

INVESTIGATING LAKE ONTARIO'S LOWER FOOD WEB: SPATIAL VARIATION AND
TEMPORAL TRENDS IN WATER CLARITY, PHOSPHORUS, SILICA,
CHLOROPHYLL-A AND ZOOPLANKTON

A Thesis

Presented to the Faculty of the Graduate School
of Cornell University

In Partial Fulfillment of the Requirements for the Degree of
Master of Science

by

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August 2016

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Changes in lower food web parameters indicate that Lake Ontario moved from a state of mesotrophy to oligotrophy since 1970. Spring total phosphorus (TP), summer chlorophyll-*a* (chl-*a*), and zooplankton density and biomass have declined, and the ability of the lake to support a recreational fishery could be compromised if these declines continue. We used Secchi depth transparency, TP, soluble reactive phosphorus, silica, chl-*a*, and zooplankton data from spatially-intensive sampling programs in 2003 and 2008 to test for differences between habitats (nearshore vs offshore) and regions (east vs west) in 2003, to test for differences between years (2003 vs 2008), and to compare 2003 and 2008 with long-term data (1970 – 2011) to test the hypothesis that oligotrophication of Lake Ontario's offshore waters has continued. Results show no spatial differences in key indicators (spring TP, summer chl-*a*) in 2003, higher values in 2008 compared to 2003, and no trend in long-term data since the mid to late 1990s. Oligotrophication has not continued in Lake Ontario in the 2000s.

BIOGRAPHICAL SKETCH

Kristen T. Holeck was born in Syracuse, New York in 1970. She graduated from Cicero-North Syracuse High School in 1988, received an A.A.S. degree from SUNY Morrisville in 1993, and a B.S. from Cornell University in 1995. Upon graduating from Cornell, she began working for the Cornell Biological Field Station in Bridgeport, New York as a chemistry technician studying Oneida Lake and Lake Ontario. Her involvement in multiple projects on nonindigenous species in the Great Lakes and the lower food web of Lake Ontario prompted her to apply to graduate school through the employee degree program in 2006. She remains employed at the field station to this day.

In memory of my mother, Lois E. Obrist

ACKNOWLEDGEMENTS

I would like to thank my undergraduate advisor at Cornell, Aaron Moen, for fostering a sense of responsibility for my own learning. Memorable quotes from include, “there are no easy answers to complex problems”, and “every day is a test”. Ed Mills and Lars Rudstam, past and present directors of the Cornell Field Station and my supervisors, provided multiple diverse opportunities for advancing my knowledge and experience in aquatic ecosystems and encouragement to complete my graduate degree. Because of their generosity I have participated in co-authoring numerous book chapters, reports, and peer-reviewed publications. Thank you to all my collaborators and co-authors from across the years; there are too many to list. Special thanks to Jana Lantry (Chrisman) for making my first two years at the field station memorable and to all past and current coworkers for making every day more colorful. The papers that appear as chapters in this thesis could not have been possible without bi-national cooperation of and funding from multiple agencies in the United States (EPA, USGS, USFWS, NYSDEC) and Canada (EC, DFO, OMNR).

TABLE OF CONTENTS

Biographical Sketch.....	iii
Dedication.....	iv
Acknowledgements.....	v
Preface.....	viii
Chapter 1. Spatial and long-term temporal assessment of Lake Ontario water clarity, nutrients, chlorophyll <i>a</i> and zooplankton	
Abstract.....	1
Introduction.....	1
Methods.....	2
Results.....	5
Discussion.....	8
Conclusions.....	13
Acknowledgements.....	13
References.....	13

Chapter 2. Lake Ontario water quality during the 2003 and 2008 intensive field years
and comparison with long-term trends

Abstract.....	16
Introduction.....	17
Materials and Methods.....	17
Laboratory Analysis.....	18
Data Analysis.....	19
Results.....	19
Discussion.....	23
Conclusions.....	24
Acknowledgements.....	24
Funding.....	25
References.....	26

PREFACE

The Lake Ontario ecosystem has been reshaped during the last 50 years by socio-political influences and the introduction (both intentional and unintentional) of nonindigenous species (Mills et al. 2003; Holeck and Mills 2004). Pacific salmon were stocked in the 1960s to reduce nuisance levels of alewife and to provide recreational fishing opportunities (Owens et al. 2003). Degraded water quality and nuisance algal growth prompted the 1970s signing of the Great Lakes Water Quality Agreement between the United States and Canada which aimed to reduce phosphorus inputs to all the Great Lakes (IJC 1988). During the 1980s and 1990s, several nonindigenous species were unintentionally introduced via the ballast water of transoceanic ships (Holeck et al. 2004). The spiny waterflea (*Bythotrephes longimanus*; 1985), zebra mussel (*Dreissena polymorpha*; 1989), quagga mussel (*Dreissena rostriformis bugensis*; 1991), and fishhook waterflea (*Cercopagis pengoi*; 1998) have all become established in Lake Ontario (Lange and Cap 1986, Mills et al. 2003). These events have permanently altered the structure and function of the Lake Ontario food web.

Food web changes in Lake Ontario have had both positive and negative consequences. Pacific salmon have flourished and play a critical role in sustaining a multi-million dollar recreational fishery supported primarily by two other nonindigenous fish species, alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*). Stocking of salmonids was so successful that fishery managers shifted from a strategy aimed at controlling nuisance levels of alewife to concern about whether the salmon fishery could be sustained with a declining alewife population. Mandated phosphorus reductions were

also a success. With declining phosphorus loadings, Lake Ontario's water quality improved and nuisance *Cladophora* blooms were reduced. However, phytoplankton and zooplankton levels also declined, decreasing the lake's capacity to support fish. The filter-feeding zebra and quagga mussel also contributed to decreased levels of phytoplankton and zooplankton, while the nonindigenous waterfleas fed on native zooplankton, thereby competing with zooplanktivorous fish like alewife. Mills et al. (2003) hypothesized that although oligotrophication drove the recovery process of the Lake Ontario ecosystem, the lake would not return to historic conditions due to the presence of these nonindigenous species.

Oligotrophication has led to competing concerns regarding Lake Ontario's productivity. First, there is a question about the ability of the lake to support current alewife production in the offshore due to declining nutrient levels and zooplankton biomass. At the same time, high nutrient levels close to shore are contributing to a resurgence of attached algae (e.g., *Cladophora*) in some shoreline and beach areas (Makarewicz and Howell 2007; Kuczyinski et al. 2016). The collapse of the alewife population and the decline in the Chinook salmon fishery in Lake Huron in 2003 may have been due to declines in lower trophic levels (Barbiero et al. 2011, Bunnell et al. 2012). Alewives had not returned to Lake Huron as of 2014 (Gorman and Weidel 2015), and concerns of a similar crash in Lake Michigan led to a decision to decrease Chinook stocking rates in that lake (Lake Michigan Committee 2016). Continued oligotrophication of Lake Ontario could compromise the lake's ability to support a recreational salmonid fishery.

This thesis contains two chapters that assess the condition of the Lake Ontario lower food web by examining status of and trends in lower food web indicators. Chapter 1 uses Secchi depth, total phosphorus, soluble reactive phosphorus, silica, chlorophyll-*a* and zooplankton (density, biomass, and mean length) to spatially characterize the lower food web. It evaluates differences between habitats (nearshore vs offshore) and regions (east vs west) across three seasons (spring, summer, and fall) during 2003. Spatial characterization is important prior to evaluation of temporal trends because it allows for visualization of differences that might otherwise be obscured by the analysis of lake-wide means. Chapter 2 uses a subset of Chapter 1 indicators (Secchi depth, total phosphorus, silica, and chlorophyll-*a*) to compare data collected in 2003 with data from a similar, spatially-intensive sampling effort in 2008 and uses additional long-term data collected by multiple agencies in the United States and Canada to test the hypothesis that oligotrophication has continued in Lake Ontario into the 2000s.

Few spatial differences of selected food web indicators were observed in Lake Ontario in 2003. For habitat comparisons (nearshore vs offshore), nearshore silica and offshore chlorophyll-*a* were both higher in fall. For regional comparisons (east vs west) Secchi depth and zooplankton mean length were both higher in the east during spring and total phosphorus was higher in the west during summer. Results from 2003 show a general lack of expected differences (e.g., higher spring total phosphorus nearshore, higher Secchi depth offshore) between nearshore and offshore habitats. Comparisons of the two lake-wide surveys showed that 2008 had higher spring total phosphorus, spring silica, spring Secchi disk transparency, and summer chlorophyll-*a* concentrations

compared with 2003. Long-term data indicate change points in Secchi depth, total phosphorus, chlorophyll-a, spring silica, and silica utilization in the mid- to late 1990s, and no significant changes since. Results indicate that oligotrophication of the offshore waters of Lake Ontario has not continued into the 2000s.

Despite the stability of lower trophic levels observed from the mid- to late 1990s through 2010-11, further oligotrophication of Lake Ontario's offshore is possible. Recent analyses show a gradual decline in total phosphorus 1980 – 2013 (Dove and Chapra 2015) and below average total phosphorus values in 2014 – 2015 compared to 1996 – 2013 (Holeck et al. 2015, 2016). Offshore summer chlorophyll-a declined significantly 2005 – 2015 (Holeck et al. 2016), and similar declines were observed in Environment Canada and United States Environmental Protection Agency data since 2005 (Dove and Chapra 2015; Rudstam et al. 2016). Continued lower productivity could impact fisheries. Kao et al. (2016) found that lower nutrient levels and the expansion of quagga mussels were largely responsible for the alewife crash in Lake Huron in 2003, and warned that similar signs were evident in both Lake Michigan and Lake Ontario. Lake Michigan alewife declined sharply in 2014 (Bunnell et al. 2015; Warner et al. 2015), but it is yet unknown whether an alewife “crash” has occurred there as in Lake Huron. In Lake Ontario, alewife year classes were poor 2013 – 2014, but the adult population remained relatively stable (Walsh et al. 2016). If lower phosphorus and chlorophyll levels persist, Lake Ontario's alewife population could decline.

The combined effect of reduced nutrient inputs and introduction of nonindigenous species on alewife in Lake Michigan and Lake Huron is not evident in Lake Ontario, possibly because fish food sources have not declined there. Despite declines in total phosphorus and chlorophyll-*a*, summer offshore epilimnetic zooplankton density and biomass increased 2005 – 2015, and in 2015 biomass was two to four times levels observed since 2005 (Holeck et al. 2016). Also, zooplankton biomass can concentrate in the deep chlorophyll layer near the base of the thermocline. Rudstam et al. (2015) found that, in 2008, most of the Lake Ontario's daytime zooplankton biomass occurred at or below the thermocline. This was also the case in 2015; over 60% of the July zooplankton biomass occurred in the metalimnion while the epilimnion accounted for just 12% (Holeck et al. 2016). The distribution of zooplankton in colder waters should benefit rainbow smelt and cisco more than alewife, but it is possible that alewife still receive some benefit from foraging in this layer. Finally, Lake Ontario alewife are consuming more *Mysis* (Stewart et al. 2010), and the *Mysis* population has been stable during the past decade (Rudstam et al. 2016). Lake Ontario's alewife population remains stable, but the contradictory patterns observed in lower trophic level parameters warrant caution.

Continued monitoring and new research on Lake Ontario's lower food web are needed to ensure that appropriate management actions can be undertaken to maintain ecosystem health and sustain the recreational fishery. First, continuation of long-term monitoring programs is key. Results presented here could not have been possible without data provided by monitoring programs conducted by multiple agencies in the

United States and Canada. The Environment Canada Surveillance Program (1970 – 2015), Department of Fisheries and Oceans Bioindex Program (1981 – 1995), New York State Department of Environmental Conservation Biomonitoring Program (1995 – 2015), and United States Environmental Protection Agency Great Lakes Monitoring Program (1986 – 2015) all perform annual monitoring at differing spatial scales on Lake Ontario. In addition, periodic intensive spatial surveys performed with binational cooperation between the United States and Canada provide much needed information on the differences present (or absent) in lower food web parameters on a horizontal scale (e.g., nearshore vs offshore, east vs west). However, periodic intensive spatial surveys should not overlook the importance of measuring variability in the vertical component of lower food web parameters. Detection of the redistribution of zooplankton from the epilimnion to the metalimnion is just one example of the value in sampling the vertical spatial component, and variability in the vertical component of other parameters such as chlorophyll and nutrients is of interest and importance as well. Finally, nutrient loadings should be measured at major points of input. Input from Lake Erie via the Niagara River accounts for 30% of Lake Ontario's annual phosphorus load (Chapra and Dolan 2012), and a new annex to the Great Lakes Water Quality Agreement aimed at reducing phosphorus loads to the western and central basins of Lake Erie by 40% could fuel further oligotrophication in Lake Ontario. Maintenance of long-term monitoring programs combined with sampling of areas and parameters that have either been overlooked (e.g. metalimnetic zooplankton) or that have not been re-measured in decades (phosphorus loading) will provide managers with the tools they need to make informed decisions regarding the future of the Lake Ontario ecosystem.

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Spatial and long-term temporal assessment of Lake Ontario water clarity, nutrients, chlorophyll *a*, and zooplankton

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*Secchi depth, total phosphorus, soluble reactive phosphorus, silica, chlorophyll a, and zooplankton (density, biomass, and average size) were sampled as part of a lake-wide, seasonal (spring, summer, and fall) assessment of Lake Ontario in 2003 to characterize the status of the lower aquatic food web. For each parameter, spatial comparisons were performed to test for differences between habitats (nearshore and offshore) and between regions (east and west) during each season. Significant differences between habitats were found only for silica and chlorophyll a; silica was higher nearshore in fall, and chlorophyll a was higher offshore in fall. Significant differences between regions were detected in Secchi depth, epilimnetic zooplankton mean length, total phosphorus and *Cercopagis pengoi* density and biomass; Secchi depth and zooplankton mean length were higher in the east in spring, total phosphorus and *Cercopagis pengoi* biomass were higher in the west in summer, and *Cercopagis pengoi* biomass was higher in the east in fall. *Cercopagis pengoi* was present lake-wide in summer and fall, but *Bythotrephes longimanus* was present only in fall in the Kingston basin. Mean spring total phosphorus, soluble reactive phosphorus, chlorophyll a, and epilimnetic zooplankton density and biomass are at or near record low levels. As we move into the future, persistent low levels of these lower food web elements will continue to stress alewife populations both through reduced food resources and food quality for zooplankton, and may force these fish to seek alternative food such as *Mysis*.*

Keywords: phosphorus, silica, *Cercopagis*, *Bythotrephes*

Introduction

The physical, chemical, and biological structure of the Great Lakes ecosystems, including that of Lake Ontario, changed considerably during the three decades from 1970 to 2000 (Madenjian et al. 2002; Mills et al., 2003, 2005; Bronte et al.,

2003; Dobiesz et al., 2005). In Lake Ontario, water clarity increased, phosphorus concentrations declined, and several non-native species became established. Reduced phosphorus loading, mandated by the Great Lakes Water Quality Agreement of 1972, was largely responsible for the oligotrophication of the lake and declines in productivity of

phytoplankton and zooplankton during this period (Johannsson 1987, 2003; Neilson and Stevens 1987; Stevens and Neilson, 1987; Johannsson et al., 1991; Johengen et al., 1994; Millard et al., 1996; Millard et al., 2003). Through the latter part of this period, several invasive, non-indigenous species (NIS) became very abundant, in particular, the zebra mussel (*Dreissena polymorpha*), quagga mussel (*D. bugensis*), spiny water flea (*Bythotrephes longimanus*), and fishhook water flea (*Cercopagis pengoi*) (Mills et al., 1993; MacIsaac et al., 1999). Addition of these species has caused changes in community structure, trophic relationships, and productivity patterns in several of the Great Lakes (Nalepa, 1991; Dermott and Kerec, 1997; Lozano et al., 2001; Johannsson et al., 2000; Benoit et al., 2002; Barbiero and Tuchman, 2004; Warner et al., 2006; Pangle et al., 2007).

Declining productivity and establishment of NIS are of particular concern relative to Lake Ontario's non-native salmonid fishery which is supported primarily by alewife (*Alosa pseudoharengus*), a non-native planktivore. A declining alewife population (Jones et al., 1993; O'Gorman and Stewart, 1999) led fishery managers to shift from a strategy of alewife control to concern about the ability of alewife to sustain the salmonid fishery. The alewife decline may be linked to the establishment of other NIS (i.e. dreissenid mussels and the invasive predatory cladocerans, *C. pengoi* and *B. longimanus*). For example, Mills et al. (2003) suggest that filter-feeding dreissenids have depressed zooplankton production, particularly in nearshore habitats where the ratio of dreissenids to water volume is highest. Also, *Cercopagis* and *Bythotrephes* have added competitive and predatory pressure on the zooplankton community and likely increased competition among zooplanktivores (Warner et al., 2006). Declines in zooplankton abundance and changes in community composition are also reflective of the overall decline in lake productivity as evidenced by low nutrient levels (Johannsson, 2003).

In this study, we examine the status of water clarity, total phosphorus (TP), soluble reactive phosphorus (SRP), soluble reactive silica (SRS), chlorophyll *a*, and zooplankton biomass, density, and mean length (ZML) in Lake Ontario in 2003. These data are compared with long-term trends and a previous large-scale spatial study to examine the possible impacts that changes in lower food web parameters may have had on the ecosystem, and to establish a baseline for future assessment. In addition, we examine the importance of season and of geography

(nearshore vs. offshore; east vs. west) in describing the present patterns in these variables. In this work we depend heavily on historical, long-term databases and studies developed and executed by Environment Canada (Surveillance Program, 1969–2003), Fisheries and Oceans Canada (Bioindex Program, 1981–1995; Lake Ontario Trophic Transfer Project, 1990–1996), and the United States Environmental Protection Agency (1986–2003).

Methods

When sampling large lakes such as the Great Lakes, resources dictate that a choice must be made between temporally intensive sampling at a few representative sites and broad spatial sampling a few times during the season. Although a temporally intensive sampling program provides a much better understanding of the dynamics and productivity of a region (El-Shaarawi and Kwiatkowski, 1977; Minns, 1984; Johannsson et al., 1998), it cannot be used to evaluate spatial patterns. Due to resource limitations and the fact that a spatially intensive survey had not been performed recently, the sampling design used in our study (the Lake Ontario Lower Aquatic Food Web Assessment or LOLA) was modeled after the earlier Canadian Lake Ontario Trophic Transfer (LOTT) program (1990–1996), the most recent lake-wide survey of Lake Ontario's lower trophic levels.

Sample collection and processing

Water and zooplankton samples were collected during the day during three lake-wide cruises in spring (April 28–May 3), summer (August 10–11 and August 19–21), and fall (September 21–25), 2003 from sites along four north-south transects (Figure 1) in Lake Ontario. The cruises were planned to coincide with organism life cycles and provide a spatial component of the season cycle. Spring is the time of isothermal water temperatures and provides the initial chemical conditions for the year prior to significant uptake of nutrients by the biota. The spring survey provides a picture of the amounts of nutrients available for the biological activity that will occur during the year. Summer and fall surveys (August and September) characterize the summer and late summer zooplankton production and community structure. The 30-m bathymetric contour was used to delineate nearshore (gray area in Figure 1) and offshore habitats (nearshore $n = 7$, offshore

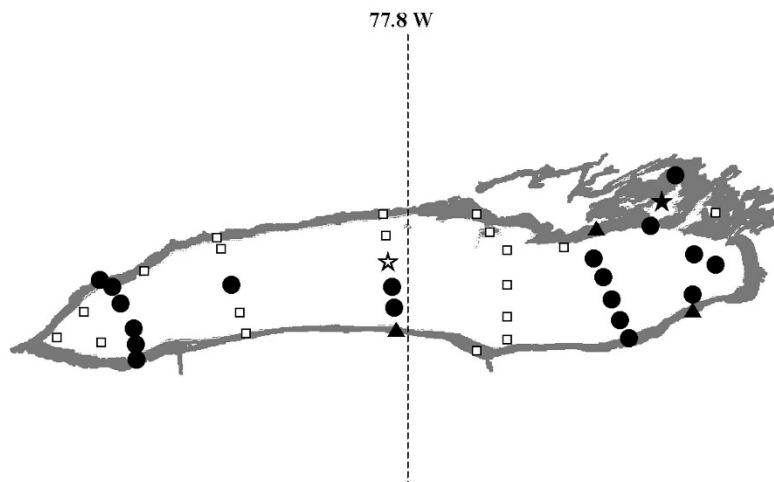


Figure 1. Sampling locations in Lake Ontario for LOLA 2003 (dark circles and star = zooplankton water clarity, nutrients, and chlorophyll *a*, triangles = water clarity, nutrients, and chlorophyll *a*) during April, August, and September 2003, for the Canadian Bioindex Program (open star = station 41; closed star = station 81), and the Lake Ontario Trophic Transfer Project (all symbols). Dashed line represents the 77.8° W longitude line. Light gray shading represents bottom depths of 30 m or less.

$n = 16$ for nutrients; nearshore $n = 4$, offshore $n = 16$ for zooplankton). The lake was divided into eastern and western regions by the 77.8° W longitude line (eastern region $n = 13$, western region $n = 10$ for nutrients; eastern region $n = 11$, western region $n = 9$ for zooplankton). Zooplankton samples were lost for three nearshore stations (black triangles in Figure 1) in the spring; therefore, those stations were omitted from all zooplankton analyses.

Sampling procedure varied with season due to the location of the thermocline. An electronic bathythermograph (EBT) or conductivity-temperature-depth (CTD) profiler was used to determine thermocline depth. During spring isothermal conditions, integrated water samples were collected from 20-m depth or two meters above the bottom (for shallow stations) to the surface. In summer and fall, integrated water samples were collected from one meter above the thermocline to the surface. Water samples were collected using an integrated tube sampler (1.9-cm inside diameter Nalgene tube), lowered to the appropriate depth, and kept perpendicular to the lake bottom. Water was transferred to 2-L Nalgene containers and processed immediately on board the ship. Water was shaken to mix thoroughly and a 100 mL aliquot was taken and preserved with 1 mL 30% H_2SO_4 for later analysis of TP. For soluble reactive phosphorus (SRP) and soluble reactive silica (SRS), water was filtered through a 0.45-micron membrane filter and 100 mL aliquots of filtrate were taken.

Water samples were stored in the dark at 4°C until returned to the lab for analysis. For chlorophyll *a*, up to 2L of water was filtered through a Whatman GF/C filter at a pressure not exceeding 300 mmHg, and the filter was frozen for later analysis. Once samples were returned to the lab, TP concentration was determined colorimetrically using the ammonium molybdate – stannous chloride method after persulfate digestion (Philbert and Traversy, 1973). SRP and SRS were analyzed in an autoanalyzer using the ammonium molybdate – stannous chloride method heteropoly – blue method, respectively (Philbert and Traversy, 1973). Chlorophyll *a* concentration was determined by 90% acetone extraction (Strickland and Parsons, 1972). Secchi depth (m) and temperature (°C) were recorded at each site.

Epilimnetic zooplankton samples (following depth protocol for water sampling; see above) were collected using a 64- μ m mesh, 50-cm diameter, flow-metered (Rigossa) net raised at a minimum rate of 0.7 m second⁻¹. Zooplankton were preserved in the field in 70% ethyl alcohol after anesthetization with antacid tablets. Zooplankton (other than *Cercopagis*) were counted using the stratified regime of Cooley et al., (1986) and biomass determined by length weight regressions (Ora Johannsson, unpublished data). To separate *Cercopagis*, the sample was first passed through a 400- μ m mesh sieve. The 400- μ m fraction was transferred to a Petri dish and examined under a microscope and all *Cercopagis*

were removed. Up to 60 animals were measured, and weights were determined using the regression equation of Makarewicz et al. (2001). If more than 60 *Cercopagis* were present, a subsample of 200–250 individuals was counted, dried, weighed, and used to estimate abundance and biomass in the entire sample. Cryovial bullet tubes were numbered and precisely weighed using a Mettler balance. *Cercopagis* from both the subsample and remainder of the sample were rinsed to remove trace ethanol and other zooplankton, transferred to the cryovials, freeze dried, and weighed. The weight of the counted fraction was then used to determine the weight of the uncounted fraction.

Data analysis

T-tests were used to compare means for each parameter to identify spatial differences during each season. Significantly different means were identified by a p-value adjusted for multiple comparisons using the Bonferroni correction. Spatial categories include east and west (separated by 77.8° W longitude line), referred to hereafter as regional comparisons, and nearshore and offshore (separated by the 30-m bathymetric contour), referred to hereafter as habitat comparisons. Analysis of variance (ANOVA) was used to compare means across seasons. Significant results, identified by a p-value <0.05, were examined using the Tukey-Kramer HSD test (JMP IN 5.1.2; SAS Institute) to identify which pairs of means were different. Water quality parameters (Secchi disc, TP, SRS, and chlorophyll *a*) and zooplankton mean length (ZML) data were normally distributed and therefore were not transformed. In the case of SRP, transformation did not improve normality; analyses were performed on untransformed data. Zooplankton density and biomass data were log₁₀ transformed after adding one. Zooplankton mean length was calculated from species average lengths after weighting for species density. Chlorophyll *a* concentrations were unadjusted for phaeophytin.

Historical Data

Programs: Intensive surveys conducted on Lake Ontario during the 1970s found more temporal than spatial variability in chlorophyll *a* and zooplankton (El-Shaarawi and Kwiatkowski, 1977; Minns, 1984), and a research program was designed accordingly. The Department of Fisheries and Oceans

Bioindex Program (1981–1995) sampled two fixed stations (midlake station 41 and Kingston Basin station 81) on a weekly basis from April to October (Johannsson et al., 1998; Johannsson, 2003; Millard et al., 2003). Recognizing that periodic, large-scale, spatial research was also essential in the overall evaluation of ecosystem change, the Department of Fisheries and Oceans participated in a study assessing whole lake, multi-trophic level productivity in Lake Ontario in 1990 (the Lake Ontario Trophic Transfer or “LOTT” Project). The LOTT Project sampled five to eight depth-defined sites on six north-south transects spaced evenly from west to east across the lake in spring, summer, and fall (Millard et al., 2003). In addition, Environment Canada (Surveillance Program, 1969 - 2003) conducted spatially intensive, whole-lake surveys for nutrients in spring (April) and summer (late July – early August) each year: a total of 98 stations per cruise (Millard et al., 2003). The USEPA (GLNPO Limnology Program, 1986–2003) sampled eight offshore sites in the spring (April) and eight offshore and five nearshore sites in late summer (August) of each year (Makarewicz et al., 1995; Barbiero and Tuchman, 2001; Barbiero et al., 2001). We obtained historical data collected by these sampling programs for comparison with data collected in 2003. All four sampling programs were instrumental in tracking the long-term decrease of phosphorus and the early impacts of dreissenid mussels on the Lake Ontario ecosystem.

Methods: Surveillance Program nutrient data were collected in spring from surface waters (1 m sampling depth) of open lake stations (sounding depth ≥ 100 m). Bioindex Program nutrient concentrations were obtained from integrated samples (0 to 20 m) collected weekly from stations 41 and 81 (spring 1981–1995). Spring averages for each year were calculated using values from April 1 to the onset of stratification. LOTT nutrient (May 22–31, 1990) and chlorophyll *a* (August 1, 1990 and July 14–15, 1995) data were from integrated samples collected from a depth of 0 to 20 m or 0 to bottom minus 1 m. EPA nutrient data (1986–2002) from stations 41 and 81 were collected in April and were integrated from a depth of 0 to 20 m.

Nutrient analyses for Surveillance, Bioindex, and LOTT were performed by the National Laboratory for Environmental Testing, Environment Canada, Burlington, Ontario (Environment Canada 1997). Soluble nutrients were analyzed onboard ship during Surveillance cruises. Bioindex and LOTT samples were filtered onboard, stored at 4°C and returned to

the lab for analysis. Total phosphorus was analyzed by acid persulfate digestion followed by automated colorimetric molybdate stannous chloride method (Philbert and Traversy, 1973). For silica, water was filtered through a 0.45-micron membrane filter and then analyzed by the autoanalyzer heteropoly-blue method (Philbert and Traversy, 1973). EPA TP data were composites of water samples taken at discrete depths with Niskin bottles (spring: surface, 5 m, 10 m, and 20 m) mounted on a SeaBird Carousel. Sample processing techniques for those data are described in detail by Barbiero and Tuchman (2001).

Zooplankton samples were collected weekly at stations 41 and 81 during the Bioindex Program from 1981–1995. A 64- μm mesh, 50-cm diameter, metered net was towed from 20 m depth (or 1 m above thermocline) to the surface. We compared LOLA densities from May, August and September to Bioindex densities (April 15– May 15; Aug 1 – Aug 31; Sep 1 – Sep 30). Zooplankton were not collected during the LOTT study.

Results

Phosphorus

In 2003, lake-wide mean spring TP concentration was $7.5 \mu\text{g L}^{-1}$, and it increased over the course of the sampling season, reaching $11.3 \mu\text{g L}^{-1}$ in the fall (Table 1). Lake-wide fall TP was significantly higher than spring TP (ANOVA $F(2, 66) = 3.99$, $p = 0.02$; Tukey-Kramer HSD). There were no significant differences in TP concentrations between nearshore and offshore habitats for any season, but TP was significantly higher in the western region in summer (Table 1 and 3b). Mean seasonal SRP con-

centrations were below $1.0 \mu\text{g L}^{-1}$ in 2003 (Table 1). For SRP, there were no significant seasonal changes lake-wide, no significant differences in concentrations between nearshore and offshore habitats for any season, and no significant differences between eastern and western regions for any season.

Silica

Mean seasonal SRS concentrations were highest in spring ($734 \mu\text{g L}^{-1}$) and lowest in summer ($265 \mu\text{g L}^{-1}$) (Table 1). Lake-wide SRS levels were significantly higher in spring compared with summer and fall (ANOVA $F(2, 66) = 60.9$, $p < 0.0001$; Tukey-Kramer HSD). A comparison of habitat by season found SRS to be significantly higher in the nearshore in the fall (t-test; $p < 0.0001$) (Table 1 and 3a), but a comparison of region by season found no differences.

Chlorophyll *a* and water clarity

Mean chlorophyll *a* concentrations did not exceed $2.7 \mu\text{g L}^{-1}$ in 2003 (Table 1). Lake-wide chlorophyll *a* was significantly higher in fall compared with summer, and significantly higher in summer compared with spring (ANOVA $F(2, 66) = 13.9$, $p < 0.0001$; Tukey-Kramer HSD). A comparison of habitat by season found chlorophyll *a* to be significantly higher in the offshore in the fall (t-test; $p = 0.0006$) (Table 1 and 3a), but there were no significant differences between eastern and western regions for any season. Mean lake-wide Secchi disc depth was highest in spring (9.8 m) and declined through the summer reaching a low of 6.7 m in the fall (Table 1). Lake-wide Secchi depth was significantly higher in spring compared with summer and fall (ANOVA $F(2, 66) = 8.26$, $p = 0.0009$;

Table 1. Seasonal means and ranges for physical and chemical parameters sampled in Lake Ontario in spring, summer, and fall (23 sites per season) 2003. Ranges are in parentheses below each mean.

	TP ($\mu\text{g L}^{-1}$)	SRP ($\mu\text{g L}^{-1}$)	Silica ($\mu\text{g L}^{-1}$)	Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	Secchi depth (m)
Spring	7.5 (4.8–17.1)	0.9 (0.6–2.3)	734 (350–870)	1.3 (0.8–3.0)	9.8 ^{b(east)} (6.0–17.0)
Summer	10.0 ^{b(west)} (1.8–26.3)	0.4 (0.2–3.8)	265 (100–1020)	1.9 (0.9–6.8)	7.6 (4.0–10.5)
Fall	11.3 (7.2–28.0)	0.7 (0.2–4.9)	344 ^{a(nearshore)} (130–610)	2.7 ^{a(offshore)} (1.6–4.1)	6.7 (5.0–9.0)

^aSignificant difference (t-test; $p < 0.05$) detected between nearshore and offshore habitats (higher value in superscript parentheses).

^bSignificant difference (t-test; $p < 0.05$) detected between eastern and western regions (higher value in superscript parentheses).

Table 2. Mean epilimnetic (64- μm mesh net) zooplankton density, biomass, and length in Lake Ontario in spring, summer, and fall 2003. Density data were \log_{10} transformed, biomass data were \log_{10} transformed after adding one, and the reported average has been backtransformed. Zooplankton mean length is weighted for density of each taxon (veligers not included). Ranges are in parentheses below each mean.

	Density (# $\text{m}^{-3} \times 10^3$)	Biomass (mg m^{-3})	Length (μm)	<i>Cercopagis</i> Density (# m^{-3})	<i>Cercopagis</i> Biomass (mg m^{-3})
Spring	1.3 (0.2 – 4.3)	3.8 (0.6 – 13.2)	675 ^{b(east)} (519 – 804)	0.0	0.0
Summer	14.9 (3.3 – 163.8)	23.7 (4.0 – 55.6)	524 (214 – 774)	18.6 ^{b(west)} (0 – 1624.8)	0.9 ^{b(west)} (0 – 12.3)
Fall	35.4 (5.0 – 155.5)	54.0 (6.7 – 311.1)	470 (251 – 645)	131.2 ^{b(east)} (9.3 – 420.1)	1.9 ^{b(east)} (0.1 – 6.3)

^aSignificant difference (t-test; $p < 0.05$) detected between nearshore and offshore habitats (higher value in parentheses).

^bSignificant difference (t-test; $p < 0.05$) detected between eastern and western regions (higher value in parentheses).

Tukey-Kramer HSD). Secchi depth was significantly higher in the eastern region in spring (t-test; $p = 0.0003$) (Table 1 and 3b).

Zooplankton

Epilimnetic zooplankton density and biomass increased significantly from spring to fall (ANOVA; $F(2,57) = 72.6$, $p < 0.0001$ and $F(2,57) = 47.5$, $p < 0.0001$, respectively) (Table 2). Regional comparisons of epilimnetic zooplankton biomass, density, and length by season showed a significant difference only for length; zooplankton length was higher in the east in spring (t-test; $p = 0.003$) (Table 2 and 3b). Habitat comparisons of epilimnetic zooplankton biomass, density, and length by season showed no significant differences in any season. Epilimnetic zooplankton mean length significantly decreased from 675 μm in spring to 524 μm in summer and 470 μm in fall (ANOVA $F(2,57) = 15.1$; $p < 0.001$) (Table 2). This size decrease is consistent with the composition shift from copepods (particularly cyclopoids) in spring

to generally smaller cladocerans in summer and fall.

We assessed change in zooplankton community composition by dividing epilimnetic zooplankton biomass into six groups: bosminids, daphnids, invasive predatory cladocerans, other cladocerans, calanoid copepods, and cyclopoid copepods. Bosminids and daphnids were dominant in the fall and summer seasons, respectively, each accounting for 46% of the biomass at those times (Figure 7). Cyclopoid copepods were dominant (85% of the total epilimnetic biomass) in spring 2003 (Figure 7). Regional comparisons of zooplankton mean length for dominant (>10% of the biomass) community groups for each season found a difference only in spring; cyclopoids were significantly higher in the east (t-test; $p = 0.008$) (Table 2 and 3b). Invasive predatory cladocerans (*B. longimanus* and *C. pengoi*) accounted for 7% of the total epilimnetic biomass in summer and 3% in fall. An examination of zooplankton species composition by biomass showed that *Diacyclops thomasi* and *Limnocalanus macrurus* were the dominant

Table 3a. Mean values for physical, chemical, and zooplankton parameters for which significant differences were detected in habitat (nearshore vs offshore) comparisons (see Table 1). Ranges are in parentheses following each mean value.

Parameter	Season	Higher in	Lower in
Silica	Fall	Nearshore 420 (260-1020)	Offshore 200 (100-300)
Chlorophyll <i>a</i>	Fall	Offshore 2.9 (1.7-4.1)	Nearshore 2.0 (1.6-2.6)

Table 3b. Mean values for physical, chemical, and zooplankton parameters for which significant differences were detected in regional (east vs west) comparisons (see Table 2). Ranges are in parentheses following each mean value.

Parameter	Season	Higher in	Lower in
Secchi depth	Spring	East 11.9 (8.0–17.0)	West 7.0 (6.0–8.5)
TP	Summer	West 14.5 (7.1–26.3)	East 7.2 (1.8–12.0)
Zooplankton mean length	Spring	East 714 (605–804)	West 628 (519–700)
<i>Cercopagis</i> biomass	Summer	West 4.2 (0.04–12.3)	East 0.1 (0.007–0.4)
<i>Cercopagis</i> biomass	Fall	East 3.2 (1.0–6.3)	West 1.3 (0.09–4.3)

spring species, *Daphnia retrocurva* and *Bosmina longirostris* dominated the summer period, and *Eubosmina coregoni* and *D. retrocurva* were dominant in the fall (Table 4).

Neither *Cercopagis pengoi* nor *Bythotrephes longimanus* were observed in spring. Epilimnetic

density (and biomass) of *Cercopagis* averaged 18.6 m^{-3} (0.9 mg m^{-3}) in summer and 131.2 m^{-3} (1.9 mg m^{-3}) in fall (Table 2). *Cercopagis* density and biomass were higher in western Lake Ontario during summer and higher in eastern Lake Ontario in fall (Table 2 and 3b). The species made up a large

Table 4. Mean percent of offshore epilimnetic zooplankton species biomass from vertical, 64- μm mesh net hauls in Lake Ontario in spring, summer, and fall 2003. Percents are based on means of $n = 16$ samples per season.

Group	Species	Spring	Summer	Fall
Bosminids	<i>Bosmina longirostris</i>	<1	14	1
	<i>Eubosmina coregoni</i>	<1	4	44
Daphnids	<i>Ceriodaphnia lacustris</i>	0	<1	<1
	<i>Daphnia galeata</i>	<1	1	3
	<i>Daphnia retrocurva</i>	0	40	29
Invasive predatory cladocerans	<i>Bythotrephes longimanus</i>	0	0	<1
	<i>Cercopagis pengoi</i>	0	8	3
Other cladocerans	<i>Alona rectangula</i>	0	<1	0
	<i>Chydorus sphaericus</i>	0	<1	<1
	<i>Diaphanosoma birgei</i>	0	<1	<1
	<i>Holopedium gibberum</i>	0	11	2
	<i>Leptodora kindtii</i>	0	3	1
	<i>Polyphemus pediculus</i>	0	3	<1
Calanoid copepods	<i>Calanoid copepodite</i>	1	1	1
	<i>Calanoid nauplii</i>	<1	<1	<1
	<i>Diaptomus minutus</i>	<1	1	<1
	<i>Diaptomus oregonensis</i>	1	1	2
	<i>Diaptomus sicilis</i>	<1	0	0
	<i>Epischura lacustris</i>	0	1	<1
	<i>Eurytemora affinis</i>	<1	1	1
	<i>Limnocalanus macrurus</i>	15	0	0
Cyclopoid copepods	<i>Cyclops vernalis</i>	0	<1	<1
	<i>Cyclopoid copepodite</i>	22	5	6
	<i>Cyclopoid nauplii</i>	<1	2	<1
	<i>Diacyclops thomasi</i>	60	2	4
	<i>Mesocyclops edax</i>	0	1	0
	<i>Tropocyclops extensus</i>	0	<1	<1
Total Seasonal Biomass (mg m^{-3})		3.9	15.4	65.4

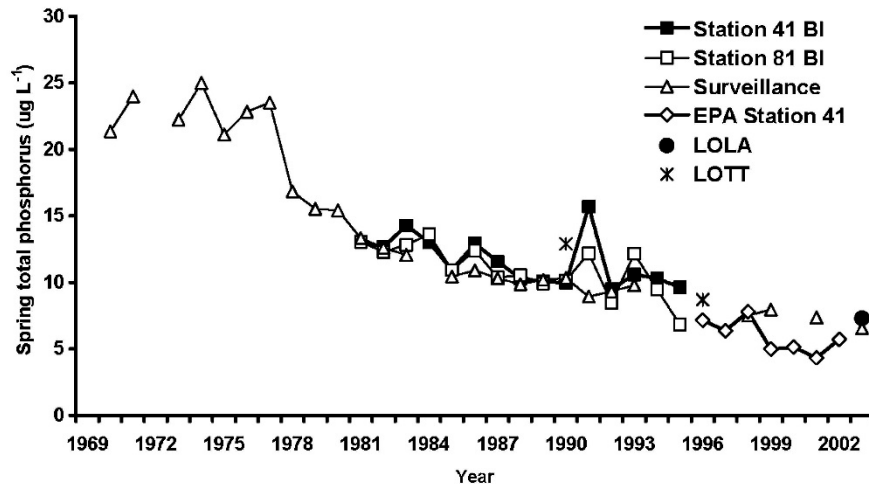


Figure 2. Spring total phosphorus trend in Lake Ontario, 1969–2003. Open and closed squares represent data from the Canadian Bioindex Program, 1981–1995. Open triangles represent data from the Canadian Surveillance project, 1969–2003. Open diamonds represent data from EPA station 41. Asterisks are the lake-wide spring means from the LOTT study. Closed circle is the spring lake-wide mean for 2003.

proportion (17%) of the total zooplankton biomass in western Lake Ontario in summer. *Bythotrephes* was only observed in fall in the Kingston Basin, with a lake-wide average density of 0.6 m^{-3} .

Discussion

Historical Perspective

Open-lake, long-term, spring TP has been steadily decreasing in Lake Ontario since 1977 (Figure 2). Offshore TP concentrations as measured by the Canadian Bioindex Program approached the target level of $10 \mu\text{g L}^{-1}$ in 1985 (Millard et al., 2003) and, with the exception of 1991, remained close to the target until 1995. Since that time, spring TP levels have continued to decline, reaching a low of $4.32 \mu\text{g L}^{-1}$ (USEPA; station 41) in 2001. However, EPA samples were processed by a different method and it is unknown if the continued downward trend is real or an artifact of differing methods. Surveillance data appear to be leveling off during the same time period, and comparable values between LOTT (1996) and LOLA data support this trend.

Phosphorus enrichment stimulates silica uptake by diatoms, and Schelske et al. (1986) contended that TP concentrations in the Great Lakes in the $8.0 - 25.0 \mu\text{g L}^{-1}$ range were required to deplete silica. Open-lake spring TP concentrations have been

below $8.0 \mu\text{g L}^{-1}$ since 1996; while silica concentrations have been gradually increasing (Figure 3). Millard et al. (2003) found no significant increase in spring silica at either station 41 or 81 for the 1981 to 1995 time period, and Surveillance data for the same time period support this finding (Figure 3). However, Surveillance data plotted from 1969–2003 show an increasing trend, and addition of data from the LOLA project for stations 41 and 81 to the long-term Bioindex data shows a trend that mirrors this increase. With silica concentrations well above growth limiting levels ($300 \mu\text{g L}^{-1}$; Schelske et al., 1986), it appears that diatoms may be experiencing P-limitation. Millard et al. (2003) questioned whether offshore spring diatom biomass could be controlled by P supply, but noted the possibility of co-limitation by both light and P supply (Healy, 1985). Spring diatom biomass was lower in 2003 (0.1 g m^{-3}) (Munawar et al., this volume) compared to historic levels (1970, 0.9 g m^{-3} ; 1978, 0.4 g m^{-3} ; 1990, 4.2 g m^{-3} ; Munawar and Munawar, 2003) while spring Secchi depth has increased (Figure 4), indicating that P-limitation may be more important now than in the past.

Summer chlorophyll *a* concentrations at station 41 in Lake Ontario, 1981–1995 did not decline in tandem with spring TP (Millard et al., 2003) (Figure 5). However, the chlorophyll *a* decline was significant at station 81 during the same time period.

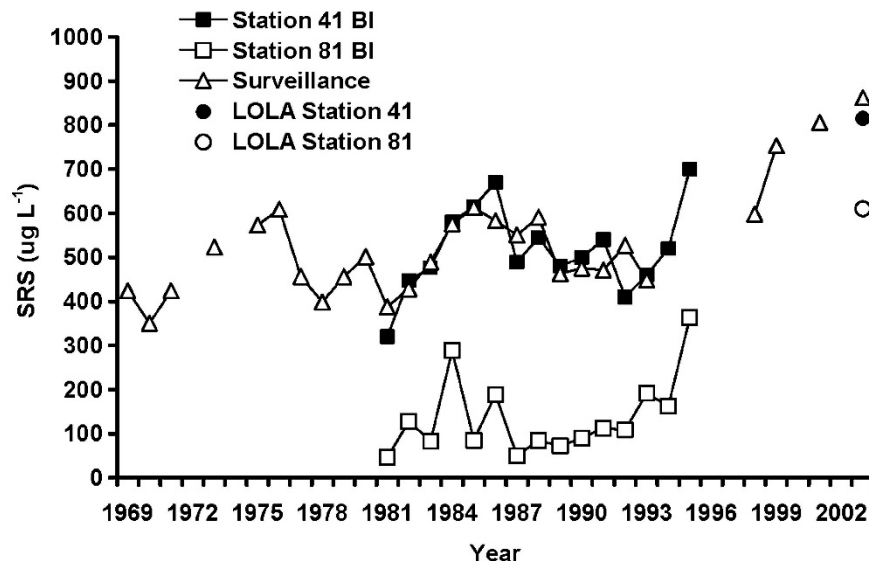


Figure 3. Spring SRS concentrations in Lake Ontario, 1969–2003. Open and closed squares represent data from the Canadian Bioindex Program, 1981–1995. Open triangles represent data from the Canadian Surveillance project. Open and closed circles (LOLA) indicate results from LOLA 2003x

In 2003, mean chlorophyll *a* concentrations at stations 41 and 81 were lower than any recorded during 1981–1995.

Offshore epilimnetic zooplankton species observed in 2003 did not differ greatly from those observed in 1992–1995 by Johannsson (2003). *Cercopagis pengoi*, *Alona rectangulara*, and *Polyphemus pediculus* were the only species present in 2003 that

were absent in 1992–1995. *Daphnia pulicaria* and *Ceriodaphnia quadrangula*, were present in 1992–1995 but not in 2003. Epilimnetic zooplankton density and biomass were high in the early 1980s and declined to relatively stable levels by the late 1980s which continued until 1995 (Johannsson, 2003). Summer and fall densities are typically an order of magnitude higher than spring densities. In 1987

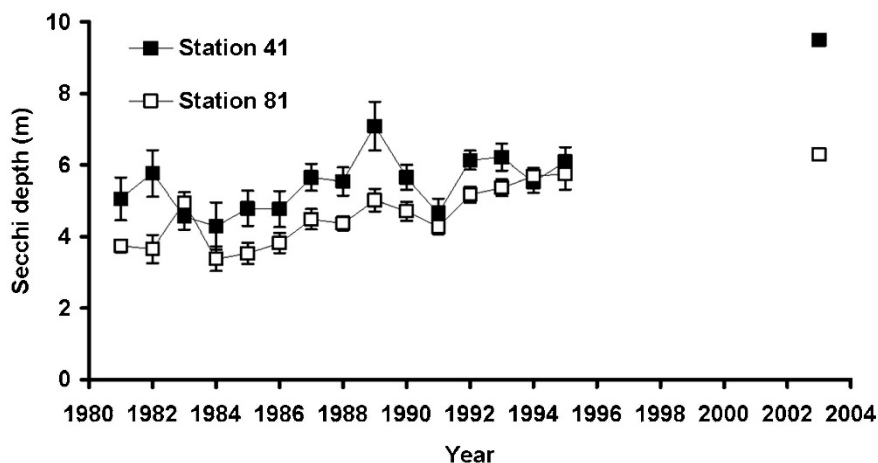


Figure 4. Mean seasonal (April–October) Secchi disc depth in Lake Ontario, 1981–1995 and 2003. Data from 1981–1995 are from the Canadian Bioindex Program. Data from 2003 are from LOLA.

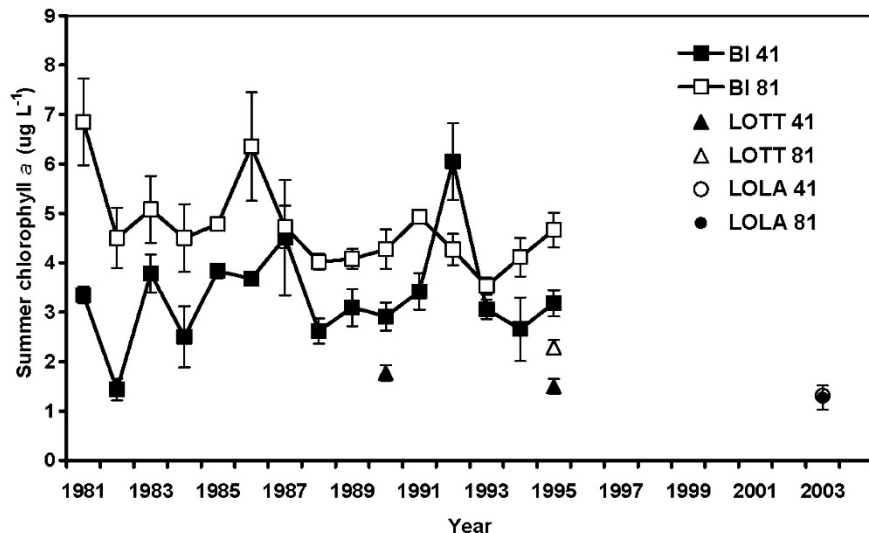


Figure 5. Summer chlorophyll *a* concentrations in Lake Ontario, 1981–2003. BI indicates data from the Canadian Bioindex Program, 1981–1995. LOTT indicates data from the Lake Ontario Trophic Transfer project, 1990 and 1996. LOLA indicates results from 2003. For Bioindex data, error bars are ± 1 SE based on all August data collected from each site. For LOTT and LOLA data, error bars are ± 1 SE based on samples from all sties sampled in summer of each year.

and 1991, spring densities approached those of fall (Figure 6). In summer of 2003, zooplankton density was as low as $17,000\text{ m}^{-3}$ and biomass had decreased to 25 mg m^{-3} . Spring and summer zooplankton densities in 2003 were the lowest recorded for the 1981 to 2003 time period (Figure 6).

Spatial considerations

Lake Ontario’s offshore waters remain oligotrophic, with TP and chlorophyll *a* concentrations at or near record low levels in 2003. Nearshore and offshore habitats in Lake Ontario are similar with

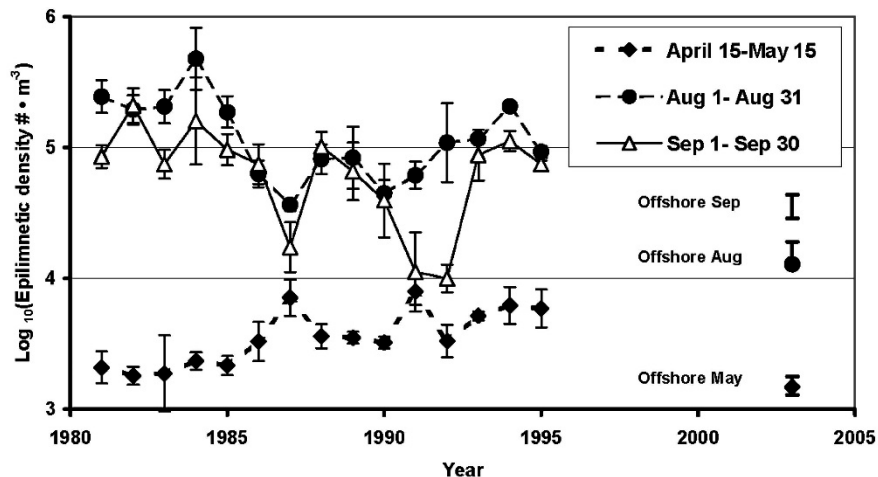


Figure 6. Epilimnetic zooplankton density in Lake Ontario at Station 41, 1981–1995 (error bars are ± 1 SE) and 2003 (error bars are ± 1 SE about mean values from all offshore stations) Station 41 was not sampled in September 2003.

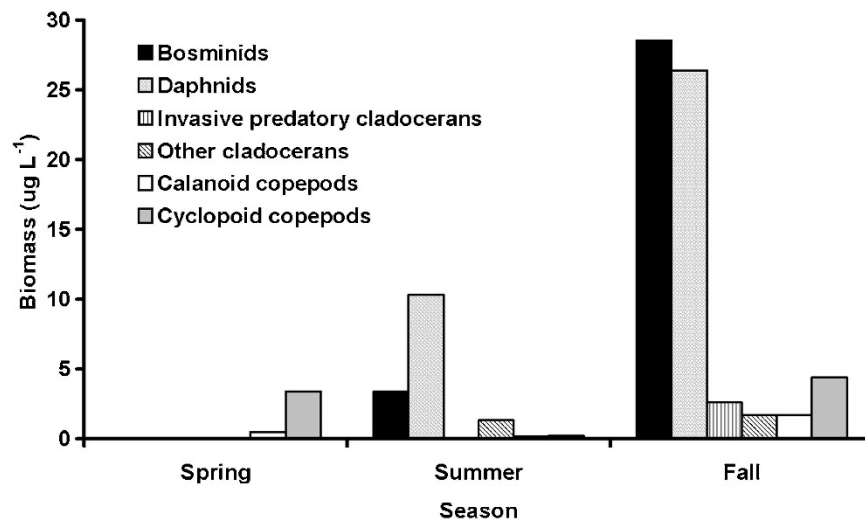


Figure 7. Mean offshore epilimnetic zooplankton biomass by category from vertical, 64- μ m mesh net hauls in Lake Ontario in spring, summer, and fall 2003.

respect to nutrient levels and chlorophyll *a*, an indication that the lake's nearshore waters are oligotrophic as well. These findings appear to contradict recent reports describing Lake Ontario's 'nearshore' zone as water-quality impaired—high phosphorus levels, algal blooms, and increased abundance of the benthic filamentous alga *Cladophora* (Makarewicz et al., 2006). However, the similarity between nearshore and offshore habitats in our study is a reflection of our operational definition of nearshore. We classified sites as nearshore based on bottom depths of less than 30 m, but actual depths of nearshore sites in our study ranged from 10 to 28 m. Other studies examining differences between nearshore and offshore waters in Lake Ontario have used a wide range of definitions (20 m – 100 m) for the boundary between the two habitats (e.g. Munawar et al. 2003; Millard et al., 2003), but none have used depths less than 10m (e.g. Hall et al., 2003). Our study did not include the coastal zone – areas with bottom depths in the range of 1–5 m (Makarewicz et al., 2006) – a habitat that requires further study.

Regional (east vs. west) comparisons in 2003 showed spring Secchi depth higher in the east, summer TP concentrations higher in the west, and spring epilimnetic zooplankton mean length higher in the east. The deeper eastern Secchi depth in spring was not explained by other variables sampled; there were no significant differences in either TP or chlorophyll

a between eastern and western regions at that time. It is possible that inputs from the Niagara River increased turbidity in the western region during spring. The higher summer TP concentration in the west may be attributed to localized phytoplankton development in the western end of the lake. Although chlorophyll *a* concentrations were not significantly higher in the west at that time, satellite imagery (<http://oceancolor.gsfc.nasa.gov>; August 18, 2003) shows higher surface chlorophyll *a* concentrations, particularly at northernmost sites on the western transect. These sites had higher TP concentrations than the two sites closest to the Niagara River.

Implications of a changing ecosystem

Millard et al. (1996) reported a decline of as much as 30% in primary productivity between 1972 and 1992 and commented that should that decline cascade up the food chain, that fish managers would be charged with the difficult task of preparing stakeholders to expect lower fish production. Should they persist, the record low nutrient and zooplankton levels observed in 2003 will have several food web implications. Low zooplankton biomass may translate into a decrease in populations of top predators. Changes in nutrient cycling may become more evident as well. Hecky et al. (2004) hypothesize the existence of a 'nearshore phosphorus shunt', a consequence of dreissenid mussel

establishment whereby nutrients are sequestered in nearshore/coastal areas and along the bottom slope. If true, nutrient levels will remain very low in offshore and nearshore waters while the coastal zone will continue to experience water quality impairment and eutrophic conditions. In any case, most of the surface area of Lake Ontario is now oligotrophic and the significance of the microbial food web is critical to the functioning of this ecosystem (Mills et al., 2003). Heath et al. (2003) noted that the significance of the microbial food web in transporting carbon and phosphorus to higher trophic levels increased as waters became more oligotrophic, and that bacterial biomass could actually exceed phytoplankton biomass under such circumstances, a scenario likely reflective of the Lake Ontario ecosystem.

Lower phosphorus concentrations and high water clarity in Lake Ontario in 2003 may impact food quality of zooplankton by altering C:N:P ratios. Research has indicated that the ratio of carbon to nutrients in algal food can be an important indicator of food quality for some invertebrates (Hessen, 1992; Sterner, 1993; Sterner et al., 1993; Sterner and Hessen, 1994; Schulz and Sterner, 1999; Schulz and Sterner, 2000; Elser et al., 2000). High algal C:P ratios are indicative of poor food quality for several important zooplankton consumers, such as large daphnids, because elemental phosphorus is required for rapid growth and reproduction. Low P content in algal food has been demonstrated to reduce growth rate and productivity of daphnids and other fast-growing species (Sterner and Schulz, 1998; Sterner and Elser, 2002). In addition, high C:N or low N:P ratios can also be indicative of protein limitation for zooplankton such as copepods (Russell-Hunter, 1970; Hatcher, 1994). In 2003, spring and summer mean phytoplankton biovolumes were the lowest ever reported for Lake Ontario while the proportion of cyanobacteria, a poor quality food source, was high (Munawar et al., this volume). Summer biomass of Cryptophyta, a high quality algal food resource for zooplankton, declined to 0.05 g m^{-3} (Munawar et al., this volume) a level less than one-third of that reported in 1995 (Johannsson et al., 1998). These changes associated with the increased oligotrophication of Lake Ontario will disrupt the food supply to zooplankton, and the microbial food web may become a more important pathway of energy transfer to zooplankton.

Nutrients, food quality, invasive species, and predation are all factors that can affect zooplankton abundance, biomass, and community structure.

Johannsson (2003) reported that the Lake Ontario zooplankton community responded to declines in TP with changes in both species composition and biomass. *Chydorus sphaericus* and *Ceriodaphnia lacustris*, species preferring nutrient-rich conditions, declined or disappeared in the early 1990s. These species were present at very low densities ($<300 \text{ m}^{-3}$) in summer and fall of 2003. Summer biomass and density of both cladocerans and cyclopoids fell by approximately 50% from the early 1980s to the mid 1990s (Johannsson, 2003). By 1995, mean summer cladoceran density and biomass at station 41 were $51,000 \text{ m}^{-3}$ and $81 \text{ g dry wt m}^{-3}$, respectively, and spring TP concentration was 9.6 ug L^{-1} . The spring TP concentration for the offshore of Lake Ontario in 2003 was 7.5 ug L^{-1} , and we saw a marked decline in zooplankton abundance and biomass, suggesting decreased productivity. Lake wide mean summer epilimnetic zooplankton density and biomass in 2003 were $15,000 \text{ m}^{-3}$ and $24 \text{ g dry wt m}^{-3}$, respectively; these means were lower than any summer data observed at station 41 in 1995. Decreases in biomass could also have resulted from increased predation by planktivorous fish, mysids or predatory zooplankton, in particular the recent invaders, *Cercopagis pengoi* and *Bythotrephes longimanus*.

Invasive predatory cladocerans have been shown to affect Great Lakes' zooplankton populations. Pangle et al. (2007) demonstrated that *Bythotrephes longimanus* decreased the productivity of *Daphnia retrocurva* and *Bosmina* spp. However, *B. longimanus* was absent in our samples collected in the summer of 2003. Several recent studies have also assessed the predatory impacts of *Cercopagis* in Lake Ontario. Warner et al. (2006) observed significant declines in abundance of bosminids, *Dia-cyclops thomasi*, and copepod nauplii during peak *Cercopagis* abundance in nearshore Lake Ontario. Similar declines were not observed during times when *Cercopagis* was absent, suggesting predation by *Cercopagis* was responsible for declines in small zooplankton. Benoit et al. (2002) found that invasion by *Cercopagis* was correlated with a decline in juvenile epilimnetic cyclopoids, and that production of juvenile copepods decreased both through direct predation and through a shift in copepod vertical distribution to colder waters. Decreases in *Bosmina longirostris* abundance in the presence of *Cercopagis* were noted as well (Warner et al., 2006; Benoit et al., 2002). Laxson et al. (2003) found that *Cercopagis* fed on small-bodied zooplankton

(*D. retrocurva* and *B. longirostris*) in laboratory experiments, and noted a decline in the abundance of *D. retrocurva*, *B. longirostris*, and *Diacyclops thomasi* between 1999 and 2001 coinciding with an increase in abundance of *Cercopagis*. *Cercopagis* densities in 2003 were lower than those reported by Laxson et al. (2003) and Warner et al. (2006), and lake wide mean density reached 131.2 m^{-3} in fall, a time when *Cercopagis* was dominant in eastern Lake Ontario. The temporal scale of our study is coarser compared to those mentioned and so it is difficult to assess predatory impacts based on our data. Fall *Cercopagis*, cyclopoid, and bosminid densities were all higher in eastern waters, but the differences were not significant.

Conclusions

Managers will continue to struggle with the issue of sustaining fishery resources given the nature of changes in Lake Ontario's lower food web. Persistent low levels of total phosphorus, soluble reactive phosphorus, chlorophyll *a*, and epilimnetic zooplankton biomass will continue to stress alewife populations both through reduced food availability and reduced food quality for zooplankton. Alewife may be forced to seek alternative food such as mysids, a shift that may have both positive and negative energetic consequences. Because the success of efforts to maintain recreational fisheries and to restore self-sustaining populations of native species depends on the condition of the lower food web, long-term assessment is critical to measure the effectiveness of remedial actions, to better understand how stressors manifest themselves across habitats and impact fish communities, and to make recommendations for future actions.

Acknowledgements

We thank the crews of the USEPA R/V Lake Guardian and CCGS Limnos. We acknowledge the leadership of Fred Luckey and Jack Kelly of the USEPA and Vi Richardson of Environment Canada in the LOLA program. This work was funded by EPA Grant CR-83209001 to Cornell University and by a Canada Ontario Agreement (COA) Grant from Ontario Ministry of Natural Resources. This is contribution # 253 of the Cornell Biological Field Station.

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CHAPTER 2



AQUATIC ECOSYSTEM
HEALTH & MANAGEMENT



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Lake Ontario water quality during the 2003 and 2008 intensive field years and comparison with long-term trends

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Phosphorus loading declined between the 1970s and the 1990s, leading to oligotrophication of the offshore waters of Lake Ontario during that time period. Using lake-wide data from the intensive field years of 2003 and 2008 and from available long-term data sets on several trophic state indicators (total phosphorus [TP], soluble reactive silica [SRSi], chlorophyll a and Secchi disc transparency [SDT]), we tested the hypothesis that oligotrophication of the offshore waters of Lake Ontario has continued in the 2000s. Significant differences between 2003 and 2008 include higher spring (April) TP, SRSi, and SDT in 2008, lower summer (July–August) SDT in 2008, higher summer chlorophyll a in 2008, and lower fall (September) TP, SRSi, and chlorophyll a in 2008. The decline in SRSi from spring to summer was greater in 2008 than in 2003. Change point and regression analyses on the long-term data revealed no trend in spring TP since 1996, in summer chlorophyll a since 1994, in spring SDT since 1998, in spring SRSi or SRSi decline from spring to summer since 1999, or in summer SDT since 2001. Neither the comparison of the 2003 and 2008 surveys nor the analysis of the long-term data supported our hypothesis of continued oligotrophication of the offshore of Lake Ontario in the 2000s.

Keywords: oligotrophication, phosphorus, silica, chlorophyll a, Secchi disc transparency, trophic state

Introduction

Lake Ontario, one of the Laurentian Great Lakes, is a large (18,960 km²), deep (mean depth 86 m; maximum depth 244 m) lake bordering the Province of Ontario to the north and west, and New York State to the south and east. The lake has undergone drastic ecological change in response to anthropogenic stressors (Mills et al., 2003). Cultural eutrophication resulting from phosphorus inputs from the watershed led to the 1972 Great Lakes Water Quality Agreement (GLWQA; revised in 1978, and amended in 1983, 1987 and 2012) between the United States and Canada, an agreement that demonstrates a commitment from both countries to address problems related to the chemical, physical, and biological integrity of the Great Lakes basin ecosystem. A major aim of the GLWQA was to reverse the effects of cultural eutrophication (Vollenweider et al., 1974; Schelske, 1991). A phosphorus abatement program was implemented, and target phosphorus concentrations were established for each of the Great Lakes. Implementation of GLWQA led to a decrease in phosphorus concentrations and to the oligotrophication of offshore waters in the Great Lakes (Environment Canada and the United States Environmental Protection Agency, 2014) including Lake Ontario (Millard et al., 2003; Mills et al., 2003; Munawar and Munawar, 2003; Holeck et al., 2008; Dove, 2009). Oligotrophication is defined here as the combined ecological response of a lake to decreased nutrient loading (Anderson et al., 2005), which may include decreased algal production, decreased secondary production, and increased water transparency (Mills et al. 2003). The target TP concentration of 10 $\mu\text{g l}^{-1}$ for Lake Ontario's offshore waters was attained in 1986 (Mills et al., 2003) and has remained below that level since that time (Dove, 2009; Holeck et al., 2013).

However, problems related to eutrophic conditions, particularly nuisance *Cladophora* growth and cyanobacteria blooms in embayments and shoreside (depth <1.2 m) areas, have returned (Makarewicz et al., 2012). This has led to a re-evaluation of targets for phosphorus loadings as called for in the GLWQA Protocol signed in 2012. At the same time, continued oligotrophication in the offshore is a concern to fisheries managers since, among the possible impacts, decreased phosphorus concentrations have been implicated in the decline of Alewife (*Alosa pseudoharengus*)

and the multi-million dollar sport fisheries in Lakes Michigan and Huron (Bunnell et al., 2014, Barbiero et al., 2009, 2012). These processes — eutrophication of the nearshore and oligotrophication of the offshore waters — may be the combined response of an overall decline in phosphorus loading to the lake coupled with increased localized phosphorus input to some nearshore areas and an increased abundance of *Dreissena* Mussels that led to a retention of phosphorus in the nearshore (Mills et al., 2003; Hecky et al., 2004; Makarewicz et al., 2012).

Simultaneous nearshore eutrophication and offshore oligotrophication present a special problem for lake managers since measures taken to reverse one of those processes could exacerbate the other. For example, reducing phosphorus inputs to the lake might improve water quality in the nearshore but could cause phosphorus declines in already nutrient-poor areas of the offshore. It is therefore important to evaluate if the oligotrophication of the offshore waters that was initiated by the GLWQA has continued in the offshore of Lake Ontario in the 2000s. Here, we evaluate several water quality parameters to help determine if the process of oligotrophication that began in the 1970s has continued in the offshore waters of Lake Ontario.

Materials and methods

Field sampling

During 2003 and 2008, the United States Environmental Protection Agency's (EPA) R/V Lake Guardian and the Canadian Coast Guard Ship Limnos performed three lake-wide surveys assessing the lower trophic levels in Lake Ontario (Figure 1, the Lake Ontario Lower food web Assessment [LOLA] project). Timing of the spring cruises was similar for the two years (4/28 – 5/1, 2003 and 4/21 – 4/24, 2008), but the timing of the summer and fall cruises differed both by date and by the seasonal development of surface temperature (summer 7/20–7/26, 2003 and 8/10, 8/11, 8/19–8/22, 2008; fall 9/2–9/5, 2003 and 9/21–9/25, 2008; Figure 2). Both the summer and fall cruises in 2008 were up to 3 weeks earlier than the corresponding 2003 cruises. Station locations and depths are in Rudstam et al. (2012).

Data collected include total phosphorus (TP), soluble reactive silica (SRSi), chlorophyll *a*, and

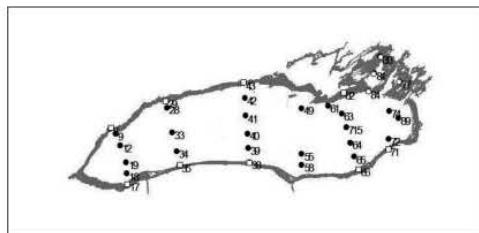


Figure 1. Map of Lake Ontario indicating sample locations in 2003 and 2008. The gray area delineates the nearshore with nearshore stations marked with open squares (<30 m deep). Kingston Basin stations are indicated with open circles. Data from nearshore and Kingston Basin stations are not analyzed in this article but are available in Rudstam et al. (2012).

Secchi depth transparency (SDT). TP, SRSi, and chlorophyll *a* were measured from integrated water samples in the epilimnion. The samples were collected either with an integrated tube (Limnos) or by pooling several discrete Niskin bottle samples (Lake Guardian) collected through the epilimnion. During stratified periods, samples were collected from the surface to a depth of 1 m above the top of the thermocline (defined as the depth where the rate of temperature decline increases relative to the mixed layer). During spring isothermal conditions,

samples were collected from the surface to 20 m depth or to two meters above the bottom (for stations <20 m depth).

Laboratory analysis

TP and SRSi were processed using an autoanalyzer at the Environment Canada laboratory in Burlington, Ontario (2003 samples) and at the EPA certified laboratory at SUNY-Brockport (J. Makarewicz, 2008 samples) using standard methods (APHA, 1998; Wetzel and Likens, 2000). Total phosphorus was determined using the ammonium molybdate – stannous chloride method after preservation with 1 mL 30% H₂SO₄ (per 100 mL sample) and persulfate digestion (APHA, 4500-P D). For SRSi, water was filtered through a 0.45- μ m membrane filter and SRSi concentration was determined by the heteropoly – blue method (APHA, 4500-SiO₂ D). Chlorophyll *a* was determined by acetone extraction after filtration through GF/C (nominal pore size 1.2 μ m) glass fiber filters followed by spectrophotometry (2003) or fluorometry (2008, Turner 10-AU unit). Values for total chlorophyll *a* were not corrected for phaeophytins. Detection limits were TP: 0.2 μ g l⁻¹ (2003), 1.2 μ g l⁻¹ (2008);

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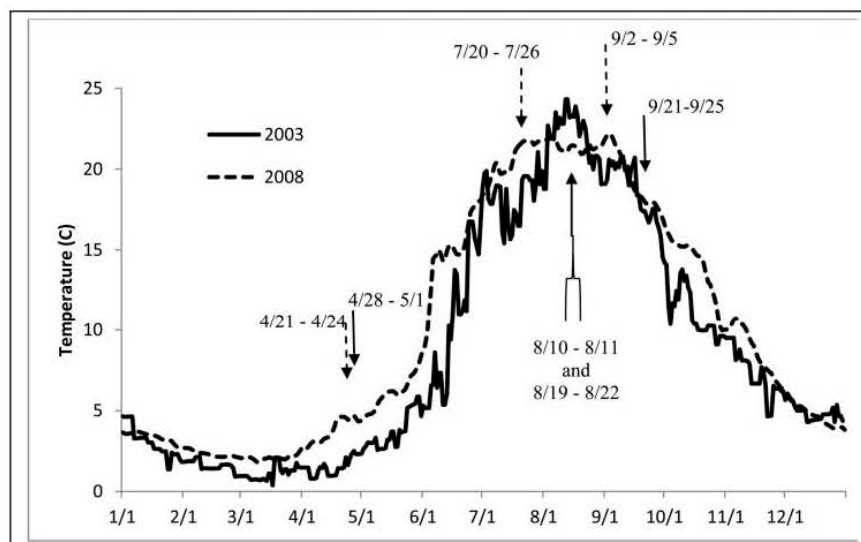


Figure 2. Lake surface temperature in Lake Ontario during 2003 and 2008 (from NOAA <http://coastwatch.glerl.noaa.gov/glseaf/>). Timing of LOLA surveys during spring, summer, and fall surveys are indicated by solid arrows (2003) and dashed arrows (2008). In 2003, the summer survey was split into two shorter time periods.

SRSi: $20 \mu\text{g l}^{-1}$ (2003), $50 \mu\text{g l}^{-1}$ (2008); chlorophyll *a* $0.5 \mu\text{g l}^{-1}$ (2003 and 2008). When concentrations were below the detection limit for any parameter, the detection limit for that parameter was used to calculate means and variability. When detection limits varied between years, the higher detection limit was used to calculate means for comparison between years. The mean of the deviations (difference between duplicates/mean) was 20% or less with the exception of TP in 2003 (48%). Replicates were averaged and mean values were used in all subsequent analyses. More details and all data are available electronically through the Knowledge Network for Biocomplexity (Rudstam et al., 2012).

Data analysis

2003 vs 2008

Samples were obtained from at least 8 and up to 17 stations depending on the season and year (Figure 1). For each parameter (TP, SRSi, chlorophyll *a*, and SDT) t-tests with unequal variance were used to compare 2003 and 2008 data. Differences were considered significant at the $p < 0.05$ level. Significance values were not corrected for multiple comparisons (see discussion in Gotelli and Ellison [2004] about the issues associated with applying Bonferroni adjustments for multiple tests).

Comparison with long-term data

Four existing Lake Ontario water quality data sets were used to compare trends to the LOLA data: the Department of Fisheries and Oceans Canada (DFO) Bioindex Program (1981–1995) sampled two stations (midlake station 41 and Kingston Basin station 81) on a biweekly basis from the beginning of April until the end of October (Johannsson et al., 1998; Johannsson, 2003; Millard et al., 2003); the Environment Canada Great Lakes Surveillance Program (EC-GLSP; 1969 – present) conducts whole-lake water quality surveys in April and August approximately every second year (Dove, 2009); the United States Environmental Protection Agency (EPA) Great Lakes National Program Office's (GLNPO) limnology program (1986 – present) samples eight offshore stations in April and August of each year (Great Lakes Environmental Database [GLENDa]); and the US Biomonitoring Program (US-BMP, 1995 – present), which is a collaboration between the New York State

Department of Environmental Conservation (NYS-DEC), the United States Geological Survey (USGS), the United States Fish and Wildlife Service (USFWS) and Cornell University, samples between 3 and 21 offshore stations 1–3 times per year (Holeck et al., 2013). Detailed methods for the long-term data can be found in Dove et al. (2009, EC-GLSP), Holeck et al. (2013, US-BMP), Johannsson et al. (1998, DFO Bioindex Program), and EPAs GLENDa database (GLNPO, 2012). To analyze trends when data were available from more than one sampling program, we calculated a simple mean of offshore data from those sampling programs. Portions of these data series have been published (Hall et al., 2003; Holeck et al., 2008; Dove, 2009). Here we extend the analyses to 2011 (2010 for SRSi) and combine data from different programs. Change point analyses were performed on long-term data using Change-Point Analyzer version 2.3 (Taylor Enterprises, 2003). Change point analysis detects changes in time-ordered data and provides confidence levels and intervals for each change. Time trends were assessed using linear regression on 1) all available years, and 2) years after the most recent change point for each parameter.

Results

Phosphorus

In 2008, offshore TP concentrations were below the target of $10 \mu\text{g l}^{-1}$ established in the GLWQA (Table 1). Spring TP was significantly higher in 2008 than in 2003 in the offshore. Summer and fall TP were significantly lower in 2008 compared to 2003. The long-term trend of spring TP indicates a decline from 1970 until the mid-1990s, with no significant trend since that time (Table 2; Figure 3). A change point analysis on spring TP showed a break point in 1996, representing a change in the mean spring TP concentration from $9.9 \mu\text{g l}^{-1}$ for the period 1985–1995 to $6.1 \mu\text{g l}^{-1}$ for the period 1996–2011. There has been no further decline in spring TP since 1996 ($r^2 = 0.01$, $n = 16$, $p = 0.71$).

Chlorophyll *a*

Although offshore spring chlorophyll *a* concentrations were similar in 2003 ($1.35 \mu\text{g l}^{-1}$) and 2008 ($1.26 \mu\text{g l}^{-1}$), summer chlorophyll *a* levels

Table 1. Mean (SE, n) values of water quality parameters from the LOLA 2003 and 2008 surveys in offshore waters of Lake Ontario. Number of stations sampled varied with season and year. Significant differences ($p < 0.05$) between 2003 and 2008 are in bold (t-test assuming unequal variance, $p < 0.05$). Note that there has been no correction done for multiple tests.

	2003		2008		p-value
	Mean (SE, n)	Range	Mean (SE, n)	Range	
SPRING					
Dates		28 Apr–1 May		21–24 Apr	
TP ($\mu\text{g P l}^{-1}$)	6.6 (0.2, 16)	4.8–8.9	9.8 (0.7, 8)	8.7–14.7	<.0001
SRSi ($\mu\text{g SiO}_2 \text{l}^{-1}$)	793 (9, 17)	730–870	868 (14, 8)	806–924	<.0001
Secchi depth (m)	10.0 (0.8, 13)	6.0–14.5	14.9 (0.9, 8)	12.0–19.0	.0010
Chl <i>a</i> ($\mu\text{g l}^{-1}$)	1.35 (0.08, 17)	0.71–2.29	1.26 (0.14, 8)	0.72–1.80	.592
SUMMER					
Dates		10–11 Aug; 19–22 Aug		20–26 July	
TP ($\mu\text{g P l}^{-1}$)	10.1 (1.7, 14)	4.6–26.3	6.6 (0.4, 16)	4.0–10.6	.040
SRSi ($\mu\text{g SiO}_2 \text{l}^{-1}$)	190 (14, 16)	100–300	155 (17, 16)	64–273	.113
Secchi depth (m)	8.9 (0.5, 8)	7.0–11.0	6.8 (0.5, 13)	4.0–9.5	.007
Chl <i>a</i> ($\mu\text{g l}^{-1}$)	1.48 (0.17, 16)	0.87–3.52	3.19 (0.30, 16)	1.52–6.28	<.0001
FALL					
Dates		21–25 Sept		2–5 Sept	
TP ($\mu\text{g P l}^{-1}$)	11.4 (0.8, 14)	7.2–18.4	8.0 (0.5, 17)	5.4–11.3	.0006
SRSi ($\mu\text{g SiO}_2 \text{l}^{-1}$)	247 (31, 14)	130–500	109 (14, 17)	40–225	.0002
Secchi depth (m)	6.3 (0.4, 11)	5.0–9.0	5.0 (0.3, 13)	3.2–6.5	.0118
Chl <i>a</i> ($\mu\text{g l}^{-1}$)	3.12 (0.17, 14)	2.31–4.25	1.61 (0.26, 17)	0.66–3.99	<.0001

in 2008 ($3.19 \mu\text{g l}^{-1}$) were about twice the values measured in 2003 ($1.48 \mu\text{g l}^{-1}$, Table 1). Fall offshore chlorophyll *a* levels were higher than summer values in 2003 and lower than summer values in 2008. Offshore epilimnetic chlorophyll *a* concentrations declined significantly from 1981 to 2011 (Figure 4; $r^2 = 0.15$, $n = 31$, $p = 0.029$). However, chlorophyll *a* concentrations are more variable among the different data series than TP, and there is greater interannual variability. Sources of variability in chlorophyll *a* include methodological differences among laboratories as well as difference in timing of sampling. For the long-term dataset, there was a change point in chlorophyll *a* in 1994 (Table 2) and no trend thereafter ($r^2 = 0.03$, $n = 18$, $p = 0.51$).

Water Transparency

Mean SDT in the offshore was greater in the spring of 2008 (14.9 m) than in 2003 (10.0 m, Table 1). Mean summer SDT in the offshore was shallower in 2008 (6.8 m) than 2003 (8.9 m) which was consistent with the difference in chlorophyll *a* (higher chlorophyll *a* = lower SDT). Long-

term SDT has increased in Lake Ontario in both spring and summer (Table 2; Figure 5). SDTs from the 2000s are roughly twice those measured in the 1980s (Figure 5), tracking a substantial increase in water transparency in Lake Ontario. Change point analyses indicate a break in spring SDT in 1998 and in summer SDT in 2001, with higher SDT recently. Spring SDT shows a marginally significant increase since 1998 ($r^2 = 0.19$, $n = 12$, $p = 0.10$), but summer SDT indicates no recent increase (2001–2011; $r^2 = 0.04$, $n = 10$, $p = 0.59$).

Silica

Soluble reactive silica concentrations were higher in the spring than summer, an observation consistent with the typical seasonal pattern in Lake Ontario (Millard et al., 2003). Offshore spring SRSi concentrations were significantly lower in 2003 ($793 \mu\text{g SiO}_2 \text{l}^{-1}$) than in 2008 ($868 \mu\text{g SiO}_2 \text{l}^{-1}$) although the difference was less than 10% (Table 1). Offshore summer SRSi values decreased from spring values (see above) to 190 and $155 \mu\text{g l}^{-1}$ in 2003 and 2008,

Table 2. Results of regression and change point analyses performed on Lake Ontario nutrient parameters. All data were log-10 transformed prior to regression analysis. Year change point detected refers to the first year following the change. The 95% confidence intervals for the change point and the average values for the period before and after the change point are given. Significant p-values are indicated in bold.

Parameter	Years tested	Year(s) change point detected	Confidence interval	Change point analysis		Regression	
				Average prior to change point	Average since change point	Long-term	Since last change point
Spring Secchi depth (m)	1981–2011	1998	(1998, 2000)	8.2	13.6	p < 0.0001 , $r^2 = 0.74$, n = 27	$p = 0.10$, $r^2 = 0.19$, n = 12
Summer Secchi depth (m)	1981–2011	2001	(1999, 2009)	5.1	8.4	p < 0.0001 , $r^2 = 0.55$, n = 30	$p = 0.59$, $r^2 = 0.04$, n = 10
Spring TP ($\mu\text{g l}^{-1}$)	1970–2011	1996	(1996, 1996)	9.9	6.1	p < 0.0001 , $r^2 = 0.88$, n = 41	$p = 0.71$, $r^2 = 0.01$, n = 16
Summer chlorophyll <i>a</i> ($\mu\text{g l}^{-1}$)	1981–2011	1994	(1982, 1996)	3.3	2.7	p = 0.029 , $r^2 = 0.15$, n = 31	$p = 0.51$, $r^2 = 0.03$, n = 18
Silica utilization (mg l^{-1})	1986–2010	1999	(1997, 2000)	0.4	0.7	p < 0.0001 , $r^2 = 0.62$, n = 23	$p = 0.58$, $r^2 = 0.03$, n = 12
Spring silica (mg l^{-1})	1986–2010	1996	(1990, 1996)	0.5	0.6	p < 0.0001 , $r^2 = 0.70$, n = 23	n/a
Summer silica (mg l^{-1})	1986–2010	n/a	n/a	0.6	0.8	$p = 0.58$, $r^2 = 0.01$, n = 23	$p = 0.52$, $r^2 = 0.04$, n = 12
				n/a	n/a		n/a

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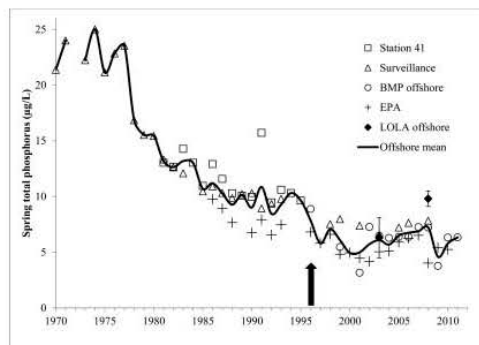


Figure 3. Long-term spring (April–May) epilimnetic total phosphorus concentrations in Lake Ontario, 1970–2011. Station 41 is from the Department of Fisheries and Oceans Canada’s Bioindex Program. USGS data are from Lake Ontario Biological Station sampling. Surveillance data are from ECs Great Lakes Surveillance Program. BMP offshore data are from the NYSDEC Biomonitoring Program. GLENDa data are from the EPAs GLENDa database. LOLA data are from this report. The arrow indicates change points in the data.

respectively. Fall SRSi concentrations were significantly lower in 2008 than in 2003 (Table 1). The increase in spring SRSi from 2003 to 2008 is consistent with the long-term trend (Figure 6). Spring silica concentrations have increased significantly between 1986 and 2010 ($r^2 = 0.70$, $n = 23$, $p < 0.0001$). There has been no concomitant increase in summer silica concentrations ($r^2 = 0.01$, $n =$

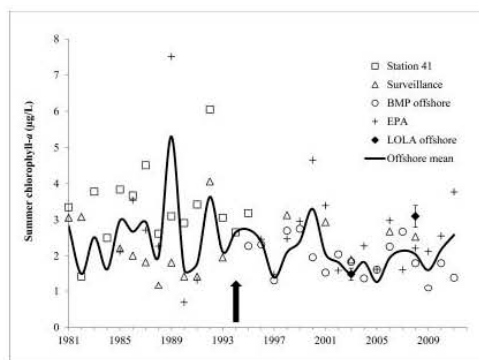


Figure 4. Long-term summer (July–August) epilimnetic chlorophyll *a* concentrations in Lake Ontario, 1981–2011. Station 41 is from the Department of Fisheries and Oceans Canada’s Bioindex Program. BMP offshore data are from the NYSDEC Biomonitoring Program. Surveillance data are from ECs Great Lakes Surveillance Program. GLENDa data are from EPA. LOLA data are from this report. Arrow indicates change point in the data.

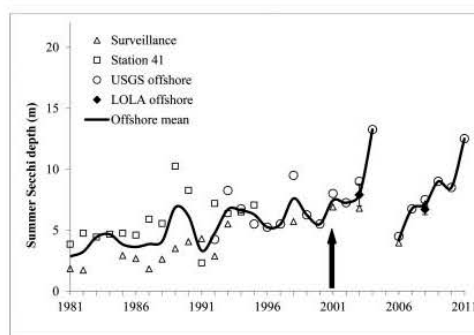
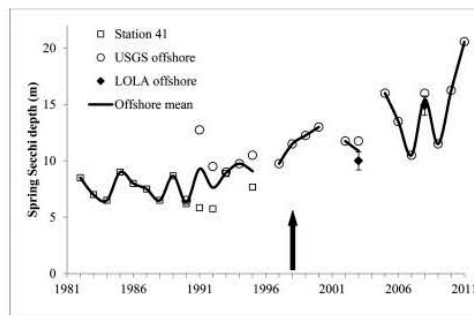


Figure 5. Long-term mean spring (April, top panel) and summer (July/August, bottom panel) Secchi depth (meters) in Lake Ontario, 1981–2011. Station 41 and Station 81 are from the Department of Fisheries and Oceans Canada’s Bioindex Program. USGS data are from Lake Ontario Biological Station sampling. Surveillance data are from ECs Great Lakes Surveillance Program. LOLA data are from this report. Arrows indicate change points in the data. Surveillance data were excluded from change point analysis.

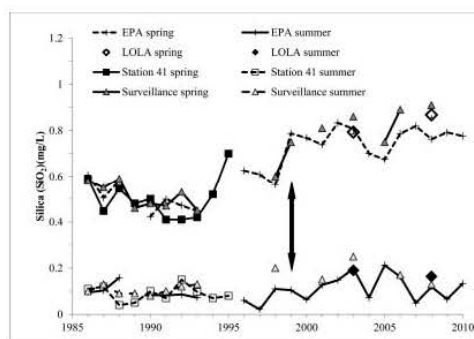


Figure 6. Mean silica concentration in spring (April) and summer (July/August) surveys in Lake Ontario, 1986–2010. Long-term data are from EPAs GLENDa database, DFOs Bioindex Program (Station 41) and ECs Great Lakes Surveillance Program. LOLA data are from this study. Arrow indicates change point in silica depletion (the difference between spring and summer values).

23, $p = 0.58$). The decline in SRSi in the upper waters between spring and summer (defined as silica “utilization” by Mida et al., 2010) has increased in Lake Ontario over the last 25 years ($r^2 = 0.62$, $n = 23$, $p < 0.0001$; Figure 6, Table 2). There is a change point in silica “utilization” in the year 1999 (Table 2), and no significant trend thereafter ($r^2 = 0.04$, $n = 12$, $p = 0.52$).

Discussion

The LOLA 2003 and 2008 programs were designed to investigate the degree of change in lower trophic levels in Lake Ontario. Here we compared nutrients (P and Si), chlorophyll *a*, and water transparency measures from the LOLA 2003 and 2008 programs to assess changes in water quality and trophic state of the lake between these two years. We also compare the results of the LOLA surveys with the long-term data available through the different agencies around the lake. We were particularly interested in whether the oligotrophication of the offshore described previously for the period from the 1970s to the early 2000s (Mills et al., 2003; Holeck et al., 2008; Dove, 2009) has continued during the most recent decade. We used total phosphorus (TP), chlorophyll *a*, and Secchi disc transparency (SDT) as indicators of water quality and trophic state (Carlson, 1977; Wetzel, 2001). These indicators are typically correlated, at least in systems where primary production is phosphorus-limited. Other companion papers in this volume present data on phytoplankton biomass and productivity (Munawar et al., 2015), zooplankton biomass and community composition (Rudstam et al., 2015) and benthos abundance (Birkett et al., 2015).

Contrary to our expectations, the results indicate no further oligotrophication in the offshore in the 2000s. The comparisons of trophic levels indicators measured during the LOLA 2003 and 2008 surveys suggest a more mesotrophic offshore in 2008 than in 2003. Spring TP, summer chlorophyll *a* and spring to summer silica “utilization” were higher in 2008. Summer and fall water clarity (SDT) were lower in 2008. Only spring SRSi and SDT suggested continued oligotrophication, and these indicators are discussed further below. Higher summer chlorophyll *a* values in our data are consistent with independent measurements by Twiss et al.

(2012). Howell et al. (2012) and Makarewicz et al. (2012) also measured relatively high chlorophyll *a* levels in 2008 at nearshore locations on both the north and south shores of the lake (north shore average $3.1 \mu\text{g l}^{-1}$; south shore average $2.9 \mu\text{g l}^{-1}$). The three long-term monitoring programs (EPA-GLNPO, EC-GLSP, and US-BMP) also show higher summer chlorophyll *a* levels in 2008 than in 2003 (Figure 4), although the difference between the two years is smaller in these three data series. Our results are also consistent with the assessment of Munawar et al. (2015) based on phytoplankton biomass composition and primary production data. According to the scale of Munawar and Munawar (1982), Lake Ontario was mesotrophic in summer 2008 ($2\text{--}3 \text{ g m}^{-3}$) (Munawar et al., 2015). These combined results suggest that Lake Ontario’s offshore waters were more mesotrophic in 2008 compared to 2003, which does not support continuing oligotrophication of Lake Ontario’s offshore in the 2000s.

Although the long-term phosphorus and chlorophyll *a* data do not support a trend toward mesotrophy, they do suggest that oligotrophication did not continue past 1999. Offshore spring TP concentrations leveled off after 1995 (Table 2; Figure 5) and have remained between 7 and $10 \mu\text{g l}^{-1}$ throughout the 2000s. Likewise, other indicators (spring and summer STD, summer chlorophyll *a*, spring SRSi) showed no significant change with time since the last change point (Table 2). These change points all occurred between 1994 and 2001. Similarly, Holeck et al. (2013) found no significant trends in spring TP in Lake Ontario’s nearshore from 1995–2012 in data from the US-BMP. Likewise, Reavie et al. (2014) did not detect a decline in phytoplankton biovolume from 2001 to 2011 in the GLNPO – EPA data, and there was no decline in satellite derived surface chlorophyll concentrations in the 2000s (Watkins et al., 2013; Barbiero et al., 2014). The change point in TP in 1996 coincides with the time Zebra Mussels (*Dreissena polymorpha*) became firmly established in nearshore areas and Quagga Mussels (*D. rostriformis bugensis*) began expanding into offshore areas of Lake Ontario (Mills et al., 1999; Watkins et al., 2007; Birkett et al., 2015). However a link between the expansion of Mussel biomass and an end to oligotrophication is in contrast to the

hypothesized increase in retention of phosphorus in the nearshore by these Mussels (Hecky et al., 2004). The apparent end to the process of oligotrophication in Lake Ontario's offshore may be attributable to the fact that phosphorus concentrations have stabilized there.

Analysis of the long-term Lake Ontario silica data showed a significant increase in spring silica concentrations but not in summer concentrations (Table 2; Figure 6). Dove (2009) warned that increasing spring silica concentrations signal a declining diatom population, since Schelske et al. (1986) noted an inverse relationship exists between spring silica concentrations and diatom biomass in the Great Lakes. However, there was no further increase in spring SRSi after 1999, and epilimnetic silica was depleted by the summer throughout the time series. Because silica is taken up by diatoms between early spring (April) and summer (July–August), the decline in silica concentration between spring and summer has been used as an indicator of diatom abundance (Conley et al., 1993; Schelske et al., 1986; Mida et al., 2010). In this context, silica utilization in Lake Ontario increased in the long-term data series as there was an increase in spring SRSi without a concomitant increase in summer SRSi levels. Thus, the SRSi utilization data suggest no further decline in diatoms through the 2000s and may even indicate an increase in diatoms over time. These results are consistent with observations in Lake Ontario of higher diatom biomass in 2008 than in any other year previously measured (1970, 1978 and 2003; Munawar et al., 2015), and with observations of no trend in diatom biovolume from 2001 to 2011 in the EPA-GLNPO data (Reavie et al., 2014).

Secchi depth transparency (SDT) is the only indicator of water quality and lake trophic state presented here that suggest continued oligotrophication of the offshore in the 2000s. Both spring and summer SDT were higher in the 2000s than in previous decades (spring mean SDT 8.2 m prior to 1998 and 13.6 m thereafter; summer mean SDT 5.1 m prior to 2001 and 8.4 m thereafter), there was a marginally significant increase in spring SDT since 1998 ($p = 0.10$, Table 2), and spring SDT was significantly greater in 2008 than in 2003. Note though that summer and fall SDT declined from 2003 to 2008. Further, SDT is also affected by various inorganic particles in the water column and may

therefore not always be a good indicator of lake trophic state. For example, Secchi depth was shallower in the fall of 2008 (5.0 m) than in the summer, despite lower fall chlorophyll *a* concentrations ($1.7 \mu\text{g l}^{-1}$), likely due to carbonate precipitation (whiting event) observed at the time (Peng and Effler, 2011; Watkins et al., 2013).

The lack of continuing oligotrophication in Lake Ontario in the last decade is likely due to Lake Ontario's location downstream from Lake Erie. The Niagara River, which connects the two water bodies, contributes approximately 27% of the phosphorus load in Lake Ontario (Chapra and Dolan, 2012), and Lake Erie TP has been increasing over the last several years (Environment Canada and the US Environmental Protection Agency, 2014; Dolan and Chapra, 2012; Scavia et al., 2014). If this trend continues in Lake Erie, we may expect increases in phosphorus concentrations in Lake Ontario in the future. This has implications for ecosystem structure and function, and fisheries management.

Conclusions

Comparisons of lake-wide surveys in of Lake Ontario in 2003 and 2008 showed higher phosphorus and chlorophyll *a* concentrations in 2008 than in 2003. Long-term data series indicate change points in Secchi depth, total phosphorus, chlorophyll *a*, spring silica, and silica utilization in the mid-to late-1990s, significant oligotrophication prior to that time, and no significant changes since. Our analysis suggests that the oligotrophication of the offshore waters of Lake Ontario has not continued into the 2000s.

Acknowledgements

We thank the crews of the USEPA R/V *Lake Guardian* and CCGS *Limnos* as well as the participants in the LOLA research cruises and contributors of the long-term data sets used for comparisons with the LOLA surveys. We thank Michael Twiss, Edward Mills, Ora Johannsson and the anonymous reviewers for their helpful comments, and Alice Dove for her valuable contributions to earlier versions of this manuscript. The opinions presented herein are those of the authors and do not necessarily represent

the position of EPA or USGS. This is contribution 1900 of the USGS Great Lakes Science Center. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. or Canadian Governments.

Funding

This work was funded by EPA Grant 97220700-0 to Cornell University as part of the Great Lakes Restoration Initiative and a grant from the International Joint Commission. Further support is provided by the agencies collaborating in the lower trophic level assessments of Lake Ontario (EPA GNLPO and Region 2, NYSDEC, USGS, USFWS, DFO, EC, OMNR).

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