A Comparison of Total Phosphorus, Chlorophyll *a*, and Zooplankton in Embayment, Nearshore, and Offshore Habitats of Lake Ontario

Spencer R. Hall[1,4], Nijole K. Pauliukonis[1,5], Edward L. Mills[1,*], Lars G. Rudstam[1], Clifford P. Schneider[2], Sandra J. Lary[3,6], and Fredrik Arrhenius[1,7]

[1]*Department of Natural Resources*
Cornell University Biological Field Station
900 Shackelton Point Rd.
Bridgeport, New York 13030, USA

[2]*New York State Department of Environmental Conservation*
Cape Vincent Fisheries Research Station
Cape Vincent, New York 13618, USA

[3]*US Fish and Wildlife Service*
Lower Great Lakes Fisheries Resources Office
405 N. French Rd., Suite 120A
Amherst, New York 14228-2008, USA

ABSTRACT. *Lower trophic levels were compared in embayment, nearshore, and offshore habitats of Lake Ontario, 1995 to 1997, in the context of oligotrophication and invasion of dreissenid mussels. Total phosphorus (TP), chlorophyll* a *(chl* a*), Secchi disk depth, temperature, and zooplankton were measured to spatially and temporally contrast these habitats and to test for recently hypothesized "decoupling" of chl* a *from TP (lower than predicted chl* a *per unit TP, consistent with dreissenid mussel grazing). The embayment habitat had higher concentrations of TP and chl* a*, greater volumetric zooplankton density and biomass, and higher springtime water temperatures than both nearshore and offshore habitats, while overall areal zooplankton biomass was highest in the offshore. Furthermore, concentrations of TP and volumetric zooplankton density in nearshore habitats are now more similar to the offshore pelagia than they were three decades ago. Finally, a lower yield of chl* a *per unit TP was found in nearshore habitat compared to offshore and embayment habitats. The current lower yield of chl* a *per unit TP in nearshore habitat can be attributed more to* Dreissena *than to erosion and/or resuspension of sediments.*

INDEX WORDS: *Dreissenids, embayments, Lake Ontario, nearshore, oligotrophication, offshore.*

INTRODUCTION

Lake Ontario, the 17th largest lake in the world (Beeton *et al.* 1999), has undergone major ecosystem-level changes over the past four decades. Some

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[4] Current address: Department of Ecology and Evolution, University of Chicago, 1101 E. 57th St., Chicago, IL 60637 USA
[5] Current address: Florida Department of Environmental Protection, NPS Management and Water Quality Standards Section, 2600 Blairstone Rd., MS 3570, Tallahassee, FL 32399
[6] Current address: Maine Department of Marine Resources, 21 State House Station, Augusta, ME 04333-21
[7] Current address: Institute of Marine Research, PO Box 4, 435 21 Lysekil, Sweden
[*]Corresponding author. E-mail: elm5@cornell.edu

of the most significant ecological changes in Lake Ontario during this period have been associated with mandated reductions in phosphorus (Millard *et al.* 2003) and unplanned introductions, including two species of dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*) (Mills *et al.* 1993, Mills *et al.* 1999) and the predatory cladoceran *Cercopagis pengoi* (MacIssac *et al.* 1999). Decreased phosphorus loading has led to a process of oligotrophication (Neilson and Stevens 1987, Stevens and Neilson 1987, Johengen *et al.* 1994, Millard *et al.* 1996*a*, Johannsson *et al.* 1998). The direct and indirect effects of this process have begun to impact lower trophic level production and dynamics. For in-

stance, offshore zooplankton production has declined with decreased phosphorus loadings (Johannsson 1987, Johannsson *et al.* 1991, Johannsson *et al.* 1998). Meanwhile, abundance of forage fish, particularly of alewife (*Alosa pseudoharengus*), has decreased, and growth rates of some salmonids have declined as well (Rand and Stewart 1998). However, understanding of these ecological changes is primarily based on studies of offshore habitats (Johannsson 1987, Rand *et al.* 1995, Millard *et al.* 1996*a*, Johannsson *et al.* 1998).

As Lake Ontario becomes more oligotrophic, trophic level responses in offshore habitat may be a poor surrogate of similar changes in nearshore and embayment habitats. Traditionally, most studies of nutrients, phytoplankton, and zooplankton in Lake Ontario have focused on offshore sites (Johannsson 1987, Taylor *et al.* 1987, Johannsson *et al.* 1991, Millard *et al.* 1996*a*, Johannsson *et al.* 1998). Some studies, however, have identified major spatial gradients of temperature, nutrients, phytoplankton, and zooplankton among different Lake Ontario habitats (Patalas 1969, Munawar and Nauwerck 1971, Gray 1987, Neilson and Stevens 1987). The extent to which offshore, nearshore, and embayment environments vary ecologically in space and time is currently not well understood.

Phosphorus and light are usually considered as the primary factors limiting offshore production of epilimnetic phytoplankton in Lake Ontario (Millard *et al.* 1996*b*). However, dreissenid mussels have the potential to reduce phytoplankton abundance and, through their intense grazing, impact interrelationships between phosphorus and algal standing crop. These effects have been described in theoretical (Madenjian 1995, Padilla *et al.* 1996) and field (Fahnenstiel *et al.* 1995, Johengen *et al.* 1995, Holland *et al.* 1995, Mellina *et al.* 1995, Nicholls *et al.* 1999) studies. In Lake Ontario, dreissenid mussels now inhabit embayment, nearshore, and offshore habitats (Mills *et al.* 1993, Mills *et al.* 1999), and their impact on this ecosystem is not fully understood. Given that phytoplankton biomass has declined in many lakes colonized by *Dreissena* spp. (Leach 1993, Fahnenstiel *et al.* 1995, Idrisi *et al.* 2001), it is of particular interest whether these mollusks have modified the yield of chlorophyll *a* per unit of total phosphorus, especially in Lake Ontario's nearshore habitat (Nicholls *et al.* 1999).

In this paper, spatial-temporal patterns of lower trophic level variables (total phosphorus [TP], chlorophyll *a* [chl *a*], and zooplankton [density, biomass, and mean length]) were examined in embayment, nearshore, and offshore habitats of Lake Ontario, 1995 to 1997. More specifically, the study centered on a comparative assessment of these lower trophic level variables in embayment, nearshore, and offshore habitats and assessing dreissenid-induced changes in chl *a* and TP.

METHODS

Sampling Sites

Offshore, nearshore, and embayment habitats of Lake Ontario were sampled during 1995 to 1997 (Table 1). "Habitat" refers to the classification

TABLE 1. *Summary of sampling design in this study of embayment, nearshore, and offshore habitats of Lake Ontario, 1995-1997.*

	Embayment	Nearshore	Offshore
Number of Sites	3	6	22–31 (depending upon month and year)
Sampling Season	May-October	May-October	August and October (May in 1996 only)
Sampling Frequency	Every 2 weeks	Every 2 weeks	Two whole-lake surveys per year
Sampling Depth	10 m (3.3 m in SPB)	10 m	25–50 m for zooplankton; 10 m for TP, chl*a*
Time of Sampling	Day	Day	Night
Boat Anchoring	Yes	Yes	No
Variable Measured:			
TP, Chl *a*[a]	XX	XX	XX
Mean Temperature, Secchi Depth[a]	XX	XX	
Crustacean Zooplankton[b]	XX	XX	XX

[a] One sample or measurement per site per sampling date. Units: TP and chl *a* in µg/L, temperature in °C, and Secchi depth in m.

[b] Crustacean zooplankton variables: density (volumetric and areal, #/L or #/m, respectively), biomass (µg dry mass/L and µg/m, respectively), and mean length (mm).
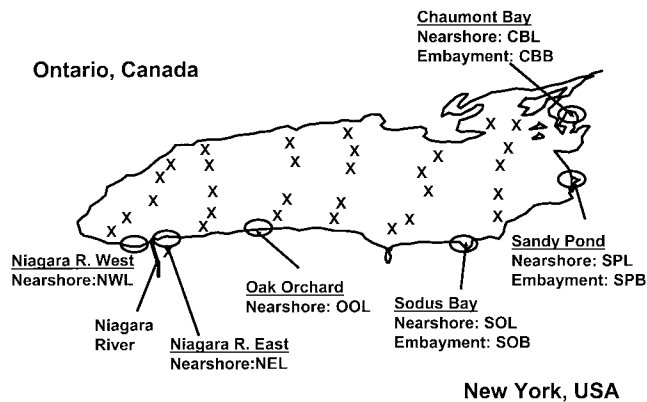
FIG. 1. *Location of study sites in Lake Ontario, 1995 to 1997. Nearshore/embayment sites are ovals. Offshore sites are denoted with "X"s. However, since number and precise location of offshore sites varied by year and month (August and October) of the survey, these labels are only approximations. Embayment sites were located at Sodus Bay, Sandy Pond, and Chaumont Bay only. Abbreviations for embayment and nearshore sites are given.*

scheme for collective sites in embayment, nearshore, and offshore areas. "Embayment" habitat was defined as shallow (depth = 3 to 10 m), bay sites relatively isolated from offshore waters of the main lake. "Nearshore" habitat was considered as relatively shallow (depth = 10 m) sites along the shoreline, but fully exposed to the main lake. The sampling depths of the nearshore sites were within the range (although on the shallower end) of sample depths in other studies of "nearshore" waters (Gregor and Rast 1982, Rockwell *et al.* 1985). Sites throughout deeper pelagic portions of the lake (depth > 20 m) were calculated as offshore habitat.

Offshore water and zooplankton samples were collected at night by the R/V *Seth Green* at each of 22 to 31 trawling sites during summer (August) and fall (October) fish assessment surveys (Fig. 1). Additionally, 11 offshore sites were sampled in mid-May of 1996 only. Offshore sampling was designed to characterize the pelagic epilimnion with extensive spatial sampling rather than intensive sampling at a few fixed sites. At six nearshore sites and three embayment sites, water and zooplankton samples were collected during daylight and usually once every 2 weeks, from 1 May to 17 October (12 occasions per year) (Fig. 1).

Transparency, Water Temperature, TP, and Chl *a*

Water transparency was measured using a Secchi disk at embayment and nearshore sites only. Mean epilimnetic water temperature was measured in nearshore and embayment habitat (not in offshore habitat) using 3.3 m (SPB site only) or 10 m (all other embayment and nearshore sites) integrated water samples or from depth profiles. When depth profiles were used, temperature was taken at 1-meter intervals and averaged from surface to a depth of 10 m or bottom if depth was less than 10 m. Integrated water samples for analysis of TP and chl *a* were collected at all sites using a 1.9 cm inner diameter Nalgene tube, lowered to a depth of 3.3 m (SPB site only) or 10 m. Raw lake water was filtered through Whatman 934-AH glass fiber filters in the field, and these filters were assayed for chl *a* using the acetone extraction method (Strickland and Parsons 1972). A 50-mL unfiltered aliquot of each sample was frozen for later analysis of TP using persulfate digestion (Menzel and Corwin 1965). Quality assurance/quality control samples for TP were done with a certified laboratory.

Crustacean Zooplankton Variables

Three variables were measured to characterize crustacean zooplankton: density, biomass, and average body length. Both density and biomass were calculated on a volumetric (per L) and areal (per m^2) basis. Volumetric measurements were more likely to reflect the feeding environment of fishes, while areal measurements indicated total amount of epilimnetic zooplankton present per unit area of the lake. Zooplankton samples were collected with vertical tows using 0.5-m diameter, 153-μm mesh, 2-m-long, nylon nets. It was assumed that there was a 100% net filtering efficiency, and volumetric density and biomass were multiplied by tow depth to calculate density and biomass on an areal basis. These gear and sampling methods are consistent with many earlier studies of Lake Ontario and elsewhere (Mills and Schiavone 1982, Johannsson *et al.* 1991, O'Gorman *et al.* 1991). At embayment and nearshore sites, boats were anchored and nets were towed vertically through the water column. At these sites, zooplankton were sampled in the top 10 m (or top 3.3 m at Sandy Pond embayment), and three replicate tows were collected to increase precision at each site. Data from these three tows were averaged prior to all data analyses.

At offshore sites, length of tow ranged between

25 to 50 m, and samples were collected from an unanchored vessel at night (as in Johannsson *et al.* 1991). Nightly epilimnetic sampling gives a better representation of vertically migrating species in the offshore (such as *Diacyclops thomasi* and *Tropocyclops prasinus*) (Johannsson 1987, Johannsson and O'Gorman 1991, Johannsson *et al.* 1994). Since the goal was to capture as much spatial coverage on Lake Ontario as possible, time did not permit anchoring of the vessel. It is possible, however, that by not anchoring, zooplankton tows may have been oblique on occasion, and that vessel drift may have led to possible overestimation of biomass and density (see discussion below). Tow depths at offshore sites were determined by maximum depth of alewife, which was found using echo-sounders and trawling. Location of alewife has been documented as a good indicator of epilimnetic depth in Lake Ontario (Olson *et al.* 1988, Johannsson and O'Gorman 1991, O'Gorman *et al.* 1991). Finally, only one sample was collected at each offshore site.

Zooplankton samples were preserved in the field using either 4% sugar formalin (1995 to 1997) (Haney and Hall 1973) or 70% ethyl alcohol (some sites in 1997). When alcohol was used, zooplankters were first anaesthetized using effervescent antacid tablets to prevent explosion of cladoceran carapaces. Crustacean zooplankton (excluding the mysid shrimp, *Mysis relicta*) were counted and measured (mm) from 1 to 3, 1-mL sub-samples (greater than 100 individuals per sample) using a microprojector at 20× magnification. Images were projected onto an electronic touch screen interfaced with a computer (Hambright and Fridman 1994). Most crustacean zooplankton were identified to species (Balcer *et al.* 1984), except nauplii and copepodites. Length (mm):dry weight (μg) regression equations (Cornell Biological Field Station, *unpublished data*) were used to estimate zooplankton biomass. Average body length of the zooplankton community was based on the length of 100 or more individuals (all species pooled). Length measurements were made from the anterior margin of the head to the base of the tailspine (cladocerans) or to the caudal setae (copepods).

Data Analysis

Comparison of Embayment—Nearshore-Offshore Habitats

Seven variables (TP, chl *a*, zooplankton density [volumetric and areal], zooplankton biomass [volumetric and areal], and zooplankton length) were compared in embayment, nearshore, and offshore habitats during both August and October. Comparisons of each month were analyzed separately. For each year between 1995 and 1997, fortnightly samples falling within August and October were averaged at each nearshore and embayment site; therefore sites were considered as "replicates" within habitat types for analysis. As a result, sample size for both August and October analyses during each of the three years was $N = 3$ for embayment habitat (three sites), $N = 6$ for nearshore habitat, and $N = 22$ to 31 for offshore habitat. Each variable was log-transformed ($\log_{10}[x]$) to achieve normality and reduce heteroscedasticity of residuals. There were two stages of analyses: Mantel tests, to test for spatial autocorrelation in offshore and nearshore habitats, followed by parametric (multivariate) analysis of variance ([M]ANOVA) and principle components analysis (PCA).

Mantel tests were first used to detect spatial autocorrelation in the offshore dataset, and the data were lumped to eliminate statistical non-independence of spatially proximate sites. For each month-year (e.g. August 1995, October 1996) and for each of the seven variables, statistical significance of the Mantel Z-statistic (and associated r-statistic) was calculated, using 2,500 randomizations, a two-tailed test (Manly 1997, Fortin and Gurevitch 2001), and a program using Matlab 5.3 (Mathworks, Inc. 1999). Autocorrelation was also tested among all of the variables for each site-year (a multivariate test). Evidence was found of significant spatial autocorrelation of at least one variable for each of the 6 month-years tested. As a result, proximate sites were spatially averaged and the reduced datasets were re-analyzed with Mantel tests until significant autocorrelation was no longer detected for any of the variables. (The only exception which was permitted concerned chl *a* in August 1997: $Z = 6.10$, $r = 0.69$, $P = 0.0012$, $N = 10$.) As a result of averaging data, the number of sites in the offshore was reduced to 10–20 sites, depending upon the month-year.

Mantel tests were used to look for spatial autocorrelation in the nearshore habitat and between nearshore and embayment sites. *A priori*, a potential west-east gradient among nearshore sites was anticipated. Subsequently, sites were chosen along the southern shore of Lake Ontario (Fig. 1) to capture as much of this gradient as possible, providing an efficient but conservative estimate of variation in

the nearshore habitat (Cochran 1977, Section 8.6). Spatial autocorrelation, *post hoc,* was then tested using Mantel tests. Similar to the offshore tests, for each month-year the significance of Mantel Z-statistics was calculated using 2,500 randomizations for each of the variables and a multivariate analysis among nearshore sites ($N = 6$), and among nearshore and embayment sites ($N = 9$). For each month-year except August 1996, no evidence was found of autocorrelations (all $rs < 0.30$, $Ps > 0.15$). In August 1996, there was marginally significant evidence of spatial autocorrelation among nearshore sites ($0.35 < r < 0.55$, $0.05 < P < 0.10$) for five of seven variables (chl a, areal zooplankton density, volumetric zooplankton density and biomass, and zooplankton length). These nearshore tests had low power due to a small number of nearshore sites ($N = 6$); with larger numbers of nearshore sites, there may be significant spatial autocorrelation in August 1996. However, without evidence of systematic (for each year) spatial autocorrelation in the nearshore, and without evidence of autocorrelation among embayment and nearshore sites as a whole (all $rs < 0.26$, all $Ps > 0.12$, $N = 9$), a parametric (M)ANOVA was used to test for differences in variables along the embayment-nearshore-offshore habitat gradient. The potential spatial gradient among nearshore sites was also documented using PCA (below).

As encouraged by Scheiner (1993), all seven dependent variables were analyzed for independent August and October comparisons in an overall MANOVA using *habitat* (embayment, nearshore, offshore), *year* (1995, 1996, 1997), and *habitat* × *year* interactions as fixed factors in the models (SYSTAT 9.0; SPSS, Inc. 1998). Analysis of significant MANOVAs with univariate ANOVAs was used to identify effects on individual variables, but overall Type I ($\alpha = 0.05$) error was controlled by using sequential Bonferroni adjusted αs using the Dunn-Sidak method (Sokal and Rohlf 1995). For models using October data, missing cells (lost samples) of each variable were filled with mean values of all years for that variable. For significant ANOVA models, *post hoc* Scheffe's pair-wise tests were used to compare embayment, nearshore, and offshore habitats or to compare years (Sokal and Rohlf 1995). Seven variables were compared in embayment, nearshore, and offshore habitats in May during 1996 only. To analyze these variables, a similar approach was used, but with only one fixed factor (*habitat*).

PCA was used to characterize the potential, although weak, gradient among nearshore sites, and between embayment and proximate nearshore sites (SYSTAT 9.0; SPSS Inc. 1998). For August and October, correlation matrices were calculated for five variables (TP, chl a, volumetric zooplankton density, volumetric zooplankton biomass, and average zooplankton length) among nearshore and embayment sites. Eigen-analysis was used to reduce dimensionality of this matrix. Component scores were plotted for each site-year, and biological meaning of the PC axes was interpreted using the loadings results.

Seasonal Variability in Embayment and Nearshore Habitats

Multivariate repeated measures (RM) ANOVA with log-transformed ($\log_{10}[x]$) data was used to examine spatial and temporal patterns of TP, chl a, Secchi depth, water temperature, and volumetric zooplankton density, size, and biomass. Since most sampling depths were similar between embayment and nearshore sites, only volumetric density and biomass of zooplankton were considered. Embayment and nearshore habitats were compared using data from each site and for each year (1995 to 1997) segregated fortnightly, testing for significance of two fixed factors (*habitat* and *year*, as above), a "*seasonal*" (within subject) factor, and all possible interactions. A multivariate approach was selected because it permits an "unstructured" variance-covariance matrix and does not require that dependent variables are equally correlated (von Ende 1993). Ideally, a doubly multivariate analysis would have been performed, which would allow taking an unstructured variance-covariance matrix approach to simultaneously analyzing repeatedly measured, multiple response variables (von Ende 1993), but the design exceeds the limitations of current algorithms for this analysis. Instead, the overall Type I ($\alpha = 0.05$) error was controlled by using a sequential Bonferroni-adjusted α levels and the Dunn-Sidak method (von Ende 1993, Sokal and Rohlf 1995). For each variable, missing cells (lost or broken samples) were filled with mean values of the entire dataset of that variable.

Relationships of Chl a and TP

Deviations of chl a were tested in the dataset from chl a predicted by three published epilimnetic $\log_{10}$ chl a (µg/L)/$\log_{10}$ TP (µg/L) relationships. The first relationship is an equation derived from spring-summer samples of north temperate, inland

lakes without dreissenids (equation 1 of Mazumder 1994). This equation is very similar to equations presented in Hanson and Peters (1984) and Pace (1984), both of which yield nearly identical results. The second relationship is based on equations in Nicholls *et al.* (1999, equation in caption of Fig. 2) and Gregor and Rast (1982, calculated from data in Table 1) for pre-dreissenid, nearshore habitat in the Great Lakes. Nicholls *et al.*'s (1999) model used May to October averaged data, collected at 17 municipal water intake sub-surface sampling sites, while Gregor and Rast (1982) used mean summer values of surface water collected during the early 1970s. Both of these studies used data from nearshore Canadian waters of the Laurentian Great Lakes.

Using these three models, significant differences were tested in yield of chl *a* per unit TP in the dataset during summer (mid-June through early September) for embayment and nearshore habitats only, and during August only for all three habitat types. Specifically, mean deviations of observed chl *a* (this study) from predicted chl *a* (published regression models) were compared with zero (zero indicating no deviation) using a *t*-test (Sokal and Rohlf 1995). Statistically significant negative mean deviations were considered, after sequential Bonferroni correction using the Dunn-Sidak method, to provide evidence of reduced yield of chl *a* per unit TP.

RESULTS

Comparison Among Embayment, Nearshore, and Offshore Habitats

Upon comparison of embayment, nearshore, and offshore habitats (Table 2, Fig. 2), it was found that embayments have statistically higher levels of TP, chl *a*, and volumetric zooplankton density and bio-

FIG. 2. Comparison of embayment (E), nearshore (N), and offshore (O) habitats of Lake Ontario during August and October. Data are averages (± 1 SE error bars) of each habitat during each year (1995 to 1997). N = 3 for embayment habitat, N = 6 for nearshore habitat, and N = 10 to 20 for offshore habitat (depending on the month and year). Differences of variables between habitats with the same lower case letter are statistically indistinguishable using Scheffe's Tests. "NS" indicates that accompanying ANOVA was not statistically significant.
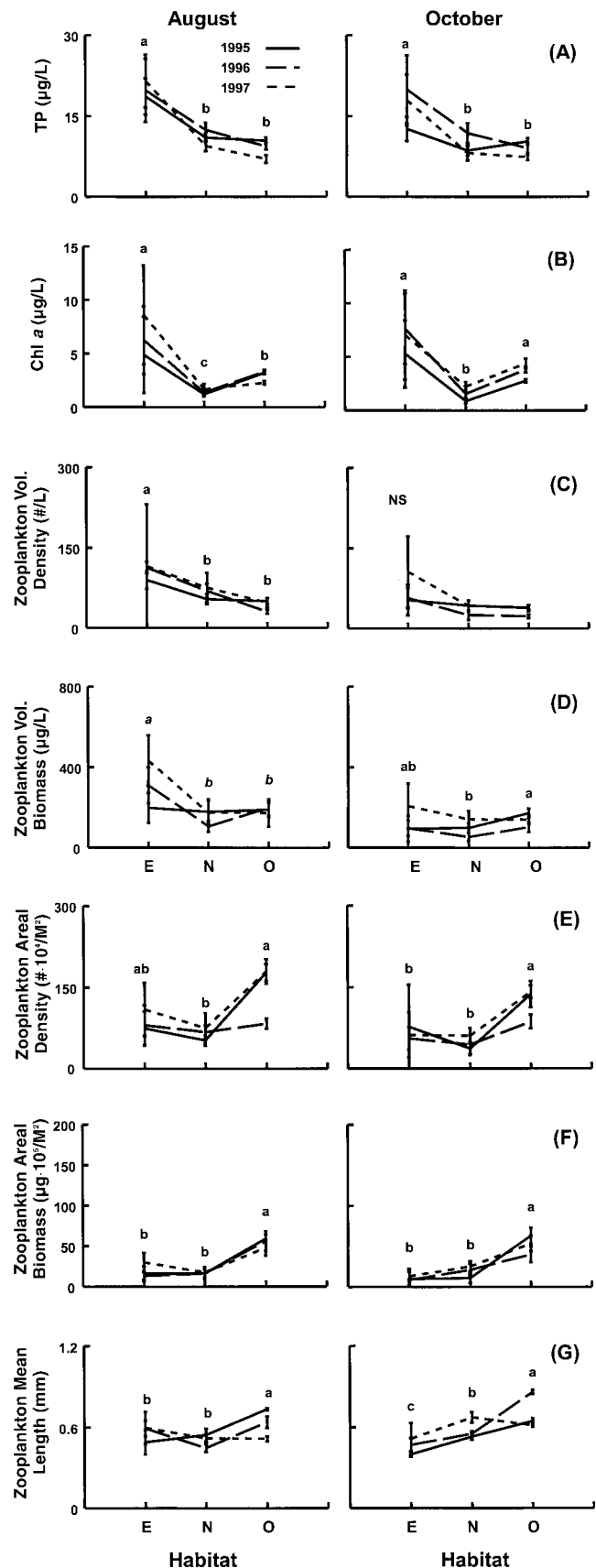
*TABLE 2.   Results (F-values) of August and October overall multivariate and individual univariate ANOVA comparisons of embayment (**N = 9**), nearshore (**N = 18**), and offshore (**N = 48 for August and N = 39 for October**) habitats in Lake Ontario, 1995 to 1997. ANOVA models used the fixed factors "Habitat" (**df = 2**), "Year" (**df = 2**), and "Habitat × Year" (**df = 4**), and log$_{10}$(x)-transformed variables for independent August and October comparisons. Sum-of-squares$_{error}$ has 66 and 57 degrees of freedom for the August and October univariate models, respectively.*

	August			October		
Variable	Habitat	Year	Habitat × Year	Habitat	Year	Habitat × Year
MANOVA	40.34**	0.959	2.27	24.78**	4.423**	4.66**
Degrees of Freedom	14,120	14,120	28,217	14,102	14,102	28,185
Wilk's λ	0.031	0.809	0.40	0.05	0.39	0.15
TP (µg·L^{-1})	21.49**	1.27	1.55	16.45**	2.60	2.72
Chl *a* (µg·L^{-1})	56.50**	0.15	1.85	25.94**	4.08*	0.91
Zoop. Density (#·L^{-1})	12.21**	0.54	1.55	2.17	1.64	0.35
Zoop. Biomass (µg·L^{-1})	3.42*	0.19	0.62	4.00*	2.02	1.44
Zoop. Density (#·m^{-2})	11.48**	1.54	2.82	12.45**	0.56	0.36
Zoop. Biomass (µg·m^{-2})	18.72**	0.97	0.48	21.81**	0.90	0.90
Zoop. Length (mm)	7.03**	0.55	3.42*	65.18**	10.63**	18.45**

** and * indicate significance at α = 0.01, and 0.05, respectively, for overall MANOVA model and for univariate ANOVA models with sequential Bonferroni-corrected significance levels.

mass than nearshore and offshore habitats in August. In October, in contrast, differences of chl *a* and volumetric zooplankton density and biomass between embayments and nearshore/offshore habitats were less pronounced and often not statistically different (Table 2, Fig. 2). However, in October, embayments still maintained higher levels of TP than nearshore and offshore habitats (Table 2, Fig. 2). Additionally, in both August and October, measures of TP, chl *a*, and volumetric zooplankton density and biomass in nearshore and offshore habitats were typically similar. Furthermore, for variables such as chl *a* (August and October) and volumetric zooplankton biomass (October only), offshore habitat had statistically higher levels than nearshore habitat. Yet, in contrast to volumetric indices of zooplankton abundance, areal measures showed a different pattern: areal zooplankton density and biomass generally was higher in offshore habitat (deeper epilimnion and sampling depth) than in nearshore and embayment habitat (shallower sampling depth) in both August and October (Table 2, Fig. 2). Additionally, zooplankton length was greater in offshore habitat than in nearshore and embayment habitat, although the magnitude of this difference was not large (Table 2, Fig. 2).

Significant differences were found between years in October for two variables, chl *a* and zooplankton length (Table 2). Overall chl *a* was lower in all habitats in 1995 than in both 1996 and 1997 (Scheffe's *post hoc* tests, *P*s = 0.032 and 0.008, respectively), while overall zooplankton were largest in 1996, smaller in 1997, and smallest in 1995 (Scheffe's *post hoc* tests, all *P*s < 0.001) (Figure 2). Detection of these significant *year* effects accounted for the significant *year* factor in the overall October MANOVA (Table 2). Significant *habitat × year* interactions were found for zooplankton length in both August and October (Table 2). These interactions reflected changes in ranking of average length in different habitats, depending upon the year considered (Fig. 2). The significant October interaction also explained the significant *habitat × year* interaction in the October MANOVA model (Table 2).

Differences among habitats were detected for TP, chl *a*, and volumetric zooplankton density and biomass using May 1996 data as well (Table 3). Embayments had higher concentrations of TP, chl *a*, and zooplankton density than both nearshore and offshore sites, while nearshore sites had lower volumetric zooplankton biomass than both embayment and offshore habitats (Table 3). Although not statistically significant, mean volumetric zooplankton biomass was twice as high (but highly variable) in embayment habitat, as compared to that in offshore

*TABLE 3. Results of spring (mid-May) individual univariate ANOVA comparisons of embayment (**n = 3**), nearshore (**n = 6**), and offshore (**n = 11**) habitats in Lake Ontario in 1996 only. Models used "Habitat" (**df = 2**) as a fixed factor and log$_{10}$(**x**)-transformed variables. Sum-of-squares$_{error}$ has 17 **df**. Mean and standard errors (in parentheses) are also presented for un-transformed variables. Differences of variables between habitats with the same lower case letter are statistically indistinguishable using Scheffe's Tests. Overall MANOVA was significant (Wilks' λ = 0.012, **F = 21.3, P < 0.001**).*

	TP (μg/L)	Chl *a* (μg/L)	Zooplankton Density (#/L)	Zooplankton Biomass (μg dry mass/L)	Mean Zooplankton Length (mm)
F-ratios	13.47**	10.63**	10.97**	9.77**	95.17**
Embayment	17.8 (1.2) a	4.0 (0.9) a	60.5 (23.5) a	113.2 (46.8) a	0.51 (0.03) b
Nearshore	11.6 (3.3) b	0.9 (0.6) b	3.4 (2.8) b	7.0 (4.8) b	0.49 (0.05) b
Offshore	8.8 (0.5) b	1.3 (0.09) b	6.5 (2.4) b	55.7 (22.8) a	0.85 (0.02) a

** and * indicate significance at α = 0.01, and 0.05, respectively, for overall MANOVA model and for univariate ANOVA models with sequential Bonferroni-corrected significance levels.

habitat. Meanwhile zooplankters were statistically longer in the offshore than in both nearshore and embayment habitats.

Using PCA, the possible presence of a highly variable west-east gradient among nearshore sites was detected. In both August and October analyses, PCA axis 1 explained over 50% of the variation of the dataset (59.9% and 54%, respectively). In addition, PC axis 1 loaded strongly with four highly correlated variables: TP (0.87, 0.73, respectively), chl *a* (0.86, 0.82), volumetric zooplankton density (0.88, 0.82) and biomass (0.84, 0.67). In October, it also loaded strongly with zooplankton length (–0.62). Patterns of PC axis 1 scores among nearshore sites, particularly in August, sometimes do follow along a west (less TP, etc.) to east (more TP, etc.) gradient, although the pattern is highly variable (Fig. 3). PC axis 2 loads strongly with zooplankton length in August (–0.99), and with volumetric zooplankton density and biomass (0.55 and 0.74, respectively) and zooplankton length (0.60) in October. In both months, sites do differentiate along east-west gradients on PC axis 2, but variation among years is even greater (Fig. 3). Embayment sites SPB and SOB group separately from each other and from their proximate nearshore sites (SPL and SOL, respectively), while embayment site CBB groups more closely with its proximate site, CBL (Fig. 3).

Spatial, Seasonal, and Inter-annual Variability in Embayment and Nearshore Habitats

Several major patterns emerge from considering overall habitat comparisons, inter-year, and sea-sonal aspects of the embayment-nearshore gradient. First, an analysis of patterns among years showed that embayment habitats overall had higher levels of TP, chl *a*, volumetric zooplankton density and biomass, higher mean water temperature, and lower Secchi depth than nearshore habitat throughout May to October (Fig. 4, Table 4). In contrast, zooplankton length was similar in embayment and nearshore habitat, but there were overall differences among years (Table 4). These results generally reiterate and support those of the August and October ANOVA analyses above. Second, an analysis of patterns within years indicated that all variables, except Secchi depth, showed significant seasonal developmental patterns (Fig. 4, Table 4). For chl *a*, volumetric zooplankton density, volumetric biomass, and temperature, significant *seasonal × habitat* effects were found, and for chl *a* alone, a significant *seasonal x habitat x year* effect was found (Table 4). Chl *a* peaked in embayment habitat in August and September, but it exhibited minimal change in nearshore habitat, May through October (Fig. 4). Additionally, volumetric zooplankton density and biomass were higher in embayment habitat than in nearshore habitat until mid-summer; in late summer and early fall, differences between embayment and nearshore habitat were reduced (Fig. 4). Furthermore, water temperature was higher in embayment habitat than in nearshore habitat in spring through mid-summer but not in autumn (Fig. 4). Finally, significant *seasonal × year* effects were detcted for both water temperature and zooplankton length (Table 4), indicating that both variables ex-
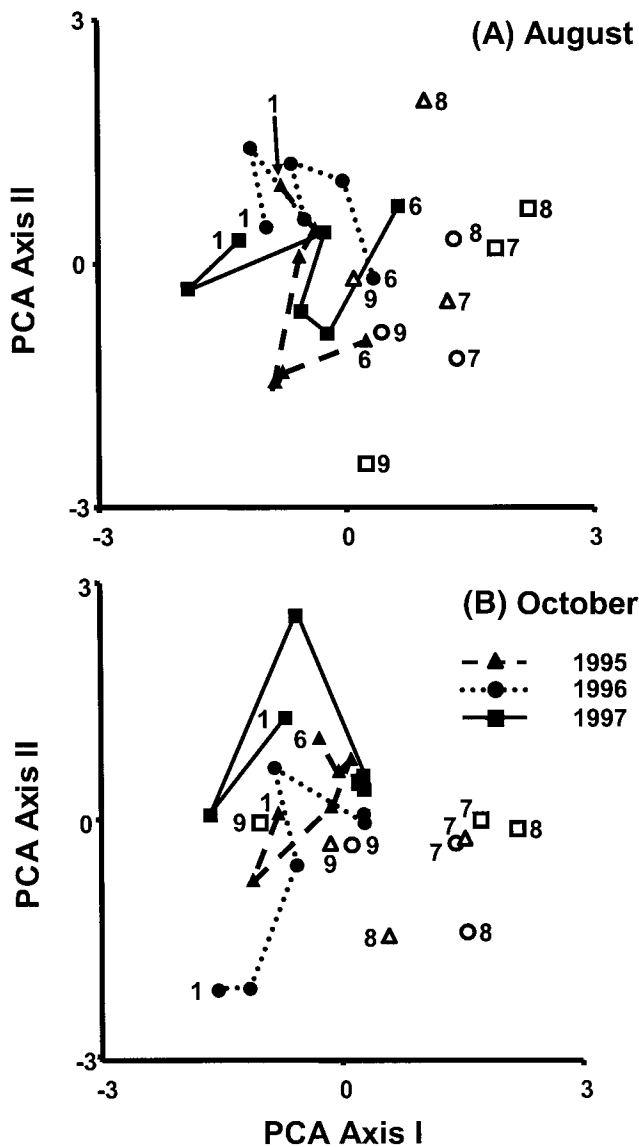
FIG. 3.   *Component scores resulting from principle component analysis of five key indicator variables (TP, chl a, volumetric zooplankton density and biomass, and zooplankton length, all log_{10}(x) transformed) in embayment sites (clear symbols) and nearshore sites (black symbols) of Lake Ontario during (A) August and (B) October. Nearshore site codes are numbered from west to east: 1 = NWL, through 6 = CBL, and adjacent sites are joined by dashed lines (1995), dotted lines (1996), or solid lines (1997). Embayment site codes are also numbered from west to east: 7 = SOB, 8 = SPB, 9 = CBB. See Figure 1 for abbreviations and geographic locations of sites.*

hibited different patterns of seasonal development between years.

Evidence of Inter-Habitat Differences of Chl *a*:TP Relationships

In the nearshore habitat, less chl *a* per unit TP than predicted by the representative equation developed from northern temperate lakes (Mazumder 1994) during both summer (mid-June through late August) and August only analyses (Table 5). Similarly, using the pre-dreissenid Laurentian Great Lakes nearshore equation developed by Nicholls *et al.* (1999), less chl *a* per unit TP was observed than predicted in the nearshore for both summer and August-only analyses (Table 5). However, the magnitude of the mean deviation from Nicholls *et al.*'s (1999) model is smaller than that calculated using the north temperate lakes equation (Table 5). In contrast, more chl *a* per unit TP was observed in the nearshore than predicted by the nearshore-specific equation of Gregor and Rast (1982) in the nearshore summer analysis, and no significant deviation was found in the August-only nearshore analysis.

These patterns in nearshore habitat contrast with those found in embayment and offshore habitat. More specifically, no significant differences were found between observed chl *a* and that predicted by the Mazumder (1994) equation in either summer or August-only analyses, but more chl *a* per unit phosphorus was observed than predicted by nearshore-specific equations (Gregor and Rast 1982, Nicholls *et al.* 1999) in embayment habitat. In offshore habitat, slightly less chl *a* per unit TP was found using the north temperate lakes equation (Table 5). Although statistically significant, it is unlikely that the magnitude of this mean deviation is biologically meaningful (Table 5). In contrast, more chl *a* per unit TP was observed than predicted by both nearshore equations in offshore habitat (Table 5).

Data for chl *a* and TP in Lake Ontario prior to the establishment of *Dreissena* were needed as evidence of possible "decoupling" between these two variables. The only published historical studies containing this information were made by Rockwell *et al.* (1985) (seven nearshore sites in 1981) and Makarewicz (1991) (June through September nearshore data at one site in 1986 and 1987). August data from these two studies were compiled, and the first seven sites and 2 years at the Makarewicz (1991) site were treated as independent samples (total $N = 9$). It was found that chl *a* per unit TP in nearshore habitats, prior to invasion by
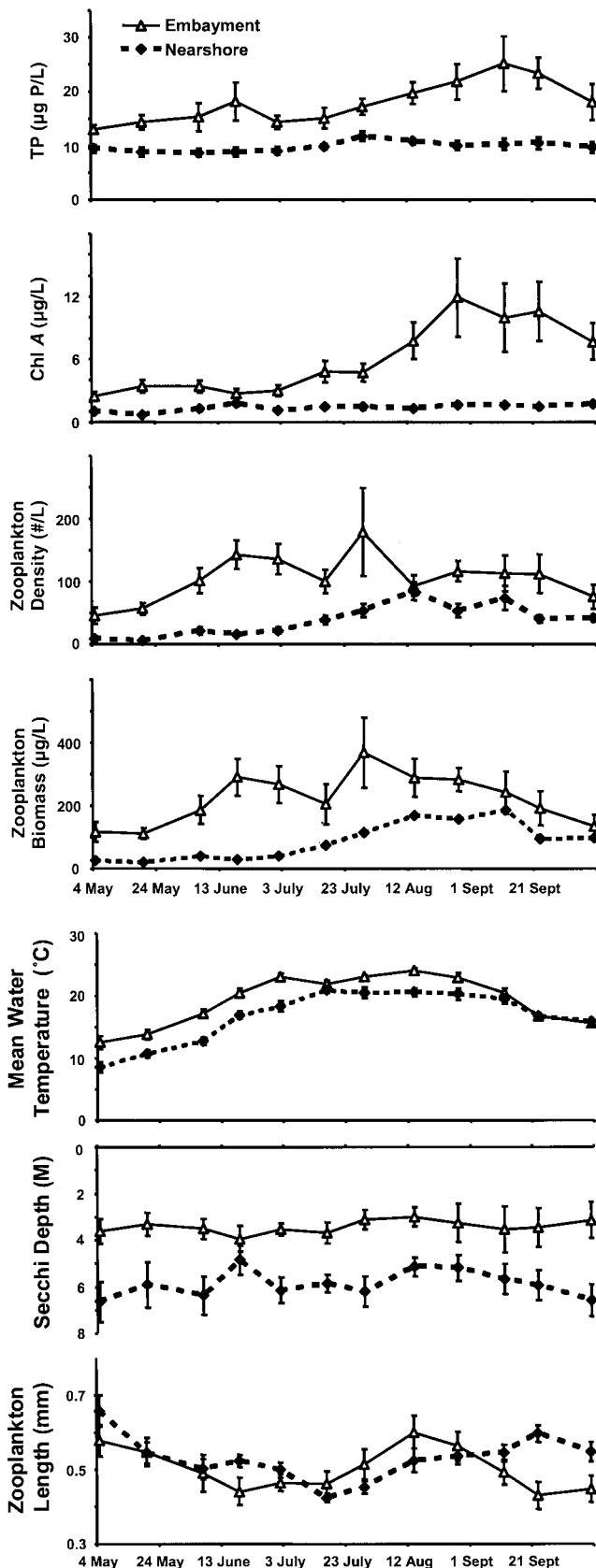
Dreissena, matched that predicted by northern temperate lakes (Mazumder 1994; mean deviation = –0.08, SE = 0.06; t = –1.24, P = 0.25, N = 9) while more chl *a* was observed than predicted by the nearshore-specific equations (Gregor and Rast 1985: mean deviation = 0.38, SE = 0.06; t = –6.55, P = 0.0002, N = 9; Nicholls *et al.* 1999: mean deviation = 0.28, SE = 0.07; t = 3.83, P = 0.005, N = 9). The implications of these findings are discussed below when considering possible scenarios causing changes in the relationship of chl *a* and TP in the nearshore waters of Lake Ontario.

DISCUSSION

Spatial and Temporal Comparisons of the Embayment, Nearshore, and Offshore Habitats

This 3-year, spatio-temporal analysis of lower trophic variables yielded two major findings. As expected, embayment habitat was more eutrophic than nearshore and offshore habitats of Lake Ontario, as reflected by generally higher concentrations of TP and chl *a*, and higher volumetric indices (density and biomass) of zooplankton. Embayment habitat was not only more eutrophic than nearshore habitat, but it also exhibited distinctly different seasonal patterns. TP and chl *a* peaked in embayments during August and September, but remained relatively constant during May through October in the nearshore habitat. Such habitat differences are not surprising, as embayments typically are sheltered (geomorphologically and probably hydrologically) from offshore pelagic waters, and they receive allochthonous inputs of nutrients from nearby watersheds and municipal waters. Perhaps more importantly for fishes (O'Gorman *et al.* 1997), the first major increases of algae and zooplankton populations in spring/early summer occurred in embayments, likely triggered by warmer temperatures and higher TP levels (as were observed in Patalas 1969, Scavia and Bennett 1980, McQueen *et al.* 1986, Neilson and Stevens 1987).

With reductions in phosphorus loading to

FIG. 4. *Time series data, binned approximately fortnightly, of averages (± 1 SE) of each site-year of indexing variables in embayment (solid lines and white triangles;* N = 9, *i.e., three sites during 3 years) and nearshore habitats (dashed lines and black diamonds;* N = 18, *i.e., six sites during 3 years) of Lake Ontario, 1995–1997.*

TABLE 4. *Results (**F**-values and **df**) of repeated measures ANOVA models examining spatial and temporal patterns of seven variables in embayment and nearshore habitats of Lake Ontario. Temporal variability was characterized on two scales: inter-annual (seasonal) and intra-annual. We used a multivariate approach to analyze the "seasonal" terms of the models: thus, Wilk's λ and **F**-values, respectively, are shown for these terms.*

	Inter-annual (Among Years)			Intra-annual (Seasonal)			
Variable	Habitat $(df = 1, 21)$	Year $(df = 2, 21)$	Habitat × Year $(df = 2, 21)$	Seasonal $(df = 11,11)$	Seasonal × Habitat $(df = 11,11)$	Seasonal × Year $(df = 22,22)$	Seasonal × Habitat × Year $(df = 22,22)$
TP (µg/L)	30.75 **	3.29	0.43	0.23, 3.30*	0.47, 1.14	0.11, 2.02	0.18, 1.36
Chl *a* (µg/L)	35.52 **	0.90	0.10	0.19, 4.42*	0.13, 6.76**	0.27, 0.93	0.36, 6.67**
Zoop. Density (#/L)	48.54 **	0.11	0.12	0.13, 6.90**	0.14, 6.11**	0.21, 1.20	0.17, 1.41
Zoop. Biomass (µg/L)	32.56 **	0.37	0.34	0.13, 6.65**	0.13, 6.57**	0.12, 1.85	0.20, 1.22
Temperature (° C)	38.41 **	0.11	2.60	0.61, 71.59**	0.15, 5.56**	0.03, 4.49**	0.23, 0.94
Secchi Depth (m)	11.33 *	0.42	0.07	0.42, 1.39	0.47, 1.12	0.09, 2.34	0.18, 1.39
Zoop. Length (mm)	1.93	10.69 **	1.62	0.13, 6.88**	0.28, 0.88	0.14, 5.95**	0.22, 1.12

* and ** indicate statistical significance at sequential Bonferroni-corrected α = 0.05 and 0.01, respectively.

nearshore waters and *Dreissena*-induced changes in water clarity in Great Lakes waters, one might expect that nearshore habitats would be more similar to offshore pelagic waters than they were in the past. Historically, TP, chl *a*, and volumetric zooplankton density and biomass were higher in nearshore than in offshore habitats (Patalas 1969, Munawar and Naurwerck 1971, Czaika 1974, Stadelmann *et al.* 1974, Gregor and Rast 1982, Johannsson *et al.* 1991). In contrast, the findings of this study suggest that levels of TP, chl *a*, and volu-

metric zooplankton in both nearshore and offshore habitats are more similar than in the past. Such similarities, coupled with observed patterns of areal zooplankton density and biomass, have significant implications for planktivorous fishes in Lake Ontario. A study by Rand *et al.* (1995) in 1990 concluded that consumption by planktivorous fishes greatly exceeded offshore production of crustacean zooplankton. Rand *et al.* (1995) suggested that the discrepancy between zooplankton production and consumption might be offset by higher production

TABLE 5. *Deviations of observed chl **a** from predicted chl **a**, in $\log_{10}(x)$-units, using two sets of chl **a**: TP regression equations: one derived from north inland temperate lakes (**North-temperate**; Mazumder 1994), and two derived from pre-dreissenid nearshore Laurentian Great Lakes (**Nearshore**; Nicholls et al. 1999, and Gregor and Rast 1982). See text for details of equations. Data used were mean summer values (mid June to late August), and August values only, during each year of 1995 to 1997 for each of the habitats. (Summer means were not available for offshore sites). Statistics given are mean deviation, in log units (standard error).*

Time Period	Regression Equation	Embayments (All Sites) $N = 9$	Nearshore (All Sites) $N = 18$	Offshore (Aug Only) $N = 48$
Summer	*North-temperate*: Mazumder (1994)	−0.13 (0.07)	−0.45 (0.03)**	—
August	*North-temperate*: Mazumder (1994)	−0.06 (0.09)	−0.51 (0.04)**	−0.09 (0.02)**
Summer	*Nearshore*: Nicholls *et al.* (1999)	0.24 (0.07)*	−0.13 (0.03)**	—
August	*Nearshore*: Nicholls *et al.* (1999)	0.32 (0.09)**	−0.18 (0.04)**	0.23 (0.02)**
Summer	*Nearshore*: Gregor and Rast (1982)	0.29 (0.06)**	0.15 (0.03)**	—
August	*Nearshore*: Gregor and Rast (1982)	0.38 (0.08)**	−0.04 (0.04)	0.52 (0.03)**

** and * indicate significance at α = 0.01, and 0.05, respectively of *t*-test comparing mean deviation with zero (Sokal and Rohlf 1995) using sequential Bonferroni-corrected significance levels.

of zooplankton in the nearshore and embayment habitats. If it is assumed that areal zooplankton biomass is strongly correlated with actual production (Shuter and Ing 1997, Stockwell and Johannsson 1997), these results suggest that zooplankton production in nearshore and embayment habitats in August does not contribute disproportionately to overall areal zooplankton production in the lake. However, zooplankters were most dense volumetrically in embayments. Consequently, embayments may represent a rich source of zooplankton for plankton-eating fishes, and this source may translate into higher growth and survival rates than for those living in nearshore and offshore habitats (Miller *et al.* 1988, O'Gorman *et al.* 1997).

While making comparisons of zooplankton indices between nearshore and offshore habitats, it is important to acknowledge a potential bias in the offshore data. In the offshore sampling regime, the vessel did not anchor during zooplankton sampling tows. If the vessel had a moderate horizontal drift of 0.5 m/s, vertical hauls could have sampled 10 to 15% more water if tow nets were retrieved at 1 m/s. In this case, the estimates of crustacean density and biomass would be 10 to 15% overestimates of actual density and biomass. However, this potential bias would not change the conclusions. For instance, a correction of this bias would reduce August offshore zooplankton biomass and make nearshore and offshore comparisons more similar, not less similar.

Crustacean zooplankton body length often indicates levels of planktivory in freshwater lakes; small average size of crustacean zooplankton indicates high levels of vertebrate planktivory (Mills and Schiavone 1982, O'Gorman *et al.* 1991). In Lake Ontario, the observed mean crustacean length was consistent with historic levels of medium to high planktivory (Johannsson and O'Gorman 1991, O'Gorman *et al.* 1991). Crustacean zooplankton length was greatest offshore (in both August and October), and fluctuated seasonally in the embayment and nearshore habitat. These spatio-temporal patterns likely reflected spring-summer influxes of alewife and other fishes into nearshore waters of Lake Ontario (O'Gorman *et al.* 1991).

Changes in Relationships of Chl *a* and TP Among Habitats

These results indicate different relationships of chl *a* and TP between nearshore habitats and embayment and offshore habitats. Specifically, lower amounts of chl *a* per unit TP were observed than predicted by Mazumder's (1994) and Nicholls *et al.*'s (1999) models for pre-*Dreissena* periods in the nearshore. In contrast, higher chl *a* per unit TP were observed in offshore and embayment habitats compared to nearshore areas. For offshore and embayment habitats, Mazumder's (1994) model closely predicted observed chl *a* per unit TP, while Nicholls *et al.*'s (1999) model predicted less chl *a* than was observed.

Four possible scenarios could explain why chl *a* per unit TP was lower in nearshore habitat compared to embayment and offshore habitat. The two possibilities that are less likely include changes in the zooplankton community and size structure, and changes in nutrient limitation. For instance, while a low yield of chl *a* per unit TP can occur in the presence of large, efficient zooplankton (large *Daphnia*) (Pace 1984, Mazumder 1994), large daphnids are uncommon in the nearshore zone of Lake Ontario (Johannsson *et al.* 1991; E.L. Mills *et al.*, *unpublished data*). Also, in nitrogen limited systems, reductions in chl *a* per unit TP might be expected. However, TN/TP ratios in Lake Ontario have been high since the 1980s (Neilson and Stevens 1987).

A more plausible hypothesis implicates grazing effects of dreissenid mussels. Theoretical (Madenjian 1995, Padilla *et al.* 1996) and field studies (Fahnenstiel *et al.* 1995, Johengen *et al.* 1995, Holland *et al.* 1995, Mellina *et al.* 1995, Nicholls *et al.* 1999) have predicted and documented intense grazing of phytoplankton by dreissenid mussels. Furthermore, Mellina *et al.* (1995) provided evidence of "decoupling" of the chl *a*-TP relationship (lower yield of chl *a* per unit TP) following invasion of zebra mussel in Lakes Erie and St. Clair. In post-zebra mussel years, Mellina *et al.* (1995) found that chl *a* per unit TP was lower than predicted by Dillon and Rigler's (1974) regression model between spring turn-over TP and summer chl *a* in these lakes. Dillon and Rigler's (1974) model had similar parameters as the model of Mazumder (1994). In Lake Ontario's nearshore habitat, dreissenid biomass is high (Mills *et al.* 1999), and as a result, the grazing potential of these filter-feeding mollusks is great. Such grazing effects could lead to lower chl *a* per unit TP in nearshore habitats (Holland *et al.* 1995, Mellina *et al.* 1995, Nicholls *et al.* 1999).

Lastly, low chl *a* per unit TP could be merely a reflection of erosion and/or resuspension processes specific to nearshore Great Lakes waters, and unrelated to grazing by *Dreissena* spp. Yield of chl *a* per unit TP in the mid-1970s in Great Lakes waters

(Gregor and Rast 1982; see also Brydges 1971) was much lower than that found in historical offshore sampling (Gregor and Rast 1982) and in the observations of embayment and offshore habitats of Lake Ontario in this study. Gregor and Rast (1982) proposed that nonbioavailable TP from bluff erosion and resuspension in nearshore sites could explain lower chl *a* yields per unit TP. Although nonbioavailable P in the form of apatite would not be measured using the persulfate digestion methods, it is possible that other resuspended tripton, measurable via persulfate digestion, could have historically contributed to lower observed yield of chl *a* per unit of TP. It is difficult to determine if this explanation accounts for the particularly large slope and large negative intercept of Gregor and Rast's (1982) model. In contrast to results produced using Gregor and Rast's (1982) regression model, Nicholls *et al.*'s (1999) nearshore-specific model predicts more chl *a* than observed in the nearshore habitat, although the difference was less than the Mazumder (1994) north temperate model. However, the chl *a* per unit TP values observed in the nearshore habitat were not as low as those predicted by Nicholls *et al.*'s (1999) post-dreissenid equation (*post hoc* August-only analysis: mean deviation = 0.17, SE = 0.04, $t = 4.07$, $P < 0.0001$; *post hoc* summer analysis: mean deviation = 0.22, SE = 0.03, $t = 7.16$, $P < 0.0001$). As a result, the yield of chl *a* per unit TP observed in the nearshore is intermediate to that predicted by Nicholls *et al.*'s (1999) pre-dreissenid and post-dreissenid equations.

It is possible that Nicholls *et al.*'s models are not appropriate for the data collected in this study. As the authors of that study pointed out, they derived their equations from samples collected in deep, subsurface waters (Nicholls *et al.* 1999). Furthermore, as the authors also noted, the low slope of their predreissenid model may reflect underutilization of P by phytoplankton at the low light levels found typically in subsurface waters (Nicholls *et al.* 1999). Thus, these differences between the data collected in this study and that used to create Nicholls *et al.*'s (1999) pre-dreissenid model makes it difficult to determine, for certain, if the lower yield of chl *a* per unit TP that was observed in nearshore sites supports a "specific-to-nearshore" hypothesis or a dreissenid-driven "decoupling" hypothesis.

Ruling out the "specific-to-nearshore" hypothesis as an explanation for the decoupling of chl *a* and TP requires pre-*Dreissena* nearshore data. Given the above analysis of data from Rockwell *et al.* (1985) and Makarewicz (1991), the "limitations" of

the Nicholls *et al.*'s (1999) pre-dreissenid model, the combination of currently highly transparent waters, suggesting limited resuspension and sediment load (mean Secchi disc > 5 m, Fig. 4), and the high abundance of dreissenids in Lake Ontario's nearshore habitat, it is likely that the Mazumder model most consistently reflects expected historical and current trends in chl *a* and TP in different habitats. The extent to which nearshore "decoupling" of chl *a* and TP occurs in other Great Lakes is unknown, but the current lower yield of chl *a* per unit TP in the nearshore habitat of Lake Ontario can be attributed more to *Dreissena* than to erosion and/or resuspension of sediments.

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