The Lake Ontario Zooplankton Community before (1987–1991) and after (2001–2005) Invasion-Induced Ecosystem Change

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ABSTRACT

We assessed changes in Lake Ontario zooplankton biomass, production, and community composition before (1987–1991) and after (2001–2005) invasion-induced ecosystem changes. The ecosystem changes were associated with establishment of invasive dreissenid mussels and invasive predatory cladocerans (*Bythotrephes* and *Cercopagis*). Whole-lake total epilimnetic plus metalimnetic zooplankton production declined by approximately half from 42.45 (g dry wt·m^{-2}·year^{-1}) during 1987–1991 to 21.91 (g dry wt·m^{-2}·year^{-1}) in 2003 and averaged 21.01 (g dry wt·m^{-2}·year^{-1}) during 2001–2005. Analysis of two independent data sets indicates that the mean biomass and biomass proportion of cyclopoid copepods declined while the same measures increased for the invasive predatory cladocerans. Changes in means and proportions of all other zooplankton groups were not consistent between the data sets. Cyclopoid copepod biomass and production declined by factors ranging from 3.6 to 5.7. Invasive predatory cladoceran biomass averaged from 5.0% to 8.0% of the total zooplankton biomass. The zooplankton community was otherwise resilient to the invasion-induced disruption as zooplankton species richness and diversity were unaffected. Zooplankton production was likely reduced by declines in primary productivity but may have declined further due to increased predation by alewives and invasive predatory cladocerans. Shifts in zooplankton community structure were consistent with increased predation pressure on cyclopoid copepods by alewives and invasive predatory cladocerans. Predicted declines in the proportion of small cladocerans were not evident. This study represents the first direct comparison of changes in Lake Ontario zooplankton production before and after the invasion-induced disruption and will be important to food web-scale investigations of invasion effects.

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Introduction

During the 1990s, invasive species disrupted the Lake Ontario food web (Mills et al., 2003; O'Gorman et al., 2008; Stewart et al., 2009). The disruption may have changed the zooplankton community. Some of the changes have been documented (Johannsson, 2003; Warner et al., 2006; Holeck et al., 2008), but to date, analyses have been insufficient to allow for comparison of whole-lake scale changes in annual zooplankton production associated with invasion. Previous studies only examined changes to zooplankton production up to 1995 (Rand et al., 1995; Kuns and Sprules, 2000; Johannsson, 2003). Additionally, Rand et al. (1995) concluded that the consumptive demand of planktivorous prey fish paradoxically exceeds zooplankton production in Lake Ontario by a factor of 1.7, without accounting for invertebrate consumption of zooplankton, suggesting possible underestimation of zooplankton production.

Studies have yet to fully examine changes to Lake Ontario zooplankton species richness and diversity associated with developing populations of the predatory cladocerans *Cercopagis pengoi* and *Bythotrephes longimanus.* Earlier assessments excluded Lake Ontario as *Bythotrephes* abundance was low (Makarewicz and Jones, 1990; Johannsson et al., 1991; Barbiero and Tuchman, 2004). Since that time, *Bythotrephes* abundance remains low, but *Cercopagis* has become well established (Holeck et al., 2008). In Lake Michigan, predation by alewife is likely limiting *Bythotrephes* abundance but not *Cercopagis* (Pothoven et al., 2007), and this may also be the case in Lake Ontario. *Bythotrephes* and *Cercopagis* consume cyclopoid copepods and cladocerans (Wahlstrom and Westman, 1999; Benoit et al., 2002; Laxon et al., 2003). Declines in the abundance of small cladocerans and cyclopoid copepods in Lake Ontario, after 1997, were attributed to *Cercopagis* predation (Laxon et al., 2003; Warner et al., 2006), but the impacts on species diversity and richness have not been assessed. Cyclopoid

copepods and small cladocerans are also eaten by alewife (Urban and Brandt, 1993; Mills et al., 1992; Stewart et al., 2009). It was predicted that combined predation by alewife and invasive predatory cladocerans would further shift the zooplankton community structure and may cause disproportionate reductions in the abundance of cyclopoid copepods and small cladocerans (Stewart et al., 2009). Updated and improved estimates of annual zooplankton production and species composition before and after invasive species disruption are needed to evaluate these hypothesized effects and to facilitate food web scale studies (Halfon et al., 1996; Rand et al., 1995).

The objectives of this study were to assess changes in the magnitude of zooplankton group biomass and production for two 5-year reference time periods before (1987–1991) and after (2001–2005) the invasive-induced disruptive influences on the Lake Ontario food web. Improvements were made to previous estimates of Lake Ontario zooplankton production by correcting for species-specific variation in metalimnetic production, included estimates of overwinter production, and accounted for temperature-mediated whole-lake spatial variation in production rates. Upper water column (epilimnion plus metalimnion) zooplankton group biomass and production for the whole-lake was estimated directly during 1987–1991. Changes in biomass ratios between 1987–1991 and 2001–2005 were used to calculate production during the post-disruption time period. Potential changes in zooplankton group biomass were assessed by comparing data collected during 1987–1991 and 2001–2005. In doing so, we tested the hypotheses that 1) zooplankton group biomass and total biomass declined after the food web disruption, and 2) the structure of the zooplankton community changed after the disruption altering the biomass proportions among zooplankton groups and changing species diversity and richness.

Methods

Zooplankton sampling

Zooplankton data were from several sources (Table 1). Detailed sampling methods are described in the source publications and are only described briefly here. Only data from epilimnetic sampling of the zooplankton community was used as it was the most frequently employed method. Monthly (April to October) south-shore data were derived from the United States Geological Survey and Cornell University (USGS-Cornell) biomonitoring program during 1987–1991 and 2001–2005 (Johannsson et al., 1991; Holeck et al., 2008). Seasonal (spring, summer, fall) data were also available from the Lake Ontario Lower Aquatic Food Web Assessment (LOLA) studies conducted during 2003 (Holeck et al., 2008). Temporally intensive data collected weekly (April to October) at two stations during 1987–1991 came from the long-term biomonitoring program conducted by the Department of Fisheries and Oceans Canada (DFO; Johannsson et al., 1998; Johannsson, 2003). A subset of the temporally intensive DFO data (1987–1991) was selected to create a seasonal data set (spring, summer, and fall) that matched the same weeks of sampling as the LOLA 2003 seasonal sampling (Table 1).

The spatial distribution and bathymetric depths of the sampling sites varied among programs (Fig. 1). The USGS-Cornell biomonitoring program sampled zooplankton 2 km from the south shore (20 to 26-m bathymetric depth) and 20 km from the south shore (190 to 210-m bathymetric depth) at two locations, one off Oak Orchard, 72 km east of the mouth of the Niagara River, and the other off Smoky Point, 66 km east of Oak Orchard. The LOLA program had the most spatially extensive data sets with sampling sites throughout the lake and station bathymetric depths ranging from 10 to 221-m (Fig. 1). Using the same methods as the LOLA program, the DFO program sampled zooplankton at Station 81 (34-m bathymetric depth) in eastern Lake Ontario and at station 41 (128-m bathymetric depth) near the center of Lake Ontario (Fig. 1).

Zooplankton species were categorized as small cladocerans (Bosminidae, Chydoridae, *Ceriodaphnia* sp., *Diaphanosoma* sp., *Alona* sp.), large cladocerans (*Daphnia sp.*, *Leptodora kindtii, Macrothrix laticornis, Holopedium* sp.), invasive predatory cladocerans (*Bythotrephes longimanus, Cercopagis pengoi*), calanoid copepods, and cyclopoid copepods. Proportions of the copepod nauplii were added to the biomass of adult calanoid and cyclopoid copepods based on the relative proportions of the adults. Rare harpacticoid copepods were not included in the analysis. Data were not available to adequately assess changes in rotifer and dreissenid veliger biomass, so they were excluded.

Only the USGS-Cornell data set was used for the analysis of species richness and diversity because sites, seasonal sampling intensity, and counting and identification methods were identical between time periods. Copepodites, nauplii, individual *Daphnia sp.* that could not be assigned to a specific species, and harpacticoid copepods were excluded. The Shannon–Weiner diversity index was calculated using zooplankton species density as measure of abundance. Species diversity and richness were compared among time periods, with and without inclusion of the invasive predatory cladocerans, using a nonparametric Mann-Whitney U test for independent samples ($\alpha = 0.05$) corrected for multiple-comparisons using a sequential Bonferroni procedure (Quinn and Keough, 2003).

Metalimnetic corrections

Zooplankton inhabit water below the epilimnion and were not captured by the sampling protocols, the extent of which varies with species group. As the epilimnion seasonally deepens, the percentage of the total water column zooplankton population captured by epilimnetic sampling increases. In Lake Ontario, metalimnetic production can account for 10 to 56% of the total annual water column zooplankton production (Kuns and Sprules, 2000) and needs to be accounted for when calculating whole-lake production. Data from 1986 and 1987 were used to develop functions to correct the 1987–1991 DFO data for the presence of animals below our epilimnetic sampling depths. On four

Table 1
Summary of data sets used in the analysis (see text for more details).

Program	Years	Season	Dates	Samples	Sampling method	
					Sampling depth	Mesh (μm)
DFO	1987–1991	Biweekly	April 03–October 30	255	epilimnion or 20-m	64
DFO Subset	1987–1991	Spring	April 24–May 7	19	epilimnion or 20-m	64
DFO Subset	1987–1991	Summer	August 10–August 20	19	epilimnion or 20-m	64
DFO Subset	1987–1991	Fall	September 16–September 27	14	epilimnion or 20-m	64
LOLA	2003	Spring	April 28–May 3	29	epilimnion, or 20-m, or 2-m above bottom	64
LOLA	2003	Summer	August 10–August 21	28	epilimnion, or 20-m, or 2-m above bottom	64
LOLA	2003	Fall	September 21–September 25	29	epilimnion, or 20-m, or 2-m above bottom	64
USGS-Cornell	1987–1991	By Season	April–May, June, July–August, September, October[a]	97	epilimnion, or 50-m, or 2-m above bottom	153
USGS-Cornell	2001–2005	By Season	April–May, June, July–August, September, October	93	epilimnion, or 40-m, or 2-m above bottom	153

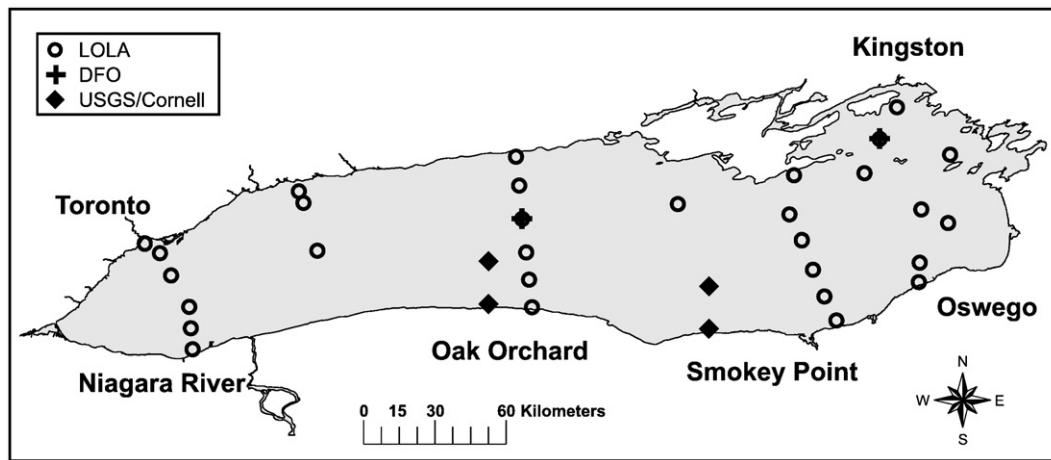[a] One sample was collected Nov 1 and included in October samples.

Fig. 1. Map of Lake Ontario showing zooplankton sampling sites (USGS is the United States Geological Survey-Cornell University, LOLA is the Lake Ontario Lower Aquatic Food Web Assessment and DFO is the Department of Fisheries and Oceans, Canada).

occasions between July 1 and September 30 1986 and twice in July 1987, zooplankton vertical profiles were determined during the day and night at stations 41 and 81 using a combination of a vertical tow (64-μ mesh, 50-cm diameter, metered net) through the epilimnion and five discrete-depth samples (41-L Shindler–Patalas trap, 75-μ sock) through the metalimnion. The percentage of each species which resided in the epilimnion was calculated as the areal abundance (no./m^2) of that species in the epilimnion divided by the sum of the areal abundances in the epilimnion and metalimnion, multiplied by 100. When the percentages of each species in the epilimnion were examined with respect to the mixed depth, similar patterns were observed at both stations, with only *Daphnia retrocurva* and *Diacyclops thomasi* undergoing distinct diurnal vertical migrations. Consequently, all data for each species were considered in the analyses of these vertical patterns with the exception of *D. retrocurva* and *D. thomasi* where only daytime data were examined; all DFO samples during 1987–1991 were collected during daylight hours.

The relationship between the percentage in the total epilimnetic and metalimnetic population captured as a function of sampling depth was described with the model

$$\log(\%) = a + b \cdot (\text{depth}) \tag{1}$$

where log (%) is the natural log of the percentage of the total epilimnetic and metalimnetic population found in the epilimnion, a is a constant and b is the slope, and depth is the depth of the mixed layer. The model was fit to the data using a generalized linear model (GLZ, STATISTICA, StatSoft Inc.) using a log linking function and assuming a Poisson error term (Quinn and Keough, 2003). It was assumed that the relationship only applied to a threshold depth, where it was observed that the percentage captured reached a plateau and did not vary with depth. Corrections were determined using the equation for depths less than the threshold depth, and mean percentage correction was used for depths equal to or greater than the threshold depth. The threshold depth was determined to the nearest 0.5-m by visually inspecting plots of the data. The plateau percentage was estimated as the mean of the observed percent captured of all observations beyond the plateau depth. Species-specific equations were developed for *Ceriodaphnia lacustris, Eubosmina coregoni, Bosmina longirostris, Daphinia retrocurva,* and *Diacyclops thomasi.* Data were combined for all small cladoceran species to develop a general small cladoceran correction function. The correction function developed for *Daphinia retrocurva* was applied to all large cladocerans. Correction functions were developed and applied for all species combined within other zooplankton groups: cyclopoid copepods, calanoid copepods, cyclopoid nauplii, and calanoid nauplii.

To estimate zooplankton biomass, species-specific, aerial epilimnetic densities were determined from the data in Johannsson et al. (1998) for the approximately weekly samples from April to October 1987–1991 for stations 41 and 81. During the stratified period, sample depth and the species or species-group correction functions were used to estimate the animals in the metalimnion. Total density was multiplied by species-specific mean dry weights based on Lake Ontario length–weight relationships and size-frequency distributions for the dominant species tabulated from published sources (Stockwell and Johannsson, 1997; Johannsson and O'Gorman, 1991) and unpublished data from the Department of Fisheries and Oceans, Burlington, Ontario, Canada.

Production 1987–1991

Annual production during 1987–1991 was calculated as the product of daily zooplankton group biomass and the daily production to biomass (P/B) ratios summed over a year (April through to the end of March). Daily P/B ratios were calculated from estimates of the daily isothermal mixed layer temperature and P/B–temperature relationships (Shuter and Ing, 1997). Daily mixed-layer isothermal temperatures were estimated from a spatially explicit empirical model (Appendix A).

Daily biomass estimates for each station were determined by interpolating between sampling events assuming exponential rates of population biomass change between weeks. Species-specific intrinsic rates of increase or decrease (r) were estimated as

$$r = \frac{\ln(B_t + 1) - \ln(B_0 + 1)}{n} \tag{2}$$

where B_0 is the biomass (mg dry weight·m^{-2}) at the beginning of the interpolation interval, B_t is the biomass at the end of the interpolation interval, and n is the size of the interpolation interval in days. Daily biomass from October 31 to April 1 the next year was estimated by assuming an exponential decline in biomass from October to April. In this case, species-specific intrinsic rates of population decline (r-values) were determined using the same formula where B_0 was the average October biomass and B_t was the average April biomass the following year.

The bathymetry of Lake Ontario was described using a 2-km^2 grid system (Robertson and Jordan, 1972) of 4621 spatially referenced cells with an estimated mean bathymetric depth. Using the spatially explicit empirical temperature models (Appendix A), temperature of the mixed layer was estimated as the average temperature from 0 to 5 m for each cell, biweekly for each year (1987–1991) from April to October. The models allowed us to estimate the biweekly average mixed-layer temperature independently for each of the 4621 cells

each year. The year effect on temperature is represented in the model by the inclusion of biweekly, year-specific, mid-lake temperatures (Appendix A). For the other months, the average monthly mixed layer water column temperatures was assigned to each cell based on average near-surface temperatures measured from 1962 to 2002 (Stewart and Bowlby, 2009). Daily temperatures were estimated by linear interpolation between biweekly or monthly estimates.

The mixed layer depth is shallower during July in the west region of Lake Ontario (Stewart and Robertson, 1991) and this spatial pattern was confirmed for other months (Appendix A; Table A5). It was assumed therefore that the daily zooplankton group biomass of station 41, which had cooler water and shallow thermocline depths was representative of western Lake Ontario and the zooplankton group biomass of station 81, with warmer water and deeper thermocline depths, was representative of eastern Lake Ontario (see Appendix A for delineation of eastern and western Lake Ontario).

Daily production for each bathymetric cell was estimated as the product of the daily zooplankton group P/B and the daily biomass (either station 81 or 41). If the bathymetric depth of a cell was <20-m the areal estimate of production was reduced proportionately. Whole-lake zooplankton group and total annual production (g dry wt·m^{-2}·year^{-1}) was the weighted average of production of each cell, using the number of cells as weights.

Changes in biomass, community structure, and production

Relative changes in zooplankton group biomass over time were assessed by comparing USGS-Cornell data from 1987 to 1991 and 2001 to 2005 (Table 1). These data were collected and processed using the same protocols (e.g., common counting methods and length–weight curves applied during both time periods). The 2003 LOLA seasonal epilimnetic zooplankton group biomasses were also compared to a 1987–1991 subset of the DFO data. The DFO subset included data only for stations 81 and 41 with sampling dates chosen to match the sampling weeks of the LOLA data (Table 1). For this comparison, neither data set was corrected for animals not sampled below the epilimnion. Unfortunately, taxon length to weight conversions or means applied to the 1987–1991 to estimate biomass from density differed from those used for the 2003 LOLA data, so this comparison needs to be qualified. Also, the DFO sampling during 1987–1991 was at only two stations, while the 2003 LOLA sampling included 29 sites throughout the lake (Fig. 1). While not an ideal comparison, it provides a valuable independent validation of the general trends detected in the USGS-Cornell comparison.

Changes in zooplankton group biomass between time periods were assessed using simple means across all years, sites, and seasons. Like many comparative studies through time, making statistical inferences is complicated because time-series observations can be autocorrelated, may not be independent, and depending on the statistical model may represent pseudoreplication (*sensu* Hurlbert, 1984). To accommodate this concern, randomization tests (Quinn and Keough, 2003; Manly, 2007) were used to assess how sampling error might influence our estimates of time period means of total zooplankton biomass, zooplankton species-group biomass, and species group proportion. For both of the USGS-Cornell data bases all observation were resampled from each time period (all years combined) within five seasonal strata (April-May, June, July–August, September, October) 5000 times with replacement. For each resampling event, the number of samples drawn from each stratum matched the original number of observations. All years and sites were treated as one set of observations and resampled at random. The mean and the 2.5 and 97.5 percentiles derived from the distribution of samples were calculated for each metric. The same method was applied to the DFO versus LOLA comparison, except that there were only three seasonal strata (spring, summer, fall).

The null hypothesis that there was no difference in total zooplankton biomass, zooplankton species-group biomass, and species group proportion between 1987–1991 and 2001–2005 was tested by first estimating the original observed difference in the sample means between the two time periods for both sets of independent comparisons [USGS-Cornell samples collected during both time periods and the DFO (1987–1991) versus LOLA (2003)].

The difference between the means of each individual resample was calculated and subtracted the original observed mean. The absolute value of this difference was used to derive the random distribution to be expected if the null hypothesis was true (Manly, 2007). These distributions were used to determine the probability that the absolute values of the observed difference could have occurred by chance as measured by the distribution of the 5000 resampled observations. The null hypothesis was rejected if the probabilities were less than 0.05. Corrections for multiple-comparisons were done using a sequential Bonferroni procedure (Quinn and Keough, 2003) among the zooplankton groups within each set of independent comparison.

The 2003 LOLA data and the 2001–2005 USGS-Cornell data were not collected frequently enough to allow for direct estimates of production. However, the sampling designs were sufficient to measure relative changes in biomass. Therefore production was estimated for these time periods by assuming that changes in production would be directly proportional to changes in mean zooplankton group biomass. For example, if a zooplankton group biomass during 2003 was estimated to be 1/3 the biomass estimated for the same group during 1987–1991, than it was assumed that production of that zooplankton group during 2003 was 1/3 the production estimated for the same group during 1987–1991. The proportional change in zooplankton group biomass from 1987 to 1991 was estimated independently for 2003 and 2001–2005. For 2003, the changes in the mean total zooplankton and zooplankton group biomass from the 2003 LOLA data set were compared to the same estimates for the 1987–1991 DFO data subset (Table 1). For 2001–2005, the changes in the mean total zooplankton and zooplankton group biomass from the 2001–2005 USGS-Cornell data set were compared to the same estimates for the 1987–1991 USGS-Cornell data set (Table 1). The production of invasive predatory cladocerans was estimated by multiplying the estimate of large cladoceran production by the ratio of the mean biomass of invasive predator cladocerans to the mean biomass of large cladocerans.

This approach assumed that there was no change in the zooplankton group P/B ratios from those estimated in 1987–1991. The assumption of no temperature induced change in P/B ratios by was evaluated comparing April to October mid-lake temperatures (Stewart and Bowlby, 2009) during 1987–1991 and 2001–2005 using a factorial analysis of variance with mid-lake temperature as the dependent variable and month and time period as categorical predictor variables.

Results

Metalimnetic corrections

An example of the observed percent total population as a function of depth and the fitted correction function for *Eubosmina coregoni* (Fig. 2) is typical of the fitted function for other species and groups (Table 2). The percentage of *Tropocyclops extensus* captured was variable and no pattern was evident; however. we assumed this was due to sampling error. Therefore the general cyclopoid copepod correction function was applied to this species as it is a warm water species and likely follows a pattern similar to the other warm-water groups.

Production 1987–1991

Total whole-lake epilimnetic plus metalimnetic mean zooplankton production during 1987–1991 was estimated at 42.43 (g dry wt·m^{-2}·year^{-1}; Table 3). Production was dominated by cyclopoid copepods (26.00 g dry wt·m^{-2}·year^{-1}), followed by small cladocerans (9.08 g dry
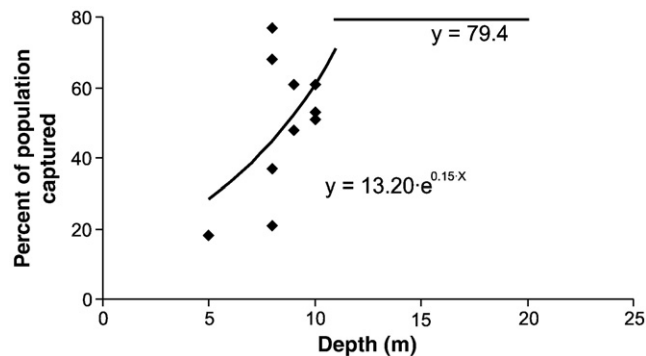
Fig. 2. The observed percentage of the total epilimnetic plus metalimnetic population of *Eubosmina coregoni* captured as a function of depth and the fitted correction function.

wt·m^{-2}·year^{-1}), large cladocerans (6.97 g dry wt·m^{-2}·year^{-1}), and calanoid copepods (0.38 g dry wt·m^{-2}·year^{-1}).

Changes in biomass, community structure, and production

The magnitude of change in biomass varied by zooplankton group and between data set comparisons. Total zooplankton biomass declined in the later time period by a factor of 1.9 to 2.0 compared to the early time period (Table 4). The analyses indicate that large cladoceran biomass did not change [USGS-Cornell P = 0.031, Sequential Bonferroni corrected (SBc) α = 0.025; DFO versus LOLA data set, P = 0.124; Table 4]. Small cladoceran biomass declined by a factor of 1.86 for the USGS-Cornell comparison (P = 0.013, SBc α = 0.017; Table 4), but no change was indicated by the DFO versus LOLA comparison (P = 0.629; Table 4). Calanoid biomass declined by a factor of 3.9 for the DFO versus LOLA data set (P < 0.001, SBc α = 0.008; Table 4), but there was no significant difference between time periods in the USGS-Cornell data sets (P = 0.726; Table 4). Cyclopoid copepods were the dominant zooplankton group, and biomass declined significantly in both data set comparisons by a factor of 3.6 to 5.7 (P < 0.001, SBc α = 0.008; Table 4).

The proportion of cyclopoid copepods decreased and invasive predatory cladocerans increased for both UGSG-Cornell and DFO-LOLA comparison (P < 0.001, SBc α = 0.008; Fig. 3). Cyclopoid copepods declined from an average of 49–52% of the biomass to 35–40% while invasive predatory cladocerans increased from a barely detectable proportion of the biomass (<0.03%, not shown) to an average of 5 to 8% of the biomass (Fig. 3). The proportions of other zooplankton groups did not change for the USGS-Cornell comparison (Fig. 3a), but the DFO-LOLA comparison indicated that the proportion

Table 2
Parameter estimates and statistics for the log-linear modelling of the % of the total epilimnion plus metalimnion population captured as a function of depth. See text for explanation of the intercept (a), slope (b), plateau and plateau %. The Wald statistics (1 df) and P-value apply to the slope.

Taxon	Intercept (a)	Slope (b)	Wald	P	Plateau Depth (m)	Plateau %
Ceriodaphnia lacustris	3.32	0.10	9.95	0.002	10.0	87.5
Eubosmina coregoni	2.58	0.15	18.53	<0.001	12.0	79.4
Bosmina longirostris	1.82	0.24	40.91	<0.001	11.0	74.0
Small cladocerans combined	2.58	0.16	65.65	<0.001	12.0	80.3
Daphnia retrocurva	2.62	0.16	8.18	0.004	12.0	85.7
Diacyclops thomasi	0.68	0.14	11.02	0.001	17.0	75.0
Other cyclopoid copepods	1.90	0.22	48.26	<0.001	11.5	71.5
Cyclopoid nauplii	0.17	0.25	141.62	<0.001	17.0	68.5
Calanoid copepods	2.53	0.08	20.99	<0.001	17.0	62.3
Calanoid nauplii	1.94	0.21	44.02	<0.001	12.0	75.5

Table 3
Mean areal zooplankton production for the time periods 1987–1991, 2003, and 2001–2005. The lower (L) 95% and upper (U) 95% refer to upper and lower 95% confidence intervals on the 1987–1991 mean (N = 5).

Zooplankton Group	Production (g/m^2/year)				
	1987–1991	L 95%	U 95%	2003 LOLA	2001–2005 USGS
Invasive cladocerans				0.47	0.79
Large cladocerans	6.97	5.05	8.88	5.57	4.29
Small cladocerans	9.08	6.74	11.42	9.78	4.87
Calanoid copepods	0.38	0.28	0.48	0.09	0.40
Cyclopoid copepods	26.00	20.46	31.55	4.54	7.24
Total	42.43	35.52	49.33	21.91	21.01

of calanoid copepods decreased and that the proportion of small and large cladocerans increased (P < 0.001, SBc α = 0.008; Fig. 3b).

Zooplankton species richness including the invasive predatory cladocerans ranged from 16 to 20 and species diversity ranged from 1.26 to 2.08 (Table 5). There was no significant difference in zooplankton species richness (P = 0.465; invasives included, P = 0.602; invasives excluded) or diversity (P = 0.047, SBc α = 0.017; invasives included, P = 0.08; invasives excluded; Table 5) between time periods.

The ANOVA model comparing April–October mid-lake temperatures during 1987–1991 and 2001–2005 indicated no significant time period effect (P = 0.351), validating our assumption of no temperature related changes in zooplankton group P/B. Changes to whole-lake annual zooplankton production (Table 3) are based directly on changes in the ratios of biomass between time periods (Table 4). Total production declined by approximately half from 42.43 (g dry wt·m^{-2}·year^{-1}) during 1987–1991 to 21.91 (g dry wt·m^{-2}·year^{-1}) during 2003 or 21.01 (g dry wt·m^{-2}·year^{-1}) during 2001–2005 (Table 3). The largest change in production was estimated for cyclopoid copepods which declined from 26.00 to an estimated 4.54 during 2003 and an average of 7.24 during 2001–2005 (Table 3). The production of large cladocerans was estimated to decline slightly in 2003 and during 1987–1991 (Table 3). Estimates of small cladoceran production derived from the changes in the USGS-Cornell biomass indicate a decline from 9.08 to 4.87 (g dry wt·m^{-2}·year^{-1}) while the DFO and LOLA comparison indicated virtually no change (Table 3). Calanoid production was estimated to decline by a factor of 0.38 to 0.09 (g dry wt·m^{-2}·year^{-1}) in 2003, but the USGS-Cornell data set comparison indicated no significant change in calanoid biomass (Table 4) or production from 1987–1991 to 2001–2005 (Table 3).

Discussion

This study compliments and extends earlier assessments of changes in Lake Ontario zooplankton biomass and production (Kuns and Sprules, 2000; Johannsson, 2003; Holeck et al., 2008). Our production estimates determined during 1987–1991 (95% CI 36–49 g dry wt·m^{-2}·year^{-1}) were higher than reported in previous studies. For example, using the egg-ratio method for Lake Ontario during 1987–1991, Johannsson (2003) estimated that seasonal epilimnetic production (June 15–October 31) ranged from approximately 8–19 (g dry wt·m^{-2}). Expansion of estimates to the entire year and the addition of species-specific estimates of metalimnetic production would result in higher estimates. Our application of daily spatially-explicit P/B ratios may be an improvement over the egg-ratio method applied by Johannsson (2003). The egg-ratio method only estimates growth after eggs are produced and can be influenced by the assumed timing of these events. The P/B ratio method estimates the growth of the population throughout the year. Kuns and Sprules (2000), using a combination of egg ratio and daily P/B ratio methods, estimated that epilimnetic plus metalimnetic

Table 4

Mean total zooplankton and zooplankton group biomass for each data set. The percentiles are the 2.5% and 97.5% percentile from the distribution of 5000 resampled observations. The ratio is the earlier time period mean divided by the later time period mean. The *P*-value is from the distribution of differences between the earlier and later time periods (see text for an explanation).
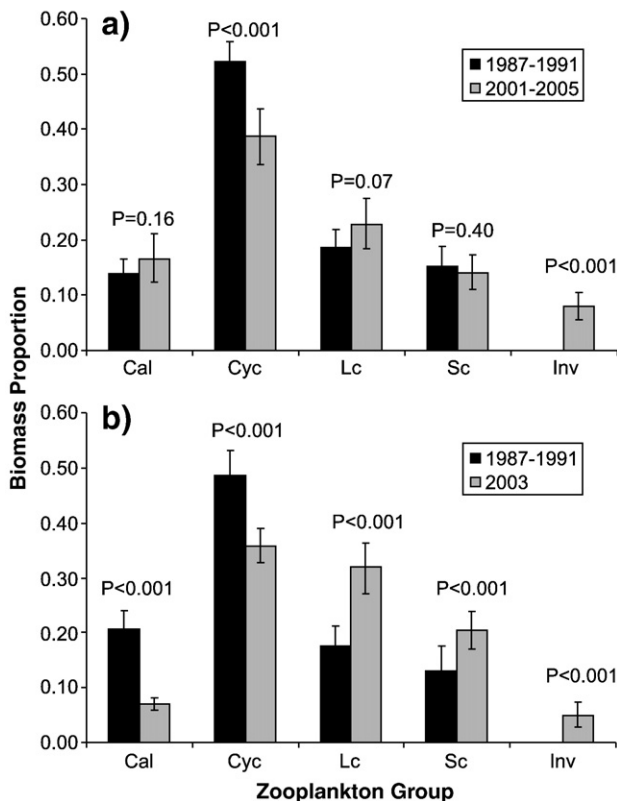
	Program	N	Total Biomass (μg/m³)	Calanoid Biomass (μg/m³)	Cyclopoid Biomass (μg/m³)	Large Cladoceran Biomass (μg/m³)	Small Cladoceran Biomass (μg/m³)	Invasive Cladoceran Biomass (μg/m³)
Mean	USGS-Cornell (1987–1991)	97	69.56	4.14	34.03	19.55	11.83	0.01
Percentiles			(56.56, 81.32)	(3.40, 4.92)	(27.53, 41.43)	(13.54, 26.42)	(7.95,16.22)	(0.00, 0.03)
Mean	USGS-Cornell (2001–2005)	93	34.44	4.36	9.48	12.04	6.35	2.23
Percentiles			(27.95, 41.19)	(2.29, 7.00)	(6.07, 13.45)	(8.10,16.48)	(4.46, 8.44)	(1.42, 3.22)
Ratio			2.02	0.95	3.59	1.62	1.86	0.01
P-value			<0.001	0.726	<0.001	0.031	0.013	<0.001
Mean	DFO Subset (1987–1991)	54	92.79	6.06	46.53	23.32	16.88	0.00
Percentiles			(71.38, 116.67)	(4.19, 8.72)	(33.94, 61.21)	(16.70, 30.60)	(10.08, 24.77)	(0.00, 0.00)
Mean	LOLA 2003	86	47.92	1.42	8.12	18.63	18.17	1.58
Percentiles			(37,75, 60.03)	(0.96, 2.00)	(5.21, 11.95)	(14.71, 23.38)	(12.34, 15.12)	(1.17, 2.07)
Ratio			1.94	4.28	5.73	1.25	0.93	0.00
P-value			<0.001	<0.001	<0.001	0.124	0.629	<0.001

production (May to October) for Lake Ontario during 1993 and 1994 ranged from 18.9 to 23.8 (g dry·m^{-2}); assuming a wet to dry conversion of 0.1). This is closer in magnitude to our annual estimates determined for 2001–2005 (20.2 to 22.7 g dry·m^{-2}·year^{-1}). This does not mean that zooplankton production had declined lakewide between 1987–1991 and 1993–1994; no downward trend in epilimnetic zooplankton production was observed in the main lake (station 41) between 1987 and 1995 (Johannsson, 2003). Declines started in the Kingston Basin (station 81) in 1994; however, production of dreissenid veliger larvae made up the difference in 1995—they were not enumerated in 1994

Fig. 3. Mean zooplankton group proportions for the DFO versus LOLA data sets (a) and the USGS-Cornell data sets (b). (Cal = Calanoid copepods, Cyc = Cyclopoid copepods, Lc = Large cladocerans, Sc = Small cladocerans, Inv = Invasive predatory cladocerans). The bars represent the 2.5% and 97.5% percentiles from the distribution of 5000 resampled observations.

(Johannsson, 2003). Significantly, phytoplankton biomass also did not decline at either station in the 1987–1995 period (Johannsson et al., 1998). Our determinations of higher levels of zooplankton production than previously estimated are most likely due to the addition of metalimnetic production and expansion to the whole year. However, the difference could also be related to our application of spatially explicit P/B ratios versus the more commonly applied non-spatial P/B ratios or egg-ratio methods. Rand et al. (1995) estimated that alewife predatory demand on zooplankton exceeded estimates of zooplankton production during 1991. Our updated zooplankton production estimates may contribute to solving this paradox.

The absence of any change in zooplankton species richness and diversity coincident with the establishment of the invasive predator cladocerans in Lake Ontario by 2001–2005 may indicate that the Lake Ontario zooplankton community is more resilient to food web effects from invasive disruption compared to inland lakes (Strecker et al., 2006) or other Great Lakes. This may be due to the suppression of the invasive predatory cladocerans by alewife predation. It may also be related to the spatial and temporal heterogeneity in zooplankton community composition. The variability in the composition of alewife diets across space and season in Lake Michigan and Lake Ontario is immense (Stewart et al., 2009; Pothoven and Vanderploeg, 2004), suggesting that alewife are exploiting a zooplankton community highly variable in species composition over space and time. Heterogeneity increases invasibility, reduces the impact of invaders, and increases coexistences of native and invading species (Melbourne et al., 2007). Due to their large size, the Great Lakes have much greater abiotic and biotic spatial and temporal heterogeneity, which may serve to mitigate the influence of the invasive predatory cladocerans and other invasives, especially in comparison to smaller inland lakes.

Zooplankton productivity has rarely been assessed in the Great Lakes following the invasion-induced post 1990s ecological change (except cf.

Table 5

Zooplankton species richness and diversity in the USGS data set with the inclusion of the invasive predatory cladocerans, during the 1987–1991 and 2001–2005 time periods. Rows are values for individual years.

1987–1991			2001–2005		
Year	Richness	Diversity	Year	Richness	Diversity
1987	20	1.48	2001	17	1.66
1988	18	1.26	2002	15	1.56
1989	16	1.45	2003	19	1.50
1990	16	1.40	2004	20	1.43
1991	16	1.48	2005	20	2.08

Johannsson et al., 2000). This study represents the first direct comparison of changes in zooplankton production before and after the invasion-induced disruption and will be important to food web-scale investigations of invasion effects. Our results confirm the predictions of a decline in zooplankton productivity following dreissenid invasion and reduced nutrient loadings (Millard et al., 1995; Johannsson, 2003; Hecky et al., 2004; Holeck et al., 2008). The 2001–2005 declines in total zooplankton group biomass and production observed from the analysis of two independent data sets were similar in magnitude, indicating the general robustness of our methods. However, the observed shifts in zooplankton community composition from 1987–1991 to 2001–2005 were not consistent between the two data set comparisons. The USGS-Cornell data set comparisons was considered more reliable as the sampling included more years, and common methods of counting and processing were applied. The inclusion of 5 years of data better accounts for annual variation in zooplankton community composition. The community composition characterized by only one year of data for the LOLA post-invasion period may be unique and not indicative of overall long-term trends. Support for this contention is evident in the similarity between the zooplankton group proportions during 1987–1991 between the 5 years of USGS-Cornell data (Fig. 3a) and the 5 years of DFO data (Fig. 3b), despite the fact that they employed different temporal and seasonal sampling designs. This suggests that monitoring programs that account for annual variation may be more robust than periodic spatially extensive sampling programs. Alternatively, the variation associated with the expanded spatial extent of the 2003 LOLA sampling (Fig. 1) may have resulted in a unique but more accurate characterization of the zooplankton community, which can only be reliably compared to programs of similar spatial extent.

Although we did account for spatial variation in P/B ratios due to epilimnetic temperature differences, only two sites were used to describe seasonal and spatial variation in biomass. The analysis may underestimate the magnitude of spatial variation in zooplankton production if other factors, such as predation or food resources, were more important in other regions of the lake. However, temperature has been shown to be a strong determinant of zooplankton community composition. Patalas (1969) documented spatial differences in the seasonal development of Lake Ontario zooplankton community related to temperature. Generally, crustacean zooplankton appeared first and reached highest densities in the warmer shallow water of the eastern region, with the difference between the east and west regions, and nearshore and offshore areas becoming less prominent as the season progressed. Lake Ontario temperatures were observed to be persistently warmest nearshore and in the eastern region and cooler offshore and in the western region (Patalas, 1969; Stewart and Bowlby, 2009, Appendix A). Seasonal zooplankton densities were strongly correlated with a site-specific index of epilimnetic heat content (Patalas, 1969). Zooplankton population growth is also positively related to temperature (Shuter and Ing, 1997), which leads to the prediction that zooplankton biomass and production in Lake Ontario should be higher nearshore versus offshore, and highest in the eastern versus western regions of the lake. Station 81 (34-m bathymetric depth) is in the warmest region of Lake Ontario and station 41 (128-m bathymetric depth) is in the coolest region, so a considerable amount of the spatial variation in zooplankton biomass was accounted for. Given the high costs associated with monitoring Great Lake ecosystems, more work is needed to better understand the relative importance of capturing spatial variation versus annual variation. Such an analysis could be used to improve the design of future zooplankton monitoring programs.

Rotifers and dreissenid veligers were not included in our analysis, but do contribute to total planktonic production. In Lake Ontario, rotifer biomass ranged seasonally from 4% to 17% of herbaceous zooplankton biomass (Johannsson, 2003) and from 1.0% to 12.0% of total zooplankton biomass, not including *Mysis diluviana* (Sprules and Munawar, 1991; Makarewicz et al., 1995). Dreissenid veligers may have been an important contributor to zooplankton production during the mid-1990s, especially

in the warmer nearshore areas (Johannsson, 2003). However, by 2003, lake-wide seasonal zooplankton sampling (Holeck et al., 2008) indicated that dreissenid veligers comprised only 0.1%, 3.7%, and 1.9% of the total zooplankton biomass in spring, summer, and fall, respectively (Cornell University Biological Field Station, Bridgeport, NY, unpublished data). Johannsson et al. (2000) estimated that Lake Erie dreissenid veligers grew on average of 0.1 day^{-1} at temperatures above 10 °C and 0.04 day^{-1} below 10 °C. Applying these rates to Lake Ontario seasonal temperatures would result in an annualized P/B for dreissenid veligers of approximately 25.6. Our average annualized zooplankton group P/Bs derived from this study were as follows: calanoids (4.6), cyclopoids (21.4), small cladocerans (29.9), and large cladocerans (27.9). Using the zooplankton group biomass as weights, the weighted average zooplankton community P/B was estimated as 22.9. Therefore as a percentage of total zooplankton production, the contribution from dreissenid veligers would be only slightly higher [by a factor of 1.11 (25.6/22.9)] than estimated by their percent contribution to total zooplankton community biomass and is estimated at approximating 2.0%.

Lake Ontario phytoplankton biomass has declined (Millard et al., 2003; Munawar and Munawar, 2003), and as demonstrated by this study and others, this has been associated with declines in zooplankton biomass and production (Johannsson et al., 1998; Holeck et al., 2008) and declines in alewife (O'Gorman et al., 2008). This overall multi-trophic level decline in productivity complicates interpretations of zooplankton community changes. While interpreting the results of this study it is important to distinguish declines in overall zooplankton biomass and production and disproportionate changes in biomass and production of some zooplankton groups, measured as changed zooplankton group proportions. Interpretation is further complicated by inconsistency between the two data set comparisons.

Do declines in Lake Ontario primary production (PP) account for the observed decline in zooplankton production from 1987–1991 to 2001–2005? Approximately 80% of the water flowing into Lake Ontario comes from Lake Erie (http://www.epa.gov/glnpo/atlas), so we applied Lake Erie post-dreissenid PP:TP ratios (Depew et al., 2006) to estimates of Lake Ontario TP during 2003 to estimate the PP in comparison to direct estimates of Lake Ontario PP during 1987–1991 (Millard et al., 1996). Lake Erie PP:TP ratios (± 1 SD) were 10.7 (2.8) and 14.3 (3.3) for nearshore (≤20-m) and offshore, respectively (Depew et al., 2006). Using theses ratios and the average seasonal TP for Lake Ontario during 2003 of 9.6 (μg·L^{-1}) from Holeck et al. (2008), annual PP in Lake Ontario during 2003 was estimated to range from 102.7 to 137.4 (g C·m^{-2}). The same TP value was applied to the PP to mean seasonal TP relationship developed by Millard et al. (1999), which excluded sites potentially impacted by dreissenids, and resulted in an estimated PP of 133.7 (g C·m^{-2}). Considering that water <20-m represents only approximately 13% of the total area of Lake Ontario, it is reasonable to assume that the offshore seasonal PP of 137.4 was most comparable to the data in Millard et al. (1996). During 1987–1991 Lake Ontario PP averaged 169.9 (Millard et al., 1996). Compared to our 2003 estimate, PP may have declined to only 80% of its 1987–1991 level, while zooplankton productivity declined by approximately half. This suggests that in addition to PP decline, some other mechanism is further reducing zooplankton productivity.

It has been hypothesized (Hecky et al., 2004) and partially confirmed (Depew et al., 2006) that dreissenids shunt nutrients and particulate organic carbon from the nearshore water column to the benthos, reducing pelagic PP. This effect would be accounted for in our estimate of PP and is not likely an explanation for a disproportionate decline in zooplankton production. Direct dreissenid grazing of phytoplankton, making it unavailable to support zooplankton production, might be a mechanism causing the disproportionate decline in zooplankton production from 1987–1991 to 2001–2005. Declines in chlorophyll-*a* following establishment of dreissenid mussels have been attributed to dreissenid grazing (Caraco et al., 1997, 2006). Grazing by dreissenids mussels was estimated to remove 26% of the available primary

production in western Lake Erie (Madenjian, 1995), which would thus be unavailable to support zooplankton production. Also, selective feeding by dreissenid mussels has been implicated in a shift in the phytoplankton community to increased prevalence of blue-green algae and other large colonial forms of algae (Makarewicz et al., 1999; Nicholls et al., 2002; Bierman et al., 2005; Miller and Watzin, 2007; Naddafi et al., 2007) which may be less edible to zooplankton (Porter, 1973; Lehman and Sandgren, 1985). A reduction in the yield of chlorophyll-*a* from a given concentration of total phosphorus (TP) has been attributed to dreissenid filtering in nearshore Lake Ontario (Nicholls et al., 1999; Millard et al., 1999). However, dreissenid filtering impacts are less likely in the offshore of deep thermally stratified Lake Ontario, where very little of the epilimnetic water is in proximity to dreissenid mussel beds. For Lake Ontario, less than 10% of the total volume of epilimnetic water (<=20-m) is in the nearshore zone over bathymetric depths <=20-m, where it could presumably be subject to mussel filtering effects. If not dreissenid filtering, changes in the depth distribution, growth, or behavior of zooplankton due to the invasive predatory cladocerans (Pangle et al., 2007) could have contributed to reduced zooplankton productivity beyond that predicted by changes in primary productivity.

Is overgrazing of zooplankton by predators contributing to overall declines in zooplankton production? Correlative studies clearly implicate predation by the invasive predatory cladocerans, especially *Cercopagis* (Benoit et al., 2002; Laxon et al., 2003; Warner et al., 2006). However, alewife and the invasive predatory cladocerans both consume common zooplankton prey and their potential predation effects cannot be considered in isolation (Stewart et al., 2009). Overgrazing by alewife may be a more likely mechanism. Lake Ontario is often characterized as having an undersupply of zooplankton production. It has been estimated that consumption by either alewife (Rand et al., 1995) or *Cercopagis* (Laxon et al., 2003) can exceed the production of their zooplankton prey. This implies intense predation pressure. Production of short-lived zooplankton species may respond quickly to declines in PP, resulting in a tight coupling between the production of small zooplankton and larger predatory zooplankton. In contrast, there may be lag of several years before the production of longer-lived multi-age class population of zooplanktivorous alewife declines in response to declines in PP. This would result in an uncoupling of the predator demand for zooplankton by alewife with the ability of the system to produce the required supply of zooplankton production, resulting in overgrazing. It is worth investigating if this is a general phenomena associated system characterized by intense predation pressure on zooplankton from prey fish and declining primary productivity.

Predation by both alewife and invasive predatory cladocerans may be the mechanism causing a disproportionate decline in cyclopoids. Cyclopoid copepods often dominate the zooplankton portion of alewife diets and are consumed by alewife during all seasons (Stewart et al., 2009). Cyclopoid copepods are also important in the diets in the early life-history stages of many other Lake Ontario fish including lake herring (*Coregonus artedii*), lake whitefish (*Coregonus clupeaformis*) and rainbow smelt (*Osmerus mordax*; Davis and Todd, 1998; Freeberg et al., 1990; Urban and Brandt, 1993; Lantry and Stewart, 1993), and alewife (Norden, 1967; Heinrich, 1981; Urban and Brandt, 1993; Hewett and Stewart, 1989; Lantry and Stewart, 1993). *Cercopagis* predation on cyclopoids is seasonal, with highest predation occurring primarily during mid-summer peak in abundance (Laxon et al., 2003). Reduced availability of zooplankton for alewife was suggested by extremely low stomach content weights at bathymetric depths <70-m following the disruptive changes of the 1990s (Stewart et al., 2009). This is consistent with overgrazing of zooplankton in nearshore waters by alewife and a switch to offshore food resources evidenced by increased offshore distribution of alewife (O'Gorman et al., 2000) and increased prevalence of *Mysis diluviana* in alewife diets (Stewart et al., 2009). These observations suggest that grazing pressure on zooplankton may have increased to the point whereby alewife needed to change their distribution to acquire enough food.

The disproportionate decline in cyclopoid biomass in both data sets was consistent with the predicted predation effect by alewife and invasive predatory cladocerans (Laxon et al., 2003; Warner et al., 2006; Stewart et al., 2009), but a reduction in the proportion of small cladocerans that could be predicted from the same studies was not detected. The USGS-Cornell data set comparisons did detect a decline in small cladoceran biomass, but this was in proportion to the overall decline in zooplankton biomass, and the proportion of small cladocerans did not change. On the other hand, the DFO and LOLA data set comparison saw no change in small cladoceran biomass and detected a significant increase in the proportion of small cladocerans. As discussed above, the DFO and LOLA data set comparison may be less robust due to differences in processing methodology, trying to compare multi-year spatially limited sampling program to a single-year spatially extensive sampling, and reduced seasonal coverage.

In an independent study, Laxon et al. (2003) observed a significant decline in both cyclopoids and small cladocerans from a comparison of data from 1986 to 1991 with data from 1999 to 2001. This is consistent with a general decline in zooplankton productivity, and is consistent with the observation from the USGS-Cornell comparison. Unfortunately, Laxon et al. (2003) did not report changes in total zooplankton community structure so it is not possible to assess changes in zooplankton group proportions from their study. The Laxon et al. (2003) study and USGS-Cornell comparison did detect a significant decline in the biomass of small cladocerans. However, both sampling programs occurred on the south shore of Lake Ontario and may be characterizing a regional rather than a lake-wide response. Regional variation in Lake Ontario temperature (Appendix A, Stewart and Bowlby, 2009) will influence zooplankton community composition and seasonal succession (Patalas, 1969) resulting in different zooplankton community structures and potentially different predator-prey interactions in different regions of lake during the same calendar seasons. This temperature-induced variability might be more problematic for measuring cladoceran biomass and detecting change as they are only abundant after thermal stratification while cyclopoid copepods are abundant throughout the year (Johannsson et al., 1998). For example, the inclusion of warmer nearshore sites in a spatially extensive sampling in the spring might elevate estimates of cladoceran biomass in comparison to less spatially extensive sampling. The weight of evidence supports a post-invasion decline in total zooplankton biomass and production with a disproportionate decline in cyclopoid copepods and an increase in invasive predatory cladocerans. Evidence for both absolute and proportionate changes in the biomass and production of other zooplankton groups is inconclusive.

The ubiquitous consumption of cyclopoids by alewife and other fish species, and additional summer consumption by the invasive predatory cladocerans, seems a likely mechanism for their disproportionate decline. However, better understanding of the interplay among the effects of various sources of predation (top-down) and reduced production (bottom-up) effects on zooplankton community structure, biomass, and production will require a more comprehensive food web analysis.

Cyclopoid abundance has been shown to be an important determinant of recruitment in marine fish (Castonguay et al., 2008), and a similar mechanism may be operating in the Great Lakes. The potential link between Great Lakes fish recruitment and cyclopoid abundance warrants further investigation. Also, cyclopoid copepods are the dominant zooplankton group, and their decline may portend important changes in the pathway of energy flow and trophic transfer efficiencies.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi: 10.1016/j.jglr.2010.07.010.

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