2006 Status of the Lake Ontario Ecosystem: A Biomonitoring Approach

Edward L. Mills, Jonathan W. Swan, Allison L. Babler and Lars G. Rudstam
Cornell University Biological Field Station

Russ McCullough, Dan Bishop, Web Pearsall and Steve LaPan
New York State Department of Environmental Conservation

Betsy Trometer
United States Fish and Wildlife Service

Brian Lantry, Robert O'Gorman
U.S. Geological Survey – Great Lakes Science Center

Ted Schaner
Ontario Ministry of Natural Resources

Introduction

The Great Lakes and Lake Ontario ecosystems have been subject to accelerated ecological change since the 1950s. These ecosystems experienced (in the 1950s and 1960s) numerous stresses including overfishing, cultural eutrophication, and contaminant discharge yielding degradation of water quality, loss of habitat, and the depreciation of fish communities. Such stresses raised public concern about the condition of the Great Lakes and led to a new period of environmental awareness and restoration in the 1970s, 1980s, and 1990s. The historic Great Lakes Water Quality Agreement (GLWQA) between the United States and Canada in 1972, later revised in 1978 and 1987 (IJC 1988), marked a new era of ecosystem management and initiated a process we term oligotrophication (reverse of eutrophication). In Lake Ontario, for example, phosphorus levels have declined over the past 20 years, but this event has come at a time when demands for a salmonid sport fishery have increased, non-native species such as the alewife have exhibited highly variable population dynamics, pelagic zooplankton production has declined, pelagic fish stocks are recovering, and exotics such as the zebra mussel, quagga mussel and the predatory cladocerans *Bythotrephes longimanus* and *Cercopagis pengoi* have proliferated (Christie *et al.* 1987, EPA 1993, Mills *et al.* 2003, Mills *et al.* 2005). Clearly, Lake Ontario is an ecosystem in transition, and the public's interest in and awareness of the Lake Ontario environment continues to increase. It is incumbent upon the scientific and management communities to understand these ecosystem changes and their implications for the life support system of this important freshwater resource.

One approach toward assessing a lake ecosystem in transition like Lake Ontario is to develop a database of key indicators that reflect ecosystem change. From 1995-2006, we have conducted a biomonitoring program in Lake Ontario that has indexed some of the primary indicators of ecosystem health as identified by the Lake Ontario Pelagic Community Health Committee (EPA 1993). The primary objective of the research was to evaluate the indexing variables of total phosphorus (TP), soluble reactive phosphorus (SRP), chlorophyll *a* (Chl *a*), Secchi depth, and crustacean zooplankton (density, biomass, size structure) (1) spatially and temporally, and (2) in critical habitats including embayments, the nearshore, and the offshore. The biomonitoring approach we describe has been successfully accomplished through interagency support of the New York State Department of Environmental Conservation (NYSDEC) including regional staffs at Watertown, Cortland, and Avon, the U.S. Fish & Wildlife Service – Lower Great Lakes Fishery Resources Office (USFWS), the Ontario Ministry of Natural Resources (OMNR), the U.S. Geological Survey – Great Lakes Science Center (USGS), and Cornell University. The program has also allowed us to (1) provide a benchmark for comparison to evaluate changes in the lower food web of Lake Ontario, and (2) link with closely allied programs such as current Sea Grant projects assessing changes in Lake Ontario's mysid population, and the benthification of Great Lakes ecosystems. The biomonitoring variables we have chosen to examine contribute to research on Lake Ontario's coastal areas and embayments which are crucial to understanding the coupling between ontogenetic patterns of habitat utilization by fish and whole-lake predator-prey interactions, and for understanding the role of inshore habitats in food web dynamics.

Report Objectives

We measured total phosphorus (TP), soluble reactive phosphorus (SRP), chlorophyll *a* (Chl *a*), water temperature, Secchi depth, zooplankton density, zooplankton size, and zooplankton biomass. With these data, we addressed the following questions:

(1) *Embayment - Nearshore - Offshore Comparisons*: Do biomonitoring variables vary between embayment, nearshore, and offshore habitats?

(2) *East-West Comparisons*: Do biomonitoring variables vary from east to west in nearshore and offshore habitats?

(3) *Seasonal and Year-to-Year Variability in Embayment and Nearshore Habitats*: Do biomonitoring variables in embayment and nearshore habitats differ significantly throughout the season? Do trends vary between embayments and nearshore habitats from year-to-year?

(4) *Relationships Among Variables*: Are any biomonitoring parameters related to each other?

(5) *Zooplankton Community Dynamics*: Does the biomass of major zooplankton groups differ between embayment, nearshore, and offshore habitats? Do trends vary seasonally between embayments and nearshore habitats? Does zooplankton community structure suggest a healthy balance between predatory and prey fish?

(6) *Cercopagis pengoi*: How was *C. pengoi* distributed lakewide during mid-summer to fall? Are there any trends in spatial distribution? Has *C. pengoi* had any major effects on the zooplankton community?

(7) *Bythotrephes longimanus* (formerly *cederstroemi*): How was *B. longimanus* distributed lakewide during mid-summer to fall? Are there any trends in spatial distribution? Has *B. longimanus* had any major effects on the zooplankton community? What are the implications of *B. longimanus* presence or absence on alewife populations?

(8) *Erie/Ontario Nearshore Comparisons*: How do biomonitoring variables differ between nearshore habitats in easternmost Lake Erie and Lake Ontario?

Methods

Sampling

The R/V's Kaho and Seth Green collected water and zooplankton samples during April through October 2006. All samples collected by these vessels were considered to be offshore for habitat comparisons. Offshore water depths ranged from 15m to 207m. The deepest nearshore site was less than 15m throughout the sampling season. Offshore sampling totaled 39 samples taken on 25 dates.

Water and zooplankton samples, as well as water temperature and Secchi depth data, were collected from six nearshore and two embayment sites during the May to October sampling season. The eastern nearshore sampling locations (Galloo Island Lake, Chaumont Bay Lake, Sandy Pond Lake), and western nearshore locations (Niagara River East Lake, Niagara River West Lake, and Oak Orchard Lake), along with the two eastern embayment sampling sites (Chaumont Bay and Sandy Pond Bay) were sampled biweekly. Figure 1 shows a map of sampling locations. The sampling sites at Sodus Bay were not sampled in 2006.

Water Chemistry

Water samples were collected for analysis of chlorophyll *a* (Chl *a*) and two phosphorus fractions: total phosphorus (TP) and soluble reactive phosphorus (SRP). Each sample was obtained by using an integrated water sampler (1.9cm inside diameter Nalgene tubing) lowered to a depth of 10m or the bottom minus 1m where total depth was less than 10m. The tube was then closed off at the surface end and the column of water transferred to 2L Nalgene containers. From each sample a 100 mL unfiltered aliquot sample was frozen for later analysis of TP (Menzel and Corwin 1965). We also filtered 1-2L 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 100mL sample of filtered water was also frozen for later analysis of SRP (Strickland and Parsons 1972).

Quality Assurance - Quality Control

In 2006, Quality Assurance and Quality Control (QAQC) analyses were conducted for TP and SRP. Water samples were collected from embayment and nearshore habitats using the standard sampling methods.

In July, 10 aliquots of raw water were taken from one sample for TP analysis. An additional 10 aliquots of filtered water were taken from the same sample for SRP analysis. One subset of these samples was analyzed at CBFS; another subset was analyzed at the Upstate Freshwater Institute (UFI), an EPA certified laboratory located in Syracuse, NY, for comparison with CBFS results. In the event that significant differences ($p<0.05$) arose between CBFS and UFI laboratory results, an adjustment equation would have been generated and applied to CBFS results (TP and/or SRP) in order to account for those discrepancies. The adjustment equation is a regression equation that adjusts the CBFS data in relation to the UFI data.

In 2006, we also conducted replicate sampling for analyses of TP, SRP, and Chl *a*. Three different samples (triplicates) were collected at each nearshore and embayment location twice in August. From each of the three samples, one aliquot was taken for TP, one for SRP, and one for Chl *a* analysis. The samples were analyzed at CBFS to determine the amount of variability between samples.

Zooplankton

We measured several zooplankton parameters: total density (#/L), size (mm), and biomass (µg/L), as well as *C. pengoi* biomass and total biomass (expressed as proportion of total) of five subgroups of zooplankton. Zooplankton samples were collected with a standard 0.5m diameter, 153µm mesh nylon net. At most embayment and nearshore sites, we strained a 10m water column. At offshore sites, we sampled a 5-40m water column. 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 replicate samples were collected per site on each date.

In the CBFS laboratory, each sample was strained through a 1.02mm mesh cup to separate *C. pengoi* and other larger organisms (>1mm in length) from smaller zooplankton (<1mm). This was done because *C. pengoi* form clumps in the sample, making the usual random subsampling of 1mL samples inappropriate. For each sample that contained clumps of *C. pengoi*, two analyses were performed, one on the smaller zooplankton and one on the larger zooplankton (including *C. pengoi*) that were caught in the 1mm mesh strainer. The larger zooplankton were measured and enumerated by subsampling at least 100 organisms from a gridded, numbered petri dish in which the sample had been homogeneously separated.

The subsample 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. The zooplankton were measured using the digitizing tablet and identified to species, excluding nauplii and copepodites (Pennak 1978, Balcer *et al.* 1984). To calculate the total number of large crustaceans and *C. pengoi* in the clumped part of the sample, we used a ratio of wet weights of the subsample to wet weights of the total sample. Wet weights were determined using a Sartorius balance. For the smaller sized zooplankton samples, we counted and measured at least 100 organisms from one or more 1mL random subsamples using the same microscope and digitizer technique. [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 Friedman 1994).]

We used length:dry-weight regression equations (CBFS unpublished data) to estimate zooplankton biomass. Biomass of *C. pengoi* was estimated using two different regression equations. Nearshore samples were analyzed using the regression $\ln W = 1.7164 + 2.3703 \ln L$, where W represents biomass (µg) and L represents length (mm). Offshore samples were analyzed using the regression $\ln W = 1.3690 + 2.7686 \ln L$. Each of these regressions is based on the original length:dry weight regressions (determined using unpreserved specimens) established in 1998, but that have since been modified to increase the estimated weight by 42% to compensate for biomass loss due to preservation (Giguere *et al.* 1989).

Data Analyses

We employed the following analyses to address the above objectives:

(1) Spatial Variability:

For each of the eight embayment and nearshore study parameters (TP, SRP, Chl *a*, water temperature, Secchi depth, zooplankton density, size, and biomass), we compared the biweekly averages between the two habitats using a paired t-test for means. For the comparisons between offshore, nearshore, and embayment habitats, we examined each of seven study parameters (TP, SRP, Chl *a*, water temperature, zooplankton density, size, and biomass) with paired two-sample t-tests assuming unequal variances. These comparisons were made with data that were collected during the same sampling week. Zooplankton density and biomass were log transformed, and each zooplankton relationship was considered significant following the Bonferroni adjusted $\alpha=0.0167$ ($p<0.0167$). Differences in each chemical / physical relationship were considered significant at $p<0.05$.

(2) East-West Comparisons:

Nearshore east-west comparisons were made for the eight study parameters (TP, SRP, Chl a, Secchi depth, water temperature, zooplankton density, size, and biomass). Comparisons were made between eastern sites (Galloo Island Lake, Chaumont Bay Lake, Sandy Pond Lake) and western sites (Niagara East Lake, Niagara West Lake, Oak Orchard Lake) using the biweekly data from May - October. We employed paired t-tests with untransformed (TP, SRP, Chl *a*, Secchi depth, water temperature, zooplankton size) and log (x+1) transformed (zooplankton density and biomass) mean biweekly values to test for east-west differences. We considered each relationship significant for two-tailed tests at $p< 0.05$.

East-west differences between offshore sites were examined for seven study parameters (TP, SRP, Chl *a*, water temperature, zooplankton density, size, and biomass). Offshore sites included all samples taken by the R/V Seth Green or R/V Kaho, all of which had depths greater than 15m. The east-west dividing line was 77.8^{o} W longitude (Figure 1). T-tests assuming unequal variance were used to examine differences between east and west locations for log-transformed (zooplankton density and biomass) and untransformed (TP, SRP, Chl *a*, water temperature and zooplankton size) data. Water chemistry and zooplankton comparisons were made with July data. Each relationship was considered significant for two-tailed tests at $p<0.05$.

(3) Seasonal and Year-to-Year Variability in Embayment and Nearshore Habitats:

We examined eight study parameters (TP, SRP, Chl *a*, Secchi depth, water temperature, zooplankton density, size, and biomass) for seasonal differences in both embayment and nearshore habitats. Year-to-year differences for TP, SRP, Chl *a*, Secchi depth, and water temperature were tested using a paired two sample t-test comparing 2005 and 2006 biweekly average data. We considered each relationship significant for two-tailed t-tests at $p<0.05$.

(4) *Relationships of Variables*:

We investigated several nearshore and embayment biomonitoring parameters for potential relationships. We examined the influence of TP, SRP, and water temperature on

Chl *a* using linear regression analysis (Zar 1984) with untransformed data.

(5) Zooplankton Community Dynamics:
We divided zooplankton into the following seven 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 quadrilangula, Chydorus sphaericus, Leptodora kindtii, Diaphanosoma sp., Alona sp., Holopedium gibberum, Polyphemus pediculus, Camptocercus sp.), Bythotrephes longimanus* (formerly *cederstroemi*); and *Cercopagis pengoi.* We compared average biweekly biomass proportions of each group between embayment and nearshore habitats using a paired t-test to determine differences in community composition between these areas. In addition, we compared the biomass of each group in July using t-tests assuming unequal variance on log (x+1) transformed data for embayment, nearshore, and offshore (water depth of 25m or more) areas.

(6) Cercopagis pengoi:
The offshore samples collected in July by the R/Vs Kaho and Seth Green provided a comprehensive view of spatial distributions of *C. pengoi* in 2006. For this time period, offshore (water depth of 25m or more) data were analyzed using t-tests assuming unequal variance on log (x+1) transformed *C. pengoi* density and biomass to assess east-west differences in spatial distribution. In addition, log (x+1) transformed mean biweekly values of *C. pengoi* density and biomass were analyzed using paired t-tests to look for an east-west difference among nearshore sites. Comparisons of *C. pengoi* density, average size, and biomass in offshore, nearshore, and embayment habitats were performed using t-tests assuming unequal variance for the following pairs of sampling periods: late August 1998 and August 1999, August 1999 and July 2000, July 2000 and August 2001, August 2001 and 2002, August 2002 and July 2003, July 2003 and mid-July to mid-August 2004, mid-July to mid-August 2004 and July 2005, and July 2005 and 2006. Finally, we compared average densities of bosminids in the summer sampling period over the nine years of this biomonitoring project (1995-2006) to further assess changes in community structure**.**

(7) Bythotrephes longimanus:
The offshore samples collected in September and October by the R/Vs Kaho and Seth Green provide a view of spatial distributions of *B. longimanus* in 2006. July offshore (water depth of 25m or more) data were analyzed using t-tests assuming unequal variance on log (x+1) transformed *B. longimanus* density and biomass to assess east-west differences in spatial distribution. In addition, log (x+1) transformed mean biweekly values *B. longimanus* density and biomass were analyzed using paired t-tests to look for an east-west difference among nearshore sites. We summarized *B. longimanus* density, average size, and biomass in embayments, nearshore, and offshore habitats over the years 1998-2006 to put data from this year in a historical context.

(8) Erie/Ontario Nearshore Comparisons:
In 2006 a site near Buffalo (in Lake Erie) was sampled eleven times (May-October) to assess potential Lake Erie contributions to Lake Ontario via the Niagara River. Paired t-tests were performed on data collected from the Buffalo site and on average nearshore data from Lake Ontario for the corresponding time period to assess potential differences. This analysis was performed on six study parameters: Chl a, TP, SRP, total zooplankton density, size, and biomass. Zooplankton density and biomass were log (x+1) transformed.

Results

QAQC

In 2006, QAQC analyses were conducted for July TP and SRP samples. A comparison of samples analyzed at CBFS with those at Upstate Freshwater Institute (UFI), showed that TP values were not significantly different (p=0.531). SRP samples did show a significant difference (p<0.006). However, some SRP values were below minimum detection levels for UFI and high sample variability prevented any meaningful adjustment to the accepted regression equation.

The analysis of August embayment and nearshore TP, SRP, and Chl *a* triplicate samples showed that slightly less than half of the samples had a coefficient of variation (CV) less than the predetermined acceptance level of 10%. The triplicate samples which were found to have a CV greater than 10% were deemed acceptable due to: (1) the low levels of TP, SRP, and Chl *a* detected in Lake Ontario, and (2) the minimal range of resulting values and corresponding standard errors within a given set of triplicate samples. Consequently, we pooled triplicate samples for each August replicate sampling effort and reported an average value for each TP, SRP, and Chl *a*, concluding that a single sample adequately reflects the conditions at the time of sampling throughout the entire field season.

Embayment-Nearshore-Offshore Comparisons:

In 2006 we observed several significant spatial differences between embayment, nearshore, and offshore habitats.

Embayment-Nearshore Comparisons of Secchi depth, Chl a, TP, SRP, and water temperature: Water clarity measured using a Secchi disc was consistently greater in nearshore areas than in embayment sites, as was the case in 2005, with the exception of the month of October. Unlike 2005, the May through October biweekly average Secchi depth for embayments (4.1m) was not significantly shallower (p>0.07) than the nearshore habitat average of 5.3m (Figure 2). The decrease in the difference between embayment and nearshore sites may be due to the exclusion of the Sodus Bay and Sodus Lake sites which were sampled in 2005 but not in 2006. If these sites are excluded from 2005 data, the embayment and nearshore Secchi depths are significantly different in both years. In 2006, mean biweekly SRP concentrations were significantly higher (p<0.002) in embayments than in nearshore habitats (Figure 4A). TP values were also found to be significantly higher (p<0.002) in embayments than in the nearshore habitats, with average May through October concentrations of 17.6µg/L and 7.9µg/L respectively (Figure 3B). Average embayment Chl *a* concentrations (8.6µg/L) were nearly five times greater than in the nearshore habitats (1.8µg/L) (Figure 3A). Water temperatures averaged 18.7^{o}C in embayments and 17.3^{o}C in nearshore habitats (Figure 4B).

Embayment-Nearshore-Offshore Comparisons of July Chl a, TP, SRP and water temperature: The average Chl *a*, TP, SRP, and water temperature of the embayment, nearshore, and offshore (collected by R/V Kaho and R/V Seth Green) sites for July are noted in Table 1. The average Chl *a* concentrations for offshore and nearshore samples were 2.4µg/L and 2.8µg/L respectively, compared to 8.3µg/L in embayments. Average TP concentrations were 7.8µg/L (offshore), 8.5 µg/L (nearshore), and 18.9µg/L (embayment). Offshore SRP averaged 2.0µg/L, compared to 1.8µg/L in the nearshore habitats, and 2.3µg/L in embayments. Water temperature for the offshore averaged 16.8^{o}C while the nearshore average water temperature was 21.1^{o}C, and the embayments averaged 24.8^{o}C.

Zooplankton Embayment – Nearshore - Offshore Comparisons: In 2006 we found May through October zooplankton density (p<0.001) and biomass (p<0.01) to be significantly greater in embayments (89.5/L, and 79.9µg/L respectively) than in nearshore sites (10.5/L and 21.1µg/L respectively) (Table 2, Figure 5A&C). Average size of zooplankton was significantly (p<0.0001) smaller in embayment sites (0.38mm) than in nearshore sites (0.54mm) (Table 2, Figure 5B).

During July, the average embayment zooplankton density and biomass (140.3/L, and 134.8µg/L, respectively) were not significantly different than the density (4.1/L), and biomass (10.8µg/L) of nearshore samples, but the embayment average size (.39mm) was significantly ($p<0.01$) less than the average size of nearshore samples (0.57mm, Table 3). The average size of zooplankton of offshore samples (0.77mm) was significantly greater than the average size of nearshore samples ($p<0.001$) and embayment samples ($p<0.001$). Offshore zooplankton biomass (13.7µg/L) was significantly different than biomass of nearshore and embayment samples (Table 3). Zooplankton density of offshore samples (3.5/L) was not significantly different than density of nearshore samples or embayment samples (4.1/L and 140.3/L respectively).

East - West Comparisons

In addition to examining spatial differences between habitats (embayment, nearshore, and offshore), we examined regional differences between the east and west sites of Lake Ontario.

East-West Nearshore Comparisons of Secchi depth, Chl a, TP, SRP and water temperature: East-West nearshore comparisons were made using biweekly data from May through October. Mean Secchi depth was found to differ significantly ($p<0.0003$) between eastern and western sampling sites in 2006. Western nearshore Secchi depths averaged 4.5m, while eastern nearshore Secchi depths averaged 6.4m (Figure 6D). No significant difference ($p>0.1$) was found between eastern and western nearshore temperatures in 2006 with average values of 17.5 ^{o}C in the eastern nearshore, and 16.7 ^{o}C in the western nearshore. There were also no significant differences observed in Chl *a*, TP, SRP between eastern and western sites. This pattern is similar to that seen in 2005 (Table 4). The average Chl *a* concentrations were 1.7µg/L in the eastern and 1.9µg/L western nearshore sites. Average TP concentrations were 7.3µg/L (east) and 8.5µg/L (west). Eastern nearshore SRP concentrations averaged 2.2µg/L and western sites averaged 2.0µg/L.

East-West, North-South Offshore Comparisons of Chl a, TP, SRP, and water temperature:

The comparisons of the offshore biomonitoring study parameters from north to south and east to west yielded no significant differences.

East-West Nearshore Zooplankton Comparisons: No significant differences were found between eastern and western regions of nearshore Lake Ontario for average size, density, and biomass of zooplankton, or for the density and biomass of *Cercopagis pengoi* and *Bythotrephes longimanus*. (Table 5).

East-West Offshore Zooplankton Comparisons: In the July east-west comparison for offshore sampling stations, there were not any significant differences. Mean density was generally greater in the west than the east, but due to smaller average size in the west the biomass was also generally smaller, although these differences were statistically insignificant (Table 6). *Cercopagis pengoi* density and biomass were not significantly different between eastern and western sites (Table 6, Figures 7, 8 & 9).

Seasonal and Year-to-Year Variability in Embayment, Nearshore and Offshore Habitats

In 2006, we observed seasonal differences in Secchi depth, Chl *a*, TP, SRP, water temperature, and all three zooplankton parameters in embayment, nearshore and offshore habitats.

Secchi depth, Chl a, TP, SRP, and water temperature: Average water clarity of nearshore habitats in 2006 decreased relative to early summer (May and June) in July and August, with averages of 4.1m and 4.3 m respectively (Figure 2). Although the October average also decreases to 4.9m this is likely due to a lack of October data for a few of the deeper sites. The sharpest decrease in clarity was at the Oak Orchard Lake site, which went from a maximum Secchi depth of 10.3m in late May to a minimum of 2.8m by mid-August. Lakewide nearshore Secchi depths ranged from a maximum of 10.4m (early October, Chaumont Bay Lake) to a minimum of 1.7m (late May, Sandy Pond Lake). Embayment Secchi depths were shallowest in August and deepest in October. Embayment Secchi depths ranged from 0.9m (Sandy Pond Bay, early August) to greater than 8.5m (Chaumont Bay, early October).

Chl *a* concentrations were higher in embayments than in nearshore areas, exhibiting an increasing trend from May to September, then decreasing into October. In 2006, nearshore concentrations increased from May to July and then declined gradually throughout the remaining sampling season (Figure 3A). Embayment Chl *a* concentrations peaked in August at 26.1µg/L, while nearshore sites peaked in July at 2.8µg/L. Embayment Chl *a* concentrations varied from <0.2µg/L in Chaumont Bay (late May) to 51.0µg/L in Sandy Pond Bay (early August). Nearshore Chl *a* ranged from less than 0.2µg/L (Sandy Pond Lake, early May) to more than 9.9µg/L at the same site in late August. Offshore Chl *a* averaged 2.2µg/L (Figure 3A), ranging from 0.2µg/L to 7.3µg/L.

TP concentrations were higher in embayments than nearshore habitats, similar to 2005 (Figure 3B). Monthly average embayment TP concentrations increased from May to August, while nearshore TP concentrations remained relatively constant during the same period. From August through October, embayment TP concentrations decreased substantially from their peak, but the nearshore values remained relatively unchanged. Average embayment TP values peaked in August at 31.2µg/L and nearshore concentrations reached 8.5µg/L in October. Embayment TP ranged from 5.8µg/L at Chaumont Bay (early September) to 52.3µg/L at Sandy Pond Bay (mid-July). Nearshore TP ranged from 3.3µg/L at Sandy Pond Lake (early September) to 13.6µg/L at Oak Orchard Lake (mid-September). The average offshore TP concentration was 7.1µg/L (Figure 3B), ranging from 2.8µg/L to 12.4µg/L.

Mean monthly embayment and nearshore SRP concentrations were both fairly constant from May through July and increased later in the 2006 sampling season (Figure 4A). Nearshore SRP concentrations had a minimum of 1.0µg/L at Sandy Pond Lake (early June) and a maximum of 5.1µg/L at Galloo Island Lake (early October). Embayment SRP ranged from 1.6µg/L at Chaumont Bay (early June) to 5.3µg/L (early October) at the same site. Monthly SRP concentrations in embayment and nearshore sites peaked in October (4.6µg/L and 3.2µg/L; respectively). Offshore sites peaked in September at 2.9µg/L.

Water temperatures for both embayment and nearshore habitats exhibited a similar seasonal pattern: warming into August, then cooling into fall (Figure 4B). Monthly average temperatures peaked in July at 24.8°C for embayments and in August at 23.2°C for nearshore sites. Embayment temperatures ranged from a minimum of 11.1°C in mid-October at Chaumont Bay to a maximum of 26.9°C in late July in Sandy Pond Bay. Nearshore temperatures ranged from 8.5°C in early May at Oak Orchard Lake to 25.3°C at Chaumont Bay Lake during early August. Offshore temperatures exhibited a similar seasonal trend to that seen in the embayments and nearshore, peaking at 16.8°C in July.

We also compared 2005 and 2006 annual means derived from biweekly data (secchi depth, Chl *a*, TP, SRP, and water temperature) in both embayment and nearshore habitats (Figures 2, 3 and 4). While embayment Secchi depths did not differ significantly between years, nearshore Secchi depth decreased significantly from 6.7m in 2005 to 5.3m in 2006 ($p<0.002$). This difference is likely due in part to the lack of data, in 2006, for the Sodus Bay Lake site, which usually had Secchi depths on the high end of the nearshore range. Embayment biweekly Secchi values averaged 3.4m in 2005 compared to 4.0m in 2006 ($p>0.27$).

Chl *a* concentrations were not found to be significantly different between 2005 and 2006 for either embayment or nearshore sites ($p>0.99$, $p>0.06$ respectively). Average embayment Chl *a* was 8.6µg/L in both 2005 and 2006. The 2006 average nearshore biweekly Chl *a* concentration was 1.8µg/L, compared with its 2005 value of 1.4µg/L.

Total phosphorous concentrations in embayments in 2006 were slightly lower (17.6µg/L) than in 2005 (18.0µg/L). The nearshore TP average was 7.9µg/L for both years. The difference in the embayment TP was insignificant ($p>0.89$).

After increasing in 2005 relative to previous years, embayment and nearshore SRP concentrations were both found to be significantly lower in 2006 compared to 2005. The embayment SRP mean in 2006 was 2.8µg/L compared to 5.7µg/L in 2005 ($p<0.002$). The nearshore SRP mean was 2.1µg/L in 2006, compared to a 2005 mean of 4.1µg/L ($p<0.0002$).

Water temperatures did not vary significantly between 2005 and 2006 in either embayment or nearshore habitats ($p>0.05$ and $p>0.5$ respectively). The biweekly embayment temperature average was insignificantly lower in 2006 (18.7^{o}C) than in 2005 (20.3 ^{o}C). The biweekly nearshore average temperature in 2006 (17.3^{o}C) was not significantly less than the 2005 average (17.7 ^{o}C).

Zooplankton: Zooplankton densities were highest in embayments during the entire 2006 sampling season, peaking in early July (Figure 5A). The lowest zooplankton densities occurred at offshore sites in May. For individual dates and habitats, the lowest nearshore zooplankton density was 0.51/L at the Chaumont Lake site in late May and the lowest embayment density was 3.87/L at Chaumont Bay in early July. The highest densities were 72.0/L at Oak Orchard in early September and 424.4/L at Sandy Pond Bay in early June. At offshore sites, the lowest density was seen in late April (0.10/L) and the highest was observed in early June (89.3/L).

Zooplankton average size at embayment sites was highest in early August (0.45mm) and lowest in late August (0.29mm; Figure 5B). At nearshore sites, average size was highest in early July (0.60mm) and lowest in late June (0.42mm). Offshore mean zooplankton size was highest in early May (0.88mm) and lowest in early August (0.58mm) (Figure 5B). Figure 10 shows mean monthly zooplankton size for each habitat in 2005 and 2006. Offshore average size was greater than both embayment and nearshore average size for each time period data were available, with the exception of nearshore habitats in September 2005. Offshore average size remained high in 2005 through August before decreasing to near 0.60mm in September and October. In 2006 the offshore average size fluctuated then stabilized at 0.64mm in September and October. Embayment and nearshore seasonal trends in zooplankton lengths in 2005 were generally similar to the trends in 2006 (Figure 10).

Mean biomass from May through October was highest at the embayment sites in early July (192.9 µg/L; Figure 5C). The lowest mean biomass occurred at the nearshore sites in early May (2.7 µg/L). Mean biomass of the zooplankton community in embayment areas was greater than in nearshore and offshore habitats during the majority of the sampling season. The nearshore mean biomass was greater in early September and mid-October and the offshore mean biomass was greater in early June and mid-September. The maximum zooplankton biomass at a single site on a sampling date in embayment and nearshore habitats was 381.9µg/L in early July at Sandy Pond Bay, and 157.8 µg/L in mid-September at Oak Orchard, respectively. The minimum biomass at an individual site on a single date for embayments was 3.8 µg/L at Chaumont Bay in early July, while it was 0.60 µg/L for nearshore sites at Chaumont Lake in late May. Offshore mean biomass values were generally similar to nearshore values, with nearshore values slightly larger in early August and mid-October (Figure 5C).

Relationships Among Variables

We examined the relationships of TP, water temperature, and SRP with Chl *a* using a linear regression analysis of biweekly data for embayment and nearshore sites (Figure 11). The 2006 biweekly water temperature-Chl *a*-relationship and TP-Chl *a* relationship were found to be positively correlated in both embayment and nearshore habitats. Unlike 2005, the SRP-Chl a relationship was not positively correlated in both habitats and there was no correlation between these variables. When Chl *a* was regressed against water temperature, temperature explained over 23% of the variability in embayment Chl *a* (insignificant at $p>0.11$), and 64% of the variability in nearshore habitats (significant at $p<0.002$) (Figure 11A). When Chl *a* was regressed against TP, we found that TP significantly explained ($p<0.05$) 88% of the Chl *a* variability in embayments, and insignificantly ($p>0.44$) explained 6% of Chl *a* variability in nearshore areas (Figure 11B).

Zooplankton Community Dynamics

Embayment - Nearshore: In 2006, two zooplankton taxa significantly differed in proportion of total biomass between embayments and nearshore sites (Table 2). Bosminids had a significantly greater proportion of biomass in embayments ($p<0.005$), while calanoid copepods had a significantly greater proportion in nearshore habitats ($p<0.001$). The proportion of *C. pengoi* biomass was on average greater in the nearshore sites (0.11) than embayment sites (0.001), but the difference was not statistically significant (Table 2).

The bosminid proportion of total biomass in nearshore habitats peaked in late June (Figure 12A). Bosminid proportion of biomass in embayments fluctuated between 0.18 and 0.62 during the first half of the sampling season, then increased beginning in August, reaching a high of 0.66 in mid-August. Daphnids peaked in percent biomass in mid-August in the nearshore and in early June for embayment sites (Figure 12B). Calanoid copepod contribution to total zooplankton biomass peaked at 0.39 in late July in embayments before dropping to zero contribution for the last third of the season. In the nearshore calanoid copepod contribution steadily increased from early July until it peaked mid-September before declining to low levels at the end of the season (Figure 12C). The proportions of cyclopoid copepods in nearshore habitats tended to steadily increase throughout the season before it plateaued at the end of the season at about 0.4. In embayment habitats the proportion of cyclopoid copepods initially peaked in late August before declining and then increasing to a maximum at the end of the season. Cyclopoid proportion of biomass reached a low for nearshore sites in late May, and was low for embayments for the first half of the season (Figure 12D). *Cercopagis pengoi* was rare in the first three and last four sampling weeks, but peaked in nearshore sites in early July, reaching 39 percent of total zooplankton biomass. *C. pengoi* percentage of total biomass peaked in early July in embayments, reaching 6.8 percent. “Other” cladocera were the greatest contributors to total zooplankton biomass at the beginning of the season. Other cladocera proportion of total biomass then declined in both nearshore and embayment sites before increasing again in both habitats at the end of the season (Figure 12F).

Offshore: Calanoid and cyclopoid copepods dominated the offshore community during May and June 2006. In early July, *Cercopagis pengoi* was the largest single contributor to zooplankton biomass, with a proportion of total biomass of 0.79, while cyclopoid copepods had a proportion of total biomass of 0.13. “Other” cladocerans had their highest proportion of total zooplankton biomass in early August (0.31). Cyclopoid copepods contributed the greatest proportion of zooplankton biomass in early May, early June and mid-October (0.56, 0.85, and 0.47, respectively), while daphnids contributed the most to biomass in mid-September (0.38). Of the species present, all except *B. longirostris* contributed to an overall large offshore zooplankton average size. In offshore habitats, the dominant cyclopoid copepod *D. thomasi* annual average size was 0.73mm, *D. retrocurva* annual average size was 0.66mm, *H. gibberum* annual average size was 0.51mm, and calanoid copepod annual average size was 1.15mm. Other less frequently detected species that contributed to large zooplankton average size when present in offshore habitats were *C. pengoi, B. longimanus*, and *L. kindti*.

Embayment - Nearshore - Offshore: In July there were two notable differences between components of the zooplankton community in the three different habitats (Table 3). Bosminid biomass values at offshore sites (0.75μg/L) were significantly lower than bosminid embayment biomass (30.2μg/L) ($p<0.01$) (Table 3, Figure 13). *Cercopagis pengoi* biomass was significantly higher at offshore sites (6.8μg/L), and nearshore sites (6.0μg/L), compared to embayment sites (0.5μg/L) ($p<0.01$, and $p<0.001$, respectively) (Table 3).

<u>*Cercopagis pengoi*</u>

Offshore and nearshore biomass and density of *C. pengoi* in late July are presented in Figures 7A and 8A, respectively. During July 2006, average densities of *C. pengoi* at offshore, nearshore, and embayment sites were 1.03/L, 0.67/L, and 0.06/L, respectively (Figure 14A). There were no statistically detectable differences in east-west nearshore data during the entire sampling season for *C. pengoi* density or biomass (Table 5). No statisticant differences in the offshore east-west comparisons of *C. pengoi* density and biomass were found (Table 6).

Longitude did not explain an appreciable amount of the variation in *C. pengoi* distribution in Lake Ontario during July 2006 (Figure 9A).

Statistical differences were detected in *C. pengoi* density, average size, and biomass when offshore samples from August 1999 and July 2000 were compared (Table 7). *C. pengoi* density, average size, and biomass in offshore habitats during July 2000 were all significantly lower (all $p<0.001$) than in offshore habitats in August 1999 (Table 7). However, *C. pengoi* average size, and biomass significantly increased again in offshore habitats in August 2001 (both $p<0.05$) (Table 7). In August 2001 offshore average size was also significantly greater than in August 2002 ($p<0.01$). In July 2003 offshore *Cercopagis* samples, significant decreases were found in density ($p<0.01$), and biomass ($p<0.001$) when compared to August 2002 data (Table 7). Statistical differences were detected in all three offshore *C. pengoi* parameters between July 2003 and mid-July to mid-August 2004. Mean density, average size, and biomass each increased ($p<0.001$, $p<0.002$, and $p<0.001$, respectively) (Table 7). No significant changes occurred in *C. pengoi* density, average size, or biomass between any pair of consecutive years sampled at nearshore habitats between 1999 and 2004, or between 1999 and 2006 for embayment habitats. When mid-July to mid-August 2004 and July 2005 nearshore samples were compared, *C. pengoi* density was significantly greater in 2004 ($p<0.03$), whereas average size was significantly greater in 2005 ($p<0.02$). No significant changes occurred in offshore *C. pengoi* density, average size, or biomass between mid-July to mid-August 2004 and July 2005. Nearshore density and biomass significantly increased between July 2005 and July 2006 (both $p<0.02$). Offshore average size significantly decreased in 2006 ($p<0.05$). No significant changes occurred in *C. pengoi* density, average size, or biomass between any pair of consecutive years sampled at embayment habitats between 1999 and 2006 (Table 7).

Trends in the mean densities of bosminids during the July/August offshore sampling efforts over the past eleven years of this biomonitoring project were examined to determine if the arrival of *C. pengoi* in Lake Ontario was associated with a change in zooplankton community structure. After more than a 20-fold increase in bosminid density from 1995 to 1996 and 1997, values plummeted in 1998 when *C. pengoi* first arrived (Figure 15). Even though the density remained low in 1999, it increased to 18 bosminids per liter in 2000 as *C. pengoi* densities simultaneously decreased. However, in 2001 bosminid density once again declined dramatically to five bosminids per liter, and appeared to be associated with an increase of offshore *C. pengoi* density. *C. pengoi* offshore density increased from 0.21/L in 2001 to 0.36/L in 2002 and was associated with a decline in offshore bosminid density to 3.2/L, again suggesting a relationship with increased *C. pengoi* density. July of 2003 saw offshore bosminid densities increase to 13.4/L while *C. pengoi* offshore density (0.05/L) was considerably lower than in August 2002 (0.36/L). During mid-July to mid-August 2004, offshore bosminid density decreased to 3.8/L and *C. pengoi* densities increased to 0.44/L. In July 2005, bosminid density again decreased to 0.62/L while *C. pengoi* density also decreased to 0.26/L. In July 2006, bosminid density remained low at 0.63/L, while *C. pengoi* density increased to 1.03/L.

Bythotrephes longimanus

Offshore and nearshore biomass and density of *B. longimanus* in September and October of 2006 are presented in Figures 7B and 8B, respectively. After detection in only one sample in 2002, no detection in 2003, and three samples in 2004, *B. longimanus* was detected in 34 samples (23%) throughout the 2005 season. The occurrence of detection increased in 2006 to 43 samples (36%). In 2005 offshore habitats, *B. longimanus* was detected in 11 samples (35%) and in 13 samples (50%) in 2006 between June and October for each respective year. The average size of *B. longimanus* in offshore samples in 2005 was 2.10mm, and in 2006 was 2.61mm (Table 8). The maximum biomass of *B. longimanus* from a single offshore sample was 7.8µg/L at Smokey Point on October 20, 2005, and was 11.2µg/L at Oak Orchard on October 18, 2006. In nearshore habitats, *B. longimanus* was detected in 18 samples (24%) and in 21 samples (33%) from May through October in 2005 and 2006, respectively. The average size of *B. longimanus* in nearshore samples was 2.19mm in 2005 and 2.52mm in 2006. The maximum biomass of *B. longimanus* from a single nearshore sample was 4.7µg/L at Sandy Pond on September 6, 2005 and was 14.2µg/L at Niagara River West Lake on September 28, 2006. In embayments, *B. longimanus* was detected in 5 samples for both 2005 and 2006 (63%, and 83%, respectively) in September and October. The average size of *B. longimanus* in embayment samples was 2.22mm in 2005 and 2.53mm in 2006. The maximum biomass of *B. longimanus* from a single embayment sample was 2.9µg/L at Chaumont Bay on September 1, 2005 and 1.1µg/L at Chaumont Bay on August 4, 2006. Longotude did not explain an appreciable amount of the variation in *B. longimanus* distribution in Lake Ontario in September-October 2006 (Figure 9B).

Erie - Ontario Nearshore Comparisons

The comparison of Lake Erie (at Buffalo) and Lake Ontario nearshore data yielded no significant differences in Chl *a*, TP, SRP, or zooplankton average size. Zooplankton density and biomass at the Buffalo site was found to be significantly greater ($p<0.001$) than nearshore Lake Ontario biomass.

Significant Research Findings

Embayment-Nearshore-Offshore Comparisons

In 2006, embayments continued to be very productive habitats in comparison to nearshore and offshore areas of Lake Ontario. In embayments, TP concentrations from May to October were slightly more than 2.0 times higher than those in nearshore habitats, and almost 2.5 times higher than concentrations at the offshore sites (Figure 3B). Only one of the TP concentrations in offshore sites in 2006 was found to exceed the target value (10µg/L) set for the offshore pelagia by the Great Lakes Water Quality Agreement (GLWQA). The R/V Seth Green collected a sample from the southwest quadrant of the lake in late July with a TP value of 16.2 µg/L. Chl *a* concentrations (May through October, 2006) for embayments were 4.6 times greater than for nearshore habitats (Figure 3A). Embayment Chl *a* was also 3.9 times greater than the offshore Chl *a* during the same time period.

May through October 2006 SRP concentrations for embayments were 1.4 times higher than for nearshore habitats. Embayment SRP concentrations were also over 1.3 times higher than offshore SRP (Figure 4A).

Annual Secchi depths were 1.4 times deeper at nearshore sites than embayments, corresponding with the elevated Chl *a* concentrations of embayment habitats.

In 2006, embayment sites had over eight times the zooplankton density and over three times the biomass of nearshore sites, but had a significantly lower average zooplankton size than nearshore sites (Table 2). For July 2006, embayment density was over 34 times greater than nearshore density and over 40 times greater than offshore density. Embayment biomass was over 12 times greater than nearshore biomass, and over 9 times the offshore biomass. Embayment average size was significantly smaller than both nearshore and offshore average size (Table 3).

East-West / North-South Comparisons

The east-west comparisons of bi-weekly study variables for nearshore sites yielded a significantly greater ($p<0.0003$) Secchi depth (1.4 times greater) in the eastern half of Lake Ontario. All eastern sites had seasonal means greater than 5m, the deepest mean among the western sites (Oak Orchard Lake). Galloo Island Lake had a Secchi depth over 1.5 times greater than Oak Orchard Lake (Figure 6D).

For the east-west comparison of nearshore data including total zooplankton density, average size, biomass, and *C. pengoi* density and biomass, no significant differences were found (Table 5). In the comparison of east-west offshore samples no significant differences were found, whereas in 2005 there was a significantly greater total zooplankton average size in eastern samples (Table 6).

Sandy Pond Bay

Sandy Pond Bay was again found to be the most productive site in 2006 (Figure 6A-C, 6E-F). A seasonal Chl *a* average of 19.4µg/L and zooplankton biomass of 155.2µg/L exceeded all other sites. The seasonal mean Secchi depth at Sandy Pond Bay (2.0m) was the shallowest of all sampled habitats (Figure 6D) and corresponded with the elevated Chl *a* values. Sodus Bay, also highly productive in 2005, was not sampled in 2006.

Seasonal Variability in Embayment and Nearshore Habitats

Several water quality parameters exhibited seasonal trends. Mean monthly Chl *a* and TP concentrations in embayments increased steadily before peaking in August, and then decreased sharply by mid-October (Figure 3A & B). Nearshore Chl *a* and TP remained fairly constant throughout the 2006 season. Embayment SRP gradually increased to a peak in October, unlike 2005 when it peaked in August and then declined into October. Nearshore SRP concentrations were fairly constant before reaching a slight peak in October (Figure 4A).

For zooplankton, whereas in 2005 embayments had the highest biomass and density for the entire May through October season, in 2006 nearshore habitats had the highest biomass in early September and mid-October and offshore habitats had the highest biomass in early June and mid-September. In 2006, density and biomass peaked in embayments in early June. For nearshore sites, density and biomass peaked early September. Offshore density peaked in early June and biomass peaked in mid-September (Figure 5A & C). Zooplankton average size was smallest in embayments throughout the season (Figure 5B). Offshore average size was greater than both nearshore and embayment habitats whenever it was available (early May, early June, July, mid-September, and mid-October), except for early August, when nearshore average size was slightly larger (Figure 5B). The average size of crustacean zooplankton was highest in early May for offshore habitats, in early July for nearshore habitats, and in early August for embayment sites (Figure 5B).

Zooplankton Community Dynamics

In 2006, cyclopoid copepods were the largest contributors to biomass in nearshore habitats, followed by calanoid copepods and bosminids contributing nearly equal biomasses. In embayments, bosminids were the largest contributors to biomass followed by cyclopoid copepods, but at half the contribution of bosminids. There were two significant differences in community composition between nearshore habitats and embayments in 2006, with greater calanoid copepod biomass in the nearshore and greater bosminid biomass in the embayments (Table 2). Cyclopoid copepods were prominent at both embayment and nearshore habitats, especially later in the season (Figure 12D). Although calanoid copepods and “other” cladocerans were the largest contributors to offshore biomass in July 2005, in July 2006 cyclopoid copepods and *Cercopagis pengoi* were the largest contributors (Table 3).

Zooplankton average size in embayment habitats was low (0.30-0.45mm) from spring through fall due to high densities of Bosminids and other small cladocerans, such as *Chydorus sphaericus* and *Ceriodaphnia quadrangula*. Cyclopoid copepods were an important contributor to embayment biomass, but cyclopoid average size in embayments was 0.55mm, as compared to 0.71mm in offshore habitats. Similar conditions existed in nearshore habitats, with cyclopoid copepods averaging 0.61mm in length. Offshore habitats had consistently large zooplankton average sizes due to an abundance of large calanoid copepods, cyclopoid copepods, and daphnids from the spring through fall, as well as large seasonal biomass contributions from *H. gibberum*. *C. pengoi, B. longimanus*, and *L. kindtii* were detected less frequently, but also increased offshore zooplankton average size when present.

Cercopagis pengoi

In 2006, *C. pengoi* was first observed in early June in both nearshore samples and offshore samples, and in late June in embayment samples. *C. pengoi* proportion of biomass peaked in early July in both nearshore sites, and in embayments (Figure 12E). The highest biomass observed in Lake Ontario was 23.6µg/L at the Tibbetts Point offshore site in mid-July. No spatial differences in biomass or density were found between east-west offshore or nearshore comparisons (Tables 5 and 6). *C. pengoi* densities in the eastern and western basins of Lake Ontario were similar; longitude did not account for any east-west difference in density. When comparing *C. pengoi* biomass and density for the month of July *C. pengoi* was greatest in biomass and density at offshore sites, similar to the pattern seen prior to 2005 (Figures 13 and 14).

C. pengoi was detected in 50.4% of all the samples in May through October in 2006, a decrease from the detection rate of 57.2% in 2005, but higher than 45.2% in 2004, 31.8% in 2003, 32.8% in 2002, and 49.3% in 2001. Yet the highest rate still remains 61.7% of the samples in 2000. Since its appearance in 1998, *C. pengoi* density has appeared to be inversely related to bosminid density, which 2006 data supports (Table 7, Figure 15). Another possible explanation why 2006 had such low bosminid density is the relatively large population of *Bythotrephes longimanus* detected (Table 8).

<u>*Bythotrephes longimanus*</u>

B. longimanus was detected in 43 samples (36%) in 2006, which was an increase from 34 samples (23%) in 2005 and after being detected in only three samples in 2004. *B. longimanus* was detected in all three habitats, but other than an early observation in late April in an offshore sample *B. longimanus* wasn't observed again until late July in any of the three habitats. *B. longimanus* densities ranged from 0.0004/L to 0.05/L, biomass ranged from 0.03µg/L to 14.2µg/L, and average size ranged from 1.07mm to 3.69mm.

<u>Linkages between Lake Ontario Zooplankton and Alewife Populations</u>.

Lake managers recognize the importance of ecological indicators, especially their utility in assessing management and restoration efforts. Zooplankton are positioned in the food chain of freshwater lakes to reflect ecological balance between algae and fish. In fact, mean zooplankton length can be used as an indicator of the balance between plankton eating fish and fish predators (Mills and Schiavone 1982). A common symptom of degraded ecosystems is distortion of the expected relationship between the biomass of organisms and body size. The virtual absence of large-bodied zooplankton like *Daphnia* in freshwater lakes in response to intense planktivory by fish, for example, is a deviation from an expected size distribution. In lakes with a diverse population of quality-sized piscivores that are sufficient in number to control populations of small plankton-eating fish, larger-bodied zooplankton are usually abundant. In lakes where plankton eating fish growth is slow and quality-sized planktivores are scarce, the density of predators is most likely low. Under conditions where predation is successfully controlling planktivore density, mean body lengths of crustacean zooplankton are greater than 0.8-1.0 mm. The dominance of small crustacean zooplankton, on the other hand, points to the absence of sufficient number of predators to suppress planktivore density.

Alewife (*Alosa pseudoharengus*) is the dominant planktivore in Lake Ontario. Intense planktivory by these fish has historically structured the zooplankton community toward small species like *Bosmina*. Zooplankton are the principal food of juvenile and adult alewife and these fish can account for more than 96% of predation on zooplankton (Rand et al. 1995). Alewife abundance declined 42% from the early 1980s to the early 1990s (O'Gorman et al. 2000), and changes in the zooplankton community were observed in response to this decline. Among the more significant changes during this period were a shift to larger zooplankton species and increased abundance of summer cyclopoid copepods.

In Lake Ontario, the impact of planktivory by alewife may be greater at one time of the year than another. For instance, adult alewife migrate inshore in the springtime and return to the offshore through July. Consequently, one would expect that the impact on offshore zooplankton by adult alewife would be highest in epilimnetic waters sometime mid-summer through early fall. For the period mid- July through mid-September 2006, we found that offshore mean zooplankton size was 0.70mm, suggesting that piscivores are either in balance with their alewife prey or are suppressing populations of adult alewife. This average size, however, represents a decrease from an average size of 0.82mm in 2005. In 2006, populations of adult and juvenile alewife appear not to have been sufficiently abundant to suppress larger sized zooplankton species like *Cercopagis pengoi, B. longimanus, D. retrocurva, D. thomasi, H. gibberum, L. macrurus, and E. lacustris.* Like the period from the early 1980s to the early 1990s when alewife densities were declining, offshore cyclopoid copepod biomass in Lake Ontario in 2006 was higher than any other offshore taxa. Finally, lakes with large populations of alewife typically have zooplankton that are very small (0.3 to 0.4 mm, CBFS unpublished data), whereas offshore crustacean zooplankton in Lake Ontario during mid summer to early fall were considerably larger, averaging 0.70mm in length.

The relationship between zooplankton average size and alewife abundance is complicated by the presence of the predatory exotic zooplankter, *Cercopagis pengoi*. *C. pengoi* possesses a tail spine several times its body length, preventing young-of-the-year planktivores from preying upon it until their gape is large enough to accommodate the spine (Bushnoe *et al*. 2003). In Lake Ontario, *Cercopagis* abundance is inversely related to bosminid density so declines in *Bosmina* could contribute to a shift in the mean size of zooplankton toward larger organisms. However, *C. pengoi* is a moderately large sized cladoceran and adult alewife are known to feed on this organism. *C. pengoi* was present in 50% of Lake Ontario zooplankton samples collected in 2006. Consequently, the high occurrence rate of *C. pengoi* observed in Lake Ontario samples in 2006 provides some additional circumstantial evidence that adult alewife numbers were likely low and were not sufficiently abundant to suppress *Cercopagis* abundance.

The exotic predatory macrozooplankton *Bythotrephes longimanus* is a large spiny zooplankton that was observed in Lake Ontario from July through October 2006. *B. longimanus* was detected in Lake Ontario in only one sample in 2002, none in 2003, and was detected in only three samples in 2004. Alewife feed on *B. longimanus* in Lake Ontario, and when they feed heavily on this organism, body condition improves. The population increase of the large cladoceran *Bythotrephes* in 2005 and 2006 provides yet one more line of evidence that adult alewife abundance is currently suppressed in Lake Ontario.

Given the dependence of Lake Ontario adult alewife on microzooplankton for food, and that high mean body size of zooplankton is inversely related to alewife abundance, we conclude that current densities of adult alewife in Lake Ontario are low. The supportive evidence for this conclusion is based on the facts that 1) a high mean body size of offshore crustacean zooplankton (0.70 mm) in mid summer to early fall, 2) the presence of the large cladoceran *C. pengoi* in 50% of all samples collected in Lake Ontario in 2006 April through mid-October, and 3) the increased presence of the macrozooplankton *B. longimanus* throughout 2006.

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Table 1. Mean Chl *a* , TP, SRP and water temperature for offshore (OS), embayment (EM) and nearshore (NS) sites during the month of July .

	Mean		
Parameter	OS	EM	NS
Chl *a* (μg/L)	2.36	8.25	2.79
TP (μg/L)	7.79	18.91	8.46
SRP (μg/L)	2.03	2.26	1.83
Water Temp (^{o}C)	16.77	24.78	21.07

Table 2. Comparisons of embayments and nearshore sites May-October, 2006 using paired t-tests on biweekly, log (x+1) transformed average values of zooplankton density and biomass, untransformed average size data, and the proportions of total biomass of zooplankton taxa (i.e. Bosminids, Daphnids, Calanoid copepods, Cyclopoid copepods, "Other" Cladocera, *Cercopagis pengoi,* and *Bythotrephes longimanus*). Italics indicate p <0.05, bold indicates p <0.001. Mean values based on all Lake Ontario sites and dates.

		Mean		
Parameter		Embayment	Nearshore	p-value
Total zooplankton:				
	Density (#/L)	89.45	10.45	**1.5E-04**
	Average Size (mm)	0.38	0.54	**1.3E-05**
	Biomass (μg/L)	79.91	21.09	*0.009*
Proportion of total biomass:				
	Bosminids	0.46	0.17	*0.005*
	Daphnids	0.09	0.17	0.379
	Calanoid copepods	0.07	0.14	**4.4E-04**
	Cyclopoid copepods	0.22	0.28	0.585
	Other Cladocera	0.13	0.06	0.231
	Cercopagis pengoi	0.001	0.11	0.113
	Bythotrephes longimanus	0.006	0.060	0.159

Table 3. Comparisons of offshore (OS), nearshore (NS), and embayment (EM) habitats during July 2006 using t-tests assuming unequal variance on biweekly, log (x+1) transformed mean values of zooplankton density and biomass, and untransformed average size data. Mean values for each habitat as well as p-values from the pairwise comparisons are stated for total zooplankton density, average size, biomass, *Cercopagis* biomass, and *Bythotrephes* biomass. Italicized values are significant at Bonferroni adjusted $\alpha = 0.0167$ ($p = 0.05$) , bold values indicate $p < 0.001$.

		Mean			Pairwise comparisons		
	Parameter	OS	NS	EM	OS-NS	OS-EM	NS-EM
Total zooplankton:							
	Density (#/L)	3.50	4.11	140.33	0.381	0.091	0.106
	Average Size (mm)	0.77	0.57	0.39	**4.7E-04**	**1.2E-04**	*0.008*
	Biomass (µg/L)	13.74	10.77	134.80	**3.6E-08**	0.042	0.219
Zooplankton biomass (µg/L):							
	Bosminids	0.75	1.80	30.19	*0.009*	0.107	0.180
	Daphnids	0.70	0.85	22.06	0.674	0.144	0.159
	Other Cladocera	0.83	0.36	61.98	0.238	0.145	0.116
	Calanoid copepods	1.09	1.08	1.92	0.753	0.929	0.957
	Cyclopoid copepods	2.96	0.50	16.70	0.086	0.292	0.132
	Cercopagis pengoi	6.81	6.00	0.45	0.975	*0.004*	**7.3E-04**
	Bythotrephes longimanus	0.56	0.06	0.00	0.141	0.085	0.120

Table 4. Comparison of mean monthly chlorophyll a (Chl a), total phosphorus (TP), and soluble reactive phosphorus (SRP) concentrations for nearshore sites in eastern and western Lake Ontario, May-October, 2005-2006; east/west division based on 77.8^{o} W longitude. Note: "nd" indicates no data were collected for that time period.

Month	**Chl *a* (µg/L)**		**TP (µg/L)**		**SRP (µg/L)**	
	East	**West**	**East**	**West**	**East**	**West**
			2005			
May	0.3	0.7	8.20	7.36	3.2	3.2
June	1.2	0.9	7.25	7.33	3.7	2.9
July	1.8	1.4	6.58	7.06	3.5	3.0
August	1.5	1.7	7.21	7.36	3.4	3.5
September	1.4	2.0	8.96	8.43	5.0	4.2
October	2.0	1.4	9.54	9.65	nd	5.7
Mean	**1.4**	**1.3**	**8.0**	**7.9**	**3.7**	**3.8**
			2006			
May	0.50	0.34	7.77	7.66	2.0	2.2
June	1.21	1.53	5.70	7.77	1.5	2.0
July	2.57	3.14	8.86	8.05	1.7	1.9
August	3.67	1.90	8.42	7.32	2.0	1.7
September	1.93	2.10	6.04	10.50	1.6	2.0
October	0.44	2.53	6.78	9.48	4.7	2.4
Mean	**1.7**	**1.9**	**7.3**	**8.5**	**2.2**	**2.0**

Table 5. East-west comparisons of mean zooplankton density, average size and biomass for nearshore sites, May - October 2006. P-values based on paired t-tests done on log (x+1) transformed density and biomass data, and untransformed average size data. Italics indicate *p* <0.05, bold indicates *p* <0.001. East-west division based on 77.8^{o}W longitude.

	Mean		
Parameter	East	West	p-value
Density (#/L)	6.82	15.08	0.200
Average Size (mm)	0.55	0.53	0.614
Biomass (µg/L)	14.64	29.36	0.295
Cercopagis density (#/L)	0.15	0.14	0.958
Cercopagis biomass (µg/L)	1.26	1.21	0.843
Bythotrephes density (#/L)	5.73E-03	3.73E-03	0.599
Bythotrephes biomass (µg/L)	0.92	0.70	0.332

Table 6. East-west comparisons of zooplankton densities, average size, and biomass for offshore sites during July 2006. P-values are based on t-tests assuming unequal variances performed on log(x+1) transformed biomass and density data, and untransformed average size data. Italics indicate *p* <0.05. East-west division based on 77.8^{o}W longitude.

Parameter	Mean		
Kaho and Seth Green (July)	East	West	p-value
Density (#/L)	3.08	4.32	0.451
Average Size (mm)	0.81	0.69	0.102
Biomass (µg/L)	14.42	12.39	0.896
Cercopagis density (#/L)	1.09	0.91	0.774
Cercopagis biomass (µg/L)	7.18	6.07	0.452
Bythotrephes density (#/L)	3.3E-03	0.00	0.106
Bythotrephes biomass (µg/L)	0.85	0.00	0.081

Table 7. Comparisons of *Cercopagis pengoi* density and average size, and biomass in offshore (OS), nearshore (NS), and embayment (EM) habitats during late August 1998, August 1999, July 2000, August 2001, August 2002, July 2003, late July - early August 2004, July 2005, and July 2006 using t-tests assuming unequal variance. Mean values for each habitat as well as p-values from the pairwise comparisons are stated for total zooplankton density, average size, and biomass. Italicized values indicate $p < 0.05$. Bold values indicate $p < 0.001$.

Cercopagis pengoi	Mean				Pairwise Comparison			
Parameter	Year	OS	NS	EM	Year	OS	NS	EM
Density (#/L)	1998	0.471	0.396	0.055	98-99	0.651	0.850	0.440
	1999	0.440	0.419	0.120	99-00	**7.7E-04**	0.548	0.773
	2000	0.157	0.371	0.235	00-01	0.226	0.461	0.556
	2001	0.210	0.688	0.079	01-02	0.148	0.486	0.171
	2002	0.358	0.305	0.000	02-03	*0.001*	0.633	0.215
	2003	0.052	0.467	0.439	03-04	**1.4E-04**	0.527	0.400
	2004	0.435	0.507	0.101	04-05	0.164	*0.024*	0.685
	2005	0.261	0.197	0.181	05-06	0.052	*0.011*	0.497
	2006	1.029	0.667	0.059				
Average Size (mm)	1998	1.266	1.085	1.090	98-99	0.301	0.078	0.367
	1999	1.304	1.189	1.196	99-00	**4.3E-05**	0.202	0.371
	2000	1.149	1.083	1.153	00-01	*0.041*	0.464	0.294
	2001	1.286	1.150	1.257	01-02	*0.005*	0.257	NA*
	2002	1.074	1.018	NA*	02-03	0.761	0.584	NA*
	2003	1.060	1.110	1.046	03-04	*0.001*	0.861	0.659
	2004	1.267	1.134	1.099	04-05	0.627	*0.016*	0.501
	2005	1.295	1.216	1.176	05-06	*0.048*	0.465	0.372
	2006	1.174	1.188	1.087				
Biomass (mg/L)	1998	3.970	2.721	0.340	98-99	0.344	0.804	0.290
	1999	5.277	3.654	1.318	99-00	**4.9E-08**	0.061	0.728
	2000	0.992	2.384	1.872	00-01	*0.017*	0.385	0.884
	2001	1.826	6.119	1.154	01-02	0.876	0.572	0.175
	2002	1.748	2.032	0.000	02-03	**9.7E-04**	0.799	0.202
	2003	0.367	2.696	3.141	03-04	**1.9E-06**	0.076	0.563
	2004	3.801	3.972	0.770	04-05	0.221	0.053	0.706
	2005	2.448	2.059	1.288	05-06	0.110	*0.012*	0.575
	2006	6.814	6.000	0.450				

NA* denotes undefined test statistic

Table 8. *Bythotrephes longimanus* density, average size, and biomass in offshore (OS), nearshore (NS), and embayment (EM) habitats for May-October 1998-2006.

Bythotrephes longimanus		Mean		
Parameter	Year	OS	NS	EM
Density (#/L)	1998	0.000	trace*	trace*
	1999	0.005	0.007	trace*
	2000	trace*	0.003	trace*
	2001	trace*	0.002	0.000
	2002	trace*	0.000	0.000
	2003	0.000	0.000	0.000
	2004	trace*	trace*	0.000
	2005	0.006	0.002	0.001
	2006	0.006	0.005	0.001
Average Size (mm)	1998	-	2.469	2.086
	1999	1.502	1.194	1.293
	2000	2.742	1.777	1.021
	2001	2.705	2.144	-
	2002	1.482	-	-
	2003	-	-	-
	2004	2.680	2.470	-
	2005	2.098	2.188	2.224
	2006	2.609	2.518	2.534
Biomass (μg/L)	1998	0.000	0.033	0.034
	1999	0.153	0.156	0.004
	2000	0.001	0.074	0.016
	2001	trace*	0.033	0.000
	2002	trace*	0.000	0.000
	2003	0.000	0.000	0.000
	2004	0.111	0.101	0.000
	2005	0.713	0.291	0.182
	2006	1.046	0.795	0.197

* trace indicates 0 < value < 0.001

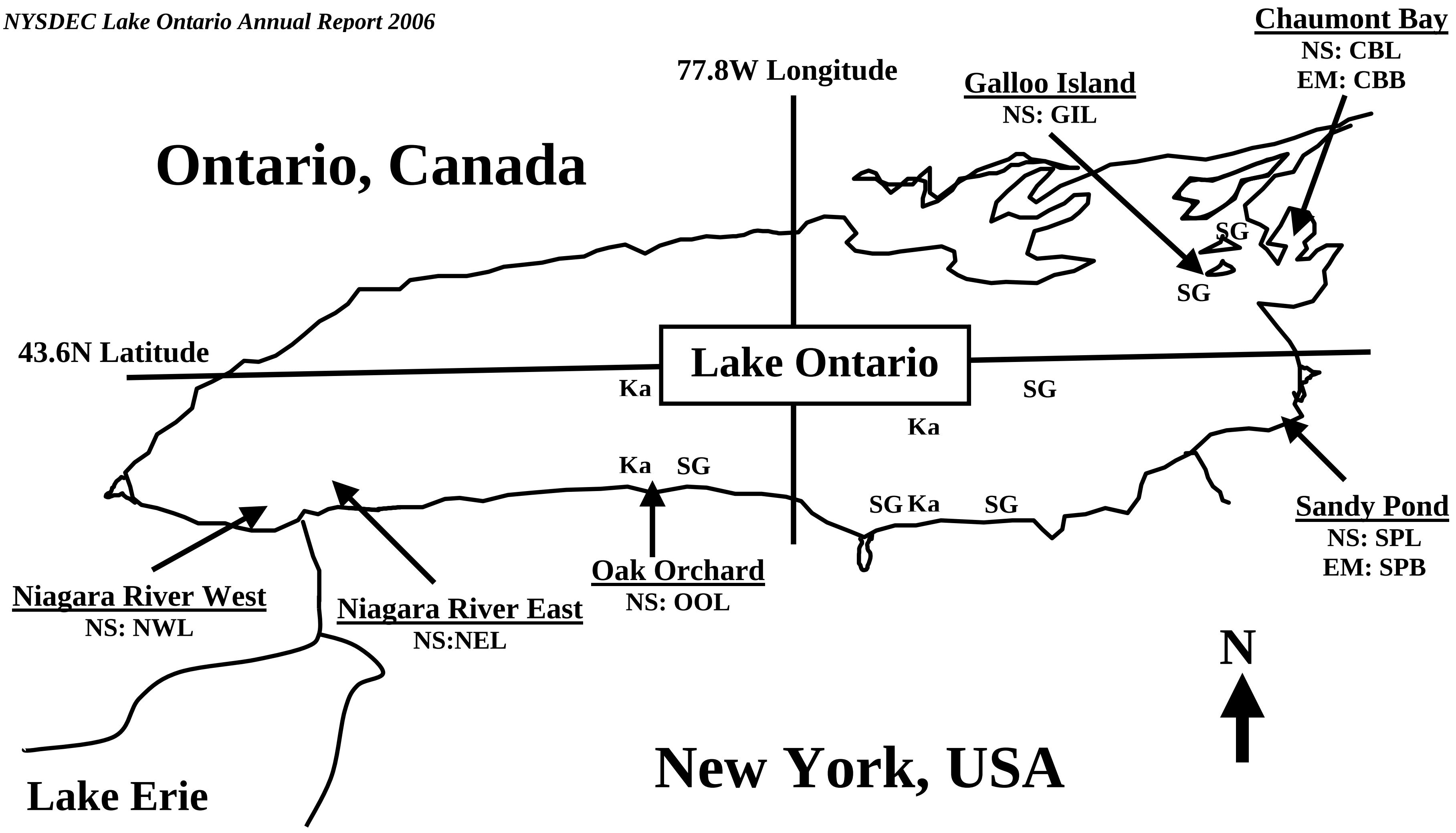

Figure 1. Sampling sites in 2006. Arrows point to nearshore (NS) and embayment (EM) sites; locations of sites sampled by the vessels Kaho and Seth Green are denoted by (Ka) and (SG), respectively.

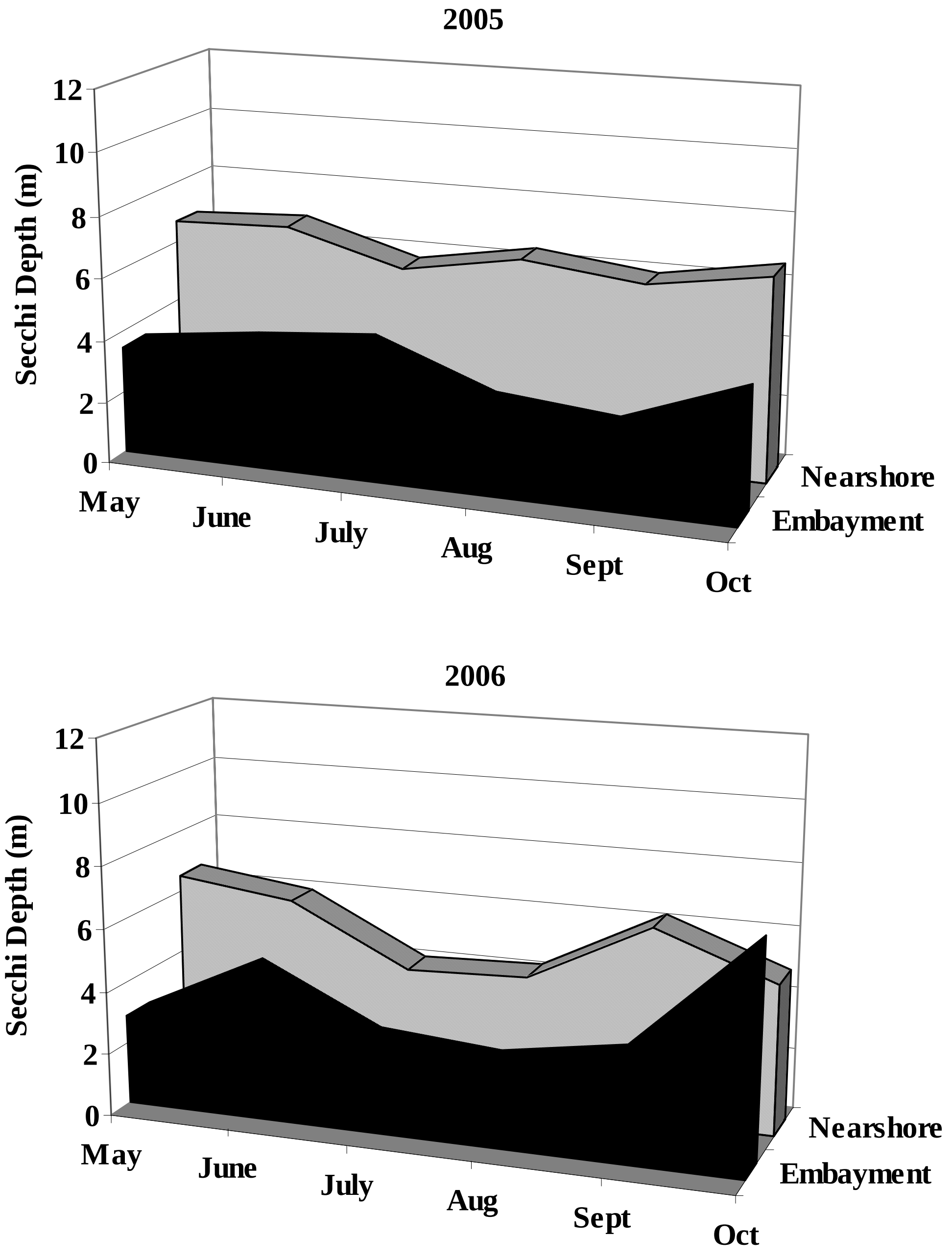

Figure 2. Mean monthly Secchi depth (meters) for all embayment and nearshore sites in Lake Ontario, May - October, 2005 and 2006.

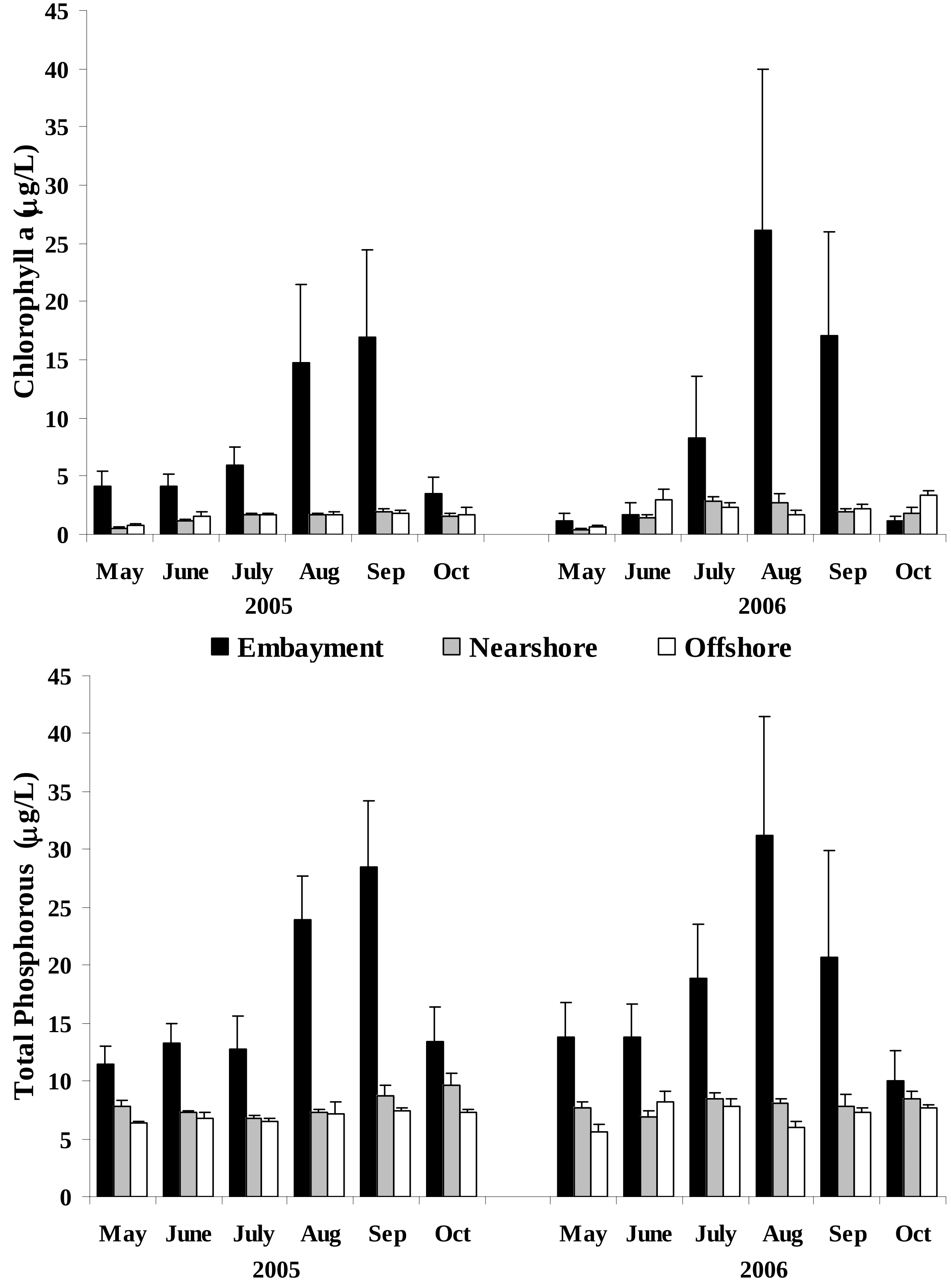

Figure 3. Comparison of mean (+ 1 SE) monthly chlorophyll a (mg/L) (A) and total phosphorus (mg/L) (B) for embayment, nearshore, and offshore habitats in Lake Ontario, May-October 2005 and 2006.

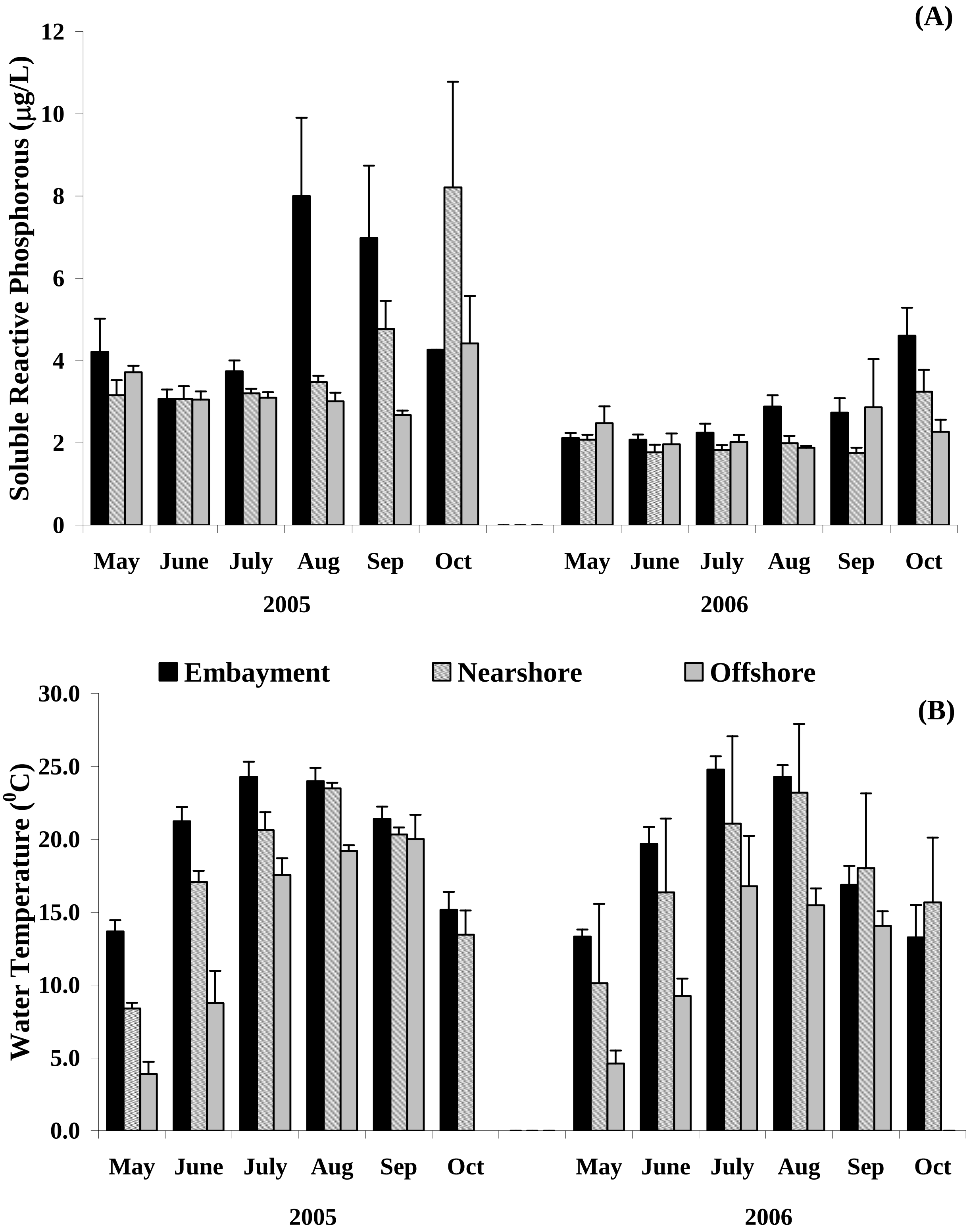

Figure 4. Comparison of mean (+ 1 SE) monthly soluble reactive phosphorus (SRP) concentrations (μg/L) (A) and water temperature (^{o}C) (B) for embayment, nearshore, and offshore habitats in Lake Ontario, May-October 2005 and 2006.

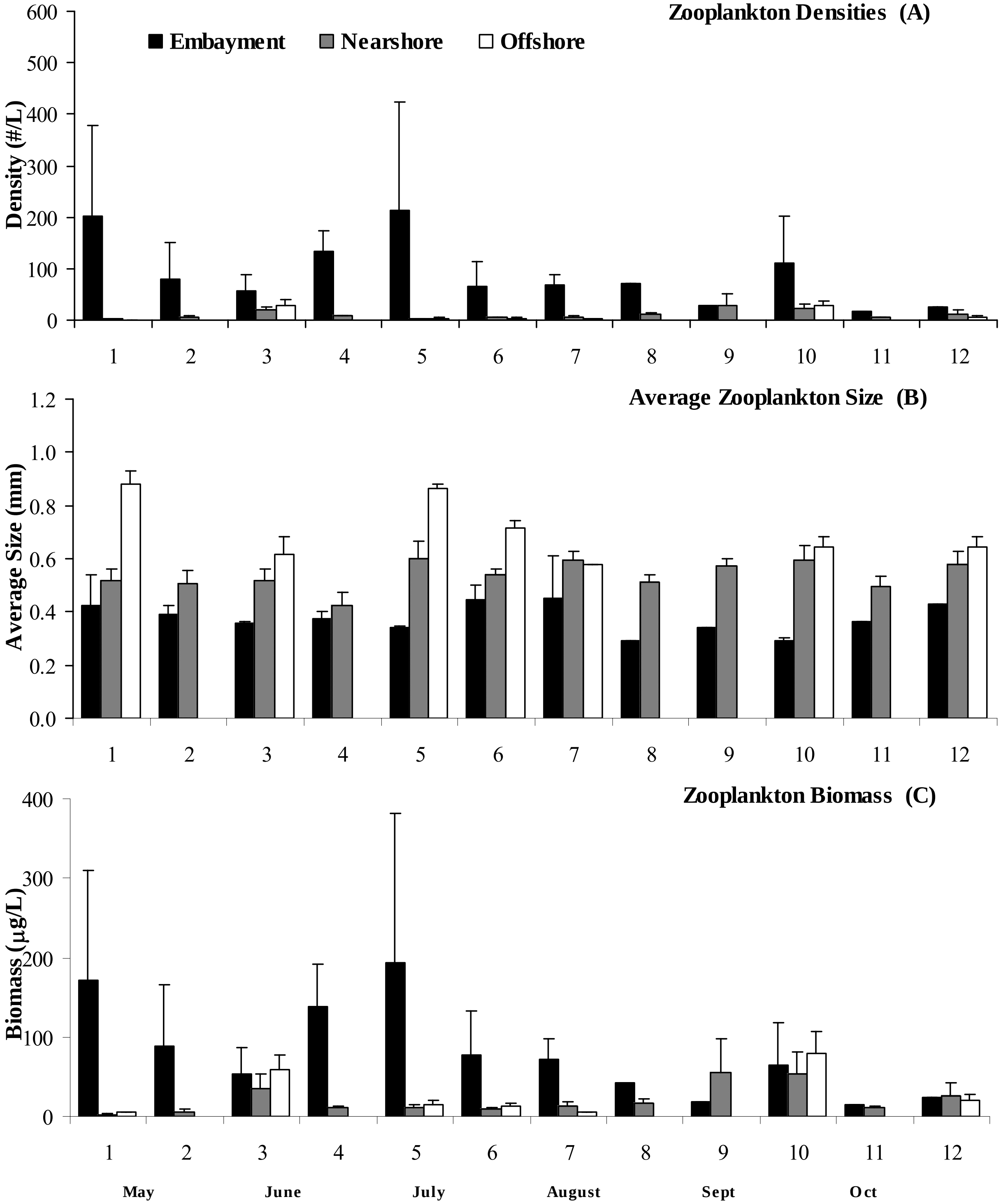

Figure 5. Biweekly means (+ 1SE) of zooplankton densities, sizes, and biomass for May through October 2006 embayment, nearshore, and offshore sites on Lake Ontario. On the x-axis, weeks sampled are designated by numbers 1-12.

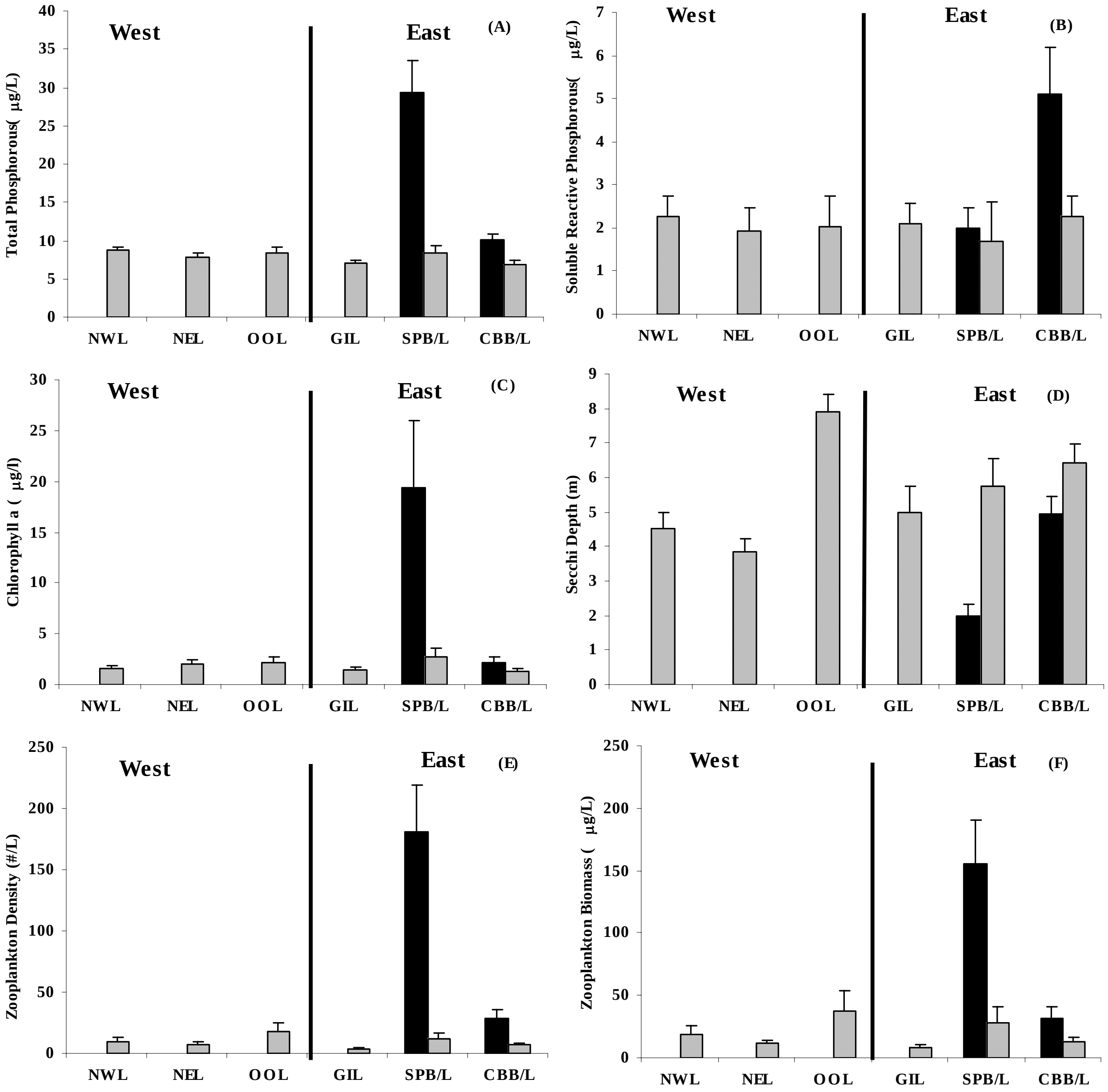

Figure 6. 2006 annual mean TP (A), SRP (B), Chl a (C), Secchi depth (D), zooplankton densities (E), and zooplankton biomass (F) at each embayment (solid bars) and nearshore (striped bars) location (+1 SE), with west-east dividing line.

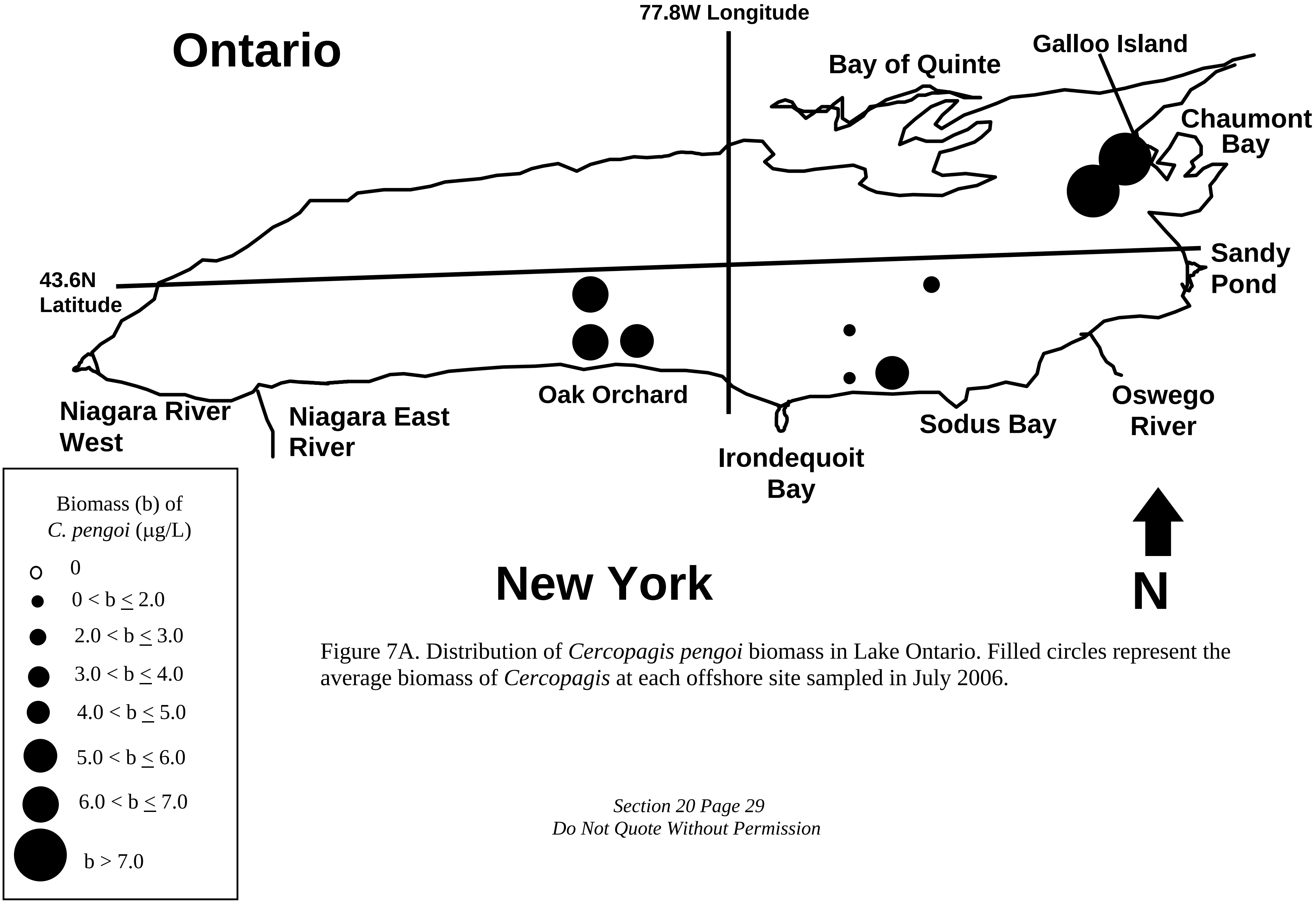

Figure 7A. Distribution of *Cercopagis pengoi* biomass in Lake Ontario. Filled circles represent the average biomass of *Cercopagis* at each offshore site sampled in July 2006.

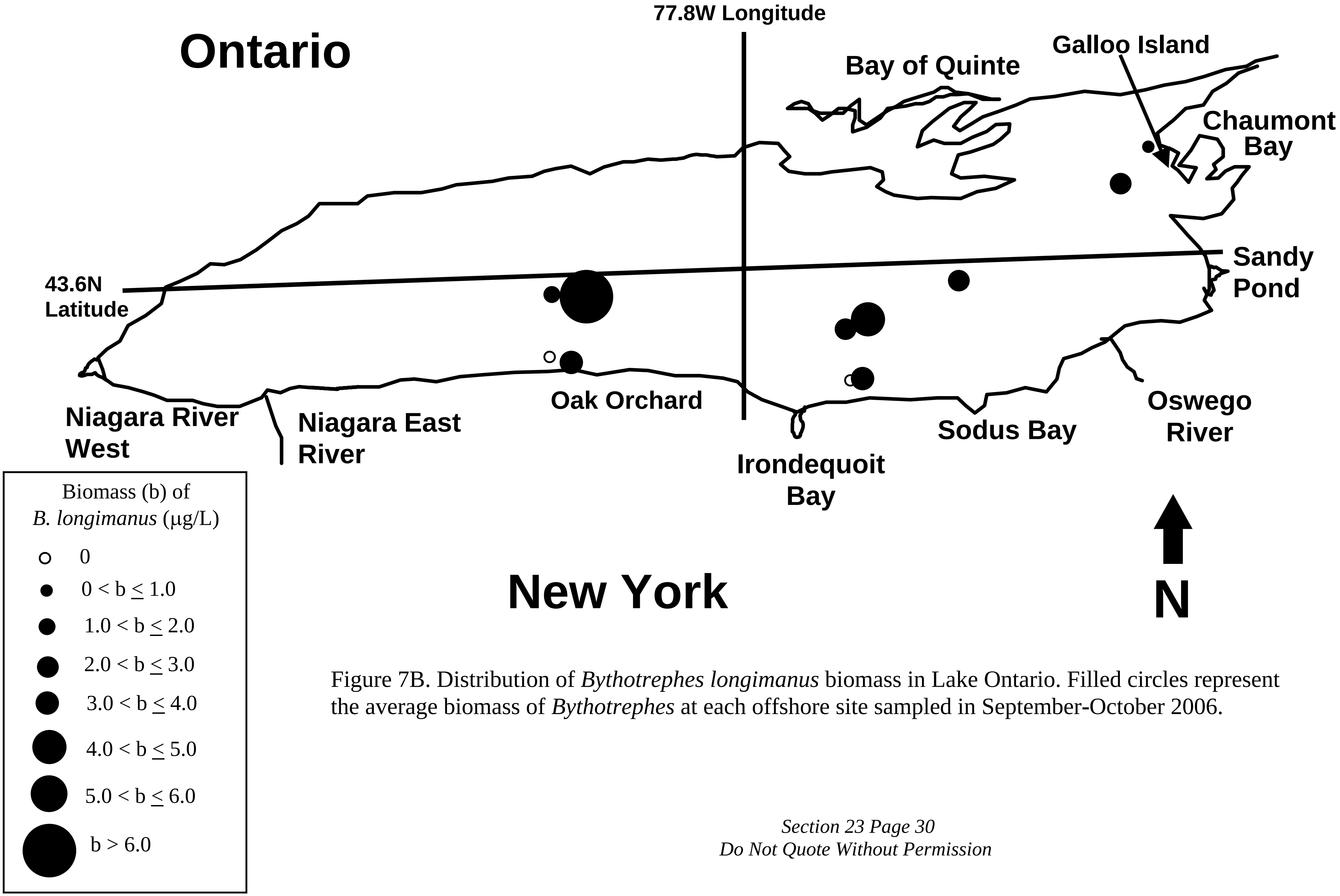

Figure 7B. Distribution of *Bythotrephes longimanus* biomass in Lake Ontario. Filled circles represent the average biomass of *Bythotrephes* at each offshore site sampled in September-October 2006.

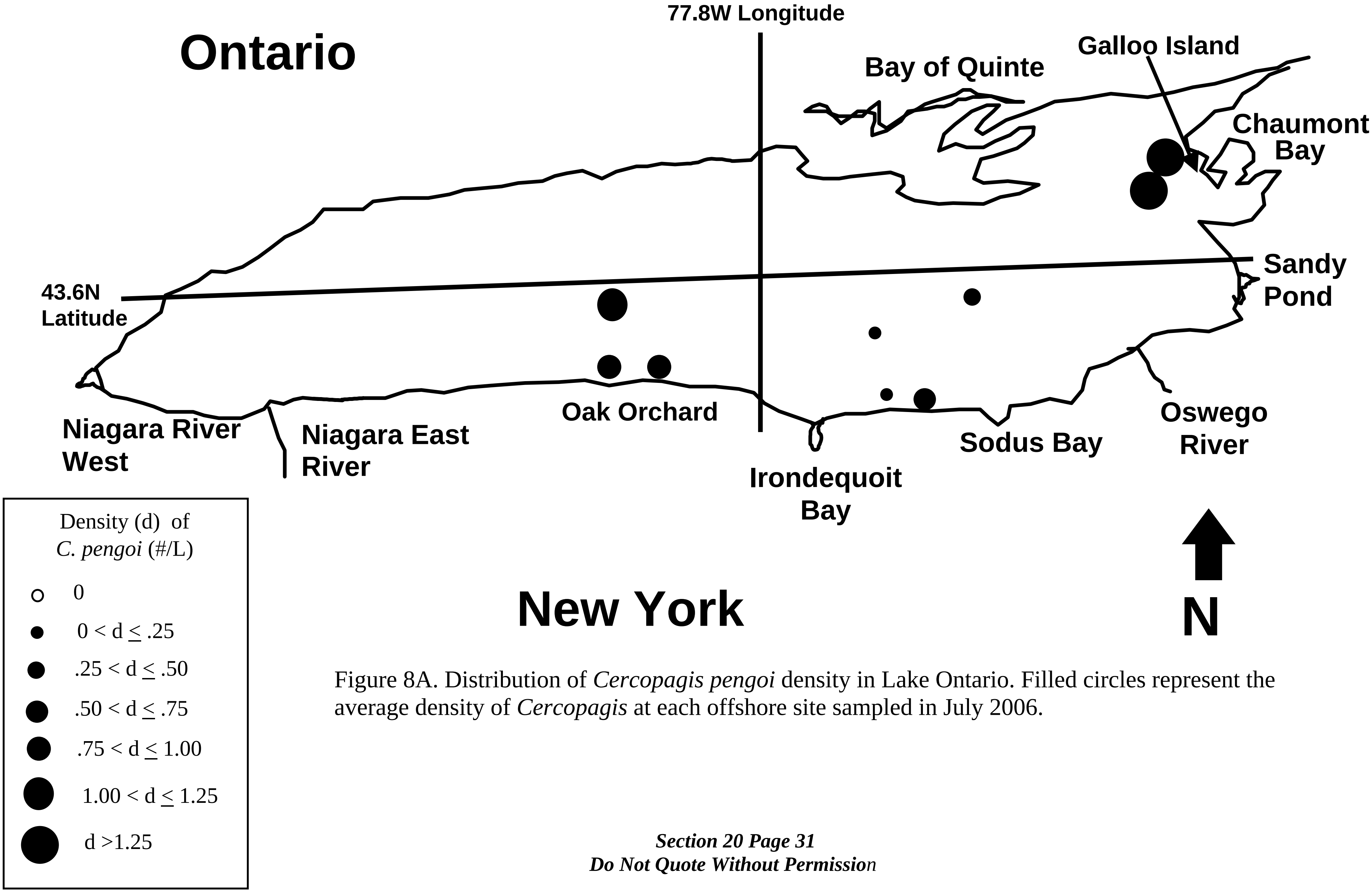

Figure 8A. Distribution of *Cercopagis pengoi* density in Lake Ontario. Filled circles represent the average density of *Cercopagis* at each offshore site sampled in July 2006.

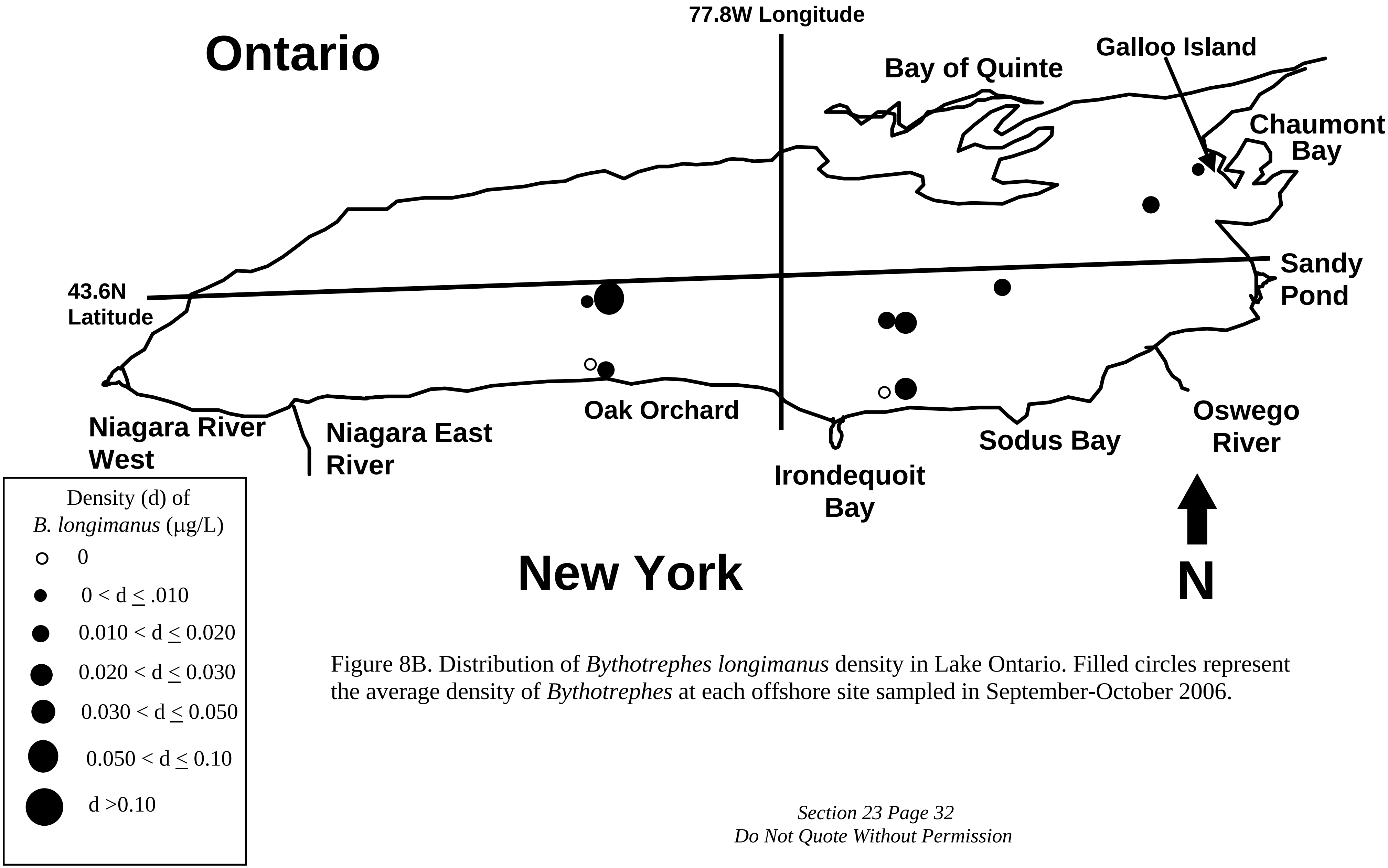

Figure 8B. Distribution of *Bythotrephes longimanus* density in Lake Ontario. Filled circles represent the average density of *Bythotrephes* at each offshore site sampled in September-October 2006.

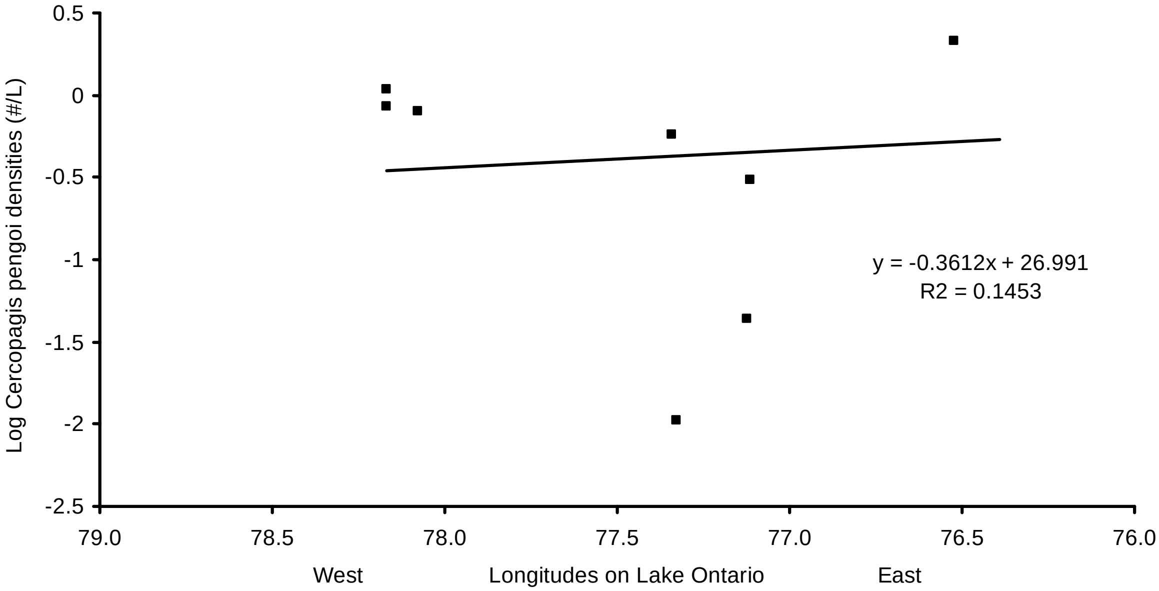

Figure 9A. Densities of Cercopagis pengoi at different longitudes from West to East in Lake Ontario for offshore sites in July 2006.

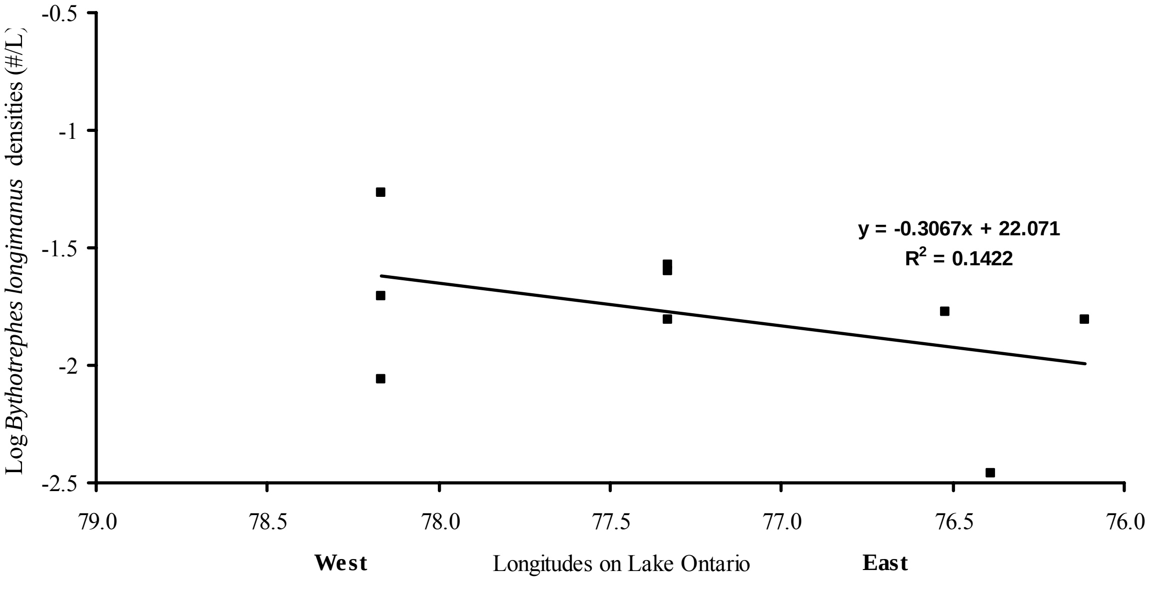

Figure 9B. Densities of *Bythotrephes longimanus* at different longitudes from West to East in Lake Ontario for offshore sites in September-October 2006.

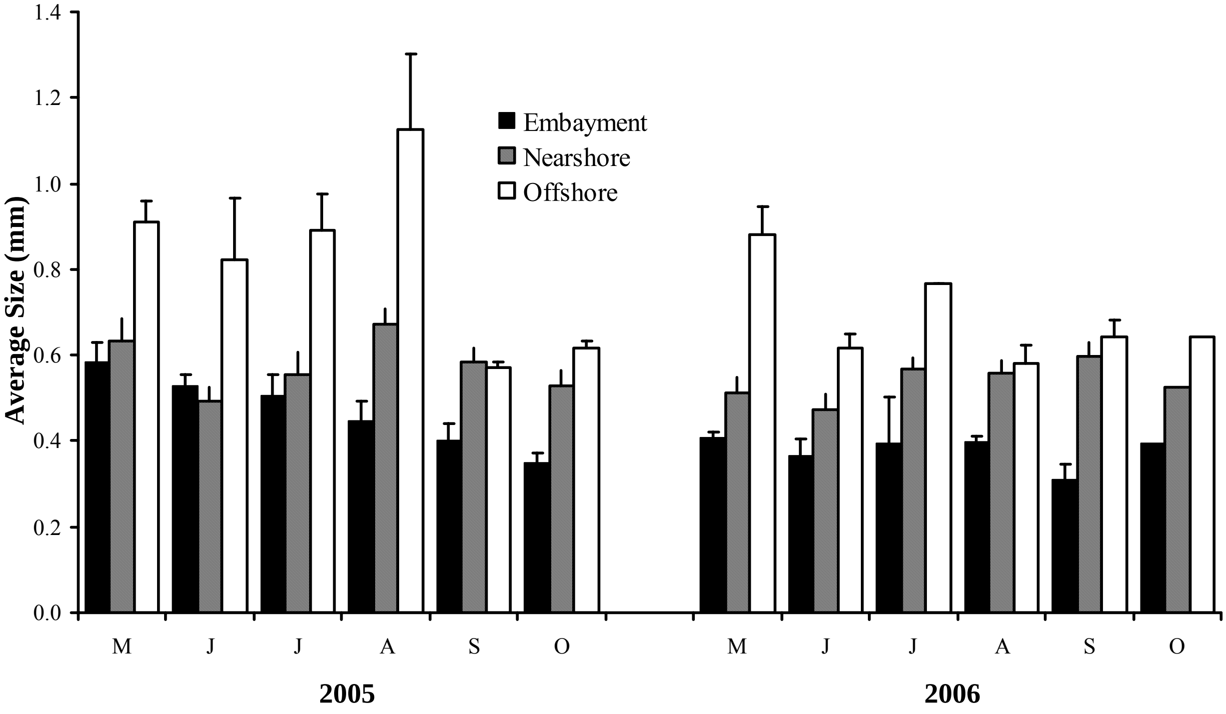

Figure 10. Comparison of mean (+ 1SE) monthly zooplankton size at embayment, nearshore, and offshore sites in Lake Ontario for May - October 2005 and 2006.

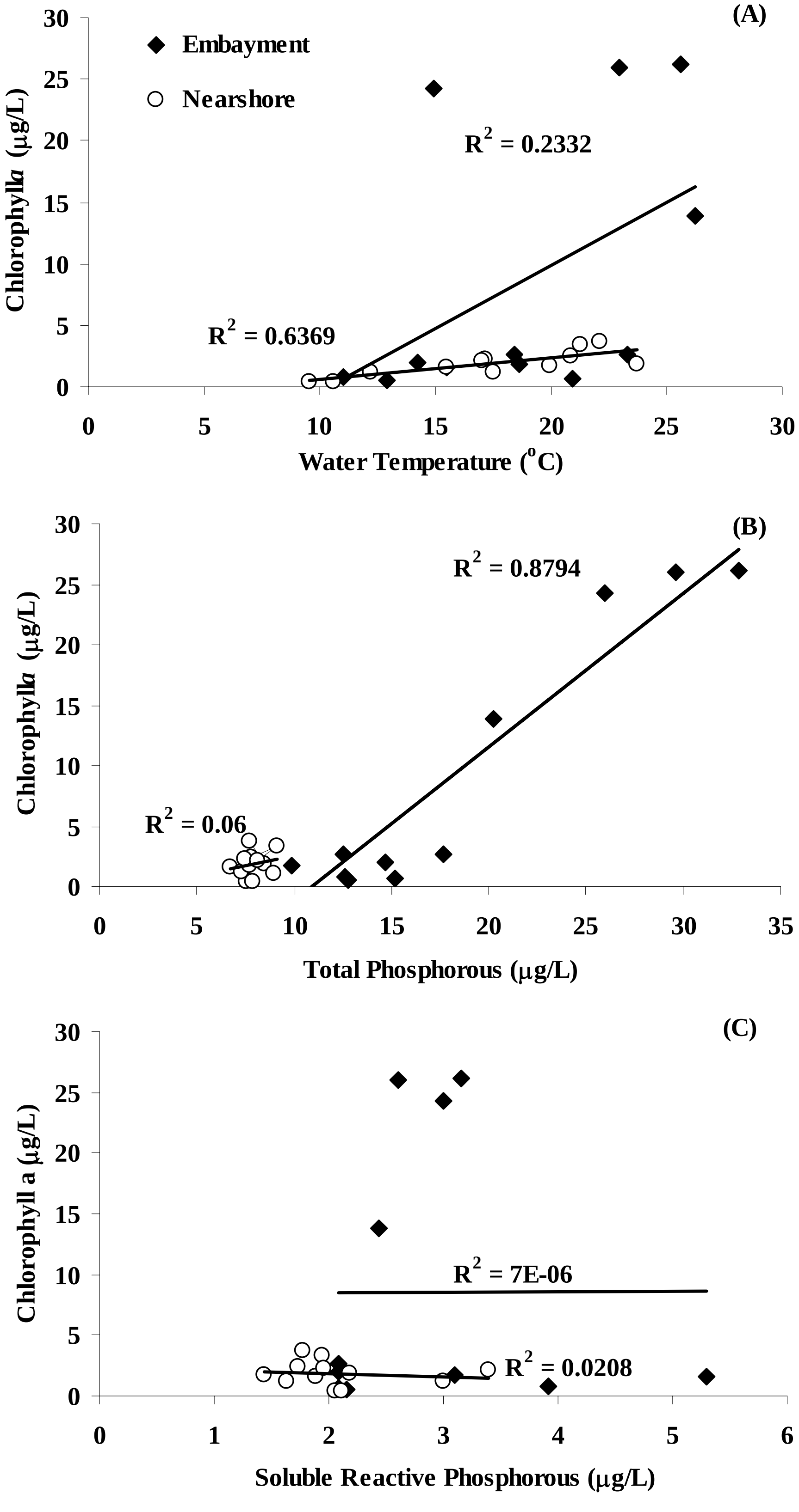

Figure 11. Relationships between 2006 mean biweekly biomonitoring variables (A) water temperature (mean 0-10m) vs. Chl a (0-10 m integrated); (B) TP vs Chl a; and (C) SRP vs. Chl a. Soild lines show the regressions.

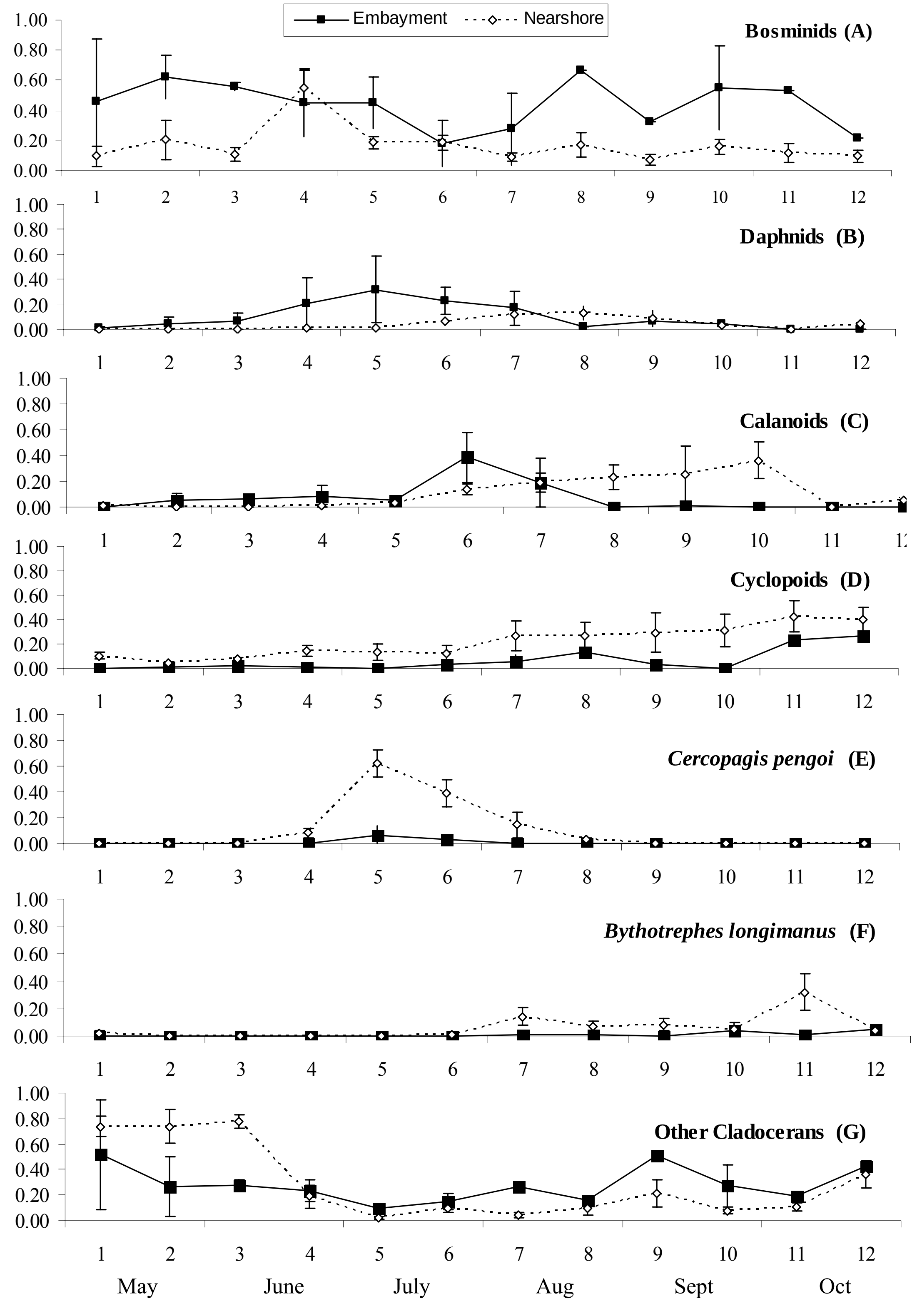

Figure 12. Proportion of total biomass of zooplankton community for embayments and nearshore areas of Lake Ontario, May - October 2006 (weeks 1-12). Zooplankton are grouped as Bosminids (A), Daphnids (B), Calanoids (D), Cyclopoids (D), Cercopagis pengoi (E), Bythotrephes longimanus (F) and Other Cladocerans (G). Bars represent + 1SE.

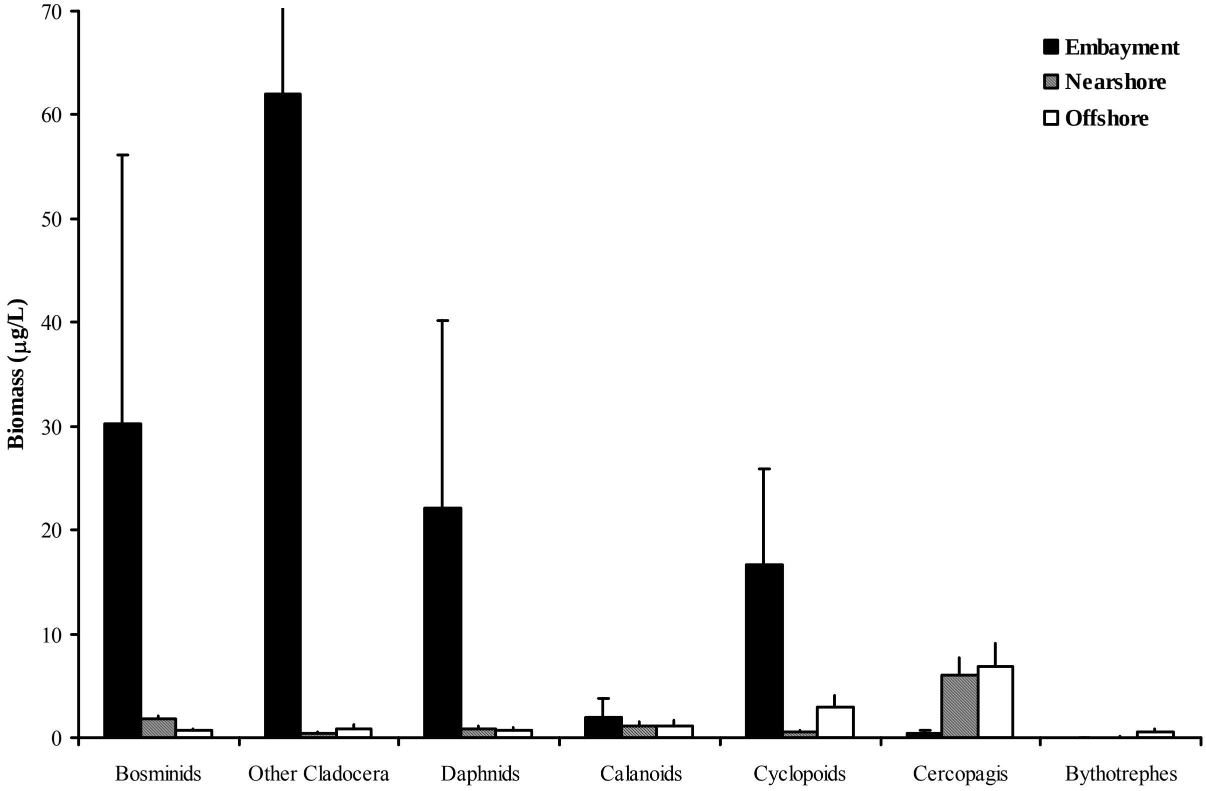

Figure 13. Comparision of average biomass of zooplankton groups from embayment, nearshore, and offshore habitats of Lake Ontario in July 2006. Bars represent + 1SE.

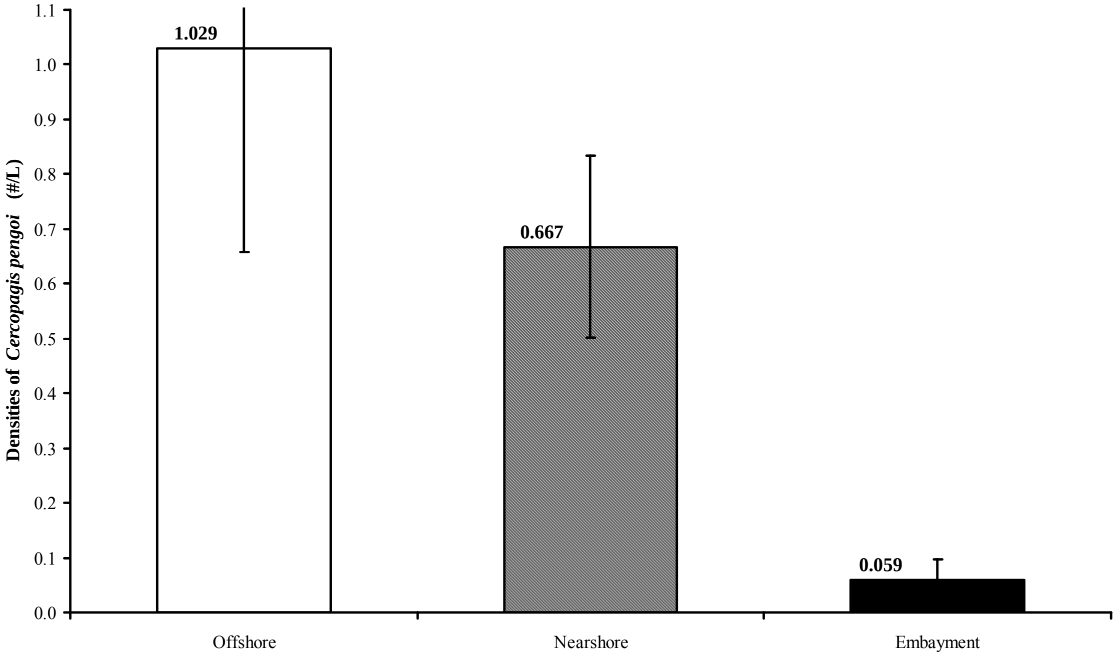

Figure 14A. Average densities of Cercopagis pengoi in July 2006 at offshore, nearshore, and embayment sites. Bars represent +1SE.

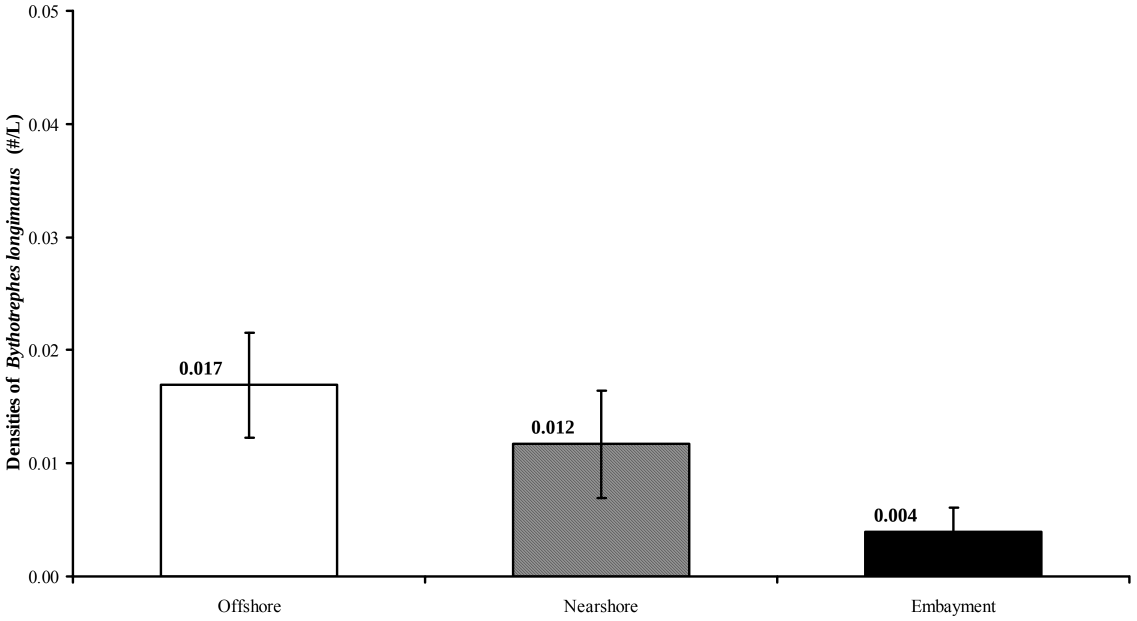

Figure 14B. Average densities of Bythotrephes longimanus in September-October 2006 at offshore, nearshore, and embayment sites. Bars represent +1SE.

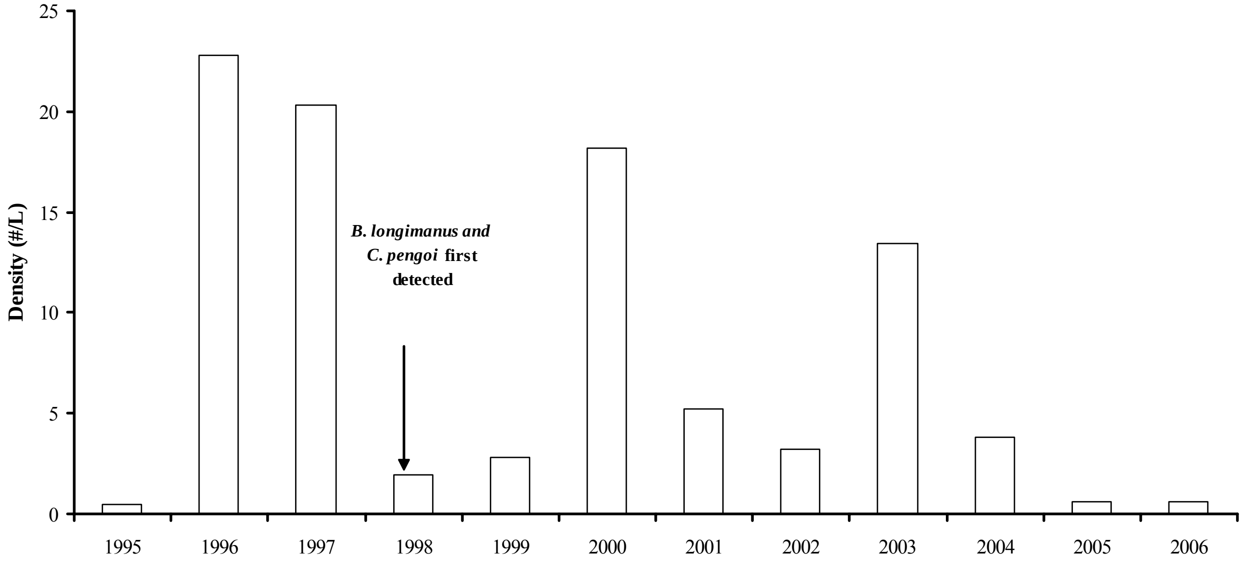

Figure 15. Mean densities of bosminids for August densities 1995-1999, 2001 and 2002, mid-July to mid-August 2004, and July 2000, 2003, and 2005-06 at offshore sites in Lake Ontario.