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Zebra Mussel (*Dreissena polymorpha*) Populations in the Seneca River, New York: Impact on Oxygen Resources†

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The character and cause of a major depletion in dissolved oxygen (DO) observed in a 16-km reach of the Seneca River, New York, in the summer of 1993 was evaluated. The decline in oxygen concentrations was attributed to a recent severe infestation by the invading zebra mussel. Zebra mussel densities of 33 000–61 000 individuals m^{-2} were found in a 1.4-km section, across which an average (n = 3) depletion in DO concentration of about 1.7 mg L^{-1} was observed. The estimated areal respiration rate for the zebra mussel population in this section (34 g m^{-2} d^{-1}) nearly matched the areal sink calculated independently from DO budget calculations (44 g m^{-2} d^{-1}). The zebra mussels also caused substantial decreases in phytoplankton biomass and increases in water clarity over the study reach. Loss in waste assimilative capacity is expected to occur in other alkaline hardwater rivers and streams with rock substrate in North America as the zebra mussel invasion spreads.

The zebra mussel (*Dreissena polymorpha* Pallas and *D. bugensis*) is a small bivalve (Mollusca: Bivalvia) native to southern Russia. It was introduced to the Great Lakes in 1985 or 1986, probably via water ballast from a foreign ship (*1, 2*) and has spread rapidly through much of eastern North America. By the year 2000, it is expected to have colonized all North America waters that meet its ecological requirements (*1*). The rapid expansion of the zebra mussel range in North America reflects its high reproductive and dispersal potential (*3*), broad physiological adaptive capabilities, and the absence of natural predators and parasites (*1*). Zebra mussels prefer relatively hard (Ca >0.7 mmol L^{-1}), alkaline (pH >7.3) waters but inhabit waters below these optimum levels (*1, 4*). Zebra mussels colonize hard substrates on which they may develop extremely dense populations, e.g., >100 000 m^{-2} (*2*). The mussel attaches by numerous byssal threads. The environmental (*1–5*) and economic (*1*) impacts of the zebra mussel invasion of North America have been the subjects of a great deal of speculation, extrapolation, and, in some cases, documentation.

The zebra mussel is an extremely efficient filter (suspension) feeder; particle retention has been reported to be 100% for particles greater than 1 μm (*6*). Particles not selected for consumption are embedded in mucus in the mussels and discharged as psuedofeces. The removal of phytoplankton and detritus by filter feeding zebra mussels has been credited with increasing water transparency in lakes in North America as well as in Europe (*1, 6–8*). However, the removal of phytoplankton from the pelagic zone reduces the energy available to pelagic food webs (*1, 3, 5*) and may negatively impact many of the commercially important fisheries (*1*). Though it has been acknowledged that zebra mussel populations can influence basic features of water chemistry (*1*), the impact of zebra mussels on the dissolved oxygen resources of invaded systems has yet to be demonstrated. Here, we document the degradation of the oxygen resources of a large river brought about by the recent invasion of zebra mussels.

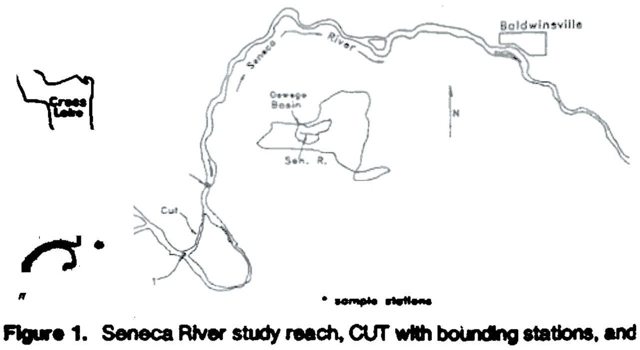

Figure 1. Seneca River study reach, CUT with bounding stations, and the Oswego River Basin.

Methods

Study Site. The Seneca River drains 9000 km^2 of the Finger Lakes region of New York, the eastern 70% of the Oswego River Basin, to Lake Ontario (Figure 1). The natural flow and mass transport characteristics of the river have been greatly altered (e.g., channelized, dams, and locks) to support navigation (part of the Barge Canal System) and hydroelectric power generation. A 16-km reach of the Seneca River, extending from Cross Lake to Baldwinsville, NY, was the focus of this study (Figure 1). The average annual flow at Baldwinsville reported by the U.S. Geological Survey for the 1951–1991 period was 96.3 m^3 s^{-1}. No significant tributaries or waste discharges enter the study reach. The depth of the channel in the study reach is 3.5–4.0 m. The reaeration capacity of the river is very low, particularly during summer low flow periods, because of the limited turbulence of the system (*9*). The State Ditch Cut (CUT), located 1.3 km downstream of Cross Lake (Figure 1), is a 1.4 km long channel, dug in 1915 as part of the construction of the Barge Canal. The channel was cut from bedrock; the walls are nearly vertical, and the bottom substrate is "cobble" size rock. The channel carries more than 90% of the river flow, as the natural "horseshoe" river course (Figure 1) is largely silted-in (unpublished flow measurements from the United States Geologic Survey).

Cross Lake (surface area of 9.0 km^2, volume of 50.8 × 10^6 m^3, mean depth of 5.5 m) is a rapid flushing (~50 times yr^{-1}), dimictic, alkaline, hardwater, hypereutrophic

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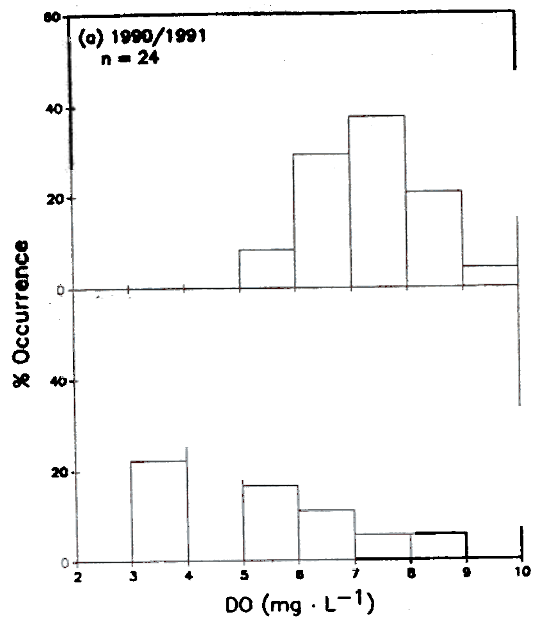

Figure 2. Comparison of distributions of summertime DO measurements for the Seneca River at Baldwinsville: (a) 1990–1991 and (b) 1993.

lake (*10, 11*). Outflow from the lake is enriched in inorganic particles as well as phytoplankton for most of the spring to fall period (*10, 11*).

Water quality monitoring during the summer of 1993 detected dramatic degradation in the oxygen resources of the Seneca River since 1990–1991 at a site just downstream of Baldwinsville (Figure 2). The median DO concentration for the population of measurements at this site in 1993 was 4.5 mg L^{-1} (Figure 2a), more than 2.5 mg L^{-1} less than the median concentration observed in 1990–1991 (Figure 2b). Field surveys of water quality and sediment type were initiated to determine the origin of oxygen depletion. Preliminary surveys, extending to the upstream (western) boundary of the basin (Figure 1), indicated the oxygen depletion was localized within the Cross Lake to Baldwinsville reach. No "unreported" discharges or sediments with high oxygen demands were discovered during the surveys. The oxygen depletion appeared to be associated with the localized occurrence of zebra mussels.

Water Quality Monitoring. Longitudinal profiles of DO, temperature, Secchi disk transparency, and chlorophyll were collected over the Cross Lake to Baldwinsville reach on five occasions during August 1993. Secchi disk transparency and chlorophyll together serve as an indicator of zebra mussel activity (*1, 3, 5–8*). Dissolved oxygen was measured *in situ* with a Hydrolab Surveyor instrument, calibrated according to the manufacturer's instructions and checked by Winkler titration (*12*). Secchi disk transparency was measured with a 20 cm diameter black and white quadrant disk. Water for chlorophyll determinations (*13*) was collected by a submersible pump from depths of 1 and 3 m from each longitudinal site. Vertical profiles of DO (1-m interval) were necessary to establish oxygen content because of the common occurrence of DO stratification associated with the limited turbulence of the system and oxygen demand localized at the river bottom. Monitoring was completed within 2–3 h in the interval of 0900 to 1500.

Biological Survey. Qualitative observations of the river bottom and associated benthic communities were made by a team of divers at sites spaced at ~2 km intervals downstream of the CUT. Quantitative sampling was restricted to three sites in the CUT. These samples were collected from upstream, downstream, and mid-regions of the CUT by use of a modified Hess sampler. Three replicate sample locations were selected at each of the three sites. Divers blindly positioned the sampler over the substrate (visibility was near zero), removed all loose substrate from the square foot area of the sampler, and transported the sample to the surface in a sieve bucket (0.5-mm mesh). All substrata and organisms were placed in plastic bags and stored on ice for transport to the laboratory.

At the laboratory, all benthic organisms were separated from the substrata. With the exception of a few gastropods, some of which were colonized by zebra mussels, all organisms in the samples were zebra mussels, *Dreissena polymorpha*. All zebra mussels were sorted by 5-mm size intervals (≤25 mm in length) and counted. Counts were converted to biomass (wet weight) and dry weight estimates by use of published empirical shell length: biomass relationships (*14, 15*)

$$W_i = 0.071 \times 10^{-3} L_i^{2.80} \tag{1}$$

$$W_{i/d} = 0.15\, W_i \tag{2}$$

where L_i (mm), W_i (g), and $W_{i/d}$ (g) are the length, wet weight, and dry weight of an individual zebra mussel, i. Individual filtration rates (F_i; m^3 individual^{-1} d^{-1}) were estimated according to the following expression (*6*):

$$F_i = 1.23 \times 10^{-4}\, W_{i/d}^{0.608} \tag{3}$$

Areal rates were calculated from the count data by summing contributions from the five size classes.

Individual respiration rates (R_i; g O_2 individual^{-1} d^{-1}) were estimated using expressions and coefficient values incorporated by Schneider (*5*) in his bioenergetics model for the zebra mussel. The value of R_i was calculated as the sum of estimates for standard respiration (basic organism maintenance, $R_{i/s}$) and active respiration (associated with feeding, $R_{i/a}$). The respective expressions include factors accommodating the temperature (assumed 25 °C) dependence of respiration, the relationship between body weight and respiration, and the effect of consumption on respiration. The simplified expressions for the two components of respiration, incorporating Schneider's (*5*) recommended coefficient values, adopted here are

$$R_{i/s} = 2.6 \times 10^{-3}\, W_i^{0.75} \tag{4}$$

and,

$$R_{i/a} = 1.6 \times 10^{-3}\, W_i^{0.61} \tag{5}$$

where $R_{i/s}$ and $R_{i/a}$ have units of g O_2 individual^{-1} d^{-1}. Areal respiration rates (R_s, R_a, and R; g m^2 d^{-1}) were calculated from the count data by summing contributions from five size classes. Substantial uncertainty accompanies the application of these expressions because of the uncertainty in supporting relationships developed from the literature (*5*). Perhaps the greatest source of uncertainty is the fraction of consumed food that is utilized in active respiration to support the cost of water transport and the physiological cost of digestive processes. Equation 5 assumes that 28.5% of consumption is diverted to active

Table 1. Features of Oxygen Budget Calculation for CUT Area of Seneca River ... 93

feature		source/reference
(1) river section for budget calculations		Figure 1
(2) av flow (n = 3; 2.18, 1.84, and 1.76 × 10^6 m^3 d^{-1})		USGS, Baldwinsville gauge
(3) av DO depletion across section (n = 3; 1.9, 1.9, and 1.3 n		Figure 3a, d, and e
(4) av DO depletion across section mass		product of items 2 and 3
(5) river bottom area over section		navigation charts
(6) av areal DO depletion rate over section		item 4 divided by item 5

Same as Canale's Analysis

respiration (*5*). Schneider (*5*) acknowledges the selection of this value was somewhat arbitrary, reflecting conditions intermediate between no cost of feeding and the respiratory cost as determined by Bayne and Scullard (*16*) for a marine mussel of 55%. Further, the estimate of the active component only considers the amount of material ingested, rather than the amount of material filtered (*5*). Thus, the active component of respiration may be expected to be greater than predicted by eq 5 in systems with high concentrations of non-food (e.g., inorganic) particles.

Results and Discussion

Water Quality. The oxygen profiles collected for the Cross Lake to Baldwinsville reach are presented in Figure 3. Each point is the arithmetic average of the vertical profile measurements. Strong DO depletions downstream of Cross Lake, with little subsequent recovery further downstream, were observed in all surveys (Figure 3). The greatest DO depletion with stream length was observed through the CUT. The New York standard of a minimum DO concentration within a day of 4 mg L^{-1} was violated for several kilometers on the day of the first survey (Figure 3a). Diurnal monitoring would probably have established violations of this standard on other survey dates (*9*). The average temperature in the CUT during the surveys ranged from 24 to 25.5 °C, corresponding to saturated oxygen concentrations of 8.2–8.05 mg L^{-1}.

The depletions in DO concentrations observed between two sites bounding the CUT (Figure 1) for the three surveys these sites were monitored are listed in Table 1. The average depletion over this sections was 1.7 mg L^{-1}. Vertical DO profiles collected in the zone of greatest DO depletion demonstrated decreasing concentrations with depth, indicating localized exertion of oxygen demand at the river bottom. Chlorophyll decreased and clarity increased dramatically from above the CUT to Baldwinsville (Figure 4). These changes are consistent with the activity of zebra mussels (*1, 3, 6, 8*).

Oxygen Budget. A simple oxygen budget calculation was made around the CUT (Figure 1) based on DO and flow monitoring data and morphometric information for the channel to provide a first quantitative representation of the net oxygen depletion in this river section. Key features of the calculation are summarized in Table 1. This river section corresponds to the zone over which the quantitative zebra mussel survey was conducted.

The calculation considers average conditions for the three surveys that included oxygen measurements at the bounds of the CUT (Table 1). This approach is consistent with the character of the river's flow regime and the quality of the flow information. Over extended periods (e.g., 1 week), the flow exiting Cross Lake is essentially equal to the flow measured at Baldwinsville. However, substantial day to day variations are reported for flow at Baldwinsville during the summer, associated largely with power genera-

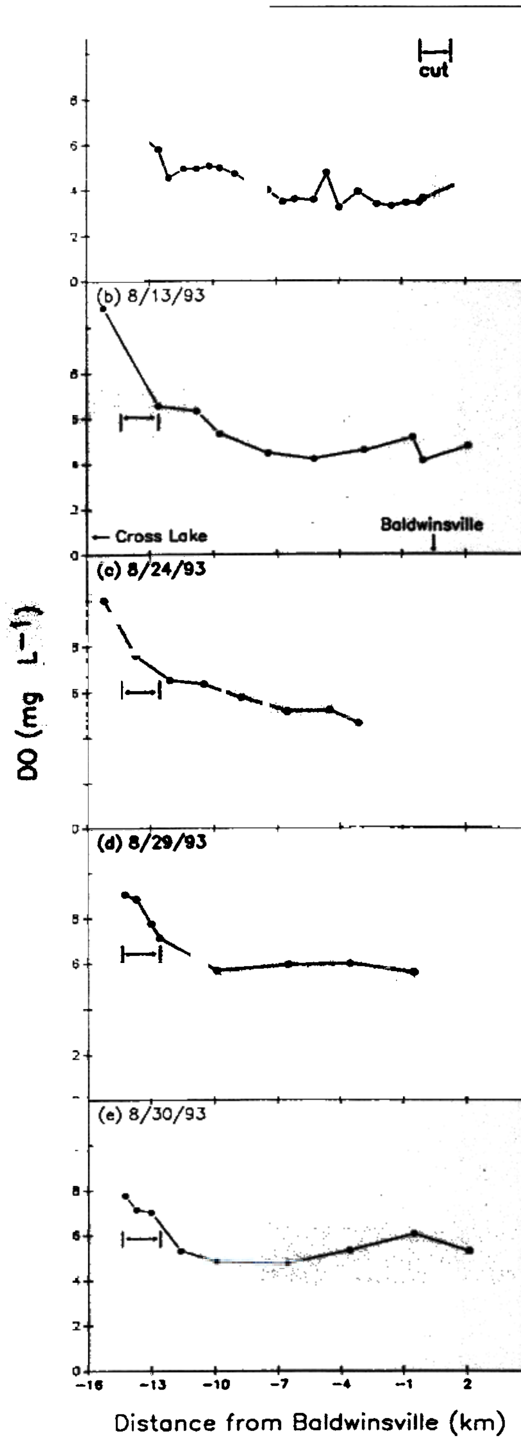

Figure 3. Longitudinal DO profiles for the Cross Lake to Baldwinsville reach of the Seneca River in 1993: (a) August 2, (b) August 13, (c) August 24, (d) August 29, and (e) August 30.

tion. The amplitudes of these variations are undoubtedly modulated in the vicinity of the CUT. As a simplifying assumption, the flow for each of the three days was

Table 2. Zebra Mussel Densities in the CUT of the Seneca River and Related Estimates

	sites			
	upstream	central	downstream	
density (individuals m^{-2})	52 400	60 700	33 200	48 770
wet weight (g m^{-2})	4 986	6 772	2 585	4 781
dry weight (g m^{-2})	748	1 016	388	717
filtration capacity (F; m^3 m^{-2} d^{-1})	18.0	23.6	10.4	17.3
standard respiration (g of O_2 m^{-2} d^{-1})	19.9	26.6	11.0	19.2
active respiration (g of O_2 m^{-2} d^{-1})	15.8	20.7	9.1	15.2
overall respiration (R; g of O_2 m^{-2} d^{-1})	35.7	47.3	20.1	34.4

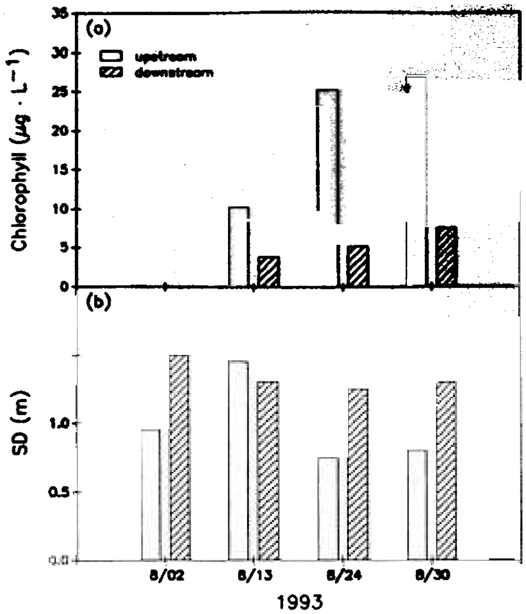

Figure 4. Comparison of upstream (above CUT) and downstream (at Baldwinsville) conditions for the study reach of the Seneca River for selected dates in the summer of 1993: (a) total chlorophyll concentration and (b) Secchi disk transparency.

calculated as the 5-d average centered on the monitoring date. The contribution of the natural ("horseshoe") channel (Figure 1) to the DO depletion can be ignored because it carries such a small fraction of the river flow (further, oxygen concentrations in this channel approach saturation).

The average net oxygen loss over the bounds of the CUT has been represented as an areal rate, with units of g O_2 m^{-2} d^{-1} (Table 1). This is consistent with the dominance of a demand exerted at the river bottom, such as would be associated with zebra mussel respiration or sediment oxygen demand (SOD). Further, it facilitates comparison with the subsequently presented independent estimates of mussel respiration. The calculated average net loss rate was 43.7 g m^{-2} d^{-1}.

Zebra Mussel Population. Zebra mussels occupied all available substrate along the bottom of the Seneca River over the Cross Lake to Baldwinsville reach (Figure 1). All hard substrata >3 cm diameter were colonized by mussels. The most complete coverage by a wide margin was observed in the CUT where a nearly continuous blanket of the invaders as thick as 15 cm, covered the cobble substrate. The less complete coverage downstream reflects the smaller contribution this form of substrate makes to the river bottom in these portions of the river. The zebra mussel population densities in the CUT were extremely high, ranging from 33 000 to 61 000 individuals m^{-2} for the three sites (Figure 5, Table 2), approaching some of the

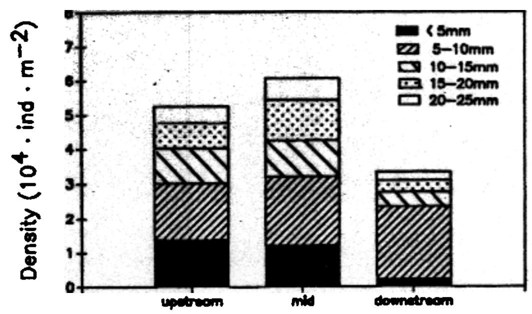

Figure 5. Zebra mussel densities and size structure for three sites in the CUT of the Seneca River in the summer of 1993.

highest densities reported for severely infested portions of the Great Lakes (*2*, *8*). Size distributions of zebra mussels were similar at the upstream and central sites in the CUT, but the mussels <5 mm and >10 mm in length made smaller contributions to the population at the downstream site (Figure 5). The size structure of the mussel assemblage indicates that most of the population was established since the summer of 1991. The vertical walls of the CUT were more sparsely colonized, e.g., 3000–7500 individuals m^{-2}. A total of 90% of the mussels colonizing the walls was <5 mm shell length.

Associated estimates of tissue weight, filtration capacity, and respiration for the populations documented for the three sites in the CUT and the average of the sites are presented in Table 2. The average zebra mussel standing crop in the CUT was estimated to be 4.8 kg m^{-2} wet weight. This corresponds to approximately 360 t wet weight or 54 t dry weight of zebra mussel tissue for the entire CUT [based on the estimated bottom area of 7.5×10^4 m^2 (Table 1)]. The estimated average filtration rate of the zebra mussel population in the CUT was about 17.3 m^3 m^{-2} d^{-1} (Table 2) or about 1.3×10^6 m^3 d^{-1} over the bounds of the CUT. At the lowest 5-d average flow reported in the month of August 1993 at Baldwinsville (1.6×10^6 m^3 d^{-1}), the mussel population of the CUT had the capacity to filter more than 80% of the Seneca River flow. About 45% of the maximum daily flow reported for the month (2.86×10^6 m^3 d^{-1}) could be filtered by this population. Based on the incomplete vertical mixing that prevailed in this portion of the river as evidenced in oxygen profiles, it is probable that the efficiency of filtration was somewhat less than these estimates.

The estimated contributions of the standard and active components to overall respiration were essentially equivalent (Table 2). The magnitude of the oxygen sink associated with zebra mussel respiration in the CUT (~34 g m^{-2} d^{-1}) can be placed into perspective by comparing it to the demands exerted by organic sediment deposits at river bottoms, described as sediment oxygen demand (SOD; g m^{-2} d^{-1}), reported in the literature. A high SOD value, corresponding to highly enriched deposits, is 5 g m^{-2} d^{-1} (*17, 18*), or about 15% of the average areal zebra mussel respiration rate estimated for the CUT (Table 2).

Despite the imperfect character of the two independent estimates and supporting data, the similarity of the oxygen budget calculation (44 g m^{-2} d^{-1}; Table 1) and the zebra mussel respiration rate for the CUT (34 g m^{-2} d^{-1}; Table 2) is compelling evidence that the depletion of oxygen in that section of the river in 1993 was largely attributable to the zebra mussel infestation. Inherent in this conclusion is that the other oxygen sinks and sources were largely in balance in this portion of the river. This assumption is consistent with the nearly saturated DO concentrations that prevailed downstream of the study reach before the infestation (Figure 2a). Decomposition of feces and psuedofeces within the mussel bed undoubtedly augments the respiration demands of the these dense mussel populations. The differences in the two independent estimates are not significant in light of the uncertainties in the inputs and assumptions incorporated in the calculations.

The features of the longitudinal DO profiles downstream of the CUT are consistent with the observed decreasing densities of zebra mussels and the poor reaeration capacity of this channelized system (*9*). The position that the degradation in the oxygen resources of the Seneca River since 1990–1991 (Figure 2) is a result of the infestation is supported not only by the closure in the oxygen budget calculation for the CUT with the independent estimate of the respiration sink associated with the mussel population but also by the age structure of the population (Figure 5).

Management Considerations. The severity of the zebra mussel infestation of this portion of the Seneca River and the coupled impact on its oxygen resources are attributable to cultural alterations to the system, including (a) cultural eutrophication [e.g., the food to support the infestation; numerous upstream discharges of phosphorus (*10, 11*)], (b) channelization (e.g., rock substrate of the CUT), and (c) elimination of the natural reaeration capacity of the system. We expect therefore that this case may approach the upper bound for the impact of this invader on the oxygen resources of streams and rivers. The persistence of the infestation at its present level would require remedial action to prevent violations of New York State water quality standards for DO (e.g., Figures 2b and 3). The European experience indicates that high density populations of lakes are usually unstable, with maximum populations lasting only 2–3 yr, followed by crashes (*3*). However, this river setting, with its relatively stable upstream food source (*11*), in contrast, may support a relatively stable population.

The loss of waste (oxygen demanding) assimilative capacity of this large river has important implications with regard to basin-wide planning. Under the conditions documented here (e.g., the new oxygen sink), the waste discharge permits issued by the state of New York to downstream discharges can no longer protect the oxygen resources of the river under critical (e.g., low flow) conditions. Further, this infestation is confounding remediation efforts for a downstream polluted lake [Onondaga Lake (*19, 20*)], which presently receives 80 MGD of domestic waste effluent. Leading management alternatives for the reclamation of the lake have included the diversion of a significant portion, or all, of the oxygen demanding effluent to the Seneca River downstream of Baldwinsville.

To support effective protection and planning for this river system, it is essential that the existing mechanistic mathematical model (*9*) for DO be modified to accommodate the zebra mussel sink and be expanded to include affected portions of the system. Application of this quantitative framework (*9*), in conjunction with supporting process studies, would provide a more rigorous analysis and resolution of the various sink and source processes than the budget analysis presented here. This effort is desirable not only to support effective management of this system but also as a test system for the study of this impact of zebra mussel infestation. The reach of the Seneca River addressed in this study appears to be a good test system, not only because of the clear signal of the impact but also because of the stability of the zebra mussel's food source [Cross Lake hypereutrophy (*10, 11*)].

A negative impact of zebra mussel respiration on oxygen resources, of the form (if not magnitude) documented here, is to be expected for other alkaline hardwater streams and rivers in North America (particularly those with large amounts of rock substrate) as the spread of this invader continues. While the severity of the impact documented here may approach the upper bound, many streams and rivers in well-developed areas cannot afford any significant loss of waste assimilative capacity. Systems susceptible to infestation need to be tracked carefully, including execution of appropriate biological surveys. Mathematical models used to manage the oxygen resources of the affected systems will need to be modified to accommodate the additional sink. Further, improved quantitative data on zebra mussel respiration and its dependence on environmental conditions (*5*) will be necessary to credibly accommodate this new oxygen sink.

Summary

Zebra mussel populations have become established on the rock bottom of the Seneca River from Cross Lake to Baldwinsville, NY. The infestation was particularly severe in a 1.4-km rock substrate channel known as the CUT, where densities as high as 61 000 individuals m^{-2} were documented in the summer of 1993. Zebra mussel respiration has degraded the oxygen resources of the river to the extent that violations of New York state water quality standards have occurred. The dominant role the zebra mussel invasion played in this degradation is manifested in the near equivalence of the observed net depletion of DO over the CUT, expressed as an areal rate and an independent estimate of mussel respiration based on relationships presented in the literature. The oxygen sink that can be exerted at a river bottom by this level of infestation (e.g., about 35 g m^{-2} d^{-1}) is much greater than that of highly enriched organic deposits (e.g., SOD = 5.0 g m^{-2} d^{-1}). The widely observed effects of this filter feeder, reduction in phytoplankton concentrations and increases in clarity, were also observed over the study reach.

The negative impact of the zebra mussel invasion on oxygen resources demonstrated here should be expected to be manifested in other infested flowing waters. The loss in waste assimilative capacity can have important management implications. Systems expected to be most severely impacted are those rich in particulate food, with large amounts of rock substrate and poor reaeration capacity.

Acknowledgments

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Notations

F_i	filtration rate of individual zebra mussel, i ($m^3\ d^{-1}$)
L_i	length of individual zebra mussel, i (mm)
R_i	respiration rate of individual zebra mussel, i (g of O_2 individual^{-1} d^{-1})
$R_{i/a}$	active respiration rate of individual zebra mussel, i (g of O_2 individual^{-1} d^{-1})
$R_{i/s}$	standard respiration rate of individual zebra mussel, i (g of O_2 individual^{-1} d^{-1})
W_i	wet weight of individual zebra mussel, i (g)
$W_{i/d}$	dry weight of individual zebra mussel, i (g)

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