# Impact of zebra mussels (*Dreissena polymorpha*) on the pelagic lower trophic levels of Oneida Lake, New York

**Nasseer Idrisi, Edward L. Mills, Lars G. Rudstam, and Donald J. Stewart**

**Abstract**: We analyzed a data series on nutrients, phytoplankton, zooplankton, and young-of-the-year fish from Oneida Lake, New York, to test several hypotheses relating the response of the pelagic food web to grazing by zebra mussels (*Dreissena polymorpha*). System-wide grazing rates increased by one to two orders of magnitude after zebra mussel introduction. The most dramatic change associated with dreissenid grazing was increased water clarity and overall decrease in algal biovolume and Chl *a*. Contrary to predictions, primary production did not decline. We attribute the lack of whole water column decline in primary productivity to the compensating effect of increased water clarity resulting in deeper penetration of photosynthetically active radiation. We observed no change in total or dissolved phosphorus concentrations. Although algal standing crop declined, *Daphnia* spp. biomass and production did not, but dominance shifted from *Daphnia galeata mendotae* to *Daphnia pulicaria*. Consistent with our findings in the lower food web, we found no evidence that zebra mussels had a negative impact on young yellow perch (*Perca flavescens*) growth, biomass, or production. Thus, despite the order of magnitude increase in grazing rates and associated decrease in algal biomass, pelagic production at primary, secondary, and tertiary levels did not decline in association with zebra mussels.

**Résumé** : Nous avons analysé des séries de données sur les nutriments, le phytoplancton, le zooplancton et les poissons de l'année au lac Oneida, New York, afin de vérifier plusieurs hypothèses relatives aux effets du broutage par les Moules zébrées (*Dreissenia polymorpha*) sur la chaîne alimentaire pélagique. À l'échelle du système, les taux de broutage ont augmenté d'un facteur de 10 à 100 après l'introduction des Moules zébrées. Le changement le plus spectaculaire amené par le broutage des moules a été une augmentation de la limpidité de l'eau et un déclin du biovolume général des algues et de la concentration de Chl *a*. Cependant, contrairement à nos attentes, la production primaire n'a pas baissé. Nous attribuons ce maintien de la production primaire dans toute la colonne d'eau à l'effet compensatoire de la limpidité accrue de l'eau qui a permis à la radiation impliquée dans la photosynthèse de pénétrer plus en profondeur. Il n'y a pas eu de changement dans les concentrations du phosphore total, ni du phosphore dissous. Bien que la biomasse des algues ait diminué, la biomasse des *Daphnia* spp. et leur production se sont maintenues; *Daphnia pulicaria* a cependant remplacé *Daphnia galeata mendotae* comme espèce dominante. Il n'y a aucune indication que les Moules zébrées ont un effet négatif sur la croissance, la biomasse ou la production de la Perchaude (*Perca flavescens*), ce qui est conforme à nos observations sur les maillons inférieurs du réseau alimentaire. Ainsi, malgré un accroissement d'environ 10 fois des taux de broutage et le déclin qui en a résulté dans la biomasse des algues, la production pélagique aux niveaux primaire, secondaire et tertiaire n'a pas diminué en présence des Moules zébrées.

[Traduit par la Rédaction]

## Introduction

The most prevalent perturbation to aquatic ecosystems that is mediated through anthropogenic vectors is the introduction of exotic species (e.g., Mills et al. 1994). To date, 146 nonindigenous species have been recorded as established in the Laurentian Great Lakes alone (Mills et al. 1994), and many studies have focused on the impact of these exotics on associated ecosystems (e.g., Strayer et al. 1999). In particular, the recent invasion of the zebra mussel (*Dreissena polymorpha*) in North American freshwater lakes and rivers has caused concern because of their high filtration capacity and their ability to alter food web structure (e.g., Padilla et al. 1996; Caraco et al. 1997).

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In this study, we analyzed a data series on nutrients, phytoplankton, zooplankton, and young-of-the-year (YOY) yellow perch (*Perca flavescens*) from Oneida Lake, New York, to test several hypotheses relating the response of a food web to grazing by zebra mussels. The importance of these processes will vary seasonally. Specifically, we hypothesized that (*i*) total phosphorus (TP) will not decrease but will be partitioned into more soluble reactive phosphorus (SRP) and less total particulate phosphorus (TPP) due to the lower algal biomass in the water column (Heath et al. 1995; Mellina et al. 1995; Caraco et al. 1997); other dissolved nutrients (nitrate, silica) will be less affected because phosphorus is the limiting nutrient (Johengen et al. 1995); (*ii*) phytoplankton biomass (as chlorophyll *a* (Chl *a*)) will decrease, leading to a decrease in primary productivity and an increase in water clarity (Holland 1993; Fahnenstiel et al. 1995; Caraco et al. 1997), and phytoplankton community composition will shift to grazer-resistant forms, such as large cyanobacteria or large diatoms (Smith et al. 1998); (*iii*) daphnid biomass and production will decline due to reduction in algal biomass and production, and the shift to larger inedible forms of phytoplankton will further inhibit daphnid production (Karatayev et al. 1997; Pace et al. 1998); and (*iv*) decreased daphnid biomass and production will lead to declines in YOY fish biomass and individual specific growth (Rutherford et al. 1999).

While we hypothesized that changes in the pelagic lower trophic levels were zebra mussel induced, two alternative hypotheses explaining a decrease in phytoplankton and associated changes in other trophic levels are also possible: (*i*) reduced phosphorus loading causes a decrease in phytoplankton biomass [as Chl *a*], daphnid biomass and production, and YOY fish biomass and an increase in water clarity (nutrient limitation: bottom-up effect) or (*ii*) decreased planktivory by fish (unrelated to zebra mussels) increase zooplankton biomass leading to a decrease in both Chl *a* and primary productivity with TP remaining stable (trophic cascade: top-down effect).

## Materials and methods

### Study site

Oneida Lake is a 20 700-ha, shallow, productive lake (mean depth 6.8 m, maximum depth 16 m) located on the Lake Ontario Plain of central New York State (Mills et al. 1978). The lake is well mixed and generally isothermal during the ice-free months. The lake has been described as naturally eutrophic, with TP concentrations typically ranging between 30 and 60 $\mu g \cdot L^{-1}$ during the 1970s (Mills et al. 1987). Centric diatom blooms (*Cyclotella* spp.) typically have dominated early-spring phytoplankton communities, whereas cyanobacteria blooms (mainly *Aphanizomenon flos-aquae*) persist for 1 or 2 months in late summer (Greeson 1971). The zooplankton community has been dominated by two daphnid species, *Daphnia pulicaria* and *Daphnia galeata mendotae*, with smaller populations of *Daphnia retrocurva* (Mills et al. 1987). The dominant zooplanktivores are YOY fish; at high densities, YOY yellow perch are able to collapse the daphnid population (Mills and Forney 1983). Populations of gizzard shad (*Dorosoma cepedianum*) expanded in 1984 and impacted daphnid populations from the mid-1980s to the early 1990s (Roseman et al. 1996; Shepherd and Mills 1996). Zebra mussels were first observed in Oneida Lake in 1991, and by autumn 1992, the population reached densities as high as 44 000 individuals$\cdot m^{-2}$ (Mellina et al. 1995).

### Limnological data

Limnological data were collected weekly at five sites (1975–1997) from April to November (Fig. 1). Sampling was conducted monthly during the winter ice-cover period (at the reference site, Shackelton Pt.; see Fig. 1). A tygon tube (2.5-cm inner diameter) was used to collect integrated water samples (surface to 0.5 m above lake bottom) for phytoplankton and nutrients. Within 2–4 h after collection, samples were filtered for Chl *a*, SRP, total soluble phosphorus (TSP), nitrate-nitrogen ($NO_3$), and soluble reactive silica as $SiO_4$ (SRS) (Strickland and Parsons 1972; American Public Health Association et al. 1976). Filtered samples were stored at a temperature of approximately –20°C prior to analysis. Unfiltered water was used to estimate TP. Dissolved organic phosphorus (DOP) was estimated as the difference between SRP and TSP and TPP as the difference between TSP and TP. Total alkalinity and phenolphthalein alkalinity of water with known pH were used to determine dissolved inorganic carbon (DIC) (Wetzel and Likens 1991).

Number of clear-water days was defined as the period between the spring and summer algae blooms when Chl *a* was less than 3 $\mu g \cdot L^{-1}$ for at least 2 consecutive weeks. In situ water column irradiance was measured with a LI-COR 4π sensor and LI-COR 1000 data logger at 0.25-m intervals from the surface to the bottom; above-surface irradiance was measured with a LI-COR 2π sensor attached to the same data logger.

Subsamples of integrated lake water from each site for phytoplankton analysis were immediately fixed in Lugol's solution upon collection and later identified and enumerated using a Wild inverted microscope. Identification was to species when possible; otherwise, phytoplankton cells were identified to genus. Biovolume estimates were determined with the use of a BASIC program (N. Idrisi, unpublished data) using average shapes and sizes for individual algal species (Reynolds 1984). All limnological, phytoplankton, and zooplankton samples were integrated over depth; thus, estimates represent water column mean values.

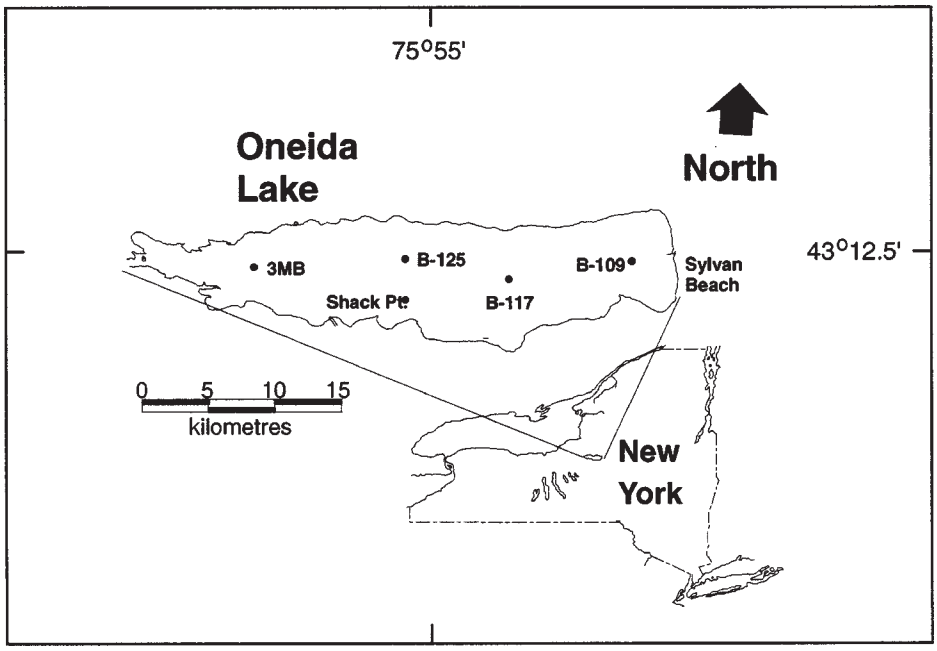
### Primary productivity

Integrated water samples were collected for $^{14}C$ photosynthesis incubations using the Fee incubator technique (Shearer et al. 1985; Fee 1990). Irradiance was measured with a LI-COR 4π sensor from the surface to the bottom to determine extinction coefficients used in calculating primary productivity. Photosynthetic–irradiance (PI) experimental procedures were modified following Lewis and Smith (1983) and Fahnenstiel et al. (1995). Modifications included the incubation of a smaller sample volume (3 mL) and a 40-min incubation period. Differences in $^{14}C$ uptake between the two procedures were minor (Lang and Fahnenstiel 1995). Water samples were kept cool in opaque 10-L containers and transferred to the laboratory for subsequent processing; time from collection of the first sample to the return to the laboratory was typically 2 h. Prior to initial experimentation, a spectral distribution analysis was carried out at the three sampling sites with a LI-COR 1800 underwater spectroradiometer on May 18, 1993, to determine the spectral quality of the euphotic zone. A colored gel, matching the spectral distribution data, was placed at the bottom of the Fee incubator (also called a photosynthetron) between the light source and the samples to act as a filter, allowing the penetration of light wavelengths similar to those in the field.

The PI curves were fitted from photosynthetic rates at specific irradiances using the simplex nonlinear curve fitting routine in Systat 5.03 (Systat®). Two PI parameters were determined, $P_m$ and $\alpha$, from the equation (Gallegos and Platt 1981)

$$P(I) = P_m \tanh\left(\frac{\alpha I}{P_m}\right)$$

**Fig. 1.** Map of Oneida Lake, New York, U.S.A., showing the main sampling sites.




where $P(I)$ is photosynthetic rate (milligrams carbon per hour) at irradiance $I$ (einsteins per square metre per hour), $P_m$ is maximum photosynthetic rate (milligrams carbon per hour), and $\alpha$ is the initial linear slope at irradiance $I$ (milligrams carbon per einstein per square metre).

Primary productivity was estimated with the computer programs developed by Fee (1990) using the PI parameters per unit chlorophyll ($P_m^B$(milligrams carbon per milligram Chl *a* per hour) and $\alpha^B$ (milligrams carbon per milligram Chl *a* per einstein per square metre)), extinction coefficients, and latitude and Julian day as input parameters. Primary productivity for years other than 1993 and 1994 was estimated using the empirical models developed in Idrisi (1997). These models, based on primary productivity measurements in 1993–1994, explained 73 and 47% of the variation for $P_m$ and $\alpha$, respectively (Idrisi 1997). The models were verified against independent data from 1988, where errors between observed and predicted PI parameters were less than 5% (Idrisi 1997).

### *Daphnia* spp. biomass and production

Zooplankton samples were collected (at the same time and locations as the limnological and phytoplankton collections) with a 153-μm-mesh Nylon net (0.5-m mouth diameter, 2 m in length) using vertical tows from approximately 0.5 m off the sediment surface to the water surface. *Daphnia pulicaria* and *D. galeata mendotae* were enumerated and body length recorded with the use of a computer-assisted plankton analysis system (Hambright and Fridman 1994). Individual weights were calculated from length – dry weight regressions (E.L. Mills, unpublished data). Numbers of eggs per female were counted for *D. pulicaria* and *D. galeata mendotae* to estimate secondary production from 1988 to 1996 according to the method of Borgmann et al. (1984). Annual average clearance rates of daphnid populations (*D. pulicaria* and *D. galeata mendotae*) were predicted for the whole data set (1975–1997) from multivariate regressions from Peters and Downing (1984). Annual averages were calculated for the period April–October for each year using eq. 4 from Peters and Downing (1984). Input data included daphnid dry weights, food concentration (wet weight converted from Chl *a*), nanoplankton biovolumes, nanoplankton biovolumes per individual daphnid for 1975–1995, median biovolume, and biovolume per individual daphnid from Peters and Downing (1984) were used for 1996–1997.

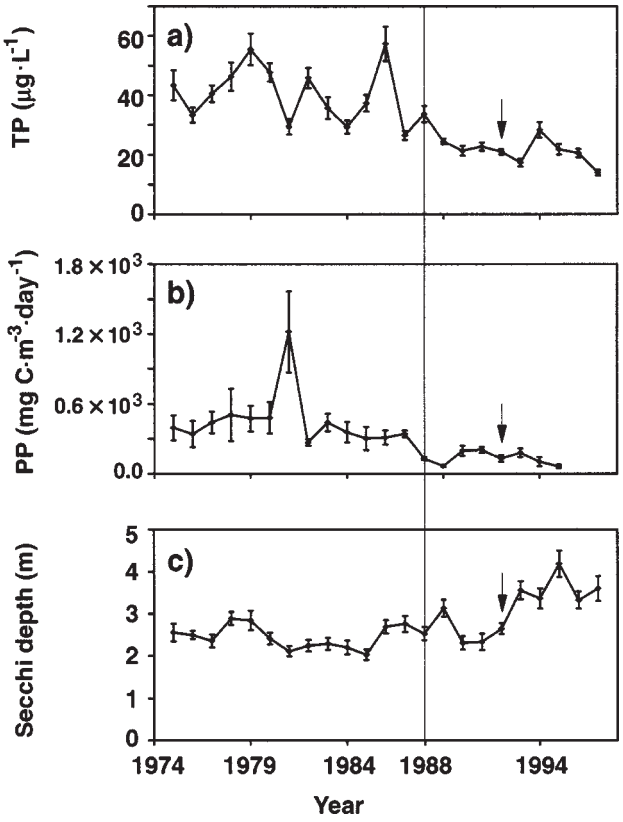
### Zebra mussel population structure

Dreissenids were collected by SCUBA using 0.5- to 1-$m^2$ quadrats placed randomly at each of 10 sites in triplicate (see fig. 1 in Mellina et al. 1995). Samples were collected in October of each year from 1992 to 1997; only nine sites were sampled in 1995. All individuals collected throughout this sampling period were *D. polymorpha*. Lake-wide wet weight biomass (including shell) means ± 95% confidence intervals were calculated by stratifying samples by substrate type (soft, sand, and hard substrates; Greeson 1971). Abundances and size frequency distributions were estimated for each substrate type and lake-wide estimates made by weighting abundances based on the total area of each substrate type (Cochran 1977). Because zebra mussels were not observed on any substrates deeper than 10 m, lake-wide values were corrected by assigning zero abundance for total lake bottom at depths exceeding 10 m. Annual zebra mussel clearance rates of the Oneida Lake zebra mussel population were estimated using the equations of Horgan and Mills (1997). Clearance rates were estimated as weight-specific rates based on zebra mussel dry weights (soft tissue only). We assumed that Oneida Lake was generally isothermal and well mixed during the ice-free season, and therefore, zebra mussels would have access to the entire water column. Daily clearance rates for zebra mussels were corrected for differential filtering activity between day and night (Horgan and Mills 1997).

### YOY yellow perch biomass, growth, and production

Abundance of a primary zooplanktivore (yellow perch) was estimated using high-speed Miller samplers (540-μm-mesh net) in June and a 5.5-m otter bottom trawl from the end of July through October each year (1975–1997). Miller sampling was conducted when YOY yellow perch attained approximately 18 mm total length (VanDeValk et al. 1999). By the end of July, YOY yellow perch typically become demersal and vulnerable to bottom trawls (Forney 1971). Weekly estimates of YOY yellow perch from the end of July through October were obtained from trawls fished at 10 sites each week. Average daily biomass was calculated from the decline in abundance in trawl samples and observed growth rates. For the pelagic period, abundance was calculated assuming a constant instantaneous mortality rate between the date of the Miller sampling survey and the end of July (Mills et al. 1987). Average weight of YOY yellow perch in October trawls was considered to

**Fig. 2.** Long-term trends of mean (±1 SE) annual concentrations of (*a*) TP from 1975 to 1997, (*b*) primary productivity (PP) from 1975 to 1995, and (*c*) Secchi depth from 1975 to 1997 for Oneida Lake. To the right of the vertical line drawn through all three panels is the time period used in the analysis for this study. Arrows indicate the time of zebra mussel invasion.

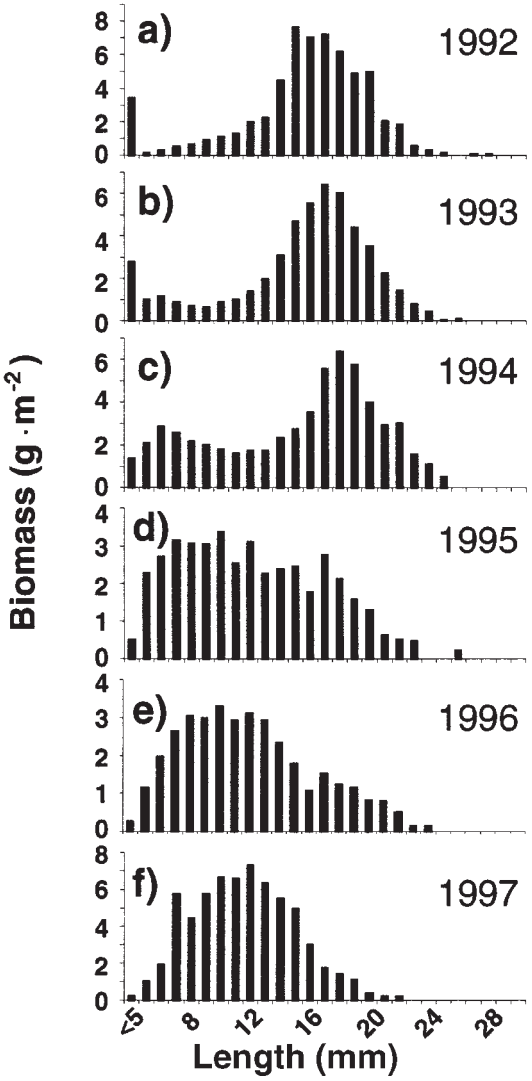



represent total annual growth. Production of YOY yellow perch was calculated from weekly changes in abundance and growth and summed to obtain annual production (Mills et al. 1987).

### Data analysis

To determine the effect of zebra mussels on the lower food web, we used data from June to October of each year. This time period is when water temperature was above 10°C, and zebra mussels would most likely have the greatest impact on the system. Laboratory experiments have determined that feeding activity by *D. polymorpha* occurs at a temperature range of 8–25°C (Stanczykowska 1977); summer temperatures in Oneida Lake did not exceed 25°C during the period when zebra mussels were present. We divided the data set into pre-zebra mussel phase (1988–1991) and post-zebra mussel phase (1992–1997; we use 1992–1995 for phytoplankton biovolumes and primary productivity and 1992–1996 for daphnid production); we also grouped data for each year by season (spring, summer, and autumn). In our analysis, we did not want to confound nutrient effects with zebra mussel impacts. Consequently, we chose to begin our data analysis with 1988, since TP concentrations from 1988 to 1997 were stable; interannual differences in TP were 10–30 $\mu g \cdot L^{-1}$ for 1975–1987 compared with a maximum difference of 10 $\mu g \cdot L^{-1}$ since 1988 (Fig. 2). We used a two-way analysis of variance (ANOVA) to test for significant differences between pre- and post-zebra mussel periods followed by a comparison of means for zebra mussel phases within each season (SAS Institute Inc. 1989). When the criterion for normality was not met, we log transformed the data prior to analysis. Comparisons were considered significant at $P < 0.05$.

**Fig. 3.** Size frequency distributions of Oneida Lake zebra mussel population biomass from 1992 to 1997.




## Results

### Zebra mussel abundance and biomass

We estimated mean areal densities and wet weight of zebra mussels for each year based on numbers and weights of individuals in shell size categories ranging from <2 to 30 mm (Fig. 3). Our results indicate that mean shell length increased over the period from 2.75 (1992) to 8.72 mm (1997), maximum mean shell length was in 1995 (9.75 mm), and shell length frequencies shifted from bimodal (1992–1994) to a single mode (1995–1997). In 1992, a high abundance of small mussels (<2 mm) contributed to the highest lake-wide mean density (>40 000·$m^{-2}$) observed in this study. In contrast, the highest mean wet weight (including shell) of mussels was observed in 1997 (1560 g·$m^{-2}$) compared with average weights ranging from 343 to 1012 g·$m^{-2}$ from 1992 to 1996. As might be expected, site-to-site variance was high; coefficient of variation among sites ranged from 84% in 1993 to 206% in 1997. Mussel densities at individual sites ranged from zero to a high of 114 300·$m^{-2}$

**Table 1.** Statistical analysis of seasonal attributes for variables used in this study.

| Parameter | Zebra mussel phase | Season |
|---|---|---|
| TP | ns | *** |
| TPP | ** (–) | *** |
| SRP | ns | * |
| DOP | ns | ns |
| $NO_3$ | ns | *** |
| SRS | ns | * |
| Secchi depth | *** (+) | ** |
| Chl *a* | * (–) | ** |
| Primary productivity | ns | ns |
| Total phytoplankton | * (–) | ns |
| Netplankton | * (–) | ns |
| Nanoplankton | ns | ns |
| Cyanobacteria | ns | *** |
| Diatoms | *** (–) | ns |
| Chlorophyta | ns | ns |
| Chrysophyta | *** (–) | ns |
| Cryptophyta | ns | ns |
| Mean zooplankton length | *** (+) | *** |
| Total zooplankton | ns | * |
| *D. pulicaria* biomass | * (+) | * |
| *D. pulicaria* production | * (+) | * |
| *D. galeata mendotae* biomass | * (–) | ns |
| *D. galeata mendotae* production | ** (–) | ns |
| Yellow perch biomass | ns | ns[a] |
| Yellow perch growth | ns | ***[a] |

**Note:** TP, total phosphorus; TPP, total particulate phosphorus; SRP, soluble reactive phosphorus; DOP, dissolved organic phosphorus; $NO_3$, nitrate-nitrogen; SRS, soluble reactive silica as $SiO_4$. Two-way ANOVA treatments are zebra mussel phase (pre- (1988–1991) and post-zebra mussel years (1992–1997)) and season (spring (April 1 – June 3), summer (June 10 – September 19), and autumn (September 26 – October 28)). Number of samples per group: pre-dreissenid, spring and autumn, 40; pre-dreissenid, summer, 44; post-dreissenid, spring and autumn, 60; post-dreissenid, summer, 66. The positive sign in parentheses indicates an increase during post-zebra mussel years and the negative sign indicates a decline for those variables having significant zebra mussel effects. ***$P < 0.005$; **$P \leq 0.01$; *$P \leq 0.05$; ns, not significant ($P > 0.05$).

[a]Summer and autumn values only.

and, likewise, site-to-site differences in mussel biomass (as wet weight including shell) ranged from zero to 11 276 $g \cdot m^{-2}$. Highest mussel densities were generally observed at 3 m depth, decreasing in density to depths of 7 m. No mussels were found beyond depths of 10 m.

## Nutrients

We hypothesized that TP would not decline in the presence of zebra mussels but that its constituents would shift to more SRP and less TPP. Other major nutrients such as $NO_3$ and SRS would exhibit minimal, if any, change. Consistent with our hypothesis, we found (using a two-way ANOVA) that there was no significant difference in mean TP concentrations in pre- and post-zebra mussel years (Table 1). While SRP concentrations did not increase in the presence of zebra mussels, there was a significant decline in TPP (two-way ANOVA, $P < 0.05$). Annual averages of $NO_3$ and SRS concentrations exhibited no significant change in the presence of zebra mussels (Table 1).

Distributions of phosphorus and other nutrients varied significantly by season from spring to summer to autumn; TP, SRP, TPP, DOP, and SRS increased from spring to autumn, whereas $NO_3$ declined over the same period (Fig. 4). Comparison of phosphorus concentrations by zebra mussel phase and by season indicated that TPP was consistently lower in post-zebra mussel years for all seasons, whereas SRP and TP concentrations were lower only in summer and autumn. $NO_3$ was significantly lower in autumn, while SRS was lower in summer during zebra mussel years (Fig. 4).

## Water clarity, Chl *a*, primary productivity, and phytoplankton community dynamics

We hypothesized that grazing by zebra mussels would lead to increased water clarity, decreased phytoplankton biomass and primary productivity, and a shift in algal composition to grazer-resistant forms. As expected, Secchi depth increased significantly (two-way ANOVA, $P < 0.05$) and Chl *a* decreased significantly (two-way ANOVA, $P < 0.05$) in the presence of zebra mussels (Table 1; Figs. 4*g* and 4*h*). The lowest annual average Chl *a* concentration was recorded in 1993 and 1997 (4.9 and 4.7 $\mu g \cdot L^{-1}$, respectively); Chl *a* was 46% lower in post-zebra mussel years. For the years 1993–1997, the annual average Secchi depth was consistently greater than that for previous years (Fig. 5*a*). Although the number of clear water days (defined as the period when mean water column Chl *a* was $<3\ \mu g \cdot L^{-1}$) increased from 60 ± 16 to 86 ± 4 days, the difference was not significant (*t* test, $P > 0.05$). This statistical outcome was likely due to the prolonged clear-water period in 1989 that extended beyond any post-zebra mussel year (Fig. 5*b*).

We found significant (two-way ANOVA, $P < 0.05$) zebra mussel effects by season for Secchi depth and Chl *a* but not for primary production (Table 1; Fig. 4). Secchi depth was greater and Chl *a* lower during post-zebra mussel years for all seasons (Figs. 4*g* and 4*h*). Primary productivity did not differ significantly (two-way ANOVA, $P > 0.05$) by season or zebra mussel presence–absence; however, higher mean primary production estimates were observed in the autumn and lower estimates in the summer in years when zebra mussels were present (Fig. 4*i*).

Primary productivity did not decline significantly during the post-zebra mussel period in spite of the significant reduction in Chl *a* (34% reduction from pre-zebra mussel Chl *a* concentrations) (Table 1; Fig. 4*i*). Primary productivity can be maintained with declining algal biomass if there is a compensatory increase in photosynthetic rate per unit chlorophyll (no observed differences in primary productivity between the two periods; *t* test, $P = 0.383$). This can occur through shifts in the PI curves or increase in light penetration. Extinction coefficient ($k_D$) values were significantly higher during the pre-zebra mussel period compared with post-zebra mussel years (0.742 ± 0.03 $m^{-1}$, and 0.564 ± 0.046 $m^{-1}$, respectively; *t* test, $P < 0.05$). Both $\alpha^B$ and $P_m^B$ increased from pre- to post-zebra mussel years ($\alpha^B$ = 14.08 ± 1.68 and 20.28 ± 6.15 mg C·mg Chl $a^{-1} \cdot einstein^{-1} \cdot m^{-2}$, respectively; $P_m^B$ = 6.53 ± 1.24 and 7.49 ± 1.2 mg C·mg Chl $a^{-1} \cdot h^{-1}$, respectively); however, these differences were insignificant.

Consistent with trends in Chl *a*, total phytoplankton biovolume in all seasons declined significantly after the zebra

**Fig. 4.** Mean (±1 SE) seasonal (spring, summer, and autumn) (*a*) TP, (*b*) TPP, (*c*) SRP, (*d*) DOP, (*e*) $NO_3$, (*f*) SRS, (*g*) Secchi depth, (*h*) Chl *a*, and (*i*) primary productivity (PP) for pre- (1988–1991, open bars) and post-zebra mussel years (1992–1997, solid bars). Asterisks indicate significance levels as determined from mean comparisons of pre- and post-zebra mussel periods.

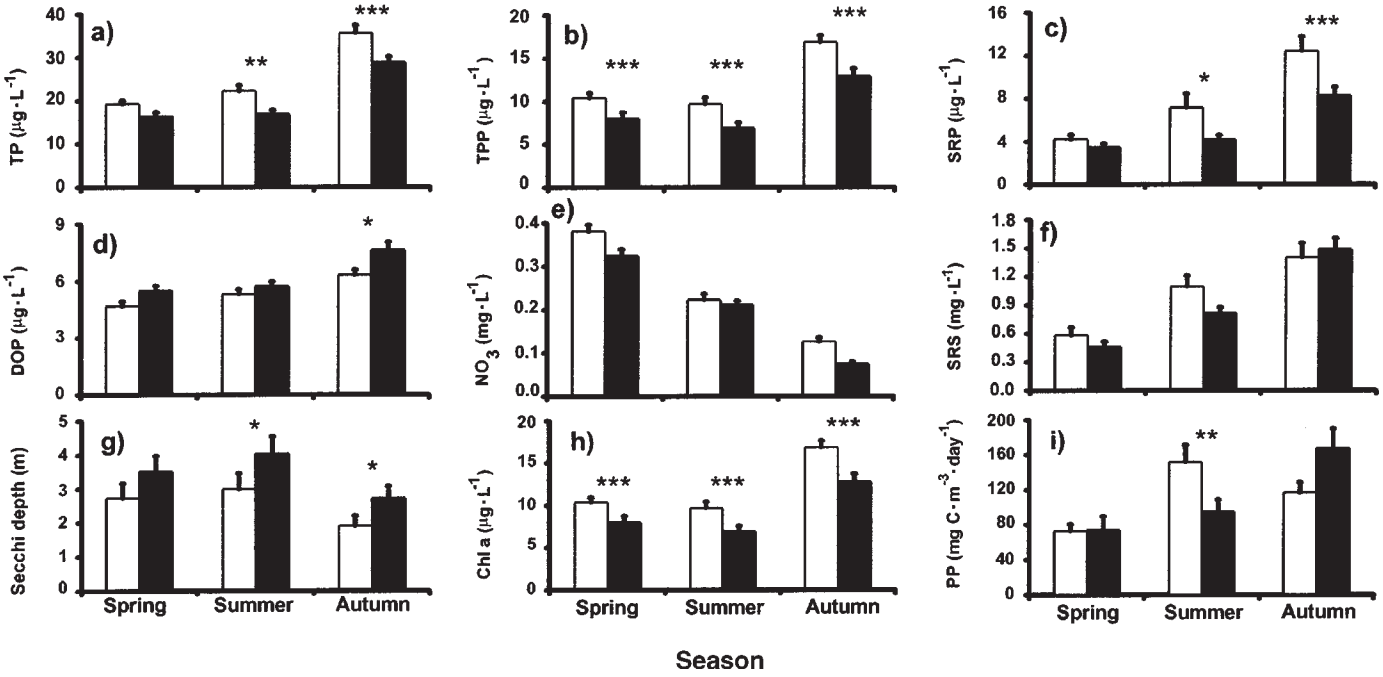
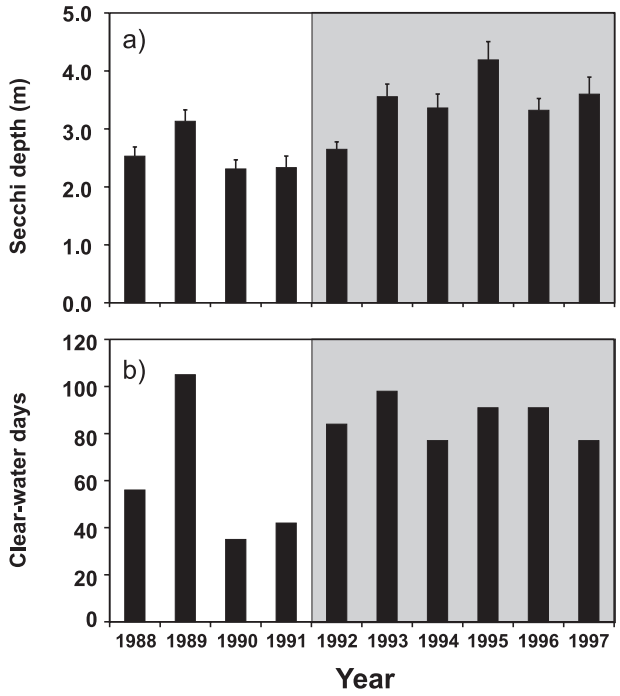



**Fig. 5.** (*a*) Mean annual Secchi depth (±1 SE) averaged from five sampling sites in Oneida Lake and (*b*) number of clear-water days during pre- and post-zebra mussel years. The gray shaded area indicates the post-zebra mussel period.



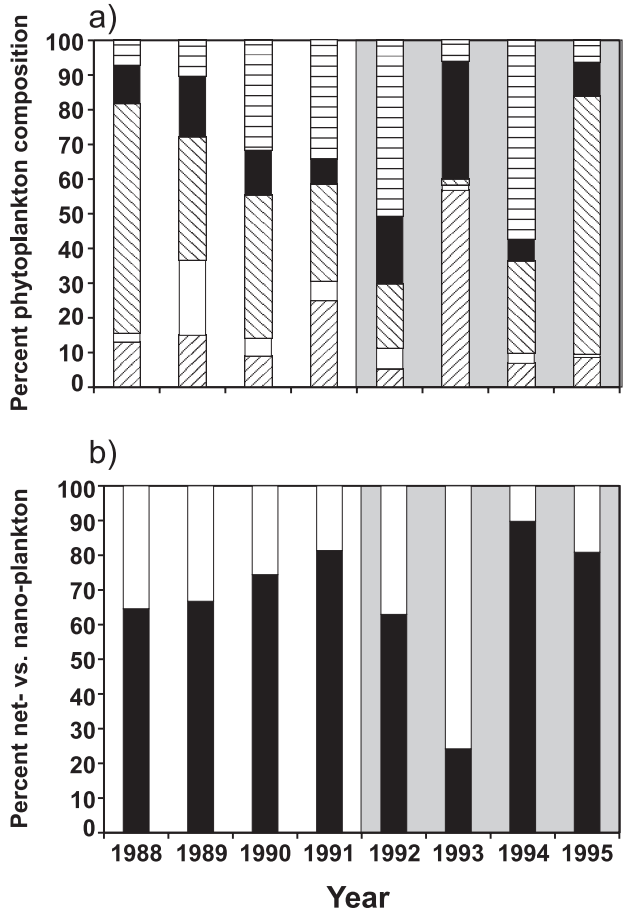

mussel invasion (Table 1). Associated with this decline was a shift in algal composition; the phytoplankton community structure shifted from a pre-zebra mussel community dominated by diatoms (1988–1990) to a community dominated by cyanobacteria (1992 and 1994), chlorophytes (1993), and diatoms (1995) (Fig. 6*a*). The phytoplankton community in 1991 was codominated by diatoms, cyanobacteria, and chlorophytes (Fig. 6*a*). The transitional year, 1992, was dominated by cyanobacteria but also had a higher proportion of nanoplankton than any pre-zebra mussel year (Fig. 6*b*). The nanoplankton (chlorophytes and cryptophytes) dominated the phytoplankton community in 1993, but this was followed by a dramatic decline in 1994.

Netplankton biovolume followed a trend similar to that of total phytoplankton and varied significantly with zebra mussel phase (Table 1; Fig. 7*b*). In contrast, nanoplankton did not vary significantly by zebra mussel phase in summer and autumn but did so in spring; the major difference in the spring was the dominance of the diatom *Cyclotella* spp. during the pre-zebra mussel period (Fig. 7*c*). Cyanobacteria biovolumes were not significantly different in the presence or absence of zebra mussels (Table 1; Fig. 7*d*). Diatom and chrysophyte biovolumes both declined significantly in the presence of zebra mussels, being most pronounced in the spring and autumn (Table 1; Figs. 7*e* and 7*g*). Diatoms recovered to pre-zebra mussel state in 1995 (Fig. 6*a*). Chrysophytes were extremely rare during the post-zebra mussel period in all seasons (Figs. 6*a* and 7*g*). Chlorophytes and cryptomonads were most abundant in summer during the clear-water phase; however, neither taxon varied significantly by zebra mussel phase or season (Table 1; Figs. 7*f* and 7*h*).

### *Daphnia* spp. dynamics

We hypothesized that daphnid biomass would decline in response to a decline in algal biomass and production. *Daphnia pulicaria* and *D. galeata mendotae* were the two dominant zooplankton species throughout the study period, accounting for more than 50% of the total zooplankton community biomass (Fig. 8*b*). *Daphnia pulicaria*, the larger of the two spe-

**Fig. 6.** Proportional annual abundance in Oneida Lake for (*a*) the five dominant phytoplankton groups (horizontally hatched bars, Cyanobacteria; solid bars, Cryptophyta; right-hatched bars, Bacilliariophyceae; open bars, Chrysophyceae; left-hatched bars, Chlorophyta) and (*b*) netplankton (solid bars) and nanoplankton (open bars) during pre- and post-zebra mussel years. The gray shaded area indicates the post-zebra mussel period.




cies, dominated the post-zebra mussel period, while *D. galeata mendotae* dominated the pre-zebra mussel period. Consistent with the dominance of the large-bodied *D. pulicaria* in post-zebra mussel years was a shift to a higher mean length of crustacean zooplankton (Fig. 8*a*). Mean zooplankton length was significantly (two-way ANOVA, $P = 0.001$) higher (39%) in years when zebra mussels were present (Fig. 9*a*). In spite of a shift to the larger *D. pulicaria* in post-zebra mussel years, total zooplankton biomass did not change significantly pre- and post-zebra mussels (Table 1). However, total zooplankton biomass was significantly greater (two-way ANOVA, $P < 0.01$) post-zebra mussels in the summer and significantly greater (two-way ANOVA, $P < 0.005$) pre-zebra mussels in the spring (Fig. 9*b*).

Mean annual *D. pulicaria* biomass and production were significantly higher in years when zebra mussels were present (Table 1; highest production estimates were in summer). Egg production may be a good indicator of feeding condition (e.g., see Pace et al. 1998 and references therein). We observed no effect of zebra mussels on combined *D. pulicaria* and *D. galeata mendotae* egg ratios (0.49 ± 0.165 and 0.502 ± 0.077 egg·individual$^{-1}$ for pre- and post-zebra mussel years, respectively). This suggests similar feeding conditions for daphnids in pre- and post-zebra mussel periods.

*Daphnia galeata mendotae* exhibited no significant seasonal variation in either biomass or production but did exhibit a significant difference by zebra mussel presence–absence (Table 1). Biomass and production of this daphnid were higher in years when zebra mussels were absent; the lowest biomass and production were in the autumn during these same years (Figs. 9*e* and 9*f*). In post-zebra mussel years, biomass and production of *D. galeata mendotae* peaked in summer (Figs. 9*e* and 9*f*).

### Zebra mussel and daphnid clearance rates

The most dramatic change in Oneida Lake post-zebra mussels was the temporal duration and depth of water clarity, reflected in Secchi depth and the number of clear-water days and the overall decrease in algal biovolume and Chl *a* (Figs. 4, 5, and 7). We attempted to determine if these changes were associated with clearance rates of zebra mussels and (or) daphnids. Estimated weight-specific zebra mussel clearance rates were highest in 1995 and corresponded to the highest mean shell length (9.75 mm) (Table 2; Fig. 3). Zebra mussel population clearance (as percentage of lake cleared per day) increased to its highest level (2.5 times total lake volume cleared per day) in 1997 when the population reached its highest biomass (Table 2; Fig. 3). In spite of a generally higher weight-specific clearance rate of daphnids compared with zebra mussels, daphnid population clearance rates never exceeded 8% of lake cleared per day (Table 2).

### YOY yellow perch biomass, growth, and production

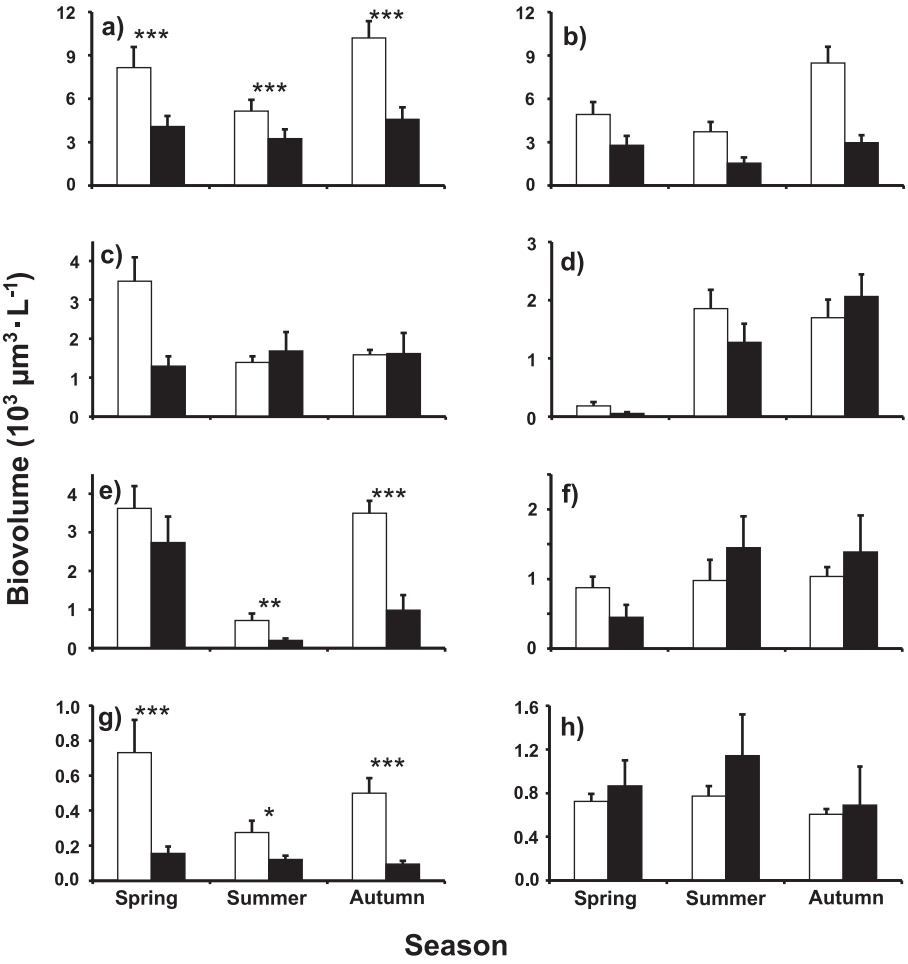
We hypothesized that YOY yellow perch biomass, growth, and production would decline in response to negative zebra mussel impacts on *Daphnia* spp. (also see Mayer et al. 2000). However, consistent with our findings at lower trophic levels, we observed no significant effects of zebra mussels on biomass, growth, and production of YOY yellow perch (comparisons of the years 1988–1991 and 1992–1997: two-way ANOVA, $P > 0.3$) (Tables 1 and 3). Growth rates indexed as weight in October ranged from 4.2 to 5.8 g in 1988–1991 (mean 5.2 ± 0.36 g) and from 4.5 to 8.7 g in 1992–1997 (mean 6.0 ± 0.59 g). Biomass of YOY yellow perch typically peak in July–August in Oneida Lake (Mills et al. 1987), and this was also observed for both the pre- and post-zebra mussel periods analyzed here. Production is usually greater in May–July, although neither biomass nor production was significantly different between pre- and post-zebra mussel years (Tables 1 and 3).

## Discussion

### Nutrient dynamics

We hypothesized that TP would not decline but would be partitioned into more SRP than TPP because of reductions in algal biomass. We did not observe a decline in TP after the establishment of zebra mussels, consistent with findings in western Lake Erie (Holland et al. 1995). Contrary to our hypothesis, however, we did not detect a significant increase in

**Fig. 7.** Mean (±1 SE) seasonal biovolumes of (*a*) total phytoplankton, (*b*) netplankton, (*c*) nanoplankton, (*d*) Cyanobacteria, (*e*) Bacilliariophyceae, (*f*) Chlorophyta, (*g*) Chrysophyceae, and (*h*) Cryptophyta for pre- (1988–1991, open bars) and post-zebra mussel years (1992–1995, solid bars). Asterisks indicate significance levels as determined from mean comparisons of pre- and post-zebra mussel periods. Note the different scales on the *y*-axis.



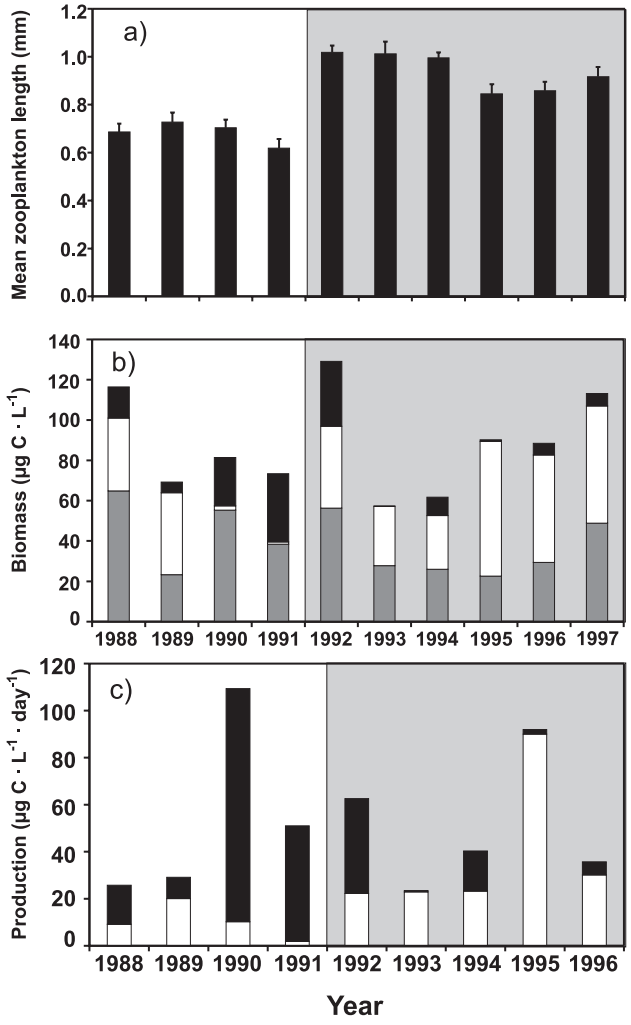

SRP or any change in DOP, although the DOP to TP ratio increased significantly (0.218 ± 0.026 and 0.302 ± 0.02 pre- and post-invasion, respectively; *t* test, $P = 0.033$) during post-zebra mussel years. While these results are consistent with those observed in Saginaw Bay (Johengen et al. 1995), they differ from those of recent studies in the Hudson River where SRP exhibited a significant increase (150%) and in western Lake Erie where SRP increased by 17% (Holland et al. 1995). In contrast with SRP, DOP concentrations were higher in the autumn in years when zebra mussels were present (but not in spring and summer). Heath et al. (1995) found higher DOP concentrations in enclosures with high densities of zebra mussels, although the results were confounded due to unusually high concentrations in one of the control enclosures. Short-term increases in phosphorus concentrations have been shown in laboratory and mesocosm experiments to be attributed to excretion by zebra mussels (Heath et al. 1995; Mellina et al. 1995; Arnott and Vanni 1996). The influence of zebra mussel excretion on phosphorus cycling, however, depends on zebra mussel population size, size of individual mussels, and the relative concentration of phosphorus in the water column (e.g., Heath et al. 1995; Mellina et al. 1995; Arnott and Vanni 1996); these conditions may account for the different responses in phosphorus dynamics among freshwater ecosystems. In any case, the lack of change in TP in Oneida Lake suggests that potential productivity has remained unchanged, and this finding may help explain why production at other trophic levels exhibited little or no change in response to zebra mussels.

### Water clarity, Chl *a*, primary productivity, and phytoplankton community structure

Observed changes in Secchi depth, Chl *a*, and phytoplankton biovolume were consistent with our hypothesis that phytoplankton biomass (and Chl *a*) would decline as water clarity increased in response to grazing by zebra mussels, as observed elsewhere (e.g., Holland 1993; Karatayev et al. 1997; Strayer et al. 1999). However, primary productivity did not decline as predicted. Higher PI parameter values and lower extinction coefficients may have compensated for low chlorophyll concentrations.

Primary productivity cannot be maintained if algal biomass declines unless there is a compensatory increase in production per unit biomass (Fahnenstiel et al. 1995). This in turn can be caused by an enhanced light environment or by changes in the phytoplankton community to species with

**Fig. 8.** (*a*) Annual mean (±1 SE) zooplankton lengths, (*b*) annual biomass of *D. galeata mendotae* (open bars), *D. pulicaria* (solid bars), and other zooplankton species including other cladocerans and copepods (gray bars), and (*c*) annual production of *D. galeata mendotae* (open bars) and *D. pulicaria* (solid bars) during pre- and post-zebra mussel years (gray shaded area).




higher growth rates. In Oneida Lake, changes in PI parameters between pre- and post-zebra mussel periods were in the direction of higher efficiency per unit chlorophyll; also, increased water clarity accounted for higher photosynthetic rates below 5 m depth. For example, areal primary production at Station B-125 on May 24, 1993, was 183 mg $C \cdot m^{-2}$; using the proportional changes in $P_m^B$, $\alpha^B$, $k_D$, and Chl *a* that occurred between pre- and post-zebra mussel years and assuming 20% variation to determine significant differences, we find no change in areal primary production (184 mg $C \cdot m^{-2}$) if Chl *a* is reduced to 65% of the original concentration. The observed changes in parameters that affect primary production require a reduction of Chl *a* by at least 50% in order to produce a significant decline in primary production (141 mg $C \cdot m^{-2}$). In other systems, the compensatory effects of increased water clarity and photosynthesis were not sufficient to compensate for the dramatic declines in Chl *a* concentration, which were greater than those observed in Oneida Lake (e.g., Fahnenstiel et al. 1995; Caraco et al. 1997). The degree of compensation will likely vary among systems depending on the combination of factors, including PI parameter values, light environment, phytoplankton species composition, and Chl *a* concentration.

The response of algal communities to dreissenid grazing varies among freshwater ecosystems (Smith et al. 1998; Makarewicz et al. 1999). In Oneida Lake, a short-term shift was observed in the phytoplankton community to more nanoplankton (Chlorophyta, Cryptophyta, and *Cyclotella* spp.) and less netplankton (Bacillariophyceae, Chrysophyceae, and Cyanobacteria). However, annual variability was high, thus precluding the observation of any clear trends in phytoplankton dynamics over the long term. A clear shift, however, occurred in the Hudson River where there was a marked decline in cyanobacteria and a relative increase in diatoms postinvasion (Smith et al. 1998). It is argued that the likely cause for the relative increase of diatoms over cyanobacteria (dominated by *Microcystis* spp. in the Hudson River) was the differential growth rates of phytoplankton in response to zebra mussel grazing (Smith et al. 1998).

On the other hand, Arnott and Vanni (1996) hypothesized that low nitrogen to phosphorus ratios (a result of zebra mussel excretion) could cause a shift in the phytoplankton community to cyanobacteria due to nitrogen limitation. Although we do not have nutrient data comparable with those of Arnott and Vanni (1996), $NO_3$ and SRP concentrations indicate possible nitrogen limitation in Oneida Lake since 1985 during the summer and autumn. Consequently, late-summer nitrogen limitation leading to cyanobacteria blooms in Oneida Lake likely preceded the invasion by zebra mussels. Makarewicz et al. (1999) found a significant increase in cyanobacteria in the western basin of Lake Erie in the spring, but this was followed by a significant decline in the summer. There were no significant differences in cyanobacteria biovolumes in all seasons analyzed in Oneida Lake.

### Daphnid community

We predicted that zebra mussels would negatively impact *Daphnia* spp. biomass and production in response to lower algal food resources. Our findings do not support this hypothesis. Although algal food resources declined, *Daphnia* spp. biomass and production did not decline significantly. We attribute the persistence of the daphnid community to our observation that primary production did not change significantly (probably due to increased water clarity; see above) and that there was no shift to less edible algal species; this result was also predicted in a simulation model (Padilla et al. 1996). Pace et al. (1998) similarly found that macrozooplankton did not significantly decline after the zebra mussel invasion in the Hudson River. Microzooplankton were significantly reduced in the Hudson River (Pace et al. 1998) but were not sampled efficiently with the 153-µm-mesh net used in Oneida Lake.

The daphnid species shift observed in Oneida Lake was not studied in the Hudson River, although Pace et al. (1998) speculated that a shift in species composition might have occurred. *Daphnia galeata mendotae* tend to dominate in years of high planktivory by fish in Oneida Lake (Mills and Forney 1983). Large year-classes of gizzard shad occurred in 1990 and 1991, leading to high planktivory rates and a dominance of *D. galeata mendotae* over *D. pulicaria* (Roseman

**Fig. 9.** Mean (±1 SE) seasonal values of (*a*) mean zooplankton length, (*b*) total zooplankton biomass, (*c*) *D. pulicaria* biomass, (*d*) *D. pulicaria* production, (*e*) *D. galeata mendotae* biomass, and (*f*) *D. galeata mendotae* production (the post-zebra mussel years for *D. pulicaria* and *D. galeata mendotae* production included 1992–1996) for pre- (1988–1991, open bars) and post-zebra mussel years (1992–1997, solid bars). Asterisks indicate significance levels as determined from mean comparisons of pre- and post-zebra mussel periods.

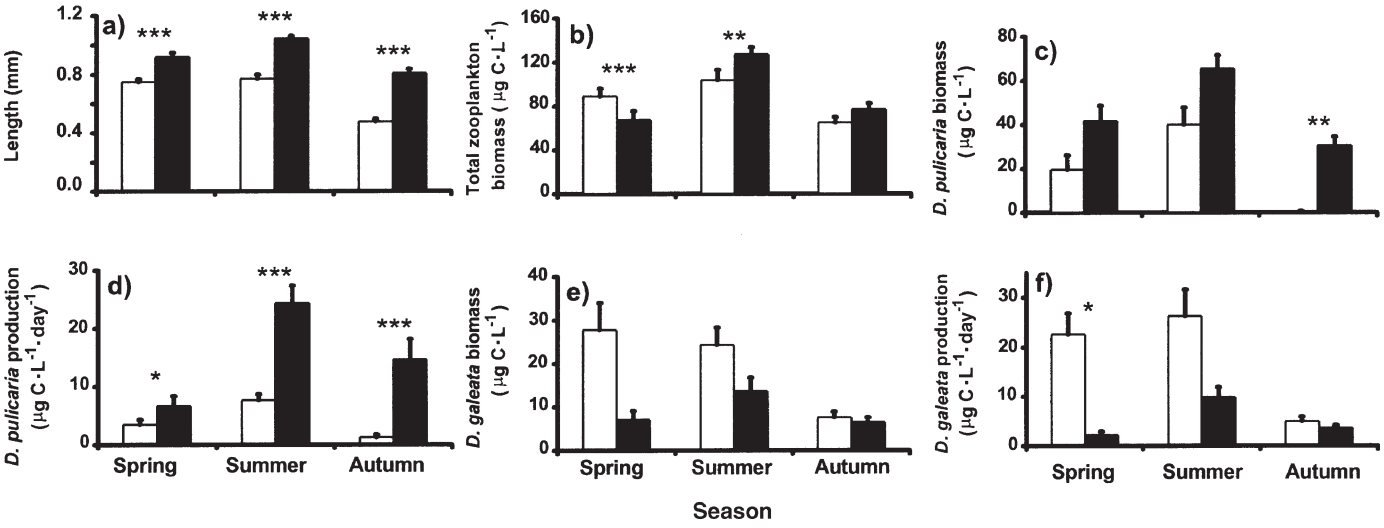



**Table 2.** Annual average clearance rates and proportion of lake cleared per day for total populations of daphnids (*D. pulicaria* and *D. galeata mendotae*) and zebra mussels in Oneida Lake.

| Year | Daphnid (mL·mg dry weight$^{-1}$·day$^{-1}$) | Daphnid (% lake cleared·day$^{-1}$) | Zebra mussel (mL·mg dry weight$^{-1}$·day$^{-1}$) | Zebra mussel (% lake cleared·day$^{-1}$) |
|---|---|---|---|---|
| 1975–1991 | 243 | 3 | — | — |
| 1992 | 430 | 8 | 15.5 | 180 |
| 1993 | 261 | 2 | 116 | 189 |
| 1994 | 262 | 3 | 287 | 198 |
| 1995 | 407 | 8 | 302 | 149 |
| 1996 | 305 | 6 | 296 | 132 |
| 1997 | 398 | 7 | 298 | 249 |

**Note:** Pre-zebra mussel clearance rates and proportion of lake cleared of daphnids are averages for the period 1975–1991.

et al. 1996; Shepherd and Mills 1996), but large numbers of these fish were not observed post-1992 (VanDeValk et al. 1999). Larger daphnids may be better competitors at low food levels (Gliwicz 1990), and this has been used to explain the dominance of *D. pulicaria* in years when planktivory rates are low (Rudstam et al. 1993). Zebra mussels could induce low food levels, leading to the dominance of *D. pulicaria*. However, in 1998 and 1999, *D. galeata mendotae* was again the dominant species, even though algal biomass did not increase (E.L. Mills, unpublished data). In those years, a resurgence of emerald shiner (*Notropis atherinoides*) and an associated increase in pelagic planktivore biomass likely caused the shift back to the smaller daphnid (VanDeValk et al. 1999). Thus, we believe that the observed shift in *Daphnia* spp. composition associated with zebra mussels was due to the concomitant decline in open-water planktivory by gizzard shad rather than a zebra mussel effect of reduced resources.

**Yellow perch**

Consistent with our observations in the daphnid community, we did not detect a decrease in YOY yellow perch growth, biomass, and production following the establishment of zebra mussels. Mayer et al. (2000) reported an increase in YOY yellow perch growth post-zebra mussels in their study of Oneida Lake (1964–1997). Although we also observed an increase in YOY yellow perch growth post-zebra mussels, this increase was not significant, probably because the power of our analysis was lower (4 versus 27 pre-zebra mussel years). Mayer et al. (2000) found increased YOY yellow perch growth after accounting for density-dependent effects and attributed such growth to increased feeding efficiency on zooplankton (mainly daphnids) associated with zebra mussel induced elevated water clarity. Increased YOY yellow perch growth could not be attributed to the presence of zebra mussel veligers. These veligers are smaller (90–200 mm; Sprung 1993) than prey generally consumed by larval yellow perch (Schael et al. 1991), and diet analysis from two post-zebra mussel years showed no veligers in YOY yellow perch diets (Mayer et al. 2000).

In conclusion, our findings suggest that compensatory factors have lessened the impact of *D. polymorpha* on the pe-

**Table 3.** Mean (±1 SE) seasonal YOY yellow perch biomass, daily specific growth rate, and production for pre- (1988–1991) and post-zebra mussel years (1992–1997).

| | | Season | |
|---|---|---|---|
| Variable | Zebra mussel phase | Summer | Autumn |
| Biomass (mg wet weight·$m^{-3}$) | Pre | 41.8±3.94 | 23.6±2.6 |
| | Post | 37.2±4.29 | 26.8±3.5 |
| Specific growth rate (mg wet weight·$day^{-1}$) | Pre | 1.1±0.203 | 4.7±0.119 |
| | Post | 1.4±0.203 | 6.0±0.179 |
| Production (kg wet weight·$ha^{-1}$·$season^{-1}$) | Pre | 12.6±5.5[a] | 7.06±3.15[b] |
| | Post | 9.6±2.3[a] | 9.02±2.17[b] |

[a]May 27 – July 15.
[b]July 15 – October 14.

lagic lower food web of Oneida Lake. Light appears to be a crucial factor, allowing phytoplankton production deeper in the water column. It appears that low food resources did not impact the daphnid community and that this community is more sensitive to top-down pressure from planktivores (Mills and Forney 1983). Consistent with these findings, we found no evidence that zebra mussels had a negative impact on young yellow perch production. While our analysis has focused on the short-term impacts of zebra mussels on the pelagic food web of Oneida Lake, the long-term effects of zebra mussels is yet to be determined. In a long-term European study (40+ years; Karatayev et al. 1997), the zebra mussel invasion caused an increase in water clarity and macrophyte and zoobenthos biomass and a decrease in phytoplankton and zooplankton biomass. However, after approximately 10 years, zebra mussel impacts were less pronounced but the lake ecosystem did not revert to pre-zebra mussel conditions. Whether Oneida Lake follows a pattern similar to that of Lake Lukomske will only be ascertained through continued and rigorous study of the pelagic food web in the coming decades.

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