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ECOSYSTEMS

Alteration of Ecosystem Function by Zebra Mussels in Oneida Lake: Impacts on Submerged Macrophytes

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ABSTRACT

Dreissenid mussels (the zebra mussel *Dreissena polymorpha* and the quagga mussel *D. bugensis*) are ecosystem engineers that modify the physical environment by increasing light penetration. Such a change is likely to affect the distribution and diversity of submerged macrophytes. Filter-feeding by these mussels has been associated with increased water clarity in many North American and European lakes. In this study, we report the increase in water clarity of Oneida Lake, New York, USA, for 1975–2002 and argue that the increase was caused by zebra mussel invasion rather than declines in nutrients. Over the study period, although mean total phosphorus decreased significantly, the main increase in water clarity occurred after the zebra mussel invasion in 1991. The average depth receiving 1% surface light increased from 6.7 m to 7.8 m after the invasion of zebra mussels, representing a 23% areal expansion. The maximum depth of macrophyte colonization, as measured by diver and hydroacoustic surveys, increased from 3.0 m before the invasion of zebra mussels to 5.1 m after their establishment. In addition, macrophyte species richness increased, the frequency of occurrence increased for most species, and the composition of the macrophyte community changed from low-light–tolerant species to those tolerating a wide range of light conditions. Comparisons with observations reported in the literature indicate that increased light penetration alone could explain these changes in macrophyte distribution and diversity. Such changes will increase the importance of benthic primary production over pelagic production in the food web, thereby representing an overall alteration of ecosystem function, a process we refer to as ''benthification''.

Key words: submerged macrophytes; dreissenid mussels; light; water clarity; Secchi depth; species diversity; Oneida Lake.

INTRODUCTION

The invasion of nonnative species has had one of the most pervasive and deleterious anthropogenic impacts on the world's ecosystems (Mills and others 1994; Wilcove and others 1998). One prominent example is the arrival of dreissenid mussels (the zebra mussel *Dreissena polymorpha* and the quagga mussel *D. bugensis*) into the rivers and lakes of North America. Dreissenid mussels have been described as ''ecosystem engineers'' (Jones and others 1994, 1997) because they alter both the structure and function of the environment they invade (Strayer and others 1998; Bailey and others 1999; Karatayev and others 2002; Mayer and others 2002). Although many abiotic and biotic effects of dreissenid mussels have been identified (see for example, MacIsaac 1996), increased water clarity in

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rivers and lakes is one of the most commonly reported impacts (Caraco and others 1997; Baldwin and others 2002; Vanderploeg and others 2002). Dreissenid mussels increase water clarity by filtering particles from the water and consuming them or binding them in pseudofeces. Karatayev and others (1997, 2002) reported similar improvements in the water clarity of rivers and lakes in Europe after invasion by dreissenid mussels. Greater water clarity leads to deeper light penetration and thus enhances benthic photosynthesis (Vanderploeg and others 2002). Such changes in light would also be expected to influence the distribution and community composition of submerged macrophytes (Wetzel 1983; Chambers and Kalff 1985).

Many ecosystem processes are mediated by submerged macrophytes (Carpenter and Lodge 1986). These plants can directly or indirectly alter the physical and chemical environment by shaping light, temperature, and nutrient dynamics (Carpenter and others 1992; Petticrew and Kalff 1992; Diehl and Kornijów 1998). They also play a significant role in shaping the structure and dynamics of pelagic and benthic food webs in rivers and lakes, even at relatively low areal coverage. For example, macrophytes are used as habitat by algae, zooplankton, invertebrates, and fishes; therefore, they directly and indirectly affect predator–prey interactions among these groups (see, for example, Covich and others 1999). Submerged macrophytes have a variety of different life histories and consequently affect processes across a wide range of spatial and temporal scales (see, for example, Diehl and Kornijów 1998). Changes in interactions controlled by macrophytes, in turn, may have cascading effects on the entire food web in both the pelagic and the littoral zones (Carpenter and others 1992; Scheffer and others 1993, 2001; Schindler and Scheurerell 2002; Scheffer and Carpenter 2003).

Biological, physical, and chemical factors all interact to shape the growth, biomass, and distribution of submerged macrophytes in aquatic ecosystems (Håkanson and Boulion 2002; Schindler and Scheuerell 2002). Important factors affecting macrophytes include depth, fetch, ice scour, latitude, temperature, and water levels. Among these factors, light is of paramount importance, because it exerts a major control on photosynthesis and declines with water depth due to attenuation, scattering, and absorption (Sand-Jensen and Borum 1991; Hudon and others 2000). Therefore any increase in light penetration associated with dreissenid invasion is likely to affect the plant community (Vestergaard and Sand-Jensen 2000; Karatayev and others 2002; Van den Berg and others 2003; Lammens and others 2004). The general effect of an increase in light penetration will be positive, promoting plant growth by increasing photosynthesis and creating a larger area of suitable sediment. Consequently, expanded distribution and diversity of macrophytes and reduction of phytoplankton biomass is an expected outcome of increased light penetration in aquatic ecosystems (see, for example, Genkai-Kato and Carpenter 2005).

In addition to increasing light penetration, there are numerous ways that dreissenids may affect submerged macrophytes (Figure 1). Dreissenid mussels attach to submerged macrophytes, disperse themselves, and inhibit plant growth (Lewandowski 1982; Horvath and Lamberti 1997; Lewandowski and Ozimek 1997; Buchan and Padilla 2000). On the other hand, dreissenid mussels may benefit macrophytes by increasing nutrient availability. The growth of submerged macrophytes depends mostly on nutrients such as phosphorus (P) in the sediments (Carignan and Kalff 1980). The mussels can relocate P and nitrogen (N) in the particles from the water column to the sediments through the production of pseudofeces and feces (Hecky and others 1993; Effler and others 1996; Roditi and others 1997). It has recently been suggested that *Dreissena* are redirecting a significant proportion of nutrients to near-shore areas at a large spatial scale in the Laurentian Great Lakes (Hecky and others 2004). Thus, a potentially important net effect of dreissenid mussel activity is the conversion of particulate forms of nutrients to dissolved chemical elemental forms in sediments, and this process may benefit submerged macrophytes (see, for example, Reusch and others 1994).

Despite the importance of macrophytes in lake communities and the widespread occurrence of increased water clarity, possible changes in the roles of these organisms in the face of environmental change caused by dreissenid mussels or nutrient abatement has received little attention. With some notable exceptions (for example, Skubbina and others 1995; Chu and others 2004; Lammens and others 2004), there have been few studies addressing the relationship between increased water clarity and submerged macrophytes in North American and European lakes. Focal studies have been conducted to assess the cascading ecosystem-level responses to changes in the plant community (Caraco and others 2000; Strayer and Smith 2001; Mayer and others 2002; Strayer and others 2004). However, to date, no one has examined the primary mechanism underlying the

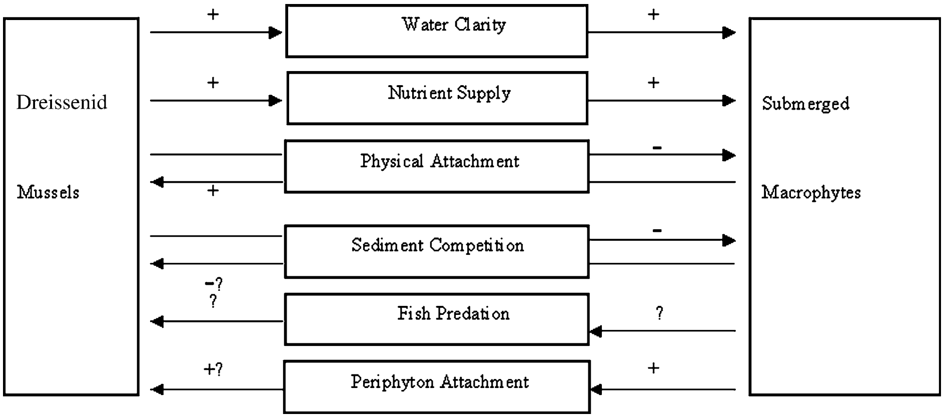

Figure 1. Possible interactions between *Dreissena polymorpha* or *D. bugensis* and submersed macrophytes in freshwater ecosystems based on European and North American studies. Benefits from *Dreissena* are indicated with a + symbol; those adversely affected are indicated by a − symbol; a question mark (?) indicates uncertain consequences.

interactions between dreissenid mussels and submerged macrophytes.

Our study focused on the response of submerged macrophytes to the zebra mussel–mediated increase of water clarity in a large freshwater lake, Oneida Lake, New York, USA. We hypothesized that the presence of dreissenid mussels in lakes would enhance the distribution, frequency of occurrence, and diversity of submerged macrophytes due primarily to increased light penetration. Previous studies on this lake have linked the observed increase in water clarity to the zebra mussel invasion (Idrisi and others 2001; Mayer and others 2002). To test our hypothesis, we first quantified changes in Secchi depth before and after establishment of zebra mussels using a 28-year time series and determined whether P abatement is an important factor for water clarity in this ecosystem. We then compared trends in changes in light penetration, maximum depth of macrophyte colonization, macrophyte species diversity, frequency of occurrence, and species composition in different periods.

METHODS

Study Site

Oneida Lake is the largest inland lake in New York State, with a surface area of 206.7 km^2, a mean depth of 6.8 m, and a maximum depth of 16 m (Figure 2). This shallow and polymictic lake (Mills and others 1978) currently has P levels approximately 40% lower than those of the 1970s (24.8 $\mu g\ L^{-1}$ in 2002 versus 40.7 $\mu g\ L^{-1}$ in 1975). Zebra mussels were first observed in the lake during the summer of 1991, and their lakewide mean densities reached as high as 44,000 mussels m^{-2} with an average shell length of 2.75 mm in 1992 (Mellina and others 1995; Idrisi and others 2001). In 1997, densities ranged from a mean of approximately 45,000 mussels m^{-2} on rock and cobble areas to approximately 10,000 m^{-2} on sand to approximately 3000 m^{-2} on shallow mud areas, with the average shell length being 8.72 mm (Idrisi and others 2001; Mayer and others 2002). In addition, the mean wet weight of zebra mussels increased from 343 to 1560 g m^{-2} between 1992 and 1997 (Idrisi and others 2001).

Secchi Depth, Total Phosphorus, and Suitable Macrophyte Area

Since 1975, Secchi depth (as an index of water clarity) has been measured at five standard stations on a weekly basis from April to November (Figure 2). Light attenuation coefficients were calculated from irradiance measurements throughout the water column to estimate lake area suitable for macrophyte beds, defined as the area from the shoreline to the bottom depth receiving 1% surface light (Wetzel 1983). In situ water column irradiance has been measured since 1993 with a LI-COR 4π sensor coupled to a LI-COR 1000 data logger at 0.5-m intervals from the surface to the bottom at the five stations; above-surface irradiance was measured with a LI-COR 2π sensor attached to the same data logger. The depth receiving 1% surface light ($Z_{0.01}$) was calculated from the definition of light attenuation (Wetzel 1983):

$$I_Z = I_O \times e^{-KZ} \tag{1}$$

where K is light attenuation coefficient, I_0 is light incidence at surface, and I_z is light incidence at depth Z.

Measurements of K were available only for 1993 to 2000, so we estimated $Z_{0.01}$ for the entire study period (1975–2002) based on the relation between K and Secchi depth from 1993 to 2000:

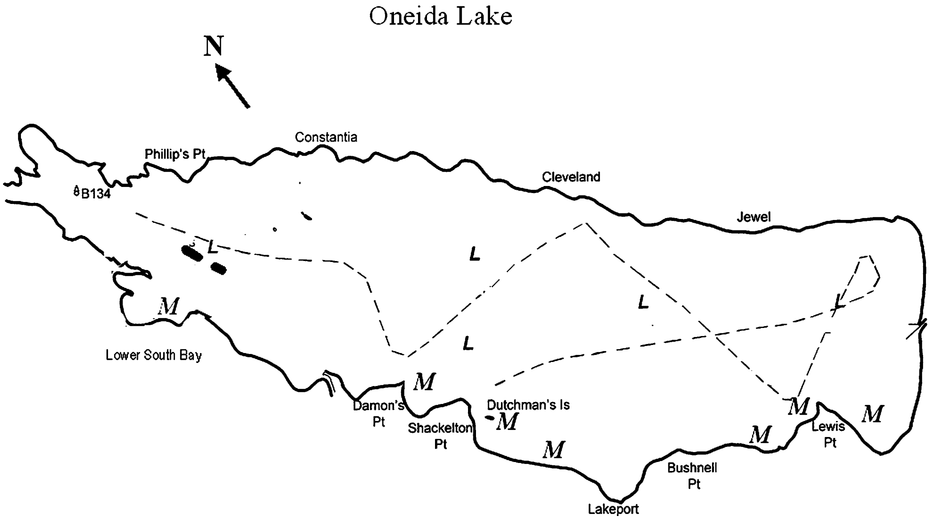

Figure 2. Sampling stations on Oneida Lake. The dashed line indicates transects across Oneida Lake for hydroacoustic survey in 1999. Transects varied slightly in each year during surveys. L, limnology; M, submerged macrophytes.

$$\mathrm{Log}_{10}\,(\mathrm{K}) = -0.520\,\mathrm{Log}_{10}(\text{Secchi depth}) + 0.049\ (R^2 = 0.638, n = 774) \tag{2}$$

From the Secchi depth data, we estimated light attenuation coefficients from Eq. (2) and the depth receiving 1% surface light according to Eq. (1). Finally, the potential areal cover of submerged macrophytes was estimated from an area-depth relationship for Oneida Lake (Greeson 1971):

$$\text{Area} = -0.094\,\mathrm{Z}^3 + 2.126\,Z^2 + 2.920\,Z + 2.7 (0 < Z \leq 16)\ (R^2 = 0.998) \tag{3}$$

where Z is the depth in Oneida Lake in m and Area is the area of the lake (in km^2) with bottom depth shallower than Z.

Total phosphorus (TP) (as an index of lake trophic conditions) has been estimated using the method of Menzel and Corwin (1965). In our study, TP and Secchi depth were averaged from April to September of each year, the months of particular importance for the growth of submerged macrophytes (Wetzel 1983).

Submerged Macrophytes

Field surveys of submerged macrophytes were conducted along the southern shore of Oneida Lake using SCUBA or skin divers in 1976, 1977, 1980, 1995, 1999, and 2002. Typically, the same five to seven sites were surveyed at one to four different depths (Figure 2). In 1976, 1977, and 1980, a single 1-m^2 quadrat was harvested at each depth along the transect, whereas in 1995, 1999, and 2002, three to four quadrats (0.25-m^2) were harvested at each depth. Only macrophytes rooted in the quadrat were harvested. All plants were identified to genus or species.

Between 1976 and 1999, we recorded maximum depth of plant colonization (Z_c) as the depth of the final plant at the edge of a macrophyte bed. Diver surveys completed during 2002 were conducted at eight sites at shallow depth only (0.5 m and 1 m); therefore we cannot estimate maximum depth of plant colonization by this method. However, these data were included in determining species composition, frequency of occurrence, and species richness because we did not find differences in species composition at different depth in the previous five surveys.

Species abundance was measured from all six diver surveys. Frequency of occurrence was calculated as the proportion of samples taken that contained a given species (Skubbina and others 1995). Diversity was estimated by the Simpson's index (D) and species evenness (E) using standard calculations (Begon and others 1990).

Chambers and Kalff (1985) identified a Secchi depth to Z_c relationship for angiosperm macrophytes in freshwater lakes without zebra mussels. To test whether zebra mussels have altered the expected Secchi depth to Z_c relationship in Oneida Lake, we compared observations from Oneida Lake with those presented by Chambers and Kalff (1985) with an analysis of covariance (ANCOVA) ($\alpha = 0.05$). Observations on Z_c of macrophytes in Oneida Lake were from hydroacoustic surveys (1995–2002). In 1995–2000, Oneida Lake was surveyed using a 70-kHz split-beam echo sounder (Simrad EY 500; full half-power, beam angle 11.1°, pulse length 0.2 ms, pulse rate 0.3–1 pings s^{-1}) along roughly north-south transects spaced from the east to the west ends of the lake (Figure 2).

Transect location varied slightly between years but still afforded complete coverage of the lake. Acoustic data were recorded directly to a laptop computer in the field and analyzed with EP500 software (ver. 5.2; Simrad, Horten, Norway). In 2001 and 2002, the surveys used a 420-kHz single-beam digital echo sounder (DT-4000) (BioSonics; transducer beam angle 6°, pulse length 0.1 ms, pulse rate 1 pings s^{-1}) and the analysis was performed with Visual Analyzer software (ver. 4.0.2; BioSonics, Seattle, WA, USA). Plant beds were readily identifiable on the echograms in shallow areas because plant echoes extend distinctly from the bottom toward the surface and are elongated (see, for example, Thomas and others 1990). Identification of echoes as plants was confirmed with underwater video observations. Maximum depths of plant beds were identified as the depth of the deepest plant-type echo continuous with the bed. Observations of rare plantlike echoes in deep water were not considered because they may represent plant material that was uprooted and transported there. Maximum depth was determined using transects collected in June to September during each year.

Statistical Analysis

For Secchi depth, TP, depth receiving 1% surface light, and suitable macrophyte habitat, as well as macrophyte species richness, evenness, and frequency of occurrence, we divided the data set into preinvasion (1975–1991) and postinvasion years (1992–2002) and used a standard *t*-test to compare the periods after testing for normality and autocorrelation between years. When necessary, we transformed the data to decrease heteroscedasticity. As a complement, we calculated all the power of one-tailed tests at $\alpha = 0.05$ (Zar 1999). We used a GLM procedure to test for the effect of zebra mussel and TP on Secchi depth (correlation and ANCOVA) and the effect of the zebra mussel and Secchi depth on macrophyte maximum colonization (ANCOVA) by using data in Chambers and Kalff (1985) and our data on macrophyte depth distribution in Oneida Lake. Regression analysis was conducted after the analysis of residuals of error variances. If necessary, weighting methods were used for the regression. All analyses were done using the GLM procedure of SAS 9.0 (SAS Institute, Cary, NC, USA).

RESULTS

Secchi Depth and TP

Water clarity (April–September) increased during the period of 1975–2002 (Figure 3). Specifically, Secchi depth in Oneida Lake increased from 2.6 ± 0.1 m (mean ± 1 SE) before zebra mussel invasion to 3.5 ± 0.2 m after the establishment ($df = 26$, $t = 5.20$, $P < 0.001$, N_1 =1 7, $N_2 = 11$, and Power = 100%). The post-mussel period was characterized by a large initial increase in Secchi depth, from 2.7 m in 1992 to 4.4 m in 1995, followed by a slight decrease to 3.6 m in 2002. Despite the decrease seen after 1998, the post-mussel average annual Secchi depth has remained higher during all but 2 years of the preinvasion period.

The mean April–September TP level in the lake declined during the period of 1975–2002 (Figure 3). Mean TP decreased from approximately 41 μg L^{-1} in 1975 to approximately 25 μg L^{-1} in 2002, with a maximum of 59.4 μg L^{-1} in 1986 and a minimum of 14.2 μg L^{-1} in 1997. The mean TP concentration decreased from 35.0 ± 2.8 μg L^{-1} before the invasion to 19.8 ± 1.6 μg.L^{-1} after the establishment of a large zebra mussel population in 1992, and this was significantly lower than the preinvasion period ($df = 26$, $t = 4.19$, $P < 0.001$, $N_1 = 17$, $N_2 = 11$, and Power = 99.9%). This decline in TP has been directly attributed to point and nonpoint source nutrient controls in the Oneida Lake watershed mandated by the Great Lakes Water Quality Agreement and specifically represented by a large decline after 1986 (Idrisi and others 2001). Concentrations of TP after the invasion in 1992 were approximately 20 μg L^{-1}, and were similar to those from the 3 years before the invasion (that is, 1989 to 1991) (Figure 3).

There was no correlation between TP and Secchi depth either before the invasion ($df = 16$, $\rho = -0.217$, $P = 0.358$) or after the invasion ($df = 10$, $\rho = 0.199$, $P = 0.547$) (Figure 4). Analysis of Secchi depth as a function of TP and zebra mussel presence/absence showed no effect of TP on water clarity ($P = 0.606$, ANCOVA), but a strong and significant effect of zebra mussel presence ($P = 0.001$, ANCOVA).

Suitable Habitat of Submerged Macrophytes

The relationship between Secchi depth and light extinction (Eq. [2]) enabled us to calculate the depth of 1% surface light for the entire data series. This depth increased from 6.7 ± 0.13 m before zebra mussels to 7.8 ± 0.17 m after the invasion ($df = 26$, $t = 5.20$, $P < 0.001$, $N_1 = 17$, $N_2 = 11$, and Power = 100%, Figure 5). The potential habitat area suitable for submerged macrophytes, as calculated from the hypsographic curve of Oneida Lake (Eq. [3]), and the depth receiving 1% surface

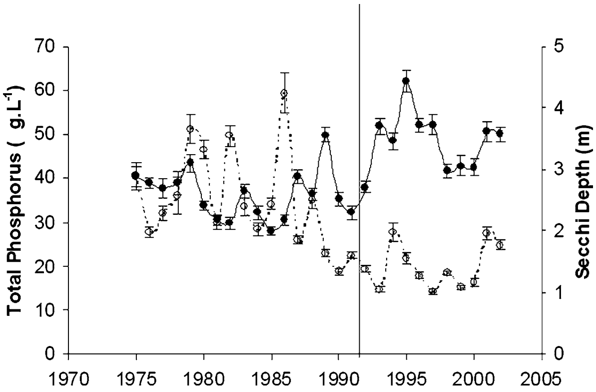

Figure 3. Long-term trends of mean (April–September) (± 1 SE) concentrations of total phosphorus (TP) and Secchi depth (SD) from 1975–2002 in Oneida Lake, New York. Open circles denote general trend of TP; solid circles denote SD changes. The vertical line indicates the time of zebra mussel invasion.

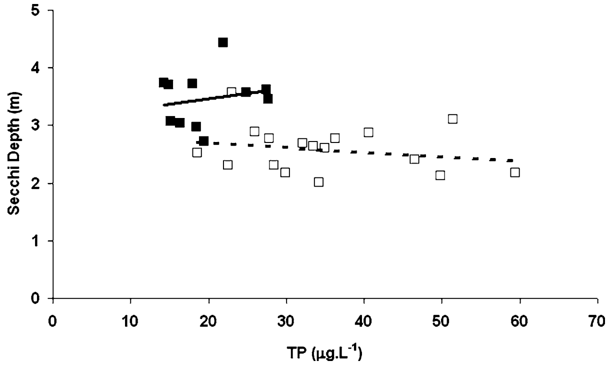

Figure 4. Correlation between total phosphorus (TP) and Secchi depth (SD) before and after zebra mussel invasion in Oneida Lake. Open squares and dashed line denote the regression of TP and SD prior to invasion; solid squares and solid line denote the regression after invasion. The correlation between TP and SD prior to invasion is $\rho = -0.217$ ($df = 16$, $P = 0.358$) and that after the invasion is $\rho = 0.199$ ($df = 10$, $P = 0.547$).

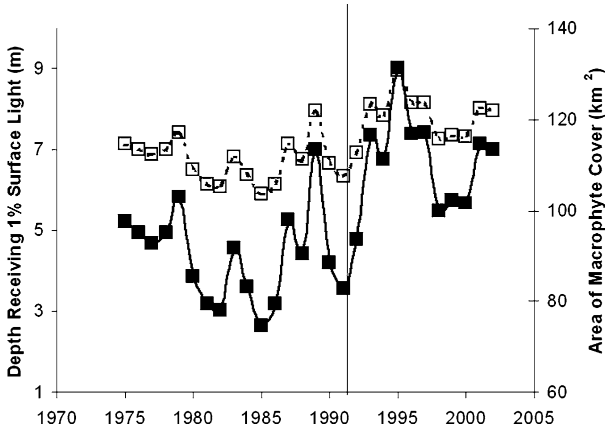

Figure 5. Changes in depth receiving 1% of surface light and potential suitable submerged macrophyte cover in Oneida Lake from 1975 to 2002. Open squares denote general trend of depth receiving 1% surface light; solid squares denote potential macrophyte cover. The vertical line indicates the time of zebra mussel invasion.

light increased from 90 ± 3 km^2 prior to zebra mussels to 111 ± 3 km^2 (that is, a 23% increase) after the invasion ($df = 26$, $t = 5.22$, $P < 0.001$, $N_1 = 17$, $N_2 = 11$, and Power = 100%).

Macrophyte Maximum Depth and Species Composition

Diver surveys in 1976, 1977, 1980, 1995, 1999, and 2002 and the hydroacoustic surveys from 1995 to 2002 revealed that the maximum depth of colonization (Z_c) increased through the entire study period (Figure 6). Specifically, Z_c averaged 3.0 ± 0.5 m before (1976, 1977, and 1980) to 5.1 ± 0.8 m after invasion (1995–2002). This represents a 70% increase in maximum depth between the pre–and post–zebra mussel periods ($df = 11$, $t = 4.67$, $P = 0.001$, $N_1 = 3$, $N_2 = 10$, and Power = 99.1%). The expansion of macrophyte distribution was concurrent with an increase in plant diversity (Table 1) and improvements in water clarity between 1975 and 2002 (Figure 3). During this time, the Simpson's diversity index increased significantly from 5.2 to 8.2 ($df = 4$, $t = 3.87$, $P = 0.018$, $N_1 = 3$, $N_2 = 3$, and Power = 98.7%), and species richness increased from eight to 12 macrophyte species after the zebra mussel invasion. Seven species were identified during each survey before the zebra mussel invasion and 10 species were present in each year after the invasion ($df = 4$, $t = 5.0$, $P = 0.008$, $N_1 = 3$, $N_2 = 3$, and Power = 100%). However, species evenness was low during both periods and did not increase significantly (0.78 to 0.81; $df = 4$, $t = 0.59$, $P = 0.590$, $N_1 = 3$, $N_2 = 3$, and Power = 13.3%).

When comparing the two time periods, we observed that the submerged macrophytes occurred more frequently in general and that between 1975 and 2002 the species composition shifted from shade-tolerant species to species that can tolerate a range of light conditions (Table 1). Before the arrival of the zebra mussels, there were six dominant macrophyte species that had a frequency of occurrence of greater than 38%. These six species were *Myriopyllum spicatum* (nonnative), *Potomogeton*

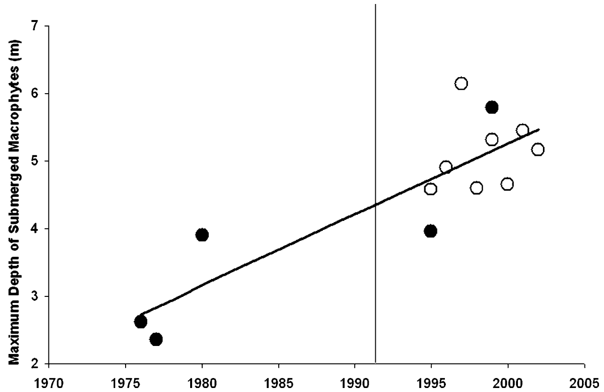

Figure 6. Submerged macrophyte maximum depth of colonization from 1975 to 2002 in Oneida Lake, New York, from SCUBA diver surveys and hydroacoustic surveys. The regression is $y = 0.105x - 204.65$ ($R^2 = 0.741$), where x is the year. This regression is significant ($P < 0.001$, ANOVA); no weighting methods were used because the analysis of the residuals showed roughly homogenous error variances. Solid circles denote data of diver surveys; open circles denote hydroacoustic data for Oneida Lake. The vertical line indicates the time of zebra mussel invasion.

zosteriformis, *Elodea canadensis*, *Ceratophyllum demersum*, *Zosterella dubia*, and *Vallisneria americana*. All but *P. zosteriformis* can tolerate low-light conditions (Stodola 1967). Among them, *Z. dubia* and *V. americana* increased significantly in frequency of occurrence after the zebra mussel invasion (the first species by 127.5%; $t_z = 3.5$, $P_z = 0.027$, $\text{Power}_z = 96.6\%$ and the second by 92.1%; $t_v = 3.1$, $P_v = 0.037$, $\text{Power}_v = 93.3\%$, $df = 4$, $N_1 = 3$, and $N_2 = 3$) whereas *P. zosteriformis* decreased significantly (by 92%; $df = 4$, $t = 5.87$, $P = 0.004$, $N_1 = 3$, $N_2 = 3$, and Power = 100%). The other three species showed no significant change. Two species that were rare before the mussel invasion, *Najas flexilis* and *P. richardsonii*, became dominant, with a pronounced increase in their frequency of occurrence ($t_n = 8.38$, $P_n = 0.001$, $\text{Power}_n = 100\%$, $t_p = 3.04$, $P_p = 0.039$, $\text{Power}_p = 92.2$, $df = 4$, $N_1 = 3$, and $N_2 = 3$) (Table 1). The four new species observed after the zebra mussel invasion included *Ranunculus trichophyllus* and three *Potamogeton* species, among them the nonnative *P. crispus*. Over this time, *P. pusillus* became a dominant species whereas *R. richophyllus* remains rare in the lake.

Changes in the depth distribution of submerged macrophytes were also observed during the study period (Table 2). Specifically, when the two different periods were compared, species richness increased significantly at each depth: three increased at shallow water (less than 2 m), five increased at the intermediate depth (2–4 m), and 10 increased at deep water (greater than 4 m). There was not much difference in species composition at shallow, median, and deep water either before or after the invasion. However, two additional species were present at the intermediate depth in the postinvasion years.

Response of Submerged Macrophytes to Light in Other Freshwater Ecosystems

Chambers and Kalff (1985) reported a range of 0.01 to 18 m for maximum depth of macrophytes with a corresponding range of 0.07 to 25 m for Secchi depth for lakes free of dreissenid mussels. The regression relationship is $y = 1.51x + 1.46$ ($R^2 = 0.60$, $P < 0.001$), where y is the square root of maximum macrophyte depth and x is $\log_{10}$(Secchi depth). In Oneida Lake, after the mussel invasion, we observed a range of 4.6 to 6.2 m for maximum depth of colonization of macrophytes from hydroacoustic data for 1995–2002 and 4.0 and 5.8 m for the 1995 and 1999 diver surveys, respectively, with a corresponding range of 2.8 to 4.4 m for Secchi depth for the period. These data from Oneida Lake fall on the regression line of other North American lakes. The analysis of ANCOVA showed that Secchi depth was significantly related to macrophyte depth (square root transformed, $P < 0.001$), but there was no significant difference between our post-zebra mussel Oneida data and the other lakes ($P = 0.642$).

Discussion

One of the most prominent ecosystem-engineering effects of zebra mussels in rivers and lakes is an increase in water clarity. In this study we have demonstrated that this habitat alteration by zebra mussels had systemwide effects on the diversity and frequency of occurrence of submerged macrophyte in a large eutrophic/mesotrophic lake. Our data suggest that the increase in water clarity in Oneida Lake from 1975 to 2002 was primarily associated with zebra mussels rather than reduced nutrient levels. Mayer and others (2002) reached a similar conclusion based on an intervention analysis with a shorter data series. Further, the observation of stable TP concentration after 1989 supports the hypothesis that the increase in Secchi depth is due to a zebra mussel effect rather than additional nutrient abatement (Idrisi and others 2001). Thus, the zebra mussel invasion offers the simplest explanation for these changes (see also Idrisi and others 2001; Mayer and others 2002).

Table 1. Submerged Macrophyte Species Diversity and the Frequency of Occurrence (%)

Submerged Species	Pre invasion			Post invasion			Mean (Pre-)	Mean (Post-)	*P* value	Power (%) ($\alpha = 0.05$)
	1976	1977	1980	1995	1999	2002				
Ceratophyllum demersum	70	25	50	43	91	50	48	61	0.548	16.1
Elodea Canadensis	20	75	100	18	82	63	65	54	0.743	10.0
Myriophyllum spicatum	90	92	83	71	86	63	88	73	0.108	66.1
Najas flexilis	10	0	0	76	91	63	3.3	77	0.001[b]	78.2
Potamogeton crispus	0	0	0	4.8	50	13	0	23	0.179	100
Potamogeton pectinatus	0	0	0	29	0	50	0	26	0.143	50.3
Potamogeton pusillus	0	0	0	0	82	38	0	40	0.167	55.9
Potamogeton richardsonii	0	0	8	24	32	63	2.7	40	0.039[a]	51.8
Potamogeton zosteriformis	60	92	67	0	18	0	73	6.0	0.004[b]	92.2
Ranunculus trichophyllus	0	0	0	0	4.5	0	0	1.5	0.374	100
Vallisneria americana	40	50	25	57	86	75	38	73	0.037[a]	25.9
Zosterella dubia	20	33	67	86	100	88	40	91	0.025[a]	93.3
Simpson's Diversity Index	5.03	5.03	5.51	6.66	8.90	8.93	5.19	8.17	0.018[a]	98.7
Evenness	0.72	0.84	0.79	0.74	0.81	0.89	0.78	0.81	0.590	13.3

Simpson's diversity index and evenness of submerged macrophyte species are statistically significant between pre- and postinvasion years at $\alpha = 0.05$.
Power was calculated at $\alpha = 0.05$ based on a one-tailed test.
There was one unidentified Potamogeton species in the 1995 survey and three in the 2002 survey. Because these unknown species were very low in abundance, we did not include them in the table.
[a] *Significant at $\alpha = 0.05$.*
[b] *significant at level $\alpha = 0.01$.*

Mussels increase water clarity by removing particles from the water column and by stabilizing sediments from resuspension (both dead and live mussels on the bottom) and thereby promote habitat change in multiple ways.

After the increase in the water clarity of Oneida Lake, submerged macrophytes increased in diversity and frequency of occurrence and shifted composition from shade-tolerant species to species that can live at a wider variety of light levels (Table 1). Our comparisons of the maximum plant depth and Secchi depth relationship in Oneida Lake with the regression based on data drawn from the literature (Chambers and Kalff 1985) suggest that the increase in light penetration is a sufficient explanation for the observed macrophyte range expansion, consistent with findings from other studies (for example, Genkai-Kato and Carpenter 2005). Similarly, macrophytes grew deeper and were more abundant after dreissenid mussel invasions in the Saginaw Bay of Lake Huron, the Bay of Quinte of Lake Ontario, and Lake Veluwe in Europe (Skubinna and others 1995; Bailey and others 1999; Chu and others 2004; Lammens and others 2004). We believe that a major effect of dreissenid mussels in lakes is the indirect effect of increased lake-wide water clarity on submerged macrophytes. This is a clear case of ecological engineering (Jones and others 1994, 1997).

Greater maximum depth of colonization and more suitable growing area following increase in water clarity can promote the growth of both low-light–tolerant species in deep areas and high-light–tolerant species in shallow areas. Conversely, only low-light–tolerant macrophyte species are likely to grow well in turbid water. In our study, five of the six dominant species prior to the zebra mussel invasion (except *P. zosteriformis*) tolerate low-light conditions (Stodola 1967) and are therefore likely to be successful in turbid lakes or deep water. However, after the zebra mussel invasion, four new, high-light–tolerant species (*R. trichophyllus*, *P. crispus*, *P. pectinatus*, and *P. pusillus*) occurred more frequently across a range of depths (Table 2). The trend for more species to be found at the intermediate depth in the postinvasion years may be due to the susceptibility of the new species to the strong waves in the near shore (Hudon and others 2000; Riis and Hawes 2003). The presence of these high-light–tolerant species suggests that changes in diversity have occurred directly because of the increase in light, and not indirectly due to the increased area available for growth.

Two exceptions to the general trend of increase in frequency of occurrence of submerged macrophytes species were declines in *M. spicatum* and *P. zosteriformis*. The trend of decline in *M. spicatum* may be due to the attachment of zebra mussel larvae, because their shells inhibit the growth of

Table 2. Comparison of Submerged Macrophytes Species at Different Depths between Pre- and Post-invasion Years

	Less than 2 m		2 – 4 m		Greater than 4 m	
Submerged Macrophytes	**Pre-**	**Post-**	**Pre-**	**Post-**	**Pre-**	**Post-**
Ceratophyllum demersum	×	×	×	×		×
Elodea Canadensis	×	×	×	×		×
Myriophyllum spicatum	×	×	×	×		×
Najas flexilis	×	×		×		×
Potamogeton crispus		×		×		×
Potamogeton pectinatus		×		×		
Potamogeton pusillus		×		×		×
Potamogeton richardsonii		×	×	×		×
Potamogeton zosteriformis	×		×	×		×
Ranunculus trichophyllus				×		
Vallisneria Americana	×	×	×	×		×
Zosteralla dubia	×	×	×	×		×

Pre-, before zebra mussel invasion; Post-,after zebra mussel invasion.
Unidentified Potamogeton species were not included due to low abundance.
×, species present in lake.

the plant by shading them from the light (B. Zhu unpublished) and weighing down the macrophytes (Lewandowski 1982; Buchan and Padilla 2000). Other species did not suffer from zebra mussel attachment because the larvae densities were lower on these plants (Lewandowski and Ozimek 1997) or the positions of attachment were different (that is, leaf or stem, top or bottom) (B. Zhu unpublished). In addition, the presence of a native weevil (*Euhrychiopsis lecontei*) and a moth (*Acentria ephemerella*) may also have contributed to the decline in this nonnative species, because these organisms feed on the growing tips of *M. spicatum* (Sheldon and Creed 1995; Johnson and others 2000). The reason for the decline in *P. zosteriformis* is not known, but interspecific competition with other macrophyte species may play an important role for these co-occurring species when water clarity and light penetration increase (Van den Berg and others 1998, 2003).

The presence of submerged macrophytes is an important feature of the near-shore zone, and an increase in macrophytes can improve the physical, chemical and biological environment in these ecosystems. For example, Caraco and others (2000) suggested that increased macrophyte photosynthesis due to greater light penetration after zebra mussel invasion might have moderated the decline of dissolved oxygen as a result of zebra mussel respiration. The physical structure provided by macrophytes is required by many zooplankton, invertebrates, and fish species for feeding, or as spawning or nursery habitats. Eggs of the copepod *Diaptomus sanguineus* were found on macrophytes for up to 5 months before either hatching or sinking to the sediment (Caceres and Hairston 1998), and benthic invertebrate densities were observed to increase significantly after the increase of macrophytes due to the zebra mussel invasion in Oneida Lake (Mayer and others 2002). Interestingly, all the macrophyte species found in Oneida Lake are useful sources of food and habitat for invertebrates, and vertebrates, from fishes to birds (Stodola 1967; Schindler and Scheuerell 2002). With few exceptions, most of the fish species present in Oneida Lake spend at least part of their life cycle in the near-shore habitat, often during the vulnerable early life stages (Keast 1980; Wetzel 1983). By extension, an increase in the presence of submerged macrophytes may be followed by an increase in the survival of individuals at early life stages (Mayer and others 2000) and increased recruitment of some littoral fish species (Strayer and others 2004).

Higher macrophyte diversity has been affected by the introduction of new species, including nonnative species such as *P. crispus*, after zebra mussel invasion. This may have important implications for ecosystem management. Although an increase in macrophytes seems to be beneficial for zooplankton, macroinvertebrates, and fish because it expands the supply of food and other resources, the introduction of other nonnative species may have unanticipated consequences for the ecosystem. Nonnative species may replace native species that have been lost due to biological or physical stressors (for example, cultural eutrophication) and serve to increase local diversity. But they may also replace endemic native species, such that their establishment would inevitably reduce diversity among habitats and regions (see, for example, Rahel 2000).

Patterns of increased diversity of macrophytes, similar to what we observed in Oneida Lake after zebra mussel invasion, have occurred in other lakes when pelagic primary production has declined (Correll 1998; Murphy 2002). The trend of increased submerged macrophyte species richness confirms the idea that lakes support a greater distribution and diversity in a mesotrophic state than they do in a eutrophic state (Scheffer and others 2001; Scheffer and Carpenter 2003). By extension, the current distribution of macrophytes in Oneida Lake is likely comparable to the conditions that were extant before cultural eutrophication reduced water clarity (Mills and others 1978). Thus a modification of habitat (ecosystem engineering) can affect ecosystem structure and function in a manner and at a level similar to changes in trophic status. Changing an important physical variable such as water clarity will increase the importance of benthic production over pelagic production in the food web, thereby representing an overall alteration of ecosystem function, a process we refer to as ‘‘benthification’’ (Mills and others 2003).

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