09 (6.954)	1.156 (15.21)
$g\sigma_{K_{ext}}$	1.516 (16.03)	1.146 (12.26)	1.178 (6.385)	1.204 (10.39)	1.389 (14.29)	1.066 (11.19)	1.166 (6.396)	1.154 (9.782)	1.328 (13.08)	0.986 (9.736)	1.124 (6.256)	1.138 (9.356)	1.409 (14.24)	1.002 (9.698)	1.16 (6.579)	1.151 (9.671)
$g\sigma 0_1$	2.175(17.05)				2.14 (16.95)				2.125 (16.98)				2.166 (17.56)			
$g\sigma 0_2$	1.816(14.81)				1.805 (14.76)				1.786 (14.31)				1.897 (19.51)			
$\mu 0$	0.193 (0.657)				0.112 (0.647)				0.053 (0.645)				0.055 (0.64)			
μ_{TP}	0.097 (0.626)				0.024 (0.623)				0.025 (0.622)				0.076 (0.623)			
μ_{NH_4}	-0.018 (0.598)				-0.022 (0.598)				-0.024 (0.598)				-0.036 (0.597)			
$\mu_{K_{ext}}$	-0.009 (0.600)				0.025 (0.598)				0.024 (0.597)				-0.039 (0.599)			
σ	0.224(0.009)				0.166 (0.006)				0.105 (0.004)				0.142 (0.006)			
$\sigma 0$	2.836(41.93)				2.672 (34.3)				2.58 (28.95)				2.535 (26.03)			
σ_{TP}	2.115(11.29)				2.114 (10.94)				2.117 (11.02)				2.11 (10.99)			
σ_{NH_4}	2.934(25.62)				2.93 (25.6)				2.928 (25.59)				2.933 (25.64)			
$\sigma_{K_{ext}}$	2.936(32.20)				2.918 (30.91)				2.917 (30.83)				2.96 (33.13)			

Table S3: Classification scheme used to characterize the relative importance of different abiotic factors on the relative abundance of total cyanobacteria, *Anabaena* spp., *Aphanizomenon* spp., and *Microcystis* spp. at four sampling locations (Belleville, Napanee, Hay Bay, Conway) in the Bay of Quinte.

Symbol	β_0	β_{TP}	β_{NH_4}	β_{Kext}	β_{temp}
⇧	$\beta_0 \geq 0.3$	$\beta_{TP} \geq 0.20$	$\beta_{NH_4} \geq 0.05$	$\beta_{Kext} \geq 0.1$	$\beta_{temp} \geq 0.15$
⇧	$0.2 \leq \beta_0 < 0.3$	$0.15 < \beta_{TP} < 0.20$	$0.03 \leq \beta_{NH_4} < 0.05$	$0.07 \leq \beta_{Kext} < 0.1$	$0.1 \leq \beta_{temp} < 0.15$
⇧	$0.1 \leq \beta_0 < 0.2$	$0.10 \leq \beta_{TP} < 0.15$	$0.01 \leq \beta_{NH_4} < 0.03$	$0.04 \leq \beta_{Kext} < 0.07$	$0.05 \leq \beta_{temp} < 0.1$
⇧	$0.05 \leq \beta_0 < 0.1$	$0.05 \leq \beta_{TP} < 0.10$	$0.005 \leq \beta_{NH_4} < 0.01$	$0.01 \leq \beta_{Kext} < 0.04$	$0.01 \leq \beta_{temp} < 0.05$
⇧	$\beta_0 < 0.05$	$\beta_{TP} < 0.05$	$\beta_{NH_4} < 0.005$	$\beta_{Kext} < 0.01$	$\beta_{temp} < 0.01$

FIGURES LEGENDS

Figure S1: Temporal trends of (a) total phosphorous (TP, µg L^{-1}), (b) reduced inorganic nitrogen (NH_4-NH_3, µg L^{-1}), (c) soluble reactive phosphorus (SRP, µg L^{-1}), (d) oxidized inorganic nitrogen (NO_3-NO_2, µg L^{-1}), (e) dissolved inorganic nitrogen**:**soluble reactive phosphorus (DIN:SRP), (f) light attenuation coefficient (m^{-1}), (g) dissolved oxygen (mg L^{-1}), and (h) surface water temperature (°C) in the four sampling locations during the study period.

Figure S2: Box plots of the pre- and post-dreissenid invasion periods for (a) total phosphorous (TP), (b) soluble reactive phosphorus (SRP), (*c*) reduced inorganic nitrogen (NH_4-NH_3), (d) oxidized inorganic nitrogen (NO_3-NO_2) (units are all in µg L^{-1}), and (e) time series of the SRP:TP ratioat the intake of the Belleville Water Treatment Plant.

Figure S3: Scatter plots of cyanobacteria biomass against light attenuation (m^{-1}) in the Bay of Quinte. (*a,b*) Total cyanobacteria, (c,d) *Anabaena*, (e,f) *Aphanizomenon*, and (g,h) *Microcystis.* Left and right panels represent the pre- and post-dreissenid invasion periods, respectively. The solid lines represent LOWESS (locally weighted scatter plot smoothing) fit.

Figure S4: Scatter plots of cyanobacteria biomass against NH_4 concentrations (µg L^{-1}) in the Bay of Quinte. (a,b) Total cyanobacteria, (c,d) *Anabaena*, (e,f) *Aphanizomenon*, and (g,h) *Microcystis.* Left and right panels represent the pre- and post-dreissenid invasion periods, respectively. The solid lines represent LOWESS (locally weighted scatter plot smoothing) fit.

Figure S5: Scatter plots of cyanobacteria biomass against the oxidized form of inorganic nitrogen (NO_3-NO_2) concentrations in the Bay of Quinte. (a,b) Total cyanobacteria, (c,d) *Anabaena*, (e,f) *Aphanizomenon*, and (g,h) *Microcystis.* Left and right panels represent the pre- and post-dreissenid invasion periods, respectively. The solid lines represent LOWESS (locally weighted scatter plot smoothing) fit.

Figure S6: Scatter plots of cyanobacteria biomass against surface water temperature (^{o}C) in the Bay of Quinte. (a,b) Total cyanobacteria, (c,d) *Anabaena*, (e,f) *Aphanizomenon*, and (g,h) *Microcystis*. Left and right panels represent the pre- and post-dreissenid invasion periods, respectively. The solid lines represent LOWESS (locally weighted scatter plot smoothing) fit.

Figure S7: Relationship between the diversity index (Gleason's D) and three abiotic factors (top panels: surface water temperature, middle panels: total phosphorous, and low panels: light attenuation coefficient) in four sampling stations: (a) Belleville, (b) Napanee, (c) Hay Bay, and (d) Conway. The solid lines represent LOWESS (locally weighted scatter plot smoothing) fit.

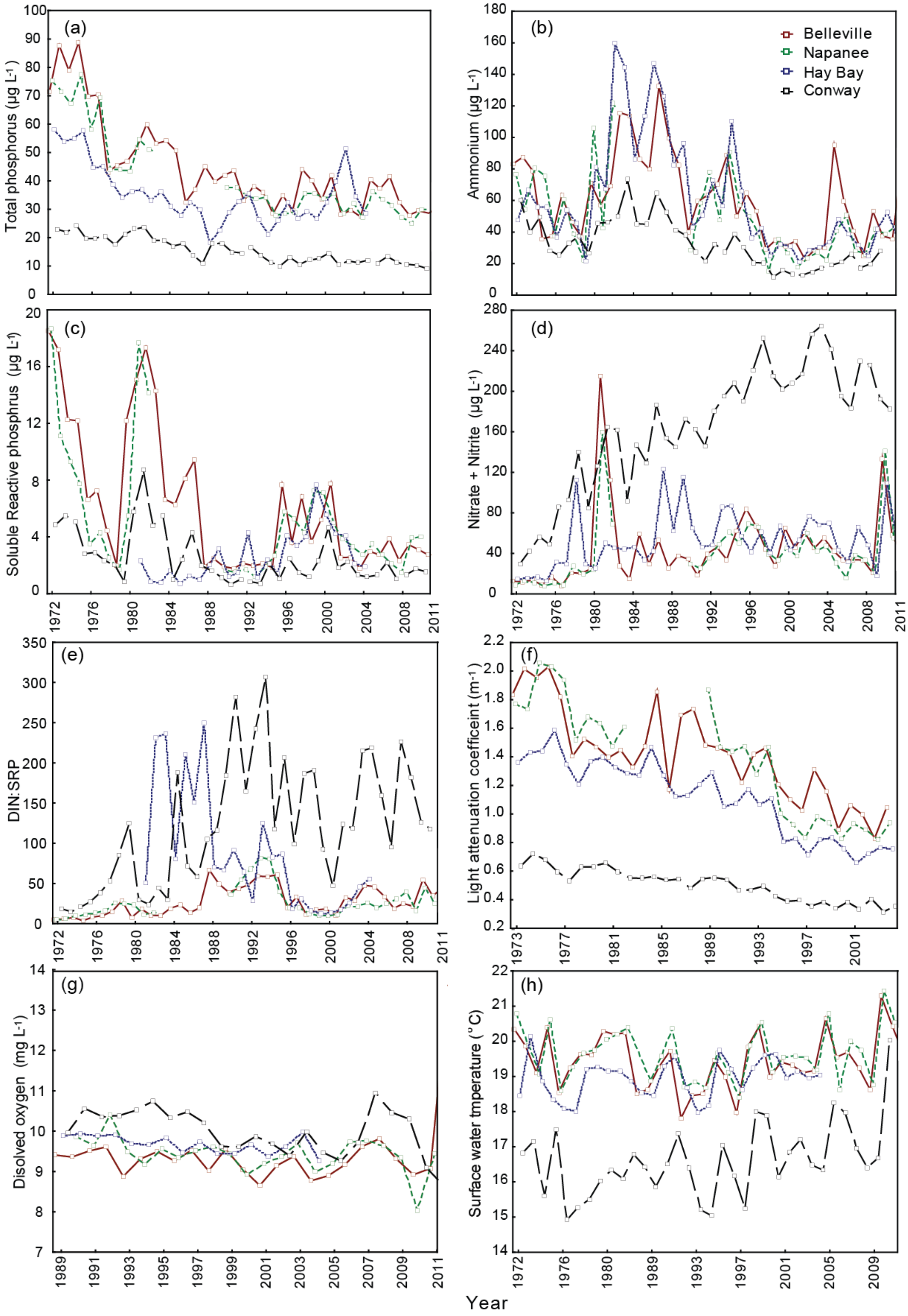

(a)
Total phosphorus (µg L-1)
0
10
20
30
40
50
60
70
80
90
100
(b)
Ammonium (µg L-1)
0
20
40
60
80
100
120
140
160
180
Belleville
Napanee
Hay Bay
Conway
(c)
Soluble Reactive phosphrus (µg L-1)
0
4
8
12
16
20
1972
1976
1980
1984
1988
1992
1996
2000
2004
2008
2011
(d)
Nitrate + Nitrite (µg L-1)
0
40
80
120
160
200
240
280
1972
1976
1980
1984
1988
1992
1996
2000
2004
2008
2011
(e)
DIN:SRP
0
50
100
150
200
250
300
350
1972
1976
1980
1984
1988
1992
1996
2000
2004
2008
2011
(f)
Light attenuation coefficeint (m-1)
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
1973
1977
1981
1985
1989
1993
1997
2001
(g)
Disolved oxygen (mg L-1)
7
8
9
10
11
12
13
14
1989
1991
1993
1995
1997
1999
2001
2003
2005
2007
2009
2011
(h)
Surface water tmperature (°C)
14
15
16
17
18
19
20
21
22
1972
1976
1980
1989
1993
1997
2001
2005
2009
Year

Figure S1

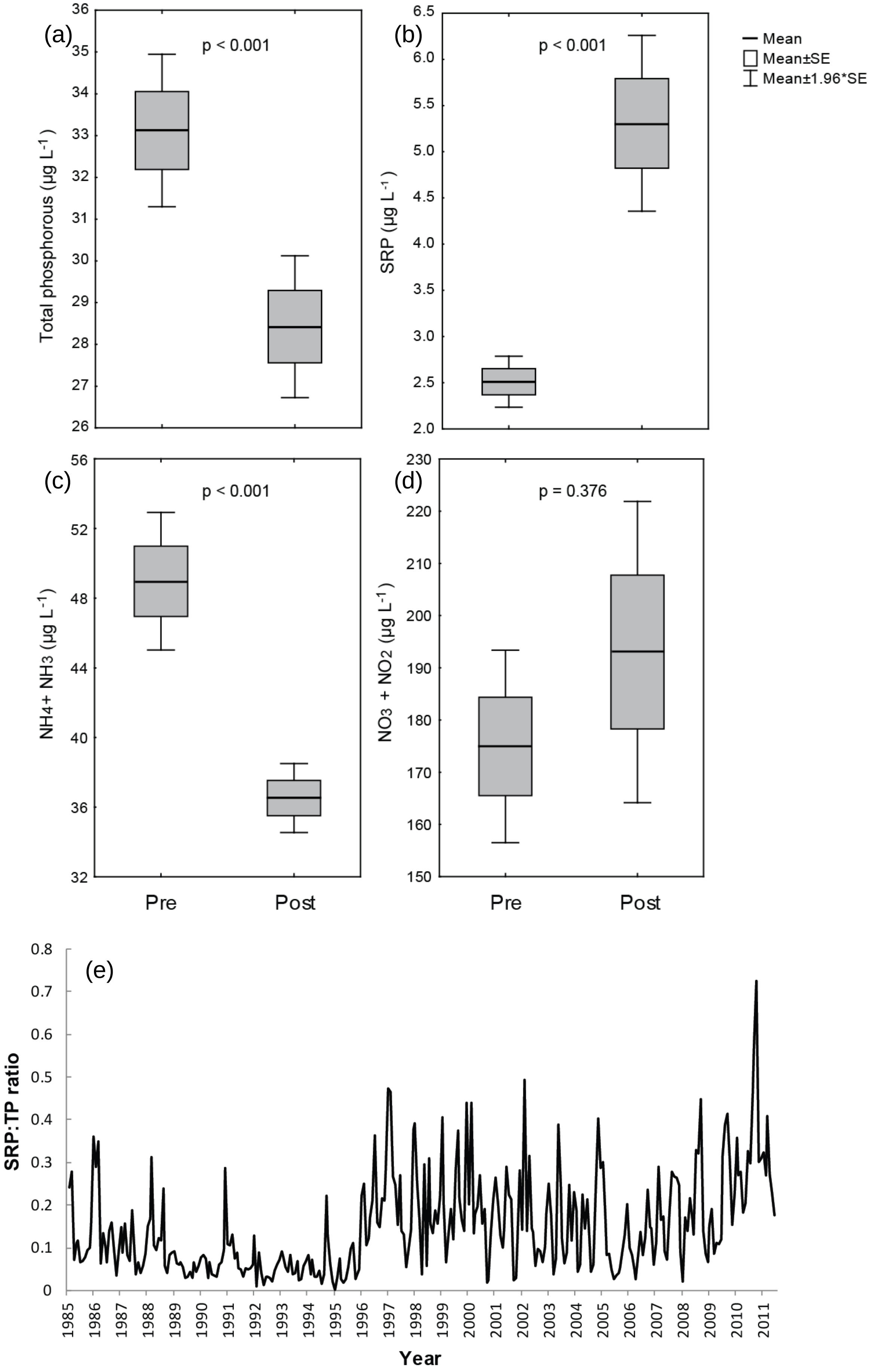

(a)
p < 0.001
Total phosphorous (µg L-1)
36
35
34
33
32
31
30
29
28
27
26
(b)
p < 0.001
SRP (µg L-1)
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
Mean
Mean±SE
Mean±1.96*SE
(c)
p < 0.001
NH4+ NH3 (µg L-1)
56
52
48
44
40
36
32
Pre
Post
(d)
p = 0.376
NO3 + NO2 (µg L-1)
230
220
210
200
190
180
170
160
150
Pre
Post
(e)
SRP:TP ratio
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1985
1986
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
Year

Figure S2

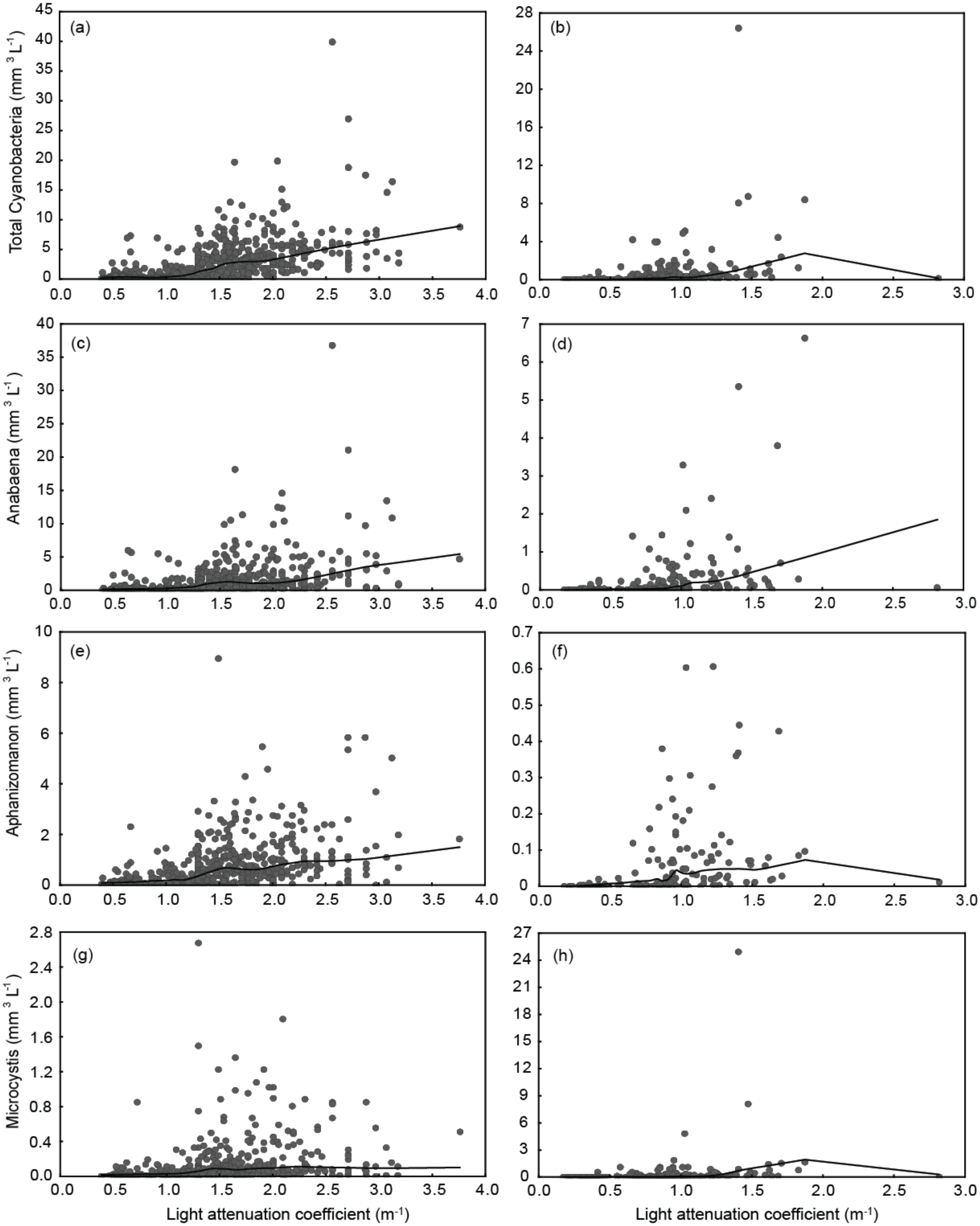

(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Total Cyanobacteria (mm ^{3} L^{-1})
Anabaena (mm ^{3} L^{-1})
Aphanizomanon (mm ^{3} L^{-1})
Microcystis (mm ^{3} L^{-1})
0 5 10 15 20 25 30 35 40 45
0 4 8 12 16 20 24 28
0 5 10 15 20 25 30 35 40
0 1 2 3 4 5 6 7
0 2 4 6 8 10
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7
0.0 0.4 0.8 1.2 1.6 2.0 2.4 2.8
0 3 6 9 12 15 18 21 24 27
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
0.0 0.5 1.0 1.5 2.0 2.5 3.0
Light attenuation coefficient (m^{-1})
Light attenuation coefficient (m^{-1})

Figure S3

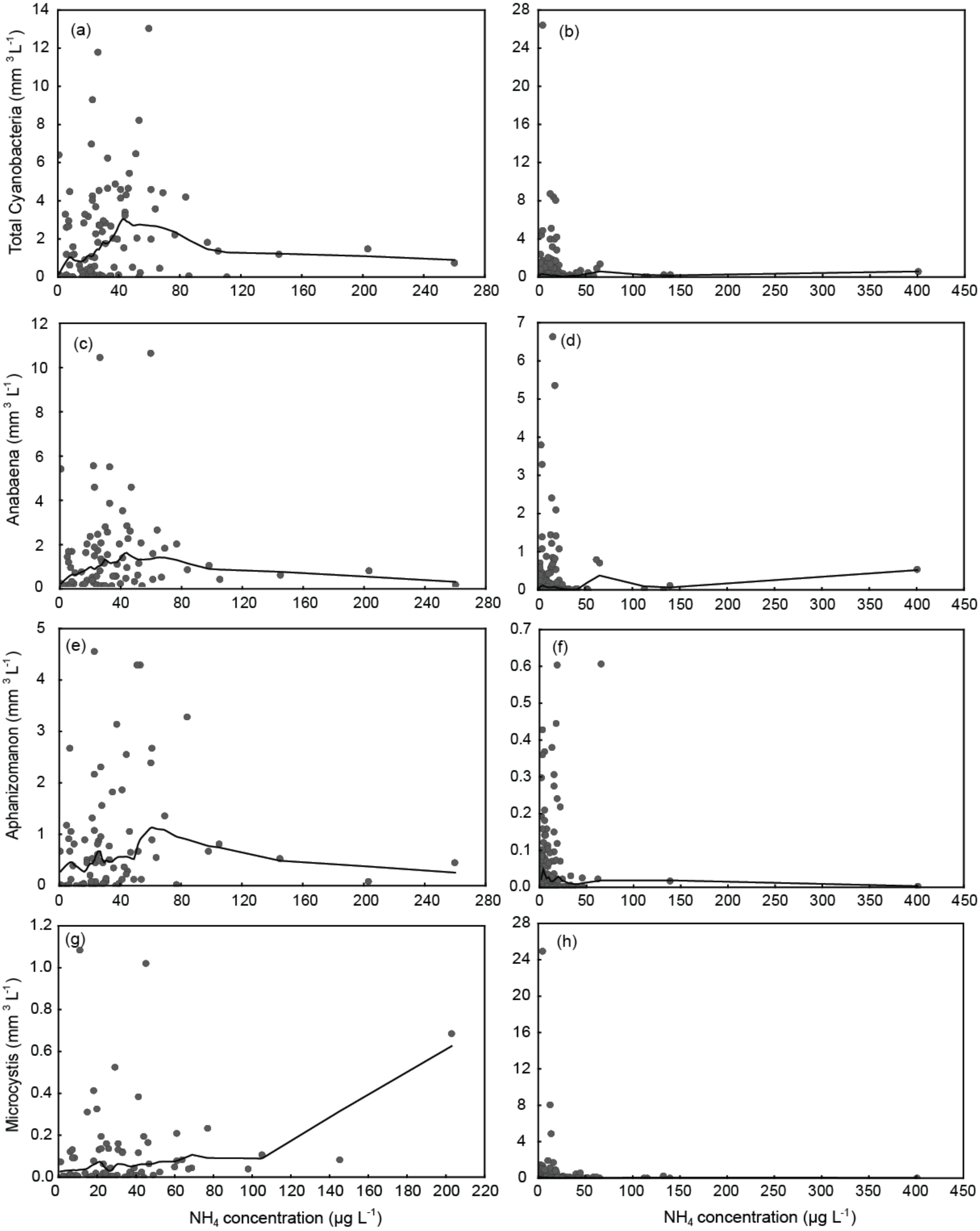

(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Total Cyanobacteria (mm 3 L-1)
Anabaena (mm 3 L-1)
Aphanizomanon (mm 3 L-1)
Microcystis (mm 3 L-1)
0 2 4 6 8 10 12 14
0 4 8 12 16 20 24 28
0 2 4 6 8 10 12
0 1 2 3 4 5 6 7
0 1 2 3 4 5
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7
0.0 0.2 0.4 0.6 0.8 1.0 1.2
0 4 8 12 16 20 24 28
0 40 80 120 160 200 240 280
0 50 100 150 200 250 300 350 400 450
0 20 40 60 80 100 120 140 160 180 200 220
NH4 concentration (µg L-1)
NH4 concentration (µg L-1)

Figure S4

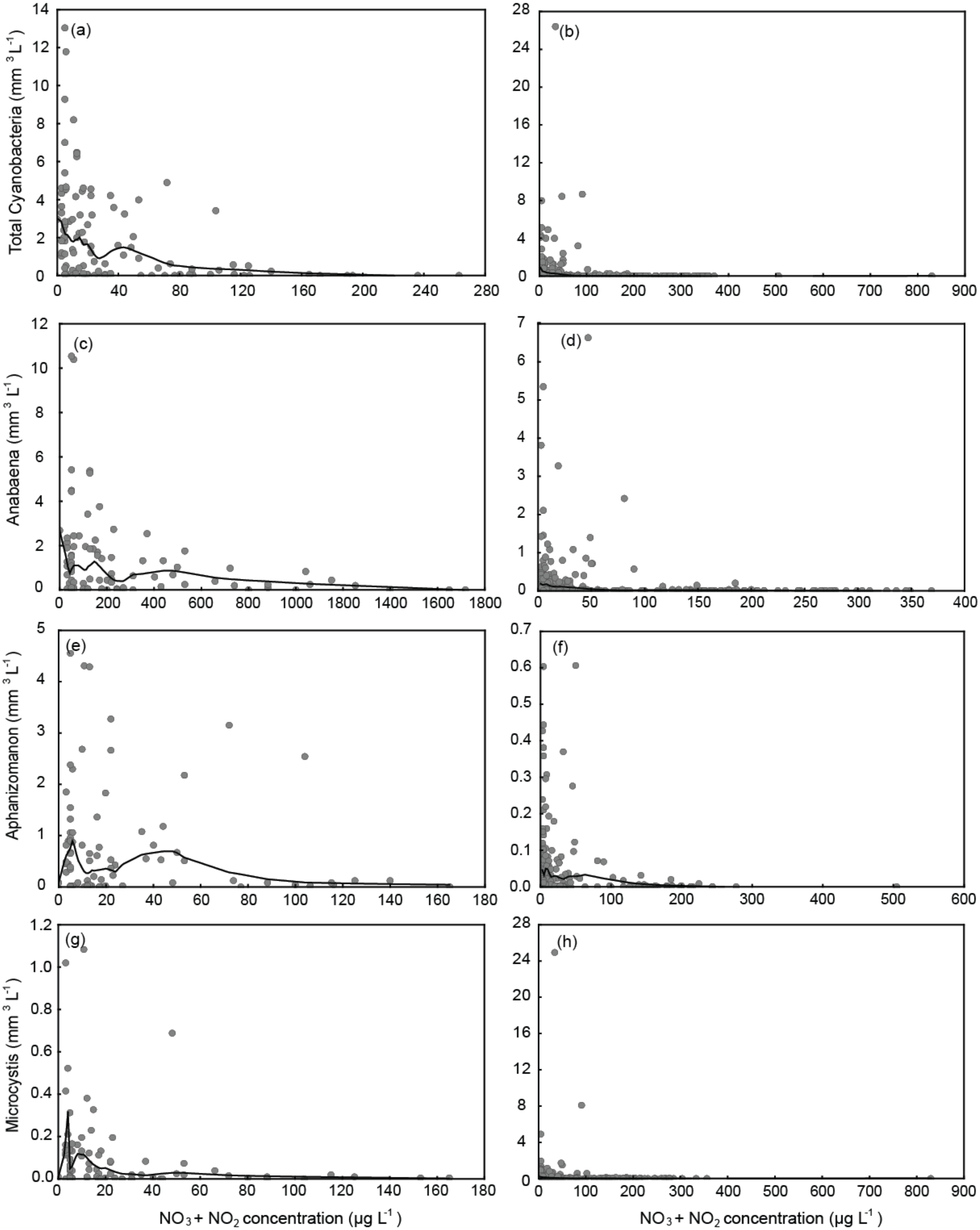
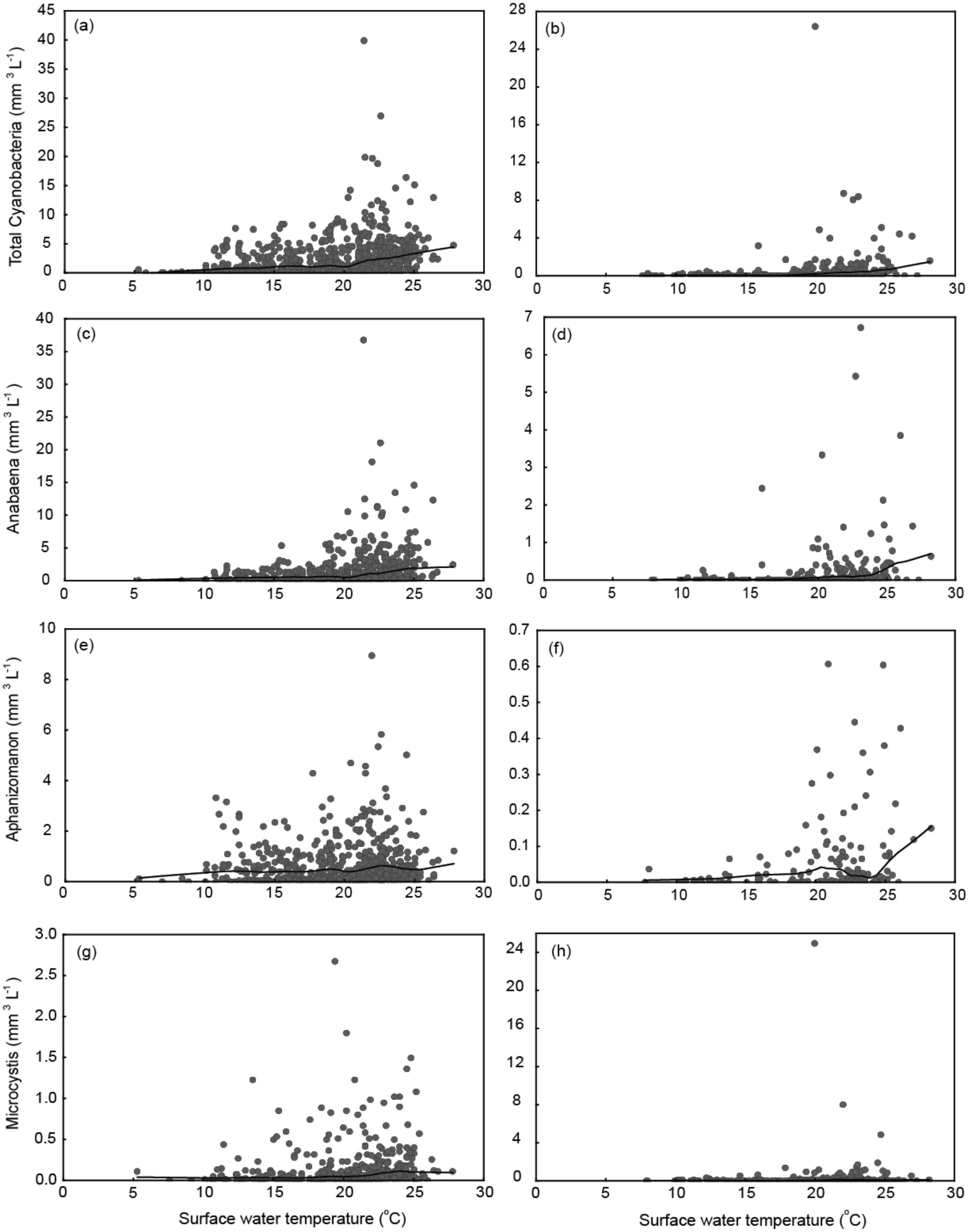

Total Cyanobacteria (mm 3 L-1)
Anabaena (mm 3 L-1)
Aphanizomanon (mm 3 L-1)
Microcystis (mm 3 L-1)
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
NO3 + NO2 concentration (µg L-1)
NO3 + NO2 concentration (µg L-1)

Figure S5



(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Total Cyanobacteria (mm^3 L^{-1})
Anabaena (mm^3 L^{-1})
Aphanizomanon (mm^3 L^{-1})
Microcystis (mm^3 L^{-1})
Surface water temperature (°C)
Surface water temperature (°C)
0
5
10
15
20
25
30
35
40
45
28
24
20
16
12
8
4
7
6
3
2
1
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
3.0
2.5
2.0
1.5
1.0

Figure S6

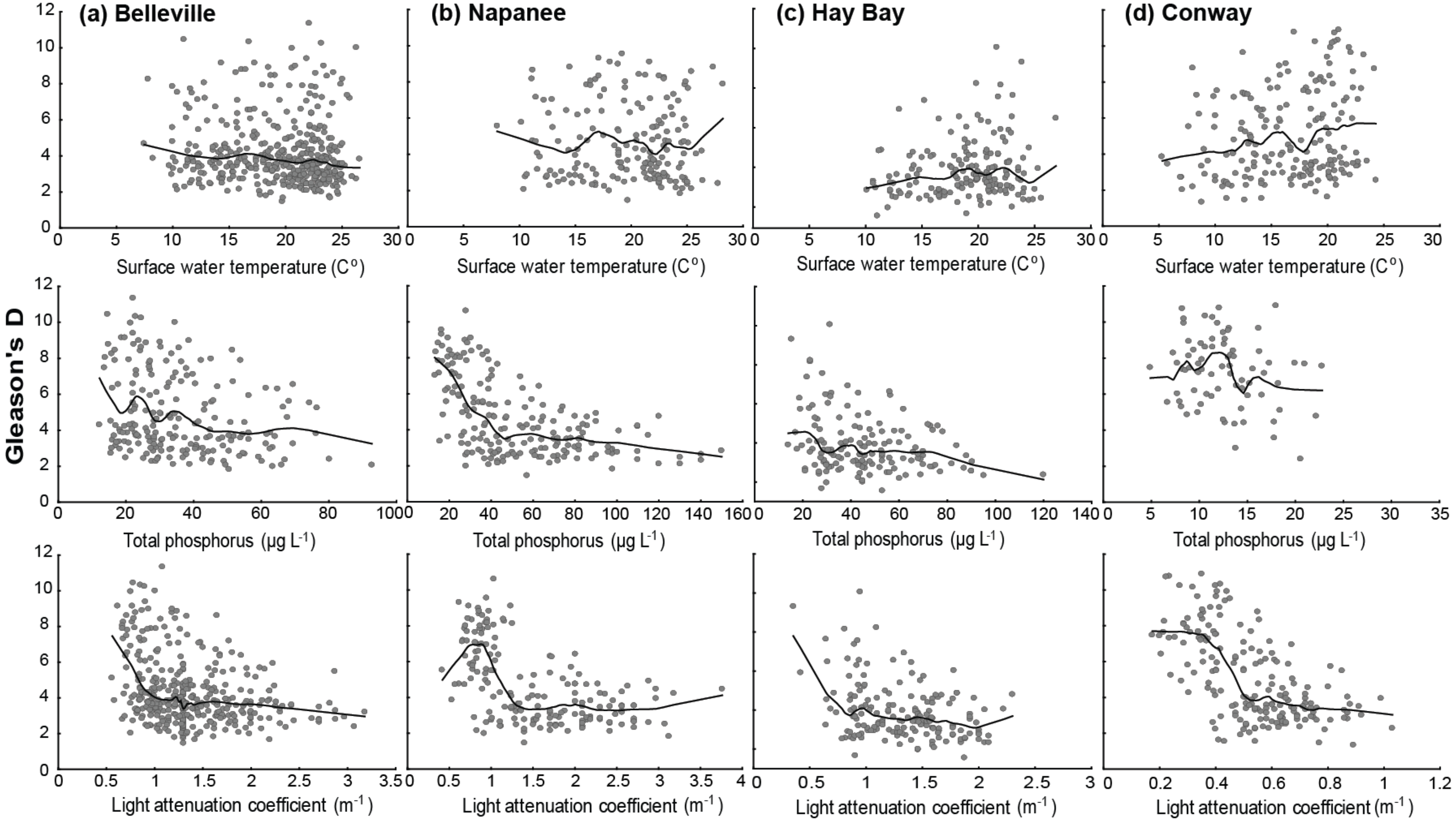

(a) Belleville
(b) Napanee
(c) Hay Bay
(d) Conway
Gleason's D
Surface water temperature (C°)
Total phosphorus (μg L-1)
Light attenuation coefficient (m-1)
0
2
4
6
8
10
12

Figure S7