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## Quantifying a shift in benthic dominance from zebra (*Dreissena polymorpha*) to quagga (*Dreissena rostriformis bugensis*) mussels in a large, inland lake

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### ABSTRACT

Dreissenid mussels are aggressive invasive species that are continuing to spread across North America and co-occur in the same waterbodies with increasing frequency, yet the outcome and implications of this competition are poorly resolved. In 2009 and 2015, detailed (700+ sample sites) surveys were undertaken to assess the impacts of invasive dreissenid mussels in Lake Simcoe (Ontario, Canada). In 2009, zebra mussels were dominant, accounting for 84.3% of invasive mussel biomass recorded. In 2015, quagga mussels dominated (88.5% of invasive mussel biomass) and had expanded into profundal (>20 m water depth) sites and onto soft (mud/silt) substrates with a mean profundal density of 887 mussels/m<sup>2</sup> (2015) compared to ~39 mussels/m<sup>2</sup> in 2009. Based on our annual benthos monitoring, at a subset of ~30 sites, this shift from zebra to quagga mussels occurred ~2010 and is likely related to a population decline of zebra mussels in waterbodies where both species are present, as recorded elsewhere in the Great Lakes Region. As the initial invasion of dreissenid mussels caused widespread ecological changes in Lake Simcoe, we are currently investigating the effects this change in species dominance, and their expansion into the profundal zone, will have on the lake; and our environmental management strategies. Areas of future study will include: changes in the composition of benthos, fish, or phytoplankton communities; increased water clarity and reduction of the spring phytoplankton bloom; energy/nutrient cycling; and fouling of anthropogenic in-lake infrastructures (e.g. water treatment intakes) built at depths >25 m to avoid previous zebra mussel colonization.

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### Introduction

Dreissenid mussels are aggressive aquatic invaders that have become widespread in many freshwater systems throughout the Laurentian Great Lakes Region. In addition to extirpating many native species of bivalves and filter feeders in these habitats, dreissenids have also caused extensive, ecosystem-scale, environmental changes such as increased water clarity, altered phytoplankton biomass and species composition, changed benthic habitat space and structure, triggered declines in filter feeding taxa while facilitating increases to deposit-feeding and predatory invertebrates, and caused benthification of resources and energy flow (see comprehensive reviews by Higgins and Vander Zanden, 2010, Karatayev et al., 2014a, Mayer et al., 2014, Nalepa and Schloesser, 2014, Ward and Ricciardi, 2014). While zebra mussels (*Dreissena polymorpha*) were reported earliest in North America (1986 in Lake St. Clair, Carlton, 2008), their congener, quagga mussels (*D. rostriformis bugensis*) arrived soon after (1989, Mills et al.,

1993) and have since replaced them as the dominant benthic species in several Great Lakes (e.g. lakes Ontario and Michigan, the central and eastern basins of Lake Erie) (Mills et al., 1999; Karatayev et al., 2014a; Nalepa et al., 2010) and the Finger Lakes of upstate New York (USA) (Mei et al., 2016; Rudstam and Gandino, 2016). Studies of this change in species dominance, and the ecological implications of this change, are limited to a small number of case studies (above). Lake Simcoe, a large (surface area 722 km<sup>2</sup>, maximum depth 42 m, Table 1) inland lake in Ontario, Canada, is currently undergoing this dreissenid species change; and, as this lake has been well studied since the 1980s, it provides a good location to investigate this species change in more detail.

Zebra mussels were first recorded in Lake Simcoe in 1992 and had a lake-wide distribution by 1995–6 (Evans et al., 2011). Quagga mussels were first recorded in Lake Simcoe in 2004 (Ontario Ministry of Natural Resources (Ontario MNR), 2004) but had a very low density (3–7 individuals per grab sample) until 2009–10 (Lake Simcoe Region Conservation Authority (LSRCA), unpublished data). Since their arrival, dreissenids have become dominant taxa of the Lake Simcoe benthic fauna and, as in many other invaded waterbodies, have altered the abundance and diversity of the benthic community (Jimenez et al.,

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**Table 1**  
Mean annual (2013–2015) lakewide physical and water chemistry data recorded at Lake Simcoe, Ontario, Canada.

Variable	
Surface area	722 km <sup>2</sup>
Maximum depth	42 m
Mean depth	15 m
Catchment area	3307 km <sup>2</sup>
Secchi disk transparency	6.9 m
pH	8.2
Alkalinity	115 mg/L
Calcium	44.6 mg/L
Chloride	42.2 mg/L
Chlorophyll <i>a</i>	1.4 µg/L
Total Kjeldahl nitrogen	0.47 mg/L
Total phosphorus	16.0 µg/L
Silicon	2.0 mg/L
Sodium	24.6 mg/L
Specific conductance	408 µS/cm <sup>2</sup>
Turbidity	0.49 NTU
Dissolved organic carbon	4.2 mg/L

2011; Ozersky et al., 2011; Rennie and Evans, 2012), and changed energy flow and foodwebs through the benthification of nutrients and resources, in particular the sequestration and storage of carbon (C), nitrogen (N), and phosphorus (P) (Ozersky et al., 2015a, 2015b). While nutrient levels and offshore phytoplankton biomass have decreased, and water clarity increased, in Lake Simcoe, these changes were synchronous with implementation of P abatement strategies that decreased P loading to the lake by 20–30% since the mid-1990s (Evans et al., 1996; Young et al., 2011). As in other lakes with dreissenid colonization and nutrient management strategies (e.g. lakes Michigan and Huron, Warner and Lesht, 2015), partitioning the proportion of change attributable to invasive mussel filtration and feeding (versus P reduction) remains challenging for Lake Simcoe.

Although several studies of the Lake Simcoe benthic community have been undertaken, these have been of relatively small spatial and temporal scales with a limited number of sample sites. Pre-dreissenid benthic data is mostly limited to “snapshots” from the 1920s (Rawson, 1928); then a gap until the 1980s–1990s when studies examined four rocky littoral sites (Ozersky et al., 2011), a single cross-lake transect (Rennie and Evans, 2012), and 40 shallow and deep sites from two of the three lake basins (Jimenez et al., 2011). Rawson (1928) described a benthos community, dominated by Chironomidae (51% of total biomass) and reported water clarity (Secchi disk transparency (SDT) ~7 m) similar to current records (mean SDT ~4–11 m) that pre-dated the severe impacts of increased P loading/depleted hypolimnetic dissolved oxygen (~1960–1980s). The remaining studies, which allow a comparison of pre- and post-dreissenid benthic communities, reported that after their establishment, zebra mussels quickly became the dominant benthic species in the nearshore zone (water depths 2–20 m). Although non-dreissenid benthic density may have decreased at sites with soft substrates and deeper than 20 m depth (Jimenez et al., 2011; Rennie and Evans, 2012), mean abundance was 45× greater at rocky littoral/nearshore zone sites mostly driven by increases in deposit-feeder taxa (i.e. amphipods, isopods, chironomids, and oligochaetes) (Ozersky et al., 2011).

In this study, we set out to provide the first, high resolution, lake-wide, targeted investigation of invasive dreissenid mussels in Lake Simcoe. The objectives of our study were to: (1) quantify the abundance, biomass, and spatial distribution of *Dreissena* in Lake Simcoe; (2) confirm a decline in zebra mussels and their replacement with quagga mussels recorded by our annual benthic monitoring data; (3) investigate differences between the 2009 and 2015 mussel surveys and explore changes within/between lake areas; and (4) determine potential impacts to benthic invertebrate community, the lake ecosystem as a whole, and our environmental management and restoration of Lake Simcoe.

## Materials and methods

### Study site

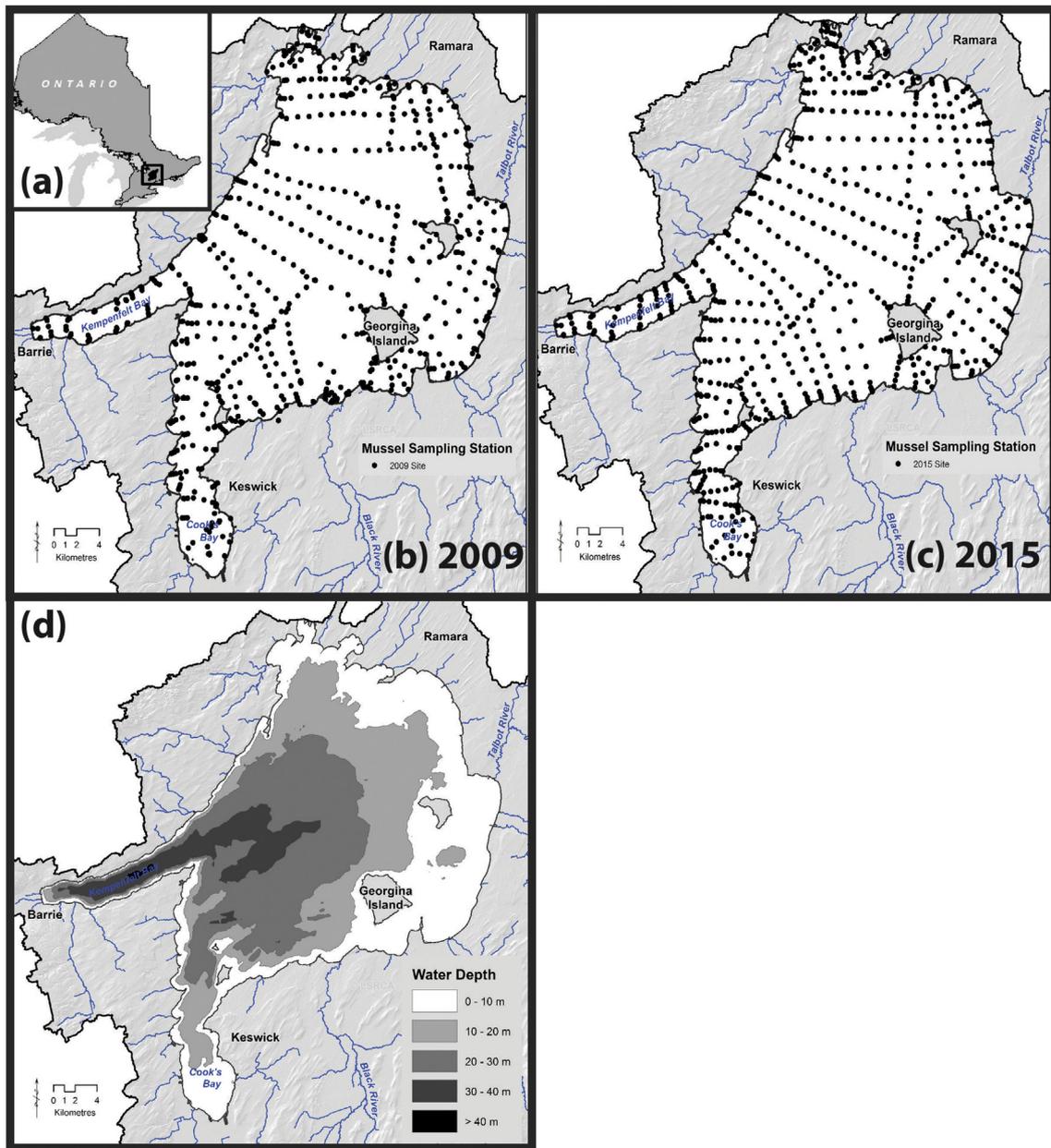
Lake Simcoe (44°25'N, 79°25'W) is the largest inland lake in south-central Ontario, Canada (Fig. 1a–d, Table 1). Agriculture and natural cover are the primary land uses in the watershed (~47% and 40% of surface area, respectively), although urban area (~12%) is increasing (Palmer et al., 2011, 2013a, 2013b), likely related to the lake's close proximity to Canada's largest city (Toronto; metropolitan area population ~6.2 million, Statistics Canada, 2017). Although the lake is currently meso-oligotrophic (mean, fall overturn, total phosphorus (TP) ~16.0 µg/L; range 9–24 µg/L; 2009–2012; Ontario MOE 2014), it has undergone environmental changes consistent with eutrophication since European settlement in the watershed (starting ~1796). P loading increased from a model-estimated, pre-European settlement 32 t/y (Nicholls, 1997) to a peak ~100 t/y by the mid-1980s. P abatement programs have since reduced P loading to a five-year mean ~85.5 t/y (2010–2014), although this value fluctuates (71–101 t/y), mostly related to total annual precipitation amounts (LSRCA, 2017). The lake experienced recruitment failure in the coldwater fish community (~1960–1980s), related to extended periods of low hypolimnetic dissolved oxygen (DO) resulting from increased P loading. Recently, likely in response to P abatement measures, the period of deepwater hypoxia has been greatly shortened and natural recruitment has been reported for coldwater fish species (e.g. lake trout, *Salvelinus namaycush*, and lake whitefish, *Coregonus clupeaformis*). The current lake management plan has set targets for an autumn hypolimnetic DO = 7 mg/L, which corresponds to a target P load of 44 t/y (Young et al., 2011).

### Sampling and laboratory protocols

Mussels were collected from Lake Simcoe by Petite Ponar Grab at 747 sites (Fig. 1b) arranged in 88 transects, perpendicular to the shoreline, spaced at 2.5 km intervals between 11 June and 14 October 2009 (with supplementary sampling 17–28 May 2010), and 715 sites (Fig. 1c) between 6 April and 23 September 2015 (the additional 32 sites from the 2009 survey were used for initially testing sampling methods/training field staff and not repeated in 2015). At each transect, grab samples were taken at water depths of 1, 3, 5, 10, 15, 20, 25, 30, and 40 m. For transects extending across the lake past the deepest sample depth of that transect (e.g. sampled at 15 m but not reaching 20 m depth), additional grab samples were taken at 1 km intervals to reach the end of the transect. As grab samplers have reduced efficacy on rocky/hard substrates, in 2015, photographs of 14 grab sample sites on hard substrata were taken with a GoPro Hero 3+ Silver camera attached to a marked 0.25 m<sup>2</sup> quadrat frame fitted with LED lighting. Mussel counts from photographs were then compared with abundance of total mussels from grab samples.

At each site, grab samples were deposited into a sieve bucket (0.5 mm mesh screen bottom) and rinsed with lake water to remove mud. Mussels were then removed, placed in 500 mL polyethylene (PET) jars, and placed in a cooler, on ice, for transport to the lab. Samples that were not processed within 24 h were frozen, and then thawed before analysis. At the lab, mussels were identified to species, sorted into respective, species-specific, size classes based on total valve length (0–10 mm, 11–20 mm, 21–30 mm, 30+ mm), and enumerated. To determine biomass, mussels of each size class had tissue removed from shells, weighed to determine shell-free wet weight, dried for 24 h at 105 °C in a gravity convection oven, and re-weighed to determine shell-free dry weight biomass.

Annual trends in dreissenid mussels (and other benthos) were tracked by an annual collection of triplicate Petite Ponar Grab samples at a subset of sites stratified by depth (littoral/nearshore 2–20 m water depth; profundal >20 m depth) (based on Kilgour et al., 2008 and Rawson, 1928). Samples were collected in October 2005 (19



**Fig. 1.** Maps of Lake Simcoe: (a) denotes location of lake and catchment basin within Ontario, Canada; (b) Lake Simcoe with 747 sample sites used in the 2009 dreissenid mussel survey; (c) Lake Simcoe with 715 sample sites used in the 2015 dreissenid mussel survey; (d) bathymetry of the lake.

sites), November 2008 (24 sites), October 2009 (32 sites), October 2010 (17 sites), May–June and October–November 2011 (48 sites), October 2012 (27 sites), and October 2013–2015 (32 sites). Grab samples were washed with lake water in a sieve bucket (0.5 mm mesh screen) and placed in 500-mL PET jars with 10% buffered formalin solution. In the lab, benthos were picked and identified to lowest practical taxonomic level (all individuals in each sample) using a Nikon SMZ 745 dissecting microscope.

Mean early spring (1 April–15 May; pre-thermal stratification of the water column) and mean late-spring–early summer (1 June–15 July; during thermal stratification) data (2008–2015) for Secchi disk transparency and chlorophyll *a* concentration from three of our bi-weekly monitoring lake stations (with water depths > 30 m) were compiled to assess the impact of profundal zone dreissenid mussels in Lake Simcoe. Water transparency was recorded using a 20-cm black and white Secchi disk. Chlorophyll *a* was recorded using a water quality sonde (YSI 6600V2, 2008–2014; EXO2, 2015–2016; both YSI Inc. Yellow Springs OH) and by laboratory analysis (colourimetry, Maxxam Analytics,

Mississauga ON) of surface water samples collected using a Van Dorn bottle at a water depth of 1.5 m. These two methods gave results that were highly correlated ( $r = 0.86$ ) in paired sampling.

*Statistical analyses*

Spatial changes in zebra and quagga mussel biomass were visualized using a GIS-based ordinary kriging technique from the Geostatistical Analyst extension of ArcGIS 10.0 (Environmental Systems Research Institute (ESRI), Redlands CA). In order to create the best interpolated layer, four semivariogram models (circular, Gaussian, spherical, stable) were compared. The model chosen best satisfied the criteria of: root mean square standardized closest to 1, root mean square and average standard errors were closest to each other in value, and standardized mean was closest to zero (Fortin and Dale, 2008, Johnston et al., 2001, Legendre and Legendre, 2012).

For comparisons of changes to mean mussel abundance and biomass between the 2009 and 2015 surveys, a Mann-Whitney *U* test was used.

To explore differences related to depth and size class between zebra and quagga mussels, in 2009 and 2015, a one-way ranked ANOVA with post-hoc Mann-Whitney *U* test was used. To analyze trends in annual benthos monitoring data in 2005, and 2008–2015, linear regression was used. For the analyses above, we used SigmaPlot for Windows 13.0 (Systat Software Inc., San Jose CA). For further comparisons of the annual benthic monitoring data between mussel species, years, and lake areas (Cook's Bay, Kempenfelt Bay, and the main basin), a nested two-way (hierarchical) ANOVA with post-hoc Tukey test of means was carried out using R (v. 3.1.1) and the "nlme" package (v.3.1–17) (The R Foundation for Statistical Computing).

#### Modeling potential impacts of dreissenid changes and profundal zone expansion

To explore the potential impacts of dreissenid changes, and the expansion of quaggas into the profundal zone, on aspects of lake ecology, a simple model was developed using biomass data (mg/m<sup>2</sup>) from the 2009 and 2015 surveys. Available mussel filter-feeding rate (mL/mg·h) from literature (Baldwin et al., 2002, Fanslow et al., 1995, Mosley and Bootsma, 2015, Vanderploeg et al., 2009), and volume of the unstratified water column above each sample site (m<sup>3</sup>) were used to calculate the time required for the mussel biomass to filter this water volume. These data were then used in a kriging analysis (as described above) to visualize benthification of planktonic resources by dreissenids in Lake Simcoe, and changes between 2009 and 2015.

#### Results

A total of 43,952 mussels were recovered and analyzed from samples in 2009 with zebra mussels accounting for 84.3% of recorded invasive mussel biomass and being the dominant dreissenid species in both abundance and biomass at nearshore (2–20 m) sites, and three profundal (>20 m) sites that had dreissenids present. In 2015, a total of 26,742 mussels were recovered and analyzed with quagga mussels comprising 88.5% of recorded biomass and dominating both nearshore and profundal sites. Total mean dreissenid abundance (both species combined) was lower in 2015 compared to 2009, but mean shell-free dry weight (SFDW) biomass was higher in 2015, indicating a larger average size of quaggas compared to zebra mussels (Table 2). Nearshore sites had the highest abundance and biomass of dreissenids in both 2009 (2080 mussels/m<sup>2</sup>; 13.3 g/m<sup>2</sup>) and 2015 (1628 mussels/m<sup>2</sup>; 17.8 g/m<sup>2</sup>), but profundal sites had an almost doubling of mussel abundance and biomass in 2015 (888 mussels/m<sup>2</sup>; 8.0 g/m<sup>2</sup>) compared to 2009 (400 mussels/m<sup>2</sup>; 4.6 g/m<sup>2</sup>) (Table 2). Differences in abundance and biomass for both species at both nearshore and profundal sites between 2009 and 2015 were highly significant ( $p < 0.001$ ).

The increase in mussel abundance and biomass at profundal sites in 2015 was due to the presence of the "profunda" morphotype of quagga mussels (Dermott and Munawar, 1993; Nalepa et al., 2014) that accounted for 97% of mussels recovered at water depths >20 m. Additionally, this profunda morph comprised 96% of quagga mussels recorded at nearshore sites with soft (mud/silt) substrates. In 2015, 78% of

sites deeper than 20 m had mussels, compared to 12% in 2009. Although numerous empty valves from native mussel species were recovered in both years of this survey and in our annual benthic sampling, only one live native mussel (Unionidae) was recovered from a site near Georgina Island on 8 July 2015, and then returned to the lake. No other live native unionid mussels were recorded in our 2009 survey or our annual benthos monitoring program in the lake; however, relict populations of unionids have been recorded in wetlands and several tributaries of Lake Simcoe (LSRCA, unpublished data).

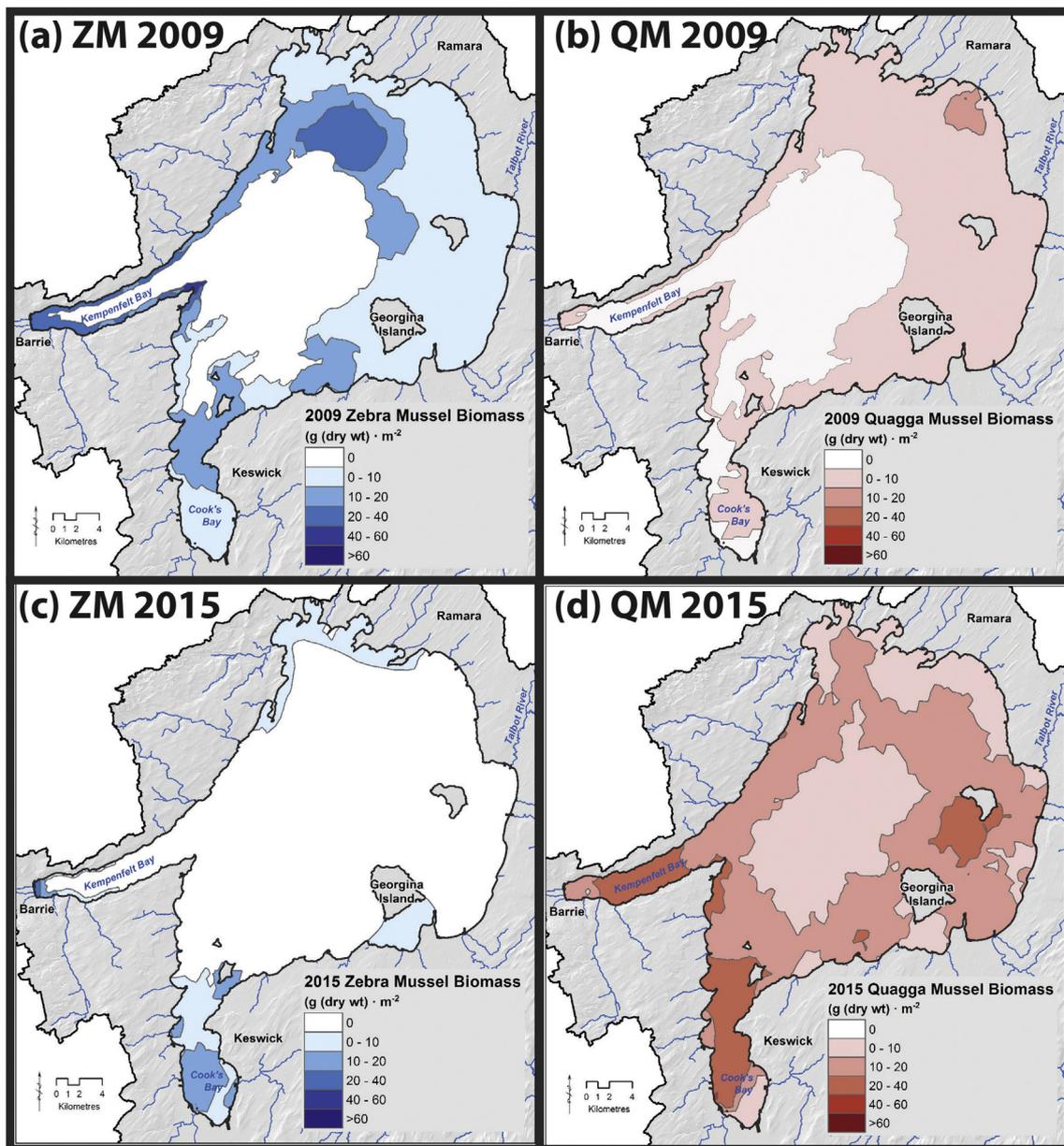
Using GIS-based kriging techniques, biomass from the two dreissenid species was visualized by interpolating our 2009 and 2015 survey data (Fig. 2). For 2009, the stable model had the best fit for both zebra and quagga mussels (root mean square standardized error (RMSSE) = 0.98 and 0.99, respectively). Dreissenids were predominantly found on hard substrates such as rock shelf, cobble, and boulders, with lower biomass found on sand substrates and attached to aquatic plants, particularly in Cook's Bay (Fig. 2a–b). In 2009, lakewide, both species were limited to water depths shallower than ~20 m, with the exception of three sites in Kempenfelt Bay where zebra mussels were recovered from ~30 m depth. For 2015 data, the Gaussian model had the best fit (zebra RMSSE = 1.147, quagga RMSSE = 0.98). Spatial coverage of zebra mussels was greatly reduced (as reflected in the abundance and biomass data in Table 2), with significant populations only being recovered attached to aquatic plants in Cook's Bay, and in shallow water depths close to Barrie (Fig. 2c). Quagga mussels were greatly expanded in 2015, particularly in profundal habitats and have been recovered from sites at the deepest part of the lake in Kempenfelt Bay ( $Z_{\max} = 42$  m) (Fig. 2d).

Similar to spatial coverage trends, dreissenid distribution and biomass in relation to water depth changed between the two surveys (Fig. 3). Zebra mussels had a decreased depth range in 2015 compared to 2009, whereas quagga mussels had expanded into the profundal zone. Results of Mann-Whitney *U* tests showed significant differences between depth intervals for zebra mussels ( $p < 0.01$ ), quagga mussels ( $p < 0.001$ ), and both species combined ( $p < 0.05$ ). When separated for depth zone (nearshore vs profundal), there was a significant difference between 2009 and 2015 at profundal depths for total dreissenid biomass ( $p < 0.01$ ), but nearshore sites showed no significant difference ( $p = 0.98$ ) between 2009 and 2015 in total dreissenid biomass (Fig. 3).

Corresponding with an increase in biomass, and a reduction in abundance, there was an increase in relatively larger size individuals (>20 mm) in 2015 compared to 2009 (Fig. 4). Zebra mussels with valve lengths of 11–20 mm dominated the lake in 2009 by biomass (Fig. 4a), but a higher density of smaller (0–10 mm) individuals was recorded (Fig. 4c). In 2015 the majority of zebra mussels were of a smaller size (0–10 mm) and found attached to aquatic plants. Quagga mussels of larger valve lengths (11–20 mm, 21–30 mm) dominated in 2015 by biomass (Fig. 4c), but were more evenly distributed across the 0–10, 11–20, and 21–30 mm size classes in terms of density (Fig. 4d). Differences between size classes of each species biomass within each year were significantly different ( $p < 0.001$ ), except for zebra mussels 0–10 mm and 11–20 mm in 2015 (Fig. 4a,b). In terms of density, differences between classes were significant except zebra mussels 0–

**Table 2**  
Comparison of mean abundance and mean shell-free dry weight (SFDW) biomass with standard error values for zebra and quagga mussels in 2009 and 2015 from Lake Simcoe, Ontario, Canada.

Lake zone	Species	Mean abundance (individuals/m <sup>2</sup> )		Mean SFDW biomass (g/m <sup>2</sup> )	
		2009	2015	2009	2015
Nearshore (2–20 m)	Zebra	2474.3 ± 238.2	407.3 ± 86.1	11.3 ± 1.1	2.3 ± 0.6
	Quagga	333.7 ± 64.2	1221.1 ± 77.6	2.0 ± 0.3	15.5 ± 1.0
Profundal (>20 m)	Zebra	361.4 ± 113.8	1.5 ± 1.1	3.8 ± 1.4	0.01 ± 0.01
	Quagga	39.2 ± 20.8	886.7 ± 121.7	0.8 ± 0.6	8.0 ± 1.2
Total	Zebra	2028.7 ± 192.0	318.8 ± 67.6	9.7 ± 0.9	1.8 ± 0.5
	Quagga	271.6 ± 51.0	1148.1 ± 66.4	1.8 ± 0.2	13.9 ± 0.8
	Both species	2299.8 ± 222.4	1468.9 ± 101.3	11.5 ± 1.0	15.7 ± 1.1



**Fig. 2.** Mean shell-free dry weight biomass of *Dreissena* spp. mussels in Lake Simcoe as interpolated by kriging analysis (darker hue indicates higher biomass): (a) zebra mussels in 2009; (b) quagga mussels in 2009; (c) zebra mussels in 2015; (d) quagga mussels in 2015. For a colour version of this figure, readers are directed to the online version available at the Journal of Great Lakes Research website.

10 mm versus 11–20 mm, and 21–30 versus 30+ mm in 2015; and quagga mussels 0–10 mm and 11–20 mm versus 21–20 mm in 2015 (Fig. 4c,d). Differences between years (2009 vs 2015) within each size class were significant ( $p < 0.001$ ).

Using dreissenid data from our annual benthos monitoring program, both zebra and quagga mussels had highly significant trends at littoral/nearshore sites between 2005 and 2008–2015 (zebra:  $r^2 = 0.81$ ,  $p < 0.001$ , quagga:  $r^2 = 0.91$ ,  $p < 0.001$ ; Fig. 5a–b). Although zebra mussels had a large decline in abundance at nearshore sites between 2005 and 2008, their abundance was relatively stable 2008–2011 (regression  $r^2 = 0.50$ ,  $p = 0.29$ ), after which a further decrease was recorded (2012–2015). At profundal sites, zebra mussels had low density in all sampling years and no significant trend ( $r^2 = 0.0002$ ,  $p = 0.97$ ), whereas quagga mussels increased in density, but this trend is currently not significant ( $r^2 = 0.38$ ,  $p = 0.07$ ). No significant differences were recorded in zebra mussel abundance between the three principal lake areas (Cook's Bay, Kempenfelt Bay, and the main basin) in the annual data. Zebra mussels

had low abundances at profundal sites ( $< 14$  individuals per grab), and no significant trends were recorded between years ( $p = 0.75$ ) or between Kempenfelt Bay and the main basin ( $p = 0.49$ ; Cook's Bay did not have any sample sites with a water depth  $> 20$  m). Quagga mussels, conversely, had a statistically significant increase at both nearshore ( $p < 10^{-8}$ ) and profundal ( $p < 0.01$ ) sites from 2008 to 2015. Although quagga mussels were first reported in Lake Simcoe in 2004 (Ontario MNR, 2004), they were not recorded in 2005 sampling and had very low numbers in 2008–2009 annual sampling (mean = 3–7 individuals per grab sample). Nearshore sites had significant differences in quagga mussel abundance between the three lake areas ( $p < 0.001$ ), whereas there was no significant differences ( $p = 0.06$ ) between years, or at profundal sites, between Kempenfelt Bay and the main basin (Fig. 5b).

To explore possible ecological impacts of the quagga mussel expansion into the profundal zone, Secchi disk transparency (SDT) and chlorophyll *a* data from spring overturn and after thermal stratification of

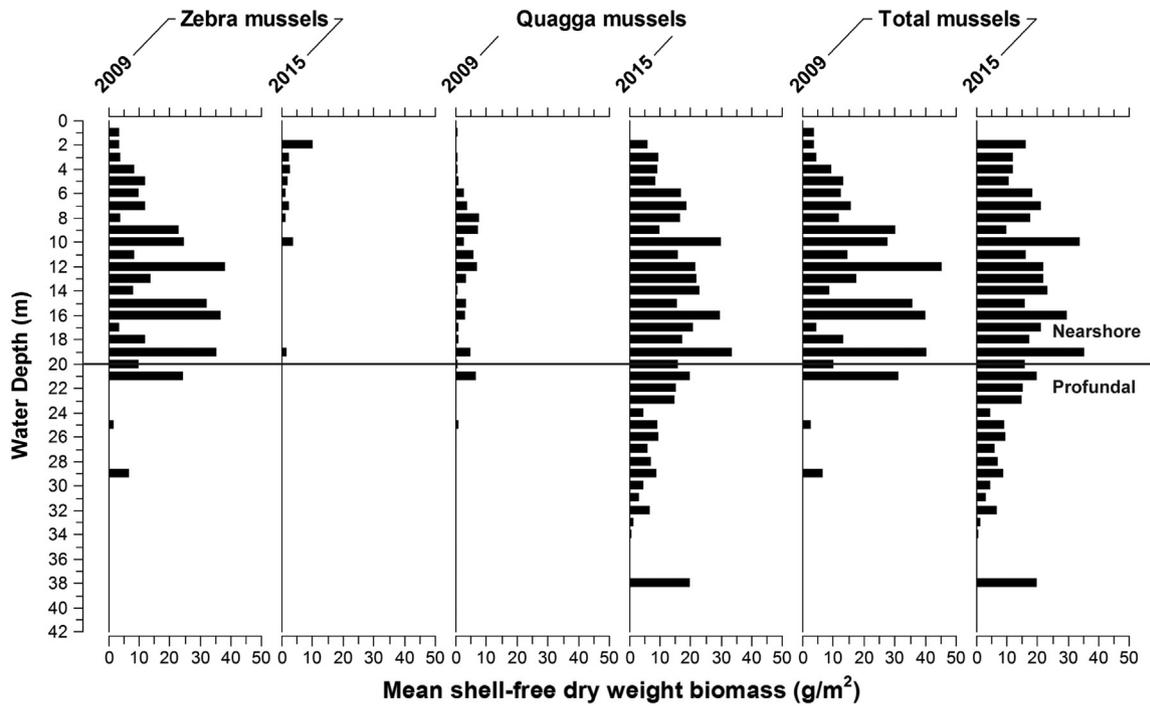


Fig. 3. Mean shell-free dry weight biomass of zebra and quagga mussels (and both species combined) in relation to water depth in Lake Simcoe recorded in 2009 and 2015.

the water column were compared (Fig. 6a,b). Before 2015, pre-stratification water clarity (mean SDT = 6.3 m) was lower, and pre-stratification chlorophyll *a* (mean = 4.2 µg/L) was higher, than after stratification (mean SDT = 7.8, mean chlorophyll *a* = 1.0 µg/L) (Fig. 6a, b). In 2016, water clarity was much higher during water column mixing (mean = 15.8 m) than after stratification (mean = 9.6 m),

whereas pre-stratification chlorophyll *a* (1.0 µg/L) had declined to values equivalent to the post-stratified period.

Using our mussel biomass data, available mussel filtration rates, and kriging interpolation, maps were developed to visualize the time taken for mussels, in areas of the lake, to filter the water column under mixed conditions in 2009 and 2015 (Fig. 7a, b; Table 3). For 2009, the spherical

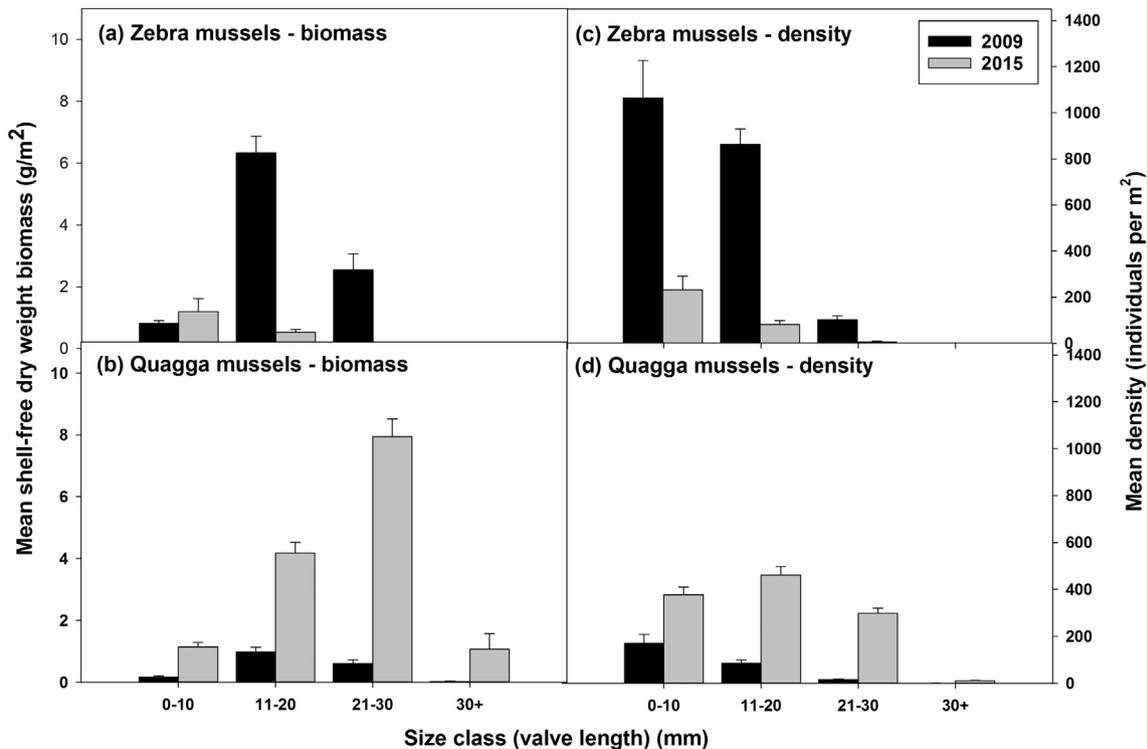
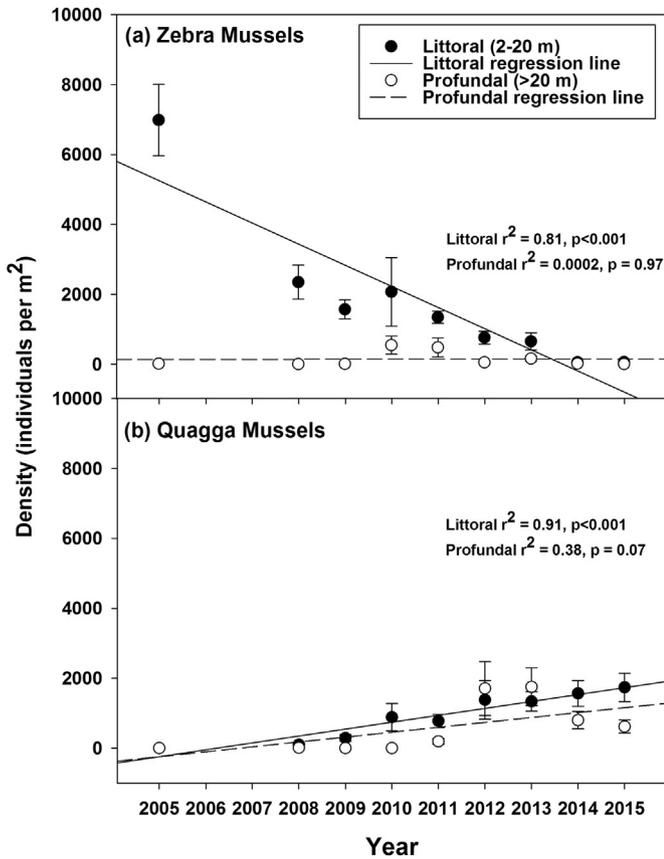


Fig. 4. Valve length size class distribution of zebra and quagga mussels from Lake Simcoe: (a) mean shell-free dry weight biomass of zebra mussels, (b) mean shell-free dry weight biomass of quagga mussels; (c) mean density/abundance of zebra mussels in each size class; (d) density of quagga mussels.

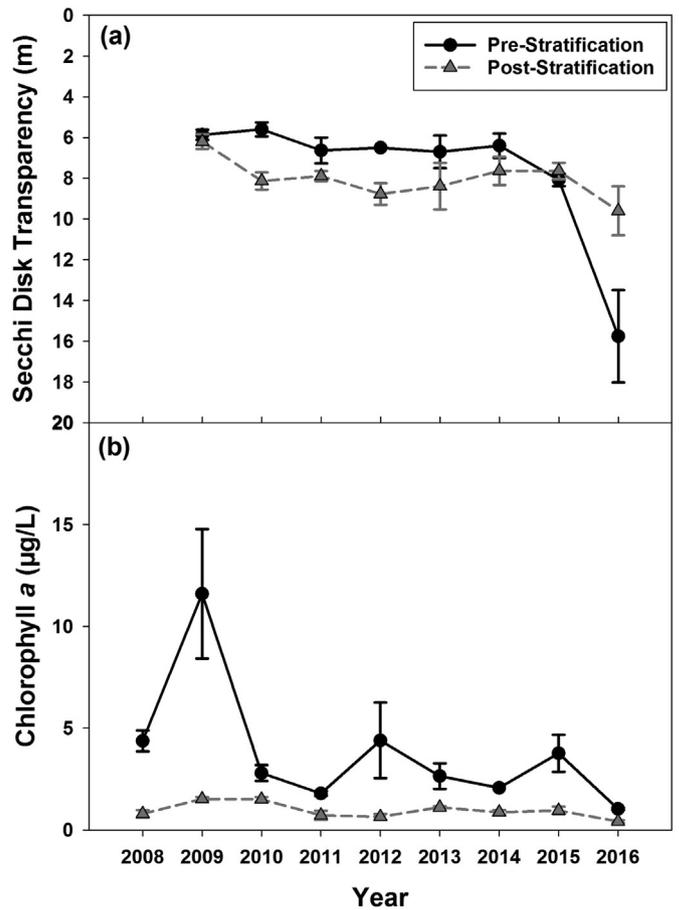


**Fig. 5.** Mean abundance of dreissenid mussels in Lake Simcoe at ~20 littoral and ~12 profundal sampling stations recorded from annual surveys in 2005 and 2008–2015: (a) zebra mussels, and (b) quagga mussels. The regression lines and statistics are added to help the interpretation of the data. Note that these numbers are different from those of the ANOVA analysis of these data discussed in the text.

model had the best fit (RMSSE = 0.58), whereas for 2015 the Gaussian model had lowest errors (RMSSE = 0.75). Mean errors were higher for this analysis than biomass data due to larger variability in filtration rates, likely driven by sample sites with a low biomass and deep water column (i.e. large volume) thus having a long estimated filtration time. Highest filtration rates, were found in areas with larger recorded biomass of mussels and relatively warmer, shallower water. In 2009, dominated by zebra mussels that predominantly inhabited the near-shore, it was estimated the total mussel population could filter 27.9% of the lake volume (11 km<sup>3</sup>) per day, (or a volume equivalent to Lake Simcoe every 3.6 days) with much of this contribution (27.1%) being from nearshore mussels. In 2015, the contribution of filtration from mussels in the profundal zone had increased (~1.95% of lake volume, compared to 0.74% in 2009), but nearshore mussels were again responsible for most of the total filtration (36.3% of total lake volume). In 2015, the total mussel population was estimated to filter 38.1% of the lake volume per day, or 2.6 days for a volume equivalent to Lake Simcoe.

**Discussion**

Lake Simcoe has undergone a large shift in the dominance of dreissenids from zebra mussels to quagga mussels (Figs. 2 and 5), similar to that observed in lakes Erie, Michigan, and Ontario (Karatajev et al., 2014a; Nalepa et al., 2010; Wilson et al., 2006). As in these other areas, this change is likely due to zebra mussels being limited by occupying all suitable habitat space and a decreasing quantity of food particles (Karatajev et al., 2015). Quagga mussels can occupy former zebra mussel habitat and have competitive advantages as they can survive on lower concentrations of food particles, have greater energetic



**Fig. 6.** Graphs of mean (a) Secchi disk transparency and (b) chlorophyll a concentration (determined by fluorescence and laboratory analysis) for pre-thermal stratification (1 April–15 May) and post-thermal stratification (1 June–15 July) in Lake Simcoe 2008–2015.

efficiency, and are active at much lower temperatures (4 °C) than zebra mussels (~12 °C) (Karatajev et al., 2015; Zaiko et al., 2014). Additionally, the profunda morphotype of quagga mussels has longer siphons that enable it to successfully occupy soft substrates (Dermott and Munawar, 1993; Claxton et al., 1998), which can provide much more habitat space (e.g. the profundal zone) than that available to zebra mussels. In Lake Simcoe, quagga mussels expanded both spatially across the lake (Fig. 2) and into deeper water depths (Fig. 3) either by outcompeting zebra mussels or occupying space made available as zebra mussel density declined. This pattern is similar to that observed in the Great Lakes, as described by Karatajev et al. (2015), and in particular Lake Michigan, where, as quagga mussels expanded into the profundal zone, their increased biomass correlated with decreased chlorophyll a concentrations during the spring phytoplankton bloom (Nalepa et al., 2010).

Although zebra mussels are, currently, not extirpated in Lake Simcoe, they have been restricted to more marginal habitats, mostly in Cook’s Bay where they are predominantly found attached to aquatic plants. In our 2015 survey, zebra mussels were mostly of a small size (0–10 mm, Fig. 4) that would be advantageous for attachment on narrow plant stems (particularly *Myriophyllum spicatum*, a dominant shallow water species in Lake Simcoe; Ginn, 2011). The small size of zebra mussels in 2015 is indicative of a rapid recruitment or generation time and suggests most zebra mussels are young-of-the-year with only a small population of reproductive mature adults in Lake Simcoe. In a study on nearshore sites in eastern Lake Erie, Diggins et al. (2004) found that despite quagga mussels accounting for 96–100% of dreissenid biomass in the benthos, zebra mussels were dominant (30–61% of dreissenids) as epibionts. Burlakova et al. (2006) reported a

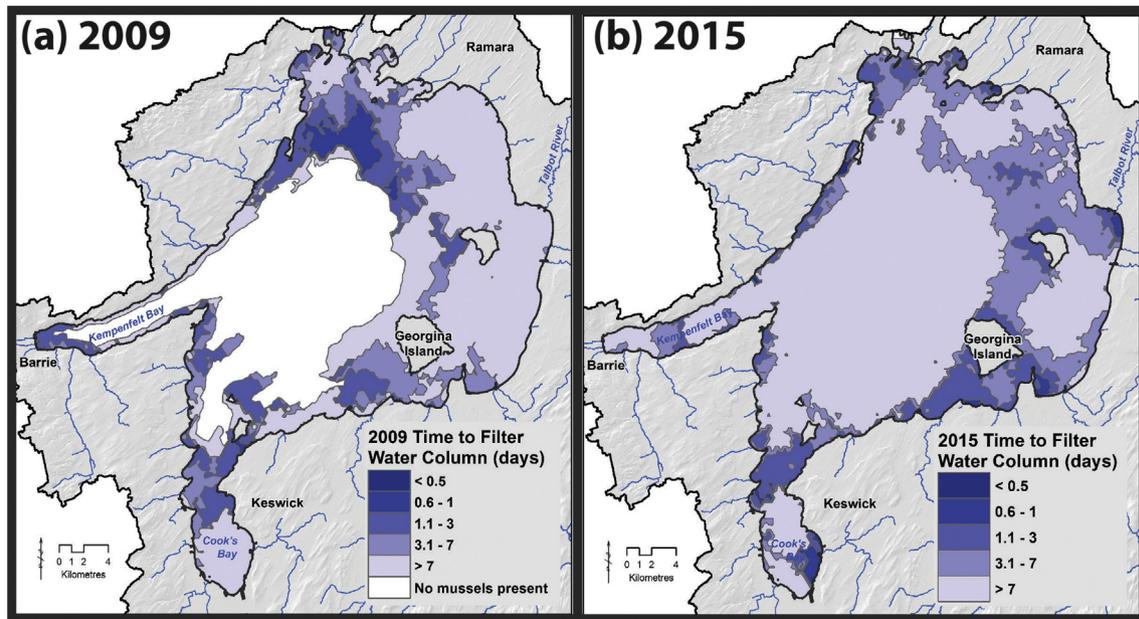


Fig. 7. Modeled time (days) for total biomass of both *Dreissena* spp. mussels to filter water column under mixed conditions in Lake Simcoe as interpolated by kriging analysis (darker hue indicates shorter filtration time): (a) 2009; (b) 2015. For a colour version of this figure, readers are directed to the online version available at the Journal of Great Lakes Research website.

similar pattern in lakes from the Ukraine, where high densities of zebra mussels of small size, and thus low biomass, attached to macrophytes but likely died following plant senescence in autumn and were covered by mud. Additionally, Cook's Bay is the more nutrient enriched portion of Lake Simcoe with a relatively higher algal biomass (Ontario MOECC, 2014) and, as such, may support the higher food requirement of zebra mussels (Baldwin et al., 2002). This inconsistency with the other areas of Lake Simcoe shows similarities with the western basin of Lake Erie, where zebra mussels have a much higher abundance (33% of total dreissenids) compared to the central and eastern basins (3% and 1% of total *Dreissena*, respectively), likely due to higher phytoplankton concentrations that allow zebra mussels to remain prominent (Karatayev et al., 2014a).

The trends reported by our two surveys and annual monitoring program supports the life strategy used by zebra mussels as proposed by Zaiko et al. (2014) and Karatayev et al. (2015) who stated that zebra mussel populations decline starting ~2.5 years after initial colonization. In lakes where both dreissenid species are present, Karatayev et al. (2015) point to a shift from zebra to quagga mussels occurring after 9 years of co-existence. In Lake Simcoe, we found this species change occurred ~7 years after quagga mussels were first reported (2004). A more rapid quagga mussel expansion may be due to Lake Simcoe's relatively smaller surface area and shallower mean depth relative to the Great Lakes and more suitable substrates being available in a relatively smaller area, and at closer proximity, enabling a faster rate of expansion. In a

study from Onondaga Lake (New York, USA), Rudstam and Gandino (2016) report that both dreissenid species were present by 1992, but remained rare until 1998 when zebra mussels increased in abundance and dominated benthic collections. While quagga mussels continued to be rare as late as 2002, they had replaced zebra mussels and accounted for 90% of the Onondaga Lake dreissenid biomass by 2009.

Although we have no extensive abundance or biomass data from Lake Simcoe for ~2–10 years after zebra mussel arrival (veligers were detected in 1991, adults reported lake-wide in 1995; Evans et al., 2011), the sharp decline between the 2005 data and 2008–2015 (Fig. 5) is indicative of a rapidly decreasing population and previous years (1995–2005) likely had much higher abundances. In addition, it is also likely that there was change in zebra mussel population size structure with 2005 having most smaller individuals, 2008 having relatively larger individuals, while biomass likely remained similar between the years. Studies by Evans et al. (2011) report zebra mussel densities (valve lengths > 12 mm) of up to 57,715/m<sup>2</sup> on rock shoals in the main basin of Lake Simcoe in 1996. With respect to our sampling protocol, which relied on grab sampling compared to other studies that used SCUBA divers and airlift samplers (e.g. Ozersky et al., 2011), we acknowledge that there is most likely bias and limitations, particularly in regards to sampling sites on hard substrates (e.g. rock shelf, boulders, and cobble). While data recorded from our hard substrate sites (100 sites or 13.8% of samples) is likely lower than "actual" abundances, hard substrate sites in our surveys did still have higher abundances/biomass than

Table 3

Estimated change in mussel filtering rates for nearshore and profundal zones of Lake Simcoe, based on laboratory values, related to shift in dreissenid species dominance.

		Estimated mussel filtering rate (10 <sup>9</sup> L/h)		Percentage of total lake volume (11 km <sup>3</sup> ) filtered per day	
		2009	2015	2009	2015
Nearshore (2–20 m)	Zebra <sup>a</sup>	107.0	22.2	22.9	4.8
	Quagga <sup>b</sup>	19.5	146.8	4.2	31.5
	Total flux	126.5	169.0	27.1	36.3
Profundal (>20 m)	Zebra <sup>a</sup>	2.6	0.07	0.6	0.01
	Quagga <sup>c</sup>	0.9	9.1	0.2	1.9
	Total flux	3.5	9.2	0.7	2.0

<sup>a</sup> Fanslow et al. (1995); Mosley and Bootsma (2015): 16.2 mL/mg·h at ~15 °C; 5 mL/mg·h at 5 °C.

<sup>b</sup> Baldwin et al. (2002): 16.2 mL/mg·h at 20–25 °C.

<sup>c</sup> Vanderploeg et al. (2009): 8.3 mL/mg·h at 4.6 °C.

sites on softer substrates (e.g. gravel, sand, and mud/silt). We feel that while sampling errors do exist, they are consistent between the two surveys and data collected in 2009 and 2015 from hard substrate sites would be comparable, although underestimated. In an effort to account for hard substrate sampling error, we deployed a GoPro camera attached to a 0.25 m<sup>2</sup> quadrat frame to photograph sample sites. Analysis of these photographs do indicate a 2–3 × higher abundance of mussels, compared to our grab samples of the same site; however, this methodology was also limited, and probably again under-represented “actual” abundance, as three-dimensional space is represented on a two-dimensional photograph, thus obscuring mussels attached to the undersides of boulders/cobble or within/behind mussel druses.

#### Effect on benthic community

Since the arrival of zebra mussels in Lake Simcoe in the early 1990s, there has been a large increase in the total abundance of benthic invertebrates, although much of this increase is due to dense populations of dreissenid mussels. When invasive mussels are excluded from analyses, [Ozersky et al. \(2011\)](#) reported that non-dreissenid biomass at shallow (water depth = 2–6 m) sites was 45 × greater in 2008, compared to 1993, mostly in groups of deposit-feeders (amphipods, isopods, chironomids, and oligochaetes). Similar trends have been reported from other areas where deposit feeders and predatory benthos exploit new food resources (i.e. nutrient-rich mussel biodeposits) and refugia in the more complex habitat space among dreissenid shells ([Burlakova et al., 2012](#); [Ricciardi et al., 1997](#); [Ward and Ricciardi, 2014](#)).

At deeper sites in Lake Simcoe, [Rennie and Evans \(2012\)](#) compared data from the 1980s with 2008–9 and reported that Chironomidae and Sphaeriidae biomass declined at 10–15 m depths, where we reported zebra mussels in 2009, but increased at 20–30 m deep sites where we reported very few zebra mussels. Comparison of our annual benthos survey data with [Rennie and Evans \(2012\)](#) suggests that, in Lake Simcoe, filter feeding benthic taxa are being outcompeted at sites where dreissenids were present. Amphipod, isopod, and gastropod (i.e. deposit feeder/grazer taxa) biomass and density increased at sites deeper than 10 m, with these groups now being found at deeper sites than before the dreissenid invasion ([Rennie and Evans, 2012](#)), likely due to these deposit feeders exploiting new food resources from dreissenid biodeposits and grazing on benthic algae that has likely increased due to increased water clarity. Increases in these benthic taxa have increased in other lakes (e.g. 20 × increase in gastropod abundance in Oneida Lake, NY; [Karatayev et al., 2014c](#)) as a result of increased grazing opportunity from higher benthic algal biomass, and the shifting of productivity from pelagic to benthic habitats ([Vadeboncoeur et al., 2003](#)). Although our annual benthic data is limited to the second decade after the arrival of dreissenids (2005–2015), there has been stability in the abundance of key benthic taxa (amphipods, chironomids, oligochaetes, gastropods) in the littoral zone despite the shift from zebra to quagga mussels. With the expansion of quagga mussels into the profundal zone, however, the abundance of non-dreissenid benthos has increased four- to five-fold (compared to data before the arrival of quagga mussels at a site, or at sites with no quagga mussels recorded; LSACA, unpublished data). This increase occurred mostly among deposit-feeding taxa, while abundance of competing filter feeding taxa has declined with increased quagga mussel presence at profundal sites.

Many studies in the Great Lakes report the loss of the deepwater amphipod *Diporeia*, coinciding with quagga mussel expansion into the profundal zone ([Dermott et al., 2006](#)). However, this amphipod species was never recorded in Lake Simcoe even before the dreissenid invasion in 1983 ([Jimenez et al., 2011](#)) or in the 1920s, before widespread eutrophication/reduced deepwater dissolved oxygen ([Rawson, 1928](#)). This lack of *Diporeia* in Lake Simcoe is interesting as other inland lakes of similar size, depth, and surface area in the Great Lakes Region (Champlain, Seneca, Cayuga, George, etc.) have records of this species ([Dermott et al., 2006](#)).

In terms of impacts to other fauna in dreissenid-invaded lakes, there is a theoretical case for increased abundance in some fish species due to more prey (benthic fauna) being available. In Lake Simcoe, however, [Trumpickas et al. \(2012\)](#) report declines in fish species richness and number of individuals captured when comparing historical (1982–1995) and more recent (2007–2009) data at nearshore sites. With the expansion of quagga mussels into the profundal zone, further investigations should target the impact on the already threatened Lake Simcoe coldwater fish community. Anecdotal information from local recreational fishermen report gut contents of lake whitefish (*C. clupeaformis*) containing mussels, so dreissenids may represent a new potential prey for the fish community, or increased biomass of non-dreissenid benthos may increase other prey for coldwater fish.

#### Consequences and management implications

The arrival of dreissenids in the Great Lakes Region resulted in large-scale, ecosystem-wide, ecological re-structuring of lakes and other freshwater systems. In Lake Simcoe, the dreissenid invasion coincided with a two- to three-fold increase in Secchi disk transparency, decreases in chlorophyll *a* concentrations, species changes to the phytoplankton community ([Ontario MOECC, 2014](#); [Hawryshyn et al., 2012](#)), and an increase in aquatic plant biomass ([Ginn, 2011](#)) although these changes also occurred simultaneously with P abatement programs and climate-related changes (i.e. increased air temperatures, reduced period ice cover, longer period of water column stratification ([Ontario MOECC, 2014](#))). As both dreissenids and P reduction are contributing factors to many of these changes, it remains challenging, with currently available data, to partition the influence of each driver to these trends. Partitioning eutrophication or dreissenid impacts as a key driver of changes in Lake Simcoe is a critical question in understanding how the ecology of the lake is changing, as well as how the effectiveness and adaptability of our lake management strategy is being impacted. Although lakes invaded by dreissenids undergo rapid ecological changes, such as those described above ([Higgins and Vander Zanden, 2010](#)), other studies on lakes Michigan and Huron, and 25 smaller USA lakes, point to changes in total P concentration and chlorophyll *a* can be more influenced by lake thermal structure and length of time the water column is stratified, air temperature, and precipitation, as opposed to dreissenid biomass ([Cha et al., 2013](#); [Warner and Lesht, 2015](#)). In an analysis of long-term (> 15 years) data from Europe and North America, however, [Mayer et al. \(2014\)](#) argue that dreissenids have augmented benthic production and escalated the flow of energy between nearshore and offshore habitats. Further targeted studies in Lake Simcoe are required to understand the role and contribution of these drivers to ecological changes.

One method to partition the effects of multiple, synergistic variables on lake dynamics, and tease out the proportion due to dreissenids in Lake Simcoe, may be a comparison of spring and summer chlorophyll *a* and water clarity. In the past few years, spring (pre-thermal stratification) chlorophyll *a* has decreased and Secchi disk transparency has greatly increased (up to 20 m in 2016, [Fig. 6a, b](#)), suggesting decreases to the spring algal bloom. As Secchi disk transparency and chlorophyll *a* concentrations return to values comparable to long-term means after lake stratification (and after profundal quagga mussels are excluded from epilimnetic productivity) it is likely that this spring phenomenon is linked to filtration by profundal zone quagga mussels. If reductions in chlorophyll *a* and increased transparency were due to changes in lake productivity, it is likely that these low values would persist into the period of water column stratification. Instead, this pre-stratification change is likely due to feeding by quagga mussels that are active at temperatures as low as 4 °C ([Karatayev et al., 2014b](#)) and have access to algae from the entire water column. Similar trends have been reported in Lake Michigan where the biomass of the winter-spring phytoplankton bloom has declined as quagga mussels have expanded into the profundal zone ([Rowe et al., 2015a, 2015b](#);

Vanderploeg et al., 2010; Kerfoot et al., 2010), and also in the eastern basin of Lake Erie where spring total phytoplankton biovolume decreased by ~80% following the invasion by quagga mussels (Barbiero et al., 2006). In Lake Simcoe, and across the Great Lakes Region, with current trends toward a longer period of thermal stratification and reduced winter ice cover (Ontario MOECC, 2014), winter algal production could be consumed by quagga mussels during the periods of a mixed water column with resulting implications to annual productivity and foodwebs (Warner and Lesht, 2015; Rowe et al., 2015a, 2015b). In Lake Michigan, the spring phytoplankton bloom was critical for sustaining secondary production in the pelagic zone. Following the expansion of quagga mussels to deepwater habitats, reductions in spring phytoplankton and chlorophyll *a* coincided with reductions in *Mysis* (Pothoven et al., 2010) and reduced growth/condition of some coldwater fish species such as lake whitefish (Madenjian et al., 2015). While impacts to phytoplankton may occur during periods of full water column mixing, there is little effect on total annual productivity that is more strongly influenced by P inputs and climate; particularly during strong winter and summer stratification of the water column that isolates deep water mussels from phytoplankton in the epilimnion (Rowe et al., 2017). Nalepa et al. (2009) reported, in Lake Michigan, that since the expansion of quagga mussels to the profundal, the offshore benthic community has become an energy sink, increasing the relative benthic energy pool from 17 to 109 kcal/m<sup>2</sup> before expansion, to 342 kcal/m<sup>2</sup> after expansion.

The sequestration of nutrients in the nearshore zone, resulting from dreissenid filter-feeding activity, has resulted in higher littoral zone P concentrations, increases to aquatic plant and benthic algae biomass, increases in deposit-feeder/grazer benthos, and a corresponding increase in some warmwater fish species biomass. According to the nearshore shunt hypothesis (Hecky et al., 2004), this sequestration of energy in shallow water habitats limits export to, and results in less production in, the offshore zone. As quagga mussels have invaded habitat space in the profundal zone previously not occupied by zebra mussels, we were interested to evaluate the potential for a breakdown of the nearshore shunt in Lake Simcoe, a possible return of nutrients/energy/production exported to the offshore, and impacts to our lake management strategies. Based on a modeling exercise, using our biomass data and available information on mussel filtering rates, there is a potential for increased filtering in the offshore zone due to presence of quagga mussels (Table 3). Despite the 2.6 times increase in estimated filtration rate in the profundal zone (3.5 to 9.2 billion litres filtered per hour, Table 3), estimates of mussel filtering in the nearshore zone remain relatively high and has also increased. Consequently, the amount of potential flux to the profundal zone has increased only slightly (2.7% to 5.2% of total filtration) compared to when zebra mussels were dominant (e.g. 2009), and is likely greatly reduced when the water column is stratified and isolate deepwater mussels from phytoplankton. The contribution of total filtration from the profundal zone may increase in future years. Nalepa et al. (2010) reported that, in Lake Michigan, profundal zone quagga mussels grew more slowly than in warmer, more productive, shallow waters. In Lake Simcoe, more quagga mussels in the smallest size class (0–10 mm valve length) were recorded in the profundal zone (43.8% of profundal quaggas) compared to the nearshore zone (29.2% of littoral quagga mussels). As such, mussel biomass at profundal sites may increase in the future. In Lake Simcoe, we find it unlikely a nearshore shunt would be altered with a shift from zebra mussels to quagga mussels, particularly because profundal quaggas, as suggested by studies from Lake Michigan, are effectively isolated from the productive epilimnion during the period of thermal stratification (Rowe et al., 2015b). Using a kriging analysis to visualize the impact of mussel filtration, we calculated that time required to filter the (mixed, non-stratified) water column varied widely across the lake, likely related to mussel biomass and water depth (Fig. 7a, b). In both 2009 and 2015, fastest filtration was estimated to occur over dense mussel populations on hard substrates in the nearshore zone. In 2015, a major

change from 2009 was filtration of unstratified offshore waters that, while relatively slow compared to the nearshore, could be responsible for increased water clarity after 2015. During the stratified period, it is probable that profundal mussels are effectively isolated from phytoplankton in the epilimnion and the filtration rate map would resemble the 2009 scenario.

Another potential consequence of the change from zebra to quagga mussels is interference with in-water anthropogenic infrastructures such as water treatment or power plant cooling water intakes. Lake Simcoe is a drinking water supply for eight municipalities and has 15 wastewater treatment plants (Palmer et al., 2011). To avoid fouling by zebra mussels, infrastructure for several of these facilities was placed at water depths >25 m, or below the recorded maximum depth of zebra mussels in the lake. Additionally, mussel deterrent procedures (e.g. chlorine diffuser operations) were timed to zebra mussel life history (i.e. mussels active when water temperatures were >12 °C). After the shift to quagga mussels, some of these infrastructures have become colonized with dense populations of mussels (LSRCA, unpublished data) which interfere with facility operations and are seen as a potential threat to drinking water quality and security. In facilities built in anticipation of projected human population expansion (and are thus currently not operating on a 24-hour basis), mussel deterrents (e.g. pre-chlorination diffusers at the intake, carbon dioxide bubblers, and polyaluminum chloride coagulation treatment) are turned off when the plant is not taking in water. Several of these facilities operate on a 12-hour on/12-hour off basis, and quagga mussels have been reported attached to intake structures, low-lift wells, and purification equipment. Similar infestations of mussels on in-lake infrastructures have been reported in the Great Lakes Region and the southwestern USA, adding high capital expenses to operation and maintenance costs (up to \$78.56 USD per one million gallons filtered per day), as well as infrastructure repairs and incorporating mussel deterrents into designs for new or retrofitted treatment plants (Chakraborti et al., 2014, 2016). As such, several drinking water facilities on Lake Simcoe are developing mussel deterrent strategies that include a dreissenid mussel monitoring program with treatment plant operations (e.g. in-lake veliger sample collection, settling plates in low lift wells), and mussel deterrents (chlorine diffusers at the intake, back flushing or heating of filtration membranes inside the facility) that are timed to maximize effectiveness and reduce costs.

## Conclusions

Two, high resolution, benthic surveys were carried out on Lake Simcoe in 2009 and 2015 for targeted assessments of dreissenid mussel populations to evaluate trends recorded by our annual lake benthic monitoring program. These surveys showed a large shift in dreissenid dominance from zebra mussels (84.3% of the dreissenid population) in 2009 to quagga mussels (88.5% of population) in 2015. Of particular note, was the expansion of quagga mussels onto the mud/silt substrates of the profundal zone, previously not available to zebra mussels. Further investigations are underway to evaluate the consequences of this species change in Lake Simcoe that may also be applicable to other lakes: changes to species diversity and abundance of the benthic community, reduction of the spring phytoplankton bloom, fouling of submersed water treatment infrastructure and protection of drinking water quality, and impacts to our lake management strategy for the environmental protection of Lake Simcoe.

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