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Analysis of Lake Ontario Lower Aquatic food web Assessment (LOLA 2003 and 2008) within the context of long-term ecological change.

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Rudstam, L., F. Luckey, and M. Koops. 2012. Zooplankton in the offshore Lake Ontario during intensive sampling years 2003 and 2008: results from the LOLA (Lake Ontario Lower food web Assessment) program. Knowledge Network for Biocomplexity, Web Data Available: http://knb.ecoinformatics.org/knb/metacat/jimont.132.5/knb.

Introduction

Lake Ontario is the 13th largest lake in the world with a surface area of 18,500 km² (Reynolds et al. 2000), has a population in the watershed of over 8 million, and provides a range of ecosystem services to the people in the watershed (freshwater for various uses, shipping, fisheries, and recreation). Over the last century, the lake has experienced numerous stresses including overfishing, colonization by non-native species, cultural eutrophication, and contaminant discharge leading to degradation in water quality, loss and change of habitat, and the decline of native fish communities (Christie 1972, Schelske 1991, Mills et al. 2003). The 1972 Great Lakes Water Quality Agreement (GLWQA) and its 1978 amendment between the United States and Canada (International Joint Commission 1988) were ratified to address these problems.

Implementation of this agreement led to a decrease in phosphorus concentrations in all the Great Lakes, including Lake Ontario, and to a process of oligotrophication and recovery. By the mid-1990s, spring total phosphorus levels had decreased to below the target goal of 10 µg/L in the offshore of Lake Ontario, algal biomass decreased, and water clarity increased (Munawar 2003, Mills et al. 2003). Nutrient and algal decreases may also have affected higher trophic levels as both epilimnetic zooplankton density (Holeck et al. 2008), and alewife (*Alosa pseudoharengus*) abundance (but not growth rate or condition) declined (O'Gorman et al. 2008, Walsh and Connerton 2012). While nutrient levels are likely similar to pre-industrial conditions, the food web is unlikely to return to pre-industrial conditions because it has been altered by the invasion of non-native species (Mills et al. 1993, 2003). Invasive species that impact the food web include two predatory cladocerans (the spiny water-flea *Bythotrephes longimanus* and fish-hook water-flea *Cercopagis pengoi*), two filter-feeding mussels (zebra mussel *Dreissena polymorpha* and quagga mussel *Dreissena rostriformis bugensis*), and the round goby (*Neogobius melanostomus*). Evaluating ecological changes and their causes in Lake Ontario must consider the influence of both changes in nutrient loading and food web configuration.

Currently, extensive surveys for each Great Lake occur on a rotating five-year schedule. In 2003, the US Environmental Protection Agency (USEPA) and Environment Canada (EC) funded a comprehensive sampling of Lake Ontario's lower trophic levels (LOLA 2003—Lake Ontario Lower food web Assessment). The lower trophic level sampling program in Lake Ontario from 2003 was repeated in 2008 (LOLA 2008) through a bi-national collaboration between the USEPA, EC, Canada's Department of Fisheries and Oceans (DFO), the National Oceanic and Atmospheric Administration (NOAA) the New York State Department of Environmental Conservation (NYSDEC), the Ontario Ministry of Natural Resources (OMNR), the US Geological Survey (USGS) and several universities (Cornell University, Clarkson University and the College of Environmental Science and Forestry in Syracuse). In 2010, Cornell University received a USEPA grant through the Great Lakes Restoration Initiative to analyze these data. This report presents the status of Lake Ontario's lower trophic levels in 2008 and a detailed comparison with similarly collected LOLA 2003 data (Watkins et al. 2007, Holeck et al. 2008). We also compare these two years with time series data collected by the collaborating agencies and Cornell University (Dove 2009, Stewart et al. 2010, Johannsson et al. 2011, Holeck et al. 2012) and discuss observed changes in relation to changes in nutrient concentration and

food web configuration in Lake Ontario. These data sets include the NYSDEC/USGS/USFWS/Cornell Biomonitoring Program (US-BMP), EC's surveillance program (EC-Surv), USEPA's GLENDA database (USEPA-GLENDA), and DFO's Bioindex program (DFO-BI).

Major findings

Spring offshore total phosphorus and soluble reactive phosphorus increased from 2003 to 2008, but summer levels did not. Lake-wide average total phosphorus levels remained at or below the target level of 10 µg/L in all three seasons of 2008.

Lake-wide nutrient concentrations have declined since the 1960s. However, phosphorus concentrations have been stable (~7-10 µg/L) since the mid-1990s. These values are higher than in Lakes Michigan and Huron (<5 µg/L).

Spring silica was similar in 2003 and 2008 and was depleted by the summer in both years. This indicates continued spring diatom production in Lake Ontario, in contrast to the upper Great Lakes where the spring diatom bloom has declined. Long-term data show no decline in the rate of silica depletion, in contrast to observations in Lakes Michigan and Huron.

Summer epilimnetic chlorophyll-*a* increased by a factor of 2, the proportion of autotrophic algae increased, and summer water clarity declined from 2003 to 2008. Summer chlorophyll-*a* levels in 2008 were similar to the concentrations in the 1981-1995 time period. This is consistent with increased spring total phosphorus concentrations leading to higher summer algal production in the lake in 2008.

However, chlorophyll-*a* did not increase in spring or fall of 2008 compared to 2003, and measurements in the offshore in longer time series do not show significant changes in chlorophyll-*a* (since 1995 in the US-BMP, since 1981 in the EC-Surv and since 1985 in the EPA-GLENDA data). The trend towards mesotrophy in the summer of 2008 may therefore be limited to that year.

Most of the chlorophyll in the water column was located in a deep chlorophyll layer in the thermocline. Twiss et al. (2012) showed that this chlorophyll layer represents an increase in algal biomass that is productive. These deep algae were not included in the LOLA assessment program.

Offshore epilimnetic zooplankton density and biomass declined from 2003 to 2008 by a factor of 5 to 12 in the summer and by a factor of 1.5 to 2.6 in the fall. Biomass but not density also declined in the spring (factor of 1.9). This is consistent with long-term trends of declining epilimnetic zooplankton abundance including a larger decline in 2004-2005 coincident with an increase in the predatory *Bythotrephes*.

Whole water column zooplankton density also declined from 2003 to 2008 in the summer and fall, but zooplankton biomass only declined in the fall (factor of 1.7). The decline in biomass was less than the decline in density because the average size of individual zooplankton increased due to large shifts in zooplankton species composition.

Large changes in whole water column zooplankton community composition occurred between 2003 and 2008 from a cyclopoid/bosminid dominated system in 2003 to a calanoid dominated system in 2008. Calanoid copepods made up 24-27% of the offshore whole water column biomass in 2003 (summer and fall) and 65-85% in 2008. Cyclopoid copepods declined from 39-42% in 2003 to 11-14% in 2008 and cladocerans declined from 51-55% in 2003 to 4-21% in 2008.

The increase in calanoid copepods was particularly strong for the larger species *Limnocalanus macrurus* and *Leptodiaptomus sicilis*. A large portion of these calanoid copepods are below the epilimnion during the day and are not caught in epilimnetic samples.

Mysid densities were similar in 2003 and 2008 indicating continued high biomass of mysids in Lake Ontario. In July of 2008, the biomass of *Mysis diluviana* was 17% of the crustacean zooplankton biomass in the offshore of Lake Ontario (depth >30m). Mysid densities appear stable in Lake Ontario.

The native benthic amphipod *Diporeia* declined further in 2008 and is almost extirpated from Lake Ontario. Quagga mussels are very abundant as deep as 90 m, but populations in shallow water declined from 2003 to 2008. Few zebra mussels were present in either 2003 or 2008.

There has been a spatial restructuring of the Lake Ontario offshore ecosystem through the increase in the deep chlorophyll layer and associated zooplankton. This has resulted in a Lake Ontario that in 2008 is more similar to Lakes Superior, Huron and Michigan than to the Lake Ontario of the 1990s.

Methods

Field sampling.

Three lake-wide cruises were performed to assess both temporal and spatial condition of the lower food web in 2008 (Table 1). Data were collected along four north-south transects (Figure 1) that were selected to overlap with previous studies such as the Lake Ontario Lower food web Assessment (LOLA) of 2003 and the Lake Ontario Trophic Transfer (LOTT) project of the early 1990s. Two ships were used - the EPA's R/V Lake Guardian and Canadian Coast Guard ship CCGS Limnos (Table 1). Timing of the spring cruises was similar in the two years, but the timing of the summer and fall cruises differed (Figure 2). This will affect our comparisons, especially for the fall.

Most parameters were measured on integrated water samples in the epilimnion. The samples were collected either with an integrator tube (Limnos) or by pooling discrete Niskin bottle samples (Lake Guardian). An electronic bathythermograph (EBT) or conductivity-temperature-depth (CTD) profile was used to determine thermocline depth (defined as the first "knee" of the temperature profile) and sampling started 1 m above this depth. During spring isothermal conditions, integrated water samples were collected from 20 m depth or two meters above the bottom (for shallow stations) to the surface. In summer and fall, integrated water samples were collected from one meter above the thermocline to the surface. Parameters measured from integrated water samples include total phosphorus (TP), soluble reactive phosphorus (SRP), soluble reactive silica (SRSi) as SiO_2, nitrates/nitrites (NO_2 + NO_3, 2008 only), chlorophyll-*a*, phytoplankton, and microbial food web components. Water chemistry was measured using an autoanalyzer. Total phosphorus concentration was determined using the ammonium molybdate – stannous chloride method after preservation with 1 mL 30% H_2SO_4 and persulfate digestion. For SRP and SRSi, water was filtered through a 0.45-µm membrane filter. SRP was analyzed using the ammonium molybdate – stannous chloride method. SRSi concentration was determined by the heteropoly – blue method. Chlorophyll-*a* was determined by acetone extraction after filtration through GF/C (nominal pore size 1.2 µm) glass fiber filters. Chlorophyll-*a* was then determined with a spectrophotometer at the Environment Canada laboratory in 2003 and with a calibrated fluorometer at SUNY-Brockport in 2008. Here we present values of total chlorophyll uncorrected for phaeophytins. Phytoplankton and microbial food web samples were processed according to the methods described in Munawar et al. (2010).

Triplicate samples were collected for chlorophyll-*a*, and duplicate samples were collected for each chemistry parameter to determine within-site variability. Results are presented as a coefficient of variation (CV; sd/mean) for chlorophyll-*a* and a percent deviation ($|n_1-n_2|$/mean) for chemistry. Variation in chl-*a* concentrations ranged from 1 to 15% with a mean of 5%. Nitrate-nitrite variability ranged from 0 to 60% (mean 9%), TP ranged from 0 to 132% (mean 18%), SRSi ranged from 0 to 105% (mean 21%), and SRP ranged from 0 to 200% (mean 57%). Replicates were averaged and mean values were used in all subsequent analyses. When concentrations were below the detection limit for any parameter, the detection limit for that parameter was used to calculate means and variability. Detection limits were TP: 0.2 µg/L (2003), 1.2 µg /L (2008); SRP: 0.2 µg /L (2003), 0.6 µg /L (2008); SRSi: 20 µg /L (2003), 50 µg /L (2008); Nitrate + Nitrite 40 µg/L (2008); chl-*a* 0.5 µg /L (2003 and 2008).

Thermocline depth was also used to guide zooplankton sampling. Epilimnion samples (following depth protocol above) were collected using a 64-µm mesh, 40-cm diameter metered net. An entire water column sample was collected with a 153-µm mesh, 50-cm diameter metered net from 100 m depth to the surface or from 2 m above the bottom to the surface at shallower bottom depths. The larger mesh net is used for the whole water column to avoid clogging of the net when filtering larger amounts of water. These samples were collected only if the bottom depth was >10 m below the depth of the 64-µm mesh sample. Flowmeter data were used to calculate efficiency and volume of water filtered. Net efficiencies in 2008 for the 64 µm epilimnetic net ranged from 64 to 122%

with a median of 88% (72 samples) and for the 153-μm whole water column net ranged from 42 to 110% (median 82%, 53 samples). Lower than 100% efficiency is to be expected due to drag and clogging, and values between 60 and 100% are considered acceptable for these surveys (LOLA Standard Field Operating Procedures). Greater than 100% efficiency is sometimes obtained as an artifact of the ship drifting during retrieval of the net (which is not accounted for in the measured tow length from the length of the wire). Net efficiencies for the 2003 samples were similar (64-μm epi net: median 85%, range 24 to 162%, 87 samples; 153-μm net: median 79%, range 45 to 130%, 74 samples).

Zooplankton used in the comparison between 2003 and 2008 were collected during daylight hours (dawn to dusk) for the epilimnetic samples and throughout the 24 hour period for whole water column samples. As most of the zooplankton are in the upper 100 m both day and night, we did not expect a difference with time of day in the whole water column samples (although such differences are expected in the epilimnetic samples due to vertical migration of different zooplankton species, see results). This was also the case as the total water column samples rarely showed a significant difference between day and night samples. Because zooplankton in Lake Ontario in recent years were more abundant in the metalimnion than the hypolimnion (Holeck et al. 2012), we compared zooplankton density and biomass on an areal basis for the whole water column tows. Otherwise, calculated densities will be diluted by the variable amount of deeper water included in these tows. Epilimnetic density and biomass was compared on a volumetric basis because the tow depths were variable (depending on the depth of the thermocline) and to be consistent with past analyses (Johannsson et al. 1998, Holeck et al. 2008).

We also compared samples collected with a 64 and a 153-μm mesh zooplankton net. Smaller mesh nets collect more small zooplankton (Johannsson et al. 1999, Mack et al. 2012) but should have little effect on the catch of larger animals as long as the net efficiencies are similar. As 90% of the nets samples had efficiencies over 71% (epi nets) and over 68% (water column nets), any bias in this comparison will primarily be towards higher epilimnetic zooplankton density and biomass compared to the whole water column samples.

Replicate tows were collected at 9 sites in 2003 and 8 sites in 2008. The deviation between replicates (as a proportion of the mean of the two replicates) varied between years and nets and between density and biomass measures. For biomass, the mean (range) of deviations were as follows: 2003 64-μm net: 43% (5-98%); 2008 64-μm net: 27% (10-82%), 2003 153-μm net: 50% (0-111%), 2008 153-μm net: 27% (1-84%). For density, these values were 2003 64-μm net: 61% (1-219%); 2008 64-μm net: 15% (5-59%), 2003 153-μm net: 51% (1-138%), 2008 153-μm net: 25% (1-88%). These deviations represent small-scale patchiness in the lake as well as uncertainty associated with the sub-sampling during sample processing. They may seem large, but deviation of 66% (a factor 2) is typical between replicate vertical tows (Winsor and Clarke 1940, Barnes 1949). There is also variation associated with counting a subsample of the total sample that can be estimated from a Poisson distribution (a precision of 10% is expected for subsamples with a mean of 400 animals Postel et al. 2000).

Zooplankton species identification, enumeration and measurements were done by different contractors in 2003 and 2008 but using the same methods. *Bythotrephes* and *Cercopagis* were counted separately by Cornell University in 2008. Biomass was calculated from length measurements using a set of length-weight equations derived from an analysis of available equations by Watkins et al. (2011). Watkins et al. selected these equations as EPA and Canada's DFO use different sets of standard length-weight regressions. The new equations use elements of both sets and attempt to minimize the number of equations used. The zooplankton data package associated with this report includes biomass calculations using all three sets of equations (Cornell, EPA and DFO).

Benthic invertebrates were collected with a standard Ponar grab (area=0.05 m^2). Triplicate samples were taken at 34 (2003) and 51 (2008) sites. Mussels were removed prior to sieving to prevent damage to the concentrating net and placed in a sample jar. Pooled triplicates were then placed in an elutriation device and washed through a nylon sieve with a 500-μm mesh. Organisms were then decanted into the jar with the mussels and preserved with 5-10% formaldehyde with a Rose Bengal stain.

Data analysis.
Data were divided into three regions (Figure 1, Table 2): the Kingston Basin (KB, stations 77, 80, 81, 84), the nearshore of the main lake (NS, stations 8, 17, 29, 38, 43, 62, 66, and 71), and the offshore of the main lake (OS, remaining stations). OS and NS regions were separated by the 30 m bathymetric contour. Variables measured in the three regions were compared using standard ANOVA followed by Tukey's HSD test. Standard t-test with unequal variance was used to compare 2003 and 2008 data from the three regions separately. Transformations were needed for zooplankton densities ($\log_e(x)$) and biomass ($\log_e(x+0.01)$), but not for zooplankton average length and chemical and physical parameters. We consider differences significant at the $P<0.05$ level. Note that we do not apply a Bonferroni correction (see discussion in Gotelli and Ellison 2004) and that we expect some differences to be significant at the $P<0.05$ level from chance alone due to the large number of comparisons.

Map overlays were constructed using the bathymetry from Virden et al. (2000).

Data curation.
Data on water quality indicators and zooplankton abundance were deposited in two locations accessible through the web – the knowledge network for biocomplexity (http://knb.ecoinformatics.org) and eCommons@Cornell, Cornell University Library, Ithaca, NY. The data packages include detailed metadata and comma separated ASCII data tables describing station location, water quality indicators, taxonomic lists, sample information, and density and biomass of each zooplankton species for each sample collected as part of the LOLA 2003 and 2008 program. Data were checked for outliers including unrealistic zooplankton sizes following the expected lengths listed in Balcer et al. (1984). Benthos data are available through Steve Lozano (stephen.lozano@noaa.gov) and mysid data through Kelly Bowen (kelly.bowen@dfo-mpo.gc.ca, size and net data) and Lars Rudstam (lgr1@cornell.edu, acoustic data).

Results

Water Quality Indicators: Nutrients, Chlorophyll-a and Secchi Transparency in the Epilimnion

In 2008, whole-lake total phosphorus (TP) concentrations remained below the target of 10 µg/L set by the Great Lakes Water Quality Agreement in all regions of the lake in spring and summer and slightly above 10 µg/L in the Kingston Basin (KB) and Nearshore (NS) in the fall. Mean soluble reactive phosphorus (SRP) concentrations were at or below 3.0 µg/L in all seasons and regions (Table 3). These levels are consistent with the classification of Lake Ontario as an oligotrophic system. Soluble reactive silica (SRSi) concentrations showed a typical pattern of high levels in the spring followed by declines through the summer associated with uptake by diatoms during this time period. Chlorophyll-*a* (chl-*a*) concentration peaked at over 3 µg/L during the summer in all regions and was below 2.1 µg/L in the spring and fall (Table 3). Water clarity was high in the spring of 2008. The lake-wide mean Secchi depth was 13.2 m in spring and declined to 5.1 m in the fall (Figure 3). Inorganic nitrogen (NO_2 and NO_3) was only measured in 2008 and ranged from 171 to 522 µg/L across the three regions. Concentrations were highest in spring and then declined to approximately half of spring levels by summer and fall. The only statistically significant differences between regions in 2008 were a greater Secchi transparency in the Offshore (OS) than NS in the summer, higher SRSi levels in OS than in KB in the spring, and higher TP in OS and NS than in KB, also in the spring. There were no significant differences among the regions in the fall. These variables are compared with 2003 below.

Phosphorus – Both spring TP and SRP were significantly higher in 2008 than in 2003 in OS but not in KB; SRP was also significantly higher in 2008 in NS (Table 3, Figure 3). This is in contrast with a long-term decline in TP since the 1970s and a stable trend since the mid 1990s (Figure 4). Summer TP values were lower in 2008 compared to 2003 in all three regions but the differences were not significant. Fall TP was significantly lower and fall SRP significantly higher in OS in 2008. NS and KB data on TP and SRP concentrations remained stable between 2003 and 2008 in all seasons.

Silica – Silica can limit primary production of diatoms and seasonal silica depletion is useful as an indicator of diatom blooms. Offshore spring SRSi concentrations were significantly lower in 2003 (793 µg SiO_2/L, s.e. 9) than in 2008 (868 µg SiO_2/L, s.e. 14) although the difference was less than 10% (Table 3, Figure 3). Spring SRSi in the NS and KB and all regions in the summer did not change significantly between the two years. Summer SRSi values decreased to 190 and 164 µg /L in 2003 and 2008, respectively. Fall SRSi concentrations were significantly lower in 2008 than in 2003. The fall samples in 2003 were collected later in the season than in 2008 which likely explain the differences in fall values between the two years. Silica typically increases in late September – October in Lake Ontario (Johannsson et al. 1998, Winter et al. 2012).

Chlorophyll-a – Chl-*a* levels were higher in the summer of 2008 than 2003 (Table 3), consistent with the higher spring phosphorus concentrations in 2008. Although OS

spring chl-*a* concentrations were similar in 2003 (1.3 µg/L) and 2008 (1.4 µg/L), summer chl-*a* levels in 2008 were 3.1 µg/L, or about double the values of 1.5 µg/L measured in 2003 (Table 3, Figure 3). The same pattern was evident in NS although differences were not significant. Fall OS chl-*a* levels were higher than summer values in 2003 (1.5 µg/L) and lower than summer values in 2008 (3.1 µg/L). The summer 2008 values were high also in Twiss et al. (2012) and in the nearshore of the north shore (3.1µg/L (range 0.7-4.9 µg/L) in Jul-Aug, 2.1 µg/L (range 1.5 – 2.4 µg/L) in Aug-Sep, Howell et al. 2012) and the nearshore of the south shore (mean 2.9 µg/L, range 2.8 – 3.0 µg/L in August, Makarewicz et al. 2012), but other data series did not show higher chl-a values in 2008 (US-BMP, EC-Surv, Figure 5). Differences are likely due to seasonal changes as both US-BMP and EC-Surv sampled later in August than LOLA 2008.

A deep chlorophyll layer characteristic of oligotrophic systems was present in 2003. Despite more mesotrophic conditions in 2008, this layer was also apparent in water column profiles collected during the summer (Figure 6, EPA Seabird SBE 25 Profiler data, see also Twiss et al. 2012). *In situ* chlorophyll concentrations in the upper 50 m of water were similar to the concentrations in the epilimnion in 2008 (average of 1.3 µg/L in both depth layers). However, an average of 84% of the chlorophyll present in the water column was below the epilimnion (SE 3.2%, range 47 to 97%, N=14 casts in July 2008). The 2008 measures of *in situ* chlorophyll from the Seabird fluorometer and the standard laboratory-based chl-*a* measurements were highly correlated and linear, although the *in situ* values were approximately half of the laboratory-based measures ($Chl_{SeaBird}$ = $0.45*Chl_{Lab} + 0.11$, $R^2 = 0.73$, N=41). Because the relationship is linear and almost intersects 0, the ratio of epilimnetic to whole water column chl-*a* will be the same with either *in situ* fluorometric values or laboratory determined values.

Water Clarity – Secchi depth in OS was greater in the spring of 2008 (14.9 m) than in 2003 (10.0 m, Table 3, Figure 3). Secchi depths from the 2000s are roughly twice that measured in the 1980s (Figure 7), tracking a substantial increase in water clarity in Lake Ontario. Chl-*a* levels were similar in the two years in the spring, suggesting that the Secchi depth increase is due more to reduced suspension of inorganic sediment than to reduced phytoplankton biomass. Satellite imagery in the spring of 2003 and 2008 confirm that remote sensing reflectance (Rrs 555) was very low, indicative of a Secchi depth >10 m (Watkins et al. submitted). Spring Secchi depths in both KB and NS were also higher in 2008 (Table 3).

Secchi depth in OS was shallower in the summer of 2008 (6.7 m) than 2003 (7.9 m) consistent with the difference in chl-*a* levels (higher chl-*a* = lower Secchi depth). This pattern was also evident in NS and KB. One interesting seasonal change observed in 2008 was that Secchi depth was shallower in the fall (5.1 m) than in the summer, despite lower chl-*a* levels (1.7 µg/L). We attribute this discrepancy to a short-term whiting event during the fall survey. Carbonate precipitation reduces water clarity and was confirmed by both shipboard observations (Peng and Effler 2011) and satellite imagery (Watkins et al. submitted). Fall sampling in 2008 occurred prior to water column overturn, unlike in 2003 where the passage of Hurricane Isabel considerably mixed the water column before the fall survey. In 2003, fall epilimnetic chl-*a* levels were higher and Secchi depth was

lower. No whiting event occurred in 2003 probably because of the low productivity during that year (Watkins et al. submitted).

Food web indicators: phytoplankton, zooplankton, mysids and benthos.

Phytoplankton/Microbial Food Web – Integrated epilimnetic microbial loop and phytoplankton samples were collected and analyzed by Fisheries & Oceans Canada from 9 – 15 stations during the 2003 and the 2008 surveys (April, July/Aug, and September). Major changes in the structure of the microbial – planktonic food web between summer 2003 and summer 2008 are reported in Table 4. At the base of the food web, phytoplankton biomass showed a nearly 10-fold increase from 0.3 ± 0.08 g m^{-3} observed in the summer of 2003 to 2.5 ± 0.3 g m^{-3} in the summer of 2008. Interestingly, Cyanophyta (blue-green algae) biomass (≈ 0.1 g m^{-3}) did not change significantly between years, however all other taxonomic groups – Chlorophyta, Chrysophyceae, Diatomeae, Cryptophyceae, Dinophyceae – increased by more than one order of magnitude.

Total microbial loop biomass, which includes bacteria, autotrophic picoplankton (APP), heterotrophic nanoflagellates (HNF) and ciliates, did not show a significant change between the summer of 2003 (1.5 ± 0.2 g m^{-3}) and the summer of 2008 (1.4 ± 0.2 g m^{-3}). However, very significant changes in the composition did occur. Both bacteria and APP biomass increased significantly, while HNF biomass declined from 1.2 ± 0.2 g m^{-3} in 2003 to 0.05 ± 0.01 g m^{-3} in 2008. The decline in HNF biomass coupled with increases in APP and phytoplankton biomass between 2003 and 2008, show a major shift in the structure of the microbial – planktonic food web from being largely heterotrophic in 2003 (Munawar et al. 2010) to being predominantly autotrophic in 2008 that is consistent with more mesotrophic conditions in the summer of 2008. However, the large gap between these lake-wide assessments of microbial-phytoplankton communities does not allow us to discern long-term time trends from inter-annual variation.

Zooplankton species composition – The species of open-water crustacean zooplankton present in Lake Ontario in 2003 and 2008 were similar with 14 copepods and 13 cladocerans identified in 2003 and 12 copepods and 12 cladocerans in 2008 (Table 5). In general the species present in 2003 and 2008 were the same as found in previous surveys (Robertson and Gannon 1981, Balcer et al. 1984, Johannsson et al. 1998, Table 5). However, there were dramatic changes in the relative abundance.

Several of the calanoid copepods were found at more stations in 2008 than in 2003, including *Leptodiaptomus minutus, Leptodiaptomus sicilis, Skistodiaptomus oregonensis, Limnocalanus macrurus* and *Epischura lacustris*, whereas only one calanoid species was encountered less frequently in 2008 than in 2003 (the non-native *Eurytemora affinis*). Cyclopoid copepods were found at a similar number of stations in both 2003 and 2008 although the abundance declined. One exception was *Acanthocyclops vernalis* which was found in 2003 but not in 2008. This species was considered common in Lake Ontario by Robertson and Gannon (1981) but is now rare. It was only found in 4 out of 15 years 1981-1995 by the DFO Bioindex program (Johannsson et al. 1998) and,

although found in 11 out of 16 years since 1995, the species only occurred in 2.6% of the US-BMP samples (Holeck et al. 2012, Table 5). The two non-native predatory cladocerans *Bythotrephes longimanus* (first found in 1982 Johannsson and O'Gorman 1991) and *Cercopagis pengoi* (first found in 1998, Makarewicz et al. 2001) were common in both years although *Bythotrephes* was found at more stations in 2008 than in 2003 and *Cercopagis* at slightly fewer stations (Table 5). The frequencies of occurrence of other cladocerans were similar in 2003 and 2008 even though abundance declined. Because of the difficulties in separating species in the genus *Diaphanosoma* and *Ceriodaphnia*, we combined species within these groups. Some of the rarer species are considered mainly littoral in past studies (such as the copepods *Eucyclops, Paracyclops* and *Leptodiaptomus reighardi* and the cladocerans *Daphnia schødleri, Alona* sp., *Camptocercus* sp. and *Sida crystalina)* and these species were rare also in the 2000s. The benthic copepod *Paracyclops fimbriatus poppei* that was not recorded as present in Lake Ontario by Robertson and Gannon (1981) was found at one station in 2003. The benthic harpacticoid copepods were primarily found as nauplii.

Zooplankton epilimnetic density and biomass (by volume) – We compared epilimnetic total crustacean volumetric density and biomass among the three regions of the lake within each year 2003 and 2008 (Table 6). Only a limited number of significant differences were detected (ANOVA followed by Tukey HSD test, $P<0.05$). In 2003, OS had higher density and biomass than NS only in the spring season, with OS significantly higher than KB for density only. In 2008, biomass in OS was higher than biomass in NS in the fall and OS density was higher than KB density in the spring. No other comparison was significant.

For comparisons between 2003 and 2008, we also tested for differences in average length and biomass of different zooplankton groups (Table 6). In the spring, copepods dominated and densities were similar in the two years. Biomass decreased in OS and increased in NS from 2003 to 2008. However, this relative consistency in spring zooplankton abundance masks a large change in species composition. Cyclopoid copepods declined in all three regions whereas calanoid copepods increased. Cyclopoids dominated in 2003 (77-86% of the biomass) and calanoids in 2008 (56-94% of the biomass). Average length in spring-OS samples decreased from 2003 to 2008.

In the summer and fall there was a large decline in total density between 2003 and 2008 (from 62 to 92% decline depending on season and region, significant in most comparisons, Table 6). This decline was consistent with observations in the US-BMP (Figure 8). The decline in biomass was also pronounced (33 to 72%) but only significant in OS in the summer. As in the spring, cyclopoid copepods declined and calanoid copepods increased. In addition, the cladoceran group bosminids, and for most comparisons also daphnids, declined. The change in the group other cladocerans was mixed. Of the predatory cladocerans, *Cercopagis* decreased in most regions and both seasons and *Bythotrephes* increased in the OS in both summer and fall. Changes in native predatory cladocerans (*Leptodora* and *Polyphemus*) were variable and not significant. Average length increased or stayed the same.

Because zooplankton migrate higher in the water column during the night, we did not use night-time epilimnetic samples in our analyses. However, these samples can be used to compare densities in the epilimnion during day and night. Although the number of epilimnetic night samples was limited (12 occasions in 2003 and 2 in 2008), we did find significant increases in abundance of many zooplankton groups during the night in the epilimnion (one tailed t-test, $P<0.05$). This was the case for cyclopoid copepods, calanoid copepods, *Limnocalanus*, daphnids, other cladocerans, and *Bythotrephes*. As observed previously (Johannsson 2003), many species migrate from the metalimnion to the epilimnion during the night in Lake Ontario.

Zooplankton areal density and biomass – whole water column – Epilimnetic samples only represented a fraction of the zooplankton in Lake Ontario in 2008 (Table 7). For example, only 2% of the zooplankton biomass in the lake was in the epilimnion during the day in the summer of 2008 (areal densities: 42 mg/m^2 in the epilimnion versus 2826 mg/m^2 in the whole water column). The proportion in the epilimnion ranged from 10 to 26% in the other surveys. The proportion of the copepod populations in the epilimnion during the day was always less than 30%, and one of the most common species in 2008, *Limnocalanus*, was rarely caught in the epilimnion. Acoustic surveys (430 kHz) from the summer 2008 show high densities of larger zooplankton in water below the epilimnion (Figure 9). On the other hand, cladocerans are relatively more common in the epilimnion, and in many cases there were no significant differences in total water column density measured with only the epilimnetic nets compared to the whole water column nets (Table 7).

Water column density and biomass were often substantially higher in OS than in NS and KB in both years due to the inclusion of deep zooplankton layers in the whole water column samples (Figure 10). In 2003 total biomass and density were significantly higher in OS than in NS on all but one comparison (density in the fall). In 2008 OS biomass and density was higher than NS in all comparisons. In both years, KB was mainly intermediate between OS and NS and some of the comparisons were significant with KB larger than NS in the summer of 2003 and 2008 and KB smaller than OS in spring 2003, summer 2008 and fall 2008. The large differences in water column density and biomass between the three regions are in contrast to the low number of significant differences among regions for the epilimnion.

Copepods constituted almost 100% of the spring zooplankton water column biomass in both 2003 and 2008. The dominant group changed from cyclopoids (80 to 95% of the total biomass in 2003) to calanoids (57 to 93% of the total biomass in 2008, Table 8, Figure 11). Calanoids also increased in the summer and fall, especially in the OS where calanoids made up 5-7% of the total biomass in 2003 (summer and fall) and 65% (fall) to 85% (summer) of the biomass in 2008. Cyclopoids and most cladoceran groups declined during the same time period in the summer and fall. This large shift in the zooplankton community from 2003 to 2008 was mostly due to an increase in *Leptodiaptomus sicilis* and *Limnocalanus macrurus*, the two largest calanoid copepods in Lake Ontario, and a decline in *Diacyclops thomasi*, bosminids, and daphnids (Table 8). Average length increased in summer and fall as a consequence of this change in the zooplankton

assemblage. Of the predatory cladocerans, *Cercopagis* declined, *Bythotrephes* increased, and the native cladoceran predators showed no significant change.

Many of these changes in water column zooplankton between 2003 and 2008 were also detected in epilimnetic data reported above. There are two exceptions. First, calanoid copepods constitute a larger proportion of the zooplankton biomass in whole water column samples than in epilimnetic samples, especially in the summer-fall of 2008 in OS where calanoids made up 24-27% of the biomass in the epilimnion and 65-85% of the biomass in the whole water column (summer-fall). Second, although density did decline in OS in both epilimnion and whole water column samples, the whole water column samples showed a larger increase in average length of the animals and a total zooplankton biomass that either did not decline (summer), or showed a more limited decline compared to density (fall). As expected, patterns in epilimnetic and whole water column samples are more similar in the shallower regions (KB and NS) where the epilimnion is representative of the whole water column present.

The tow depth varied between 2003 and 2008 as samples were taken from the slightly above the bottom in 2003 even at depth of over 200 m, whereas samples taken in 2008 followed the EPA standard operating procedure using 100 m as a maximum depth. If significant zooplankton biomass occurs at depth deeper than 100 m, the comparison will be biased towards higher areal density in 2003 than in 2008. This is only an issue in the OS. We tested this by comparing only OS samples in water shallower than 110 m. Although power of detection change decrease due to smaller sample sizes, there was only three occasions when a previously significantly higher biomass in 2003 became non-significant (bosminids and cyclopoids in the spring and *Cercopagis* in the summer). This indicates that the areal comparisons are robust to the differences in tow depth in 2003 and 2008.

Mysids – Abundance and size structure of *Mysis diluviana* was measured in April, July and September by the Department of Fisheries and Oceans, Canada, from samples collected during the LOLA cruises, and again in November at station 41 and 64. In addition, 14 net tows were collected as part of the OMNR/NYSDEC acoustics survey. Average mysid abundance at stations 41 and 64 ranged from 249 to 605 mysids/m^2 in April through September (Table 9). Mysid abundance in the OMNR/NYSDEC tows deeper than 50 m ranged from 61 to 993 mysids/m^2. The population declined somewhat in November with average densities of 173-266 mysids/m^2. Embryo-carrying females were present in November confirming that the main time for the release of the young is during the winter and spring. The population consisted of two age classes in July and August 2008 (the 2007 and 2008 cohorts, Figure 12). The average weight of a mysid (DFO samples) was 2.15 mg dwt in April (high proportion adults), declined in July as adults die (1.99 mg), and then increased through September (2.19 mg) and November (3.39 mg) with the growth of individuals in the 2008 cohort.

Mysids were also assessed with hydroacoustics during the July 2008 LOLA cruise and as part of the standard hydroacoustic survey for forage fish in Lake Ontario (Connerton and Schaner 2010). Mysids were separated from fish echoes with a threshold mask, as

described in Rudstam et al. (2008a). Mysid density is based on acoustic backscattering scaled by the average target strength calculated from the relationship between acoustic backscattering in the mysid layer and the density of mysids in the 11 net tows through at least 50 m of water from the OMNR/NYSDEC survey. Calculated average target strength of the mysids from the net tows was -88.93 dB. Abundance around the two sampling stations was similar to the net tows (Table 10)). Density varied with bottom depth with higher abundance of mysids in deeper water. Resulting lake-wide densities averaged 196 mysid/m^2 for the whole lake and 250 mysid/m^2 in OS (Table 10). There are few mysids in NS. This translates to a biomass of 497 mg dwt /m^2 using the average weight of mysids in July 2008. Mysid biomass was therefore 17% of the zooplankton biomass present in OS in July of 2008. Spatial distribution is relatively uniform in deeper water, but some patterns emerge such as an area of lower density around stations 715 in the eastern part of the lake (Figure 13). These spatial structures are similar to observations in 2005 (Rudstam et al. 2008a). Comparisons with other years suggest that mysid density declined from values around 300 /m^2 in 1988-1994 to values varying between 60 and 250 /m^2 without a time trend from 2001 to 2008 (Johannsson et al. 2011, this report).

Benthos – The benthic component of the LOLA 2008 study was led by Steve Lozano of NOAA's Great Lakes Environmental Research Laboratory (GLERL) in Ann Arbor, Michigan. A detailed presentation of the data is in Lozano (2011).

Populations of the native benthic amphipod *Diporeia* were very low in 2008. *Diporeia* populations in the shallow Kingston Basin and habitats of intermediate depth (30-90 m) disappeared already during the mid-late 1990s (Watkins et al. 2007). Deep populations that averaged 2181/m^2 in 1999 and 545/m^2 in 2003 were by 2008 nearly extirpated (Figure 14). In 2008, only 4 sites out of 52 had *Diporeia* populations larger than 100/m^2 and all were at depths greater than 90 m (Lozano 2011). The maximum abundance of *Diporeia* at any station was only 257/m^2. Deep (>90 m) populations that averaged 545/m^2 in 2003 (Watkins et al. 2007) were by 2008 nearly extirpated averaging only 42/m^2 (Table 11, Figure 15). Fingernail clams (sphaeriids) also declined whereas oligochaetes and chironomids had similar biomass in 2003 and 2008 with no time trends (Figure 15).

In 2003 and 2008 the dreissenid population of Lake Ontario was nearly entirely quagga mussels (*Dreissena rostriformis bugensis*) (Table 11). The replacement of zebra mussels (*Dreissena polymorpha*) in shallow habitats occurred between 1995 and 1998, the same time quagga mussels expanded to deeper habitats (Watkins et al. 2007, Figure 14). Quagga mussels were still abundant (averaging near 5000/m^2) as deep as 90 m, but populations at shallow habitats (0-30 m) noticeably declined from 9146/m^2 in 2003 to 912/m^2 in 2008 (Table 11, Figure 16). As in 2003, few zebra mussels were collected.

Discussion

The lower trophic levels of Lake Ontario are surveyed intensively every five years by collaborating agencies in the US and Canada. These lake-wide surveys were completed in three seasons, spring (April), summer (July-August) and fall (September) in 2003 (LOLA 2003) and again in 2008 (LOLA 2008). We have presented the 2008 data and compared these measurements with 2003 and other time series. We will now use these results to discuss several questions of importance for our understanding of the Lake Ontario ecosystem and for the management of this important resource: 1) Is the process of oligotrophication that started with the implementation of the Great Lakes Water Quality Agreement continuing? 2) Is there a coupling between increased nutrient concentrations observed shoreside (<1.2m) and offshore processes? 3) How important is the deep chlorophyll layer and associated zooplankton for lake-wide primary and secondary production? 4) What is the possible mechanism behind the substantial decline in epilimnetic zooplankton and the dramatic changes in dominant zooplankton groups? 5) Is there a decline in spring diatom production associated with quagga mussel filtering that may help explain the almost complete extirpation of *Diporeia* (as hypothesized for Lake Michigan by Vanderploeg et al. 2010)? 6) Is Lake Ontario becoming similar to Lakes Huron and Michigan with associated concerns for an alewife collapse and declines in salmonid fisheries?

Is the oligotrophication of offshore waters continuing in Lake Ontario?

Do available data indicate an end and possible reversal of the long-term trend towards more oligotrophic conditions (or desertification – Dove 2009) in the offshore of Lake Ontario? Total phosphorus, summer chlorophyll-*a* and Secchi transparency are often used as indicators of lake trophy (Carlson 1977, Wetzel 2001). These indicators are correlated, at least in systems where primary production is phosphorus limited. Although there is clearly a long-term trend of oligotrophication in Lake Ontario (Mills et al. 2003, Dove 2009), the LOLA data indicated an increase in spring TP, spring SRP, and spring SRSi from 2003 to 2008. Higher spring nutrients were likely the cause for higher summer chlorophyll levels and lower transparency in 2008 compared to 2003. These patterns were significant in the offshore and show similar trends in the Kingston Basin and the nearshore, although the smaller number of samples did not result in many significant changes in those regions. The elevated phytoplankton biomass observed in the summer of 2008 also defies the historic trend towards increasingly oligotrophic conditions. According to the scale of Munawar and Munawar (1982), Lake Ontario with 2.5 g m^{-3} of phytoplankton was mesotrophic in 2008 which is in contrast to the ultra-oligotrophic conditions observed in 2003 (0.3 g m^{-3}) and the oligotrophic conditions observed in 1990 (1.8 g m^{-3}) and 1978 (1.2 g m^{-3}). In fact, only in the pre-phosphorous abatement period of 1970 – when the lake was highly eutrophic – was a higher summer (mean) biomass of phytoplankton observed (8.6 g m^{-3}). Analysis of phytoplankton and microbial web communities are consistent with this difference in chlorophyll levels - 2008 was characterized by mesotrophic species while 2003 was dominated by ultra-oligotrophic species. In addition to increases in epilimnetic productivity indicators, we

note that a large proportion of the chlorophyll in the summer and fall is in water deeper than what is traditionally sampled-in the deep chlorophyll layer. The largest contributor to nutrient loading in Lake Ontario is the Niagara River (Chapra et al. 2009). Lake Erie has shown an increase in nutrient concentrations over the last several years (Reutter et al. 2011) and we may therefore expect an increase in nutrient levels and algal production in Lake Ontario.

Available data from other sources also indicate that there has not been any further oligotrophication in Lake Ontario through the 2000s. Holeck et al. (2012) reported no significant change in nutrient concentrations and chlorophyll levels in the lake since 1995 in either the nearshore or offshore data, the EC-Surv data show no further decline in phosphorus after 1998 (Dove 2009) and the EPA – GLENDA data show no further decline since 1999. The LOLA-2008 data even suggest that spring TP and summer chlorophyll have increased, but this was likely due to a process specific to year 2008 as the other data sets did not support such an increase. Thus we conclude that although Lake Ontario remains oligotrophic but that there has been no further decline in offshore epilimnetic production in the last decade. Phosphorus concentrations were mostly around or below the target goal of 10 µg/L throughout the 2000s. If nutrient levels have increased, they are primarily located in water below the epilimnion (see below).

The lack of a decline in indicators of primary production is not consistent with the strong decline in epilimnetic zooplankton observed between 2003 and 2008. Rather, we believe the decline in epilimnetic zooplankton is due to increased predation by predatory cladocerans and possibly omnivorous copepods (see below).

Is there a connection between increased nutrient concentrations observed shoreside and offshore processes in Lake Ontario?

During 2008, there was also a large effort to quantify nearshore processes and to understand the reasons that *Cladophora* blooms are fouling the shoreline of Lake Ontario (LONNS, Makarewicz et al. 2012a, b, Howell et al. 2012a, b). These authors and others from the special issue on the Lake Ontario nearshore published by the Journal of Great Lakes Research in 2012 have shown that total phosphorus (TP) concentrations shoreside (depth <1.2m) in Lake Ontario can be high, sometimes exceeding 100 µg/L. High TP concentrations coupled with increased water clarity associated with mussel filtering activities are the likely reasons for increases in attached algae and fouling of beaches (Hecky et al. 2004, Malkin et al. 2008, Auer et al. 2010, Higgins and Vander Zanden 2010). Makarewicz et al. (2012a, b), Howell et al. (2012a, b) and Twiss and Marshall (2012) all show the high variability in the nearshore associated with local nutrient inputs. But does this increase in local nearshore nutrient concentrations affect the offshore? Although indications of local nearshore nutrient hotspots may be observed up to 4 km from shore, this is not always the case and the distance can be substantially less (Makarewicz et al. 2012b, Howell et al. 2012b). We see little evidence of similar increases even at depth as shallow as 8 to 10 m in the LOLA data or in the US-BMP data. Nearshore (8 to 30 m depth) and Kingston Basin TP and chlorophyll tend to be lower, not higher, than these levels in offshore waters. These observations indicate that the effect of

increased nearshore nutrient concentration is limited to water shallower than what is sampled in the LOLA program or the US-BMP (about 10 m bottom depth).

Although the local nearshore conditions are not likely to have large effects on the offshore, the opposite may not be true. Malkin et al. (2012) recently suggested that the deep chlorophyll layer was feeding the benthic mussels closer to shore in the area were this layer intersects with the bottom. These nutrients could potentially be captured, retained, and therefore accumulated by the mussels and represent a nutrient subsidy from the offshore to the nearshore. The spatial context of the coupling between benthic and pelagic systems and the nearshore-offshore needs further exploration.

How important is the deep chlorophyll layer and associated zooplankton for lake-wide primary and secondary production?

Primary production in Lake Ontario may be higher than previously thought due to the presence of a deep chlorophyll layer (DCL; Twiss et al. 2012). This layer has been observed in the past in the lake (Barbiero and Tuchman 2001) and was present in the summer in both 2003 and 2008. However, the September 2003 LOLA cruise began a day after the remnants of Hurricane Isabel passed over the region. This intense event caused deep mixing, as evidenced by distinct thermal strata (cf. Gouvea et al. 2006) such that any DCL would likely have been entrained into the epilimnion. It appears that the importance of the DCL has increased over time as the depth of maximum chlorophyll has increased over time since the 1980s (B. Weidel, USGS Lake Ontario Biological Station, unpubl data).

Deep chlorophyll layers are seasonally important in deep oligotrophic lakes (Abbott et al. 1984, Moll and Stoermer 1982, Pilati and Wurtsbaugh 2003). In Lake Michigan, 30 to 60% of the areal primary production has been attributed to the DCL (Moll et al. 1984, Fahnenstiel and Scavia 1987). There are several non-exclusive hypotheses for why DCLs are formed. Higher nutrient availability in the metalimnion would increase algal growth rates at these depths. Grazing may be lower in the metalimnion if more zooplankton reside in the epilimnion, and temperature is higher there which likely increase grazing rates. The DCL may not equate to high algal biomass and production as algae adapted to a low light environment typically have higher chlorophyll to carbon ratio than light adapted algae (Pilati and Wurtsbaugh 2003, Reynolds 2006). In addition, productivity in the DCL may be lower per unit algal biomass or unit chlorophyll than in the epilimnion due to light limitation. These caveats made Barbiero and Tuchman (2001) question if the deep chlorophyll layer also meant high algal biomass and production in the deeper waters of Lake Ontario.

The standard LOLA 2003 and 2008 sampling was not designed to sample the DCL. However, Dr. Michael Twiss from Clarkson University participated in the LOLA 2008 summer cruise and investigated the DCL at nine stations (Twiss et al. 2012). At eight of these stations there were substantial DCLs in the metalimnion that consisted of heterokontophytes (diatoms and chrysophytes), pyrrophytes (dinoflagellates) and small pico-cyanobacteria. This represented a large portion of the phytoplankton biomass in

Lake Ontario. Further, the productivity per unit chlorophyll was similar in the epi- and the metalimnion (Twiss et al. 2012). Therefore, it is possible that 50% or more of the primary production in Lake Ontario was excluded in the LOLA 2008 samples. Information on the DCL needs to be included in future assessment of the productivity of Lake Ontario.

We expect that production in the DCL is increasingly important also for secondary production including microzooplankton (Twiss et al. 2012), zooplankton, mysids, and fish. Zooplankton species that dominated in 2008 (*Limnocalanus macrurus* and *Leptodiaptomus sicilis*) are large calanoid copepods that prefer colder water. These animals will likely feed extensively on algae and microzooplankton present in the DCL. Further, mysids that make up a large portion of the crustacean biomass in Lake Ontario prefer temperatures around 7 ^{o}C and often concentrate in the metalimnion and upper hypolimnion (Boscarino et al. 2009). These crustaceans should benefit from both feeding on the metalimnetic zooplankton and grazing on the larger algae in the DCL. The shift of zooplankton biomass to cool water habitats also has important implications for bioenergetics of organisms and the restoration of native fish such as deepwater coregonids. It appears that the increasing water clarity has resulted in a re-organization of the Lake Ontario offshore ecosystem towards one with substantial production in deeper water (Weidel et al. in prep). Clearly, we cannot understand the Lake Ontario ecosystem without attention to the DCL and the associated animal community. Future monitoring should include direct measures of the DCL and an expansion to lakewide estimates of primary and secondary production in the DCL to put this layer in whole lake perspective.

What is the possible mechanism behind the substantial decline in epilimnetic zooplankton and the dramatic changes in dominant zooplankton groups?

In the past, epilimnetic samples were used to assess zooplankton abundance over time in Lake Ontario (Holeck et al. 2008). The epilimnetic zooplankton density declined almost an order of magnitude between the 1980s and 2003 (Holeck et al. 2008), and there was an additional decline of almost an order of magnitude from 2003 to 2008. Biomass also declined by a factor of 5 during the stratified period. This decline was primarily due to declines in cladocerans and cyclopoid copepods whereas calanoid copepods increased some. A change-point analysis using the longer term US-BMP data showed that the decline occurred around 2005 and was associated with an increase in *Bythotrephes* (Holeck et al. 2012).

Declines in bosminids and cyclopoids and increases in calanoids and daphnids are typical responses to decreased fish planktivory, in particular from alewife (Brooks and Dodson 1965, for New York examples see Harman et al. 2002 and Wang et al. 2010). As fish planktivory declines, larger and more efficient cladocerans that are selected by fish will increase and out-compete smaller grazers like bosminids (size efficiency hypothesis, Brooks and Dodson 1965). Alternatively, invertebrate predators that are controlled by alewife will increase when alewife decline and these small predators feed preferentially

on the smaller zooplankton (Dodson 1974, Lane 1979). In Lake Ontario, we suspect that the decline after 2005 in cyclopoids, bosminids and daphnids is related more to increased predation by invertebrate predators, in particular *Bythotrephes.* This species has been implicated in declines in cladocerans in Lake Michigan (Lehman and Caceres 1993, Schulz and Yurista 1995, Vanderploeg et al. 2012), Lake Huron (Bunnell et al. 2011, 2012), and smaller lakes (Yan et al. 2001). *Bythotrephes* is likely depressed by high alewife planktivory and is present in Lake Ontario primarily in years with lower alewife abundance (e.g. 1994, end of the 2000s). In addition, *Bythotrephes* is known to induce vertical migration in daphnids (Pangle et al. 2007) which would cause a shift in vertical distribution and a decline of epilimnetic zooplankton during the day when most samples are collected. Thus, the decline in epilimnetic densities is likely also the result of a behavioral response to this new invertebrate predator. We note that adult copepods are often omnivores and that in particular *Limnocalanus macrurus* is known to consume other zooplankton (Bowers and Carter 1977). This species has also increased in Lake Ontario as well as in Lake Michigan and Huron (Barbiero et al. 2009, 2012). However, alewife and *Mysis* remain abundant and important zooplanktivores (Stewart and Sprules 2011), and future food web studies need to re-examine the consumptive role of all zooplanktivorous predators to better understand zooplankton community changes.

As in the epilimnetic samples, whole water column density declined but not summer-OS biomass. This was due to the increase in average size of the zooplankton associated with the increase in large calanoid copepods. These calanoids are primarily residing in the metalimnion and upper hypolimnion during the day and are therefore not included in the epilimnetic samples. As calanoid copepods have increased in Lake Ontario, the epilimnetic samples taken during the day are less representative of the zooplankton population in Lake Ontario in 2008 than in earlier years (including 2003).

Unfortunately, we do not have long term data available for the whole water column zooplankton to compare time trends. However, zooplankton densities were higher in the epilimnion than in the meta and hypolimnion during the 1990s (Johannsson 2003, Kuns and Sprules 2000) and higher in the metalimnion in 2010 and 2011 (Holeck et al. 2012). Barbiero et al. (2001a) found cyclopoids and cladocerans dominated over calanoid copepods in spring and summer of 1998 which was in contrast to the Upper Lakes. It is clear that there has been a shift in the depth distribution of zooplankton biomass in Lake Ontario since the 1990s and we believe this shift happened in the middle of the 2000s, possibly associated with the large decline in epilimnetic zooplankton in 2004 to 2005 (Figure 8). Cyclopoid and bosminids decreased since 2005 also in the US-BMP data.

Is there a decline in spring diatom production associated with quagga mussel filtering that may help explain the almost complete extirpation of Diporeia?

Prior to the mid-1990s, the native benthic amphipod *Diporeia* was the largest component of benthic invertebrate biomass in Lake Ontario. Within little more than a decade quagga mussels essentially replaced *Diporeia* (Barbiero et al. 2011). Fingernail clams (sphaeriids), a small but important component of overall benthic biomass, also declined

during this time. Despite the similarity in timing of the *Diporeia* and sphaeriid declines with the expansion of dreissenid mussels, no dreissenid-induced mechanisms for these declines have been confirmed for Lake Ontario. *Diporeia* populations at many sites have disappeared despite little direct contact with mussels (Watkins et al. 2007, Nalepa et al. 2009) and elsewhere, the two species coexist (e.g. New York Finger Lakes, Watkins et al. 2012).

A potential dreissenid-based mechanism for the *Diporeia* decline has been proposed for Lake Michigan. Diatoms are nutritionally rich, and settling diatoms from the spring bloom are believed to contribute a large fraction of the annual food of *Diporeia* in the Great Lakes (Gardner et al. 1985). Declines in spring diatom blooms in southern Lake Michigan in 2004 have been associated with filtering impact of expanding quagga mussels at intermediate depths (Vanderploeg et al. 2010). This filtering may have decreased flux to offshore *Diporeia* populations and hence contributed to their decline. Dreissenid biomass and filtering capacity has similarly increased in Lake Ontario - dreissenids could filter up to 25% of the water column for the 30-50 m depth interval in 2003 and in 2008 that filtering rate was near 10% (Lozano 2011) and mussel densities in the nearshore remains high (Pennuto et al. 2012). However, we detected no change in spring chlorophyll in the April EPA surveys since 1995 (USEPA - GLENDA). Short-term spring blooms are often missed by surveys, but chlorophyll estimates from satellite images averaged over the entire spring period were also similar in 2003 (1.22 µg/L) and 2008 (1.28 µg/L) and we detected only a small decrease (<30%) of spring chlorophyll concentrations in satellite data between 1998 and 2010 (Figure 17).

The change in silica from spring to summer can also be used as an indicator of diatom production. Mida et al. (2010) showed that silica remained high through the summer in Lake Michigan, which indicates minimal diatom production in that lake. In 2003 and 2008 in Lake Ontario, silica declined from high levels in spring to levels that are limiting to diatoms by the summer. The offshore silicate utilization rate in Lake Ontario was 603 µg/L over three months in 2003 and 704 µg/L in 2008. Similar rates of silica utilization occurred in years from 1998 to 2010 (Figure 18). These rates offer strong evidence that diatom production is still active in Lake Ontario. Such rates of silica utilization have not been seen in Lakes Michigan and Huron since 2004 (Mida et al. 2010). Similarly, nitrogen depletion can be used as an indicator of primary production. In 2008, levels of nitrate (plus nitrite) averaged 470 µg/L in the spring and declined to 238 µg/L in the summer. This represents a nitrogen utilization rate of 232 µg/L over three months between surveys. In comparison, for Lake Michigan nitrogen utilization was 100 µg/L over the three months prior to 2004 and in recent years declined to only 50 µg/L over three months (Mida et al. 2010).

Thus there is no evidence of a decrease in diatom production in the available data from Lake Ontario comparable to the observations in Lakes Michigan and Huron. Although other mechanisms could be operating in Lake Ontario (see Watkins et al. submitted for discussions of changes in whiting events), it seems more likely that the basin-wide decline in *Diporeia* (Lakes Michigan, Huron and Ontario) would have the same mechanistic explanation. Thus the results from Lake Ontario lead us to question the

hypothesis that a decline in the spring bloom is the main mechanism for the *Diporeia* decline. Also, Barbiero et al. (2011) reported declining *Diporeia* in Lake Huron despite much lower abundances of quagga mussels there, implying that dreissenids may not be directly implicated in the *Diporeia* decline. We believe we need to continue to search for the reason(s) for the decline of one of the key indicator species of ecosystem health in the Great Lakes.

Is Lake Ontario becoming more similar to the Upper Lakes with associated concerns for an alewife collapse and declines in salmonid fisheries?

Barbiero et al. (2012) recently analyzed data from 2000 to 2006 for the Upper Great Lakes and suggested that the oligotrophication of Lakes Huron and Michigan have made these lakes similar to Lake Superior, both in terms of zooplankton biomass and species composition. The mechanisms involved included decreases in nutrient loading (phosphorus, in particular), decreases in epilimnetic chlorophyll-*a* levels, increases in water clarity, increases in large calanoid copepods, increases in deep chlorophyll layers, and declines in cladocerans (both bosminids and daphnids). These changes in Lakes Huron (see also Bunnell et al. 2012) and Michigan are almost identical to the changes observed in Lake Ontario. Other similarities include large densities of quagga mussels and the near extirpation of *Diporeia* in Lakes Huron and Michigan (but not Lake Superior). Barbiero et al. (2012) proposed that these changes in lower trophic levels caused the collapse of alewife in Lake Huron and the subsequent return of some of the native coregonids and natural lake trout reproduction. With changes in Lake Ontario moving in similar directions, should we expect a similar collapse of alewife in Lake Ontario?

It is clear that many of the changes documented in this report have made Lake Ontario more similar to the three Upper Lakes than was the case in the 1980s and 1990s, but there are also some important differences. Nutrient concentrations in Lake Ontario are governed by processes occurring in Lake Erie, and nutrient concentrations in the Niagara River are increasing again, not decreasing. Possibly as a consequence of this, we have not observed any decline in indicators of primary production in Lake Ontario that are comparable to observations in Lakes Huron and Michigan, nor have we observed a decline in spring diatom production. Summer conditions in Lake Ontario in 2008 were more similar to mesotrophic conditions than in recent years, although this could be limited to the year 2008. We have observed a more prominent DCL than in the past, but this is not at the expense of lower epilimnetic chlorophyll or nutrient levels. This DCL is likely to promote mysid and calanoid production in Lake Ontario. Alewife do utilize zooplankton and mysids in Lake Ontario as at least part of the alewife population moves into this deeper layer during the night to feed on mysids and larger copepods (Boscarino et al. 2010). Mysids are an increasingly large portion of the alewife diet (Stewart et al. 2009). We note that large copepods and mysids are more lipid rich than cladocerans, and that alewife growth rates have increased since 2004 rather than declined as a response to the shifts in zooplankton community composition (O'Gorman et al. 2008, Walsh and Connerton 2012). Thus there is little change in overall productivity on the offshore Lake

Ontario in the last decade and we therefore do not expect that a decline in lower trophic levels would cause further declines in alewife populations. This does not preclude an alewife decline due to increased abundance of salmon in the lake, which is possible through wild production (as suggested as an alternative or contributing cause for the collapse of alewife in Lake Huron, Riley et al. 2008). The restructured Lake Ontario may, however, be more conducive to coregonid and rainbow smelt production than alewife, as is the case in Lake Superior. These species are better adapted at feeding and growing at cold temperatures than alewife (Stewart and Binkowski 1984, Rudstam et al. 1994, Lantry and Stewart 1993). This could have implications for the restoration of native coldwater coregonids such as deep-water ciscoes that are abundant in the upper lakes.

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Table 1. Summary of field sampling efforts during LOLA 2003 and 2008

	LOLA 2003	LOLA 2008
Spring survey	April 28-May 1	April 21-24
Spring vessel	CCGC Limnos	CCGC Limnos
Summer survey	August 10-11, August 19-22	July 20-26
Summer vessel	R/V Lake Guardian and CCGC Limnos	R/V Lake Guardian
Fall survey	September 21-25	September 2-5
Fall vessel	R/V Lake Guardian	R/V Lake Guardian and CCGC Limnos

Table 2. Stations sampled in 2003 and 2008 during each season. Abbreviations are C: chemistry, P: phytoplankton and microbial food web, Z: zooplankton with a subscript E for epilimnetic samples and T for total water column samples. Site depth is in m.

Station	Region	Site depth	Lat	Long	Spr 2003	Sum 2003	Fall 2003	Spr 2008	Sum 2008	Fall 2008
8	NS	15.6	43.6231	79.4528	Z_E,C,P	Z_E,C,P	Z_E,C	Z_E,C,P	Z_E, C,P	Z_E, C,P
9	OS	60.3	43.5867	79.3944	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C		$Z_{E,T}$,C	$Z_{E,T}$,C
12	OS	104.8	43.5033	79.3531	$Z_{E,T}$,C,P	$Z_{E,T}$,C,P	$Z_{E,T}$,C	$Z_{E,T}$,C,P	$Z_{E,T}$,C,P	$Z_{E,T}$,C,P
17	NS	14.4	43.2247	79.2719	Z_E, C, P	Z_E, C, P	Z_E, C	Z_E, C,P	Z_E, C,P	Z_E, C,P
18	OS	85.5	43.3036	79.2781	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C			C
19	OS	106.3	43.3836	79.2853	$Z_{E,T}$,C,P	$Z_{E,T}$,C,P	$Z_{E,T}$,C	Z_T, C	$Z_{E,T}$,C	$Z_{E,T}$,C
28	OS	61	43.7750	78.8533			$Z_{E,T}$,C			
29	NS	30	43.8183	78.8700			$Z_{E,T}$,C			
33	OS	138.1	43.5964	78.8008	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C		$Z_{E,T}$,C	$Z_{E,T}$,C
35	NS	37	43.36	78.73						
38	NS	18.8	43.3833	77.9894	Z_T,C,P	$Z_{E,T}$,C,P	Z_E, C	Z_E, C,P	Z_E, C,P	Z_E,C,P
39	OS	154.8	43.4867	78.0000	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C		$Z_{E,T}$,C	$Z_{E,T}$,C
40	OS	182.7	43.5903	78.0108	$Z_{E,T}$,C,P	$Z_{E,T}$,C,P	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C	Z, C
41	OS	128.9	43.7150	78.0264	$Z_{E,T}$,C,P	$Z_{E,T}$,C,P		$Z_{E,T}$,C,P	$Z_{E,T}$,C,P	$Z_{E,T}$,C,P
42	OS	65.6	43.8408	78.0381	$Z_{E,T}$,C	$Z_{E,T}$,C			$Z_{E,T}$,C	$Z_{E,T}$,C
43	NS	16.8	43.9500	78.0497	Z_E,C, P	$Z_{E,T}$,C,P		$Z_{E,T}$,C,P	$Z_{E,T}$,C,P	$Z_{E,T}$,C,P
49	OS	49.5	43.7706	77.4383	Z, C				C	C
62	NS	18	43.8800	76.9994	Z_T, C, P	$Z_{E,T}$,C,P	Z_E, C	Z_E, C	Z_E, C	Z_E, C
63	OS	87.5	43.7311	77.0158	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C		$Z_{E,T}$,C	Z_T, C
64	OS	213.1	43.5250	76.9275	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C
65	OS	146.6	43.4233	76.8833	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C
66	NS	17.6	43.3331	76.8392	Z_E,C, P	$Z_{E,T}$,C,P	Z_E, C	Z_E, C	Z_E, C	Z_E, C
71	NS	11.6	43.4772	76.5269	Z_T, C, P	$Z_{E,T}$,C,P	Z_E, C	Z_E, C,P	Z_E, C,P	Z_E,C,P
72	OS	108.6	43.5503	76.5250	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$		$Z_{E,T}$,C	$Z_{E,T}$,C
74	OS	67.6	43.7497	76.5186	$Z_{E,T}$,C,P	$Z_{E,T}$,C,P	$Z_{E,T}$,C	$Z_{E,T}$,C,P	$Z_{E,T}$,C,P	$Z_{E,T}$,C,P
77	KB	28.4	43.9569	76.4086	Z_E, C		$Z_{E,T}$,C		C	
80	KB	22	44.1358	76.6097	Z_E, C	$Z_{E,T}$,C	$Z_{E,T}$,C	Z_E, C,P	Z_E,C,P	Z_E,C,P
81	KB	36.3	44.0164	76.6750	$Z_{E,T}$,C,P	$Z_{E,T}$,C,P	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C
84	KB	36.6	43.8867	76.7333	$Z_{E,T}$,C	$Z_{E,T}$,C,P	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C
89	OS	81.6	43.6983	76.4164	$Z_{E,T}$,C	Z_E	$Z_{E,T}$,C			
715	OS	153.5	43.6356	76.9694	$Z_{E,T}$,C,P	$Z_{E,T}$,C,P	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C	$Z_{E,T}$,C
716	OS	150	43.60	77.44					C	
717	NS	16.8	43.30	77.44					C	
ROC	NS	19	43.2460	77.5450			Z_E			

Table 3. Average of water quality indicators from the LOLA 2003 and LOLA 2008 surveys in the three regions. Number of stations sampled varied with survey and year. Significant differences (P<0.05) between 2003 and 2008 are in bold (underlined red font is the higher value, t-test assuming unequal variance, P<0.05). Note that there has been no correction done for multiple tests. NO_x refers to $NO_2 + NO_3$

	Kingston Basin			**Offshore**			**Nearshore**		
	2003	**2008**	**P-val**	**2003**	**2008**	**P-val**	**2003**	**2008**	**P-val**
SPRING									
TP (µg P/L)	8.5	3.9	.205	**6.6**	**9.8**	**.0025**	8.0	9.9	.197
# of stations	4	3		17	8		7	7	
SRP (µg P/L)	0.8	1.3	.226	**1.0**	**2.6**	**.0019**	**0.9**	**1.8**	**.031**
# of stations	4	3		17	8		7	7	
SRSi (µg SiO_2/L)	660	619	.759	**793**	**868**	**.0005**	623	741	.232
# of stations	4	3		17	8		7	7	
NO_x (µg N/L)		371			470			522	
# of stations		3			8			7	
Secchi (m)	14.8	15	.906	**10.0**	**14.9**	**.0007**	8.8	10.5	.450
# of stations	3	3		13	9		4	7	
Chl-*a* (µg/L)	1.1	1.7	.221	1.4	1.3	.609	1.2	1.7	.252
# of stations	4	3		17	8		7	8	
SUMMER									
TP (µg P/L)	9.4	6.0	.122	10.1	6.7	.069	9.2	8.9	.891
# of stations	3	4		15	17		7	8	
SRP (µg P/L)	0.6	0.7	.391	0.6	0.7	.242	1.1	0.8	.504
# of stations	3	4		16	17		7	8	
SRSi (µg SiO_2/L)	287	160	.146	190	164	.251	396	176	.085
# of stations	3	4		16	17		7	8	
NO_x (µg N/L)		171			238			232	
# of stations		4			16			8	
Secchi (m)	6.6	5.0	.376	7.9	6.7	.296	**8.6**	**4.5**	**.0039**
# of stations	3	3		8	14		3	7	
Chl-*a* (µg/L)	**1.8**	**4.3**	**.008**	**1.5**	**3.1**	**<.0001**	2.7	3.3	.522
# of stations	3	4		16	17		7	8	
Temp (°C)	**22.8**	21.4	**.0298**	22.3	21.2	.149	**23.1**	20.3	**.0425**
# of stations	3	4		11	17		5	8	
FALL									
TP (µg P/L)	9.1	11.6	.253	**12.5**	**8.0**	**.0051**	10.8	10.5	.920
# of stations	4	3		14	16		7	7	
SRP (µg P/L)	1.0	1.5	.237	**0.8**	**1.4**	**.0262**	1.8	1.7	.892
# of stations	4	3		13	16		6	7	
SRSi (µg SiO_2/L)	**410**	**138**	**.024**	**256**	**110**	**.0002**	**466**	**144**	**<.0001**
# of stations	4	3		14	16		7	7	
NO_x (µg N/L)		182			216			231	
# of stations		3			16			7	
Secchi (m)	6.8	5.9	.291	**6.3**	**5.0**	**.0131**	**7.8**	**5.1**	**.0178**
# of stations	3	3		11	14		3	6	
Chl-*a* (µg/L)	2.5	2.1	.164	**3.1**	**1.7**	**.0001**	2.2	1.8	.237
# of stations	4	3		14	16		7	8	
Temp (°C)	19.4	n/a		17.8	**21.9**	**<.0001**	17.1	**21.7**	**.0017**
# of stations	2	0		14	10		7	2	

Table 4. Results from the 2003 and 2008 summer microbial food web surveys of Lake Ontario by Fisheries & Oceans Canada. Sample size (n) and mean ± 1 S.E. are reported.

Parameter	2003	2008
Microbial Loop (mg m^{-3})	n = 15	n = 13
Total Biomass		
Bacteria	184.7 ± 10.7	522.0 ± 45.9
APP	87.8 ± 13.4	822.1 ± 148.5
HNF	1249.4 ± 210.9	46.2 ± 10.6
Ciliates	36.4 ± 7.4	77.75 ± 13.79 (n=12)
Phytoplankton (mg m^{-3})	n = 15	n = 9
Total Biomass	285.7 ± 82.2	2450 ± 333.1
Cyanophyta	117.3 ± 88.0	131.2 ± 18.7
Chlorophyta	34.6 ± 5.9	492.8 ± 61.8
Chrysophyceae	26.4 ± 4.8	271.7 ± 43.3
Diatomeae	22.1 ± 5.7	258.9 ± 44.6
Cryptophyceae	50.4 ± 9.8	563.4 ± 222.2
Dinophyceae	34.4 ± 10.6	732.2 ± 179.9

Table 5. Frequency of occurrence of different zooplankton taxa in the 2003 and 2008 LOLA epilimnetic and whole water column samples. Groupings used for subsequent analyses are in bold (see Tables 5-7). Numbers represent the proportion of stations with the particular taxa present (in %). Taxa were classified as common (C) if found in four or more surveys, as uncommon (U) if found in 2 or 3 surveys and as rare (R) if found in only 1 survey. Classification in 1967-73 surveys as rare, uncommon or common is from Robertson and Gannon (1981) for copepods and Balcer et al. (1984) for cladocerans. Balcer et al. (1984) classified abundance as rare, uncommon, present, common and abundant. Here we combined uncommon and present as U (uncommon) and common and abundant as C (common). The number of years the species was present in the 1981-1995 period is from the Canadian Bioindex program (total number of years 15, Johannsson et al. 1998) and for 1995 – 2010 period from the US Biomonitoring Program (excluding embayments, Holeck et al. 2012). Copepods only identified as calanoid, cyclopoid or harpacticoid copepodid/nauplii were present in most samples and are not reported here. NR is not recorded.

Species/Group	2003	2003	2003	2008	2008	2008	1967-1973	1981-1995	1995-2010
Survey/# years	Spr	Sum	Fall	Spr	Sum	Fall		15	16
Calanoid copepods									
Leptodiaptomus ashlandi	7	0	0	11	0	0	R	5	4
Leptodiaptomus minutus	18	19	7	72	75	71	C	6	16
Leptodiaptomus sicilis	43	15	7	100	75	83	C	15	11
Leptodiaptomus siciloides	0	4	0	28	0	0	U	1	4
Skistodiaptomus oregonensis	75	31	85	83	75	92	C	14	16
Skistodiaptomus reighardi	4	0	0	0	0	0	R	0	0
Epischura lacustris	4	17	36	5	73	100	R	2[a]	15
Eurytemora affinis	4	19	33	0	21	4	C	14	12
Limnocalanus macrurus	100	38	22	100	75	75	C	14	16
Cyclopoid copepods									
Acanthocyclops vernalis	0	8	11	0	0	0	C	2	11
Diacyclops thomasi	100	100	100	100	96	96	C	15	16
Eucyclops agilus	0	0	0	0	4	0	R	0	4[b]
Mesocyclops edax	0	8	30	0	13	42	U	2	16
Paracyclops fimbriatus poppei	4	0	0	0	0	0	NR	0	0
Tropocyclops prasinus	11	15	48	0	0	38	C	15	15
Bosminidae									
Bosmina longirostris	86	100	96	28	100	100	C	15	16
Eubosmina sp.	68	100	100	28	71	100	C	15[c]	16
Daphniidae									
Daphnia mendotae	36	96	100	6	88	100	U-C	11	15
Daphnia pulicaria[d]	0	0	0	0	4	0	R	1	12
Daphnia retrocurva	0	100	100	11	54	100	C	15	16
Daphnia longiremis	0	0	0	0	0	0	R-U	4	1
Daphnia schødleri	0	0	0	0	0	0	NR	0	5
Ceriodaphnia sp.[e]	0	69	63	0	0	0	U-C	14	16
Other Cladocerans									
Alona sp.	0	4	0	0	4	4	R	0	11
Chydorus sphaericus	4	35	59	6	29	63	U	8	14
Camptocercus sp.	0	0	0	0	0	0	C	0	6
Diaphanosoma sp.[g]	0	15	70	0	17	79	R-U	5	16
Sida crystalina	0	0	0	0	0	0	R	0	4
Holopedium gibberum	0	92	100	6	96	88	U	12	16
Predatory Cladocerans									
Leptodora kindtii	0	65	78	0	92	83	U-C	13	16
Polyphemus pediculus	0	77	11	0	54	29	U	10	14
Bythotrephes longimanus	0	0	33	11	46	75	NR	2[f]	12
Cercopagis pengoi	0	96	100	0	88	63	NR	0	13

a) Found in 1994 and 1995; b) Identified as *Eucyclops sp*.; c) Identified as *Eubosmina coregoni* in all years with the addition of *Eubosmina longispina* in 4 of the 15 years; d) Identified as *Daphnia pulex* by Balcer et al. (1984) and Johannsson et al. (1998); e) Identified as *Ceriodaphnia lacustris* in 2003 and as *Ceriodaphnia* sp. in 2008. Johannsson et al. (1998) reports *Ceriodaphnia lacustris* in most years with the addition of *C. quadrangular* in 3 of the 15 years. f) *Bythotrephes* found in 1987 and 1994, g) Identified as *Diaphanosoma birgei* in 2003 and mostly as *D. brachyrum* in 2008.

Table 6. Zooplankton data from the epilimnion in Lake Ontario collected during LOLA 2003 and 2008. Data represent volumetric densities and biomass for samples collected from dawn to dusk; night samples are excluded. Significant differences between 2003 and 2008 are in bold with the higher values underlined and in red (t-test assuming unequal variance). Significance values are given based on comparisons of $\log_e(x)$ (density) and $\log_e(x+0.01)$ (biomass) transformed data. Average lengths were not transformed. Means are arithmetic means. Note that there has been no correction done for multiple tests. A Bonferroni adjusted alpha value for significant effect at the $P<0.05$ level with 12 tests per region and season would be 0.0042. Biomass is in mg dry wt/m^3, Density in #/m^3 and Length in mm. Group-specific values are in biomass.

	Kingston Basin			Offshore			Nearshore		
	2003	**2008**	**P-val**	**2003**	**2008**	**P-val**	**2003**	**2008**	**P-val**
Spring									
Density	371	397	0.922	1,576	1,428	0.785	419	940	0.158
Avg Length	0.71	1.15	0.142	**0.67**	**0.42**	**<.0001**	0.63	0.61	0.805
Biomass	1.3	7.7	0.159	**5.3**	**2.7**	**0.015**	**1.4**	**3.7**	**0.031**
Calanoids	**0.1**	**0.8**	**0.004**	**0.1**	**1.0**	**<.0001**	**0.03**	**2.1**	**<.0001**
Limnocal.	0.2	6.4	0.085	0.6	0.5	0.209	**0.3**	**0.9**	**0.017**
Cyclopoids	1.1	0.5	0.238	**4.5**	**1.2**	**0.002**	1.0	0.7	0.227
Bosminids	0.0	0.0	0.423	**0.01**	**0.0**	**<.0001**	**0.0**	**0.0**	**0.014**
Daphnids	0.0	0.0	0.184	0.0	0.0	0.130	0.01	0.0	0.520
Cercopagis	0.0	0.0	n/a	0.0	0.0	n/a	0.0	0.0	n/a
Bythotrephes	0.0	0.0	n/a	0.0	0.0	n/a	0.0	0.0	n/a
Lept./Polyph.	0.0	0.0	n/a	0.0	0.0	n/a	0.0	0.0	n/a
Other Clad.	0.0	0.0	0.423	0.0	0.0	n/a	0.0	0.01	0.356
# Stations	3	3		16	7		5	7	
Summer									
Density	18,122	4,831	0.095	**40,535**	**3,244**	**<.0001**	16,818	4,857	0.100
Avg Length	0.44	0.44	0.993	0.51	0.64	0.089	0.51	0.51	0.976
Biomass	17.2	5.9	0.062	**28.9**	**5.3**	**<.0001**	24.2	6.8	0.133
Calanoids	0.3	1.0	0.105	**0.5**	**0.9**	**0.037**	**0.1**	**0.7**	**0.034**
Limnocal.	0.0	0.2	0.196	**0.1**	**0.4**	**0.023**	0.0	0.2	0.184
Cyclopoids	0.7	0.2	0.429	6.1	0.2	0.079	0.7	1.5	0.786
Bosminids	6.2	1.8	0.275	**4.9**	**1.4**	**0.0003**	2.6	2.0	0.751
Daphnids	7.4	0.8	0.079	**12.1**	**0.0**	**<.0001**	**16.0**	**0.1**	**0.011**
Cercopagis	**0.0**	**1.0**	**0.010**	1.7	0.6	0.383	4.0	1.3	0.501
Bythotrephes	0.0	0.0	n/a	**0.0**	**0.9**	**0.004**	0.0	0.1	0.172
Lept./Polyph.	0.96	0.5	0.402	2.1	0.1	0.167	0.4	0.2	0.617
Other Clad.	1.65	0.2	0.053	1.5	0.6	0.191	0.4	0.8	0.321
# Stations	3	3		12	14		5	7	
Fall									
Density	**39,616**	**7,749**	**0.032**	**47,695**	**18,079**	**0.032**	**70,621**	**12,629**	**0.026**
Avg Length	0.57	0.54	0.739	**0.48**	**0.64**	**0.0005**	0.39	0.51	0.052
Biomass	83.0	19.6	0.054	73.2	48.3	0.647	94.3	23.2	0.119
Calanoids	2.9	17.2	0.060	**3.1**	**12.1**	**0.0003**	4.8	6.5	0.682
Limnocal.	0.0	0.1	0.285	0.0	1.2	0.201	0.0	0.2	0.176
Cyclopoids	**2.6**	**0.5**	**0.018**	**10.9**	**4.3**	**0.043**	**19.4**	**4.7**	**0.048**
Bosminids	**44.9**	**0.3**	**0.008**	**31.4**	**4.2**	**0.007**	**45.4**	**2.3**	**0.034**
Daphnids	**27.2**	**0.5**	**0.029**	23.5	17.4	0.390	19.0	4.4	0.231
Cercopagis	**2.6**	**0.01**	**<.0001**	**2.7**	**0.1**	**<.0001**	**3.3**	**0.2**	**0.008**
Bythotrephes	0.5	0.6	0.898	**0.0**	**0.2**	**0.018**	0.1	0.1	0.882
Lept./Polyph.	0.5	0.5	0.432	**0.1**	**0.8**	**0.0004**	0.9	0.6	0.809
Other Clad.	**1.9**	**0.5**	**0.005**	**1.4**	**8.1**	**0.033**	1.4	4.3	0.153
# Stations	4	3		13	12		7	6	

Table 7. Ratio (in %) of epilimnetic to whole water column areal abundance of major zooplankton groups in different seasons in 2003 and 2008 in the offshore of the main lake. Significant differences between epilimnetic and whole water column areal densities are in bold.

	Spring 2003	**Summer 2003**	**Fall 2003**	**Spring 2008**	**Summer 2008**	**Fall 2008**
Total Biomass	**15**	**10**	**22**	**11**	**2**	**26**
Calanoids	**17**	**25**	**25**	**17**	**1**	**30**
Limnocalanus	**12**	**0**	**0**	**7**	**0**	**2**
Cyclopoids	**16**	**5**	**9**	**12**	**1**	**19**
Bosminids	**27**	**18**	47	0	21	68
Daphnids	100	**13**	**21**	Not caught	11	70
Cercopagis	Not caught	**12**	**33**	Not caught	**19**	47
Bythotrephes	Not caught	Not caught	18	Not caught	41	78
Lept/Polyp	Not caught	79	**8**	Not caught	**14**	112
Other Clad.	0	83	42	Not caught	44	127

Table 8. Zooplankton data from whole water column samples in Lake Ontario during LOLA 2003 and 2008. Epilimnetic samples are only included when no whole water sample was taken and the epilimnetic sample represented more than 50% of the water column (several of the nearshore and eastern basin stations). Data represent areal densities and biomass for the water column sampled which in most cases includes the depth from 2 m above the bottom (or 100 m) to the surface. All samples representing the whole water column are included, regardless of time of day. Significant differences between 2003 and 2008 are in bold with the higher values underlined and in bold red. Significance values are given based on one-way comparisons of $\log_e(x)$ transformed data for density and $\log_e(x+0.01)$ transformed data for biomass. Average lengths were not transformed. Means are arithmetic means. Note that there has been no correction done for multiple tests. A Bonferroni adjusted alpha value for significant effect with 12 tests per area and season would be 0.0042. Biomass is in mg dw/m^2, Density in #/m^2 and Length in mm. Group-specific values are in biomass (mg dw/m^2).

	Kingston Basin			Offshore			Nearshore		
	2003	**2008**	**P-val**	**2003**	**2008**	**P-val**	**2003**	**2008**	**P-val**
Spring									
Density	27,055	9,636	0.403	175,320	124,889	0.532	9,494	15,834	0.257
Avg Length	**0.75**	**1.29**	**<.0001**	**0.75**	**0.64**	**<.0019**	0.66	0.71	0.822
Biomass	116.8	196.2	0.154	700.6	475.4	0.477	34.9	63.36	0.081
Calanoids	1.3	17.6	.060	**8.3**	**119.0**	**<.0001**	1.4	37.7	0.057
Limnocal.	**4.8**	**165.1**	**<.003**	101.5	149.8	0.738	5.5	17.3	0.104
Cyclopoids	110.7	13.5	0.115	**589.2**	**205.7**	**0.021**	27.9	8.4	0.297
Bosminids	0.0	0.0	n/a	**1.6**	**0.3**	**0.012**	0.07	0.01	0.106
Daphnids	0.0	0.02	0.225	0.02	0.0	0.079	0.1	0.0	0.389
Cercopagis	0.0	0.0	n/a	0.0	0.0	n/a	0.0	0.0	n/a
Bythotrephes	0.0	0.0	n/a	0.0	0.6	0.174	0.0	0.0	n/a
Lept./Polyph	0.0	0.0	n/a	0.0	0.0	n/a	0.0	0.0	n/a
Other Clad.	0.0	0.0	n/a	0.01	0.0	0.332	0.0	0.0	n/a
# Stations	4	3		17	8		7	5	
Summer									
Density	**1,189,074**	**136,915**	**0.022**	**1,100,167**	**304,485**	**<.0001**	**227,030**	**48,683**	**0.021**
Avg Length	0.51	0.54	0.848	**0.59**	**0.97**	**<.0001**	0.57	0.55	0.826
Biomass	2209.1	340.2	0.122	2558.3	2826.0	0.437	**425.2**	**82.8**	**0.021**
Calanoids	6.4	140.5	0.141	**13.9**	**1040.6**	**<.0001**	**1.5**	**10.1**	**0.038**
Limnocal.	0.0	2.3	0.423	**168.8**	**1366.4**	**0.0002**	0.00	2.4	0.374
Cyclopoids	254.0	74.5	0.205	**1082.4**	**303.7**	**0.0003**	47.0	14.0	0.313
Bosminids	**310.8**	**51.3**	**0.044**	**277.0**	**37.9**	**0.0002**	50.5	20.6	0.081
Daphnids	1489.8	21.5	0.310	**830.0**	**3.4**	**<.0001**	**247.7**	**1.3**	**0.001**
Cercopagis	1.2	36.7	0.069	**138.7**	**31.6**	**0.024**	19.8	14.6	0.310
Bythotrephes	0.0	0.0	n/a	**0.0**	**18.4**	**0.0004**	0.00	1.5	0.374
Lept./Polyph	121.1	6.1	0.114	28.6	9.1	0.932	35.0	2.4	0.338
Other Clad.	25.7	7.4	0.087	18.9	14.9	0.117	23.6	15.8	0.538
# Stations	3	3		15	14		7	5	
Fall									
Density	1,210,212	333,859	.135	**2,182,066**	**551,033**	**<.0001**	**1,213,906**	**173,725**	**0.011**
Avg Length	0.61	0.62	0.925	**0.63**	**0.83**	**<.0001**	0.42	0.55	0.084
Biomass	3163.6	1132.9	0.234	**5234.7**	**3156.6**	**0.032**	1866.5	375.0	0.088
Calanoids	**214.4**	**775.8**	**0.207**	**148.2**	**1086.5**	**<.0001**	84.1	101.7	0.927
Limnocal.	0.0	59.0	0.422	**121.4**	**966.4**	**<.0001**	**0.0**	**2.6**	**0.076**
Cyclopoids	287.1	180.2	0.554	**2066.0**	**457.4**	**0.005**	696.4	102.3	0.099
Bosminids	1171.0	36.3	0.071	**1031.4**	**110.9**	**<.0001**	**595.6**	**35.1**	**0.020**
Daphnids	1240.2	61.0	0.121	**1640.2**	**406.3**	**0.0002**	382.4	71.3	0.161
Cercopagis	**147.3**	**0.0**	**<.0001**	**159.4**	**2.1**	**<.0001**	**54.6**	**3.3**	**0.017**
Bythotrephes	11.1	11.5	0.732	**0.8**	**5.6**	**0.016**	0.8	1.6	0.434
Lept./Polyph	38.7	8.4	0.254	23.0	25.1	0.202	37.6	5.2	0.759
Other Clad.	**53.6**	**0.5**	**0.047**	47.5	97.1	0.291	15.0	51.8	0.225
# Stations	6	3		15	14		8	6	

Table 9. Whole water-column abundance (#/m^2, mean (range)) of *Mysis diluviana* at station 41 and 64 from net samples in 2008. Total abundance and the number of gravid females are given. N is the number of samples per date and station. Acoustic estimates of mysid density at Station 41 and 64 in July were 233 (175-298) and 434 (386-493) mysid/m^2, respectively.

Date	Station	N	Tow depth/bottom depth m	Mysids (#/m^2)	# gravid females	Mysid biomass (mgdw/m^2)
April 22	41	4	131/134	530 (311-994)	30 (25-37)	1290 (870-2450)[a]
April 22	64	4	228/231	249 (84-675)	7 (2-13)	405 (155-980)[a]
April 23	81	4	33/37	5 (4-6)	0 (0-0)	8 (5-10)
July 25	41	4	127/129	316 (244-387)	0 (0-0)	730 (710-860)
July 23	64	4	230/233	513 (442-562)	0 (0-0)	830 (660-980)
Sep 3	41	4	125/127	464 (290-553)	0 (0-0)	1110 (510-1370)
Sep 3	64	4	213/216	605 (514-756)	1 (0-1)	1260 (1040-1750)
Nov 13	41	2	131/135	173 (159-186)	8 (7-9)	615 (570-660)[b]
Nov 14	64	2	232/235	266 (232-299)	5 (3-7)	855 (750-960)[b]

a) Average weight from 3 tows applied to the 4th tow for biomass estimates

b) Average weight from 1 tow applied to the 2nd tow for biomass estimates

Table 10. Hydroacoustic density estimates of *Mysis diluviana* in Lake Ontario Aug 1 to 5, 2008 based on a mysid TS of -88.93dB (see text). Each of five transects was divided in 200 m sections and average densities calculated for each depth region. Variance is calculated using the north, south and middle regions of each transect as independent estimates. Whole lake estimates are weighted by the proportion of the lake area represented by each depth region. CV for whole lake is calculated from standard error propagation formulas for sums. Net samples are for the upper 60 m (variable) and collected with vertical tows during the acoustic survey. Densities were corrected for boat drift.

Depth Region	Proportion of lake area	Density (#/m^2)	CV (%) (SE/mean)	N	Average Density in Net tows (#/m^2)	N
0–30m	0.217	4.0	47.5	10	No samples	
30–50m	0.115	53.9	45.4	10	No samples	
50–75m	0.127	152.6	31.3	10	166	2
75–100m	0.112	257.3	19.5	10	119	3
100+m	0.429	329.3	7.6	5	534	6
Whole lake		196.5	15.4			

Table 11. Summary of *Dreissena* and *Diporeia* abundance (#/m^2) from LOLA 2003 and 2008. Abundance is given as the arithmetic mean. Significant differences between years in bold ($p<0.05$, t-test assuming unequal variances). Values were $\log_e (x+1)$ transformed prior to statistical analyses.

Depth	# Stations		*Dreissena polymorpha*			*Dreissena r.bugensis*			*Diporeia*		
Interval	2003	2008	2003	2008	P-val	2003	2008	P-val	2003	2008	P-val
0-30 m	9	13	47	0	0.12	**9,146**	**912**	**0.0013**	0	1	0.17
31-50 m	5	4	0	0	n/a	10,949	4,434	0.32	1	9	0.31
51-90 m	9	15	1	0	0.35	6,525	6,814	0.41	97	7	0.23
> 90 m	13	19	0	0	n/a	1,099	736	0.97	**545**	**42**	**0.0015**

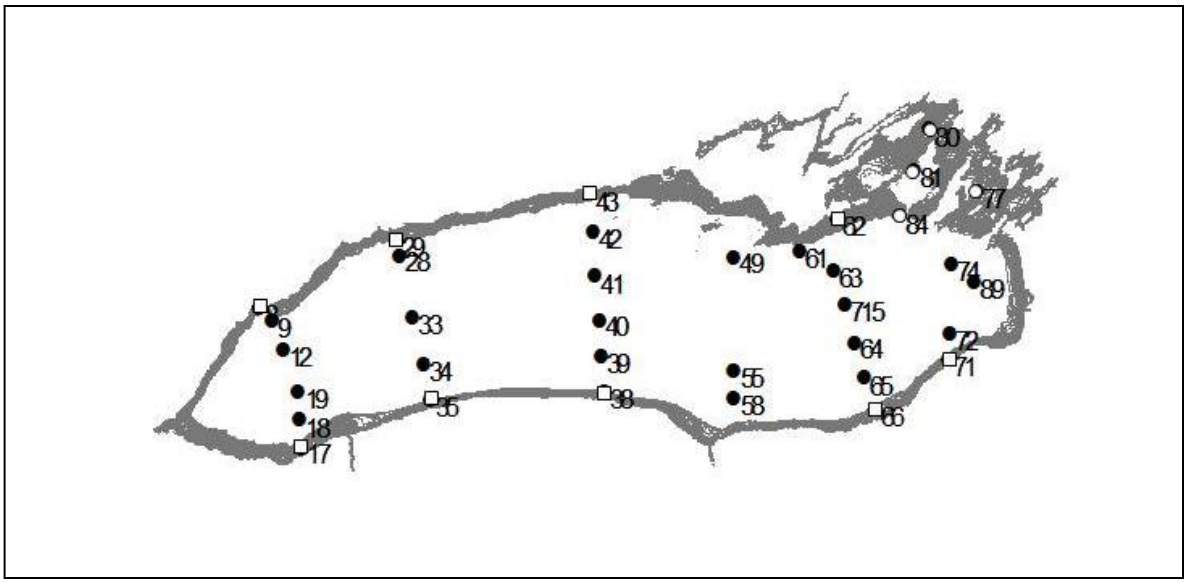

Figure 1. Map of Lake Ontario indicating sample locations used in 2003 and 2008 (see Table 2 for locations). Grey area delineates the nearshore with nearshore stations marked with open squares (<30 m deep). Kingston Basin stations are indicated with open circles.

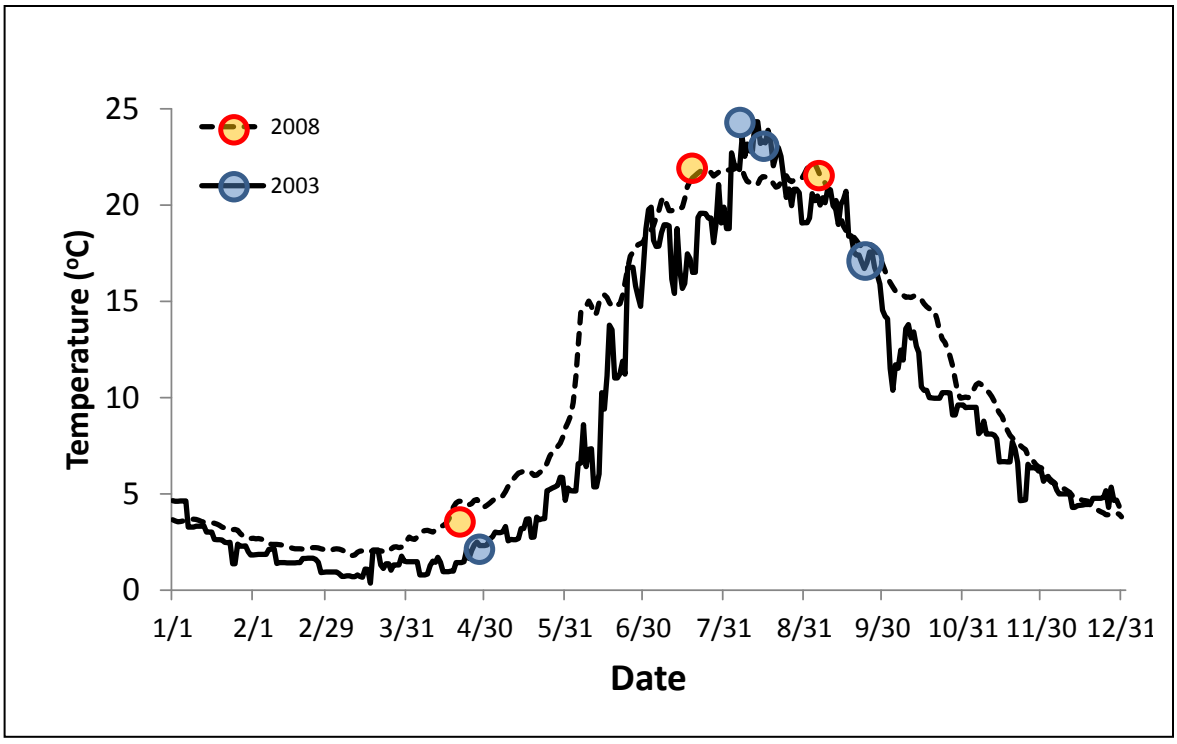

Figure 2. Lake surface temperature in Lake Ontario during 2003 and 2008 (from NOAA http://coastwatch.glerl.noaa.gov/glsea/). Timing of LOLA surveys during spring, summer, and fall surveys are indicated in blue (2003) and yellow (2008). In 2003, the summer survey was split into two shorter time periods (see Table 1).

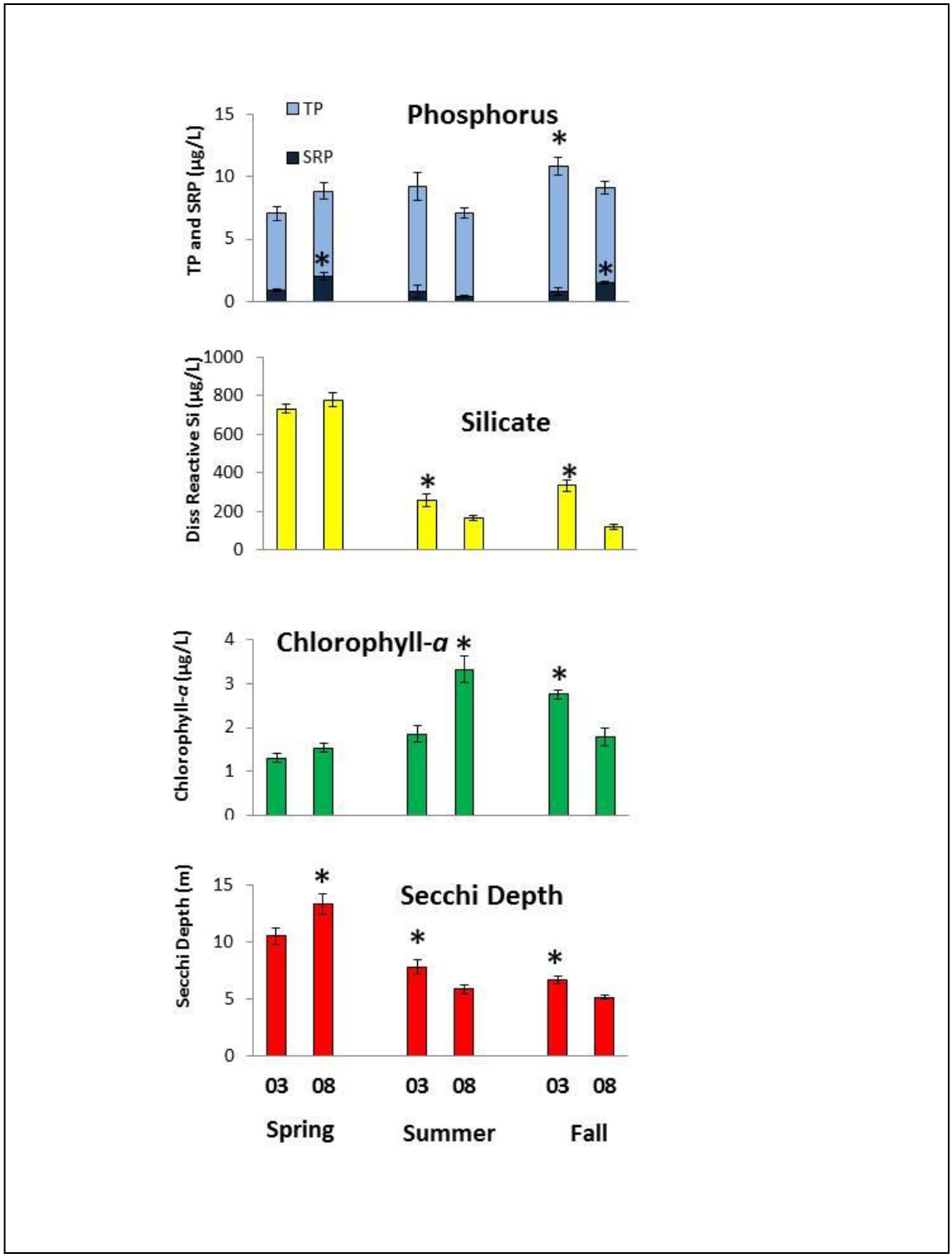

Figure 3. Average of water quality indicators from the LOLA 2003 and LOLA 2008 surveys during spring (2003 N=20-28; 2008 N=18-19), summer (2003 N=14-26; 2008 N=24-29), and fall (2003 N=17-25; 2008 N=23-27). Significant differences between 2003 and 2008 are indicated by an asterisk. Error bars indicate 1 SE.

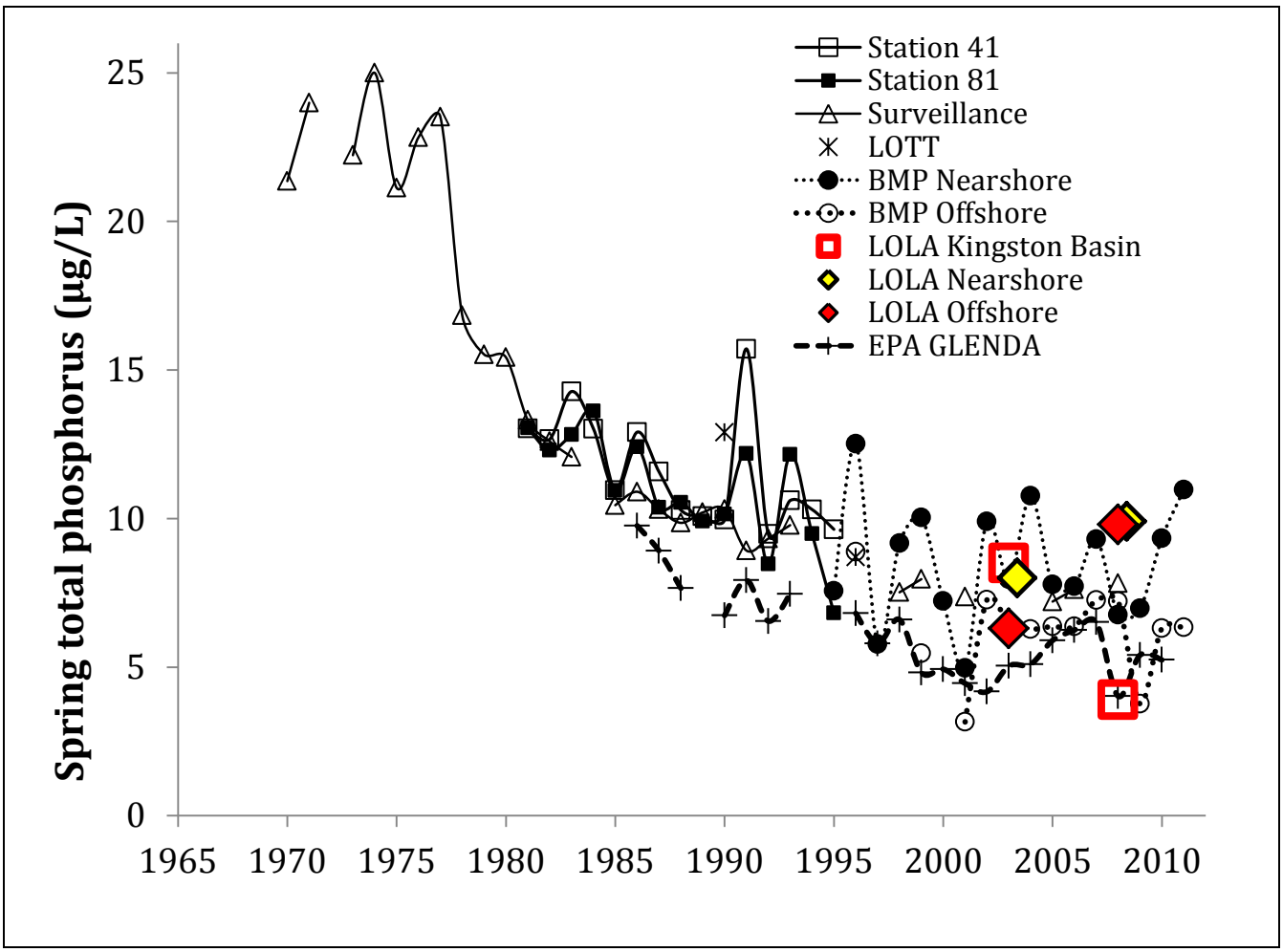

Figure 4. Long-term spring (Apr – May) epilimnetic total phosphorus concentrations in Lake Ontario, 1970 - 2011. Data from 1970 – 2008 are from EC-Surv (Dove 2009). Station 41 and 81 (1981 – 1995) are from the Department of Fisheries and Oceans Canada's Bioindex Program. LOTT data (1990 and 1996) are from the Lake Ontario Trophic Transfer Project. Data from 1995 – 2011 are from the US-BMP. Data from 1985 to 2010 are from EPA-GLENDA. LOLA data are from this report.

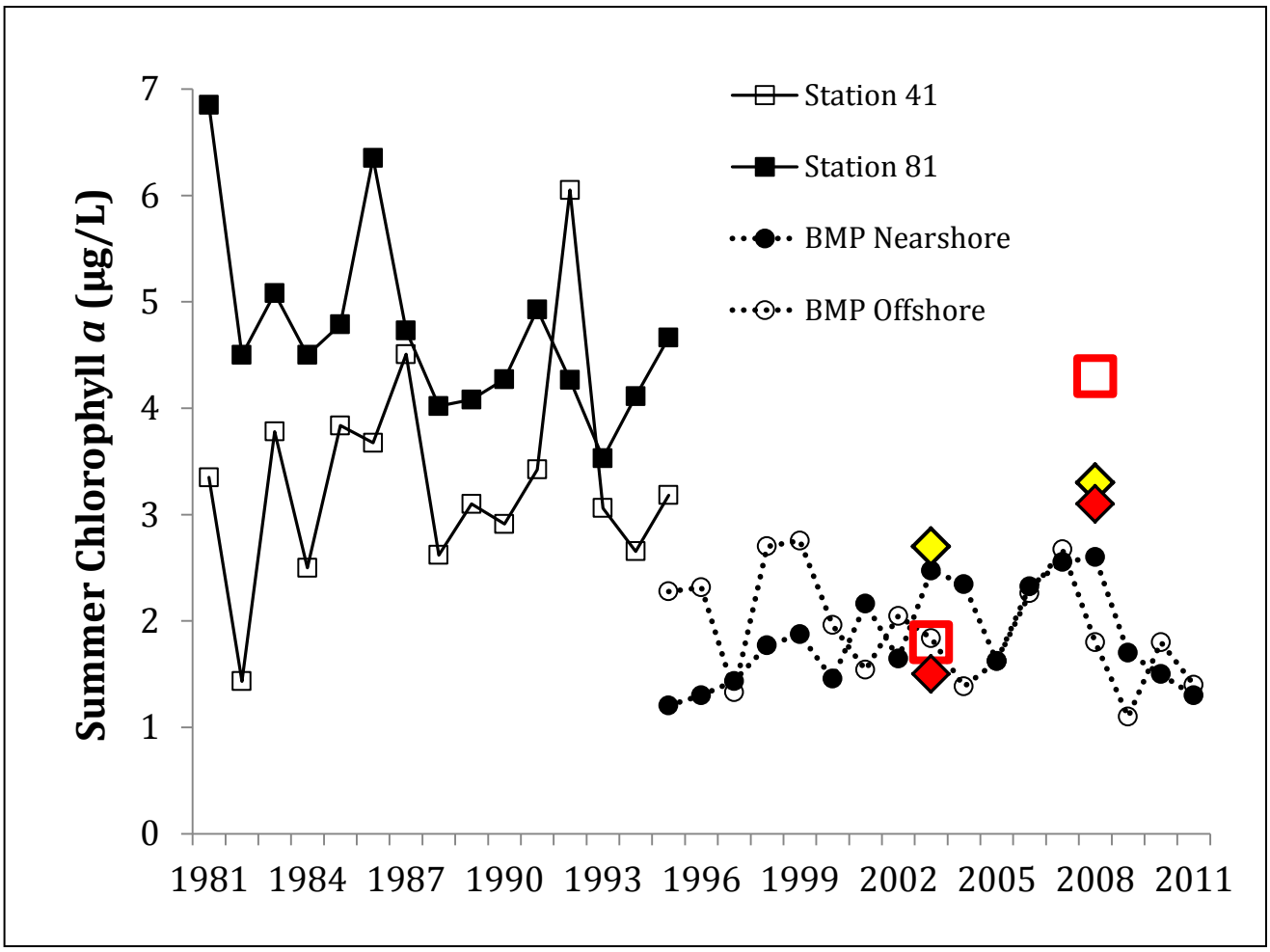

Figure 5. Long-term summer (Jul – Aug) epilimnetic chlorophyll-*a* concentrations in Lake Ontario, 1981 - 2011. Station 41 and Station 81 are from the Department of Fisheries and Oceans Canada's Bioindex Program. Data from 1995 – 2011 are from the US-BMP. LOLA data are from this report.

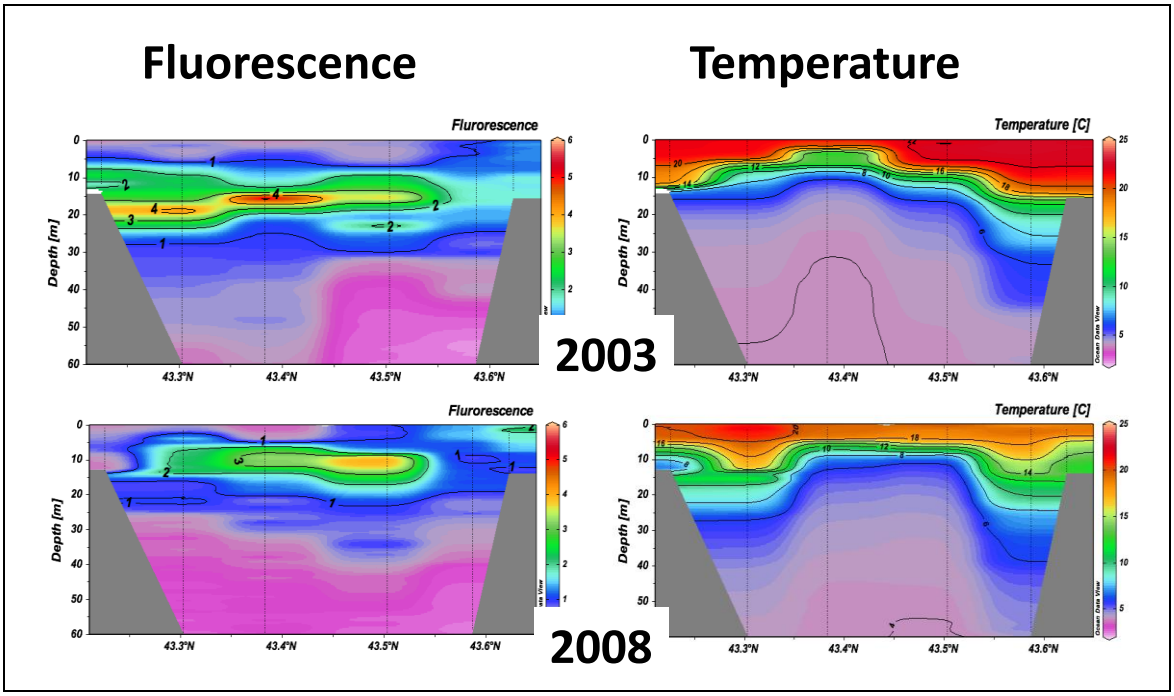

Figure 6. Fluorescence measures of chl-*a* along the western transect surveyed with SeaBird profiler in both 2003 (top panel) and 2008 (bottom panel) during the summer survey. Color scale indicates chl-*a* concentrations and is identical in both years. The DCL is evident in both 2003 and 2008 as a band of higher chloropohyll in 10-20 m deep water. Data plotted using Ocean DataView.

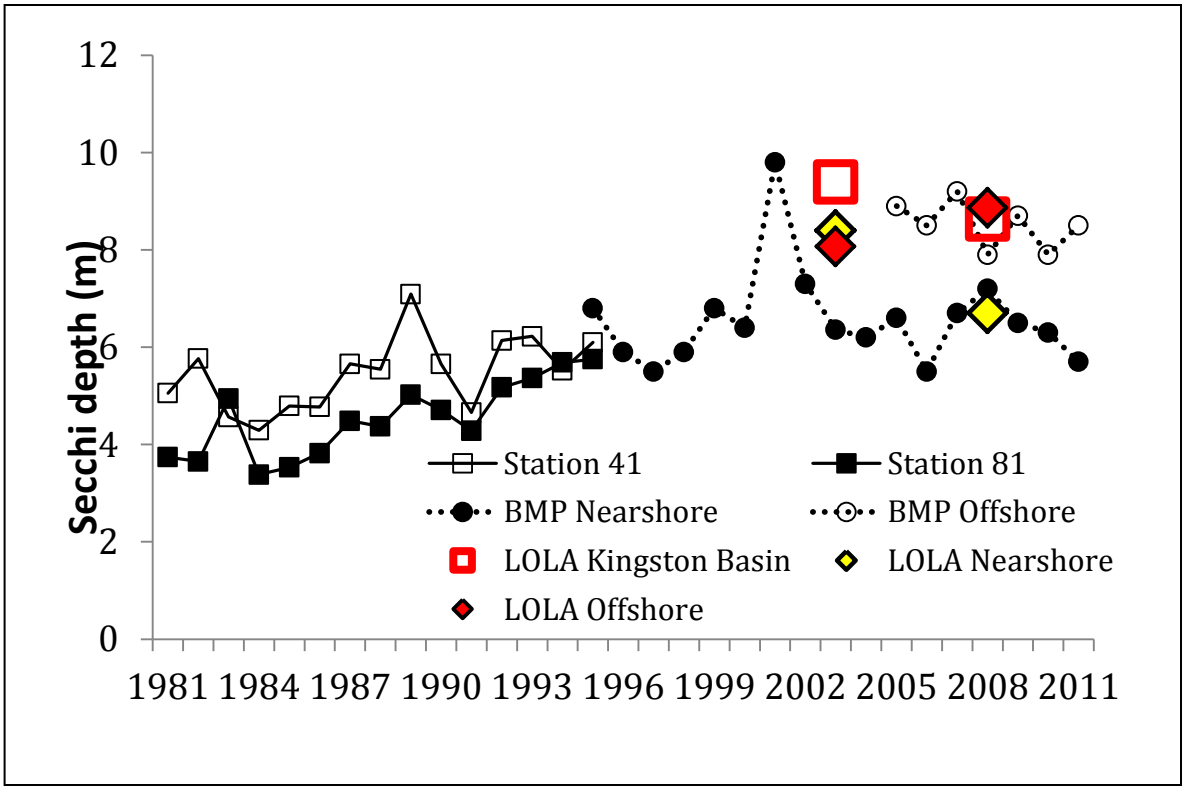

Figure 7. Long-term mean Apr/May – Oct Secchi depth (meters) in Lake Ontario, 1981 – 2011. Station 41 and Station 81 are from the Department of Fisheries and Oceans Canada's Bioindex Program. Data from 1995 – 2011 are from the US-BMP. LOLA data are from this report.

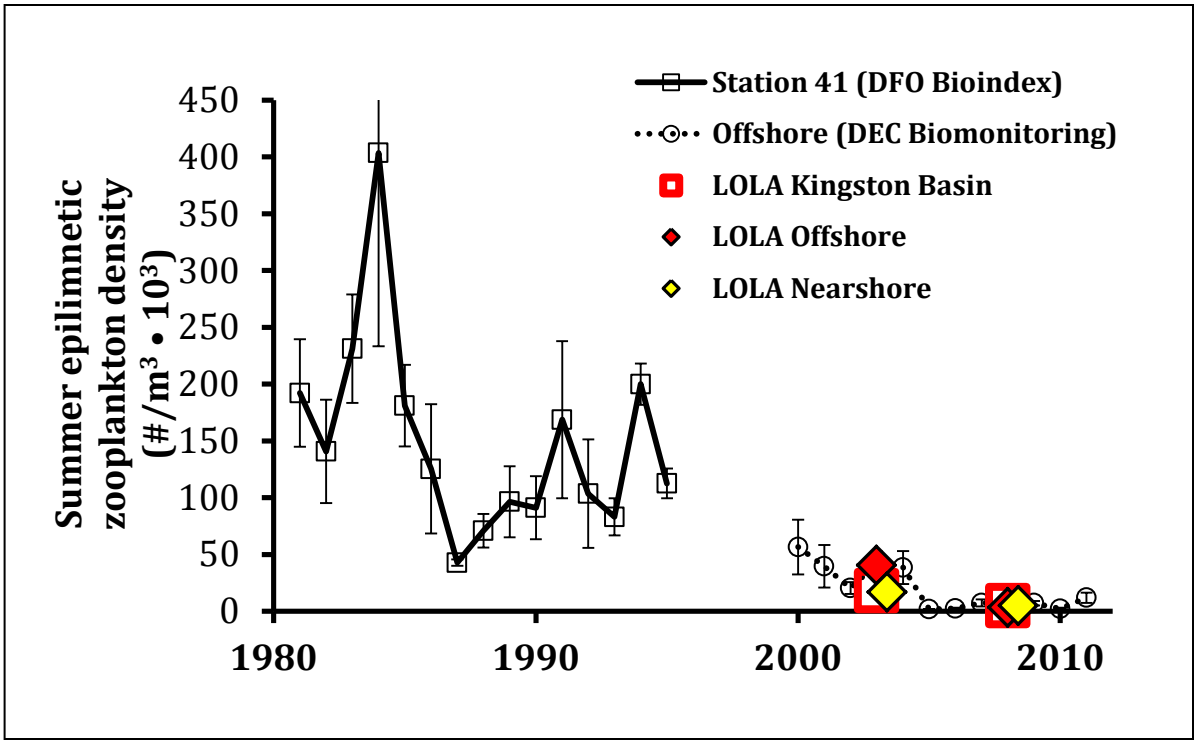

Figure 8. Mean summer epilimnetic zooplankton density in Lake Ontario's offshore, 1981 – 2011. Station 41 is from the Department of Fisheries and Oceans Canada's Bioindex Program. Data from 2000 – 2011 are from the US-BMP (day samples). LOLA data are from this report.

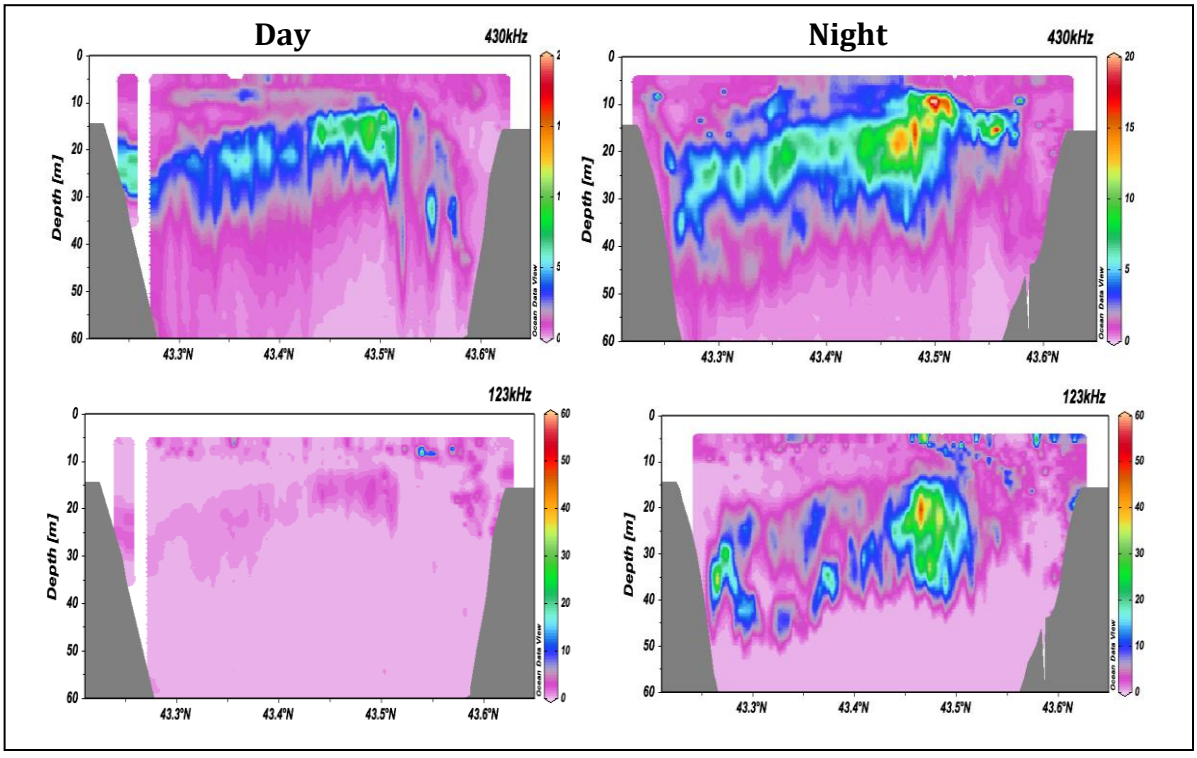

Figure 9. Depth distribution of acoustic backscattering at 430 kHz during the day (Upper panel, indicting zooplankton biomass) and 123kHz during the night (lower panel, mysis and zooplankton). Data is from the Niagara to Toronto transect which was surveyed both day and night in July 2008. Similar night time data for the whole lake are used to estimate mysid abundance with acoustics (see below).

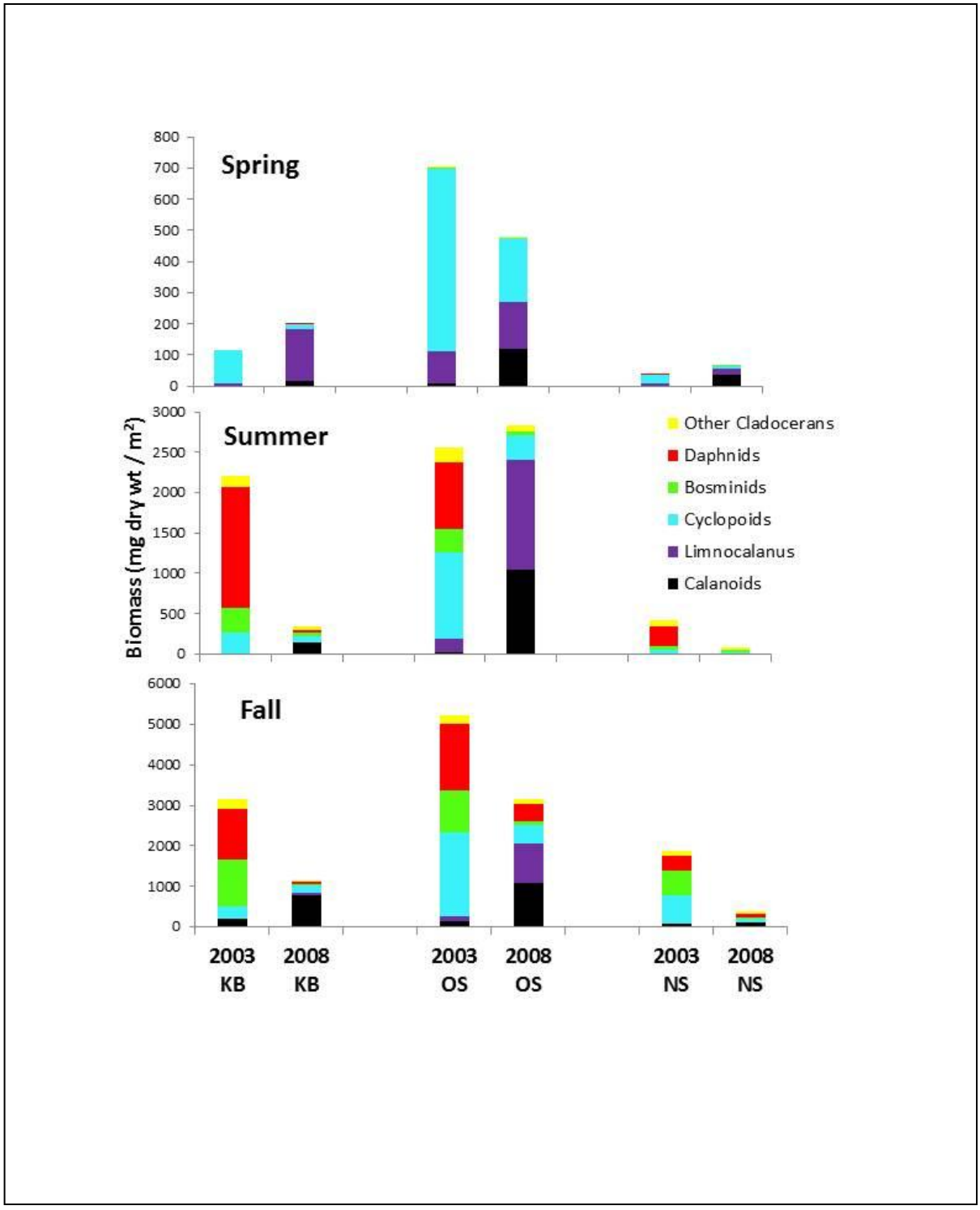

Figure 10. Lake Ontario zooplankton biomass (mg dry wt/m^2) in 2003 and 2008 in three regions (Kingston Basin, Offshore, and Nearshore). Biomass is divided by major groups.

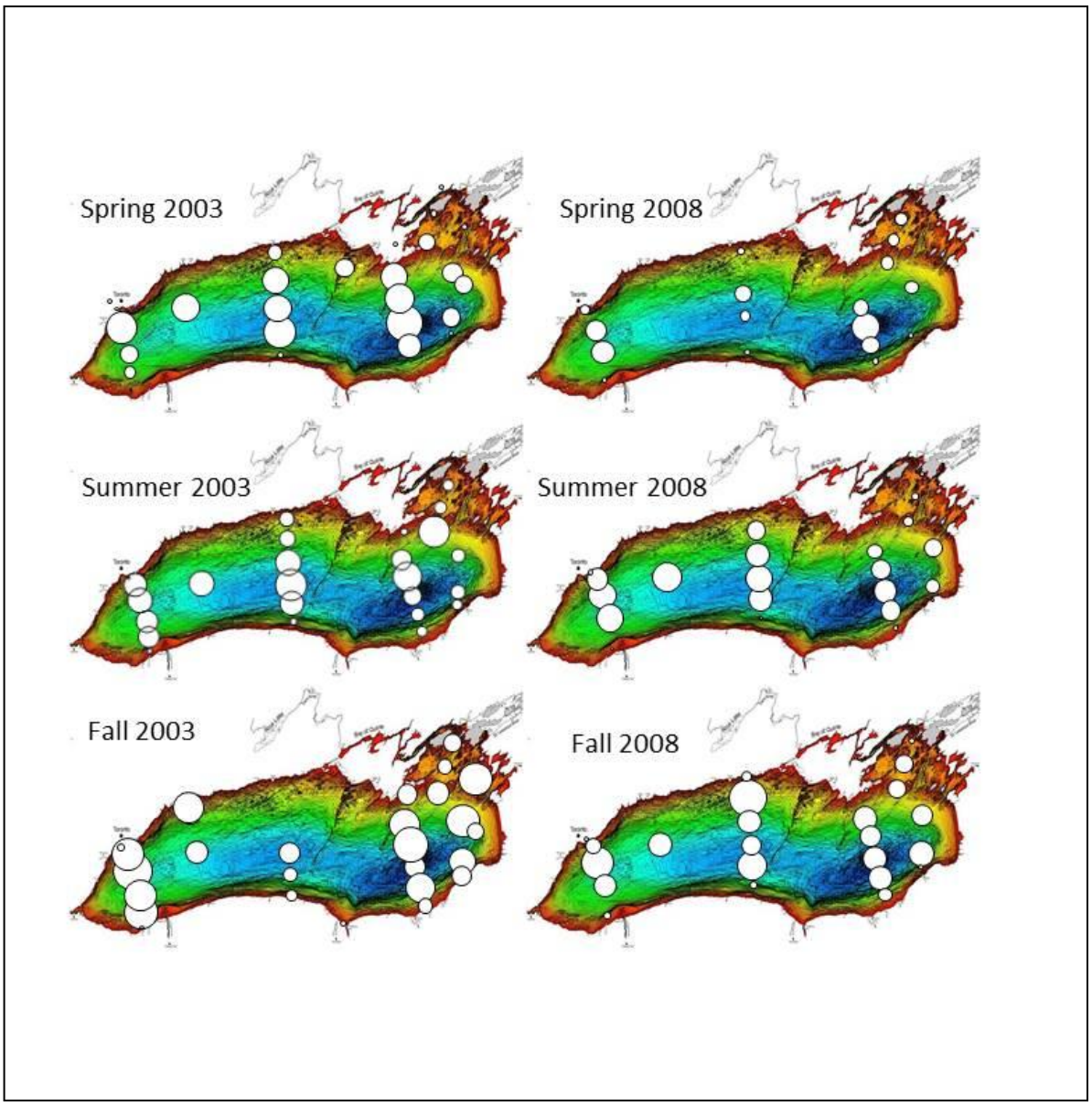

Figure 11. Zooplankton biomass distribution in whole water column nets in the three survey period in 2003 and 2008. Note that the size of the bubble does not represent the same biomass in each survey, rather it is relative to the maximum observed in each survey.

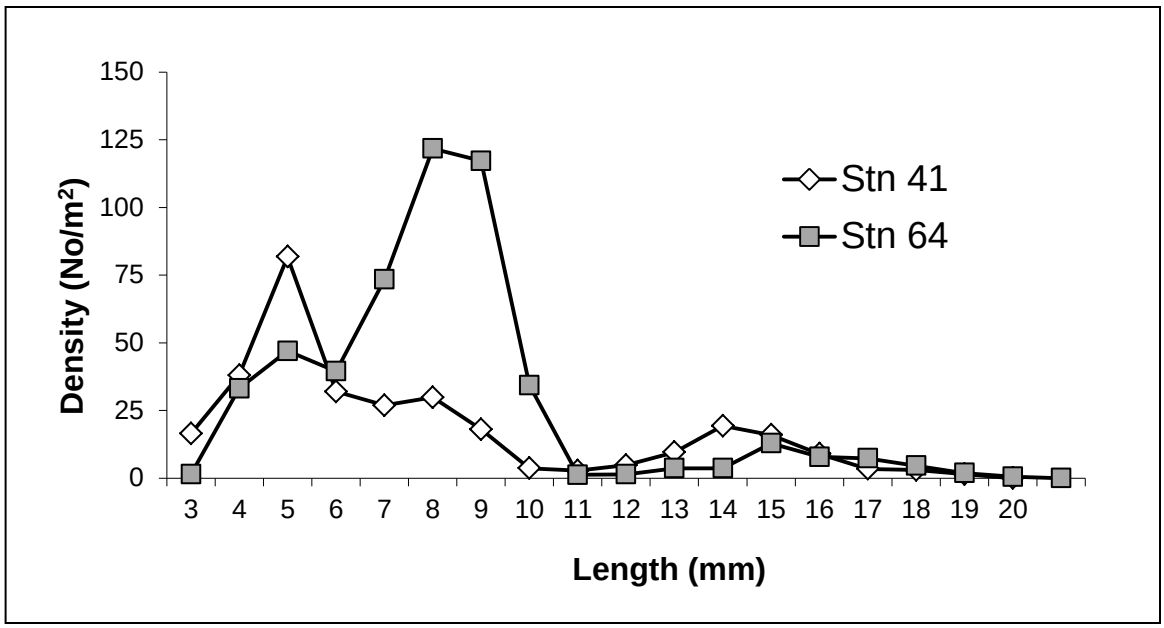

Figure 12. Length distribution of *Mysis diluviana* in the July 2008 samples at station 41 and 64. Length is standard length (tip of rostrum to end of the abdomen).

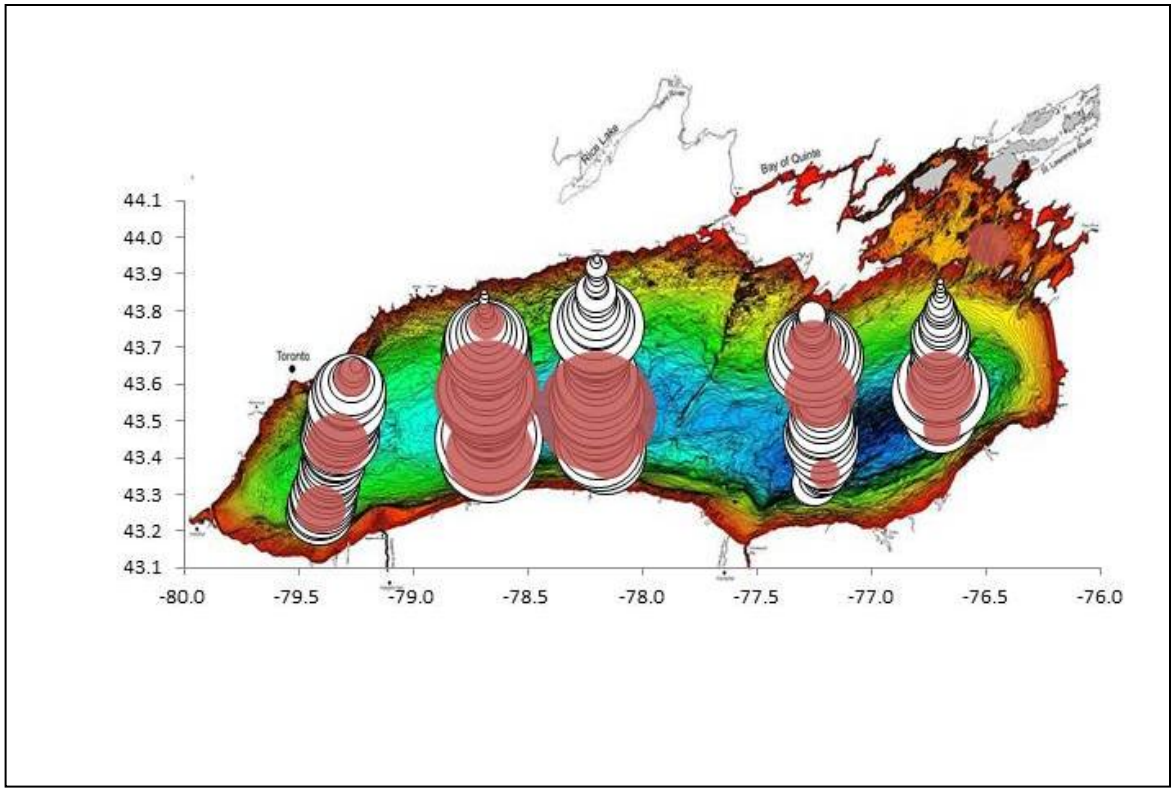

Figure 13. Spatial distribution of *Mysis diluviana* in Lake Ontario as measured with 120 kHz hydroacoustic surveys at night. Net tows are in maroon color with some transparency to also show the underlying acoustic data. Area of the bubbles are relative, the largest bubble size represent 992 individuals/m^2 (net tow). Net tows and acoustic areal densities are on the same scale.

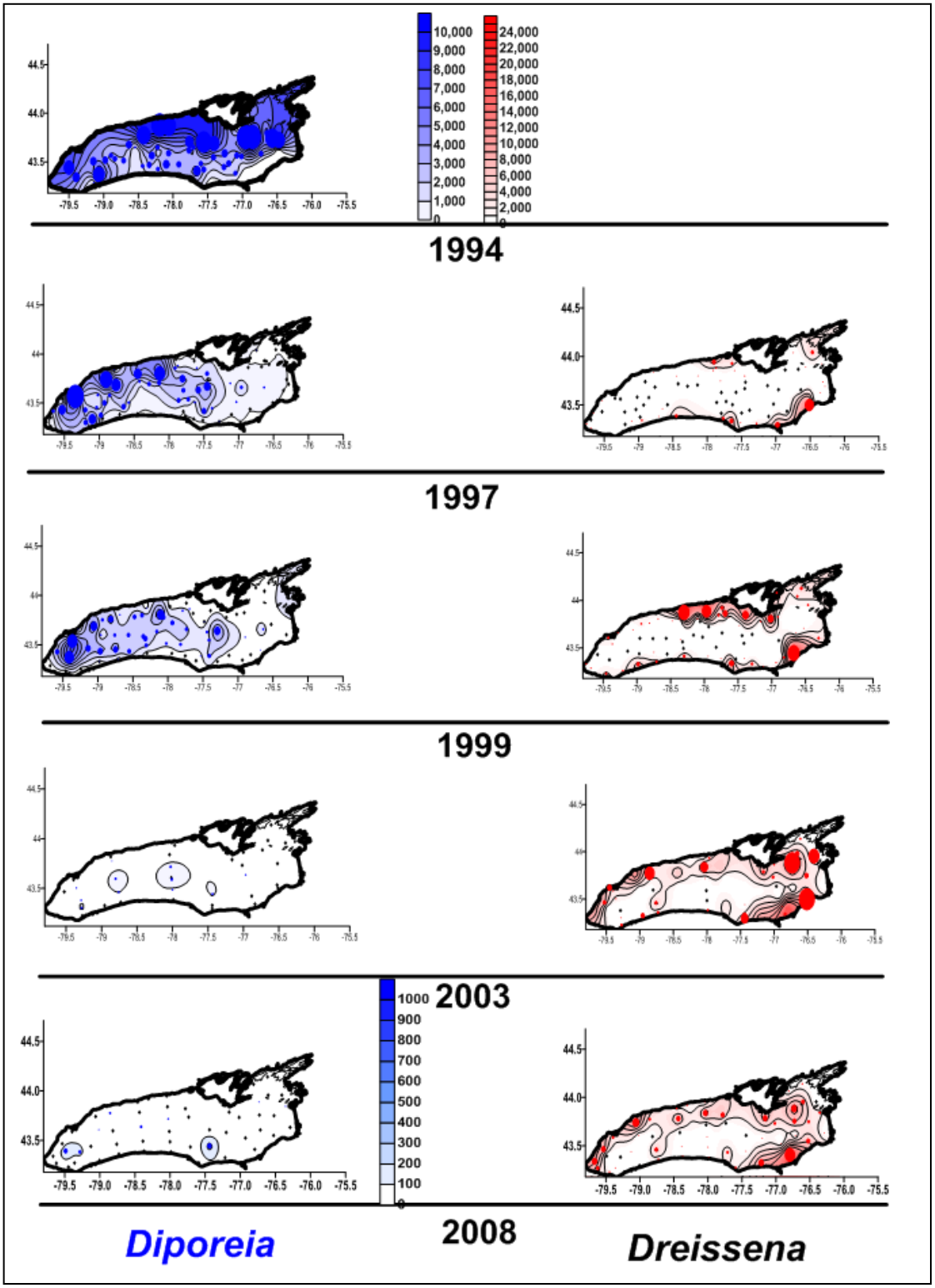

Figure 14. Contour maps of densities of *Diporeia* and *Dreissena* are displayed for the years between 1994 and 2008. Contours of *Diporeia* density are scaled from 0 to 10,000/m^2 for 1994 to 2003 and from 0 to 1,000/m^2 in 2008. Dreissena are scaled from 0 to 25,000/m^2. From Lozano (2011).

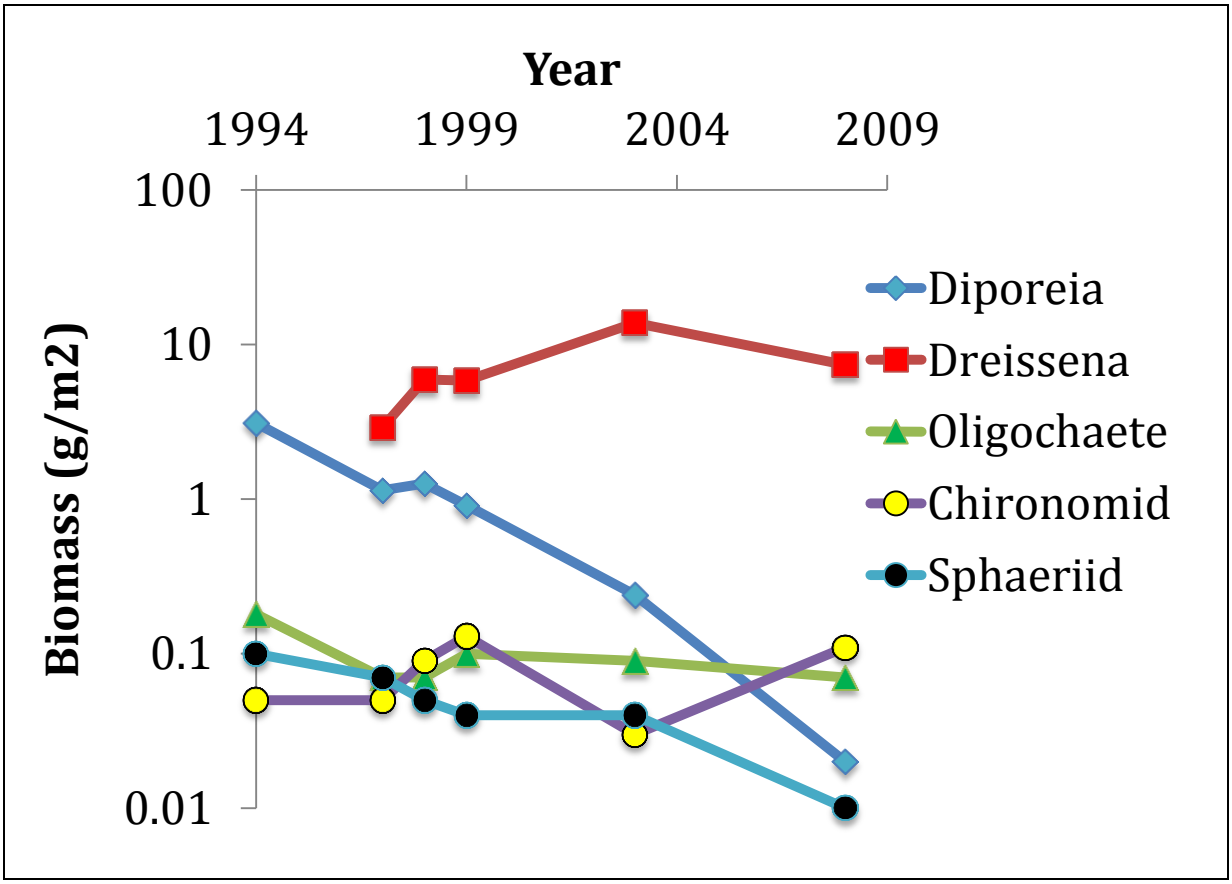

Figure 15. Time trend of major benthic invertebrate groups from 1994 to 2008 in Lake Ontario. From Lozano (2011).

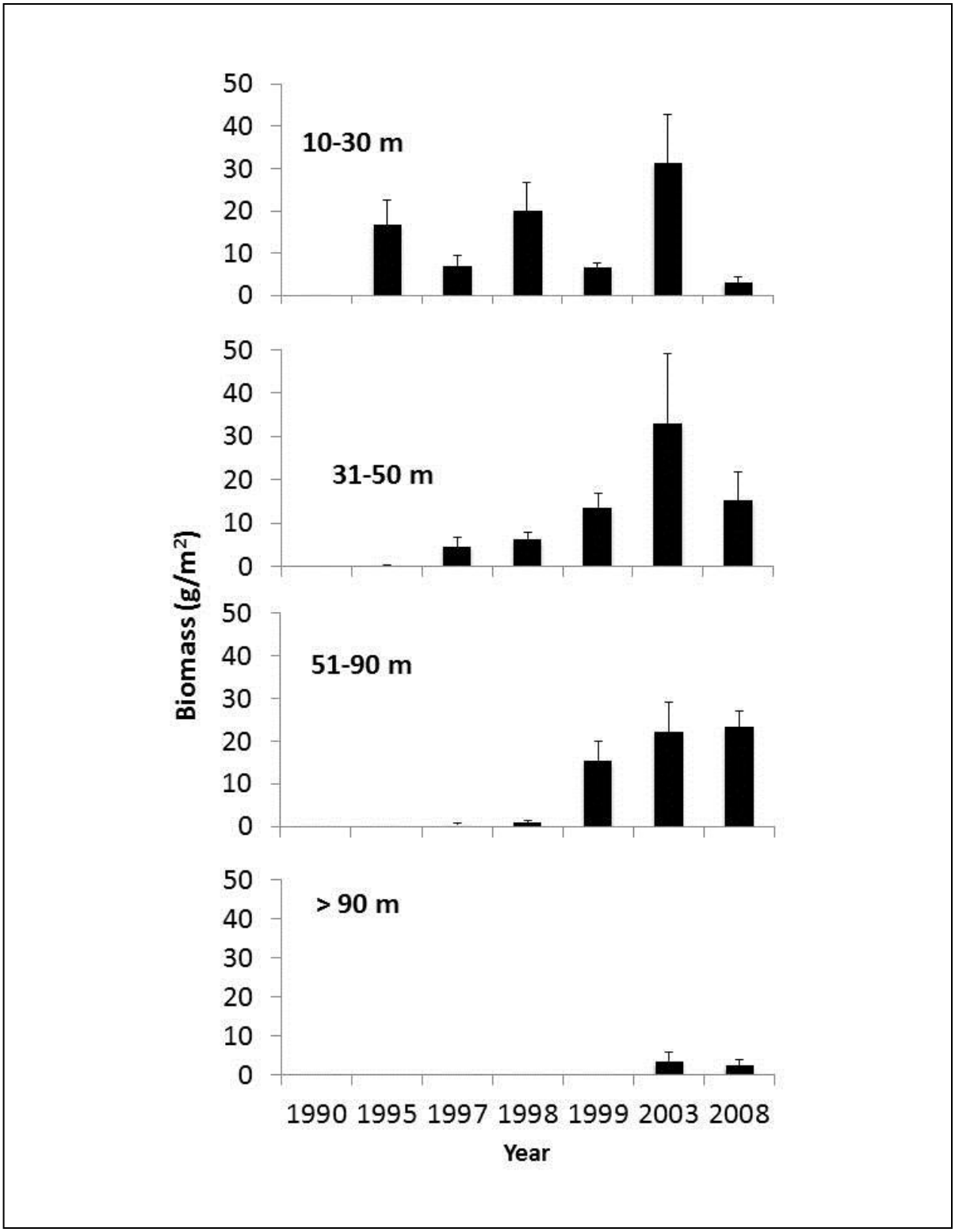

Figure 16. Time trends in quagga mussel biomass in Lake Ontario from 1997 to 2008 in four depth layers. From Lozano (2011).

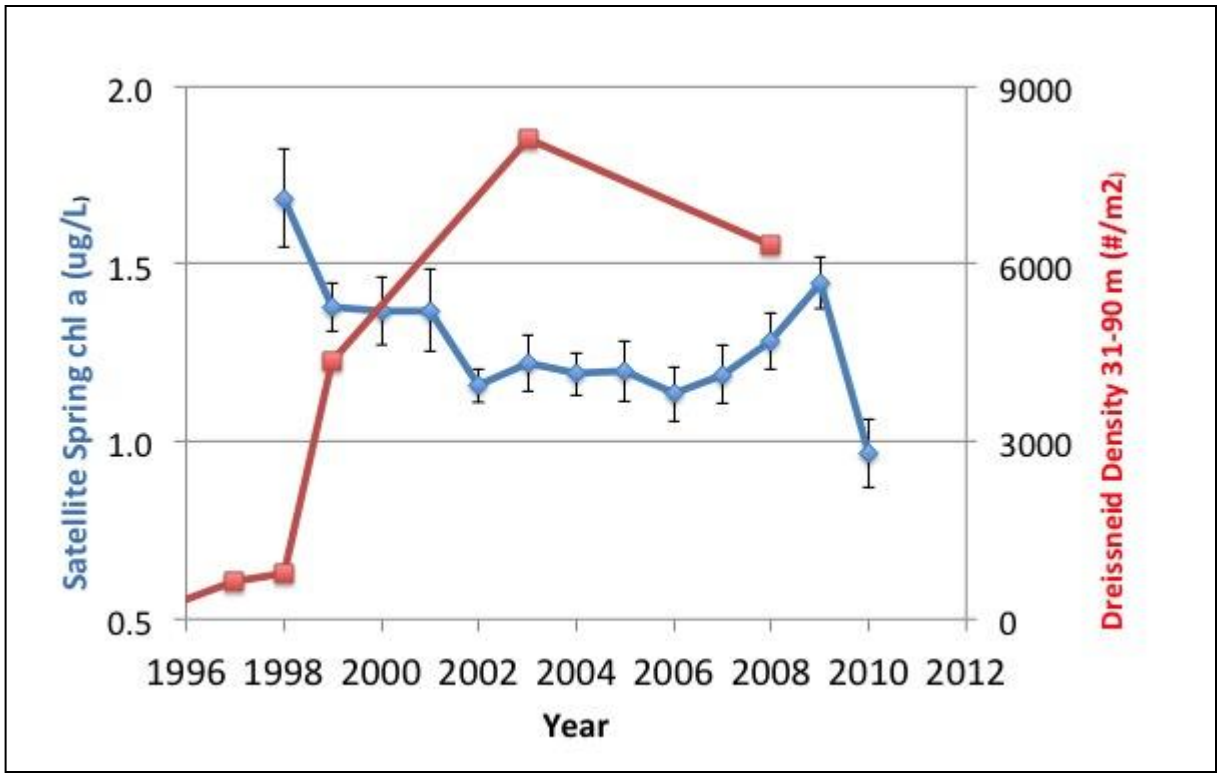

Figure 17. Spring chlorophyll-*a* (blue) based on satellite data from 1998 – 2010. Satellite data from the SeaWIFS platform (Level 2 GAC, 4 km resolution) for Lake Ontario were downloaded from the Ocean Color Web Page (http://oceancolor.gsfc.nasa.gov, details in Watkins 2009). Dreissenid density is in the 30-90 m depth layer.

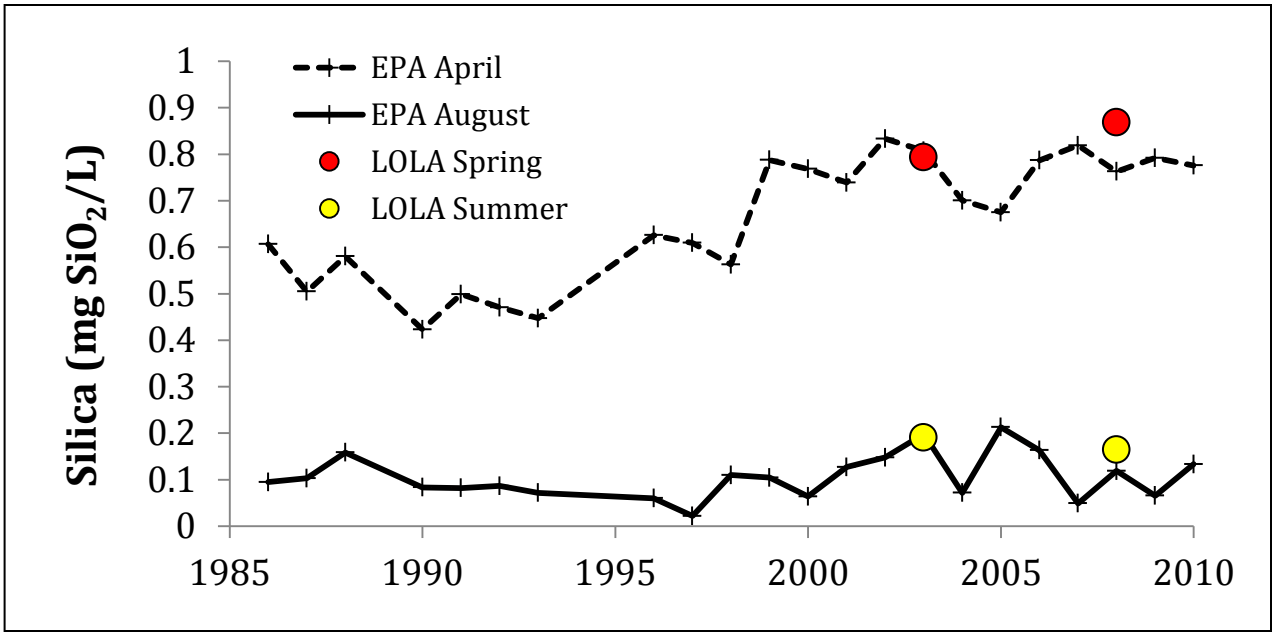

Figure 18. Concentration of SRSi (µg SiO_2/L) in April and August surveys (Source: EPA-GLENDA database).