Review

The ecological history of Lake Ontario according to phytoplankton

Lisa R. Estepp *, Euan D. Reavie

Natural Resources Research Institute, University of Minnesota Duluth, 5013 Miller Trunk Highway, Duluth, MN 55811, USA

ABSTRACT

Lake Ontario's condition has fluctuated since European settlement, and our understanding of the linkages between observed ecosystem shifts and stressors is improving. Changes in the physical and chemical environment of the lake due to non-indigenous species, pollution, sedimentation, turbidity, and climate change altered the pelagic primary producers, so algal assessments have been valuable for tracking long-term conditions. We present a chronological account of algal assessments to summarize past and present environmental conditions in Lake Ontario. This review particularly focuses on pelagic, diatom-based assessments as their fossils in sediments have revealed the combined effects of environmental insults and recovery. This review recap's the long-term trends according to three unique regions: Hamilton Harbour, the main lake basin, and the Bay of Quinte. We summarize pre-European impact settlement; eutrophication throughout most of the 20th century; subsequent water quality changes due to nutrient reductions; and filter-feeding dreissenid colonization and contemporary pelagic, shoreline, and embayment impairments. Recent data suggest that although phytoplankton biovolume is stable, species composition has shifted to an increase in densities of spring eutrophic diatoms and summer cyanobacteria. Continued monitoring and evaluation of historical data will assist in understanding and responding to the natural and anthropogenic drivers of Lake Ontario's environmental conditions.

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Introduction

Lake Ontario, easternmost of the Laurentian Great Lakes, has been subjected to anthropogenic stressors since the early 1800s that have affected the lake’s water quality and ecology (Dove, 2009; Holeck et al., 2008; Mills et al., 2003a). A recent study by the Great Lakes Environmental Assessment and Mapping project ranked Lake Ontario the most environmentally stressed of the five Great Lakes largely due to phosphorus (P) loading, invasive species such as zebra and quagga mussels, nitrogen (N) runoff, and toxic pollution from mercury and polychlorinated biphenyls (Allan et al., 2013). Nutrients and toxic
Chemicals are transported to Lake Ontario from the cities and industries along the Oswego, Genesee, and Niagara rivers (Groom, 2013), as well as metropolitan drainages such as those from Toronto, Hamilton, and Rochester. Nutrients flow into these tributaries as a result of runoff from obsolete municipal sewage systems (e.g., Toronto, Kingston, and Ottawa per Zerbisias, 2011) and excess agricultural applications of fertilizers. Other stressors include power plants at Scriba and near Rochester (that often cause degradation to nearshore waters) and ballast-borne species introductions in port areas (Groom, 2013).

Although the third deepest lake (after Lake Superior) of the five Great Lakes, Lake Ontario has the smallest surface area (18,960 km²) and the highest ratio of watershed to lake surface area. More than 80% of surface water inputs originate from the upstream Great Lakes via the Niagara River, which drains Lake Erie, with the St. Lawrence River as the outlet (Lucykey, 2002; Schelske and Hodell, 1991). The lake has a water residence time of 6 years (Michigan Sea Grant, 2000) and is comprised of four axial sedimentation basins separated by three ridges that occupy the lake’s floor from west to northeast, the Niagara, Mississauga, Genesee, and Rochester basins (NGDC-NOAA, 2000; Thomas et al., 1972) (Fig. 1). The Niagara Basin includes the greatest diversity and abundance of plankton and a mix of lakebed invertebrates tolerant of enriched conditions. The central two basins are deeper, colder, and nutrient-poor (Reid, 2001) and the Rochester Basin is the deepest within the lake (244-m depth) (Mills et al., 2003a; NGDC-NOAA, 2000; US EPA, 2012). Several small, shallow basins (West Kingston, East Kingston, Galloo, and Stoney) occur in the northeastern extremity of the lake with overall depths less than 40 m. More than half of Lake Ontario’s shoreline is comprised of the Kingston basins because of embayments, peninsulas, and islands. Hamilton Harbour is a 22-km² embayment on the western end of Lake Ontario and bordered by the Niagara Escarpment and the cities of Hamilton and Burlington; the harbor is separated physically from the lake by a sandbar and a shipping canal connects the waters bodies (Duthie et al., 1996; Sofowote et al., 2008). The Bay of Quinte, a large, complex embayment at the northeastern end of Lake Ontario, extends from the city of Trenton where water depth is 1 to 3 m, past the city of Belleville and deepening progressively downstream to a maximum depth of approximately 60 m near Amherst Island (Nicholls, 1999).

Circulation in Lake Ontario shapes the distributions of temperature, nutrients, contaminants, and planktonic organisms. Westward prevailing winds blow across the lake and during summer cause upwelling of deep water, lowering water temperatures along the north shore and higher temperatures along the south shore (Hall, 2008). This condition results in coastal currents which usually flow counterclockwise around the lake (Poissant et al., 2000). While coastal regions have unique physicochemical characteristics, there is exchange with deeper waters, allowing transport of materials (e.g., nutrients and contaminants) and energy that drive the biological processes of the lake (Rao and Schwab, 2007). The effects of parameters like watershed development, wind and wave circulation, water and air temperatures, river discharges (including nutrient inputs), and invasive mussels all require consideration of spatial uniqueness of shoreside, nearshore, and pelagic waters of Lake Ontario (Makarewicz et al., 2012b, 2012c, 2012d).

Species composition and biomass of phytoplankton have been used to track environmental shifts because they are sensitive gauges of ecosystem health in the Great Lakes (e.g., Allinger and Reavie, 2013; Barbiero and Tuchman, 2001; Reavie et al., 2014a; Stoermer, 1978). Throughout decades of algal research, diverse techniques for collection, preservation, concentration, enumeration, and taxonomic identification have been employed. Consistency is generally lacking among studies.
(Conroy et al., 2005), but ongoing multi-decade monitoring programs [e.g., US Environmental Protection Agency (US EPA) Great Lakes National Program Office’s (GLNPO) Open Lake Water Quality Survey of the Great Lakes] and paleolimnological observations (e.g., Stoermer, 1993; Stoermer et al., 1996) have furnished essential long-term evidence for establishing environmental trends relevant to primary producers. Limnological conditions and historic shifts in physical and chemical properties in Lake Ontario have been explained using modern and fossil indicator assessments (e.g., Stoermer et al., 1985a, 1985b; Wolin et al., 1991; Yang et al., 1993), which were particularly important during a time when few direct measurements of water quality were available. Summaries were recently published for Lake Erie (Allinger and Reavie, 2013) and Lake Superior (Reavie and Allinger, 2011) in an attempt to put recent, rapid changes in a context of long-term lake conditions. We similarly present an extensive retrospective assessment of Lake Ontario diatom-based fossil analyses and algological monitoring collections.

The phytoplankton history of Lake Ontario has been summarized previously in the literature (e.g., Munawar and Munawar, 2003), but no review presents an integrated consideration of paleoecological and monitoring data. Recent, rapid shifts in Great Lakes water quality and food web structure (Bunnell et al., 2014; Reavie et al., 2014a) warrant a reevaluation of historical trends so that current conditions (e.g., invasive species, excess nutrients) can be placed in an appropriate historical context. In this review we provide a chronological account of previous and ongoing assessments of phytoplankton to summarize past and present environmental conditions of Lake Ontario’s pelagic water quality. Much of this focuses on diatom-based assessments due to their prominence in paleolimnological studies, but other algal and physicochemical indicators are cited where relevant. Trends in benthos where shifts were coupled with pelagic changes are also characterized. We discuss the Lake Ontario phytoplankton timeline during three historical periods for which we have phytoplankton collections: pre-European impact settlement prior to large-scale anthropogenic intervention; early transitional and accelerated anthropogenic impacts through the 1960s; and finally the recent five decades of more intensive study following eutrophication, nutrient load reductions, invasive species establishment, and efforts to understand the complex relationships among phytoplankton, zooplankton, water quality, and stressors. For each period we summarize studies from (1) Hamilton Harbour, (2) nearshore and offshore regions of the main body of the lake, and (3) the eastern Bay of Quinte. Volumetrically, Hamilton Harbour and the Bay of Quinte are small components of Lake Ontario that have histories that are symptomatic of Lake Ontario issues overall. We summarize them separately because of the substantial study of their individual ecological conditions which represent perturbed limnological systems undergoing rapid change. To complement the discussion, Table 1 summarizes a timeline of major trends and associated drivers of Lake Ontario’s pelagic primary producers. Where outdated taxa names from older literature are presented, we added contemporary genus names (in parentheses) based on the latest understanding of diatom taxonomy (e.g., Reavie and Kireta, 2015).

**Pre-European impact**

Around 2700 B.C. the hemlock forests of the Lake Ontario region declined, the Nipissing Flood from a significant influx of water from Lake Erie began, and the receding Lake Ontario shoreline drowned productive marshes (Ford, 2009). Ford reported that by 2500 B.C. maple and beech groves became dominant, newly formed marsh environments matured, and an expanding aboriginal people who participated in a seasonal subsistence pattern settled near lakeshores and river mouths to exploit aquatic resources. From A.D. 600 and continuing after European arrival, agriculture, archery, hunting and foraging prevailed, and the lake margin was mostly hardwoods interspersed with southerly species and substantial stands of pine (Ford, 2009). Plankton and benthic invertebrates as food sources sustained large numbers of lake trout, burbot, and Atlantic salmon as the top predators, with a diverse mix of ciscoes, sculpins, and other prey fish that since have become scarce, extinct, or replaced by non-native species (Smith, 1995). European settlement of Lake Ontario’s catchment began in the early 1600s, so a “pre-settlement” period could be considered as prior to that time. However, as is typical for impacted North American lakes (Stoermer, 1993), a near-pristine condition probably persisted for many decades after 17th-century settlement.

**Hamilton Harbour**

Yang et al. (1993) analyzed siliceous microfossils in radionuclide dated core sediments from Hamilton Harbour, a 21.5-km² bay at the western tip of Lake Ontario (Environment Canada and the Ministry of Ontario, 2011) (Fig. 1) to assess historical effects of human activities on the aquatic environment, particularly from the industrial city of Hamilton. They reported that, prior to European settlement, microfossil deposition rates were low, chrysophyte cysts were abundant, and planktonic diatoms comprised about 50% of the flora. The diatom assemblage was dominated by *Melosira (Aulacoseira) islandica* which is a principal winter/early spring diatom (Reavie et al., 2014b; Stoermer and Ladewski, 1976, 1978; Stoermer et al., 1981) and is eutrophic but appears inhibited by high eutrophic conditions (Kreis et al., 1985; Stoermer and Yang, 1970), along with a relative abundance of mesotrophic *Aulacoseira ambiguus* and benthic diatoms including mesotrophic *Martyana (Staurosirella) martyi* and *Fragilariella* (Staurosirella) pinnata, mesosaprobic *Gyrosigma attenuatum,* and xenosaprobic * Mastogloia smithii* (Beaver, 1981; Lowe, 1974; Yang, 1990) per Yang et al. (1993). Authors deemed Hamilton Harbour an oligotrophic environment during this period due to the considerable relative abundance of *A. islandica* (30%, which they interpreted as an oligotrophic habitat indicator in their assessment), a greater abundance of oligotrophic and oligomesotrophic diatoms, and low abundance of eutrophic taxa. Based on a more recent understanding of *A. islandica’s* ecology (Reavie et al., 2014a,b), it is probable the harbor was at least seasonally mesotrophic. It is worth noting that the harbor is physically separated from the main basins of Lake Ontario by a sand bar and therefore does not necessarily reflect lake-wide conditions.

**Main Lake Region**

Duthie and Sreenivas (1971) reported early qualitative evidence of the long-term trophic status of Lake Ontario based on changes in siliceous microfossils in a sediment core (E-30), collected in 1969 or 1971 as described by (Kemp et al., 1974) from the deep Rochester Basin. Diatoms in pre-European sediments were moderately abundant and included *Cyclotella kutzingiana* and *Cyclotella ocellata* which prefer oligotrophic waters (Stoermer and Yang, 1970; Stoermer et al., 1996); *Melosira italica* subsp. *subartica* (currently named *Aulacoseira subartica*) which is a known winter species (Stoermer and Ladewski, 1976) that is intolerant of enrichment (Gibson et al., 2003) and characteristic of oligotrophic offshore waters (Stoermer and Yang, 1970); and *Cyclotella (Handmannia) bodanica* (previously confounded with *Cyclotella comta*) which is eutrophic and common in the upper Great Lakes (Wolin et al., 1988). Other moderately abundant species recorded were *Cyclotella atomus,* often found in polluted waters (Stoermer and Ladewski, 1976; Yang et al., 2005), *Discostella glomerata* (previously *Cyclotella glomerata*) which prefers eutrophic waters (Hutchinson, 1967), *Stephanodiscus minutula* which is eutrophic with eutrophic affinities (Stoermer and Yang, 1970), and *Tabellaria fenestrata* that is found over a wide range of ecological conditions (Wolin et al., 1988). Eutrophic *A. islandica,* which appears less tolerant of nutrient stress (Stoermer et al., 1985a), notably increased near the end of this period. The diverse ecological affinities of the long-term pre-settlement flora of Lake Ontario suggested seasonal shifts in productivity, ranging from oligotrophic to mesotrophic. Duthie and Sreenivas (1971) tentatively concluded that the steady parallel decline in oligotrophic and...
Table 1
Historical summary of major events and environmental conditions that affected primary production in Lake Ontario.

<table>
<thead>
<tr>
<th>Period</th>
<th>Major conditions/trends</th>
<th>Drivers</th>
</tr>
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<tbody>
<tr>
<td>Pre-European Settlement</td>
<td>Species known to be tolerant to eutrophic conditions (e.g., <em>C. atomus</em>, <em>A. subarctica</em>) and common in nutrient-loaded waters and oligotrophic to mesotrophic lakes (e.g., <em>A. distans</em>, <em>C. ocellata</em>, <em>C. bodanica</em>, <em>A. italica</em>) were relatively abundant, inferring that the lake was naturally oligotrophic to mesotrophic, and seasonally productive.</td>
<td>Lake Ontario is divided into four basins with many embayments, peninsulas, and islands, and most of the lake inflow originating via the Niagara River. Lake Ontario receives more land runoff than any of the five lakes, so naturally high seasonal productivity is not surprising.</td>
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<td>1830–1900</td>
<td>Phytoplankton production increased by the end of the period along with diatoms favoring enrichment (e.g., <em>A. granulata</em>, <em>C. stelligera</em>, <em>A. islandica</em>), summer blooming (e.g., <em>C. comensis</em>), and eurytopic conditions (e.g., <em>F. crotonensis</em>), Oligotrophic diatoms declined.</td>
<td>Euro-American settlement included deforestation, wetland dredging and filling, canal building, farming and commercial fishing resulting in ecological modification, excessive nutrient inputs, and other widespread pollution effects.</td>
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<td>1900–1945</td>
<td>Dramatic increase in phytoplankton biomass, including nearshore cyanobacteria and green algae blooms and a dominance of eutrophic diatoms (e.g., <em>S. alpinus</em>); species sensitive to nutrient enrichment (e.g., <em>S. translucens</em>) disappeared or mesotrophic species (e.g., <em>C. bodanica</em>) decreased. Nuisance <em>Cladophora</em> blooms increased.</td>
<td>Introduction of phosphate detergents, and use of commercial fertilizers, compounded by a continuous population expansion, rapidly impacted the system.</td>
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<td>1945–1975</td>
<td>Massive shoreline <em>Cladophora</em> blooms developed. Phytoplankton biomass increased into the 1960s, and nutrient-tolerant and hyper-eutrophic diatoms (e.g., <em>S. parvus</em>, <em>A. normani</em> f. subbals., <em>D. tenue</em> v. <em>elongatum</em>, <em>S. binderanus</em>), along with cyanobacteria and green algal blooms increased.</td>
<td>Population expansion resulted in substantial increases in soluble P (phosphate detergents), N (commercial fertilizers), and industrial wastes. Realization of problems initiated legislative action.</td>
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<tr>
<td>1975–2000</td>
<td>Significant decline in phytoplankton biomass and overall primary productivity, but not in rivers or nearshore waters. The spring diatom <em>A. islandica</em> dominated with a scarcity of <em>Cyclotella</em> spp. characteristic of oligotrophic systems. Nearshore the non-indigenous zebra mussel invades during the late 1980s followed by the quagga mussel in the early 1990s. Massive blooms of <em>Cladophora</em>, cyanobacteria and green algae reappeared in the late 1980s and <em>Diporeia</em> almost disappeared.</td>
<td>Reduced P inputs by 1983 improved water quality by the mid-1990s. Exotic zebra and quagga mussels began colonizing in Lake Ontario in the late 1980s/early 1990s, changing energy cycling to favor nearshore problems and depriving the offshore pelagic zone of nutrients. Phytoplankton biomass decreased while the relative biomass of cyanobacteria increased.</td>
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<td>2001–2014</td>
<td>Overall phytoplankton biomass did not change, but species composition shifted to high spring densities of centric diatoms (<em>S. parvus</em>) and cryptophytes, and summer increases in cyanobacteria, particularly <em>Aphanocapsa</em> (in 2012), and <em>Oscillatoria limnetica</em>. Recent decades of 2013 sedimentary profiles from the Mississauga and Rochester basins have revealed changes in the diatom community including an increase in <em>Cyclotella</em> species possibly associated with climate shifts.</td>
<td>Watershed nutrient inputs, particularly from tributaries, are driving summer blooms likely compounded with dreissenid effects. Climate warming appears to be reorganizing the pelagic diatom community.</td>
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**Bay of Quinte**

To reconstruct the history of trophic conditions in Lake Ontario’s Bay of Quinte, a 225-km² Z-shaped bay on the northeastern shore of the lake at the head of the St. Lawrence River (Fig. 1), Stoeber et al. (1985b) analyzed the algal microfossils in a sediment core collected around 1965 by Warwick (1980) with the aid of 210Pb dates to develop a chronology. Absolute abundance of overall microfossils was low with planktonic production of mostly chrysophycean flagellates or species that (as determined by carbon fragment analyses) did not generate silicified remains. The pre-settlement assemblage tended to be epipelagic diatoms (Stoebner et al., 1985b), particularly those with high silica content, as determined by sedimentary silica analysis (Carrick and Lowe, 1988). This suggested that the bay waters were transparent and unproductive. These variations in the sediments as early as the late 1600s (when human impacts in the watershed were minimal) emphasized the sensitivity of the phytoplankton community to nutrient enrichment and the value of using the sediment record to study these changes.

**Post Euro-American settlement through the 1960s**

The cause and mechanisms of the compositional and functional changes in Lake Ontario’s ecosystem due to human modification have undergone considerable debate (Stoebner et al., 1985a). Because of its geographic position, Lake Ontario was the first of the Great Lakes influenced by European settlers in North America (Ball et al., 2003). The Hamilton Harbour area of western Lake Ontario had been inhabited for more than 100 years by native Americans when the first European explorers arrived during the early 1600s, with permanent European settlement during the late 1700s (Threader, 1984; Yang et al., 1993). The
first major increase in Lake Ontario phytoplankton production around the mid-1800s was in response to increased P loadings from land runoff driven by forest clearing (Schelske, 1991). In addition, Lake Ontario receives water from Lake Erie via the Niagara River, with additional nutrient input from tributaries and precipitation (Luckey, 2002), thus additional settlement upstream compounded impacts to the lake.

Intensive mining activities during the 1880s resulted in losses to the northern coastal marshes west of the Bay of Quinte when these areas were filled and dredged for shipping and industrial and urban uses (Ontario Ministry of the Environment et al., 1990). Overfishing, habitat destruction, revised water levels, aquatic macrophyte changes and shoreline pollution adversely affected fish communities in bays around Burlington, Toronto (Whillans, 1979) and in the Bay of Quinte (Ontario Ministry of the Environment et al., 1990). In 1825, the Niagara River was diverted to the Erie Canal, followed by the 1829 opening of the Welland Canal linking Lake Ontario and Lake Erie and finally the 1859 opening of St. Lawrence Seaway, all connecting the upper Great Lakes and the Atlantic Ocean for shipping. Fertile lands were converted for lumber and agricultural products. Fishing increased and shoreline towns such as Hamilton, Niagara Falls, Toronto, and Rochester quickly became urbanized, industrial centers (Flint and Stevens, 1989). The advent of the long distance railway dramatically increased immigrants, commerce, and industry as had the Lake Ontario ships entering port at Toronto, which together enabled the city to become a major gateway linking the world to the interior of North America (Careless, 2002). By the 1930s the waters of Hamilton Harbour, which was a manufacturing center for iron, experienced increased concentrations of contaminants (e.g., chloride, ammonia, iron) from industrial and municipal waste and road salt (Threader, 1984). An exponential increase in P loading of Lake Ontario beginning in the late 1940s came from urban phosphate-based detergent use, expanding domestic sewering and agriculture (Schelske, 1991). Schelske (1991) also reported that organic carbon increased, and Si reserves were depleted via increased diatom production. Regulated water levels since 1959 with construction of the St. Lawrence Seaway reduced wetlands and coastal plant and wildlife diversity (JC, 1989; Wilcox et al., 1993). Whillans (1982) reported that the marshlands of the Canadian shoreline west of the Bay of Quinte declined by approximately 43% by the late 1970s. Emergent plants declined, submerged aquatic macrophyte beds increased due to hydrologic stabilization, algal abundance thrived on excessive nutrients, and invasive plants began dominating wetland communities (Ball et al., 2003). Makarewicz (1991) demonstrated that wind-induced turbidity plumes and upwelling were the most important variables affecting short-term fluctuations in the chemical, physical, and biological parameters in the nearshore zone of the lake. High sediment loads and increased turbidity, compounded by excessive nutrients and contaminants along with shoreline modification, are still major stressors on Lake Ontario’s coastal wetlands (Ball et al., 2003; Crowder et al., 1989; Painter et al., 1989). The direct discharge of industrial and municipal wastes and leakage of chemical waste from toxic waste dumps (e.g., Hyde Park, Love Canal) into the Niagara River also compounded pollutant accumulation in Lake Ontario (Allan et al., 1983). Human modifications, invasive species, and possible climatic influences extended to pelagic ecosystems as well, affecting all trophic levels including algal abundance and species composition.

Lake Ontario water chemistry has been greatly altered since European settlement (Beeton, 1965, 1966, 1969, 2002). Most early Lake Ontario monitoring studies that included phytoplankton observations were in bays or areas otherwise not representative of the pelagic water (Johnson and Matheson, 1968; Matheson and Anderson, 1965; Schenk and Thompson, 1965; Tucker, 1948), but they provided a better understanding of early anthropogenic impacts on water quality. Nearshore water quality studies were initially focused in the Hamilton area, the northern shore around Toronto and in the Bay of Quinte before expanding to include the pelagic regions. Beeton (1969) cited an increase in total dissolved solids from 1910 to 1965, along with the collapse of fisheries (e.g., lake herring, lake trout, blue pike) during 1955 to 1965, as evidence of the water quality degradation in Lake Ontario. The International Lake Ontario–St. Lawrence River Pollution Board (ILOWPB) (1969) reported that comprehensive geographic surveys indicated the water quality of Lake Ontario was morphometrically oligotrophic or mesotrophic because of its large area of deep water, with some eutrophic areas (e.g., Hamilton Harbour, Bay of Quinte, Toronto Harbour). The ILOWPB attributed 57% of total phosphorus (TP) loading to municipalities and industry and 33% from upstream Lake Erie, with detergent phosphates contributing about 70% of the entire TP input. Consequently, the Board recommended that phosphates be removed from detergents and that municipal treatment plants mandated to achieve a further 80% reduction in P levels (Stevens and Neilson, 1987).

Lake Ontario sediments have been studied by numerous researchers to calculate and compare sedimentation rates, estimate lake oscillations and flushing rates, determine primary productivity associated with nutrients, and understand the fate and transport effects of contaminants (e.g., Eisenreich et al., 1989; Hodell et al., 1998; Kemp and Harper, 1976; Kolak et al., 1998; Pearson et al., 1997; Robbins et al., 1978; Rosa, 1985; Schelske and Hodell, 1991; Schelske et al., 1988; Song et al., 2005). These lake sediments also recorded a long history of phytoplankton modification dating to the earliest European settlement (Duthie and Sreenivas, 1971; Kemp et al., 1974; Stoeermer et al., 1985a) with substantial alterations in the primary production base occurring well before similar changes at higher trophic levels (Beeton, 1969).

Hamilton Harbour

Yang et al. (1993) reported that initial eutrophication of Hamilton Harbour coincided with large-scale watershed settlement between 1700 and 1820 with a small peak in mesosaprobic taxa abundance around 1800 that inferred organic pollution. This complements the findings of Stoeermer et al. (1985a) who described mild eutrophication of the Lake Ontario system around 1780. Diatoms that reached maximum abundance in the harbor during this time were mesotrophic to eutrophic Fragilaria (Staur sighta) construens, F. (S.) construens var. venter (Bennion et al., 2004), and A. ambigua; eutrophic indicators A. granulata and Navicula (Cavinula) scutelloides [which is also found in mesotrophic to eutrophic conditions (Reavie et al., 2006)], while eurytopic A. islandica (reported as oligotrophic per Yang et al., 1993) declined. Between 1820 and 1926 evidence of increasing nutrient load and water contamination with expanding urban and industrial development were indicated by mesotrophic to eurytopic dominants: A. ambigua, F. (S.) construens, C. (H.) bodanica, T. fenestrata, F. (St.) pinnata; benthic Amphora ovalis var. pedalics; Stephanodiscus parvus which prefers eutrophic environments (Stoermer and Håkansson, 1984; Stoermer et al., 1985b); pollution tolerant S. alpinus; and F. (P.) brevistriata which is considered eutraphentic per Witkowski et al. (2009).

Water quality problems related to raw sewage were noted in Hamilton Harbour as early as the 1850s (Ontario Ministry of Environment and Environment Canada, 1992), Kindle (1915) reported observations of the green filamentous algae Cladophora profunda during 1914 at a depth of around 50 m, 25 km southwest of Presque Isle near Brighton, Ontario. Mackay (1930) and Neil and Owen (1964) described visual accounts of extensive pollution and algal growth (Cladophora) reported prior to the 1930s in localized areas of Lake Ontario (per Nicholls, 1980) such as the western end of the lake and around Toronto (Flint and Stevens, 1989). Hamilton Harbour became so polluted by sewage, oil, and other industrial inputs that swimming was banned during 1924 (Hamilton Spectator, 2006). With further human population expansion pollution accelerated in Hamilton Harbour between 1926 and 1961, eutrophic diatom indicators S. parvus and A. granulata increased in the sediment record from that time while some mesotrophic indicators [e.g., F. (St) pinnata, F. (S.) construens and C. (H.) bodanica] almost disappeared (Yang et al., 1993). During the 1960s meso-eutrophic and
eutrophic diatom abundance increased and included *Fragilaria capucina* which is found in areas of high nutrient loading (Stoermer, 1978) while many previously important species disappeared [e.g., *S. alpinus, Ma. (St.) martyi, Achnanthes spp.*, *A. ovalis var. pediculus*].

City of Hamilton sewage was discharged untreated into the harbor until a primary treatment plant was installed in 1964 (Johnson and Matheson, 1968). Matheson and Anderson (1965) reported that measurements from 1959 and 1960 indicated that Hamilton Harbour was the major pollution source in the western end of the lake. Johnson and Matheson (1968) found that no macroinvertebrates occurred in sediments with iron (ferric oxide) content greater than 25%, the origin of which was industrial waste discharge to the bay, or within 2 km² of sediments near steel mills. The authors attributed the differences between lake and harbor community diversity and abundance were at least partly due to the influence of municipal and industrial pollution in harbor sediments. The harbor was subsequently identified as one of the most polluted areas in North America by the Water Quality Board of the International Joint Commission (IJC, 1972).

**Main Lake Region**

Duthie and Sreenivasa (1971) reported that the timing of *Ambrosia* (ragweed) pollen concentration increases in their Rochester Basin sediment core correlated with extensive watershed forest clearing and human settlement that occurred around 1820 to 1830 per McAndrews and Boyko (1972). Increases in sediment diatom abundance with an increasing abundance of eurytopic–eutrophic species after the *Ambrosia* horizon indicated greater nutrient loading, likely from soil erosion and leaching associated with the clearing of forests. Oligotrophic *C. kuitzingiana*, oligotrophic to mesotrophic *C. (H.) bodanica*, and eutrophic *C. atomus* peaked before a subsequent overall decline after the pollen horizon period. Of the two most abundant species found in the core, *A. islandica* displaced the winter/early spring *M. (A.) subarctica*, which often appears with *A. islandica* but is less tolerant of nutrient stress (Wolin et al., 1988). Eurytopic *S. minutula*, which also has eutrophic affinities, also increased in abundance.

Stoermer et al.’s (1985a) Rochester Basin sediments subsequently cored in 1981 indicated that Lake Ontario was affected by mild eutrophication around 1769, an occurrence that was not correlated with a cored in 1981 indicated that Lake Ontario was affected by mild eutrophication, and the authors conjectured that Si limitation became the major pollution source in the western end of the lake. Johnson and Matheson (1968) found that no macroinvertebrates occurred in sediments with iron (ferric oxide) content greater than 25%, the origin of which was industrial waste discharge to the bay, or within 2 km² of sediments near steel mills. The authors attributed the differences between lake and harbor community diversity and abundance were at least partly due to the influence of municipal and industrial pollution in harbor sediments. The harbor was subsequently identified as one of the most polluted areas in North America by the Water Quality Board of the International Joint Commission (IJC, 1972).

Stoermer et al.’s (1985a) Rochester Basin sediments subsequently cored in 1981 indicated that Lake Ontario was affected by mild eutrophication around 1769, an occurrence that was not correlated with a known historical event. Impacts reduced total diatom production and nutrient sensitive *C. ocellata* but favored more nutrient-tolerant summer species [e.g., eurytopic *C. (H.) bodanica* per Stoermer (1978) and Stoermer and Ladewski (1978)] and winter flora such as *Stephanodiscus niagarae* which occurs under a wide variety of trophic conditions though it is most abundant in eutrophic areas of the Great Lakes (Stoermer, 1978). Subsequent to this event, primary production increased and the authors observed summer *Cyclotella* (Discostella) *stelligera*, which is tolerant of nutrient enrichment (Stoermer, 1978), and *Fragilaria crotonensis* which is eurytopic (Stoermer et al., 1985a) but also tolerant of eutrophication (Hartig, 1987; Stoermer, 1978).

Beginning at the *Ambrosia* horizon (approximately 1831–1847) diatom production increased including more eutrophic species (e.g., *C. stelligera*) and summer blooms of *Cyclotella comensis*, a species which is found more in oligotrophic lakes and can utilize low levels of Si (Stoermer and Kreis, 1980) and may favor high nitrate (NO₃⁻) concentrations (Stoermer et al., 1996). Microfossils deposited between 1855 and 1900 reflected increasing eutrophication, and the authors conjectured that Si limitation became important by about 1860. Some indigenous species declined including *F. (S.) construens var. minuta* [which appears to be associated with oligotrophic waters (Stoermer et al. 1985b)] and *Melosira (Hulacoceira) distans* (which also prefers oligotrophic habitats per Stoermer, 1978).

Duthie and Sreenivasa (1971) observed that after 1900 oligotrophic and mesotrophic diatom abundance continued to decline and *A. islandica*, a taxon that is currently forming large winter/spring blooms in Lake Erie (Reavie et al., 2014a), almost completely displaced the winter/early spring *A. subarctica*. Eurytopic *F. crotonensis* occurred near the core surface (we estimate the core collection in the late 1960s) along with *Stephanodiscus tenuis* and *Stephanodiscus hantzschii* which occur in enriched lakes (Nalewajko, 1967, 1966; Stoermer and Yang, 1970). The authors suggested that reduction in frustule abundance was due to increasing organic matter in the sediment promoting frustule dissolution, changing currents or most likely vastly greater sedimentation rates due to increased anthropogenic productivity. Duthie and Sreenivasa (1971) did not benefit from modern isotopic dating, so lower algal abundance in sediments does not necessarily reflect lower algal production. The authors concluded that an increase in eurytopic and eutrophic species through the 1960s in their upper core sediments suggested continued cultural eutrophication.

Between 1900 and 1945, Stoermer et al. (1985a) reported the extinction of oligotrophic *C. ocellata* and *S. transylvanica*, and *Fragilaria intermedia* var. *fallax*, which is common in oligotrophic regions (Stoermer and Ladewski, 1978). These species were replaced by widely trophic tolerant *Asterionella formosa* (Stoermer and Ladewski, 1978, 1976) and a documented indicator species of moderate N enrichment in oligotrophic alpine lakes (Saros et al., 2005), eutrophic *S. parvus,* and *Diatoma tenue* var. *elongatum* which is tolerant of highly eutrophic conditions and is indicative of high conservative ion loading (Stoermer, 1978). By 1920, Lake Ontario’s Rochester Basin species composition was substantially altered, and by 1945 the increase in seaweed and phosphate detergent usage resulted in extreme P loadings to the lake and Si depletion. Stoermer et al. (1985a) reported that increased P input lead to a sufficient increase in epiplanktonic production by non-siliceous phytoplankton species to “shade out” the deep plankton, including the elimination of some indigenous flora (e.g., *S. alpinus*). After 1945, the authors suggested that the further decrease in production or preservation of siliceous microfossils was due to year-round silica limitation which limits growth of even the most stenothermal diatoms. The preserved assemblage comprised a large portion of benthic and planktonic nearshore species such as meroplanktonic *Surirella angustia*, eutrophic *Stephanodiscus binderanus* (Stoermer et al., 1987), and nutrient-tolerant *Nitzschia* spp. which can use organic N substrates for maximal growth (Cholnoky, 1968).

Schenk and Thompson (1965), who studied the phytoplankton records of the Toronto Island Filtration Plant collected from lake intake water from 1923 through 1964, reported that annual mean algal quantity doubled between 1923 and 1953, with *Asterionella* prevalent during spring until 1937 when dominance switched to *Cyclotella* and *Melosira*. The earliest Lake Ontario phytoplankton composition and seasonal succession studies found species either tolerant of or requiring eutrophic conditions for growth (Stoermer et al., 1975). Ogawa (1969) and Reinwand (1969) sampled lakewide for phytoplankton and diatoms, respectively, although their collections were confined to September 1964. Ogawa reported that overall abundance of phytoplankton was low, but greater nearshore and green algae were more dominant than diatoms. Reinwand reported that diatom numbers were low with greater abundance nearshore. Widely trophic tolerant *A. formosa, F. crotonensis* and *T. fenestrata* were dominants in surface waters. Diatoms that dominated deep water included *Stephanodiscus astra* and *S. astra* var. *minutulus* (currently *S. minuta*), which are found in eutrophic waters (Grimes et al., 1984; Hutchinson, 1967; Kilham, 1971), and *F. crotonensis*. *Stephanodiscus minutulus* has a high P requirement with low optimum N:P and Si:P ratios (Lynn et al., 2000) and is found abundant during spring circulation (Bradbury et al., 2002). Reinward (1969) generally observed diatoms *S. binderanus* and *A. islandica* near the lake bottom and suggested an early spring/summer abundance that sank after thermal stratification. The abundance of *S. tenuis*, which prefers nutrient enriched waters, was low throughout Lake Ontario in 1964 but reported as the most abundant diatom during the subsequent spring by Nalewajko (1966).

Nalewajko (1966) and Sreenivasa and Nalewajko (1975) studied phytoplankton from Lake Ontario surface waters from 0.8 km south of Gibraltar Point (near Toronto) between January 1964 and July 1965.
Abundant diatoms were *S. tenuis*, *A. islandica* and *Diatoma elongatum* (*D. tenue var. elongatum*), with *S. tenuis* comprising about 87% of total phytoplankton during spring maxima with green algae (e.g., *Actin astrum hantzschii*, *Ankistrodesmus falcatus*) dominant (90%) during summer. Nalewajko (1966) then compared these results to adjacent and one midlake stations during late April 1965. Nearshore phytoplankton densities were 2 to 3 times greater than offshore (> 10 km) probably due to a thermal bar effect which develops 1 to 10 km offshore during spring and early summer and effectively isolates nearshore waters with higher nutrient loads from colder, offshore waters. Based on species abundance, Nalewajko (1966) concluded the lake was oligotrophic offshore, but nearshore dominance of *S. tenuis* indicated eutrophic conditions.

**Bay of Quinte**

Based on diatom accumulation rates, Stoermer et al. (1985b) estimated that the earliest European immigration to the Bay of Quinte watershed was around 1682, causing appreciable changes in floral composition but little quantitative effects or permanent alterations in the bay ecology. By the 1850s major accumulation increases in siliceous algae associated with heavy deforestation and poor agricultural practices provided quantitative evidence of rapid and severe eutrophication. This transitional period became dominated by eurytopic *A. formosa*, *F. crotonensis*, and *T. fenestra* and eurytopic *M. (A.) granulata*, *S. niagarae* and *D. tenue var. elongatum*, as well as some known pollution-tolerant taxa in the Great Lakes per Stoermer (1978): *S. purpureus*, and hyper-eutrophic *Actinocyclus normani* fo. *subalsa* (Stoermer, 1978). Overall diatom abundance then decreased. Oligo-mesotrophic *C. comta* [C. (H.) *bodanica*] increased in relative and absolute abundance around 1879; eutrophic diatoms remained abundant; and *Syndra* (Tabularia) *fasciculata*, found in areas of known industrial water and brine discharges (Stoermer et al., 1985b), occurred until 1888 corresponding to local mining. The massive influx of dissolved nutrients and sediments in the bay from anthropogenic activities resulted in high diatom production with rapid use of Si and greater microfossil preservation until about 1900, followed by a decline. Assemblage composition indicated increasing eutrophy and displacement of summer blooming species with those favoring Si-limited diatom growth. We interpret this as evidence of the beginning of summer Si limitation. Although siliceous microfossil flux decreased, by 1928 a hypereutrophic flora was established (Stoermer et al., 1985b). Bay waters were severely Si limited and thus production shifted to phytoplankton other than diatoms and chrysophytes, i.e. “soft” taxa that did not leave siliceous microfossils in the sedimentary record (Stoermer et al., 1985b). Absolute numbers of diatoms declined until 1956, possibly brought about by even greater P input, then slightly increased at the core top (1965).

Tucker (1948) studied summer phytoplankton populations during 1945 and 1946 in Adolphus Reach within the lower Bay of Quinte (Fig. 1) to understand productivity associations with whitefish populations. Although taxonomic determination was not at the species level, generally the diatoms *Melosira (Aulacoseira)*, *Tabellaria*, and *Fragilaria* were most abundant except in July when cyanobacteria, especially *Aphanizomenon* and *Microcysts*, were dominant. McCombie (1967) assessed phytoplankton in 1963 and 1964 in the same region and in the greater Bay of Quinte and reported that phytoplankton abundance was 100 times greater in the highly developed inner bay waters versus the waters at the mouth of the less developed and river-impacted outer bay.

Johnson and Owen (1970) reported mean relative phytoplankton dominance for 1967 and 1968 at locations east of Belleville to a location 8 miles offshore. Cyanobacteria decreased (65 to 18%) and diatoms increased (30 to 76%) from the upper bay to offshore Lake Ontario, corresponding with inner bay nutrients from municipal and industrial waters and land drainage that decreased lakeward with dilution. During 1968, the net input of 50% of lake water N and 85% of P were from municipal-industrial sources that Johnson and Owen (1970) suggested were controlling algal productivity. McCombie (1966) observed hypoxia during summer subsurface waters in the early 1960s. Low Secchi disc readings in the inner and middle bays also accompanied heavy algal abundance in 1967 and 1968 per Johnson and Owen (1970) that collectively confirmed cultural eutrophication of the Bay of Quinte and eastern Lake Ontario.

**1970s to Present**

Amidst growing concern over the continuing decline of water quality in Lake Ontario by sewage and industrial waste, the governments of Canada and the United States directed the International Joint Commission (IJC) to investigate and report upon the extent, causes, sources, and effects of pollution in the waters of Lake Erie, Lake Ontario, and the international section of the St Lawrence River and recommend the most practical remedial measures (ILOWPB, 1969). As a result, the Great Lakes Water Quality Agreement (GLWQA) between the United States and Canada was created in 1972 to mitigate effects of nutrient inputs on Great Lakes ecosystems (GLNPO, 1997). Vollenweider et al. (1974) modeled the correlation between P loadings, primary production, and algae (chlorophyll a) that served as the basis for establishing targets for P load reductions (Munawar et al., 2012). Mandated policies of the GLWQA and the subsequent 1978 TP reduction guidelines (IJC, 1988) resulted in significant declines of P and chlorophyll a concentrations in offshore waters (Dove, 2009; Dobson, 1994; Holeck et al., 2008; Millard et al. 2003; Nicholls et al., 2001). Oxygen exhibited an orthograde distribution in Lake Ontario pelagic waters, indicative of oligotrophic lakes (Wetzel, 1975). Dove (2009) reported that TP declined from 21 μg/L in 1975 to 7.82 μg/L in 2008. Spring nitrate plus nitrite–nitrogen (NO3 - + NO2 -) increased in the open waters of Lake Ontario from 245 μg/L in 1969 to 447 μg/L in 2008, although the rate slowed after 1987. The spring mean concentration of soluble reactive phosphorus (SRP) in the open lake decreased from a 15.3 μg/L in 1973 to 1.2 μg/L in 2001, but increased to 2.6 μg/L in 2008. Spring soluble reactive silica also increased from 0.04 mg/L during 1969, especially since 1993, to 0.91 mg/L in 2008. Unfortunately similar results were not realized in rivers, embayments, and some localized nearshore waters (Makarewicz et al., 2012d). Extensive urban/industrial and rural/ agricultural land use within the Lake Ontario drainage basin still continues to account for pollutants entering the lake including suspended solids, dissolved solids, bacteria, nutrients, metals, and trace organic contaminants.

Hartig et al. (1991) suggested that up until 1983 summer algae was limited by N, allowing N-fixing cyanobacteria an advantage over green algae and diatoms. By the early 1980s, the target P concentration level of 10 μg/L for Lake Ontario was achieved (Millard et al., 2003). Lean et al. (1987a) and Pick (1987a,b) demonstrated that soon after spring thermal bar formation nearshore plankton became P deficient but midlake plankton were not P deficient until stratification. Summer upwelling events and deep water column mixing apparently reduced the amount of P deficiency. Between 1981 and 1995 concentrations of P, algal biomass, and chlorophyll a declined considerably in eastern Lake Ontario, although in the midlake Mississauga Basin chlorophyll and algal biomass were not significantly altered (Johannsson et al., 1998). Along the northern shore *Cladophora* biomass declined by 58% from 1972–1983 which Painter and Kaimatits (1987) attributed to less SRP in response to strict P-abatement implementation strategies. However, by the late 1980s the invasion of the non-indigenous zebra mussel (Dreissena polymorpha), followed by the quagga mussel (*Dreissena bugensis*) during the early 1990s (Mills et al., 2003a), transformed the Lake Ontario ecosystem and altered the food web with changes that are still under study. Several researchers reported that large filter-feeding mussel communities increased water clarity and reduced water-column nutrients and phytoplankton density (Dermott, 2001; Hecky et al., 2004; Leach, 1993; Makarewicz et al., 1999) by direct and
indirect removal of a large portion of the algae that had previously settled offshore.

The Lakewide Management Plan (LaMP) Management Committee initiated a process in 2006 to create a binational biodiversity conservation strategy for Lake Ontario (LaMP, 2004). Recommended priority actions were to conserve watersheds and shorelines; reduce aquatic invasive species impacts and non-point source pollution; and restore the natural hydrology, water quality, and native species (Lake Ontario Biodiversity Strategy Conservation Strategy Working Group, 2009).

**Hamilton Harbour**

Yang et al. (1993)) reported from the paleolimnological record that the greatest change in microfossil composition in Hamilton Harbour sediments occurred after 1970. *Cyclorella meneghiniana*, a high nutrient indicator (Potapova and Charles, 2007), and eutrophic *F. capucina* and teratological forms of *S. niagarae* and *S. parvus* became dominant; several eurytopic species obtained maximum relative abundance (*A. normannii* fo. *subsalta*, *F. crotonensis*); and oligotrophic diatom species were rare. The authors attributed the shift in the siliceous microfossil assemblage structure to accelerated heavy metal contamination. Collectively, this shift indicated poorer water quality.

Long-term eutrophication issues in Hamilton Harbour were primarily manifested as excessive algal blooms, low transparency, and low hypolimnetic oxygen levels during the late summer (Charlton, 1997; Hiriart-Baer et al., 2009). Hamilton Harbour was designated as an Area of Concern by the IJC in 1987, and a remedial action plan was developed in 1992 with a set of actions intended to improve harbor water quality and environmental conditions (Environmental Canada and the Ontario Ministry of the Environment, 2011). Haffner et al. (1982)), who studied phytoplankton during 1977 in the harbor, suggested the water retention time was long enough to allow the algal population to adapt to and exploit nearshore nutrients, thus permitting greater phytoplankton abundance. *Harris and Piccinin (1980)* reported that the extremely high summer N:P ratios in the harbor favored green algal dominance and a prevalence of cryptophytes and chrysophytes. Although municipal sewage treatment discharge greatly improved, excessive eutrophication from P, ammonia (*NO₃*), suspended solids, and other contaminant loading still continues in Hamilton Harbour (Dermott et al., 2007; Gudimov et al., 2010). Dermott et al. (2007)) reported that eutrophication symptoms included offensive algal growths, poor water clarity and depleted oxygen. Hypoxia occurs in the hypolimnion of the harbor every year during the summer stratification period, and oxygen undersaturation also occurs in winter with extensive ice cover (Hiriart-Baer et al., 2009; Rodgers, 1998): Between May and October 2002, 2004, 2006, and 2007 Munawar and Fitzpatrick (2007) reported on phytoplankton succession in the harbor. Although high TP concentrations and extended durations of hypoxia in the lower thermal stratum reflected eutrophic conditions, phytoplankton biomass indicated a mesotrophic status. Algal dominants of greens (*e.g.*, *Coenochloris pyrenoidosa, Coelastrum reticulatum*), diatoms (*e.g.*, *S. niagarae, F. crotonensis*), cryptophytes (*e.g.*, *R. minuta, Cryptomonas reflexa*), and dinoflagellates (*e.g.*, *Gymnodinium helveticum, Ceratium furcoides*) varied, not always following expected seasonal patterns possibly due to ship traffic and wind and storm events.

Gerlofsma et al. (2007) observed that the zooplankton community in Hamilton Harbour from 2002 through 2004 reflected a highly productive and eutrophic system indicated by greater abundances of cladocerans and cyclopoïds, which are more abundant in the nutrient enriched waters of the Great Lakes (Gannon and Stemberger, 1978) compared to calanoids. Since the mid-1970s the zooplankton community changed to one less dominated by rotifers, which are a poor quality food source for fish (Warner, 1999), and with a higher biodiversity that indicated substantial improvement. *Gudimov et al. (2010)* developed a biogeochemical model that suggested the water quality goals for TP (17 μg/L) and chlorophyll a concentrations (5–10 μg/L) in Hamilton Harbour would likely be met by achieving a P loading target of 142 kg/day. *Munawar and Fitzpatrick (2011)* revised and applied the classical Vollenweider eutrophication models (Vollenweider et al., 1974) to provide guidance for remediation of beneficial use impairments. The revised models, based on the relationship between P loading and annual primary production, and the relationship between algal standing crop (chlorophyll *a*) and annual primary production indicated that Hamilton Harbour is hyper-eutrophic despite continued P abatement.

In summary, while there are disagreements in the harbor’s prevailing trophic condition, these studies collectively indicate that the harbor is still in a degraded condition that varies seasonally in trophic character. The Bay Area Restoration Council (2012) reported that cyanobacteria blooms in the harbor continued to occur annually from 2007 to 2012, causing beach closings. Public health officials issued advisories during August 2013 and August 2014 over the spreading and potentially toxic cyanobacteria (Fragomeni, 2014; Hayes, 2013).

**Main Lake Region**

*Munawar and Nauwerck (1971)* performed monthly lake wide sampling during 1970 to better understand seasonal phytoplankton abundance and composition. Annual average algae biomass was low and more homogeneously distributed in the central lake surface waters versus inshore where densities were 25% greater, more so in areas of major nutrient inputs or regions of upwelling (e.g., Toronto, near the outlets of the Welland Canal and Niagara River, north off Brighton and Murray Canal, south of Oswego). Diatoms dominated overall, but were more abundant inshore with species commonly found in eutrophic habitats. In decreasing order, diatoms, cryptomonads, green algae, and cyanobacteria were prevalent with diatoms comprising 80% of the biovolume during winter (e.g., *A. formosa, D. tenue var. elongatum, Su. angustata*) and spring (e.g., blooms of *S. hantzschii, S. binderanus* and *S. tenuis*) with green algae dominant during the summer (e.g., *Pediastrum simplex, Actinamira hantzschii*) and then fall (e.g., *Chlamydomonas globosa, Pedinomonas minusitissima*) along with cyanobacteria (*e.g.*, *Chroococcus dispersus var. minor, Oscillatoria limnetica*). *Stephanodiscus binderanus* comprised most of the nearshore spring phytoplankton biovolume. *Munawar and Munawar (1982)* later used a classification scheme for lake trophic status based on maximal and average algal biomass (Vollenweider, 1969), to suggest that Lake Ontario inshore and offshore waters were meso-eutrophic in 1970.

Under the International Field Year on the Great Lakes (IFYGL), Lorefice and Munawar (1974) focused an investigation during April and May 1972 on phytoplankton distributions at 45 stations between the Niagara River and the City of Rochester, NY in southern Lake Ontario. Diatom biomass showed an inshore to offshore decreasing trend except near the mouth of the Niagara River where the trend was opposite. Diatoms were dominant during April (e.g., *Su. angustata, S. binderanus, A. islandica subsp. helvetica, S. tenuis*) with flagellates increasingly abundant during May including *P. aciculiferum* and *Rhodomonas minut*a. The authors reported that *A. islandica* subsp. *helvetica*, which they claimed is more associated with oligotrophic conditions offshore, did not closely follow temperature contours of the thermal bar that possibly trapped nutrients nearshore. In contrast, eutrophic *S. binderanus* proliferated nearshore due to warmer temperatures and higher nutrients (as observed by Munawar and Nauwerck, 1971) and was likely responsible for inshore depletion of Si and orthophosphorus (per Munawar and Munawar, 1975a).

Extreme weather forced the IFYGL into 1973 (Stoermer et al., 1975). *Munawar et al. (1974)* analyzed phytoplankton collected between April 1972 and March 1973 at one nearshore station between Toronto and Cobourg and a mid-lake station in Mississauga Basin, consistently noting nutrient depletion due to spring and summer phytoplankton growth. Nanoplankton (< 64 μm) and small phytoflagellates dominated total phytoplankton biomass throughout the study period, an observation generally previously neglected due to limitations of sampling.
preservation, and enumeration of these smaller entities (Munawar et al., 1974; Pick and Caron, 1987). The < 20 μm fraction accounted for about 40% of total algal biomass at the midlake station during Munawar et al. (1974) study. Nearshore waters averaged 100% more phytoplankton biomass and 50% more chlorophyll a and photosynthetic activity compared to mid-lake (Munawar et al., 1974). Nearshore dominants were phytoflagellates (cryptomonads and dinoflagellates) with winter, spring and fall diatoms contributing up to 56% of total biomass, cyanobacteria at maximum (12%) abundance during July with green algae comprising 20 to 30% in September (summarized by Munawar and Munawar, 1975b). Diatoms dominated during cold periods (e.g., A. islandica subsp. helvetica, Stephanodiscus astreia var. minutula). Under stratified conditions maximum phytoplankton biomass, chlorophyll a and primary production occurred in the mid-thermocline region where phytoflagellates dominated. Munawar et al. (1974) found phytoplankton biomass was better correlated to chlorophyll a, and photosynthesis rates than cell densities, and they concluded that cell numbers provided poor information about primary production.

Stoermer et al. (1975)) also monitored the lake monthly for phytoplankton during the IFYGL from May 1972 through June 1973, reporting algal dominants reflecting degraded water quality, including potentially nuisance species. The authors observed a general pattern of spring bloom development and successional changes starting at the eastern and western lake ends, then spreading along the southern shore before becoming apparent along the northern shore, and eventually occurring in the mid-lake region. Stephanodiscus subtilis, which comprised 25% of diatom abundance, is characterized as preferring highly eutrophic and “slightly salty” waters (Cleve-Euler, 1951) and is otherwise described as S. parvus per Druart et al. (1987)) and resembles S. tenuis per Stoermer and Yang (1970). oligotrophic diatoms (e.g., C. comensis, C. comta and M. (A.) distans (Stoermer, 1978)) characteristic of the pelagic, low-nutrient waters of upper Great Lakes were few (Stoermer et al., 1975). Other dominants were A. formosa (22%), Stephanodiscus minutus (likely synonymous with S. minutulus) (10%), S. tenuis (9%), S. hantzschii (8%), and A. islandica (4%). The authors cautioned that use of monthly sampling periods may result in missing peaks in assemblages, as their results suggested considerable yearly differences related to weather conditions.

Stoermer and Ladweski (1978)) reviewed the IFYGL monthly offshore samples and reported that phytoplankton in a highly perturbed system such as Lake Ontario undergo rapid and complex responses to environmental forces such as weather events. Scavia (1979) subsequently developed an ecological model for Lake Ontario to help interpret the IFYGL data. He concluded that phytoplankton biomass was controlled by sinking, incoming solar radiation and vertical mixing in spring and fall, Si and P limitation during early summer and grazing by zooplankton in late summer. He reported that 87% of the P load to the stratified epilimnion during summer was due to regeneration processes taking place in that layer and due to rapid internal recycling rates; sufficient P levels were maintained for phytoplankton. Stoermer et al. (1985a) observed that the pollution tolerant diatom Ac. normanii fo. subsalsa reached maximum abundance in 1972 based on their Kingston Basin sediment core. The subsequent decline in diatom species associated with hypereutrophic conditions and increase in more eurytopic taxa (e.g., S. alpinus, A. islandica) near the core surface (after 1972) along with water chemistry records suggested P reduction provided some recovery in Lake Ontario. The authors concluded that P was a major driver of species succession, and they emphasized the importance of any particular species’ physical niche in determining its response to a modified nutrient supply (e.g., morphological changes in A. islandica suggesting decreasing Si:P ratios per Stoermer et al., 1985c).

Haffner et al. (1982)) hypothesized that a lake’s physical processes influence the biological activity of enclosed harbors, and this affected harbor responses to the nutrient control programs. Hydrologically isolated Toronto Harbour consists of a natural inner harbor and an artificially constructed outer harbor. Haffner et al. (1982)) collected phytoplankton bimonthly in Toronto Harbour from May to October in 1977. During the spring, A. islandica and S. hantzschii dominated nearshore waters within and outside of the harbor with a post-spring community of green algae and cryptophytes of mostly Cryptomonas erosa, Cryptomonas ovata, and R. minuta. The authors concluded that because Toronto Harbour water has a low residence time, the development of large standing crops was prevented despite a continuous input of nutrients. So despite known pollution issues, physical conditions in the harbor minimized algae blooms.

Munawar et al. (1987)) compared their lake wide phytoplankton samples collected from April to September 1978 with the 12-month, 1970 study results of Munawar and Nauwerck (1971). Between 1970 and 1978 total phytoplankton biomass decreased, particularly during the summer. Spring chrysophytes and dinoflagellates increased while diatoms and cryptophytes declined. Diatoms, which were spring and fall dominants during 1970, and flagellates increased during summer 1978 while green algae and cyanobacteria declined considerably, shifting summer dominance away from the cyanobacteria and green algae biomass observed previously.

In southeastern Rochester Basin, Makarewicz (1987) analyzed Oswego River (Fig. 1, the second largest inflow to Lake Ontario), harbor, and nearshore lake phytoplankton abundance and distribution during July through October 1981. He reported greater abundances of eutrophic S. tenuis, F. capucina, and Scedesmus in the harbor and river compared to the nearshore lake regions. Diatoms C. atomus, Cyclotella cryptica which prefers brackish water per Reimann et al. (1963)), and eutrophic C. meneghiniana were harbor and river mouth dominants comprising 37% of the total diatom abundance. Makarewicz (1987) pointed to potential chloride (Cl−) sources that provide salty environments favoring halophilic species including large, unpotted piles of de-icing salt at storage facilities adjacent to the Oswego River mouth; potash storage (Bertram, 1985); winter use of salt in the drainage basin; and the eventual outflow from an Onondaga Lake Chlor-al-kali plant (Effler et al., 1985). In addition, the ballast discharge of sea water from transoceanic ships may have provided a pathway for introduction of halophilic diatom species.

As phytoplankton studies were ongoing, reductions in nutrient flux and standing loads followed Clean Water Act mandates. The TP loading to Lake Ontario declined from 14,600 metric tons/yr in 1969 to 8,900 metric ton/yr in 1982 (Stevens and Neilson, 1987). Midlake spring TP responded rapidly from 1973 to 1982 to these reductions, decreasing 58%, while SRP decreased 66%. Stevens and Neilson (1987) reported that mean summer epilimnetic TP declined less, from 16.7 to 14.4 μg/L, and exceeded spring TP, suggesting that loading to the lake during the stratified period did not exhibit a similar decline. Spring NO3 + NO2 increased such that the N:P ratio elevated from 10 to 32.

Gray (1987) compared seasonal Lake Ontario phytoplankton biomass and composition variation between a northshore and midlake stations in the Mississauga Basin from April through November 1982 to similar stations sampled previously in 1970 (Munawar and Nauwerck, 1971) (Munawar et al., 1974). Overall mean biomass was 42% (nearshore) to 57% (midlake) less in 1982 than a decade earlier. Gray (1987) did not observe the high-nutrient M. binderana (S. binderanus), S. tenuis, S. hantzschii var. pusilla, and S. alpinus present in earlier studies (Munawar and Nauwerck, 1971; Nalewajko, 1967, 1966). During spring 1982 A. islandica and S. hantzschii were northshore dominants and A. islandica at midlake. F. flocculosa, found over a wide range of ecological conditions (Wolin et al., 1988), and S. astreata, which is an eutrophic indicator (Stoermer and Ladewski, 1976), were found during fall 1982 at the northshore station. Gray attributed the distinct nearshore and offshore community differences to physical events such as boundary currents intensified by summer storms that result in upwelling along Lake Ontario’s north shore.

Pick and Caron (1987) estimated the seasonal and vertical abundance of phototrophic and heterotrrophic nanoplanckton (2–20 μm) and picoplankton (0.2–2 μm) from April through November 1982 at a
northshore, midlake, and south shore station by epifluorescence microscopy. By late summer, picoplankton biomass represented 74% and pico-cyanobacteria 50% of total weight biomass of microorganisms < 20 μm, accounting for a substantial portion of primary production often missed or ignored in standard phytoplankton enumerations.

Based on a case study of data collected between 1970 and 1983 at a midlake Mississauga Basin station, Munawar et al. (1987) reported that the health of the pelagic phytoplankton had improved. A greater abundance of microalgae (<5 μm), ultraplankton (5–20 μm) which they reported were sensitive to metals and nutrients, and the highest chlorophyll/biomass and production/biomass ratios were observed in 1983 (Munawar and Munawar, 1975b; Munawar et al., 1978). Munawar et al. (1987) reported that changes in the pelagic species composition reflected the decrease in P concentrations particularly with the absence of eutrophic diatoms found previously (e.g., S. binderanus, S. minuta, S. hantzschii var. pusilla) and presence of species commonly found in oligotrophic Canadian lakes by Rawson (1956) (A. islandica, T. fenestrata, and A. formosa).

Wolin et al. (1991) found that Stoermer et al.’s (1985a) hypothesis that P reductions altered Lake Ontario’s phytoplankton was not adequately supported by more current data from the lake during the 1980s (IJC, 1987), reflecting greater pressures from growing human populations and industries and non-point source loading. Lean et al. (1987a, 1987b) did not observe a significant reduction in chlorophyll a during 1982 with reduced P loading. They attributed the control of algal biomass to the physical transport of lake water masses in lieu of nutrient loadings. Taylor et al. (1987) reported that Lake Ontario zooplankton measured in 1982 did not change in response to changes in nutrient loading and salmonid predators during the 1970s. To examine this discrepancy, Wolin et al. (1991) collected a surficial sediment core in 1987 from the Rochester Basin (Fig. 1), just northeast of the 1981 location cored previously by Stoermer et al. (1985a), to determine lake recovery according to siliceous microfossil shifts. In concurrence with Stoermer et al.’s (1985a) findings, Wolin et al. (1991) reported species tolerant of highly eutrophic conditions and high conservative ion loadings, e.g., Ac. normannii f. subsalsa, D. tenue v. elongatum, S. binderanus (Hustvedt, 1930; Stoermer, 1978; Wolin et al., 1988) from the late 1950s to early 1970s (Dobson, 1984; IJC, 1987). With the onset of nutrient loading reductions, Wolin et al. (1991) more recent flora and Stoermer et al.’s (Stoermer et al., 1985a) surface sediment (about 1976) flora reflected a decrease in eutrophic species. The high-nutrient Stephanodiscus binderanus, which was present in 1970 and 1972 (Gray, 1987) per Wolin et al. (1991), was absent in 1982 Lake Ontario phytoplankton samples.

Wolin et al. (1991) reported increased relative abundance in the 1987 sediment core top of the eurytopic A. formosa and A. islandica, and S. parvus and other smaller Stephanodiscus usually associated with eutrophication and early spring conditions (Lorence and Munawar, 1974; Stoermer, 1968; Stoermer and Ladewski, 1976). Synedra species common to more mesotrophic open lake conditions also increased. These indicators suggested that the water column periodically experienced Si limitation and a shift in species dominance to winter or early spring blooms that favor high Si supplied during vernal circulation. Even with the decline in hyper-eutrophic species that indicated some recovery, Wolin et al. (1991) emphasized that further reductions in P were necessary to remediate the lake.

Johannsson et al. (1998) associated P input reductions with declines in water column TP, algal standing crop, and zooplankton productivity between 1981 and 1987 in the Mississauga basin and the eastern Kingston basins. In contrast, Mills et al. (2003a) reported significant NO{sub}3 concentration increases from 1968 to 1987, paralleling N fertilizer application and probably resulting in summer P limitation in deep pelagic waters (Lean et al., 1987a, 1987b; Millard et al., 1996a). Millard et al. (1996b) also measured seasonal phytoplankton photosynthesis from 1987 to 1992 and compared results to locations from the 1972 Lake Ontario IFYGL. Phytoplankton photosynthesis had declined about 30% since the IFYGL, but algal biomass, as indicated by summer chlorophyll, did not respond to reduced P loadings. The authors reported that the decline in photosynthesis was not proportional to the 50% P decline because of the positive compensating effect that increased light penetration had on the depth of photosynthesis.

Substantial nearshore Lake Ontario chemical and biological changes followed the invasion of exotic zebra mussels (Dreissena polymorpha) in 1989 and quagga mussels (Dreissena bugensis) in 1991 (Mills et al., 2003a) from European transoceanic ship’s ballast water (Griffiths et al., 1991; Hebert et al., 1989; Mills et al., 1993). The dreissenid population exploded in the Great Lakes, fouling water intake pipes, disrupting water supplies and altering the ecosystem (Roberts, 1990), affecting industries, power plants and water supply facilities, and municipal wastewater treatment plants such as those at Grimsby, South Peel, and R.L. Clark around Toronto, Cobourg and Kingston (Nicholls, 2001; Winter et al., 2012) (Fig. 1). Dove (2009) reported that after 1989 open water spring TP concentrations declined based on data collected via Environment Canada’s Great Lakes Surveillance Program. However, from 2001 to 2008 mean SRP increased in the open lake, possibly due to selective filtration by mussels that take in particulate P and excrete dissolved P (Hecky et al., 2004). A major sink for calcium and magnesium was the precipitation and sedimentation of calcite, but after mussel establishment major ions that are utilized in mussel shells (e.g., calcium) declined, while elements such as magnesium, which is proportionally excluded in calcite formation, increased. Dove (2009) concluded that elevation of spring Si concentrations, which are indicative of a declining diatom population, suggested mussel proliferation while increases in N compounds (NO_{3{\text{-}}}NO_{2{\text{-}}}N) were likely a result of increasing watershed and atmospheric sources. Later, Dove and Chapra (2015) reported that NO{sub}3 deposition declined during the past 30 years and nonpoint source inputs (e.g., agricultural fertilizer usage or runoff) decreased. Dove and Chapra (2015) suggested the lakes are now adjusting to the decline in nitrate precipitation. Johannsen et al. (1994) also observed significant reductions in chlorophyll a by the early 1990s. Johannsson et al. (1998) attributed a decline in TP, particulate organic carbon, N, and chlorophyll a in the Kingston Basin and increased water clarity and SRP between 1987 and 1995 to dreissenid effects. Johannsson et al. (1998) also suggested that a zooplankton decline may be associated with the decrease in edible algal biomass, particularly cryptophytes. From a 1995 to 1997 survey of the lake and embayments, Hall et al. (2003) reported a lower yield of chlorophyll a per unit TP (decoupling) was consistent with mussel grazing in nearshore habitats compared to those offshore and in embayments.

To fulfill the Great Lakes Water Quality Agreement provisions the USEPA GLNPO has conducted annual, synoptic spring and summer surveillance monitoring from standard stations throughout the Great Lakes offshore waters since 1983 to detect changes reflective in quantity and quality of water parameters. Eight stations have been surveyed in Lake Ontario since 1986. These pelagic surveys include nutrient concentrations and phytoplankton abundance and species composition (methods are described in detail by US EPA, 2010) to aid in lake trophic status assessment. Barbiero and Tuchman (2001), who reported results collected under the surveillance program in 1998, observed a Lake Ontario spring diatom community overwhelmingly dominated by A. islandica, consistent with previous studies (Gray, 1987; Munawar and Munawar, 1975b, 1982, 1986; Munawar and Nauwerck, 1971; Munawar et al., 1974), with a green algae, cryptophyte and dinoflagellate summer community. Barbiero and Tuchman (2001) suggested that Lake Ontario supported a unique flora relative to the other Great Lakes that may be associated with its low Si levels. They found that phytoplankton communities did not align predictably along gradients of nutrients or productivity. In particular, spring communities in Lake Ontario were more closely similar to the less productive Lake Superior versus the more productive lower lakes.
The USEPA and Environment Canada funded a comprehensive Lake Ontario lower aquatic food assessment (LOLA) during 2003 and compared results with historical data collected by Canadian and U.S. sampling programs (Mills et al., 2003b). Green algae comprised 89% of spring phytoplankton abundance (#/mL) and cyanobacteria were highest during summer (70%). Diatoms (55%) and green algae (19%) dominated total phytoplankton biomass (μm/m³) during the spring 2003 while summer dominants were cyanobacteria (42%) and cryptophytes (17%). No significant differences were found in total phytoplankton abundance or biomass between nearshore and offshore habitats or east and west regions for either season. Mills et al. (2003b) stressed that the phytoplankton compositional changes between 1995 and 2003 were detrimental to ecosystems, suggesting spring diatom declines were likely impacting the invertebrates Diporeia, Mysis relicta, and copepods with the relative increase in summer cyanobacteria (a poor food source for zooplankton) and decrease in cryptophytes (a preferred food resource).

Diporeia density declines were first reported from the 30- to 90-m depth interval between 1990 and 1997 (Dermott and Geminiuc, 2003). Watkins et al. (2007) reported continued declines in 2003 but also observed declines at deeper (>90 m) depths for the first time. Mills et al. (2003b) found that few zebra mussels remained and quagga mussels dominated the benthic community at depths less than 90 m. To better understand the structure and function of the base of the Lake Ontario food web, Munawar et al. (2010) compared the microbial loop, chlorophyll a, phytoplankton biomass and size structure and primary productivity in the lakewide pelagic zone during spring and summer 2003. The authors found that more than 50% of the organic carbon was comprised of heterotrophic nanoflagellates (HNFs) (including some chrysophytes without chloroplasts) which are a poor quality food resource for zooplankton, and the carbon sequestered by HNF is likely unavailable to higher trophic levels. Munawar et al. (2010) reported that net plankton (>20 μm in size) had the highest carbon turnover rates. The authors concluded Lake Ontario was oligotrophic and healthy from a water quality perspective (with low P and chlorophyll a and high water clarity), but its microbial food web was unhealthy because of HNF dominance, low zooplankton abundance, and low quality food sources. Munawar et al. (2010) suggested that carbon or autotrophonous energy is sequestered by HNF, thus inhibiting energy transfer that would instead be available to zooplankton and passed up the food chain.

Large mussel colonies on shoals and nearshore have increased water clarity and diminished nutrients and phytoplankton density since 1990 (Leach, 1993; Markarewicz et al., 1999; Millard et al., 1999). Dense dreissenid populations on lake slopes can also reduce the amount of suspended planktonic “food” before transport to offshore depositional areas (Dermott et al., 2005). Hecky et al. (2004) proposed coastal dreissenid colonies reengineered nutrient recycling nearshore by serving as traps that shunt nutrients (e.g., P) via filter feeding and release to sediments as feces and pseudo-feces, making these nutrients more available for nearshore algae production such as Cladophora. Wilson et al. (2006) reported that dreissenids physically alter the lake environment by increasing hard surface availability, producing intermittent habitat between shells and live mussels, reducing particle re-suspension, altering optical conditions, and increasing sediment accumulation (Mills et al., 1996, 2003a; Vanderploen et al., 2002). Although there are no conclusive data for Lake Ontario, it is probable that filter feeding by dreissenids has caused a shift in size distributions of phytoplankton, as observed in Lake Erie (e.g. Munawar et al. (2005) suggested larger sized phytoplankton were being selectively grazed by dreissenids; Barbaro et al. (2006) found that after the mussel invasion in eastern Lake Erie small centric diatoms increased while the larger taxa F. crotonensis and the dinoflagellate Gymnodinium declined). Other studies also revealed that dreissenid impacts have shifted the Lake Ontario zooplankton balance. For example, Stewart et al. (2010) assessed changes in zooplankton biomass, production, and community composition before (1987 to 1991) and after (2001 to 2005) the dreissenid invasion, confirming the predictions that zooplankton productivity declined following dreissenid establishment (Hecky et al., 2004; Holeck et al., 2008; Johannsson, 2003). Holeck et al. (2008) also attributed low zooplankton biomass to poor food quality supplied by phytoplankton (e.g., cyanobacteria).

The LOLA was repeated during three seasons in 2008 through a binational collaboration to compare changes in nutrient concentration and food web configuration. Rudstam et al. (2012) reported that only the spring offshore TP and SRP levels increased between the two LOLA studies, but Ontario lake wide TP averages remained around the P target level (10 μg/L). Spring Si was similar and depleted by summer, indicating a continuation of spring diatom blooms in Ontario verses the concurrent declines in the upper Great Lakes. Most of the chlorophyll in the water column was located in a deep chlorophyll layer (DCL) at the thermocline, but these deep algae were not included in the LOLA assessment program. However, Twiss et al. (2012) sampled the lake in 2008 during summer thermal stratification and recorded a substantial DCL in the metalimnion comprising diatoms, chrysophytes, dinoflagellates, and small pico-cyanobacteria that represented a large portion of the phytoplankton biomass. They further reported that the productivity per unit chlorophyll was similar in the epi- and the metalimnion. Twiss et al. (2012) suggested that the deep chlorophyll maximum is as active a layer as the epilimnion during summer thermal stratification. Rudstam et al. (2012) found that although spring and fall chlorophyll a did not change between 2003 and 2008, summer epilimnetic chlorophyll a doubled, the proportion of autotrophic algae increased, and summer water clarity decreased. The authors also observed a decline in offshore epilimnetic zooplankton abundance, except during the spring. Rudstam et al. (2015) reported that between 2003 and 2008 the offshore epilimnetic crustacean zooplankton density declined by a factor of 12 and biomass by a factor of 5 during summer with smaller decreases during the fall. The authors reported that the decrease in crustacean zooplankton coincided with greater abundance of the invasive invertebrate Bythotrephes, suggesting possible predation or behavioral affects. Whole water column zooplankton density declined in the summer and fall by a factor of 4 with a fall biomass decline by a factor of 2, which Rudstam et al. (2015) attributed to a zooplankton community composition shift from a cyclopoid/bosminid-dominated community in 2003 to a calanoid-dominated community in 2008. Most of these are cold water species found in and below the thermocline associated with a DCL. Rudstam et al. (2012) concluded that due to spatial restructuring the Lake Ontario offshore ecosystem was becoming more similar to lakes Superior, Huron, and Michigan.

Cladophora is currently widely distributed across Lake Ontario shorelines, especially in the western region (LOSAAC, 2008; Malkin et al., 2008; Wilson et al., 2006). Wilson et al. (2006) estimated that Cladophora mats covered 57% of the Canadian shoreline lake bottom at 5-m depths and at 20-m depths in some locations during late August and early September 2003, suggesting that abundance is enhanced with proximity to point sources and dreissenids. Higgins et al. (2012) found that Cladophora growth rates on the southern and northern Lake Ontario shores are P limited, with P inputs from local watersheds likely driving patterns in abundance. They suggested that Cladophora production was more sensitive to P input after the dreissenid invasion as mussels can transform particulate P into bioavailable forms. Although nearshore dreissenid populations in 2008 (Pemuto et al., 2012) were lower than levels reported in 2003 (Wilson et al., 2006), large populations still persist (Howell et al., 2012).

Water quality changes since the 1980s through 2008 in Lake Ontario recorded during routine monitoring at four municipal water treatment plant intake pipes (Winter et al., 2012; near Toronto and on the south-western shore of the lake) were consistent with survey trends reported by Dove (2009), Holeck et al. (2008), and Millard et al. (2003). Winter et al. (2012) found that TP concentrations decreased dramatically then stabilized after 1996; Si and NO3−−NO2−N levels increased while Cl−
declined until the mid-1990s and then increased. Chlorophyll a and algal cell densities of cyanobacteria, green algae, and particularly diatom dominants which peaked in abundance in spring and late fall/early winter, significantly declined when dreissenids became established. Increasing annual Si concentration patterns were likely associated with dramatic decreases in diatom abundance reducing Si demand. Seasonal trends indicated melt water runoff as an important source of NO$_3$–N, and increased Cl$^-$ levels were attributed to more road salt application and land use. Since 2001 the Cl$^-$ concentration in the open waters of Lake Ontario increased from 20.3 mg/L to 22.3 mg/L in 2008 (Dove, 2009). Per Chapra et al. (2009), the most likely non-industrial source is road salt usage for highway deicing which has increased in the U.S. at a rate of 2–3% annually since the late 1970s (Kostick, 1993) with increases in the Province of Ontario at a similar or greater amount since the 1960s (Morin and Perchanok, 2003). Another source could be new industrial Cl$^-$ discharges that are not tracked by permit compliance databases (Chapra et al., 2009).

Under the GLNPO monitoring surveillance of the profundal zone of Lake Ontario, Barbiero et al. (2011) reported that between 2004 and 2009 no Diporeia were found at sites deeper than 90 m. They observed a Diporeia decline in Lake Huron even with much lower quagga mussel abundance, implying that dreissenids may not be directly involved in Diporeia reduction and that Diporeia at many sites have disappeared despite little direct contact with mussels (Nalepa et al., 2009; Watkins et al., 2007). Edlund and June (2011) analyzed Diporeia gut contents and fossil remains of diatoms from southern Lake Michigan onshore and offshore sediment cores between 1987 and 2009 to resolve historical conditions. They further reported that nearshore epilimnetic zooplankton assemblages. Holeck et al. (2010) reported that from 1995–2010 epilimnetic TP ranged between 6 and 11 mg/L in both nearshore and offshore waters with higher concentrations in embayments, and chlorophyll and water clarity were similar to 1990s levels, suggesting oligotrophic conditions. They further reported that nearshore epilimnetic zooplankton density and biomass were among the lowest ever recorded; a 99% reduction during the last three decades.

Reavie et al. (2014a) analyzed lake-specific pelagic phytoplankton trends throughout the Laurentian Great Lakes from 2001 through 2011, including seven stations in Lake Ontario. Lake Ontario phytoplankton biomass found did not significantly change over the 11-year study period, but summer cell densities largely attributed to cyanobacteria increased. The authors reported that spring relative densities of cyanobacteria declined and in 2007 assemblage composition shifted to relatively greater numbers of spring centric diatoms and dinoflagellates. Summer transitioned from the early to late 2000s to an increased relative dominance of dinoflagellates, pennate diatoms and small-celled cyanobacteria (e.g., *Aphanocapsa*). With the inclusion of 2012 data (Fig. 2) the pelagic phytoplankton revealed little discernible change in pelagic algal biomass in Lake Ontario from 2001 through 2012, but summer densities of cyanobacteria (e.g., *Aphanocapsa sp.*, *O. limnetica*) increased significantly (Kendall tests of the relationship between total algal abundance in all sample observations and year, $P < 0.05$, per Reavie et al., 2014a), particularly during 2012. Spring phytoplankton cell density and biomass were dominated by the small eutrophic diatom *S. parvus*, which had previously declined at the onset of P reduction (Stoermer et al., 1985a; Wolin et al., 1988). Other dominant centric diatoms included *S. hantzschii* and eutrophic forms of *S. alpinus*. Many *Stephanodiscus* spp. make use of abundant nutrients (e.g., P, Si) before nutrient limitation occurs later in the year. Both large-celled dinoflagellates *Peridinium* (which is cosmopolitan in hard waters but can also be found in waters of low pH and nutrients; Bak et al., 2012) and *Gymnodinium* (particularly *G. helvetica*, which inhabits diverse nutrient conditions per Munawar et al., 2008) were also spring dominants. These larger-celled taxa governed higher biomass calculations during spring and summer but not necessarily higher densities. Meso-eutrophic *Ceratium hirundinella* (Szlap-Wasielewski, 2006) comprised the greatest summer phytoplankton biomass, and eutrophic *D. tenuel vari. elongatum* was also a summer dominant by biomass. Eurytopic *F. crotonensis* was dominant based on both biomass and cell density. Cyanobacteria *O. limnetica* and particularly small-celled *Aphanocapsa*, which increased in 2012, dominated summer cell densities.

This higher spring diatom abundance in Lake Ontario is not yet explained, but it mirrors that occurring in Lake Erie’s central basin (Allinger and Reavie, 2013; Reavie et al., 2014a). The increasing numerical abundance of cyanobacteria in Lake Ontario may be due to changing nutrient flux and selective feeding by dreissenids as suggested by Kane et al. (2014) and Vanderploeg et al. (2001) in Lake Erie. Lozano (2011) reported that the benthic macroinvertebrate community of Lake Ontario has undergone a major transformation between 1994 and 2008. Although lake-wide average dreissenid densities in 2008 were lower than in 2003, dreissenids continued to expand in deeper waters, filtering 5% to 8% of the water per day at depths between 0 and 90 m. Pennuto et al. (2012) reported that quagga mussels comprised
about 99% of the nearshore mussel community during summer 2008. Vanderploeg et al. (2010) postulated that the filtering effect of dreissenids whether via the nearshore shunt or offshore sink reduces the delivery of P and carbon to the open water in Lake Michigan. Whether this applies to Lake Ontario is still under study, but there may be linkages to the changing structure of phytoplankton assemblages.

Recently, paleolimnological data revealed longer-term changes that were not detected in monitoring efforts. Preliminary analyses of two Lake Ontario sedimentary profiles collected from the Mississauga and Rochester basins in 2013 revealed the increase in the diatom Cyclotella sensu lato in recent decades (Allinger and Reavie, 2014), which has been recognized in freshwater lakes in arctic, alpine and temperate environments that otherwise have not been impacted by nutrient enrichment and other stressors (Rühland et al., 2008, 2010, 2015; Smol, 2008). The Lake Superior diatom community has recently shifted to a composition dominated by Cyclotella spp. (Shaw Chraïbi et al., 2014). Similar changes in the algae are now being observed in sediment core profiles from lakes Erie, Michigan, and Huron, even though the phytoplankton

![Fig. 2. Basin-wide averages of phytoplankton abundance in spring (April, top) and summer (August, bottom), from 2001 to 2012 at eight offshore stations in Lake Ontario. Integrated phytoplankton samples represented composite water samples taken from the homogenous water column (spring) or the euphotic zone (summer) (Reavie et al., 2014a). Algal cell densities (left) and biovolume (right) are presented. Numbers at the bottom of each absolute abundance bar indicate the number of samples averaged (those with 2 are from master stations only; Fig. 1), and below that are the relative abundances as proportions. Error bars represent a standard error of the sample totals. Taxon group codes are: BAC = centric diatoms, BAP = pinnate diatoms, CHL = chlorophytes (green algae), CHR = chrysophytes, CYA = cyanobacteria, PYR = pyrrophytes (dinoflagellates), UNI = unidentified entities. Data source: US Environmental Protection Agency Great Lakes National Program Office open lake water quality survey (US Environmental Protection Agency, 2010).]
assemblages in these lakes are greatly shaped by other stressors including nutrients, pelagic grazers, and invasive species. Rühland et al. (2015) identified climatically induced change in lake-ice cover with associated limnological alterations as primary drivers for hemispheric-scale increases in Cyclotella. More details on the magnitude and importance of this shift in Lake Ontario’s algal community are forthcoming, and many researchers are examining possible mechanisms for this worldwide increase in C. sensu lato (Catalan et al., 2013; Chen et al., 2014; Guinder and Molinero, 2013; Rühland et al., 2008, 2010, 2015; Saras and Anderson, 2014; Saras et al., 2013; Van Nieuwenhuyze et al., 2013; Winder et al., 2008). Additional studies to include the effects of nutrients, native and non-native and plankton community interactions, and physical properties of lakes affected by climate-related drivers will assist in understanding the role of bottom-up and top-down drivers affecting Lake Ontario. These recent studies highlight that paleo-limnological tools and contemporary empirical studies will allow for a richer understanding of multiple stressor effects on primary production including climate-driven changes.

Bay of Quinte

The Bay of Quinte algae and zooplankton densities between 1950 and 1975 were among the highest ever recorded for Canadian freshwater systems (Ontario Ministry of the Environment et al., 1990). The bay was identified by the IJC as a problem area due to excessive nutrient enrichment, nuisance algal growth, low dissolved oxygen in bottom waters, bacterial issues, and degraded benthic communities (GKR Consulting and French Planning Services, 2013). Nicholls (1980) reported that TP discharge to the Bay of Quinte was more than 50% less during 1978 than at the onset of water treatment discharge monitoring in 1972. Belleville water treatment plant records concurrently indicated algal densities in water intakes were 50–60% less. Based on monitoring data collected after 1971, total algal biomass dramatically declined in the inner bay around Belleville, especially in diatoms and cyanobacteria, coinciding with lower TP and increases in Si and NO3 (Nicholls, 1980).

The effects on Bay of Quinte phytoplankton from point source P reduction in the late 1970s and 1995 post-establishment of zebra mussels were studied by Nicholls et al. (2002). After P reduction, the total phytoplankton biovolume decreased by half with declines in green algae (66%), dinoflagellates (58%), diatoms (56%, particularly Aulacoseira), cryptophytes (52%), and mostly non-N-fixing cyanobacteria (26%). However, once dreissenids were established the biovolumes of total greens (42%), N-fixers and non-N-fixing cyanobacteria (51%), and dinoflagellates (55%) significantly declined. Diatoms maintained a consistently high abundance of Aulacoseira, but declines in numbers of Stephanodiscus, Synedra, and Tabellaria were observed. Nicholls et al. (2002) also emphasized that the only taxon to increase with zebra mussel colonization was the non-N-fixing cyanobacterium Microcystis, which increased 13-fold. Nicholls and Carney (2011) updated the Nicholls et al. (2002) assessment for the upper bay by including 9 more recent years of data and extending the analysis to similar phytoplankton data from the middle and lower Bay of Quinte from 1972 to 2008. The relative declines in phytoplankton densities were greater after the Dreissenina intervention than after the P loading reduction, whereas biomass reductions associated with P loading intervention were greater than post dreissenid establishment. Nicholls and Carney (2011) reported that the arrival of the mussels altered the trophic efficiency and ecosystem health integrity of the bay with desirable shifts (e.g., a decline in cyanobacteria Anabaenopsis and Oscillatoria; and undesirable effects, e.g., Microcystis dramatically increased particularly in the middle and lower bay).

Despite the positive effects of P reduction and the “clarifying” effect of dreissenids, recent data suggest a downturn in phytoplankton quality. Bay of Quinte trophic conditions were recently assessed by Munawar et al. (2012) by integrating structural, functional and chemical parameters into ecosystem health models that indicated continued eutrophication and phytoplankton community degradation, particularly primary production from nonpoint sources of P. One shallow station at Belleville was sampled biweekly from May through June from 2000 to 2008 for primary production, chlorophyll a, and species composition of phytoplankton and zooplankton. During July and August, they observed dominant cyanobacteria Anaabaena spiroides, Anaabaena circinalis, Anaabaena planktonica, and Microcystis aeruginosa which are strongly characteristic of eutrophic waters (Hutchinson, 1967; Munawar and Munawar, 1996). The dominant late-summer species was the cyanobacteria Lyngbya limnetica which outcompetes other algae for N if enough P is available and thrives in turbid, light-limited habitats (Reynolds, 1984; Salmasso, 2000; Scheffer et al., 1997).

Some targets developed for the Bay of Quinte beneficial use impairment (BUI) criteria since the bay was officially designated as an Area of Concern in 1986 have been met (Environment Canada and the Ontario Ministry of the Environment, 2011). Although phytoplankton species composition remains diverse, a prevalence of diatoms and inedible algae (including eutrophic species of Aulacoseira, Anaabaena, and Microcystis) and variable chlorophyll a results indicate BUI criteria have been achieved about 50% of the time since 2000 (GKR Consulting and French Planning Services, 2013). Bay conditions may never meet the current targets, as zebra mussels and cladocerans have a substantial impact on phytoplankton and zooplankton and were not accounted for in establishing the initial BUI target. As the bay supports a healthy and diverse fish community, the report recommended more thought into appropriate goals in a post-dreissenid environment (GKR Consulting and French Planning Services, 2011). Eutrophic conditions persist and large cyanobacteria blooms are still reported (e.g. Browne, 2014).

Summary

The last ~200 years manifested a substantial and repeated reorganization of the primary producers in Lake Ontario as a result of multiple anthropogenic drivers. Early oligotrophic and eutrophic phytoplankton were displaced by an increased abundance of eutrophic taxa with European settlement activities during the 1800s. By the 1930s phytoplankton production increased and dominant taxa reflected eutrophy and high conservative ion loading. With mandatory P input control during the 1970s, subsequent Si limitation, and increased NO3–NO2–N concentrations, the phytoplankton species succession indicated some recovery by the late 1980s. Subsequent monitoring data in Lake Ontario indicate decreases in P levels; increases in water clarity, spring Si and NO3, greater Cl– concentrations; declines in phytoplankton and zooplankton production and summer chlorophyll a; and a significant decrease in the invertebrate Diporeia since the early-1990s. Phosphorus and algae are significantly higher in nearshore areas versus offshore, and P occasionally exceeds the mandated 10 μg/L IJC goal for Lake Ontario. Pelagic phytoplankton data since 2000 suggest that although algal biovolume is stable, species composition is still shifting. The effects of dreissenids, including those now becoming established in deeper benthos, may be influencing the species composition of offshore phytoplankton. Impacts from nutrient modifications and non-native species have been demonstrated in Lake Ontario while other emerging issues compound ecosystem dynamics in the lake such as continued urban sprawl, chemical pollutants, agricultural intensification, land-use changes, climate change effects (e.g., temperature, water levels, storm intensities), habitat loss, and invasive species. Long-term and persistent stressors continue to have notable effects on Hamilton Harbour and the Bay of Quinte. To anticipate or resolve effects of stressors requires an understanding of relationships among pelagic phytoplankton, water quality, stressors, and other trophic levels. These emerging problems in the offshore planktonic food web warrant a better understanding of the underlying mechanisms. Advances in monitoring and paleolimnological technologies (e.g., Bouchard et al., 2011; Makarewicz et al., 2012d, Pienitz et al., 2009) can provide vital long-term evidence in order to inform management.


