

2010 Status of the Lake Ontario Lower Trophic Levels

Kristen T. Holeck, Christopher Hotaling, Jonathan W. Swan, and Lars G. Rudstam
Cornell University Biological Field Station

Russ McCullough, Dave Lemmon, Web Pearsall, Jana Lantry, Mike Connerton, and Steve LaPan
New York State Department of Environmental Conservation

Betsy Trometer
United States Fish and Wildlife Service

Brian Lantry, Maureen Walsh, and Brian Weidel
U.S. Geological Survey – Lake Ontario Biological Station

Significant Findings:

- 1) Total phosphorus ranges between 6 and 11 $\mu\text{g/L}$ in both nearshore (10m depth) and offshore waters of Lake Ontario. Embayment levels are higher.
- 2) Spring TP has declined in the longer data series (1970-1994), but not in the last 15 years (since 1995). It is close to or lower than 10 $\mu\text{g/L}$ (the goal of the Great Lakes Water Quality Agreement of 1978) in both nearshore and offshore habitats.
- 3) Epilimnetic chlorophyll and water clarity were similar to measurements from the last decade and are indicative of oligotrophic conditions.
- 4) Summer nearshore epilimnetic zooplankton density and biomass are among the lowest recorded in Lake Ontario. Offshore epilimnetic zooplankton density and biomass are at all-time lows.
- 5) Zooplankton biomass in the offshore epilimnion of Lake Ontario has been declining since the late-1990s at a rate of 16% per year. Similar rates of decline also occurred in the 1980s resulting in a 99% reduction in epilimnetic zooplankton biomass in the last three decades.
- 6) Average summer crustacean zooplankton length is significantly higher in the offshore than in nearshore and embayments.
- 7) Both bosminids and cyclopoid copepod densities are low in offshore and nearshore waters compared to historic data.
- 8) The predatory cladoceran *Cercopagis* continues to be abundant in the summer.
- 9) The biomass of the larger predatory cladoceran *Bythotrephes* was at an all-time high in both the nearshore and offshore samples in 2010.
- 10) Zooplankton biomass in the metalimnion is higher than the biomass in the epilimnion and includes high abundance of *Daphnia mendotae*, *Diaptomus sicilis*, and *Limnocalanus macrurus*. Total water column abundance of zooplankton in the offshore may not have declined to the levels suggested by epilimnetic samples.
- 11) Changes in the zooplankton community structure are consistent with a decline in fish predation and an increase in invertebrate predation.

Introduction

This report presents data on the status of lower trophic level components of the Lake Ontario ecosystem (zooplankton, phytoplankton, nutrients) in 2010 and compares the 2010 data with available time series. Lower trophic levels are indicators of ecosystem health [as identified by the Lake Ontario Pelagic Community Health Indicator Committee (EPA 1993) and presented in the biennial State of the Lake Ecosystem Conference (SOLEC) reports] and determine the lake's ability to support the prey fish upon which both wild and stocked salmonids depend. Understanding the production potential of lower trophic levels is also integral to ecosystem-based management. Continued evaluation of lower trophic levels is particularly important for fisheries management, as the observed declines in alewife and Chinook salmon in Lake Huron in 2003 may have been partly the result of changes in lower trophic levels (Barbiero et al. 2009).

From 1995-2010, we conducted a research program (hereafter referred to as the biomonitoring program, BMP) in Lake Ontario with the primary objective of evaluating temporal and spatial patterns in a number of ecological indicators: total phosphorus (TP), soluble reactive phosphorus (SRP), chlorophyll *a* (chl *a*), Secchi depth, and crustacean zooplankton (density, biomass, species composition, and size structure). Samples were collected from April to October. Different indicators are best assessed during different seasons. Spring conditions represent the nutrients available for biological activity that will occur during the year, making spring TP a logical indicator choice. The summer stratified period characterizes the peak production period for many species; therefore, summer chl *a* and zooplankton biomass were chosen as indicators. The September-October time period is useful to track species such as *Bythotrephes* whose biomass typically peaks later in the year. The biomonitoring program is a collaborative project that in 2010 included the New York State Department of Environmental Conservation (NYSDEC) Lake Ontario Unit and regional staff at Watertown, Cortland, and Avon; the U.S. Fish & Wildlife Service Lower Great Lakes Fishery Resources Office (USFWS); the U.S. Geological

Survey–Lake Ontario Biological Station (USGS); and Cornell University.

Report Objectives

Using data from 1995 to 2010, we address the following questions:

- (1) What is the status of Lake Ontario's lower trophic levels in 2010 and are there differences among embayment, nearshore and offshore sites this year?
- (2) What are the time trends in key indicators and are there changes over time in these trends (change-point analysis). How does the year 2010 compare to these time trends (using the biomonitoring data and other long-term data sets)?
- (3) What is the status of the two exotic predatory cladocerans, *Bythotrephes* and *Cercopagis*?
- (4) Are there changes in zooplankton community structure (biomass, size, species composition) that are indicative of changes in alewife predation, changes in predatory invertebrates (*Cercopagis*, *Bythotrephes*, *Mysis*, *Hemimysis*) or decreased overall productivity of the lake?
- (5) Are observed declines in zooplankton during the last several years limited to the epilimnion (traditionally sampled by the BMP) or are the changes observed throughout the water column?

Methods

Sampling

We measured total phosphorus (TP), soluble reactive phosphorus (SRP), chlorophyll *a* (chl *a*), water temperature, Secchi depth, and zooplankton density, size and biomass by species at offshore, nearshore, and embayment sites in Lake Ontario (Figure 1). Samples were collected from three embayment and seven nearshore sites biweekly from May through October 2010 (Table 1, 12 potential sampling weeks). Inclement weather precluded sampling in at least one week at all sites; however all sites were sampled on at least 7 occasions (Table 1). Offshore samples were collected during April, June, July, and September by the R/V Seth Green, and approximately monthly (April–October) by the R/V Kaho. Samples collected

during July night-time hydroacoustics assessments were included in offshore zooplankton analyses through 2008 but not in 2009 and 2010. Only one station was sampled at night in 2010. Embayment site bottom depths ranged from 3.0 m to 12.5 m (10 to 41 ft), nearshore sites had depths ranging from 8.5 m to 14.0 m (28 to 46 ft), and offshore sites ranged from 18 m to 206 m (59 to 676 ft). Offshore sampling totaled 29 daytime samples taken from 7 sites.

Water Chemistry

Water samples were collected for analysis of chl *a* and two phosphorus fractions: TP and SRP. Each sample was obtained by using an integrated water sampler (1.9 cm inside diameter Nalgene tubing) lowered to a depth of 10 m or bottom minus 1 m where site depth was 10 m or less. The tube was then closed off at the surface end and the column of water transferred to 2 L Nalgene containers. From each sample, a 100 mL unfiltered aliquot was frozen for later analysis of TP (Menzel and Corwin 1965). We also filtered 1-2 L of water through a Whatman 934-AH glass fiber filter that was frozen for later analysis of chl *a* using the standard acetone extraction method (Strickland and Parsons 1972). A 100 mL sample of filtered water was also frozen for later analysis of SRP (Strickland and Parsons 1972).

Quality Control and Variability

To measure the precision of the analytical methods used at the Upstate Freshwater Institute (UFI) and at the Cornell Biological Field Station (CBFS), we processed replicate samples for TP and SRP at both laboratories. In July, 10 aliquots of water were taken from the same sample at nearshore and embayment sites (n=10 sites). Five of the ten replicates were analyzed at CBFS and five at UFI. At offshore sites, duplicates (TP, SRP, and chl *a*) were collected throughout the sampling season. For TP and SRP, one sample was analyzed at CBFS and one at UFI. For chl *a*, replicates were processed only at CBFS.

In 2010, we also collected replicate samples at each sampling site to determine within site variability of TP, SRP, and chl *a*. Triplicate samples were collected at each nearshore and embayment location twice in August (except in

the case of Sandy Pond - bay [SPB] and Sandy Pond - lake [SPL] where only one triplicate sample was collected). From each of the three samples, one aliquot was taken for TP, one for SRP, and one for chl *a* analysis. TP and SRP samples were analyzed at UFI and chl *a* was analyzed at CBFS.

We note that water samples from SPB and SPL thawed as a result of freezer failure. The samples were refrozen, transported to CBFS, and processed in the same manner as the rest of the samples. The data obtained from SPB and SPL were in line with expectations from the other sites.

Zooplankton

Zooplankton samples were collected with a standard 0.5 m diameter, 153 μm -mesh nylon net equipped with a calibrated flowmeter (all sites except SPB and SPL). At embayment and nearshore sites, we strained a water column between 2.7 and 10 m. At offshore sites, we sampled a 5 to 40 m water column (to the thermocline when stratification was present). In June and July, a total water column sample (referred to as “hypolimnetic” hereafter) was obtained in addition to the epilimnetic sample on three occasions (sampled by NYSDEC), and in July and September, one 50 m (“metalimnetic” hereafter) and one 100 m tow (“hypolimnetic” hereafter) was obtained from two offshore sites sampled by USGS in addition to the standard epilimnetic sample. Zooplankton were anesthetized using antacid tablets, then preserved in the field with 95% ethyl alcohol. Single samples were collected on a biweekly basis at embayment and nearshore sites from May to October, except for July and August when two or three replicate samples were collected at several of the sites.

At CBFS, each sample was strained through a 1.02 mm mesh cup to separate *Cercopagis* and other larger organisms (>1 mm in length) from smaller zooplankton (<1 mm). This was done because *Cercopagis* and *Bythotrephes* form clumps in the sample, making the usual random sub-sampling of 1 mL samples inappropriate. For each sample that contained clumps of *Cercopagis* or *Bythotrephes* two analyses were performed, one on the smaller zooplankton and one on the larger zooplankton (including

Cercopagis and *Bythotrephes*) that were caught in the 1 mm mesh strainer. At least 100 larger zooplankton (or the whole sample) were measured and enumerated by sub-sampling organisms from a gridded, numbered Petri dish in which the sample had been homogeneously separated. In some cases different subsamples were used for *Bythotrephes* and *Cercopagis*. To calculate the total number of large crustaceans and *Cercopagis* in the clumped part of the sample, we used a ratio of wet weights of the sub-sample to wet weights of the total sample. Wet weights were determined using a Sartorius balance.

For smaller sized zooplankton, we counted and measured at least 100 organisms from one or more 1 mL random sub-samples. The sub-sample was examined through a compound microscope at 10-40X magnification. Images from the sample were projected onto a digitizing tablet that was interfaced with a computer. Zooplankton were measured on the digitizing tablet and identified to species (with the exception of nauplii and copepodites) (Pennak 1978, Balcer et al. 1984). In earlier years of this project an electronic touch screen (1995-1997) and a 20X microprojector (1998-2000) were used for measuring the zooplankton (Hambright and Fridman 1994). We then used length:dry-weight regression equations (CBFS unpublished data) to estimate zooplankton biomass. Densities from all counts of the same sample (large and small animals) are summed to yield an overall density of all organisms in each sample.

Data Analyses

For embayment and nearshore sites, we compared the biweekly averages (TP, SRP, chl *a*, water temperature, Secchi depth, zooplankton density, size, and biomass, and zooplankton group biomass proportion) between the two habitats (nearshore n=7 and embayment n=3) using paired t-tests for means. Logarithmic transformations were needed for zooplankton density and biomass to reduce heteroscedasticity. We divided zooplankton into the following eight groups: daphnids (*Daphnia mendotae*, *D. pulicaria*, *D. retrocurva*); bosminids (*Bosmina longirostris*, *Eubosmina coregoni*); calanoid copepods (*Diaptomus minutus*, *D. oregonensis*, *D. sicilis*, *D. ashlandi*,

Epischura lacustris, *Eurytemora affinis*, *Limnocalanus macrurus*); cyclopoid copepods (*Acanthocyclops vernalis*, *Diacyclops thomasi*, *Mesocyclops edax*, *Tropocyclops prasinus*); other cladocera (*Ceriodaphnia quadrangula*, *Chydorus sphaericus*, *Leptodora kindtii*, *Diaphanosoma sp.*, *Alona sp.*, *Holopedium gibberum*, *Polyphemus pediculus*, *Camptocercus sp.*); *Bythotrephes longimanus*; *Cercopagis pengoi*; and nauplii.

Summer (Jul–Aug) zooplankton density, biomass, average size, and group proportions were compared among offshore, nearshore, and embayment habitats using ANOVA followed by Tukey's HSD to determine which pairs of habitats differed significantly. Zooplankton density and biomass were log transformed, and differences were considered significant at $p < 0.05$.

Change point analyses (Taylor Enterprises, Inc. 2003) were performed on long-term trends in two time stanzas (1998–2010 and 1981–2010) to look for breaks in the data. These were performed on spring TP, summer chl *a*, summer epilimnetic zooplankton density and biomass, and on zooplankton group biomass. Change point analysis uses cumulative deviations from the mean to assess if there are significant changes in time trends and when those changes occurred. This is done by resampling the data series 10,000 times to construct confidence intervals based on the inherent variability in the data series, and testing if and when the observed data series differ significantly from these confidence intervals.

Regression analyses (Jump v8, SAS Institute Inc. 2008) were performed on the same two time stanzas (1998–2010 and 1981–2010) using spring TP, summer chl *a*, summer epilimnetic zooplankton density and biomass, and on zooplankton group biomass. Significant trends and the slopes associated with those trends are reported.

Results

Quality Control and Variability

We analyzed 50 SRP and TP samples (10 sites x 5 samples per site) at both UFI and CBFS. SRP QAQC replicates processed at UFI had CVs

(SD/mean) ranging from 5 to 50% (mean of 17%) while CBFS CVs ranged from 7 to 58% (mean of 27%). For TP, UFI CVs ranged from 1 to 16% (mean of 6%) and CBFS CVs ranged from 5 to 38% (mean of 12%). Overall the CV at UFI was lower than at CBFS.

To compare the absolute concentrations obtained by the two laboratories, we used an additional 29 duplicate samples collected throughout the year as well as the means of the QAQC replicates for a total of 39 paired samples. SRP was significantly higher when measured at CBFS than at UFI (paired t-test, $p < 0.0001$, CBFS mean SRP at 3.0 $\mu\text{g/L}$, UFI mean SRP at 0.9 $\mu\text{g/L}$). Further, the results from the two labs were not significantly correlated ($r^2 = 0.05$, $p = 0.17$, $N = 39$). In contrast, TP results from the two labs were highly correlated ($r^2 = 0.94$, $p < 0.0001$, $N = 39$), with a slope not significantly different from 1 and an intercept not significantly different from 0. Still, the more sensitive paired test revealed significant differences between the labs ($P < 0.0001$), with mean UFI TP concentration at 9.5 $\mu\text{g/L}$ and mean CBFS TP concentration at 8.2 $\mu\text{g/L}$.

We believe these differences can be attributed to methodological differences between labs. UFI uses a more recent version of Standard Methods which may have released more P from the TP samples and therefore resulted in slightly higher TP measurements in the UFI data. For SRP, UFI used an additional filtration step where samples were passed through a 0.45 μm cellulose filter. This could account for the lower SRP levels measured by UFI compared to CBFS. We note that SRP concentrations in most samples were close to the detection limit of the methods used (UFI gives a detection limit of 0.4 $\mu\text{g/L}$ and a quantification limit of 1.4 $\mu\text{g/L}$). This was not the case with TP as all TP concentrations were above UFI's detection limit of 1.1 $\mu\text{g/L}$, and all but one sample had concentrations that were above their method's quantification limit of 4.7 $\mu\text{g/L}$. It is therefore not surprising that the correspondence was better between the two laboratories for TP measurements. Here, we present TP and SRP from UFI for 2010. Given the similarity between TP measurements from the two laboratories, we consider the analysis of time trends for TP to be valid, but will have to

evaluate the SRP data from CBFS further before presenting SRP time series.

The analysis of August embayment and nearshore TP and SRP triplicate samples (processed only at UFI) showed that the CV for TP ranged from 1 to 31 % (mean of 9%), and the CV for SRP ranged from 0 to 44% (mean of 15%). This is similar to the within sample precision in the analytical method at UFI (see above). Therefore, we cannot determine the relative contribution of within sample and between sample variability in TP and SRP and conclude that the inherent variation in these measurements at any one site has a CV (SD/mean) of about 10% for TP and about 15% for SRP.

The analysis of August embayment and nearshore chl *a* triplicate samples (processed only at CBFS) showed that the CV ranged from 2 to 56% (mean 21%). We pooled triplicate TP, SRP, and chl *a* samples for each site when those were available for the analysis of spatial and temporal changes in the lake.

2010 Water Quality

Embayments at Sandy Pond and Sodus were characterized by higher concentrations of TP compared to the Chaumont embayment and other nearshore and offshore sites (Table 1). Sandy Pond had higher chl *a* and lower Secchi depth than the other two embayments. The nearshore sites east and west of the Niagara River had higher TP and SRP concentrations and lower water clarity compared with other nearshore sites but not higher chlorophyll levels. The three embayments and the two Niagara nearshore sites had the lowest water clarity; seasonal mean Secchi depth was less than 5 m at those locations. Secchi depths at other nearshore and offshore sites were between 6 m and 12 m (Table 1, Figure 2a). May through October chl *a* concentrations were low in general; means by habitat and most individual sites averaged below 2 $\mu\text{g/L}$ (Table 1, Figure 3a). Average May-Oct TP concentrations at other nearshore and offshore sites were mostly below 10 $\mu\text{g/L}$ (Table 1, Figure 4a), which is the current target established by the Great Lakes Water Quality Agreement (IJC 1988). The Sandy Pond Lake site and the Niagara sites were slightly above 10 $\mu\text{g/L}$. SRP concentrations were very low; May-

Oct means were less than 2 µg/L at all sites (Table 1). Nearshore sites had highest concentrations in July and October while offshore concentrations peaked in June (Figure 5). May through October water temperatures were significantly higher in embayments compared with nearshore habitats (Tables 1 and 2), and with the exception of October, nearshore sites were warmer than offshore sites throughout the season (Figure 6).

Total phosphorus, chlorophyll *a*, and Secchi depths are typically correlated, as all are indicators of phytoplankton abundance. This was also the case in 2010, with the exception of the Niagara River sites which had relatively high total phosphorus concentrations and low Secchi depth even though chlorophyll concentrations were not higher than at the other nearshore sites. The Niagara River sites may be affected by sediment load or turbulence associated with the river inflow. The Sandy Pond-Lake site had both higher chlorophyll and lower Secchi depth suggesting that the lower transparency at this site was due to phytoplankton rather than sediment load. The other nearshore sites (Chaumont Lake, Galloo Island, Oak Orchard and Sodus Lake) were similar to each other and to the offshore sites. Soluble reactive phosphorus was more similar among habitats. SRP is a more dynamic component of the ecosystem and is typically taken up quickly by phytoplankton. Low SRP values primarily indicate phosphorus limitation and are often decoupled from phytoplankton abundance as SRP can be below the detection limits during phytoplankton blooms.

Water Quality Trends Since 1995

Comparisons with available time series show 2010 to be a low productivity year with clear water. May-Oct nearshore Secchi depths were slightly lower in 2010 compared to 2009, but they were similar to recent years (Figure 2b). Average nearshore and offshore chl *a* concentrations have stayed below 3 µg/L since 1995 and although the 2010 mean summer offshore value (1.4 µg/L) was close to last year's all-time low (Figure 3b), it is not substantially different from the last decade. Spring TP concentrations at nearshore and offshore sites increased but remained below the GLWQA

target of 10 µg/L (Figure 4b) and similar to last decade.

2010 Zooplankton Density, Biomass, and Mean Length

In 2010, mean (May-Oct) zooplankton density and biomass were significantly greater in embayments than at nearshore sites (Table 2, Figure 7a & 7c). Average size of zooplankton was significantly smaller at embayment sites than at nearshore sites (Table 2, Figure 7b), a finding consistent with previous years.

During July-August, the average embayment zooplankton density and biomass were significantly greater than the density and biomass at nearshore and offshore sites. Zooplankton size was significantly greater in the offshore compared with nearshore and embayment habitats (Table 3, but see below for metalimnetic zooplankton).

Zooplankton Trends Since 1998

Total summer epilimnetic zooplankton biomass at nearshore and offshore sites remained low in 2010 (Figure 9). In fact, offshore epilimnetic zooplankton summer biomass was at an all-time low. A change point analysis using data from 1998–2010 showed that a break occurred in offshore density and biomass after 2004 (Figures 9 and 10, Table 4). Offshore bosminid and cyclopoid copepod biomass also showed a break after 2004. A break was detected in nearshore density after 2004 but not in biomass; however, mean biomass for 2005–2010 (20 µg/L) was lower than for 1998–2004 (44 µg/L), and the difference was marginally significant (t-test, $p=0.06$; Table 4). The decline in zooplankton biomass was due to decreases in bosminids and cyclopoids (Table 4).

Changes in lower trophic indicators vary by habitat. In the offshore, TP and chl *a* were stable from 1998 – 2010 while zooplankton density and biomass declined. In nearshore waters, TP was stable but chl *a* increased; zooplankton density decreased, but biomass did not (but see previous paragraph). Bosminids and cyclopoid copepods declined significantly in the offshore while calanoids increased significantly in nearshore waters (Table 4). While the nearshore regression for bosminids and cyclopoid copepods was not significant, a break

occurred after 2004 for these groups, just as it did in the offshore. A positive break in nearshore calanoids occurred after 2006, the same year that a negative break occurred in *Cercopagis* biomass.

Longer Term Trends

Longer term trends (1981-2010) were significant for several lower trophic level indicators. These trends were evaluated by adding BMP data to available data series from the Department of Fisheries and Oceans Canada, Environment Canada, and EPA (Table 4). Significant long-term trends were a decrease in spring TP, a decrease in summer zooplankton density, and an increase in Secchi depth (see also Mills et al. 2003, Holeck et al. 2008; Figures 2b, 4b, and 10). Chlorophyll levels cannot be evaluated for the same time period due to unresolved differences in methods.

Zooplankton Community Dynamics

Four zooplankton taxa differed significantly in proportion of total biomass between embayments and nearshore sites, May-October 2010 (Table 2; Figure 8). Cyclopoid copepods and other cladocerans represented significantly greater proportion of biomass in embayments than in the nearshore, while calanoid copepods and nauplii represented a significantly greater proportions of biomass in nearshore habitats than in embayments. The proportions of *Cercopagis* and *Bythotrephes* biomass were greater at nearshore sites compared with embayment sites but the difference was not statistically significant (Table 2). Combined biomass of *Cercopagis* and *Bythotrephes* represented 10% of the zooplankton community at nearshore sites.

A comparison of eight zooplankton groups across the three different habitats during summer (July-August; Table 3) showed similar significant differences. Bosminid biomass was significantly higher in embayment habitats compared with nearshore and offshore habitats, and significantly higher in nearshore habitats compared to offshore habitats (Table 3). Biomass of cyclopoid copepods, other cladocerans, and nauplii were significantly higher in embayments compared with nearshore and offshore habitats.

Cercopagis and *Bythotrephes*

In 2010, *Cercopagis* and *Bythotrephes* were detected in samples from each of the three habitats (Figure 8, Tables 3, 5 and 6). *Cercopagis* was first detected in late-April at the Smoky Point-N offshore site. After that, it did not reappear until mid-June at the Chaumont nearshore site and was last seen in mid-October at the Oak Orchard-N offshore site. *Cercopagis* peaked during July at most locations. *Bythotrephes* was first detected in early-June at the Galloo Island Lake site but was not present again until mid-July when it began appearing in most samples taken from nearshore and offshore locations. Peak *Bythotrephes* biomass occurred in September through early October (Figure 8). *Cercopagis* summer biomass showed a marginally significant decline in nearshore areas since 1998 with a break occurring after 2006 (Table 4). During the same time, the trend in *Bythotrephes* summer biomass has been positive in both nearshore and offshore locations (Table 4).

Stratified Zooplankton Hauls

Comparison of hypo-, meta-, and epilimnetic zooplankton tows showed that much of the total zooplankton biomass is concentrated in the meta- and hypolimnion, particularly under stratified summer conditions (Figure 11). During July and September, *Daphnia mendotae* accounted for most of the meta- and hypolimnetic zooplankton biomass. Other important meta- and hypolimnetic species included *Limnocalanus macrurus*, and *Diaptomus sicilis*. In the absence of strong stratification (e.g. early-June and mid-September), zooplankton are more evenly distributed throughout the water column.

Results of the hypo-, meta-, and epilimnetic tows made in summer and fall showed that biomass of *Bythotrephes* was greater than that of *Cercopagis* at all depths. *Bythotrephes* biomass was greatest in the metalimnion in the summer and in the epilimnion in the fall. *Cercopagis* biomass was greatest in the hypolimnion in the summer and in the epilimnion in the fall. The limited number of samples taken makes it difficult to interpret any patterns present. However, there is a significant negative relationship between mean *Bythotrephes* and *Cercopagis* biomass by habitat.

Discussion

As in previous years, embayments were the most productive habitat in 2010 with highest zooplankton density and biomass, chl *a*, TP, and SRP as well as lowest water clarity (low Secchi depth). Embayments and other similar areas are important nursery habitats for native fish species (whitefish, cisco, yellow perch, walleye, McKenna and Johnson 2009, Mason and Brandt 1996, Klumb et al. 2003).

The lower trophic level indicators were similar in the nearshore and offshore habitats and indicative of oligotrophic conditions. Excluding the Niagara River sites, the average values by sites were 0.8 to 1.9 µg/L for chlorophyll *a*, 7.1 to 10.2 µg/L for TP and 6.2 to 8.9 m for Secchi depth. These values are within the suggested range for oligotrophic (low productivity) systems (0.3-3 µg/L chlorophyll *a*, 1-10 µg/L TP; Wetzel 2001). Spring TP is a good indicator of summer phytoplankton production (Dillon and Rigler 1975) and the low chlorophyll levels observed in both the offshore and nearshore are consistent with the low spring TP values.

Both spring TP and summer chlorophyll increased from last year but remained low. Spring TP has declined from values around 20 µg/L in the 1970s to values between 5 and 10 µg/L in the 2000s in the offshore and 8-15 µg/L in the nearshore (Figure 4a). Spring TP has been below the goal of 10 µg/L set by the Great Lakes Water Quality Agreement of 1978 in the offshore sites since 1995 (not all years available) and in the nearshore sites since 2005 (Figure 4a). There were no significant declining time trends in spring TP or summer chlorophyll data since 1995, suggesting relatively stable nutrient loading and stable but low summer primary productivity through the last 15 years.

The low nearshore TP and chlorophyll values observed here are in contrast to the results of Makarewicz et al. (2009). They observed high nutrient levels (often over 50 µg/L TP) at depths <5 m at several stations along the US southern shore. These were significantly higher than the offshore, and accompanied by nuisance growth of benthic attached algae (*Cladophora*), which is also promoted by increased water clarity caused by mussel grazing (Malkin et al. 2008, Higgins

et al. 2008, Hecky et al. 2004). Our nearshore sites at 10 m depth are apparently outside the area affected by nearshore nutrient enrichments from mussels. In a more detailed study of the nearshore, Makarewicz (pers. comm.) found increased nutrient levels between 1 and 4 km from shore depending on season and station. This is consistent with our data from 10 m depth being more similar to the offshore stations than the embayments.

Epilimnetic crustacean zooplankton biomass and density were low at nearshore and offshore sites in 2010 compared to the long-term mean (Figures 9 and 10). Offshore density and biomass had declined significantly by more than 15% per year since the early 1980s and by 2010, biomass was at an historic low (Table 4; Figures 9 and 10). Epilimnetic zooplankton biomass has been particularly low since 2005 in both nearshore and offshore data, and there is a significant change point after 2004 in the offshore data set. The nearshore data is more variable; however, average values below 20 µg/L have been observed in all of the last five years compared to in only 2 out of 7 years in 1998-2004. Average size shows no trend in time although nearshore and embayments have smaller average sizes than the offshore. Average size in the nearshore was smallest in June, coinciding with alewife concentrating in the nearshore to spawn (O’Gorman et al. 1991, Klumb et al. 2003).

The decline in epilimnetic zooplankton biomass is primarily the result of declines in bosminids and cyclopoids (particularly *Diacyclops thomasi*), particularly since 2005. Daphnids also declined although not significantly, and calanoid copepods showed no change. Trends in the nearshore showed a significant increase in calanoid copepods and a marginally significant decline in *Cercopagis* but no change in other groups. The biomass of *Bythotrephes* increased in both the nearshore and offshore areas since 2005. There were negative change points for bosminids and cyclopoids in 2005, a negative change point for *Cercopagis* in 2007, and a positive change point for calanoids in 2007 (Table 4).

What are the possible causes for the decline in epilimnetic zooplankton and these shifts in

zooplankton community composition? We discussed these possibilities at some length in last year's report (Holeck et al. 2010). *Bythotrephes* and *Cercopagis* are important prey for larger alewife (Mills et al. 1992, Bushnoe et al. 2003, Storch et al. 2007), and *Bythotrephes* likely increased as a response to decreases in alewife predation (Mills et al. 1992, 2003). *Bythotrephes* and *Cercopagis* made up 11% of the May-Oct nearshore zooplankton biomass in 2010. Clearly, a relative predatory biomass that high could have large effects on other crustacean zooplankton, especially smaller zooplankton and daphnids. Larger calanoid copepods are better at avoiding predation from relatively slow invertebrate predators. Changes in other invertebrates such as *Mysis* have not been as large (Johannsson et al. in press), and this species is restricted to water below the thermocline during the summer (Johannsson et al. 2003). The new mysid invader (*Hemimysis anomala*) is a warmwater zooplanktivore that can be abundant in the nearshore area (Walsh et al. 2010). However, we do not find this species in the offshore of the lake where the main changes are occurring and it was not found in Lake Ontario before 2006 (Walsh et al. 2010). In the past, the Lake Ontario zooplankton community responded to declines in TP with changes in species composition (Johannsson 2003), but both TP and chl *a* remained at approximately the same levels since 1995.

Further support for the *Bythotrephes* hypothesis is evidenced by seasonal changes in zooplankton abundance at nearshore sites. All cladoceran groups in the nearshore declined in the fall when *Bythotrephes* increased in abundance whereas calanoid copepods did not decline to the same extent. Elsewhere, *Bythotrephes* has been implicated in declines in cladocerans (Lehman and Caceres 1993, Yan et al. 2001, Pangle et al. 2007, Bunnell et al. 2011). *Cercopagis* is also likely to cause declines in smaller zooplankton like copepod nauplii, bosminids, and small daphnids (Benoit et al. 2002, Laxson et al. 2003, Warner et al. 2006). However, *Cercopagis* appears sensitive to predation by *Bythotrephes* and there is a negative correlation between *Cercopagis* and *Bythotrephes* in our data. Thus, the changes in zooplankton abundance and community structure in Lake Ontario are consistent with an increase in invertebrate

predators, in particular *Bythotrephes*, which in turn is the result of declining alewife populations. Therefore, we consider the decrease in smaller zooplankton to be an indirect effect of decreased alewife planktivory in the epilimnion.

Conversely, meta- and hypolimnetic zooplankton biomass is higher than epilimnetic biomass (under stratified conditions) and is dominated by larger zooplankton (i.e. *Daphnia mendotae*, *Limnocalanus macrurus*, and *Diaptomus sicilis*). Of seven sites sampled with depth stratified net hauls, five had higher metalimnetic or hypolimnetic zooplankton biomass (Figure 11b). The two sites that had lower hypolimnetic biomass were sampled in early June, prior to the establishment of a well-defined epilimnion. The BMP was designed to sample the epilimnion, but now it is clear that we need to expand sampling to the whole water column at offshore locations. Zooplankton abundance and biomass were higher in the meta- and hypolimnion, particularly during mid-summer (Figure 11a & 11b)—the season used to evaluate long-term trends (see Figures 9 and 10). Total abundance and biomass of zooplankton in Lake Ontario may not have declined—a possible explanation for the lack of decline in growth rates of *Mysis* (although population abundance declined) (Johannsson et al. in press), and alewife (O'Gorman et al. 2008, Walsh et al. 2011).

It is possible that a deep chlorophyll maxima is driving production in Lake Ontario in recent years. Deep chlorophyll maxima can be common in the upper Great Lakes (Barbiero and Tuchman 2004). Such maxima develop when nutrients are limiting and water clarity sufficient to allow for positive algal growth at depth with elevated nutrient concentrations. Zooplankton then graze in this layer. Whether this results in a decline in overall productivity of the lake needs to be evaluated. Algae in the deep chlorophyll maxima are not always photosynthesizing, and the zooplankton in that layer live at lower temperatures and therefore have lower growth rates. Another explanation is that the presence of *Bythotrephes* has induced diel vertical migration of zooplankton in Lake Ontario. If this is the case, we expect increased epilimnetic zooplankton abundance during the night. Deeper distribution of zooplankton could affect

alewife growth, as alewife feed with lower efficiency at low light levels (Janssen and Brandt 1980, Boscarino et al. 2010).

Our observation of relatively high zooplankton abundance in deeper water needs substantial further analysis. At this time it is unclear how or if 2010 meta- and hypolimnetic zooplankton biomass, density and species composition differ from previous years. It is clear, however, that epilimnetic offshore zooplankton and nearshore zooplankton (where we sample the whole water column) has declined.

Finally, we note that an increase in deeper zooplankton may not be available for young-of-year alewife. These fish consume primarily small cladocerans and cyclopoids in the nearshore or offshore epilimnion (Urban and Brandt 1993, Klumb et al. 2003). Further, they cannot handle the large tail spines of the invasive predatory cladocerans (Bushnoe et al. 2003). Therefore, the observed changes in zooplankton biomass, community composition and spatial distribution could decrease growth rates of young-of-year alewife and increase over-winter mortality (O’Gorman et al. 2004, Höök et al. 2007).

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