Harmful Algae 55 (2016) 121–136

Contents lists available at ScienceDirect

Harmful Algae

journal homepage: www.elsevier.com/locate/hal

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

Yuko Shimoda [a], Sue B. Watson [b], Michelle E. Palmer [c], Marten A. Koops [d], Shan Mugalingam [e], Andrew Morley [f], George B. Arhonditsis [a,*]

[a] Ecological Modelling Laboratory, Department of Physical & Environmental Sciences, University of Toronto, Toronto, ON M1C 1A4, Canada
[b] Environment Canada, Canada Centre for Inland Waters, Burlington, ON L7R 4A6, Canada
[c] Ontario Ministry of the Environment& Climate Change, Environmental Monitoring and Reporting Branch, Toronto, ON M9P 3V6, Canada
[d] Department of Fisheries & Oceans, Burlington, ON L7S 1A1, Canada
[e] Lower Trent Conservation, Trenton, ON K8 V 5P4, Canada
[f] Kingston Regional Office, Ontario Ministry of the Environment& Climate Change, Kingston, ON, K7 M 8S5, Canada

ARTICLE INFO

Article history:
Received 5 September 2015
Received in revised form 5 February 2016
Accepted 5 February 2016
Available online 19 March 2016

Keywords:
Bayesian hierarchical modelling
Phosphorus loading
Dreissenid mussels
Phytoplankton patterns
Areas of concern

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

* Corresponding author. Tel.: +1 416 208 4858; fax: +1 416 287 7279.
E-mail address: georgea@utsc.utoronto.ca (G.B. Arhonditsis).

http://dx.doi.org/10.1016/j.hal.2016.02.005
1568-9883/

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