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Responses of Onondaga Lake, New York, to Early Stages of Rehabilitation: Unanticipated Ecosystem Feedbacks

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ABSTRACT: Responses of polluted Onondaga Lake, New York, to early stages of a phased program to rehabilitate the lake from the effects of domestic waste inputs are documented. The analysis is based on more than 10 years of paired monitoring of the effluent (total ammonia and total phosphorus) of a wastewater treatment plant (WWTP) that discharges to the lake as well as the lake itself (including total ammonia, nitrite, total and dissolved forms of phosphorus, plankton biomass and composition, Secchi disc transparency, and zebra mussel density). Major reductions in total ammonia and total phosphorus loading relative to the preceding decade are reported for the WWTP for the November 1998 through October 1999 interval. Dramatic and, in some cases, unanticipated changes in the lake's water quality and biota in response to the reductions in loading are documented for the April to October interval of 1999 including: (1) major decreases in total ammonia concentrations and improved status with respect to ammonia toxicity standards, (2) development of dense populations of zebra mussels, (3) decreases in fall concentrations of nitrite and improved status with respect to the related toxicity standard, (4) decreases in total phosphorus and total dissolved phosphorus concentrations, and (5) a severe *Microcystis* (phytoplankton) bloom that caused nuisance conditions and poor clarity. The zebra mussel invasion is attributed to the reductions in total ammonia concentrations to below toxic levels. The *Microcystis* bloom was probably related to the abrupt increase in the zebra mussel population. Additional reductions in phosphorus loading from the WWTP will be required to limit phytoplankton production and avoid the potential for continued nuisance conditions. Potential complications in resolving lake responses to future reductions in loading associated with the zebra mussel invasion are considered. *Water Environ. Res.*, 73, 691 (2001).

KEYWORDS: ammonia, eutrophication, lakes, nuisance blooms, phosphorus, rehabilitation, toxicity, zebra mussels.

Introduction

The efficacy of rehabilitation programs for polluted surface waters is important to environmental managers because of their great costs and public expectations (Cooke et al., 1993). Despite rapid advancements in the scientific and engineering understanding of these complex ecosystems (Chapra, 1997, and Wetzel, 2001), there remains substantial uncertainty concerning the response to major reductions in anthropogenic inputs (pollutant loads). Each major rehabilitation initiative represents a potentially invaluable experiment from which the understanding of these ecosystems, including the behavior and effects of the pollutants, can be greatly advanced. Where rehabilitation programs are complex, such as with multiple pollutants and temporal phasing of reduced loadings, it is important to separate the various responses to resolve cause-and-effect relationships. Ultimately, rehabilitation

programs are judged on their success in meeting water quality standards and in eliciting desired ecological responses.

Inputs of nitrogen and phosphorus from domestic wastewater treatment plants (WWTPs) have been a primary concern of receiving water quality for several decades (Brezonik, 1972; Hutchinson, 1973; Metcalf and Eddy, Inc., 1991; Thomann and Mueller, 1987; Vollenweider, 1975; and Wetzel, 2001). Large nitrogen inputs in the form of ammonia are of particular concern in terms of water quality because ammonia (1) is toxic to aquatic life at low concentrations (U.S. EPA, 1985, 1998, and 1999); (2) is the preferred form of nitrogen to support algae growth (Harris, 1986, and Wetzel, 2001); and (3) can promote oxygen depletion through the nitrification process (Gelda, Brooks, Effler, and Auer 2000, and Hall, 1986). Phosphorus loading is the principal regulator of primary productivity in most lakes (e.g., Vollenweider, 1975 and 1982, and Wetzel, 2001). Elevated inputs of phosphorus to lake ecosystems enhance phytoplankton growth and thereby promote the associated symptoms of cultural eutrophication, such as low clarity and increased hypolimnetic oxygen depletion (Hutchinson, 1973, and Wetzel, 2001). Lake reclamation efforts have often focused on reducing external phosphorus loads to ameliorate these undesirable characteristics (Cooke et al., 1993). Diversion of WWTP effluents, advanced wastewater treatment of nitrogen and phosphorus at these facilities, or both have become frequently applied lake rehabilitation approaches (Cooke et al., 1993). A wide range of lake responses, with respect to the time course and extent of improvement, has been observed for both diversion (e.g., Ahlgren, 1978; Edmondson and Lehman, 1981; and Welch et al., 1986) and advanced wastewater treatment (e.g., Larsen et al., 1979).

Diversion and advanced wastewater treatment programs to reduce nitrogen and phosphorus loading rely primarily on "bottom-up" forcing processes, that is, reduction in primary production from increased nutrient limitation (Cooke et al., 1993). However, "top-down" mechanisms associated with biological ("food web") interactions and feedback processes can result in unforeseen changes in lake community structure and primary productivity as well as related measures of water quality (Carpenter et al., 1987, and Shapiro and Wright, 1984). For example, shifts in fish populations and the zooplankton assemblage (Brooks and Dodson, 1965, and Siegfried et al., 1996) and the introduction of exotic filter feeding bivalves (mollusks) (Alpine and Cloern, 1992; Cohen et al., 1984; and Mills et al., 1993) have produced cascading effects (Carpenter et al., 1987) in food webs in affected systems that have confounded the relationships between nutrient loading, phytoplankton biomass and composition, and clarity. Increases in

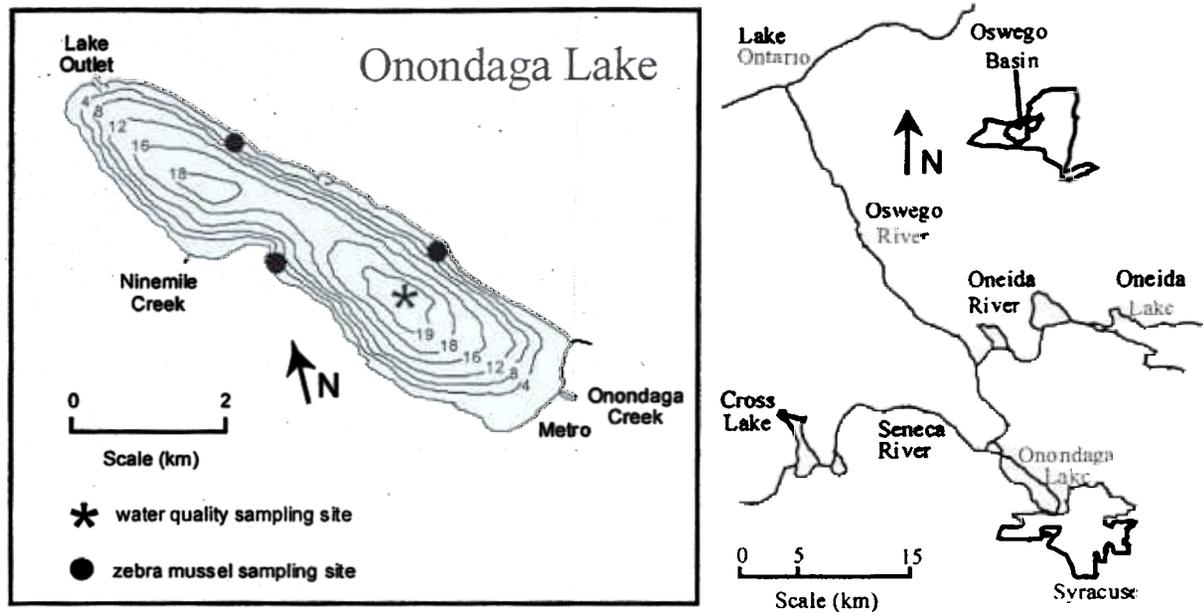


Figure 1—Onondaga Lake water quality and zebra mussel monitoring sites, Metro, and tributary inflows (left) and position among local surface water systems (right).

water clarity have been reported in many surface waters of North America that accompanied the rapid spread of the zebra mussel, an exotic bivalve mollusk (Cope, 2000), in the absence of reductions in nutrient loading (MacIlsac, 1996). Programs to reduce nitrogen and phosphorus loadings from WWTPs can intersect with the zebra mussel problem and related top-down responses in at least two ways. First, bivalves are sensitive to ammonia toxicity (U.S. EPA, 1985). Second, phosphorus loading drives, in part, the potential severity (e.g., standing crop) of a zebra mussel infestation by controlling the growth of phytoplankton (the primary food source for mussels) (Effler, Brooks, and Whitehead et al., 1996, and Karatayev et al., 1997).

This study documents reductions in ammonia and phosphorus loading to a polluted hypereutrophic urban lake (Onondaga Lake, Syracuse, New York) associated with the early phases of an advanced wastewater-treatment-based rehabilitation program. Response of this ecosystem to loading reductions is documented for water column concentrations of forms of nitrogen and phosphorus, phytoplankton composition and biomass, clarity, and zebra mussel density in the near-shore zone. Potential linkages between reduced ammonia loading, a major zebra mussel invasion, and a severe *Microcystis* (cyanophyta) bloom are evaluated. The interaction between bottom-up and top-down forcing mechanisms and the potential implications for the lake's response to future phases of the rehabilitation program are considered.

System Description

Onondaga Lake and Domestic Waste Inputs. Onondaga Lake is an alkaline, hard water, stratifying system located in metropolitan Syracuse (Figure 1). The lake has a volume of $131 \times 10^6 \text{ m}^3$, a surface area of 12.0 km^2 , and a maximum depth of 20 m. A population of approximately 450 000 people presently resides in the lake's watershed. The lake flushes rapidly (an average of approximately 4 times per year), although strong seasonal and interannual variations occur (Effler, Gelda, and Brooks, 2001, and

Effler and Whitehead, 1996). This is a particularly important feature in terms of tracking the effects of rehabilitation efforts, as the lake responds rapidly to changes in external loading (e.g., Doerr et al., 1994, and Effler, Gelda, and Brooks, 2001). The lake discharges through a single outlet to the Seneca River, which, after combining with the Oneida River (becoming the Oswego River), flows into Lake Ontario at Oswego (Figure 1). Intrusion of Seneca River water to Onondaga Lake, particularly during low runoff intervals, occurs, in part, because of the nearly equal elevation of these systems (Owens and Effler, 1996).

Onondaga Lake was oligomesotrophic before European settlement in the late 1700s (Rowell, 1996). Increasing inputs of domestic and industrial waste that accompanied development and urbanization in the watershed led to severe degradation and loss of uses of the lake (Effler, 1996). The commercial cold-water fishery was eliminated by the late 1800s (Tango and Ringler, 1996), and the lake was closed to ice harvesting in 1901, swimming in 1940, and fishing in 1970 (Effler and Harnett, 1996). Onondaga Lake has been described as perhaps the most polluted lake in the United States (Hennigan, 1990, and U.S. Senate Committee on the Environment and Public Works, 1989). An important source of industrial ionic waste, a soda ash-chlor-alkali manufacturing facility that operated on the western shore of the lake, closed in 1986. Lake salinity has decreased from approximately 3 to 1‰ (parts per thousand) as a result of the closure (Effler, 1996). Enforcement actions were taken against this industrial facility for residual impacts on the lake and against local government (Onondaga County, New York) for violations of the U.S. Clean Water Act associated with the discharge of domestic waste. An amended consent judgment (ACJ) agreed to in federal court in early 1998 is presently guiding cleanup of the lake's domestic waste problems. Domestic waste inputs of phosphorus and forms of nitrogen as well as related lake conditions that prevailed before the ACJ are briefly reviewed in this section.

The Metropolitan Syracuse Wastewater Treatment Plant (Metro) presently serves approximately 300 000 residents of Onondaga County and a number of local industries. The effluent from this facility is discharged to the southern end of Onondaga Lake (Figure 1) via a surface outfall. This discharge (average flow of approximately $3.0 \text{ m}^3/\text{s}$ [68 mg/d]) represents nearly 20% of the annual inflow to the lake, and often is the single largest inflow in late summer (Effler, Brooks, and Whitehead, 1996). The most recent comprehensive upgrade of Metro (completed in 1981, before the ACJ) provided secondary treatment by the contact stabilization modification of the activated-sludge process and phosphorus removal by chemical treatment (permit limit for total phosphorus of 1 mg/L to meet the Great Lakes basin standard). In the interim, some substantive improvements beyond the original design were achieved for ammonia (no significant nitrification originally anticipated) and phosphorus treatment. Substantial nitrification has been attained in the summer months, although rather large interannual differences in the extent and duration were observed (Gelda, Brooks, Effler, and Auer, 2000). By the early 1990s, the total phosphorus concentration in the effluent was reduced to approximately 0.6 mg/L (Effler, Brooks, and Whitehead, 1996). Metro remained the dominant source of total phosphorus, total nitrogen, total ammonia, and nitrite for the lake through 1997, representing approximately 60, 80, 90, and 90%, respectively, of the external loads of these constituents (Effler, Brooks, and Whitehead, 1996, and Gelda et al., 1999).

Inputs to Metro from a pharmaceutical manufacturing facility represented approximately one-third of the total loads of total Kjeldahl nitrogen (TKN) and total ammonia received by the WWTP (Effler, Gelda, and Brooks, 2001). Recently, the pharmaceutical facility has implemented pretreatment of this waste to reduce this source to approximately 3% of the total TKN and total ammonia load to Metro. Diluted untreated domestic waste has also been received via lake tributaries during runoff events from the combined sewer system (Effler and Hennigan, 1996). Although this source of nitrogen and phosphorus is minor compared to Metro (Effler and Whitehead, 1996), the inputs do cause in-lake violations of public health standards (fecal coliform bacteria) (Canale et al., 1993).

The Metro loads of nitrogen and phosphorus have caused violations of receiving water standards and, therefore, the U.S. Clean Water Act. Specifically, standards to protect against the toxic effects of ammonia (Brooks and Effler, 1990; Effler et al., 1990; and Matthews et al., 2000) and nitrite (Gelda et al., 1999) were routinely violated in the upper waters by a wide margin. Concentrations of total ammonia were often greater than 2 mg nitrogen/L, and at times approached 4 mg nitrogen/L (Matthews et al., 2000). Annual maximum margins of violation (concentration divided by standard) of the New York State chronic standard for ammonia toxicity (U.S. EPA, 1985) during the 1989 to 1997 interval ranged from 2.5 to 5.0 (Matthews et al., 2000). The maximum margin of violation of the New York State standard for nitrite ranged from 1.9 to 10 during the 1989 to 1997 interval (Gelda et al., 1999). Metro's phosphorus load caused the lake to be hypereutrophic, which was manifested by (1) severe phytoplankton blooms including nuisance cyanobacteria (Auer et al., 1990); (2) poor clarity that was often below the swimming safety standard of 1.2 m (Perkins and Effler, 1996); (3) rapid loss of oxygen from the hypolimnion (Effler, Brooks, and Whitehead, 1996); (4) subsequent accumulations of reduced byproducts of anaerobic metabolism (Adress and Effler, 1996, and Effler et al., 1988); and (5) depletion of dissolved

oxygen (DO) in the upper waters during the fall mixing period associated with oxidation of these byproducts (Gelda and Auer, 1996). The New York State standard for minimum DO within a day (4 mg/L) was violated annually during the fall mixing period and, in some years, by a wide margin (Effler, Brooks, and Whitehead, 1996, and Gelda, Brooks, Effler, and Auer, 2000). A large fraction of the lake's fish population exited to the Seneca River during the period of depressed DO in the fall (Tango and Ringler, 1996). The New York State "guidance" value (some regulatory discretion) for the summer total phosphorus concentration in the upper waters (20 $\mu\text{g/L}$) was exceeded by a wide margin.

Rehabilitation Program for Domestic Waste. Onondaga County has committed, as part of the ACJ, to a major rehabilitation program to eliminate water quality violations in Onondaga Lake associated with its discharge of municipal waste. This program, which consists of three phases, will be phased in during a 15-year period at a cost of approximately \$380 million. The intent of the program is to achieve full compliance with the U.S. Clean Water Act by the end of 2012. Features of the program related to the upgrade of Metro are described in this section. The point of discharge of the effluent will remain unchanged during this interval. The first phase limits total ammonia and total phosphorus concentrations (averages) in the Metro effluent to 1997 levels. The aeration system for biological treatment was upgraded in 1998.

Phase 2 requires Onondaga County to reduce total ammonia in the Metro effluent to 1.65 and 3.3 mg nitrogen/L for the June-to-October and November-to-May intervals, respectively, starting in May 2004. In addition, concentrations of total phosphorus must be reduced to 0.12 mg/L by April 2006. Phase 3 requires that total ammonia concentrations be reduced to 1.0 and 2.0 mg nitrogen/L for the June-to-October and November-to-May intervals, respectively, and that total phosphorus be reduced to 0.02 mg/L, by December 2012. Although not formally embedded in the ACJ, effective pretreatment of pharmaceutical waste (continued input to Metro) (Effler, Gelda, and Brooks, 2001) is an important component of the rehabilitation program that could affect the success of Metro meeting the effluent limits for ammonia. Failure of the three-phase program to meet receiving water quality standards would result in the alternative plan of diverting the Metro effluent to the Seneca River to be revisited (e.g., Effler, Brooks, and Whitehead, 1996).

Regional Invasion of Zebra Mussels. The zebra mussel (*Dreissena polymorpha*, Pallas) is a small bivalve mollusk that is native to southern Russia (Ludyanskiy et al., 1993). This exotic invader was introduced to the Laurentian Great Lakes in the mid-1980s, probably via water ballasts from a foreign ship (Hebert et al., 1989, and Mackie, 1991). Selected features of the biology of this bivalve invader are presented in Table 1. The zebra mussel has spread rapidly in North America because of a lack of natural ecological constraints (Ludyanskiy et al., 1993), its high reproductive rate (Ramcharan et al., 1992), and the facility for dispersal of its planktonic larvae (veligers) (Table 1). By 1991, zebra mussels had spread to all of the Great Lakes and a number of major adjoining river systems. Today, the zebra mussel is continuing to spread through much of the United States and Canada (Cope, 2000).

Zebra mussels have been particularly successful in colonizing the hard waters of central and southern New York, including systems adjoining Onondaga Lake (Cope, 2000). The Seneca River, both upstream and downstream of Cross Lake (Figure 1), was colonized by 1991. Particularly dense populations of zebra mussels (20 000 to 120 000 individuals/m²) have persisted down-

Table 1—Zebra mussel (*Dreissena polymorpha*) biology fact sheet (modified from Effler et al. 1996b).

Feature	Description and comments
Life span	2 to 5 years
Adult shell size	25 to 35 mm long
Attachment to substrate	Sessile organism; byssal threads to solid substrate
Reproduction	2 to 5 spawnings annually; fertilization at 12 to 24 °C
Dispersal	Swimming larvae-veligers; in plankton 1 to 5 weeks
Feeding	Filter feeder, particles > 1 µm diameter
Waste production	Feces, pseudofeces [rejected (e.g., inorganic) particles], and enriched excretions
Environmental requirements	Salinity ≤ 4; pH ≥ 7.3; calcium (Ca ²⁺) concentration ≥ 20 mg/L; solid substrate; food particles (e.g., phytoplankton)

stream of Cross Lake (Effler, Siegfried, and Hassett, 2001). Substantial population densities have been documented downstream to the Oswego River (Effler and Siegfried, 1998) (Figure 1). Profound changes in common measures of water quality have been imparted to the river from Cross Lake to Oswego (Figure 1) by zebra mussel metabolism (Effler, Brooks, and Whitehead et al., 1996; Effler and Siegfried, 1998; and Effler, Siegfried, and Hassett, 2001). Zebra mussels have also colonized other adjoining systems, including the Finger Lakes, Oneida Lake, Oneida River, and Cross Lake (Figure 1). Densities in the colonized systems seem to have been limited largely by the availability of solid substrate (to support attachment) (Ludyanskiy et al., 1993) and suitable food (e.g., phytoplankton) (Ramcharan et al., 1992) (Table 1).

Despite the presence of zebra mussels in Onondaga Lake since at least 1992, their densities remained low (approximately 1 individual/m²) in the near-shore zone through 1998 (Spada, 2000). These low densities seemed to be inconsistent with the available food (high concentrations of phytoplankton biomass) (Effler, 1996) and solid substrate (which remained largely uncolonized) (Spada, 2000) in the lake. Veliger surveys and colonization experiments in 1997 and 1998 indicated the Seneca River was a source of zebra mussels for the lake, but that survivorship in the lake was poor (Spada, 2000). Spada (2000) evaluated several features of the lake's chemistry commonly considered as influencing the distribution of this invader (Ludyanskiy et al., 1993, and Ramcharan et al., 1992) and concluded that the pH, DO, salinity, and calcium conditions of Onondaga Lake were not limiting. Ammonia concentrations were identified as potentially limiting to zebra mussels in the lake (Spada, 2000).

Methods

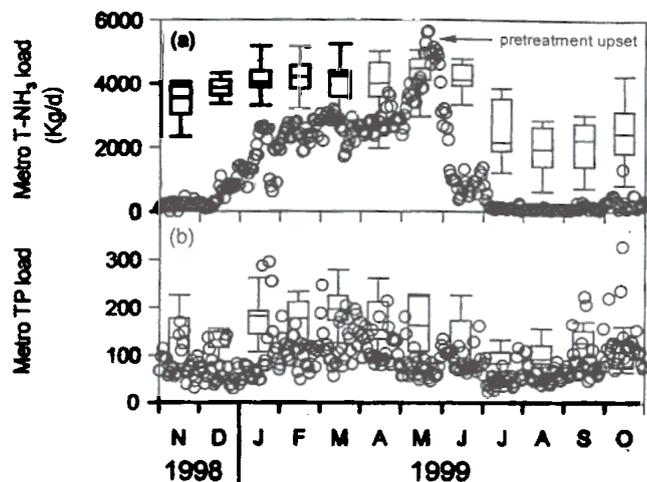
Metro Load Calculations. Estimates of mass loading rates of total ammonia and total phosphorus were based on effluent flows and concentrations measured at Metro and reported as part of the facility's permit requirements. Concentrations of total ammonia (5 days per week, Monday through Friday) and total phosphorus (daily) were determined on flow-weighted composite samples according to *Standard Methods* (APHA et al., 1992, and U.S. EPA, 1983). Effluent loads from Metro were estimated as the product of daily flows and daily concentrations. Effluent concentrations of total ammonia for days without measurements were estimated by time interpolation (e.g., Canale et al., 1996, and Effler, Brooks, and Whitehead, 1996).

Lake Monitoring and Status with Respect to Ammonia Toxicity Standard. Onondaga Lake was monitored weekly at a buoyed deep-water (approximately 19.5 m) location (Figure 1) in

the lake's southern basin for the April-to-October interval during the period from 1989 to 1999. This site has been found to be representative of lakewide conditions (Effler, 1996). Field measurements of temperature and pH were made at 1-m depth intervals with a Hydrolab Surveyor 3 (Hydrolab Corp., Austin, Texas). Secchi disc transparency was measured with a 20-cm (diameter) black and white quadrant disc. Samples for laboratory analyses were collected at 2-m depth intervals. All nitrogen (total ammonia, nitrite, and nitrate) and phosphorus (total phosphorus, total dissolved phosphorus, and soluble reactive phosphorus) analytes were measured according to *Standard Methods* (APHA et al., 1985 and 1989, and U.S. EPA, 1983), and chlorophyll a (Chl), the most widely used surrogate measure of phytoplankton biomass, was measured according to Parsons et al. (1984). Lake sampling and field measurements were conducted at mid-morning, when hydrogen ion concentrations were expected to approach the daily average value (Matthews et al., 2000).

The national toxicity criteria for ammonia, intended to protect aquatic life in surface waters, have been revised five times during the last 15 years (Heber and Ballentine, 1992, and U.S. EPA, 1985, 1996, 1998, and 1999). The details of these revisions and their implications for Onondaga Lake have been described by Matthews et al. (2000). The water quality status of Onondaga Lake with respect to ammonia is evaluated here for the April-to-October interval of 1999 by comparing measured ammonia concentrations to the current New York State standard. The New York State standard for ammonia corresponds to the U.S. Environmental Protection Agency's 1985 chronic criterion for ammonia toxicity, the criterion continuous concentration (CCC). The value of the CCC incorporates the effects of pH and temperature as they influence ammonia toxicity and the equilibrium between ammonium ion (i.e., NH₄⁺) and free ammonia (i.e., NH₃), the more toxic form (U.S. EPA, 1998). As pH and temperature increase, the equilibrium shifts toward free ammonia, and the CCC decreases (i.e., more stringent limit). Concentrations of free ammonia were calculated for the upper waters of the lake for the 1989 to 1999 period from the paired measurements of total ammonia, pH, and temperature (samples and field instrumentation measurements collected at the same depths and times), according to protocols presented by Effler et al. (1990). Status with respect to the ammonia CCC is presented based on both total ammonia measurements and free ammonia calculations (U.S. EPA, 1985).

Plankton Composition and Biomass and Zebra Mussel Density. Water for phytoplankton analysis (50 mL) was collected weekly from a depth of 1 m. Samples were preserved in the field by adding Lugol's solution (acidic) and placed in the dark for



transport to the laboratory. All samples were examined to determine the dominant and common phytoplankton. Quantitative analysis used the Utermohl inverted microscope technique. Three to six strip counts were made on each sample. Cells in filamentous forms were estimated by measuring the length of filament and dividing by mean cell length or by directly counting all cells in each filament. Average counts included more than 250 cells, ranging from fewer than 50 to more than 3500 cells. Abundance results were converted to biovolume estimates ($10^6 \mu\text{m}^3/\text{mL}$) by use of geometric formulas appropriate for the shape of each species and converted to biomass (mg/L), assuming a density of phytoplankton cells of 1 g/mL (e.g., Siegfried, 1987).

Zooplankton samples were collected weekly at the buoyed deep-water site (Figure 1) by vertical tows with a plankton net (30-cm diameter, 64- μm openings) covering the oxic depth interval. Samples were washed into bottles and carbonated water was added to narcotize the zooplankton. A formalin-rose Bengal solution was added after approximately 5 minutes for preservation and staining purposes. Counts were made of all zooplankton (rotifers and crustaceans) in appropriate subsamples (subsample volume adjusted to include at least 100 individuals of each dominant species). Abundance results were converted to biomass estimates by using literature and empirically derived conversion factors (Dumont et al., 1975, and Makarewicz and Likens, 1979).

Density estimates of zebra mussels on bottom substrates were obtained from single surveys conducted in the summers of 1997, 1998, and 2000 at three locations in the near-shore zone of Onondaga Lake (Figure 1). In 1997 and 1998, mussels located within randomly placed 1- m^2 frames were counted in situ. In 2000, mussels were collected from substrates located inside randomly placed 0.25- m^2 frames and returned to the laboratory for enumeration.

Results and Discussion

Metro Inputs. Daily loads of total ammonia and total phosphorus from Metro are presented here for the November 1998 to

October 1999 interval (Figure 2). These loads are compared to distributions of monthly average loads (represented by "box" plots) from Metro for the 1989-to-1997 interval to place the recent reductions in a historical context (Figure 2). Average effluent flows from Metro were essentially equal for the two study periods (i.e., 3.0 m^3/s and 2.9 m^3/s for the 1989-to-1997 and 1998-to-1999 intervals, respectively). Loads received from Metro during the antecedent winter interval have been demonstrated to regulate in-lake concentrations at spring turnover (e.g., Effler, Gelda, and Brooks, 2001). With the exception of May, dramatic reductions in total ammonia loading from Metro were achieved during this 12-month interval (Figure 2a). The nearly complete treatment (nitrification) achieved in November and early December of 1998 (that extended back through much of the summer of 1998) and during the July-to-October interval of 1999 (Figure 2a) reflects, in part, the benefit of industrial pretreatment at the pharmaceutical facility (Effler, Gelda, and Brooks, 2001). However, the primary driver of these dramatic reductions in loading was improved treatment of total ammonia at Metro (Effler, Gelda, and Brooks, 2001), which was largely associated with the recent upgrade in the aeration system. Effluent concentrations were 3.3 mg nitrogen/L or less (the phase 2 limit of the ACJ for November to May) on 25% of the monitored days during the November 1998 to May 1999 interval, and 1.65 mg nitrogen/L or less (the phase 2 limit of the ACJ for June to October) on 74% of the monitored days during the June-to-October interval of 1999.

The higher total ammonia-loading rates of January through April, when temperatures of the treated wastewater were 15 °C or lower (Effler, Brooks, and Whitehead, 1996), reflect the well-known dependence of the nitrification process on temperature (Bowie et al., 1985, and U.S. EPA, 1975). As in previous years (Effler, Brooks, and Whitehead, 1996), Metro provided essentially no nitrification treatment during this interval (Effler, Gelda, and Brooks, 2001). The systematically lower levels during this interval in 1999 (approximately 30%) reflect the benefits of pretreatment of the pharmaceutical waste (i.e., reduced influent concentrations) (Effler, Gelda, and Brooks, 2001). The increased loading of total ammonia in May, representing a retreat to the earlier levels (Figure 2a), was associated with an "upset event" at the pretreatment facility (Effler, Gelda, and Brooks, 2001). The increased industrial load to Metro in May was largely transferred to the lake as it preceded establishment (seasonal) of effective nitrification treatment (Figure 2a). The decrease in loads in June 1999 reflects the establishment of nitrification within the facility that accompanied the increased temperature of the wastewater.

Although the reductions in total phosphorus loading from Metro (Figure 2b) were not as dramatic compared with the earlier levels as observed for total ammonia (Figure 2a), they were nonetheless substantial. Effluent total phosphorus concentrations tended to be lower than the earlier monthly averages throughout the 12-month interval, except in October 1999 (Figure 2b). These improvements were achieved before implementation of major process upgrades that are anticipated to reach the mandated limits of the ACJ. The average effluent concentration for the 12-month interval was 0.38 mg/L. Only a single (daily) measurement of the effluent concentration was as low as the phase 2 (ACJ) limit of 0.12 mg/L. The 1999 load was 35% lower than the annual average Metro total phosphorus load for the 1989 to 1997 period; moreover, the 1999 load was 5% less than the lowest load (1997) for that period.

In-Lake Signatures: Nitrogen and Zebra Mussels. Dramatic decreases in total ammonia concentrations in the lake's upper

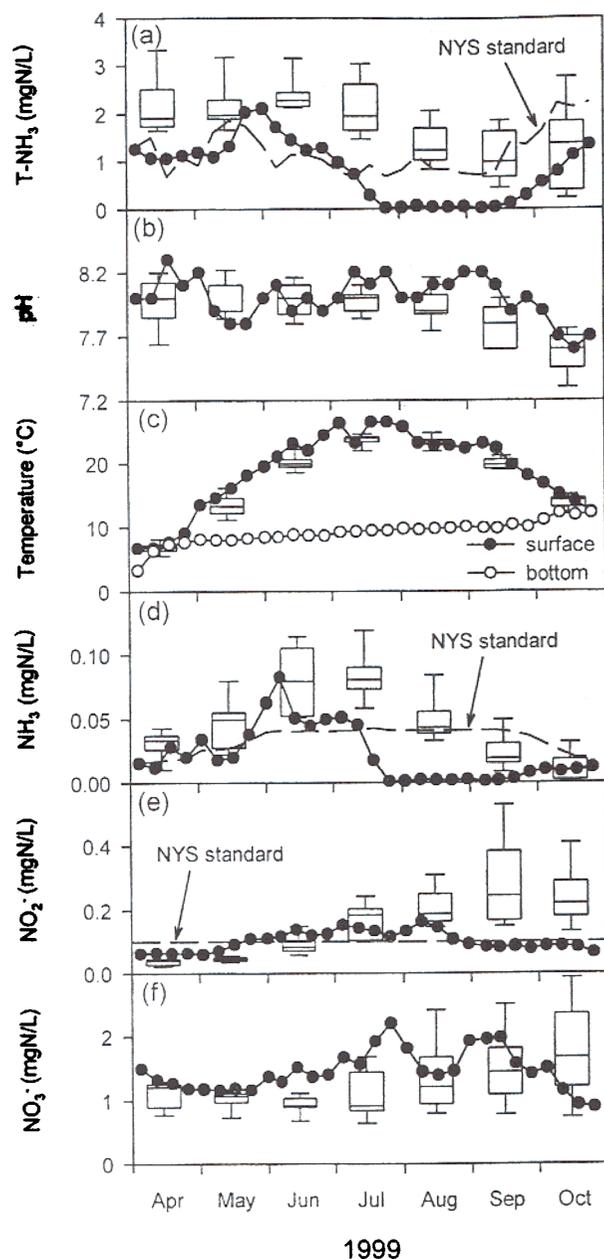


Figure 3—Time series for upper waters (mean of 0-, 2-, and 4-m values) of Onondaga Lake in 1999, compared to historic (1989 to 1997) monthly average values (boxes depict median, 10th, 25th, 75th, and 90th percentiles): (a) total ammonia (T-NH₃), dashed line is New York State standard for 1999 conditions; (b) pH (from average of hydrogen ion concentration values); (c) temperature; (d) free ammonia (NH₃), dashed line is New York State standard for 1999 conditions; (e) nitrite (NO₂⁻), dashed line is New York State standard (0.1 mgN/L); and (f) nitrate (NO₃⁻).

waters occurred in the summer of 1999 (Figure 3a) in response to reductions in loading from Metro (Figure 2a). The concentrations in 1999 were the lowest recorded in the lake during the study interval (1989 to 1999) by a wide margin. The concentration at spring turnover, 1.3 mg nitrogen/L, was the lowest value recorded;

the average for the 1989-to-1997 interval was 2.2 mg nitrogen/L. The 1999 spring-turnover concentration was successfully predicted with a mass-balance model, establishing this reduced level was a result of the lower antecedent wintertime load from Metro (Effler, Gelda, and Brooks, 2001). Total ammonia concentrations peaked in the lake at approximately 2 mg nitrogen/L in late May as a result of the upset event at the pharmaceutical pretreatment facility (Figures 2a and 3a) (Effler, Gelda, and Brooks, 2001). Concentrations of total ammonia subsequently declined during June and July to concentrations less than 0.1 mg nitrogen/L, and remained low from late July through mid-September (Figure 3a). The rapid decrease reflects the reductions in loading from Metro, mediated by the rather rapid flushing rate of the lake, and the preferential uptake of ammonium ion (versus nitrate, the alternative source of nitrogen) by phytoplankton (Wetzel, 2001). The low concentrations of total ammonia during the late July to late September interval of 1999, while typical of many lakes, are unprecedented for Onondaga Lake (Matthews et al., 2000). The observed increase in total ammonia concentrations during October, a recurring feature in Onondaga Lake, is associated with the entrainment of the enriched hypolimnion (Brooks and Effler, 1990, and Effler et al., 1990) that occurs during fall mixing (Figures 3a and 3c). The size of the total ammonia pool in the lake's hypolimnion is driven largely by primary production (Gelda, Effler, and Doerr O'Donnell, 2001) and, thus, is not substantively driven by Metro's total ammonia load. Concentrations of total ammonia in 1999 remained lower than the New York State standard for nonsalmonid systems from mid-July through the end of the study period (Figure 3a). This improvement is particularly noteworthy in light of the severe and extended violations of this standard that have prevailed annually in the system (Effler et al., 1990, and Matthews et al., 2000).

The distributions of pH (Figure 3b) and temperature (Figure 3c) in the lake's upper waters are of interest in this study primarily because of their mediating influences on the equilibrium between free ammonia and ammonium ion and, therefore, status with respect to the toxicity standard for ammonia (U.S. EPA, 1985). The extent to which the temporal patterns of total ammonia (Figure 3a) and free ammonia (Figure 3d) did not coincide reflects the effects of variations in temperature and pH. Observations for pH and temperature were, for the most part, within the bounds of historic measurements (e.g., Driscoll et al., 1994). Values of pH were somewhat lower than normal in May and higher than usual in parts of August and September (Figure 3b). The decrease in pH in October is a recurring event associated with turnover (Brooks and Effler, 1990). Temperatures were slightly higher than normal in late spring and early summer (Figure 3c). The temporal pattern of free ammonia in the upper waters (Figure 3d) largely tracked that of total ammonia (Figure 3a). This factor, along with the lack of substantive shifts in pH and temperature conditions, supports the position that the major decreases in free ammonia concentrations observed in 1999 (Figure 3d) were driven largely by the decreases in total ammonia concentrations (and thereby Metro loading). The most noteworthy differences in the total ammonia and free ammonia patterns were in early June and October (Figures 3a and 3d). The abrupt peak in free ammonia in early June reflected a peak in pH, while the relatively modest increase in free ammonia in October was a result of compensating decreases in pH (Figures 3a and 3d) (e.g., Brooks and Effler, 1990). Concentrations of free ammonia in the lake remained well less than the New York State standard for nonsalmonid systems during the mid-July through

Table 2—Density estimates of zebra mussels in summer 1997, 1998, and 2000 at three locations in the near-shore zone of Onondaga Lake.

Site	1997 and 1998 (Individuals/m ²)	2000 (Individuals/m ²)
2	<1	5984
3	<1	6768
—	<1	12 208

September interval (Figure 3d), which was consistent with the status reflected in the total ammonia pattern (Figure 3a).

Numerous small (younger than 1-year-old) zebra mussels were found on a variety of artificial substrates (e.g., buoys and fishnets) in the lake during the fall of 1999. Benthic sampling conducted in 2000 established that hard substrates (Table 1) in the littoral zone had experienced dense colonization (up to 12 000 individuals/m²) (Table 2). The mussels collected in 2000 represented essentially two size classes that corresponded to colonization during the summers of 1999 and 2000. The timing of the sudden zebra mussel invasion coincided, and almost certainly was associated, with the dramatic decrease in the upper water concentrations of ammonia that occurred in 1999 (Figures 3a and 3d) as a result of reductions in loading from Metro (Figure 2a). A wide range of ammonia sensitivities has been reported for freshwater mollusks (Goudreau et al., 1993, and U.S. EPA, 1985). Ammonia toxicity bioassays on glochidia (the parasitic larval stage of unionids) of *Villosa iris* (Goudreau et al., 1993) and juvenile *Musculium transversum* (fingernail clam) (Anderson et al., 1978, and Sparks and Sandusky, 1981) have established that bivalves can be among the most ammonia-sensitive freshwater organisms. Zischke and Arthur (1987) found that total ammonia concentrations as low as 1 mg nitrogen/L had substantial effects on the reproduction of fingernail clams. Zebra mussels reared under laboratory conditions are extremely sensitive to ammonia concentrations greater than 1 mg nitrogen/L (Nichols, 1992). Nichols (1992) found that total ammonia concentrations of 2 mg nitrogen/L caused severe stress in laboratory-reared zebra mussels, and concentrations of 3 mg nitrogen/L caused 90 to 100% mortality. Coon et al. (1993) reported that total ammonia concentrations greater than 3 mg nitrogen/L cause 100% mortality in veligers. The high concentrations of total ammonia maintained in the upper waters of Onondaga Lake (> 2 mg nitrogen/L) before 1999 apparently prevented the dense colonization of this system by zebra mussels. Spada et al. (2001) presented evidence that the earlier failure of the invasion was due to toxic effects on early life stages.

Progressive increases in nitrite continued to be observed through July 1999, as reported in previous years (Gelda et al., 1999) (Figure 3e). This has been attributed to loads from Metro (i.e., incomplete nitrification at the facility) (Gelda et al., 1999). However, the irregular, abrupt, "pulsing" (increase followed by decrease) observed in most of the previous years (Gelda et al., 1999) was absent, and concentrations in September and October were the lowest of the study interval (Figure 3e). These improvements are likely a manifestation of the improvement in total ammonia treatment at Metro (Figure 2a). Concentrations of nitrite remained greater than the New York State standard for nonsalmonid systems (0.1 mg nitrogen/L) from late May through late August (Figure 3e).

Concentrations of nitrate in the upper waters increased progressively during the period of late May through late July (Figure 3f), reflecting the influence of nitrification at Metro (e.g., Effler, Brooks, and Whitehead, 1996a, and Gelda et al., 1999). However, concentrations of nitrate decreased sharply during late July and early August (Figure 3f) following depletion of the total ammonia pool (Figure 3a) and during a major phytoplankton bloom (subsequently), which probably indicates a switch to nitrate as the primary source of nitrogen to support phytoplankton growth (Canale et al., 1996). Concentrations of nitrate increased in late August, apparently in response to continued Metro loading (e.g., Effler et al., 1996a, and Gelda et al., 1999) and reduced phytoplankton demand (Figure 3f). The decrease in nitrate concentrations observed during September and October (Figure 3f) was associated with the entrainment of nitrate-depleted waters (due to denitrification) (Effler, 1996) from the hypolimnion that occurs with the approach of fall turnover (Brooks and Effler, 1990).

In-Lake Signatures: Phosphorus and Plankton Communities. Trophic state conditions in 1999, as reflected by average values (April to September) of the most widely used indicators (total phosphorus, chlorophyll *a*, and Secchi disk transparency) (Chapra, 1997), were not substantively improved compared with the 1989-to-1997 interval (Table 3), indicating that Onondaga Lake remained hypereutrophic. This general unresponsiveness to reductions in external phosphorus loading is consistent with the position that the lake was essentially a nutrient-saturated system (Connors et al., 1996). This further suggests that greater reductions in phosphorus loading will be necessary to establish substantial nutrient limitation of phytoplankton growth and, thereby, improve trophic state conditions through bottom-up processes. However, analysis of detailed temporal patterns depicts substantial changes in the phosphorus pools and phytoplankton of the lake (Figure 4) that reflect a combination of direct and indirect effects of the reductions in phosphorus and total ammonia loading (Figure 2). Further, the signatures of forms of phosphorus, chlorophyll *a*, the plankton community structure, and Secchi disk transparency observed in 1999 (Figure 4) may be expected to be modified in subsequent years as the newly established zebra mussel community ages and expands.

Concentrations of total phosphorus in the upper waters of the lake in 1999 were substantially lower than the 1989-to-1997 averages during April, May, June, September, and October (Figure 4a). The reductions during the April to June interval are largely the result of decreased total phosphorus loading from Metro (Figures 2b and 4a). The Metro total phosphorus load during the December to March interval explained 67% of the interannual variation observed in total phosphorus at spring turnover during the 1989-to-1999 period (with 1991 eliminated as an outlier). The spring-

Table 3—April to September averages and standard deviations (in parentheses) of widely used trophic state indicators for the upper waters (mean of 0-, 2-, and 4-m values) of Onondaga Lake.

Year	Total phosphorus (µg/L)	Chlorophyll <i>a</i> (µg/L)	Secchi disk (m)
1999	54 (11)	31 (19)	2.0 (1.5)
1989–1997	81 (11)	26 (8)	2.3 (0.4)

turnover total phosphorus concentration of 84 $\mu\text{g/L}$ in 1999 was the lowest observed during the 1989-to-1999 interval and 37% lower than the 1989-to-1997 average of 134 $\mu\text{g/L}$. The total phosphorus concentration at spring turnover has been used as a predictor of the subsequent summer average chlorophyll *a* concentration (Dillon and Rigler, 1974). According to the expression of Dillon and Rigler (1974), a spring-turnover total phosphorus of 30 $\mu\text{g/L}$ would correspond to a summer average chlorophyll *a* concentration of 10 $\mu\text{g/L}$, which was described by Chapra (1997) as the boundary between mesotrophy and eutrophy. Concentra-

tions of total phosphorus remained in a rather narrow range (39 to 64 mg/L) from mid-April through September (Figure 4a). The increases in total phosphorus concentrations during October (Figure 4a) are observed annually, reflecting the entrainment of enriched waters from the hypolimnion with the approach to fall turnover. The summer average (mid-May to mid-September) total phosphorus concentration of the upper waters in 1999 exceeded the state guidance value by a factor of approximately 2.5.

Dissolved forms of phosphorus are used by phytoplankton to support growth (Hutchinson, 1973). Soluble reactive phosphorus is considered a form that is immediately available to support growth, while dissolved organic phosphorus (approximately total dissolved phosphorus—soluble reactive phosphorus) can be made available through enzymatic hydrolysis (Currie et al., 1986, and Gage and Gorham, 1985). Values of soluble reactive phosphorus were at, or lower than, detection limit concentrations (approximately 1 $\mu\text{g/L}$) in the upper waters of the lake through most of the April to September interval (Figure 4b), reflecting efficient use of this highly available pool. This observation is generally consistent with observations from earlier years (Connors et al., 1996); in addition, it is widely observed in lakes representing a broad range of trophic state conditions (Wetzel, 2001). Exceptions were the abrupt increases in soluble reactive phosphorus during the clearing events (abrupt decreases in phytoplankton biomass associated with zooplankton grazing) (Figures 4b and 4c) that reflected reductions in uptake, continued external loading, and rapid recycling within the upper waters (Auer et al., 1990). Connors et al. (1996) found that the soluble reactive phosphorus pool was an inadequate representation of the status of phosphorus limitation of phytoplankton in Onondaga Lake, in part because of the effective use of the dissolved organic phosphorus pool. Use of this pool is indicated by the rather rapid decrease in dissolved organic phosphorus in early April (Figure 4b) during the spring phytoplankton bloom, and the more gradual decrease during the July to August bloom (Figures 4c and 4d). Concentrations of dissolved organic phosphorus were substantially lower in 1999, particularly in the April to June interval, compared with earlier years (Figure 4b), presumably in response to reductions in Metro phosphorus loading (Figure 2b). Reductions in this pool suggest the approach to increased nutrient limitation. The approach to, and passage into, phosphorus-limited growth in the lake from additional reductions in Metro loading may be tracked through further reductions in the summer dissolved organic phosphorus pool. The high phytoplankton biomass levels that were maintained in August (Figures 4c and 4d), when the seasonal minimum dissolved organic phosphorus values were observed (approximately 5 $\mu\text{g/L}$), suggest that concentrations at least

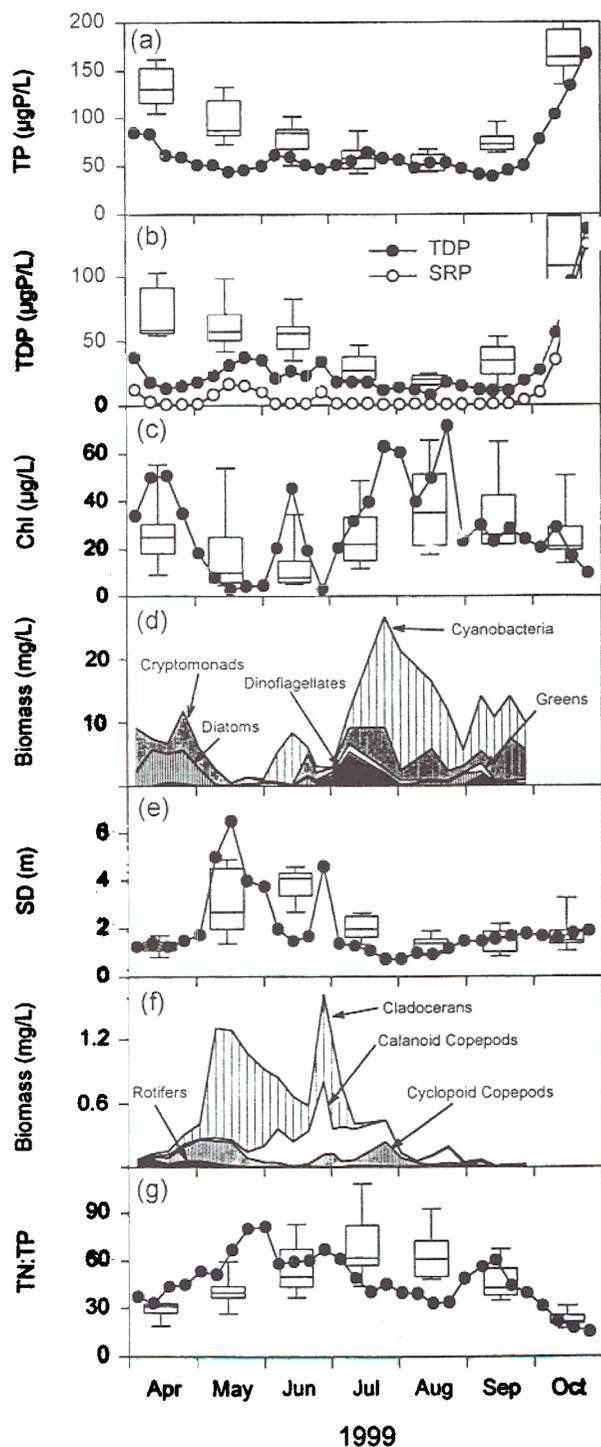


Figure 4—Time series for upper waters (mean of 0-, 2-, and 4-m values; except plankton and Secchi disc data) of Onondaga Lake in 1999, compared to historic (1989 to 1997) monthly average values (boxes depict median, 10th, 25th, 75th, and 90th percentiles, except for plankton data): (a) total phosphorus (TP); (b) soluble reactive phosphorus and total dissolved phosphorus (TDP, boxes are for total dissolved phosphorus); (c) chlorophyll *a* (Chl); (d) phytoplankton biomass and composition (1 m); (e) Secchi disc (SD); (f) zooplankton biomass and composition (oxic, depth interval); and (g) total nitrogen/total phosphorus ratio (TN:TP, by mass).

that low will need to be maintained throughout the growing season to achieve nutrient limitation and, therefore, substantial reductions in phytoplankton biomass and improvements in clarity (through bottom-up pathways).

The temporal patterns of the two measures of phytoplankton included in this analysis, chlorophyll *a* and biomass (Figures 4c and 4d), were well correlated (correlation coefficient $R = 0.75$) within the context of the limitations of these measurements (e.g., geometric approximations, differences in chlorophyll content of various species) (Wetzel and Likens, 1991) and the differences in the depths represented (average of 0-, 2-, and 4-m results for chlorophyll *a*; 1-m sample for biomass). Conspicuous blooms were manifested in April, June, July to August, and September (Figures 4c and 4d). The minima in phytoplankton biomass that occurred in May and late June of 1999 have been a recurring characteristic of the lake since 1987, although interannual differences in timing and the occurrence of one versus two events have been observed (Effler, 1996, and Perkins and Effler, 1996). These minima cause abrupt increases in Secchi disc transparency, termed *clearing events* (Auer et al., 1990, and Siegfried et al., 1996) or *clear water phases* (Lampert et al., 1986), which were clearly manifested in 1999 as Secchi disc maxima of 6.5 and 4.5 m (Figure 4e). These events have been attributed to efficient grazing by large-bodied cladocerans (daphnids) in Onondaga Lake (Siegfried et al., 1996) and elsewhere (Lampert et al., 1986). Significant reductions in blooms of cyanobacteria have been attributed to viral infections in some systems (e.g., Coulombe and Robinson, 1981, and Daft et al., 1970). However, the paired zooplankton data of 1999 continue to support efficient grazing by large-bodied cladocerans as the principal cause for these clearing events because the coincident peaks of cladoceran biomass (Figure 4f) were composed mostly of large daphnids [*Daphnia pulex/pulicaria*]. This phenomenon was largely responsible for the systematic improvement in summer average clarity conditions in the lake starting in 1987 (Perkins and Effler, 1996). This is an example of a top-down effect that was not associated with a change in nutrient loading. Interestingly, the "trigger" for the shift in the zooplankton assemblage that causes the clearing events was a major reduction in the salinity of the lake that resulted from the closure of the soda ash-chlor-alkali facility (Siegfried et al., 1996).

Phytoplankton composition data are often considered a subtlety for lake managers unless nuisance forms are present. Certain cyanobacteria (formerly blue-green algae) are of particular concern because of their propensity to form noxious floating scums and, in some cases, produce toxic effects (Cooke et al., 1993). A number of environmental conditions have been identified as favoring cyanobacteria blooms (Hyenstrand et al., 1998, and Paerl, 1988), including (1) high nutrient levels, (2) low nitrogen/phosphorus ratios, (3) high temperatures, (4) high water column stability, and (5) high pH. The nitrogen/phosphorus ratio has received particular attention for structuring the summertime phytoplankton community. Nitrogen-fixing cyanobacteria have a competitive advantage over green algae and diatoms when nitrogen concentrations, or nitrogen-to-phosphorus ratios, are low (Fogg et al., 1973; McCarthy, 1980; and Tilman et al., 1982). Non-nitrogen-fixing cyanobacteria, such as *Microcystis*, may also be favored under these conditions because they can store nitrogen (Fogg et al., 1973, and Smith, 1983). Smith (1983) reported that cyanobacteria tended to be rare when epilimnetic total nitrogen-to-total phosphorus ratios (by mass) were greater than 29:1. Efficient filter feeding by large daphnids may select for large or colony-forming cyanobac-

teria because of their inability to consume these phytoplankton (Siegfried et al., 1996, and Svensson and Stenson, 1991). Recently, Vanderploeg et al. (2001) argued that zebra mussel populations can promote blooms of *Microcystis*.

The elimination of nuisance cyanobacteria as a dominant component of Onondaga Lake's phytoplankton community in the early 1970s was attributed to an increase in the nitrogen-to-phosphorus ratio associated with major reductions in phosphorus loading resulting from a ban on high phosphorus detergents in the watershed (Effler, 1996, and Murphy, 1973). However, starting in 1987, coinciding with the beginning of the period of dominance of large daphnids in the zooplankton community, filamentous cyanobacteria (particularly *Aphanizomenon flos-aquae*) returned as a dominant component of the lake's phytoplankton (Effler, 1996, and Siegfried et al., 1996). This factor was unrelated to bottom-up effects such as relative nutrient availability; for example, the frequency of heterocysts (specialized cells that function in the fixation of molecular nitrogen) was low and the nitrogen-to-phosphorus ratio remained high. The primary driver for this major shift in composition was attributed instead to a top-down process, the effect of selective feeding (phytoplankton other than filamentous cyanobacteria were effectively consumed) of zooplankton (large daphnids) (Siegfried et al., 1996, and Svensson and Stenson, 1991). Late summer blooms of *Aphanizomenon flos-aquae* in the lake did not cause nuisance conditions that approached the severity of those manifested with the next major shift in the phytoplankton assemblage that emerged in late summer of 1999.

The seasonal succession of phytoplankton in the lake through June in 1999 was typical of conditions observed since the late 1980s (Figure 4d). A combination of diatoms and cryptomonads was responsible for the spring bloom (Figure 4d). The June cyanobacteria bloom (Figure 4d) was composed mostly of *Aphanizomenon flos-aquae*. However, the dominance of *Microcystis* during the subsequent bloom of July and August (approximately 80% of the cyanobacteria biomass) (Figure 4d) represents the single greatest change in the phytoplankton community (within the context of water quality management) since the late 1980s. The average chlorophyll *a* concentration for July and August (Figure 4c) was the second highest observed during the study interval and Secchi disc values dropped lower than the 1.2-m New York State standard for swimming safety (Figure 4f). The measures of biomass presented in time series (Figures 4c and 4d) do not completely portray the magnitude and character of the bloom. Concentrations were often systematically higher in the surface waters during the bloom; for example, a peak chlorophyll *a* concentration of 159 $\mu\text{g/L}$ was observed at the surface on August 23. Further, large accumulations of *Microcystis* (promoted by its colonial organization within a gelatinous matrix) developed along the lake's shores as surface scums that created noxious conditions. This shift in the phytoplankton assemblage had important implications for the management program for the lake because its manifestations were interpreted by the public as a degradation in water quality (e.g., related news media coverage). Moreover, hepatotoxins produced by certain strains of *Microcystis* have been linked to the poisoning of aquatic organisms, wildlife, and domestic animals that drink or ingest algae in the water (e.g., Carmichael, 1996).

This shift in the phytoplankton community does not seem to have been driven by bottom-up processes such as changes in nutrient concentrations or nutrient ratios. Epilimnetic total nitrogen/total phosphorus (by mass) values remained greater than 29 (Smith, 1983) throughout the summer months (i.e., 33:49)

(Figure 4g). McQueen and Lean (1987) found a high likelihood for cyanobacterial blooms in Lake St. George, Ontario, when temperature was greater than 21 °C and the ratio of nitrate to total phosphorus was less than 5. Epilimnetic temperatures were greater than 21 °C in Onondaga Lake from mid-June to mid-September in 1999 (Figure 3c), but the nitrate/total phosphorus ratio remained greater than 25 for the entire interval. Blomqvist et al. (1994) reported *Microcystis* was favored over other cyanophytes when the ratio of ammonia to nitrate increased. This observation was counter to those made in 1999 for Onondaga Lake when the ratio decreased dramatically (Figures 3a and 3f) as a result of the reductions in loading from Metro (Figure 2a).

The emergence of *Microcystis* as the dominant cyanophyte responsible for the severe late summer bloom of 1999 was probably primarily driven by a top-down process that was most likely associated with the coincidental invasion of zebra mussels. The occurrence of blooms of this genus of cyanobacteria has been reported elsewhere after the establishment of zebra mussels (e.g., Saginaw Bay, Lake Michigan [Vanderploeg et al., 2001], western basin of Lake Erie [Budd et al., 2001], Gull Lake and Gun Lake in Michigan, and the Bay of Quinte, Lake Ontario [Vanderploeg et al., 2001]). Zebra mussel metabolism apparently selects for "unpalatable" strains of *Microcystis* that occur as large colonies such as those observed in Onondaga Lake in 1999. These colonies have been observed to be rejected by the mussels after filtration as loosely consolidated (viable) pseudofeces (Table 1), while smaller, more desirable algae are ingested (Vanderploeg et al., 2001). This process of selective rejection, perhaps along with increased nutrient recycling (e.g., zebra mussel excretion) (Bierman et al., 1998, and Mellina et al., 1995), was probably largely responsible for the major *Microcystis* bloom observed in the lake in 1999.

Synthesis and Summary

Major reductions in external loading of total ammonia and total phosphorus from Metro have been achieved in the early stages of a phased rehabilitation program for domestic waste inputs to Onondaga Lake, although substantial further decreases will be required to meet the final mandated effluent limits. The lake responded rapidly (less than 1 year) to these reductions because of the nonconservative character of these constituents and its rapid flushing rate, an attribute that should be taken advantage of in tracking responses to subsequent phases of the rehabilitation program. A detailed monitoring program documented dramatic changes in measures of water quality and the lake's biota in 1999 compared with observations during the preceding decade, including: (1) major decreases in total ammonia and free ammonia concentrations; (2) the development of dense populations of zebra mussels in the lake's near-shore zone; (3) decreases in fall concentrations of nitrite; (4) nitrate depletion by phytoplankton (for the first time, following depletion of total ammonia); (5) decreases in total phosphorus concentrations, particularly in the spring to early summer interval; (6) reductions in total dissolved phosphorus (dissolved organic phosphorus) concentrations; (7) a severe *Microcystis* bloom and related nuisance conditions in late summer; and (8) unusually low Secchi disc values during the *Microcystis* bloom. The status of the lake with respect to water quality standards for forms of nitrogen and total phosphorus improved as the margins and durations of violations decreased, although violations continued to occur. However, based on aesthetic features that are important and recognizable to the public, such as the occurrence of nuisance conditions and poor water clarity during the *Microcystis*

bloom, the changes were viewed as further degradation. These later responses apparently reflect top-down effects mediated by the zebra mussel invasion. The responses underscore the need for additional reductions in phosphorus loading from Metro (e.g., Effler and Doerr, 1996) that would limit phytoplankton growth through bottom-up mechanisms, regardless of the operation of top-down processes.

Uncertainties in the cause-and-effect relationships for the observed changes in the biota are unavoidable. The circumstantial evidence for the coupling of the major increase in zebra mussels and decrease in ammonia concentrations is compelling based on the temporal coincidence of the occurrences and the weight of the related scientific literature concerning toxicity of ammonia for bivalves, in general, and zebra mussels, specifically. However, coupling of the *Microcystis* bloom to the zebra mussel invasion is less certain. This interaction can fairly be described as likely, based on the recent related research of Vanderploeg et al. (2001) and the similar observations reported for a number of other invaded systems.

The establishment of dense populations of zebra mussels in Onondaga Lake marks the second major shift in the system's biota in recent years in response to a major reduction in pollutant concentrations. The first case was the emergence of large daphnids as a dominant component of the zooplankton community following the decrease in salinity that attended the closure of an industrial polluter (Siegfried et al., 1996). The expansion and growth of the lake's zebra mussel population could potentially have important implications for the lake's food web and measures of water quality. Various aspects of zebra mussel metabolism have caused major changes in water quality in densely populated systems. Decreases in phytoplankton and attendant increases in clarity as a result of mussel filter feeding have been reported for a number of invaded systems (Caraco et al., 1997; Effler, Siegfried, and Hassett, 2001; Fahnenstiel et al., 1995; Holland, 1993; and Reeders and Bij de Vaate, 1990). Filter feeding by this invader may also influence water quality indicators of the hypolimnion, such as the rate of oxygen depletion, by routing much of the organic material that had previously reached the lower layers (via deposition) to the near-shore zone instead. Zebra mussels effectively recycle important nutrients (such as soluble reactive phosphorus and total ammonia) from consumed food via excretion [Arnott and Vanni, 1996; Effler et al., 1997; and Mellina et al., 1995] that could act to sustain phytoplankton growth. Respiration by the bivalve represents a new oxygen sink (Caraco et al., 2000, and Effler et al., 1998). Fortunately, this sink remains isolated in the near-shore area of the lake, where photosynthetic and reaeration inputs can satisfy this demand (Gelda and Auer, 1996). Zebra mussels can also exert important direct and indirect influence on other biological communities. This bivalve consumes smaller zooplankton (e.g., rotifers) (Strayer et al., 1999) and has promoted expansion of rooted plant growth into deeper waters through increased light penetration (Skubinna et al., 1995). These effects, and direct interactions with the invader, may also influence the structure of the fish and benthic communities (MacIsaac, 1996). The stability of zebra mussel populations and related food web effects are important management issues for invaded systems. The European experience indicates that instability is observed for most systems (e.g., maximum densities lasting 2 to 3 years, followed by crashes and subsequent cycles of diminished amplitude) (Ramcharan et al., 1992).

The phased program to rehabilitate the domestic waste-based problems of Onondaga Lake represents a rare opportunity to

advance the understanding of the effects of these pollutants on lakes. Responses to future incremental reductions in loads from the WWTP can be well resolved because of the phasing of increased treatment and the inherently rapid response of the system. The top-down effects of the coincidental zebra mussel invasion will undoubtedly complicate the cause-and-effect analysis of responses to the rehabilitation program. These influences should be recognized and separated from the bottom-up effects of the program for both scientific and management reasons. Therefore, managers and the public should not rely primarily on the potential benefits of top-down effects (e.g., improved clarity) and, specifically, zebra mussel metabolism to meet long-term water quality goals for polluted systems, such as Onondaga Lake, because these effects depend on rather delicate balances within complex food webs that are subject to uncontrolled changes.

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