

The state of Lake Simcoe (Ontario, Canada): the effects of multiple stressors on phosphorus and oxygen dynamics

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Abstract

Lake Simcoe, the largest lake in southern Ontario outside of the Laurentian Great Lakes, is affected by numerous stressors including eutrophication resulting from total phosphorus (TP) loading, climate change, and invasions of exotic species. We synthesized the long-term responses of Lake Simcoe to these stressors by assessing trends in water quality and biological composition over multiple trophic levels. Evidence for climate change included increasing thermal stability of the lake and changes in subfossil diatom communities over time. Although the deep water dissolved oxygen (O₂) minimum has increased significantly since TP load reductions, it is still below estimated historical values and the Lake Simcoe Protection Plan end-of-summer target level of 7 mg O₂ L⁻¹. Low deep water O₂ concentrations corresponded with a decline in coldwater fish abundance. Since 1980, some nutrient concentrations have decreased (spring TP) while others have increased (silica), but many show no obvious changes (ice-free TP, nitrate, ammonium). Increases in water clarity, combined with declines in chlorophyll *a* and phytoplankton biovolumes in Cook's Bay, were temporally consistent with declines in TP loading and the lake-wide establishment of dreissenid mussels as a major

component of the Lake Simcoe ecosystem. Using an investigative tool, we identified 2 periods when abrupt shifts potentially occurred in multiple parameters: 1986 and 1995–1997. Additional ecosystem level changes such as declines in zooplankton, declines in offshore benthic invertebrate abundance, and increased nearshore invertebrate abundance likely reflect the effects of invasive species. The interaction of these multiple stressors have significantly altered the Lake Simcoe ecosystem.

Key words: coldwater fishery, dreissenids, eutrophication, groundwater, hypolimnetic oxygen, nearshore shunt hypothesis, paleolimnology, phosphorus

Introduction

Lake Simcoe is the largest lake in southern Ontario, Canada, with the exclusion of the Laurentian Great Lakes. The lake provides drinking water for several municipalities and supports tourism and recreational activities that generated more than C\$200 million of annual revenue, including a large year-round recreational fishery (Palmer et al. 2011, Liddle and Moles Forthcoming). Since European settlement (~1796), the ecological health of Lake Simcoe has been degraded by human activities, particularly those associated with agriculture and urbanization. A collapse of the coldwater fishery in the 1960s and 1970s was attributed to anthropogenic total phosphorus (TP) inputs that increased algal production and resulted in low hypolimnetic oxygen (O_2), which limited the availability of suitable habitat for coldwater fish (Evans et al. 1996). In 2009, the Government of Ontario approved the Lake Simcoe Protection Plan (LSPP 2009), making Lake Simcoe the only lake in Canada with its own environmental legislation.

There are multiple stressors acting on Lake Simcoe. Observations from the last 3 decades show that climate change, eutrophication, increased shoreline development, changes in land use, and the introduction of invasive aquatic plant and animal species have and will continue to alter the ecosystem. Excessive loading of TP has been the most significant cause of water quality impairment in Lake Simcoe and its tributaries (Evans et al. 1996, Winter et al. 2007). As such, reducing the load of TP to the lake has been a primary objective of Lake Simcoe management initiatives since the 1980s (Winter et al. 2011). To date, the success of nutrient management efforts has been difficult to discern. Initially, loading seemed to decrease (Winter et al. 2007); however, the loading estimates and the lake monitoring data showed large interannual variability, likely due to differences in annual precipitation (OMOE and LSRCA 2009, O'Connor et al. 2011, Young et al. 2011), making changes over short time periods uncertain.

One of the greatest challenges to managing nutrient loads to the lake is the growing human activity in the

watershed, which over the past 30 years has seen increased shoreline development and significant increases in urban land use (Winter et al. 2007). Land use in the watershed is predominantly agricultural (47%) with approximately 2000 crop and livestock operations collectively generating more than C\$500 million annually (Winter et al. 2007). Agricultural operations include the province's largest cultivated marsh (the Holland Marsh), an extensive wetland that has been converted to polders for market gardening and drains into the southern end of Lake Simcoe (Cook's Bay) via the West Holland River. The south shore of Lake Simcoe forms the northern border of the Greater Toronto Area (Canada's largest urban centre at nearly 6 million people; Statistics Canada 2012), making it a popular recreational destination and home to commuters. Urban development (both residential and commercial) and roads account for 12% of the land use in the watershed, and continued expansion is expected (Winter et al. 2007). The municipalities within the Lake Simcoe watershed are among the fastest growing urban centres in Canada, expected to nearly double current population levels by 2031 (Palmer et al. 2011). Nutrient loads to the lake can also come from beyond the borders of the watershed; atmospheric deposition of P is a major nonpoint source contributing 25–50% of the TP load to the lake. Recent research has shown that atmospheric particulate transport from soils susceptible to wind erosion outside the Lake Simcoe watershed is a major contributor to the atmospheric P load (Brown et al. 2011).

The effects of invasive species on the structure and functioning of ecosystems are well documented globally and can result in the degradation of human health and wealth (Vitousek et al. 1997). More than 180 invasive species have been recorded in the Laurentian Great Lakes (Ricciardi 2006), and due to its proximity and connectivity through the Trent-Severn waterway, Lake Simcoe is vulnerable to invasion by these aquatic species. Arguably, the most ecologically significant recent invasion to Lake Simcoe has been that of the dreissenid mussels. Zebra mussels (*Dreissena polymorpha*) were first observed in the lake in 1994 and became abundant by 1996 (Evans et al. 2011). Quagga

mussels (*D. rostriformis bugensis*) were first noted in Lake Simcoe in 2004 and continue to maintain low densities throughout the lake (Ozersky et al. 2011a). Other invertebrate aquatic invaders to Lake Simcoe include the spiny water flea (*Bythotrephes longimanus*, established in ~1994; Kelly et al. 2013), the rusty crayfish (*Orconectes rusticus*, ~2004; Mason and Evans 2011), and the amphipod *Echinogammarus ischnus* (~2005; Kilgour et al. 2008). The invasive macrophyte *Myriophyllum spicatum* invaded Lake Simcoe in 1984, and by 2008 comprised 27.4% of the submerged aquatic vegetation (SAV) community by dry mass (Ginn 2011). Lake Simcoe has also experienced the introduction of several nonnative fish (Mason and Evans 2011), including rainbow smelt (*Osmerus mordax*, ~1962), black crappie (*Pomoxis nigromaculatus*, ~1987), bluegill (*Lepomis macrochirus*, ~2000), and most recently, the round goby (*Neogobius melanostomus*, ~2006).

It is difficult to isolate the ecological consequences of individual stressors in a heavily impacted system such as Lake Simcoe where climate change, changes in land use, nutrient control measures, and invasion by exotic species all occurred over the same time period. These overlapping factors have direct management implications as lake managers are constantly challenged to manage these systems in the face of multiple stressors and many unknowns. This type of situation can lead to “ecological surprises” resulting from the cumulative impacts of multiple anthropogenic stressors (Christensen et al. 2006). Here, we provide new insights into the identification of the relative importance of multiple stressors through the synthesis of ecosystem-level variables. In this observational study, we examined the temporal changes in physical, chemical, and biological attributes of a large, temperate, freshwater lake subjected to multiple ecosystem stressors. We incorporated information from multiple government agencies and academic institutions to form a holistic view of Lake Simcoe. The Lake Simcoe Protection Plan sets a target of 7 mg L⁻¹ volume-weighted end-of-summer hypolimnetic dissolved O₂ (VWHDO) concentration (LSPP 2009), which is required to maintain the coldwater fishery based on the metabolism of juvenile lake trout (Evans 2007); thus, management efforts are focused on constraining the TP levels to achieve this VWHDO target.

The objectives of this study were to analyze and synthesize long-term trends in multiple ecosystem variables, apply TP loading and O₂ profile models, and perform stable isotope and paleolimnological analyses of sediment cores to elucidate any overlying patterns in this heavily impacted ecosystem, with an emphasis on the effects of multiple stressors on hypolimnetic O₂ concentrations.

Study site

Lake Simcoe is a large, relatively shallow lake with a surface area of 722 km², shoreline perimeter of 303 km, mean depth of 16 m, and approximate volume of 11 × 10⁹ m³ (Winter et al. 2007). It is linked to Lake Huron (Georgian Bay) to the northwest and Lake Ontario to the southeast by the Trent-Severn waterway (Fig. 1). The Lake Simcoe watershed has a total area of 2899 km² and is fed by 35 tributaries, the majority of which originate in the southern portion of the watershed and flow northward before discharging into the lake (Palmer et al. 2011). The lake has an approximate flushing time of 11 years and empties to Lake Couchiching at its north end through a single outflow. The lake consists of the main basin (mean depth 14 m, maximum depth 33 m) and 2 large bays, Kempenfelt Bay on the west side of the lake (area 34 km², mean depth 20 m, maximum depth 42 m), and Cook’s Bay at the south end (area 44 km², mean depth 13 m, maximum depth 15 m; Fig. 1). The littoral zone of Lake Simcoe is dominated by hard substrates such as cobble, pebble, and boulder, with areas of sand and softer sediments in sheltered and deeper areas (Ozersky et al. 2011b). Detailed descriptions of the lake can be found in Palmer et al. (2011) and Young et al. (2011).

Methods

Sampling regimes and laboratory methodologies

Physical properties, water quality, algae, and zooplankton: The Ontario Ministry of the Environment (OMOE) monitored water quality in Lake Simcoe at 7 stations (C1, C6, C9, K39, K42, K45, and E51) from 1980 to 2010 in partnership with the Lake Simcoe Region Conservation Authority (Fig. 1). Sampling at one additional station (S15) began in 1985. The stations were sampled every 2 weeks through the ice-free season and reported as annual ice-free (May 1–Oct 31) means. Integrated samples were collected through the euphotic zone (lower depth determined as 2.5 times the Secchi disk depth) to a maximum depth of 15 m. The water chemistry parameters (TP, reactive silica, nitrate [NO₃⁻ + NO₂⁻], ammonium [NH₃ + NH₄⁺], chlorophyll *a* [Chl-*a*]), phytoplankton biovolumes (cyanobacteria, dinoflagellates, cryptomonads, euglenoids, chrysophytes, chlorophytes, diatoms), and zooplankton abundances (calanoids, cyclopoids, small cladocerans, large cladocerans) were analyzed following standard OMOE protocols (Winter et al. 2011, Kelly et al. 2013). Temperature and O₂ concentrations were also measured on each sample date with a profiler at 1 m increments. The stratification duration was calculated as in Stainsby et al. (2011), with Cook’s Bay, Kempenfelt

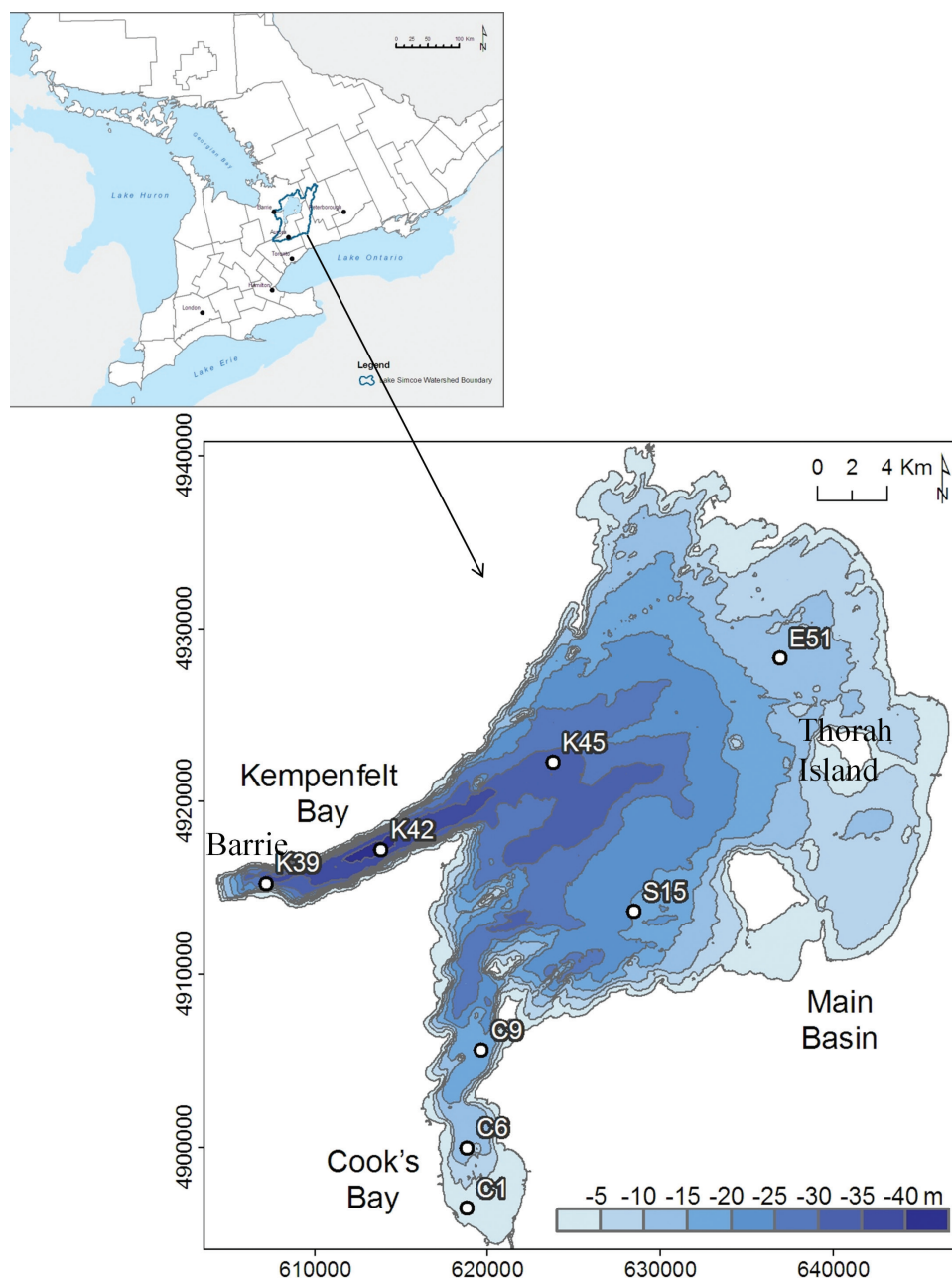


Fig. 1. Bathymetry of Lake Simcoe, Ontario, Canada, showing the 8 Ontario Ministry of the Environment (OMOE) long-term monitoring stations. Bathymetry information derived by OMNR from Canadian Hydrographic Service original depth sounding field sheet, 1957, scale 1:36 000. This map should not be relied on as a precise indicator of routes or locations, nor as a guide to navigation. The OMNR shall not be liable in any way for the use of, or reliance upon, this map or any information on this map.

Bay, and the main basin represented by stations C9, K42, and K45, respectively (Fig. 1). A single whole-lake value of TP concentration was calculated based on the spring (mean of ~3 sampling dates from ice-off to June 20) TP concentrations when the water column was assumed to be fully mixed (Nicholls 1997, Young et al. 2011). To calculate volume-weighted concentrations, the volume (based on area [m^2] in 1 m depth intervals) of the lake

sector represented by each of the 8 monitoring stations (as delineated and computed by Nicholls 1997) was calculated and used consistently across the long-term dataset. For water chemistry, Secchi depth, and Chl-*a* datasets, Cook's Bay, Kempenfelt Bay, and the main basin were represented by stations C1, K42, and E51, respectively (Fig. 1). Minimum volume-weighted hypolimnetic dissolved O_2 (MVWHDO) concentration was the lowest calculated

VWHDO value on or before 15 September (end-of-summer date) at station K42. The hypolimnion was consistently defined as 18 m to bottom (the tropholytic zone, as calculated based on the morphometry of Lake Simcoe by Nicholls 1997), regardless of possible year-to-year changes in its depth. Phytoplankton biovolumes were averaged across the long-term monitoring stations in each area of the lake, with Cook's Bay represented by stations C1, C6, and C9; Kempenfelt Bay by K42 and K39; and the main basin by K45, S15, and E51 (Fig. 1). Zooplankton abundance was represented by station C9 for Cook's Bay, K42 for Kempenfelt Bay, and K45 for the main basin (Fig. 1).

Benthic communities: The SAV survey followed the methods of Ginn (2011) and included 2008 survey data (215 sites) as well as additional annual samples (20 sites) collected in fall 2009–2011.

We compared the results of quantitative benthic invertebrate surveys from both the nearshore and offshore areas of the lake in 1926, 1983, 1993, 2005, and 2008 (see Table S1 for methodological details). We defined nearshore sites as ≤ 7 m and offshore sites as > 19 m in depth. Densities were standardized to abundance per unit area for comparative purposes.

Crayfish relative abundance was determined using baited wire-mesh minnow traps set on rocky habitat at 2, 4, and 6 m in the main basin of Lake Simcoe during 13 July–18 August 1993, and again from 22 July–3 September 2009. The mean catch per trap is expressed as the number of crayfish captured per trap over a 24 ± 2 h duration. Groupings of 4 traps were set at each depth on a single occasion at each of 14 sampling sites during 1993 and 2009; 10 of those sites were sampled in both years (D.O. Evans, OMNR, 2012, unpubl. data).

Dreissenid distribution data were compiled from sampling by 6 different research groups at 834 locations between 2005 and 2010 (Kilgour et al. 2008, Jimenez et al. 2011, Ozersky et al. 2011a, Rennie and Evans 2012) with collection methods referenced within. In 2009–2010, 624 samples were collected throughout the lake with a Petite Ponar grab and processed on 500 μ m mesh sieves to obtain estimates for shell-free dry mass (B. Ginn, LSRCA, 2012, unpubl. data). Dreissenid density was estimated for sites where only biomass data were available (724 sites), and biomass was estimated for sites where only density data were available (110 sites). These estimates were based on the following assumptions (Patterson et al. 2005, Ozersky et al. 2011a): (a) mussel biomass consisted of 7% small mussels (~ 5 mm length), 36% medium-sized mussels (~ 15 mm length), and 57% large mussels (~ 25 mm length); (b) the different size classes had a different dry weight per individual: 0.0008 g individual⁻¹ (small size), 0.0084 g individual⁻¹ (medium size) and 0.027 g

individual⁻¹ (large size); (c) mussel density consisted of 65% small mussels, 30% medium-sized mussels, and 15% large mussels. Data from the 834 discrete sampling sites were interpolated across the lake with the geostatistical gridding method of kriging (Isaaks and Srivastava 1989) using the default variogram model settings in the commercial software Surfer (grid-based mapping program that interpolates irregularly spaced XYZ data into a regularly spaced grid). The grid was then filtered through a Boolean mask of the lake boundary, which guarantees valid grid cell values inside the shoreline. The 500 m resolution used for the interpolated grid matches the bathymetric dataset implemented for the numerical modeling of the lake.

Fish populations: Fish communities were described by both summer and winter surveys. The warmwater (nearshore) fish community data were collected using the Nearshore Community Index Netting method as part of a provincial monitoring program (Stirling 1999). The study encompassed the lake and island shoreline of south-eastern Lake Simcoe. Fish were captured using a 1.8 m trap net set in the littoral zone for ~ 24 h. All fish were identified to species level and counted. Some of these data were previously reported by Robillard (2010) for the period 1992–2007. Estimated winter angling effort and angling catch data spanned the period from 1961 to 2010 and were adjusted to a standard 50-day fishing season to allow interannual comparisons of the angling effort and catch of recreationally important species. Winter roving, randomly stratified creel survey projects were performed every 1–5 years as described in Liddle and Moles (Forthcoming). Angling effort and catch estimates were generated through FISHNET v.2 software (Lester and Korver 1996). Some of these data were previously reported by Evans and Waring (1987) for the period 1961–1983, by Evans et al. (1996) to 1993, and by McMurtry et al. (1997) to 1995.

Bird populations: Water bird data, including cormorants, were obtained from a variety of sources including the Ministry of Natural Resources (MNR) Cormorant count, MNR Heron count, MNR Winter Waterfowl count, Marsh Monitoring Program, Christmas Bird Count, Ontario Breeding Bird Atlas, Project Feeder Watch, Species at Risk Records, and Great Backyard Bird Count (K. Gee, OMNR, 2012, unpubl. data).

Model descriptions

Two TP concentration-loading models were used to predict how changes in TP loading were expressed as lake TP concentrations. The models were evaluated using long-term (1999–2008) volume-weighted spring, volume-weighted ice-free, and areally weighted ice-free TP con-

centrations, and tested in the whole lake, Cook's Bay, Kempenfelt Bay, and the main basin. The steady-state Dillon-Rigler TP model (Dillon and Molot 1996) assumes no internal loading, treating each basin as a separate lake, and estimates a settling coefficient, a mass transfer coefficient describing removal of P to sediments expressed as m yr^{-1} (Dillon and Molot 1996) for each basin. The LakeMab/LEEDS model described by Håkanson and Bryhn (2008) is a process-based mass-balance model, based on ordinary differential equations regulating inflow, outflow, and internal fluxes with a temporal resolution of 1 month to reflect seasonal variations.

Three hypolimnetic dissolved O_2 (HDO) profile models were also evaluated using long-term (1998–2008) HDO concentrations obtained by the OMOE with a Yellow Springs Instruments (Ohio, USA) profiler (1 m intervals) from stations K42 (Kempenfelt Bay; Fig. 1) and K45 (main basin; Fig. 1; Lin 2010). The models tested were empirical multivariate regressions (Molot et al. 1992) used to predict end-of-summer HDO using a steady-state model based on lake morphometry and spring TP concentrations. We also applied the model of Uchmanski and Szeligiewicz (1988), a semiductive framework combining empirical volumetric hypolimnetic O_2 depletion rate (VHOD) and profile models. The third model used was based on the definition of the relative O_2 loss defined by Hutchinson (1957) and involved a deductive model for the areal hypolimnetic O_2 depletion rate (AHOD) developed by Livingstone and Imboden (1996).

Sediment core datasets

The oxygen and hydrogen isotope compositions of sediment porewater, surface water, and groundwater were compared to investigate the possibility of deep-water submarine hollows in Kempenfelt Bay. In June 2007, 2 piston cores were collected: core PC1 from Kempenfelt Bay (core length, ~ 5.1 m; water depth, 24 m) and core PC5 from the northwest region of the main basin (core length, ~ 7.6 m; water depth, 21 m). The cores were subsectioned into ~ 1 m long segments, capped, and sealed. Lake Simcoe surface water samples were also collected at both coring sites and a water sample was collected from an artesian spring overflow located in Hawkestone, Ontario. Groundwater samples were collected in the fall and winter of 2011 and 2012 respectively, from the 10th Line Essa Monitoring Well and 3 deep City of Barrie municipal drinking wells. The extraction of porewater from the sediment as well as oxygen and hydrogen isotope analyses of all of the samples followed the methodology of Macdonald (2012). The oxygen and hydrogen isotope data are reported in the delta (δ) notation in parts per thousand (‰) relative to Vienna Standard Mean Ocean

Water (VSMOW; Coplen 1996). Means from replicate determinations of standards for $\delta^{18}\text{O}$ (EDT, $n = 44$; MID, $n = 18$) and $\delta^2\text{H}$ (EDT, $n = 10$; MID, $n = 8$) were within accepted limits. The standard deviation for replicate analysis of unknown samples was better than $\pm 0.1\text{‰}$ (^{18}O , $n = 13$) and $\pm 2\text{‰}$ (^2H , $n = 13$).

Chironomid- and diatom-based paleolimnological techniques were used to assess long-term changes in water quality using two ^{210}Pb -dated profundal sediment cores collected in 2007 from the main basin and Kempenfelt Bay. Both cores were analyzed for chironomids as described in Rodé (2009) and for diatoms as in Hawryshyn et al. (2012). The chironomid and diatom assemblages were used to qualitatively track historical water quality trends through an examination of their compositional changes (Rodé 2009, Hawryshyn et al. 2012).

Data analysis

An abrupt shift (AS) analysis (sequential t -test STARS; Rodionov and Overland 2005) was used to investigate the possibility of AS in the long-term datasets for a selection of the examined variables. The STARS test uses sequential t -tests to search for changes of a specified magnitude over a chosen number of years (the “cut-off length”), with the caveat that the probability of finding an AS increases as the length of the entire time series increases. Mean annual values were tested using a threshold significance level of $p = 0.05$ and a cut-off length of $L = 5$ years, meaning that all shifts detected were bounded by time periods with a 5-year duration. If STARS detected a shift, the mean of the years before and after the shift was reported to reflect the direction of change. If an AS was not detected, we proceeded to test for long-term monotonic trends with Mann-Kendall trend tests and reported on the Sen's slopes to show directionality of trends. For Mann-Kendall trend analyses, p values were corrected for potential false discovery rates based on the significance level of 0.05 (Benjamini and Hochberg 1995).

Results

Trends in physical and water quality parameters and modeling results

The duration of stratification increased between 1980 and 2010, and an AS was detected in 1995 in all 3 basins of the lake, with an additional shift occurring in Cook's Bay in 1987 (Table 1; Fig. 2).

Whole lake spring TP concentrations experienced an AS in 1997, resulting from a decline of 4.1 mg L^{-1} from the 1980–1996 time segment mean to the 1997–2010 mean (Table 1; Fig. 3). Ice-free TP concentrations only

experienced declines in Kempenfelt Bay, with an AS detected in 1986. No long-term changes occurred in either Cook's Bay or the main basin (Table 1; Fig. 4).

There was a reduction in estimated TP loadings for the hydrological years 1990–1991 to 2006–2007 (the period for which data were available; Winter et al. 2002, 2007, OMOE and LSRCA 2009). Phosphorus loads varied during this period from a maximum of 157 t yr⁻¹ in 1990–1991 to a minimum of 53 t yr⁻¹ in 2001–2002. As reported in Young et al. (2011), the estimated loading was consistently lower since the 1998–1999 hydrologic year, and neither the STARS AS nor Mann-Kendall monotonic trend analyses showed ASs or significant trends from 1998–1999 to 2006–2007 ($Q = 0.74$ metric tonnes yr⁻¹, $p = 0.329$). Trends in TP loadings were temporally consistent with the changes in spring TP concentrations.

An AS in 1996 was detected for the MVWHDO concentrations calculated at the deepest station in the lake, K42. The MVWHDO concentrations increased from a 1980–1996 mean of 3.22 mg L⁻¹ to a 1997–2010 mean of 4.99 mg L⁻¹, and in 2010 the MVWHDO concentration was 5.08 mg L⁻¹ (Table 1; Fig. 3). The target concentration of 7 mg O₂ L⁻¹ required to maintain the coldwater fishery has only been achieved once (2005) since records began. There seems to be some correspondence between the declines in TP loading, spring TP concentrations, and increases in MVWHDO concentrations, which all occurred in the mid-1990s.

Multiple ASs were detected in each basin of the lake for reactive silica (Si) concentrations, resulting in 3 periods of increasing means for Cook's Bay, and in both Kempenfelt Bay and the main basin the means more than doubled from the 1980–1996 time segment mean to the 1997–2005 mean, followed by an overall decline in the mean in the 2005–2010 time segment, although, increases have been observed in recent years (Table 1; Fig. 4). There were no changes in nitrate concentrations in both Cook's Bay and the main basin; however, an AS was detected in 2004 in Kempenfelt Bay consistent with an increase in nitrate concentrations. Long-term changes in ammonium concentrations occurred in the 2 bays, but not in the main basin of the lake. In Cook's Bay, the AS in 1991 was consistent with an increase in ammonium concentrations, but the subsequent shift in 1997 tracked ammonium declines. Declines in ammonium concentrations also occurred in Kempenfelt Bay in 1986. Increases have been again observed in recent years for all basins (Table 1; Fig. 4).

The 2 TP load-concentration models (Dillon-Rigler and LakeMab) used to predict how changes in TP loading affect lake TP concentrations gave comparable results for whole-lake TP reduction scenarios even though the models were constructed differently. There was close

agreement between the Dillon-Rigler steady-state model for whole-lake predictions and observations using annual, volume-weighted spring and ice-free TP concentrations, with observed TP values within 2.8 mg L⁻¹ (22 %) of model predictions. However, the Dillon-Rigler model is a steady-state model and is not ideal for predicting

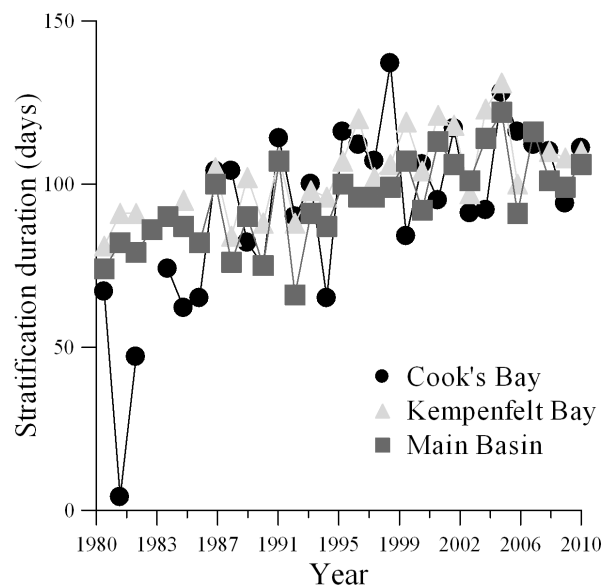


Fig. 2. The length of the stratified period displayed as the number of days in Cook's Bay (circles), Kempenfelt Bay (triangles), and the main basin (squares) for each year from 1980–2010.

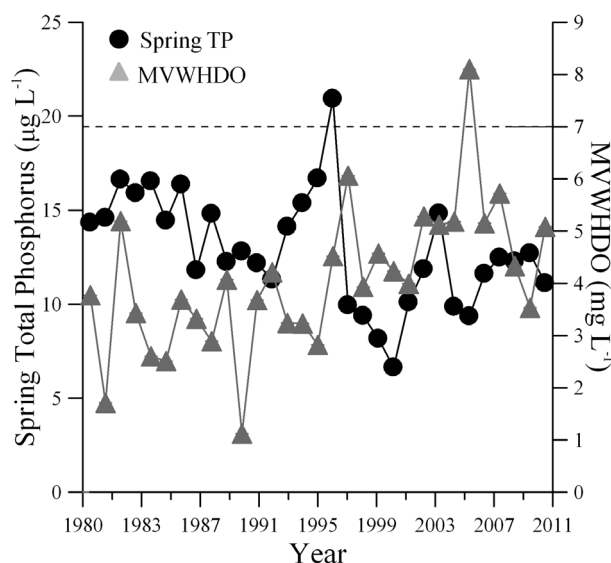


Fig. 3. Temporal (1980–2010) trends in spring total phosphorus concentration (mg L⁻¹; circles) volume-weighted across all 8 stations, and minimum volume-weighted hypolimnetic dissolved oxygen (MVWHDO) concentration at station K42 on 15 Sep (mg L⁻¹; triangles). The dashed line represents the target MVWHDO concentration of 7 mg O₂ L⁻¹.

Table 1. Detection of abrupt shifts (AS) and trends in long-term annual ice-free mean values from stations located in Lake Simcoe, including physical trends (1980–2010: Cook's Bay, 30 yr; Kempenfelt Bay, 28 yr; and main basin 31 yr), water quality parameters, and major phytoplankton (1980–2010: 31 yr trends), zooplankton (1989–2010: 22 yr trends), and warmwater fish (1992–2010: 19 yr trends) groups. The years that STARS AS occurred and the mean of each identified time segment, shown chronologically, are reported. If a significant AS was not detected, Sen's slopes (Q) were reported, showing the changes in units per year (e.g., Secchi Disk [m yr⁻¹]) from Mann-Kendall (MK) monotonic trend tests. A hyphen indicates that no AS was detected.

Parameter		Units	Cook's Bay	Kempenfelt Bay	Main Basin	Whole lake
Physical						
Stratification duration	AS	year days	1987, 1995 53, 92, 108	1995 94, 112	1995 85, 104	
Water Quality						
Spring TP	AS	year µg L ⁻¹				1997 14.8, 10.7
TP	AS	year µg L ⁻¹	–	1986 16.6, 13.9	–	
	MK	Q	–0.18		0.00†	
Si	AS	year mg L ⁻¹	1996, 2001 0.57, 1.00, 1.25	1997, 2005 0.53, 1.20, 1.03	1997, 2005 0.50, 1.17, 1.04	
Nitrate	AS	year mg N L ⁻¹	–	2004 0.024, 0.035	–	
	MK	Q	0.00†		0.00†	
Ammonium	AS	year mg N L ⁻¹	1991, 1997 0.023, 0.045, 0.031	1986 0.048, 0.016	–	
	MK	Q			0.00†	
MVWHO	AS	year mg L ⁻¹		1996 3.22, 4.99		
Secchi Disk	AS	year m	§	1996, 2002 4.5, 5.8, 6.9	1996, 2002 3.8, 6.6, 7.6	
Chl- <i>a</i>	AS	year µg L ⁻¹	–	2000, 2009 2.3, 3.0, 1.3	1986, 2009 2.6, 1.9, 0.7	
	MK	Q	–0.14*			
Phytoplankton						
Cyano	AS	year mm ³ m ⁻³	1992 58, 29	1986 64, 15	1986 45, 17	
Dino	AS	year mm ³ m ⁻³	1997 69, 23	1990, 1995 39, 73, 20	1982, 1996 64, 32, 17	
Crypto	AS	year mm ³ m ⁻³	–	1991, 2001 62, 41, 79	1984, 1988 28, 47, 36	
	MK	Q	–1.14			
Eugleno	MK	Q	0.00†	0.00†	0.00†	
Chryso	AS	year mm ³ m ⁻³	–	2005 15, 43	–	
	MK	Q	–0.64		0.33	
Chloro	AS	year mm ³ m ⁻³	–	–	1986, 1996, 2004 29, 13, 4, 11	
	MK	Q	–1.00*	–0.61*		

Parameter		Units	Cook's Bay	Kempfenfelt Bay	Main Basin	Whole lake
Diatoms	AS	year mm ³ m ⁻³	1987, 1997 898, 547, 249	–	–	
	MK	Q		1.84	2.71	
Total	AS	year mm ³ m ⁻³	1987, 1997, 2006 1279, 778, 381, 695	–	–	
	MK	Q		1.25	–0.25	
Zooplankton						
Calanoids	AS	year # m ⁻³	–	1999 26885, 11640	1997 29675, 15607	
	MK	Q	–1041.8*			
Cyclopoids	MK	Q	–267.28	–246.84	–314.11	
Small cladocerans	AS	year # m ⁻³	–	–	2007 4383, 2314	
	MK	Q	–156.60	5.24		
Large cladocerans	AS	year # m ⁻³	1996 8415, 5383	2000 3980, 1990	1994, 2001 5329, 3508, 2092	
Warmwater Fish						
Rockbass	AS	year Catch (24 h) ⁻¹				2004 26.1, 32.1
Pumpkinseed	AS	year Catch (24 h) ⁻¹				2008 10.1, 6.0
Yellow perch	MK	Q				0.22
Smallmouth bass	AS	year Catch (24 h) ⁻¹				2007 11.4, 3.8
Largemouth bass	MK	Q				–0.01
Black crappie	MK	Q				–2.76

MK monotonic trends that were significant at $p < 0.05$ and after correcting for false discovery rate are printed in bold and with an asterisk (*), respectively.

† Significance was not reported due to nonlinearity of trends over time.

= individuals

§ Secchi disk depths in Cook's Bay often exceeded lake bottom depths and were not reported.

individual years: the average observed and predicted volume-weighted spring TP concentrations for 2004 to 2007 were 10.8 and 10.1 mg L⁻¹, respectively, and the average observed and predicted volume-weighted ice-free TP concentrations were 14.1 and 13.3 mg L⁻¹, respectively. The Dillon-Rigler model also provided evidence of mixing between the bays and the main basin; the settling coefficient (averaged over the period 1999–2002) in the 2 bays was estimated to be 3–4 times higher than the settling coefficient for the main basin and the whole lake. This result is evidence of rapid P removal from the bays through exchange with the main basin rather than sedi-

mentation. The whole-lake Dillon-Rigler and LakeMAB models described above can be used to predict the effect of TP reductions. The Dillon-Rigler model predicts a TP concentration of 11.6 µg L⁻¹ under a 15% loading reduction scenario, and 9.0 µg L⁻¹ with a 36% reduction. The LakeMAB model makes similar predictions of a TP concentration of 11.9 µg L⁻¹ under a 15% loading reduction scenario, and 9.9 µg L⁻¹ with a 36% reduction.

Several O₂ modeling exercises were also performed to assess the predictive capacity of 3 different HDO profile models. The agreement between the predicted end-of-summer HDO from the 3 different HDO profile models

and observed concentrations varied depending on the model used and perhaps more interestingly, the station sampled. The prediction of HDO at station K42 in Kempenfelt Bay was consistently in poor agreement with the observed values. The predictive capabilities of the 3 models are expressed as the number of years that gave equal to or better than 5% significance level in Pearson correlations expressed as a percentage of the number of years tested. The Molot et al. (1992) model yielded a good fit 90% of the time for the main basin station but was only effective 22% of the time for the Kempenfelt Bay station. Similarly, the Livingstone and Imboden (1996) model was 90% successful in the main basin and only 30% successful in Kempenfelt Bay. The poorest agreement was from the Uchmanski and Szeligiewica (1988) model, which performed well only 50% of the time in the main basin and 11% in Kempenfelt Bay.

Stable isotopic characterization of water sources

The oxygen and hydrogen isotopic compositions of porewater from the main basin sediments (PC5; Fig. 5) showed limited variation along the length of the core and had values that clustered close to that of modern Lake Simcoe, which suggests that surface water has replaced the original porewater trapped within the sediment. Porewater from the Kempenfelt Bay core (PC1) had a wide range of isotopic compositions that likely arose from mixing among ancient lake water trapped in the sediments, modern Lake Simcoe water, and groundwater derived from underlying aquifers (Fig. 5).

Paleolimnological trends

Trends in chironomid and diatom compositional changes over the past ~300 years were assessed from ^{210}Pb -dated sediment cores taken from the main basin and Kempenfelt Bay (Fig. 6). These high-resolution data provide evidence for historical changes in lake water quality and watershed disturbances and showed close agreement between the 2 indicators. Chironomid-inferred patterns of volume-weighted hypolimnetic O_2 (CI-VWHO) in the main basin suggest that predisturbance (pre-1820 AD) conditions had high VWHO levels ($>7 \text{ mg L}^{-1}$), with inferred declines as low as $\sim 3 \text{ mg L}^{-1}$ occurring during watershed deforestation (late 19th century) and during increased urbanization in the 1970s and 1980s (Rodé 2009); relative abundances of chironomid taxa with high VWHO optima (Fig. 6) closely mirror CI-VWHO. Beginning ~1970s, the CI-VWHO concentration ($\sim 3\text{--}4 \text{ mg L}^{-1}$) was low, and in the 1990s there was an inferred modest recovery in VWHO that coincided with the initiation of sewage treatment improvements and diversions (Rodé 2009). In

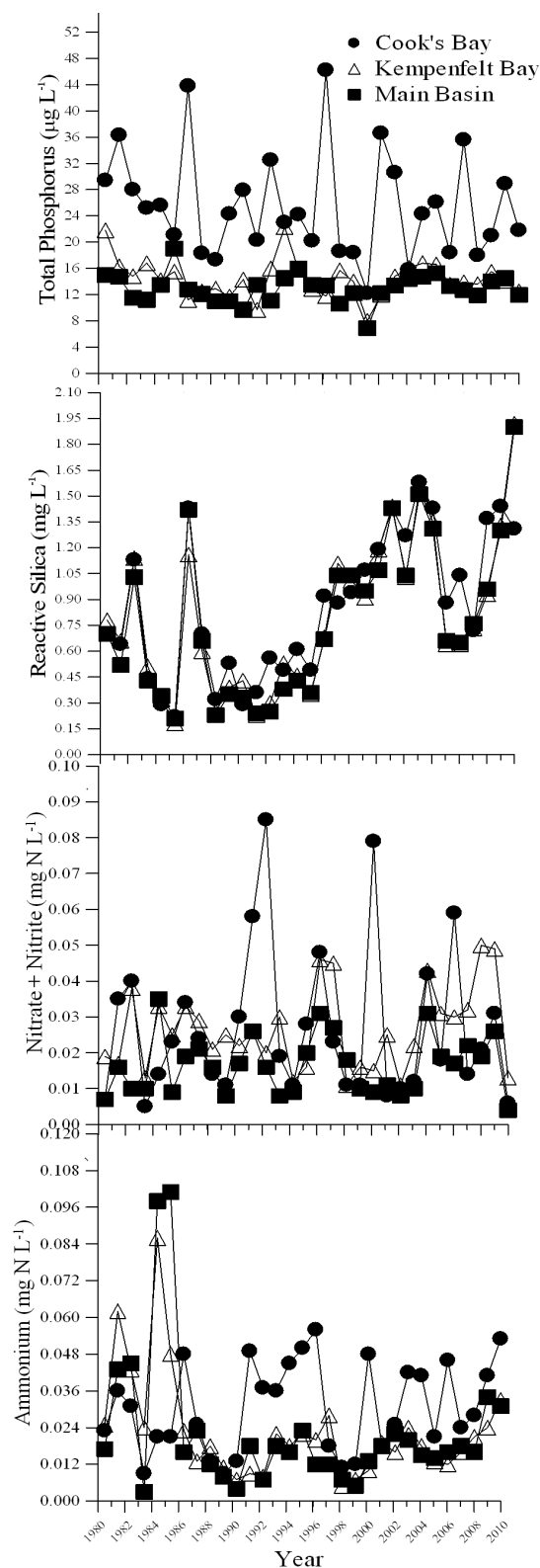


Fig. 4. Temporal (1980–2010) trends in nutrient chemistry including total phosphorus, reactive silica, nitrate and nitrite, and ammonium for Cook's Bay (circles), Kempenfelt Bay (triangles), and the main basin (squares).

2006, CI-VWHO inferences showed an increase in CI-VWHO to 5.27 mg L^{-1} (Rodé 2009), which corresponded to the OMOE monitored MVWHO concentration of 5.15 mg L^{-1} .

Early (pre-1850) diatom assemblage composition suggests that Lake Simcoe was naturally mesotrophic. Notable but modest lake-wide diatom assemblage changes were concurrent with land clearance (mid to late 19th century), canal construction (1920s), and damming of the Holland River (1930s; Hawryshn et al. 2012). In the early to mid-20th century, distinct lake-wide increases in diatoms indicative of nutrient-rich water occurred in correspondence with the onset of extensive agriculture and urban development. The most pronounced and synchronous basin-wide diatom shift (~1970) corresponded to the warmest air temperatures on record from nearby Wiarton climate station and to reduced ice cover on Kempenfelt Bay, consistent with increases in planktonic taxa. The most recent lake-wide diatom (Hawryshn et al. 2012) and chironomid (Rodé 2009) shifts occurred ~1995, consistent with the timing of dreissenid invasion in Lake Simcoe. These biological proxies show a high degree of similarity in the timing of changes to the lake ecosystem, with the highest rate of change in the ~300-year record observed in the past ~50 years (Fig. 6), concordant with the compounded effects of Lake Simcoe's multiple stressors described in this manuscript.

Water clarity, algal, and zooplankton trends

Abrupt shifts were detected in Secchi disk depth in both Kempenfelt Bay and the main basin, with increases in water clarity occurring in both 1996 and 2002 (Table 1; Fig. 7). There were decreasing monotonic trends in Chl-*a* concentrations in Cook's Bay ($0.14 \text{ mg L}^{-1} \text{ yr}^{-1}$), and 2 ASs were detected in both Kempenfelt Bay and the main basin in both 2000 and 2009, and both 1986 and 2009, respectively. In Kempenfelt Bay, there was an overall decrease in Chl-*a* concentrations; however, there were no ASs in the initial ~20 years (1980–1999), but an increase in concentrations was observed from 2000–2008, followed by a halving of the concentrations after the AS in 2009. The main basin experienced consistent declines in Chl-*a* concentrations between both ASs, with a halving of the previous (1986–2008) concentrations in 2009–2010 (Table 1; Fig. 7).

ASs were detected in total phytoplankton biovolumes in 1987, 1997, and 2006 in Cook's Bay, with declines occurring until 2006. Between 2006 and 2010, the biovolumes almost doubled from the mean of the previous 8-year period. There were no significant ASs or monotonic trends in total phytoplankton biovolume in Kempenfelt Bay and the main basin (Table 1; Fig. 8). The phytoplankton community composition in Lake Simcoe has been primarily (>70%) composed of diatoms since the 1980s,

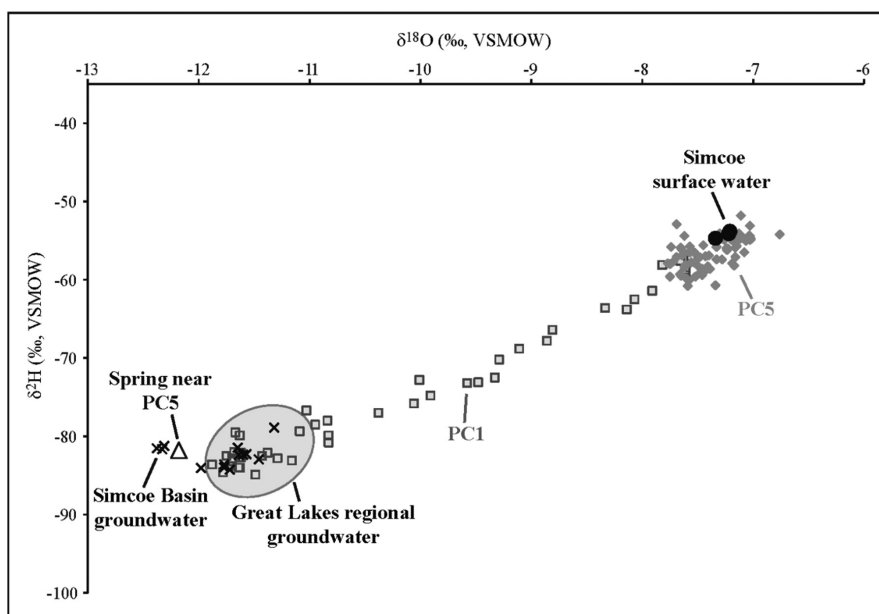


Fig. 5. The oxygen- and hydrogen-isotope compositions of sediment porewater, surface water, and groundwater are reported here in delta (d) notation in parts per thousand (‰). VSMOW refers to the Vienna Standard Mean Ocean Water. The porewater samples were obtained through piston cores in Kempenfelt Bay (PC1; filled squares) and the main basin (PC5; filled diamonds). Lake surface water (filled circles) was also collected near the coring sites as well as an artesian spring outflow (open triangle) near the coring site in the main basin. Simcoe basin groundwater (x's) was collected from deep aquifers, and the range in isotopic signatures for the Laurentian Great Lakes regional groundwater is represented by the large gray oval.

and the diatom biovolumes displayed similar long-term patterns to those of the total population, with the exception of Cook's Bay in recent years. The AS analyses did not detect any changes in the diatom biovolumes post-1997. Notable changes in the community composition over the last 3 decades did occur in all 3 areas of the lake. In Cook's Bay, ASs resulting in biovolume declines were found for cyanobacteria in 1992 and for dinoflagellates in 1997, while chlorophyte biovolumes had a significant declining monotonic trend. In both Kempenfelt Bay and the main basin, a decline in cyanobacteria biovolumes occurred between the time segment 1980–1985 and the time segment 1986–2010. More varied trends occurred in the dinoflagellate, cryptomonad, chrysophyte, and chlorophyte populations in Kempenfelt Bay and the main

basin, with some phytoplankton groups showing no evidence of trends (e.g., euglenoids) over the 30-year period.

The abundance of the major taxonomic zooplankton groups varied over the 22-year monitoring period, with cyclopoid copepods generally dominating the zooplankton community. In all 3 areas of the lake, cyclopoid copepods showed no changes over time. Monotonic declining trends were found for calanoid copepods and small cladocerans. An AS toward a lower abundance of large cladocerans in Cook's Bay was detected in 1996. Reductions in abundance were also detected in Kempenfelt Bay in 1999 and 2000 for calanoids and large cladocerans, respectively. In the main basin, ASs toward lower abundances of calanoids and small cladocerans were detected in 1997

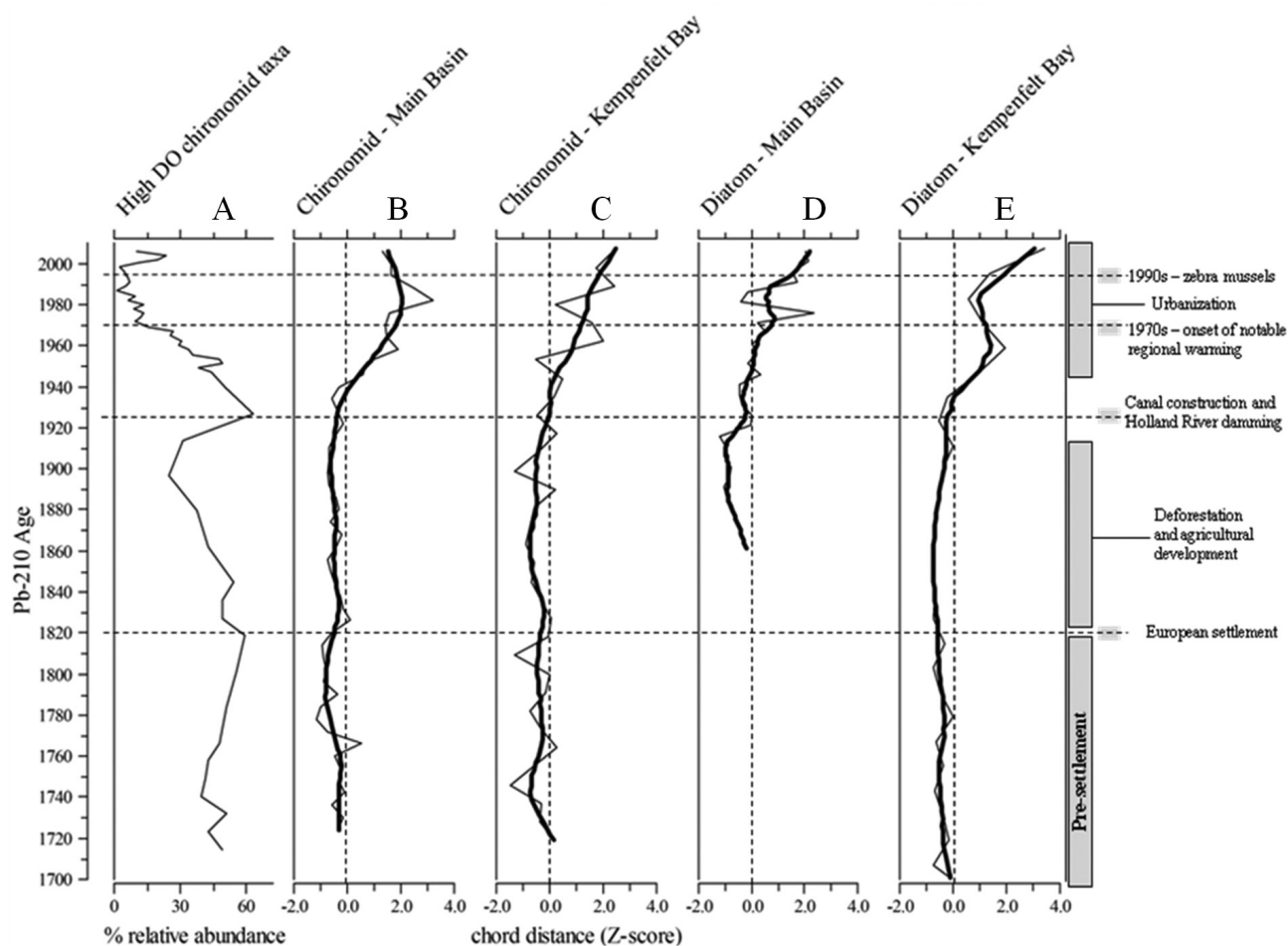


Fig. 6. Chironomid- and diatom-based paleolimnological analyses showing long-term changes. (A) Percent of chironomid assemblage consisting of taxa with high dissolved oxygen (DO) optima (DO expressed as volume-weighted hypolimnetic oxygen [VWHO; mg L^{-1}]) from a ^{210}Pb -dated profundal sediment core collected in 2007 from the main basin. (B) Rate of chironomid community change, expressed as Z-scores of chord distance, for main basin and (C) Kempenfelt Bay; and the rate of diatom community change, expressed as Z-scores of chord distance, from (D) main basin and (E) Kempenfelt Bay, from sedimentary assemblages from 2 ^{210}Pb -dated profundal sediment cores collected in 2007. Vertical dashed line represents mean rate of change for the dataset (Z-score = 0). Time intervals were standardized to the series' mean time interval, which ranged from 5 to 12 years. A LOESS smoother (span = 0.20) has been fitted to highlight the major trends in the rate of change values (thick solid line).

and 2007, respectively, and in 1994 and 2001 for large cladocerans (Table 1; Fig. 9).

Trends in benthic communities

The surveys of the distribution of SAV identified 5 areas of high SAV biomass (Fig. 10; Cook's Bay, Barrie, Ramara, Beaverton, and Georgina), with communities consisting of 20 species, 4 of which were dominant (*Ceratophyllum demersum*, *Myriophyllum spicatum*, *Elodea canadensis*, and *Chara* spp.). In addition to the 16 species listed in Ginn (2011), in the recent 2009–2011 surveys, 4 additional species were identified: *Potamogeton stricti-*

folius, *Potamogeton friesii*, *Nitella* spp., and the *Elodea* spp. listed in Ginn (2011) were further identified to species level (*E. canadensis* and *E. nuttallii*).

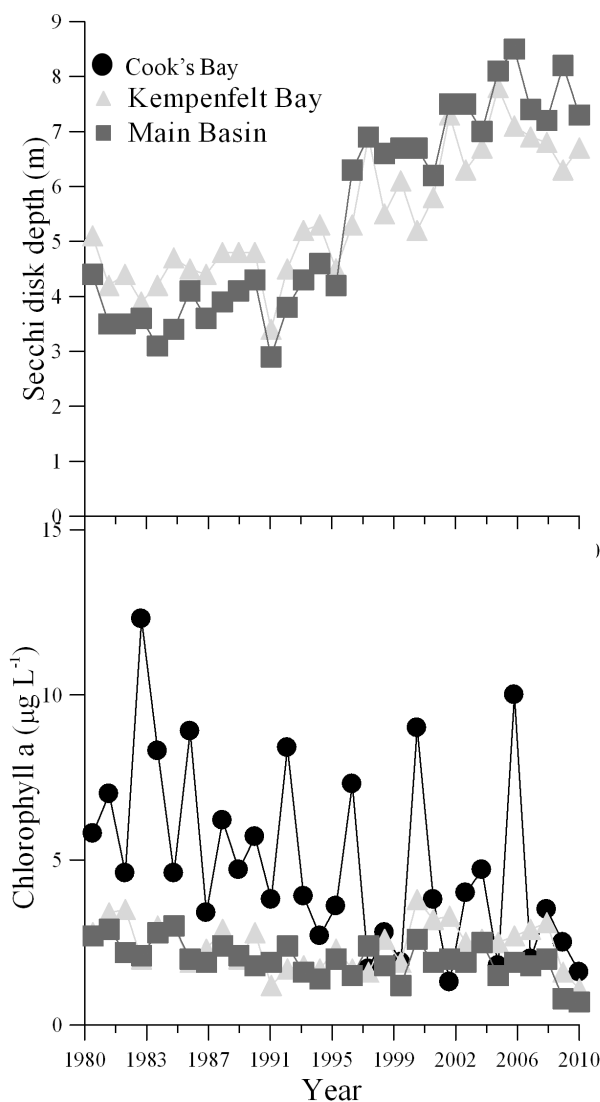


Fig. 7. Temporal (1980–2010) trends in Secchi disk depth and chlorophyll *a* concentrations for Cook's Bay (circles), Kempenfelt Bay (triangles), and the main basin (squares). Secchi disk depths in Cook's Bay were often lake bottom depths and not reported.

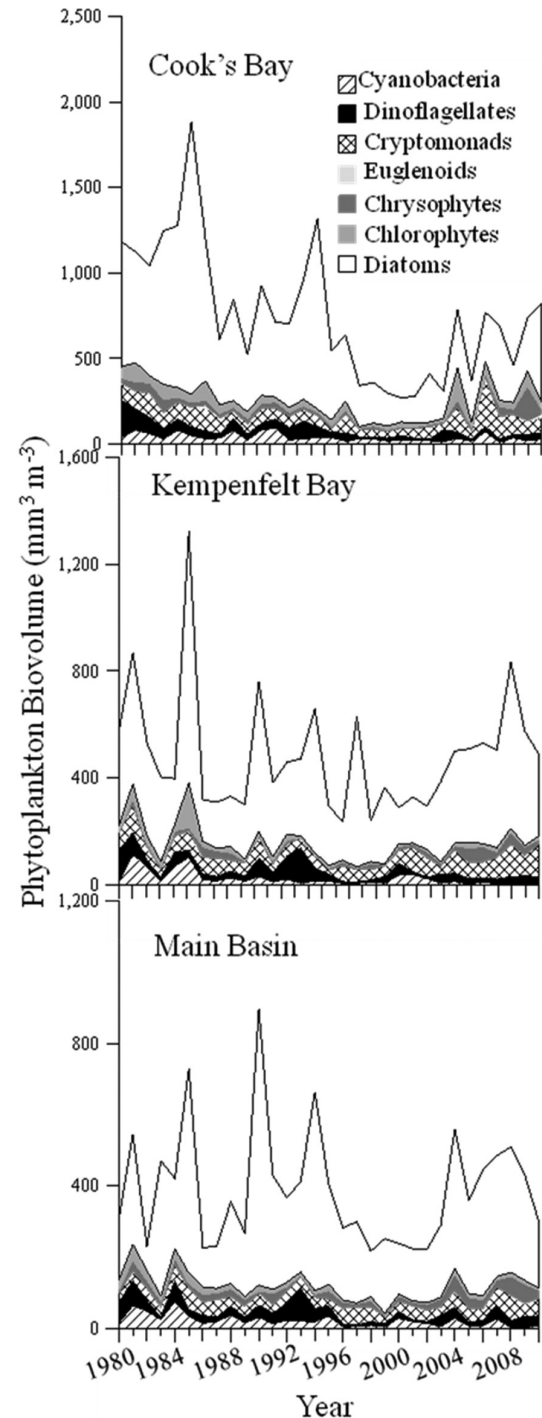


Fig. 8. Temporal (1980–2010) trends in the biovolume (mm³ m⁻³) of major phytoplankton groups in ice-free season composite samples from 8 stations representing Cook's Bay, Kempenfelt Bay, and the main basin.

The abundance of benthic invertebrates also changed over the 82-year period for which data were available, as did their distribution between littoral (nearshore; <7 m) and profundal (offshore; >19 m) areas of the lake (Fig. 11). Invertebrate abundances were lower in 1926 than the mean of all subsequent years at both nearshore

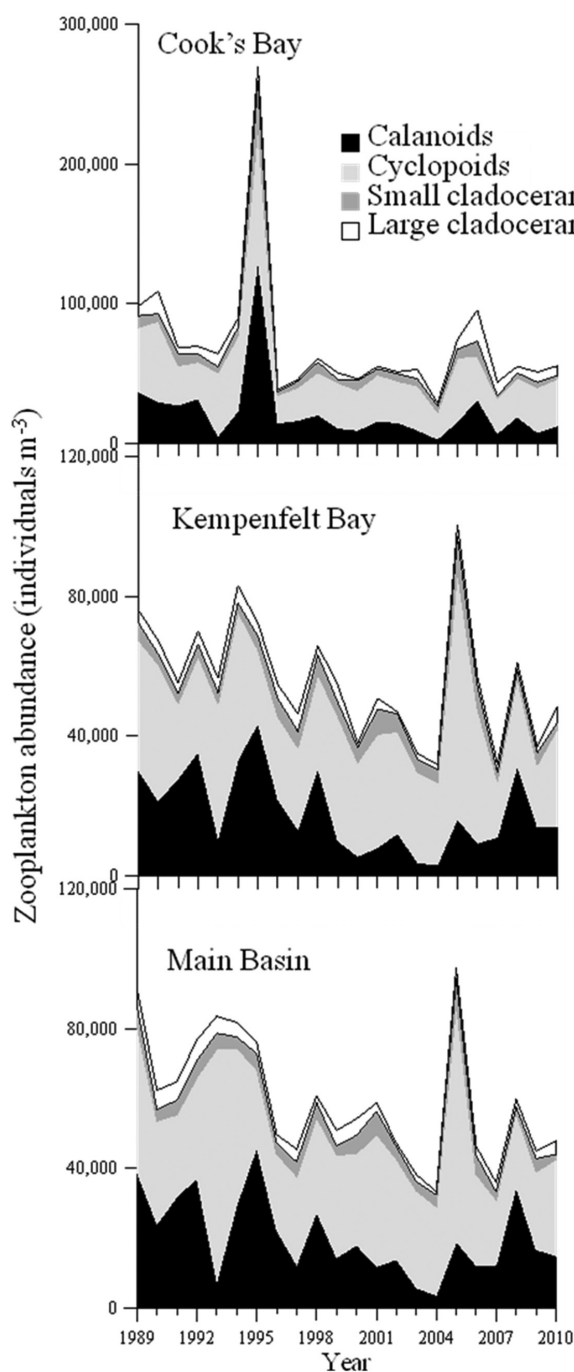


Fig. 9. Temporal (1989–2010) trends in the abundance (individuals m^{-3}) of major taxonomic zooplankton groups in ice-free season samples from Cook's Bay, Kempenfelt Bay, and the main basin.

and offshore sites. In 1983 and 1993, densities of benthic invertebrates were higher in the offshore region than at nearshore locations. By 2005 and 2008 there was a reversal of spatial trends with offshore density becoming lower than in the nearshore. The community composition in the offshore was relatively stable over time with chironomids and oligochaetes numerically dominating the benthos (Jimenez et al. 2011, Rennie and Evans 2012). The nearshore benthos was typically dominated by amphipods and chironomids, but dreissenids became either the most or second-most abundant member of the benthos since their establishment (Ozersky et al. 2011a, Rennie and Evans 2012). Although greater compared with measurements made in the late 1920s, offshore benthic invertebrate abundance declined by nearly an order of magnitude between 1983 to 1993 in comparison to abundance between 2005 to 2008. In contrast, nearshore invertebrate abundance has increased by more than an order of magnitude during the same time period.

Three crayfish species currently inhabit Lake Simcoe. *Orconectes virilis* and *O. propinquus* have coexisted in the lake since at least the 1920s. *O. virilis* was prominent on rocky substrates during the 1920s (Rawson 1930), but *O. propinquus* became the dominant species on these habitats by the 1990s (Mason and Evans 2011). Comparison of crayfish catch rates (# crayfish trap⁻¹ \pm standard deviation) in overnight sets of wire minnow traps at various sites in the main basin of Lake Simcoe revealed that in 2009, total crayfish catches were lower lake-wide than in 1993. In 1993, prior to *O. rusticus* establishment, catch rates of *O. propinquus* (4.07 ± 5.95) were much higher than *O. virilis* (0.64 ± 1.61). In 2009, *O. rusticus* catch rates were relatively high (1.01 ± 1.14), and catch rates of *O. propinquus* (0.23 ± 0.68) and *O. virilis* (0.10 ± 0.41) were very low. Lower catch rates of *O. propinquus* and *O. virilis* in 2009 at sites not yet inhabited by *O. rusticus* suggested that some factor other than the presence or competition from *O. rusticus* had resulted in lower overall abundance of the 2 species of crayfish compared to 1993. At sites where *O. rusticus* was abundant, *O. propinquus* and *O. virilis* catch rates were low or zero.

The lake-wide spatial distribution pattern of dreissenids revealed that the highest biomass (80–160 g m^{-2}) and density (12 000–30 000 individuals m^{-2}) of mussels occurred between the 5 and 15 m isopleths (Fig. 12). This distinct “ring” of high dreissenid abundance was present in both Cook's and Kempenfelt bays, as well as around the islands in the eastern part of the main basin, primarily Georgina and Thorah islands. Few dreissenids were found deeper than 20 m. We estimated potential lake-wide filtration rates with our 2005–2010 biomass and density estimates as a function of

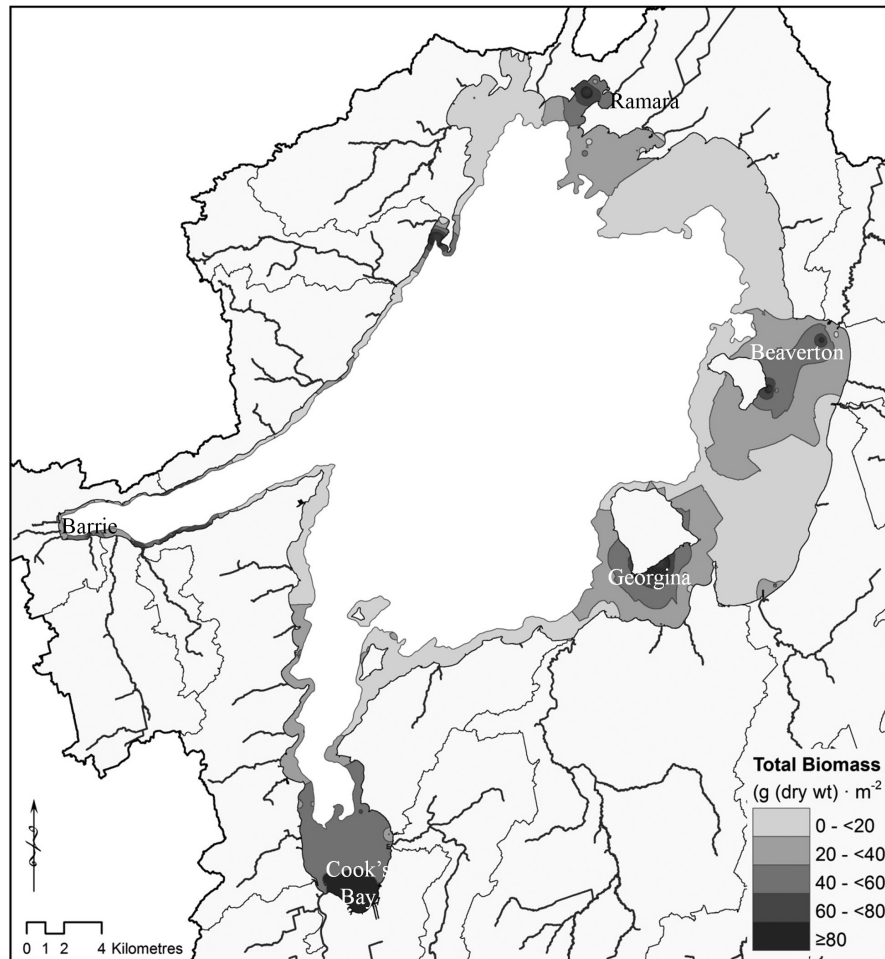


Fig. 10. Lake Simcoe showing mean biomass (g dry weight m^{-2}) of submerged aquatic vegetation distribution from surveys in the fall of 2008–2011. Darker shading indicates higher biomass (refer to legend).

individual shell-free dry tissue weight (g) for *Dreissena polymorpha* at 19–20 °C as in Kryger and Riisgård (1988). We assumed individual dreissenids were filtering at this rate ($\sim 0.08 \text{ L h}^{-1}$) for 6 months of the year, based on our lake-wide estimates of mussel standing stocks, assuming our 834 sites were representative of the lake and the bottom area of the lake was comparable to the surface area. Our estimate revealed that the dreissenid population in Lake Simcoe was capable of filtering the entire volume ($11.4 \times 10^9 \text{ m}^3$) of the lake 47 times during the 11-year hydraulic residence time.

Trends in fish populations

Fish species that were frequently captured in nearshore Lake Simcoe waters included rock bass (*Ambloplites rupestris*), pumpkinseed (*Lepomis gibbosus*), yellow perch (*Perca flavescens*), smallmouth bass (*Micropterus dolomieu*), black crappie (*Pomoxis nigromaculatus*), and

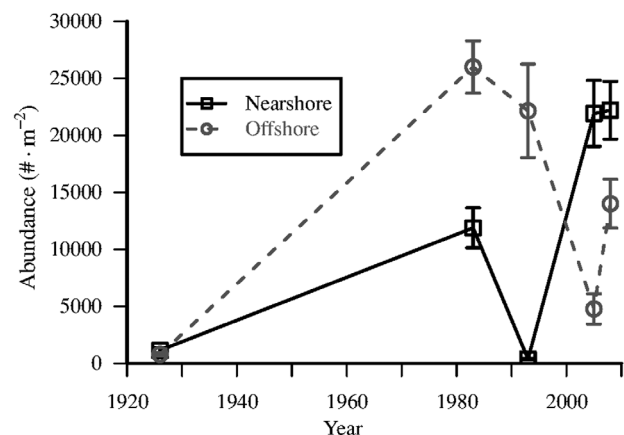


Fig. 11. Temporal (1926–2008) and spatial (littoral [$<7 \text{ m}$; open squares] vs. profundal [$\geq 19 \text{ m}$; open circles]) trends in the abundance (# of individuals m^{-2}) of benthic macroinvertebrates throughout Lake Simcoe. Data derived from a variety of sources outlined in the methods section.

to a lesser extent largemouth bass (*M. salmoides*). While there have been no long-term trends in the catch-per-unit-effort of yellow perch, largemouth bass, and black crappie from 1992–2010, ASs in some of the warmwater species

did occur. In 2004, there was an AS in rock bass catch consistent with an increase in catch-per-unit-effort, while declines were experienced by smallmouth bass and pumpkinseed in 2007 and 2008, respectively (Table 1;

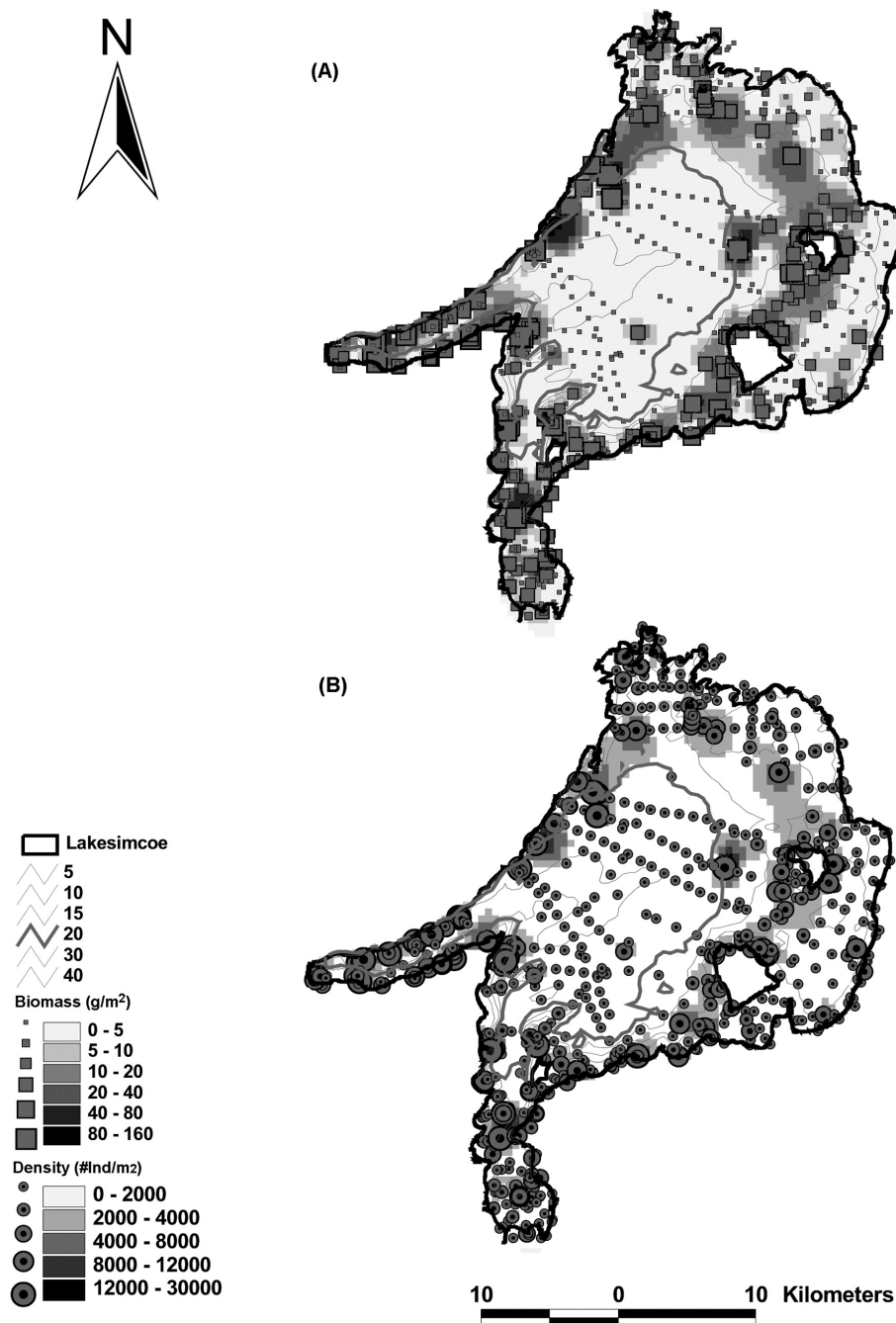


Fig. 12. Bathymetric map showing the distribution of dreissenids in Lake Simcoe based on results of 6 different surveys (see methods section). (A) Squares representing point data of shell-free dry tissue biomass (g m⁻²) and (B) circles representing the point values for mean density (# of individuals m⁻²). Darker grid shading indicates higher biomass (squares) and density (circles). Data from the 834 discrete sampling sites were interpolated across the lake with the kriging geo-statistical gridding method.

Fig. 13). There were also large, short-term fluctuations in the abundance of many species.

In 2010, the winter recreational fishery accounted for more than ~75% of the angling effort on Lake Simcoe (the 50-day winter survey and the 112-day summer survey). There has been a steady increase in winter angling effort over the past 5 decades (Fig. 14), although no large increases were observed over the most recent 20 years. The most sought after species in the winter over the past 20 years were lake whitefish (*Coregonus clupeaformis*), lake trout (*Salvelinus namaycush*), and yellow perch. The coldwater fish community, as observed through the recreational fishery, has undergone changes from 1961–2010 (Fig. 14). Lake trout, lake whitefish, rainbow smelt, and lake herring (*Coregonus artedii*) have at one point displayed declines in abundance with documented recruitment failures. Lake trout and lake whitefish experienced recruitment failures in the 1960s and 1970s followed by a decline in relative abundance, which continues to be low compared to historical levels, although some natural reproduction in lake trout has been observed in recent years (La Rose and Willox 2006, Dolson 2012). Rainbow smelt was introduced to the lake in the early 1960s, and there was a dramatic increase in its population in the 1970s, which remained high until the 1990s. Declines in the winter catch of smelt began in 1991, and it is no longer abundant in the winter recreational fishery. Lake herring catch experienced a decline beginning in the early 1980s that continued into the 1990s, resulting in a closure of the lake herring fishery in 2001. While coldwater species catches have declined at various points in the past, yellow perch catch in the

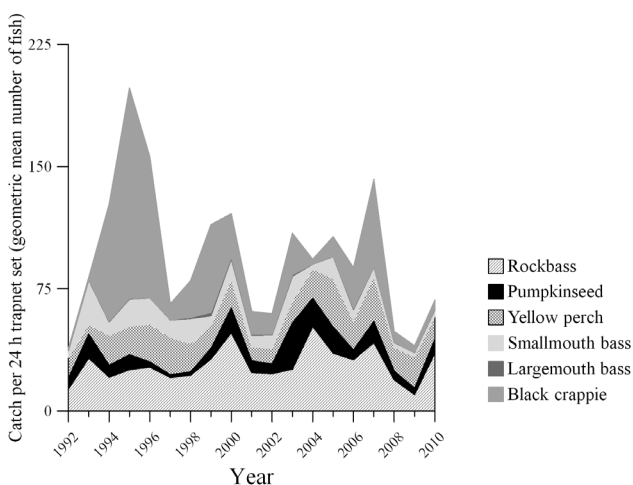


Fig. 13. Temporal (1992–2010) trends in the catch rate (catch-per-unit-effort) expressed as the geometric mean number of fish caught per night (24 h) per trap net set targeting for nearshore warmwater fish species. Number of sites sampled ranged from 25–48 depending on the year.

winter fishery has increased from 8% of total catch composition (all species) in 1963 to 94% in 2010 (Liddle and Moles Forthcoming).

Trends in water bird populations

Water bird population levels, both in 1-day point counts and breeding bird surveys, were fairly constant from the 1990s onward (K. Gee, OMNR, 2012, unpubl. data). In 2001, double-crested cormorants became a member of the Lake Simcoe water bird population and first started nesting on Thorah Island with 80 nests. The number of nests increased to 426 on 3 islands in 2006, and as of the 2008 count there were 242 nests on 4 islands (K. Gee, OMNR, 2012, unpubl. data).

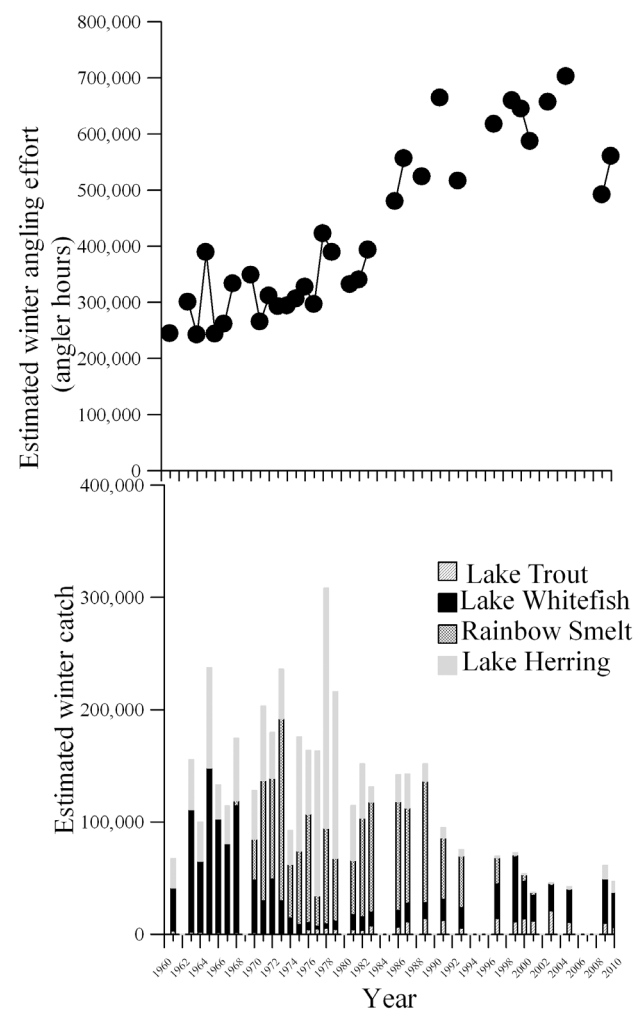


Fig. 14. Discontinuous temporal (1961–2010) trends in the winter angling effort (angler hours) and the winter catch of coldwater fish species as estimated by the Ontario Ministry of Natural Resources' Lake Simcoe Fisheries Assessment Unit winter creel survey program.

Discussion

A multitude of changes has occurred in physical, chemical, and biological parameters in the 30-year period of record for Lake Simcoe. In the context of the past ~300 years, sedimentary chironomid and diatom compositional changes identified that the last ~50 years of environmental change on Lake Simcoe have been exceptional. In Lake Simcoe as a whole, there have been increases in the duration of stratification and MVWHDO concentrations and declines in spring TP concentrations, but no sustained change in ice-free TP, nitrate, or ammonium concentrations. There have been increases in Si concentrations and water clarity, and decreases in Chl-*a* concentrations and biovolumes of many of the phytoplankton taxa. There has been some decline in abundance within the zooplankton community, along with declines in the profundal zoobenthos, but the littoral zoobenthos populations have increased. The long-term responses in the warmwater fish community are variable, while earlier declines in the coldwater fish community have been observed. The analysis of these long-term trends allows us to examine the timing of these changes relative to known ecosystem stressors. Identified stressors acting on Lake Simcoe include climate change (Stainsby et al. 2011, Hawshryn et al. 2012), nutrient loading from the watershed (Evans et al. 1996, Winter et al. 2007), and the introduction of aquatic invasive species (Evans et al. 2011, Mason and Evans 2011, Kelly et al. 2013). The correspondence between the predicted timing of stressor effects and numerous ecological parameters during long-term monitoring in the lake has allowed new insights only made possible through the synthesis of these datasets. Of the 66 long-term datasets tested for ASs, 39 datasets had ASs, and many had multiple ASs, resulting in 59 ASs detected in total. Of these 59 ASs, the year with the greatest number was 1997 (15%), with another 12% occurring in 1996. There was a 10% occurrence in 1986, while ASs for the rest of the years were $\leq 7\%$. On a decadal scale, 22% of the ASs occurred in the 1980s, 44% in the 1990s, and 34% in the 2000s, indicating that the largest decade of change was the 1990s. The time period 1995–1997 was also one of change in the paleolimnological record, when the most recent lake-wide diatom and chironomid shifts occurred ~1995.

The temporal coherence of the multiple potential stressors makes the identification of individual drivers difficult to discern. The impact of changes to nutrient loading to the lake is also difficult to assess on a temporal basis because TP load reductions occurred during 2 time periods; 1984 and the early 1990s (Winter et al. 2007, 2011). Also occurring in the mid-1990s was the establishment of *B. longimanus* in ~1994. The time period

1995–1997, however, is remarkably consistent with the timing of dreissenid establishment in Lake Simcoe. We estimated that the Lake Simcoe dreissenid population was capable of filtering the entire volume of the lake 47 times during the 11-year lake hydraulic residence time, indicating that strong impacts should be apparent upon their establishment. Dreissenids have also been implicated elsewhere in altering P cycling in lakes (Hecky et al. 2004, Cha et al. 2011). In general, the mid-1990s seem to be a period of major change in Lake Simcoe, evidenced in the declines in spring TP concentrations (which seem to reflect the TP loadings), and also the time frame in which dreissenids invaded and became established in the lake.

Climate change

The observed increases in the duration of stratification in Lake Simcoe have previously been attributed to climate change (Stainsby et al. 2011). Hawryshyn et al. (2012) also suggested that lake-wide shifts in diatom assemblages from sediment cores occurred in response to regional climate warming. Further evidence for climate change effects in Lake Simcoe were seen in the lake ice records from 1853 to 2007 for Kempenfelt Bay and Sutton, Ontario, where the total ice-free period has been extended by ~16 days, with ice-off occurring ~4 days earlier, and ice-on occurring ~13 days later (Hawryshyn et al. 2012). Whether or not these climate-associated changes in winter ice conditions are related to the recent reporting of an under-ice phytoplankton peak (Baranowska et al. Forthcoming) and possible changes in the winter catch of coldwater fish species is currently unknown.

Nutrient loading

We suggest that changes in TP loading to the lake have influenced spring and ice-free TP concentrations and deepwater O₂ concentrations. Understanding the causes and consequences of hypolimnetic O₂ depletion in Lake Simcoe is critical to successful management of this important freshwater resource because O₂ concentrations and temperature define habitat for most fish species (contaminants notwithstanding). Based on the combination of paleolimnological long-term monitoring and modeling results, the relationship between TP loading and MVWHDO has been well established for the lake. This relationship has been empirically quantified by Young et al. (2011), who predicted that a TP load of 44 tonnes yr⁻¹ would yield the target minimum volume-weighted hypolimnetic DO of 7 mg L⁻¹ and a corresponding whole-lake ice-free TP concentration of 8.1 µg L⁻¹ under current hydrological conditions.

An interesting result arising from our modeling work presented here was the large difference between the settling coefficients in the 2 bays relative to the main basin and the whole lake. While TP retention mechanisms could operate at different rates in the lake's basins, high settling coefficients in the 2 bays most likely indicate that flushing time is significantly underestimated, perhaps because of significant groundwater discharge into the basins and/or significant water exchange between the bays and the main basin. There is also the possibility that the City of Barrie sewage treatment plant effluent that discharges into Kempenfelt Bay is having an impact on the water quality. Differences in O_2 concentrations between Kempenfelt Bay and the main basin were suggested by both the poor agreement between O_2 profile model predictions and measured profiles in Kempenfelt Bay relative to the main basin and by the differences in CI-VWHO concentrations (Rodé 2009). Predisturbance CI-VWHO concentrations in Kempenfelt Bay ($2\text{--}5\text{ mg } O_2\text{ L}^{-1}$) were much lower compared to the main basin ($>7\text{ mg } O_2\text{ L}^{-1}$; Rodé 2009). These results suggest that groundwater discharge into Kempenfelt Bay may be affecting Lake Simcoe's water balance, hypolimnetic O_2 concentrations, and by extension, the fragile coldwater fish habitat. There is seismostratigraphic evidence for fluid seepage through conduits on the floor of Kempenfelt Bay, indicating a zone of probable groundwater flow to the lake (Lewis et al. 2007). Based on the oxygen and hydrogen isotope results presented here, regional groundwater is likely the source of water in the sediments that we believe to be in proximity to what may be submarine hollows. This observation remains speculative, however, because there is currently no quantitative evidence regarding the O_2 or the nutrient concentrations in this groundwater.

The results of paleolimnological reconstructions yield some clues to the causes of trends in hypolimnetic O_2 levels. Inferred patterns of VWHO in the main basin suggest that predisturbance (pre-1820 AD) Lake Simcoe had high VWHO levels ($>7\text{ mg } O_2\text{ L}^{-1}$), and that anthropogenic disturbances in the watershed were the likely cause of decreases in VWHO (Rodé 2009). Independent lines of evidence from the paleolimnological trends corroborate the long-term monitoring data presented here. Rates of chironomid and diatom community compositional change suggest a strong relationship between the chironomid and diatom records and infer strong linkages between epilimnetic processes such as increased productivity and consequent hypolimnetic processes such as increased O_2 depletion.

Accelerated eutrophication and sedimentation have been attributed to recruitment failure of coldwater fish such as lake trout and lake whitefish in Lake Simcoe. Additional factors have also been considered, such as the

degradation of nearshore spawning habitat and O_2 depletion in the hypolimnion (Evans et al. 1996), crayfish predation of lake trout and whitefish embryos (Mason and Evans 2011), and the introduction of rainbow smelt (Evans et al. 1996). The coldwater fish populations have also been subjected to increased angling effort. The importance of warmwater and coldwater fish in the diet of double-crested cormorants varies among ecosystems depending on the availability of different prey items (Doucette et al. 2011). Further study of the diets of the Lake Simcoe double-crested cormorant population is required to understand their potential effects on the lake's fish populations. Summer gill netting programs conducted from 2003 to 2010 have corroborated the recent winter catch data but also show an increased relative abundance of naturally reproducing lake trout, lake whitefish, and lake herring. They also showed an increase in rainbow smelt and a significant decline in the relative abundance of stocked lake trout (Dolson 2012).

The decomposition of phytoplankton and SAV in the bottom waters of Lake Simcoe is likely the main factor contributing to the low hypolimnetic O_2 concentrations (Young et al. 2010). Chl-*a* concentrations are commonly used as an indicator of phytoplankton biomass; however, as a light- and nutrient-responsive pigment, comparison of Chl-*a* concentrations with measurements of phytoplankton biovolumes is often poor, as previously documented in Lake Simcoe (Eimers et al. 2005). Independent trend analyses of Chl-*a* concentration and phytoplankton biovolume have been previously published (1980–2008, Young et al. 2011; 1980–2007, Winter et al. 2011). There have been major changes in these two parameters in the years following, however; in Kempenfelt Bay and the main basin, there was an abrupt decline in Chl-*a* concentration detected in 2009, with the 1980–2008 mean dropping to about half in 2009–2010. One possible explanation for these declines could be that the seasonal phytoplankton peak previously thought to occur in the fall (Nicholls 1995) may now be occurring outside of the ice-free sampling period (Baranowska et al. Forthcoming).

The total phytoplankton biovolume data do not reflect these recent changes in Chl-*a* concentrations, however. From 2008–2010 for the whole lake, there was a slight increase in biovolume relative to previous years, which is largely influenced by high biovolumes in Cook's Bay, possibly the result of increased TP loading from the watershed resulting from increased discharge in recent years. An alternative explanation is that the input of algae via the Holland River, analogous to the role of the Maumee River and Lake Erie (Conroy et al. 2008), is significant. Extremely high Chl-*a* concentrations at 3 Holland River sites suggest this may be a possibility (OMOE, 2012, unpubl. data). Although this trend is

contrary to that seen in the 2008–2010 Chl-*a* data, the lower Chl-*a* concentrations are possibly a response to improving light conditions in Cook's Bay, which are difficult to assess due to its shallow depth.

In Cook's Bay, SAV biomass has nearly tripled from 1.2 kg m⁻² in 1984 to 3.1 kg m⁻² in 2008, in conjunction with areal expansion extending the maximum depth of plant colonization from 6 m in 1984 to 10.5 m in 2008 (Ginn 2011). The areal coverage of SAV inferred from echograms has almost doubled from 9.5 km² in 1984 to 18.1 km² in 2007 (Depew et al. 2011a). Increases in SAV biomass have been attributed to increased water transparency in the littoral areas of the lake (Depew et al. 2011a, Ginn 2011). There were no obvious changes in SAV abundance or community structure between that reported in 2008 (Ginn 2011) and the updated 2009–2011 surveys shown here.

The increased biomass of primary producers (both phytoplankton and SAV) in Cook's Bay in recent years may have contributed to the low Kempenfelt Bay (K42) MVWHO concentrations via high water exchange rates between the basins. While the MVWHO in 2009 (3.5 mg L⁻¹) was the lowest recorded concentration in the past 15 years, 2009 was an exceptionally wet year (Environment Canada, unpubl. data), and increased tributary discharge may have resulted in high TP loading (OMOE, 2012, unpubl. data).

Although trends in P concentration are of primary interest in Lake Simcoe because of P control of primary production (Depew et al. 2011a; R.L. North, Trent University, 2012, unpubl. data), there have been some notable trends in the other dissolved nutrients in the lake. The large increases in reactive Si concentrations may be associated with the pelagic declines in diatom populations (at least in Cook's Bay). In lakes Huron and Erie, increases in spring soluble Si and Secchi depth were indicative of reduced primary production (Barbiero et al. 2009) and declines in diatoms (Barbiero et al. 2006). In the Laurentian Great Lakes, nitrate concentrations are much higher than Lake Simcoe and have shown a positive temporal trend (Millard et al. 2003, Finlay et al. 2007). The lack of any temporal trends in dissolved N species in Lake Simcoe is unexpected given the increasing predominance of urban land use in the watershed, which is known to be a significant nonpoint source of N loading (Howarth et al. 1996).

Aquatic invasive species

The invasion and establishment of aquatic species to Lake Simcoe has been well-documented (Kilgour et al. 2008, Evans et al. 2011, Ginn 2011, Mason and Evans 2011, Kelly et al. 2013). To date, the majority of studies on the

effects of aquatic invasive species in Lake Simcoe have focused on dreissenid mussels (Eimers et al. 2005, Ozersky et al. 2011a, Young et al. 2011, Baranowska et al. Forthcoming). Temporal trends of dreissenid populations in Lake Simcoe are difficult to assess due to the lack of abundance data between 1997 and 2004; however, we can make some speculations by comparing recent observations with a limited survey conducted in 1996 at depths of 2–6 m (Evans et al. 2011). In 1996, the mean dreissenid density was estimated to be 32 500 mussels m⁻² with a mean shell-free dry biomass of 34.8 g m⁻² (Evans et al. 2011), numbers that are larger than both the mean density (2077 mussels m⁻²) and mean biomass (14.0 g m⁻²) estimates from our 0–10 m isopleth from 2005–2010 combined. The higher densities observed by Evans et al. (2011) in 1996 are typical of the initial years after invasion (Dermott et al. 1993). These biomass and density differences between 1996 and 2005–2010 suggest that in the shallow littoral, dreissenid filtration effects would be less in recent years than immediately after the dreissenid invasion in 1994. Dreissenids have been known to use SAV as a substrate for attachment, however, particularly in Cook's Bay (Ozersky et al. 2011b); therefore, the increased areal extent and biomass of SAV in Lake Simcoe (Depew et al. 2011a, Ginn 2011) may have provided increased substrate availability for dreissenids. Petite Ponar grab samples may have underestimated dreissenid densities in Cook's Bay due to the inefficiency of the grab on SAV, but the significance of this is difficult to assess because juvenile mortality can be high in the fall when macrophytes (except *Chara*) undergo senescence (Hunter and Simons 2004).

Compared to other large systems with documented dreissenid impacts such as inner Saginaw Bay (Lake Huron), Lake Simcoe has 3.6 times higher dreissenid densities and 6.5 times higher biomass than 2008 estimates from Saginaw Bay, where dreissenids have the capacity to filter the entire volume of the inner bay >10 times during the reported hydraulic residence time of 120 days (Cha et al. 2011). We estimated that dreissenids could potentially filter the water column of Lake Simcoe (not accounting for stratification) at a rate of 0.24 times per day, similar to rates reported for inner Saginaw Bay in 1992 at higher mussel densities (Fanslow et al. 1995). Our estimate was also likely conservative, given our assumption that mussels did not filter at all for the 6 coldest months of the year. In Lake St. Clair, with dreissenid densities 3 times larger than Lake Simcoe, Hebert et al. (1991) estimated that dreissenids could filter the volume of Lake St. Clair twice a day. We acknowledge that our filtration rate estimate for Lake Simcoe was coarse, especially because it did not account for the effects of stratification or the formation of a benthic boundary

layer (Schwalb et al. Forthcoming). Nevertheless, our estimated filtration rate and the long residence time of the lake suggest that the Lake Simcoe water column has been sufficiently filtered through dreissenids to expect large, whole-lake changes.

The nearshore shunt hypothesis proposed by Hecky et al. (2004) predicts that dreissenid mussel filtration and excretion processes occurring primarily in the nearshore littoral zones of lakes result in interception of both primary and secondary production from the offshore to the nearshore. They suggested that dreissenid mussels were impacting nutrient cycling, and that the impact was most strongly affecting the shallow, nearshore regions of large lakes. In a recent review paper, Higgins and Vander Zanden (2010) identified consistent impacts of dreissenids from lakes and rivers across North America and Eurasia (Table S2). Of the 11 predicted effects, our long-term data from Lake Simcoe are consistent with 6 of these “symptoms” (Table S2). The nearshore shunt hypothesis is well supported by the benthic invertebrate studies on Lake Simcoe. Ozersky et al. (2011b) provided evidence of an increase in abundance and diversity of the littoral benthos, while Jimenez et al. (2011) and Rennie and Evans (2012) showed decreases in the abundance of non-dreissenid profundal benthos. Changes in littoral benthic invertebrate populations could also be an indirect effect due to the increase in SAV, attributed to increases in water clarity; in addition, nutrient remineralization (Depew et al. 2011a, Ginn 2011) could also increase the amount of food and habitat available to littoral benthic consumers.

Some trends in Lake Simcoe are inconsistent with the nearshore shunt hypothesis (Table S2), however. For example, the lack of a trend in TP concentration is contrary to the expected decline (Higgins and Vander Zanden 2010), most likely due to the variable TP loading to the lake that overwhelms any primarily nearshore dreissenid filtration effects. Young et al. (2011) found that Chl-*a* predicted from a relationship with TP was either less than or close to the measured values (with the exception of Cook’s Bay station C1), and that Chl-*a*/TP ratios increased at all stations immediately after dreissenids were established. In an examination of the long-term trends in phytoplankton in Lake Simcoe, Winter et al. (2011) concluded that although there was a period of low and interannually consistent total algal biovolume at stations in Cook’s Bay and the main basin of the lake following dreissenid establishment, increases after 2004 were inconsistent with a sustained dreissenid grazing effect.

Another predicted outcome of the nearshore shunt is the increased abundance of filamentous benthic algae (e.g., *Cladophora*), which is occurring in nuisance proportions in the dreissenid-impacted Laurentian Great

Lakes (Auer et al. 2010). Depew et al. (2011b) surveyed Lake Simcoe in 2006 and 2007 and found a surprising lack of *Cladophora* growth. They concluded, however, that their results were consistent with the nearshore shunt hypothesis, and that the manifestation in Lake Simcoe was very different than that observed in the lower Great Lakes, perhaps due to the availability of Si.

Since the 1990s, zooplankton abundance has declined throughout the lake. Bottom-up effects on zooplankton populations have possibly resulted from reduced food availability corresponding with the decline in phytoplankton biovolumes in 1987 and 1997 in Cook’s Bay, an effect also documented in Lake Huron (Barbiero et al. 2009, 2011). The declining trends in zooplankton populations do not correspond with the increase in phytoplankton in 2006 in Cook’s Bay, however, or with the lack of change in both Kempenfelt Bay and the main basin. Zooplankton populations were at relatively high abundances in 1989, perhaps due to reduced predation pressure from visual planktivorous fishes such as rainbow smelt and lake herring, both of which experienced large population declines in the late 1980s (Nicholls and Tudorancea 2001). The earliest abrupt decline in zooplankton populations occurred in 1994 for large cladocerans in the main basin, perhaps associated with the establishment of the predaceous zooplankter (*Bythotrephes longimanus*) in the same year (Kelly et al. 2013). Additionally, preliminary analyses identified shifts in zooplankton community composition in 1994, which was prior to the establishment of dreissenids, suggesting that *Bythotrephes* has had an effect on the zooplankton species abundances (J.D. Young, OMOE, 2010, unpubl. data).

Conclusions

The qualitative analysis of chironomid and diatom community compositional change over time provided important insight into the dynamics of multiple stressors affecting Lake Simcoe. Specifically, the combination of recent warming, extensive urbanization, dreissenid invasions, and P abatement measures has had a substantial ecological impact and effect on the water quality of Lake Simcoe. Early large-scale land clearance, damming, and canal construction pale in comparison to the magnitude and rate of chironomid and diatom compositional changes observed in the past ~50 years, suggesting that the combined effects far exceed the individual effect of any single stressor on the Lake Simcoe ecosystem (Hawryshyn et al. 2012). We suggest that the nearshore P shunt hypothesis is partially supported in Lake Simcoe, as indicated by 6 of the 11 potential shunt effects. There are inconsistencies relative to expected behaviour involving the shunt hypothesis, including no change in ice-free TP

concentrations and phytoplankton biovolumes, and the lack of filamentous benthic algae; however, we believe these results reflect multiple stressors interacting in a novel way in Lake Simcoe. We synthesized temporal trends and shifts that can be attributed to multiple ecosystem stressors causing changes in Lake Simcoe on physical, chemical, and biological scales, impacting every trophic level. The prevalence of potential ASs, in particular, warrants further investigation of the time periods when ASs were detected and the stressors that may have caused these changes. Overall, this study provides a framework for whole-ecosystem models to better understand the connections between physical and trophic linkages. Although there has been some success over the last 30 years in understanding and mitigating the combined effects of multiple stressors on the Lake Simcoe ecosystem, research, monitoring, and restoration efforts must continue if Lake Simcoe is to be managed effectively for source water protection and recreational use.

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