

RIVER DISSOLVED OXYGEN MODEL WITH ZEBRA MUSSEL OXYGEN DEMAND (ZOD)



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ABSTRACT: The development, calibration, and application of a dynamic two-dimensional mass balance model for dissolved oxygen (DO) for rivers are documented for the first time accommodating the oxygen demand associated with zebra mussels. The test system is a short (2.3 km) phytoplankton-rich section of the Seneca River, N.Y., which is believed to represent an upper bound of the impact of this exotic invader on oxygen resources because of the unusually high population densities and limited turbulent mixing that prevail. Model calibration is supported by comprehensive measurements of DO, which resolve diurnal and seasonal patterns, and various forcing conditions over a four-month period. Wide temporal variations in the areal consumption rate of DO by zebra mussels [zebra mussel oxygen demand (ZOD), $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$] were determined through model calibration. These determinations are supported by closure with earlier estimates based on simple DO budget calculations, and with laboratory biomass-specific oxygen consumption rates published in the scientific literature. Values of ZOD at times (e.g., $>50 \text{ g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) were an order of magnitude greater than the sediment oxygen demand associated with organically enriched deposits. The model performs well in simulating important features of the complex patterns of DO observed, including (1) DO depletion across the study section; (2) vertical DO stratification; and (3) diurnal changes. ZOD was the dominant sink for DO over the river study section; it was entirely responsible for the substantial observed DO depletion, and it was the major cause of the DO stratification during periods of low flow. A preliminary extension of the model is demonstrated to be successful in simulating the persistence of DO depletion 15 km downstream. The model is expected to have management utility for this and other phytoplankton-rich rivers that have been, or will be, invaded by zebra mussels.

INTRODUCTION

Mechanistic mass balance models represent the primary engineering tools to guide the management of surface water quality (Thomann and Mueller 1987; Chapra 1997). The complexity of these mathematical tools has evolved to meet increasing societal needs as computing capabilities and scientific understanding of these ecosystems have advanced (Chapra 1997). Much of the increasing sophistication of water quality models has been devoted to more detailed treatment of the "metabolism" of these ecosystems. The management models that have been developed, often at great cost, reflect the biological structure or metabolism of the ecosystems that prevailed at the time of their development. These tools may remain appropriate only as long as substantial changes in structure and function of an ecosystem do not occur. Exotic invaders can dramatically alter the structure and function of surface water ecosystems (Mills et al. 1993), thereby requiring modification of model frameworks to accommodate influences of the metabolism of the invader.

The zebra mussel (*Dreissena polymorpha*, Pallus), a small bivalve mollusk native to southern Russia, has been one of the most successful invaders of the aquatic ecosystems of North America (Ludyanskiy et al. 1993). Following the introduction into the Laurentian Great Lakes in the mid-1980s (e.g., water ballast from a foreign ship) (Herbert et al. 1989), this filter-feeding bivalve has spread throughout the Northeast, and much of the Southeast and Midwest of the United States, and much of Canada. Dense populations of the zebra mussel have been demonstrated to cause major changes in common measures of

water quality associated with various aspects of its metabolism (Effler et al. 1996). These changes have included (1) decreases in the concentrations of phytoplankton and inanimate particles (tripton) and attendant increases in clarity, as a result of filter feeding (Caraco et al. 1997; Effler and Siegfried 1998); (2) increases in ambient concentrations of nutrients associated with excretion (Arnott and Vanni 1996; Effler et al. 1996, 1997a; Caraco et al. 1997); and (3) decreases in dissolved oxygen (DO) and pH associated with respiration (Effler and Siegfried 1994; Effler et al. 1996; Caraco et al. 2000). The most dense populations of zebra mussels occur where there is abundant food (e.g., phytoplankton) and rock substrate to support attachment (Ramcharan et al. 1992). The magnitude of changes in fluxes and in pools of key constituents that have accompanied the zebra mussel invasion in severely infested systems has rendered water quality models developed before the invasion essentially useless.

The focus of this paper is the appropriate accommodation of the effect(s) of zebra mussel metabolism in a mass balance model for dissolved oxygen in rivers. Though the population densities of this invader are generally lower in rivers and streams than in lakes (Madon et al. 1998), the additional oxygen sink represented by zebra mussel respiration is a particular concern in lotic systems in developed areas. Many urban rivers have little or no available assimilative capacity to lose because of inputs of oxygen-demanding wastes. Oxygen depletion has been reported from zebra mussels in at least four large rivers in the United States—the Illinois River (Illinois Natural History Survey 1994), the Hudson River (Caraco et al. 2000), the Seneca River (Effler and Siegfried 1994; Effler et al. 1996), and the Oswego River (Effler and Siegfried 1998). Undoubtedly, the oxygen resources of a much larger number of rivers in the United States and Canada have been impacted. The most dense populations of zebra mussels and the most severe depletions of DO for a lotic system have been reported for the Seneca River (Effler and Siegfried 1994). Depletions in this river have been severe enough to cause violations of related New York State standards for minimum DO concentrations ($<4 \text{ mg} \cdot \text{L}^{-1}$) (Effler et al. 1996).

This paper documents the development, calibration, and application of a dynamic two-dimensional mass balance model

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for DO for a 2.3 km section of the Seneca River, N.Y. An array of metrics is utilized to depict salient features of the complex DO patterns and to evaluate model performance. The temporal pattern of oxygen demand associated with zebra mussels [zebra mussel oxygen demand (ZOD), $g \cdot m^{-2} \cdot day^{-1}$] (Effler et al. 1996) in the study reach is determined through model calibration. The calibrated model is applied to evaluate the relative roles of ZOD, primary production and respiration, and limited vertical mixing in regulating the observed signatures of DO depletion across the study reach, diurnal variations in DO, and vertical differences in DO. Preliminary testing of the DO model over a longer section (~15 km) of the river is presented, and critical features of the inclusion of the effect of the zebra mussel invasion in a DO management model for the river system are considered.

SYSTEM DESCRIPTION

Setting

The Seneca River is an alkaline hardwater system that drains 9,000 km² of the 13,200 km² Oswego River basin of New York (Fig. 1). The Oswego River, formed by the combination of the Seneca and Oneida Rivers, is the second largest inflow into Lake Ontario (Fig. 1), after the Niagara River. The annual average flow of the Seneca River at Baldwinsville for the 1951–91 period was $96.3 m^3 \cdot s^{-1}$; the average at the mouth of the Oswego River over the 1933–91 interval was $188.6 m^3 \cdot s^{-1}$ (U.S. Geological Survey).

The natural hydrodynamic features of the river system have been greatly modified (e.g., dams, locks, and channelization) to support power generation and navigation, which has increased water depth and reduced turbulent mixing and the reaeration capacity of the system (Canale et al. 1995). Numerous small domestic waste discharges are received by the Seneca River upstream of Cross Lake, none are received over the Cross Lake to Baldwinsville reach, and several effluents enter the river system downstream of Baldwinsville (Fig. 1) (Canale et al. 1995; Effler et al. 1996). The domestic waste loads from the largest urban area in the watershed, Syracuse, are received instead by the adjoining Onondaga Lake (Fig. 1). Onondaga Lake is severely polluted as a result of the reception of this waste (Effler 1996), and the outflow from the lake

causes negative impacts in downstream portions of the Seneca River (Canale et al. 1995; Effler et al. 1997b). The assimilative capacity of this portion of the river is an important management issue, as a leading alternative for rehabilitation of Onondaga Lake is diversion of the wastewater treatment plant (WWTP) discharge (following treatment upgrade) received from metropolitan Syracuse to the Seneca River (Canale et al. 1995; Effler et al. 1996).

Cross Lake, located ~16 km upstream of Baldwinsville and ~23.8 km upstream of the inflow from Onondaga Lake, is a dimictic, rapid flushing lake. The Seneca River inflow (Fig. 1) represents ~98% of the total flow received by this lake (Effler and Carter 1987). There are no significant inflows to the Seneca River between Cross Lake and the entry of Onondaga Lake (Fig. 1). Cross Lake is hypereutrophic because of the nutrient loading received by the upstream portion of the river (Effler and Carter 1987) from WWTP discharges and agricultural activity. This intervening lake essentially acts to convert nutrient loading carried by upstream portions of the Seneca River to phytoplankton biomass (Effler and Siegfried 1994). Water exiting Cross Lake during summer low flow intervals largely reflects lakewide epilimnetic conditions (Effler et al. 1989). However, during high runoff intervals substantial short-circuiting of the river inflow to the lake outlet occurs (Schindler et al. 1977; Effler and Carter 1987).

An artificial channel, described as the "cut," located 1.3 km downstream of Cross Lake (Fig. 1), is one of the modifications of the river to support navigation. This channel (depth of 5 m) was dug out of bedrock in 1915 as part of the construction of the Barge Canal system. The bottom of this channel is covered with cobble size rock (no rooted plants). The cut carries >90% of the river flow (Coon 1994), as the natural "horseshoe" channel of the river (Fig. 1) is largely silted in.

Zebra Mussel Invasion and Impacts on DO

Ludyanskiy et al. (1993) reported the zebra mussel invasion had spread to this river by the early 1990s. An abrupt reduction in DO concentrations was observed in the Seneca River at Baldwinsville in the summer of 1993: the median concentration decreased from $7.3 mg \cdot L^{-1}$ for 1990 and 1991; to $4.7 mg \cdot L^{-1}$ [1993, Fig. 2(a)] (Effler et al. 1996). Longitudinal DO

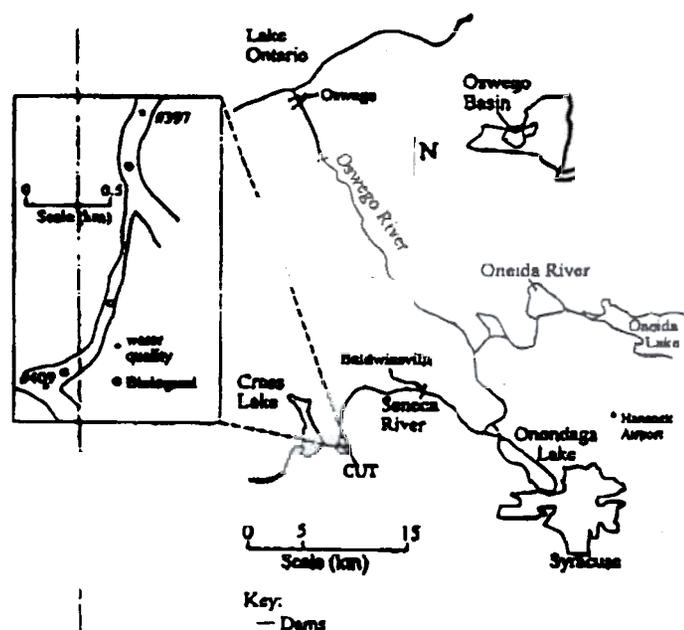


FIG. 1. River System, the Cut Section of the Seneca River, N.Y., with Water Quality Monitoring Stations

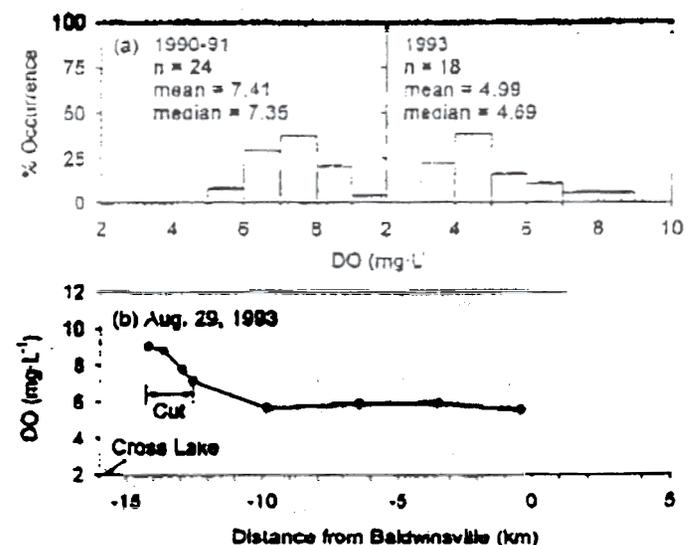


FIG. 2. Dissolved Oxygen Concentrations in the Seneca River: (a) Comparison of Summertime Concentrations near Baldwinsville before the Zebra Mussel Invasion to after the Invasion (Modified from Effler et al. (1996)); (b) Longitudinal DO Profile (Vertically Averaged Values) from Downstream of Cross Lake to Baldwinsville, August 29, 1993 (Modified from Effler and Siegfried (1994))

profiles in the same summer [Fig. 2(b)] depicted decreases downstream of Cross Lake without recovery at Baldwinsville. The greatest depletion occurred across the cut. No such depletions in DO were found for the Cross Lake to Baldwinsville reach in earlier data sets.

Zebra mussels were found to occupy all available solid substrate >3 cm diameter along the entire Cross Lake to Baldwinsville reach in a benthic survey of August 1993. Particularly dense populations of the bivalve were observed in the cut (~50,000 individuals·m⁻²), where the contribution of large rock substrate was the greatest (Effler and Siegfried 1994). The size structure of the community indicated that the population was established in 1992 and 1993 (Effler and Siegfried 1994). The population density found in the cut is the highest reported for any river in the United States, approaching maxima observed for productive portions of the Great Lakes (Effler et al. 1996). This has been attributed to the abundant food supply provided by Cross Lake in the form of phytoplankton, the supply of veligers (planktonic larvae of the zebra mussel) by the lake, and the abundance of appropriate substrate (Effler and Siegfried 1994, 1998). High densities of the invader have persisted at this location for at least seven years, though substantial seasonal and interannual variations have occurred.

Scientific evidence supports the position that the decrease in DO in the river was associated with the zebra mussel invasion. Reasonably good closure was obtained between the estimated average DO depletion across the cut (based on longitudinal DO profiles in 1993), expressed as an areal sink process (44 g·m⁻²·day⁻¹), and an areal respiration rate for the mussels (34 g·m⁻²·day⁻¹), based on laboratory rates (Schneider 1992) and the measured population density of 1993 (Effler and Siegfried 1994). Similar budget calculations made around the cut based on much more intensive DO monitoring in 1994 (Effler et al. 1998) continued to establish the existence of a large oxygen sink in this river section and rather good closure with more recent (Aldridge et al. 1995) laboratory data for zebra mussel respiration.

The cut has been adopted as the test system in this paper to incorporate the effects of zebra mussel metabolism into a mass balance model for DO, and to quantify the associated sink. This site likely approaches the upper bound of the impact of zebra mussels on the oxygen resources of a river, not only

because of the particularly high population densities maintained, but also because of the limited amount of compensation provided by recretion.

The loss of assimilative capacity of the river system for oxygen-demanding waste associated with the zebra mussel invasion has had important implications for basinwide planning. Waste discharge permits issued by New York State before the invasion can no longer protect the oxygen resources of the river. Further, this infestation is confounding rehabilitation efforts for Onondaga Lake, as plans to divert the WWTP effluent from metropolitan Syracuse to the river have been discontinued because of the loss of assimilative capacity.

SUPPORTING MEASUREMENTS

Monitoring Program

1 state variable?

An intensive field program conducted in 1994 supported model development and testing (Table 1). The array of monitored parameters included the model state variable, a number of model inputs, and several auxiliary measurements of conditions that may have influenced the dynamics of zebra mussel respiration and DO. Water quality measurements were made at two longitudinal positions (navigation buoys 409 and 397) bounding the cut (Fig. 1). Zebra mussel population estimates for this section were based on benthic surveys conducted at multiple sites (and replicate samples) within its bounds (Effler et al. 1997a). Temperature, DO, and meteorological conditions were measured the most frequently (hourly). Temperature and DO measurements were made at depths of 1 and 3 m at each of the two sites with remote monitoring units (Effler et al. 1998). Other field and laboratory analyses were conducted less frequently (two to three times·week⁻¹, Table 1). Meteorological measurements were made at Syracuse Hancock Airport, except for incident irradiance, which was measured near the southern end of Onondaga Lake (Fig. 1).

Upstream Boundary/Ambient Conditions

Rather strong dynamics of potential drivers of zebra mussel respiration and DO occurred over the modeling interval (Fig. 3). For example, major variations in river flow (Q , m³·s⁻¹) occurred (Fig. 3(a)). The most conspicuous temporal features were two intervals of low flow from mid-July through mid-

TABLE 1. Monitoring Program Supporting DO Model Testing for 1994 Conditions

Param	Depth/Frequency	Function	Reference
(a) Field			
DO ^a	1 and 3 m; hourly	State variable	Effler et al. (1998)
Temperature ^a	1 and 3 m; hourly	Model input	Effler et al. (1997a)
Secchi disk ^b	Two to three times·week ⁻¹	Model input	—
Incident irradiance	Hourly	Model input	UFI/NOAA ^c
Air temperature ^a	Hourly	Model input	NOAA records
Dew point temperature ^a	Hourly	Model input	NOAA records
Wind speed ^a	Hourly	Model input	NOAA records
River flow	Daily average	Model input	U.S. Geological Survey
Irradiance profiles ^d	Five times	Model input	—
(b) Laboratory			
Suspended solids	1 and 3 m; two to three times·week ⁻¹	Ancillary	Effler et al. (1997a)
Chlorophyll	1 and 3 m; two to three times·week ⁻¹	Ancillary	Effler et al. (1997a)
Total ammonia	1 and 3 m; two to three times·week ⁻¹	Ancillary	Effler et al. (1997a)
Nitrate	1 and 3 m; two to three times·week ⁻¹	Ancillary	Effler et al. (1997a)
Zebra mussel biomass	Monthly	Ancillary	Effler et al. (1997a)

^aHydroLab Soade.

^bTo estimate attenuation coefficient.

^cUpstate Freshwater Institute—measurements in Syracuse.

^dNational Oceanic and Atmospheric Administration weather station, Hancock Airport (Fig. 1).

^eTransport/temperature submodel inputs.

^fTo determine attenuation coefficient.

why short-circuited, why less retention time so less prim prod so less VSS?

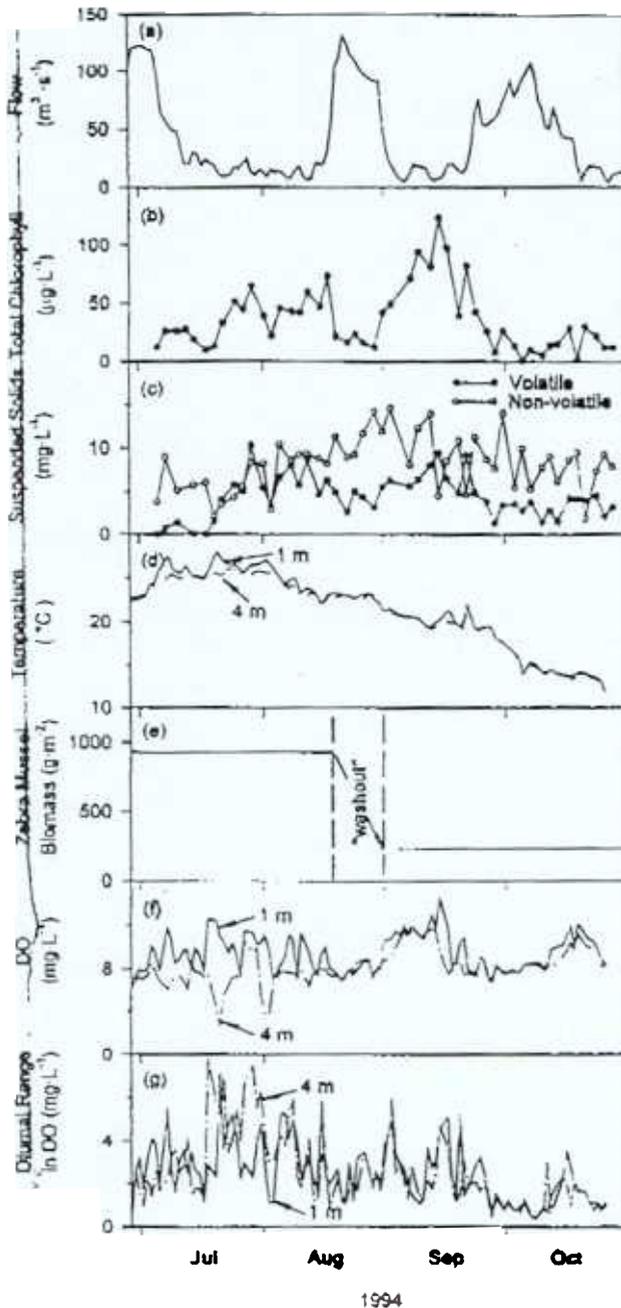


FIG. 3. Dynamics of Selected Environmental Conditions in the Seneca River at the Upstream Boundary of the Cut, July–October 1994: (a) Flow; (b) Total Chlorophyll; (c) Suspended Solids, Volatile and Non-volatile; (d) Temperature at Depths of 1 and 4 m; (e) Average Zebra Mussel Biomass within the Cut, for Two Intervals [from Data Presented by Effler et al. (1997a)]; (f) Daily Average DO at Depths of 1 and 4 m; (g) Diurnal Range in DO at Depths of 1 and 4 m

August and much of September, which separated three intervals of high flow in early July, late August, and late September through mid-October [Fig. 3(a)]. The minimum average flow for a 30 day period, with a return frequency of one in 10 years (MABOCD10), is $17.6 \text{ m}^3 \cdot \text{s}^{-1}$ for this reach. The levels of chlorophyll (Chl, $\mu\text{g} \cdot \text{L}^{-1}$) that entered the cut [buoy 409, Fig. 3(b)] reflect the hypereutrophic state of Cross Lake (Effler and Carter 1987), and indicate a rich food supply for resident zebra mussels. The dynamics of the concentrations of Chl [Fig. 3(b)] and suspended solids [Fig. 3(c)] were in part linked to variations in flow [Fig. 3(a)]. The contribution of inorganic solids to the total was greater during the three high flow intervals,

and the concentrations of the organic component of suspended solids (VSS, $\text{mg} \cdot \text{L}^{-1}$) and Chl were lower, consistent with short-circuited flow from the upstream portion of the river. Higher Chl levels [Fig. 3(b)] were observed during the lower flow (e.g., minimal short-circuited component) intervals [Fig. 3(a)]. The disproportionate decrease in Chl during the late August runoff event suggests the food value of organic particles may have diminished during this interval.

The dynamics of temperature (T , $^{\circ}\text{C}$) were more gradual by comparison [Fig. 3(d)], typical of the seasonality experienced in the region (Effler 1996). Temperature ranged from 12 (late October) to 26°C (July and August) over the simulation period. Temperatures decreased in a largely progressive manner after early August [Fig. 3(d)]. Vertical T differences were minor relative to the seasonal changes [Fig. 3(d)]. These differences were greatest during low flow intervals and depict incomplete vertical mixing in the river water column, and therefore the potential for stratification for reactive constituents such as DO.

The presented temporal pattern of zebra mussel biomass for the study period [Fig. 3(e)] is an oversimplification (Effler et al. 1997a), but it depicts the most important feature, the major decrease during the August runoff event (described as "wash-out"). Average zebra mussel population densities and total biomass in the cut decreased from $\sim 40,000 \text{ individuals} \cdot \text{m}^{-2}$ and $930 \text{ g (dry weight)} \cdot \text{m}^{-2}$ to $\sim 18,000 \text{ individuals} \cdot \text{m}^{-2}$ and $240 \text{ g} \cdot \text{m}^{-2}$, respectively (Effler et al. 1997a) [Fig. 3(e)]. The mechanism for the loss of biomass from the cut is uncertain. The increase in velocity was inadequate to remove healthy zebra mussels from the substrate. However, the colonies in the cut were several centimeters thick, made up of numerous layers of individuals. Many of the individuals in the bottom (i.e., older) layer may have been dead or degraded, such that detachment of colonies could have occurred in response to the increase in current velocity.

The DO signal received by the cut from Cross Lake during the study period was complex with respect to temporal and vertical patterns. The concentration of DO varied strongly at time scales of day-to-day [Fig. 3(f)], within a day [Fig. 3(g)], and seasonally, and differed with depth in the water column of the river. These features reflect dynamics in DO concentrations that are commonly observed in the epilimnia of hypereutrophic lakes, that are driven by the timing of primary production and wind driven turbulence (Effler and Carter 1987; Effler et al. 1989; Effler 1996). The unusually low turbulent mixing in this river acts to sustain both the temporal and the vertical features of the lake's signal. These complex features are to be expected for a river study site where the maximum impact of zebra mussels on oxygen resources is approached (e.g., hypereutrophy and limited turbulence). Further, they offer a challenge for proper quantification of the effects of primary production and limited vertical mixing in a DO model framework, and an opportunity to make related advancements.

DISSOLVED OXYGEN MODEL

Transport/Temperature Submodel

The transport/temperature submodel adopted here has been modified from that incorporated in CE-QUAL-W2 (Cole and Buchak 1995), a model that is widely applied for reservoirs. The framework is two dimensional, consisting of longitudinal and vertical segments (i.e., conditions are laterally averaged), to address related features in the DO patterns of this system [e.g., Figs. 2(b), 3(f), and 3(g)]. Segmentation was based on a bathymetric survey and was consistent with the need to avoid numerical dispersion in model predictions. A segmentation of 12 vertical layers of 0.5 m each, and three longitudinal segments, $\sim 0.8 \text{ km}$ long, was adopted to represent the cut. Thus, the cut was divided into 36 (12×3) cells; concentrations

within each cell are assumed to be uniform. Increasing the number of longitudinal segments (i.e., reduced length of individual cells) did not influence model predictions. An additional 13 longitudinal segments of ~1 km length, with vertical layers of 0.5 m thickness, were added downstream of the cut to support preliminary simulations of DO over the cut to Baldwinsville (Fig. 1) reach.

The submodel simulates T and transport. The heat budget that supports T simulations includes terms for evaporative heat loss, short- and long-wave radiation, convection, conduction, and back-radiation (Cole and Buchak 1995). Meteorological data necessary to drive the predictions include air temperature, dew point temperature, wind speed, and incident solar radiation (Table 1).

Features of transport are simulated by specifying the interaction of adjacent model cells through the processes of longitudinal and vertical advection and dispersion. The vertical mixing component of the transport framework of CE-QUAL-W2 was modified for this river application. The vertical eddy diffusion coefficient (D_z , $m^2 \cdot s^{-1}$) was calculated as a function of flow according to relationships reviewed by Martin and McCutcheon (1999). The value of D_z increased with Q ; at $Q = 65 m^3 \cdot s^{-1}$, the lower threshold for no DO stratification, a value of $D_z = 0.008 m^2 \cdot s^{-1}$ was predicted. The value of D_z was calculated to be much lower during the low flow interval of mid-July to mid-August when substantial DO stratification was observed [Fig. 3(f)]; e.g., average of $\sim 0.002 m^2 \cdot s^{-1}$.

The model performed well in simulating T at time scales of within a day to seasonal (root-mean-square error at buoy 397 = $0.44^\circ C$). However, the success of simulations in the cut was largely ensured by the frequent update of the boundary conditions. The results of an earlier dye study conducted over the Cross Lake (outlet) to Baldwinsville reach ($Q = 30 m^3 \cdot s^{-1}$) (Schindel et al. 1977) provided a test for the submodel's simulation of time of travel (t_r , h), an important feature of river transport (Martin and McCutcheon 1999). The predicted t_r was approximately equal to the observation of 70 h (Schindel et al. 1977). The predicted value of t_r to traverse the shorter length of the study site at the same Q was 4.2 h.

Dis

The generalized kinetic expression for DO, which includes the ZOD sink [exerted at the river bottom (Effler et al. 1996)] is

$$dDO/dt = K_L \cdot (DO_{sat} - DO_s) / H_s + (P - R) - (k_d \cdot CBOD_t) - (k_r \cdot NBOD) - (SOD + ZOD) \left(\frac{W_T - W_B}{A} \right) \quad (1)$$

where dDO/dt = rate of change of DO due to kinetic processes ($g \cdot m^{-3} \cdot day^{-1}$); K_L = oxygen transfer coefficient ($m \cdot day^{-1}$); DO_{sat} = DO concentration at saturation ($g \cdot m^{-3}$); DO_s = surface layer DO concentration ($g \cdot m^{-3}$); H_s = surface layer thickness (m); P = gross photosynthetic production of oxygen ($g O_2 \cdot m^{-3} \cdot day^{-1}$); R = uptake of oxygen due to endogenous respiration of phytoplankton ($g O_2 \cdot m^{-3} \cdot day^{-1}$); k_d = CBOD decay rate (day^{-1}); $CBOD_t$ = ultimate CBOD ($g \cdot m^{-3}$); k_r = NBOD decay rate (day^{-1}); SOD = sediment oxygen demand rate ($g \cdot m^{-2} \cdot day^{-1}$); ZOD = zebra mussel oxygen demand rate ($g \cdot m^{-2} \cdot day^{-1}$); W_T = width of channel cross section at top of segment (m); W_B = width of channel cross section at bottom of segment (m); and A = cross-sectional area of segment (m^2). Temperature adjustments for the kinetic processes, other than ZOD, were made according to the Arrhenius format (Bowie et al. 1985). Values of the kinetic coefficients used in this model are listed in Table 2.

TABLE 2. Summary of Kinetic Coefficients

Coefficient	Value	Reference
a_{cr} C:Chl a	$75 mg \cdot mg^{-1}$	Chapra (1997)
a_{oc}	$2.67 mg O_2 \cdot mg C^{-1}$	Chapra (1997)
$f(N)$	1.0	Bannister (1974)
k_d	$0.015 day^{-1}$	Cloern et al. (1995)
k_r	$1.9 m^{-1}$	This study
K_L	$180 \mu B \cdot m^{-1} \cdot day^{-1}$	Canale et al. (1995)
$K_L - N/A/M/T/W$	$0.69 m \cdot day^{-1}$	Canale et al. (1995)
r	10% of μ	Eq. (6); Chapra (1997)
ϕ	0.09	Eq. (6); computed
θ_p	1.03°	Canale et al. (1995)
θ_r	1.05°	Canale et al. (1995)
μ_{max}	$1.5 day^{-1}$	Chapra (1997)

^a θ_p and θ_r are temperature correction coefficients for phytoplankton production and respiration, respectively.

Development of Kinetics

SOD, NBOD (k_r), and CBOD

Certain features of this study system have simplifying effects on the application of the kinetic framework. For example, there are no deposits of organic sediments; thus, there is no significant exertion of SOD. A very low value for k_r was reported for downstream portions of the Seneca River [from Baldwinsville to just past the confluence with the Oneida River (Fig. 1)] (Canale et al. 1995). This was attributed largely to its great depth, as nitrification is localized at the sediment-water interface (Cavari 1977; Pauer and Auer 2000). Ammonia is depleted seasonally (by midsummer) in the epilimnion of Cross Lake (Effler et al. 1989), which further discourages nitrification. Increases in ammonia have been reported across the cut, associated with excretion by zebra mussels (Effler et al. 1997a). However, the lack of any increase in nitrate (end product of nitrification) across the cut over the study period supports the position that the rate of nitrification was very low (assumed zero here) (Gelda et al. 2000). Concentrations of labile organic carbon in the epilimnia of productive lakes are low within the context of potential oxygen demand (Wetzel 1992). Further, no changes in the DO_s concentration pool were observed across the study site (unpublished data). Thus, there was assumed to be no oxygen sink associated with the stabilization of CBOD.

K_L

Determinations of K_L were based on in situ experiments with the relatively insoluble gas SF_6 for downstream portions of the river (continuous injections near Baldwinsville for several weeks in the summer of 1991) as part of a DO modeling study conducted before the zebra mussel invasion (Canale et al. 1995). The values of K_L were calculated from the SF_6 transfer coefficient determinations based on differences in molecular diffusion coefficients for the two gases (Canale et al. 1995). Values of K_L consistent with those reported by Canale et al. (1995) were adopted for the present study (Table 2), as substantial longitudinal differences were not reported by those investigators over a 12 km reach.

PIR

The gross photosynthetic production of oxygen (P) was simulated according to the following phytoplankton growth kinetics (Bowie et al. 1985; Chapra 1997):

$$P = \mu \cdot Chl \cdot a_{cr} \cdot a_{oc} \quad (2)$$

$$\mu = \mu_{max} \cdot f(T) \cdot f(I) \cdot f(N) \quad (3)$$

where μ = growth rate of phytoplankton (day^{-1}); a_{cr} = carbon

D_z
= calibrated ???

What about inputs = outputs

DO

to chlorophyll ratio; a_{oc} oxygen to carbon ratio; μ_{max} = maximum growth rate of phytoplankton at 20°C under optimal light and nutrient conditions; and $f(T)$, $f(I)$, and $f(N)$ = limitation factors (≤ 1.0) associated with ambient temperature, light, and nutrient availability conditions, respectively. The simplifying assumption of nutrient saturation (Bannister 1974) is appropriate here because of the high concentrations of nutrients in water delivered to the cut from the epilimnion of Cross Lake (Effler et al. 1989), and the increase in available forms of phosphorus and nitrogen over the cut associated with zebra mussel excretion documented for the modeled interval (Effler et al. 1997a).

Light limitation [$f(I)$] is represented by

$$f(I) = \frac{I}{I + K_I} \quad (4)$$

where I = photosynthetically available solar radiation (PAR, $\mu E \cdot m^{-2} \cdot day^{-1}$); and K_I = light half-saturation constant ($\mu E \cdot m^{-2} \cdot day^{-1}$). Light at depth in the water column was calculated according to Beer's Law; the magnitude of the light attenuation coefficient (k_d , m^{-1}) was held constant (Table 2) based on the uniformity of Secchi disk measurements (Table 1). The independence of k_d from the variations in concentrations of Chl [Fig. 3(b)] reflects the high nonalgal turbidity in this portion of the river, a situation that is common to many large rivers.

The uptake of oxygen due to the endogenous respiration of the phytoplankton (R) was simulated according to

$$R = r \cdot Chl \cdot a_{CP} \cdot a_{OC} \quad (5)$$

where r = phytoplankton respiration rate (day^{-1}). This rate was simulated as the summation of two components, the basic maintenance or basal component, and an active component that increases as production increases, represented by the expression (Laws and Chalup 1990)

$$r = \phi \cdot \mu + k_b \quad (6)$$

where ϕ = coefficient for the active component of respiration (dimensionless); and k_b = basal component of respiration (day^{-1}).

ZOD

ZOD includes zebra mussel respiration as well as all other local oxygen consumption processes that operate within the colonies (e.g., stabilization of feces and pseudofeces). Respiration is the dominant component (Schneider 1992). Zebra mussel respiration has been partitioned into two components by the scientific community—(1) the standard minimum for maintenance (no feeding); and (2) the active component associated with feeding, which includes the mechanical cost of water transport and the physiological cost of digestive processes (Schneider 1992). Both components depend on the weight of mussel tissue and temperature (Schneider 1992; Aldridge et al. 1995). The active component is quite variable, depending on a number of ambient environmental conditions that remain poorly defined and unquantified (Effler et al. 1998).

ZOD is exerted at the river bottom because of the sessile habitat of zebra mussels (Table 1). The magnitude of the oxygen sink exerted by the invader depends on the area of colonization and the density (i.e., biomass), size structure (Schneider 1992; Effler et al. 1996), and metabolic state (i.e., ambient environmental conditions) of the mussel population. Thus, it is appropriate to express the ZOD (Effler et al. 1996) in the same areal units used for SOD ($g \cdot m^{-2} \cdot day^{-1}$) and to accommodate this new oxygen sink in the DO mass balance in the same manner [(1)]. The dynamics of ZOD are deter-

mined here for the cut (with the simplifying assumption that ZOD is uniformly distributed along the bottom of this river section) for the study period using the mass balance model.

Modeling Protocol

Initial conditions were based on measured T and DO profiles at buoys 409 and 397 on June 29, 1994. These observations were linearly interpolated in space (i.e., longitudinally and vertically) such that all model cells were assigned an initial value of these two state variables. Upstream boundary conditions were those measured at buoy 409. The necessary vertical resolution for the configuration of the model cells at this site was obtained from linear interpolation of the values from the two monitored depths (Table 1).

The model's autosteppping algorithm (Cole and Buchak 1995) calculates a maximum time-step, within a specified range, based on hydrodynamic numerical stability requirements, and then uses a fraction of this value for the actual time-step. The minimum and maximum time-steps were 1 s and 1 h, respectively. Boundary and meteorological conditions were supplied to the model at hourly intervals, Q daily, and Chl weekly. Linear interpolations of these reports were conducted by the model consistent with the autosteppping algorithm. Chlorophyll concentrations were specified from measurements for this modeling effort. Values of Chl were interpolated vertically and longitudinally, such that all model cells were assigned a concentration. Model simulations were conducted for the June 29–October 25 interval of 1994. Values of ZOD were specified in calibration at time-steps ≥ 1 day; i.e., no variations within a day were allowed.

MODEL PERFORMANCE AND APPLICATION

Calibration

Performance

Several salient features of the complex patterns observed for DO at the downstream station, and depletion over the study reach, were selected as metrics of the performance of the calibrated model (Figs. 4 and 5). The strong variations in these measures (Figs. 4 and 5) reemphasize the highly dynamic character of the signatures imparted by the array of forcing conditions over the study period. Model testing considered (1) vertical differences; (2) daily average DO concentrations at the downstream buoy (Figs. 4(a), 4(b), 4(c), and 4(f)); (3) differences in daily average DO between the upstream and downstream sites (Figs. 4(e), 4(d), 4(g), and 4(h)); (4) magnitudes (Figs. 4(i) and 4(j)) and distributions of magnitudes (Figs. 4(k) and 4(l)) of the maximum difference in DO within individual days (diurnal); and (5) DO concentrations measured hourly at the downstream buoy (Fig. 5). Conditions before the mid-August "washout" of zebra mussels have been differentiated from those after (two symbols, Figs. 4(a)–(j)).

The model performed well in matching the complex patterns of DO documented at the downstream site and the DO depletion over the study reach. The largest deviations between predictions and observations occurred in the interval before the washout (Figs. 4(a) and 4(b)) when the zebra mussel population (Fig. 3(e)) and DO depletion (Figs. 4(c) and 4(d)) were the greatest. The calibrated model explained 79% of the variability observed in DO concentrations at the downstream site (Figs. 4(e) and 4(f)) and $\geq 74\%$ of the DO depletion across the study reach (Figs. 4(g) and 4(h)), for both the upper and the lower river depths. Model performance was particularly impressive in simulating the vertically disparate signatures in DO depletion across the cut (Figs. 4(c) and 4(d)) during the low Q interval before the washout, features that depended importantly on the proper accommodation of incomplete vertical mixing and ZOD (also subsequently).

→ what about Chl initial/boundary conditions

→ How Chl model kept speci

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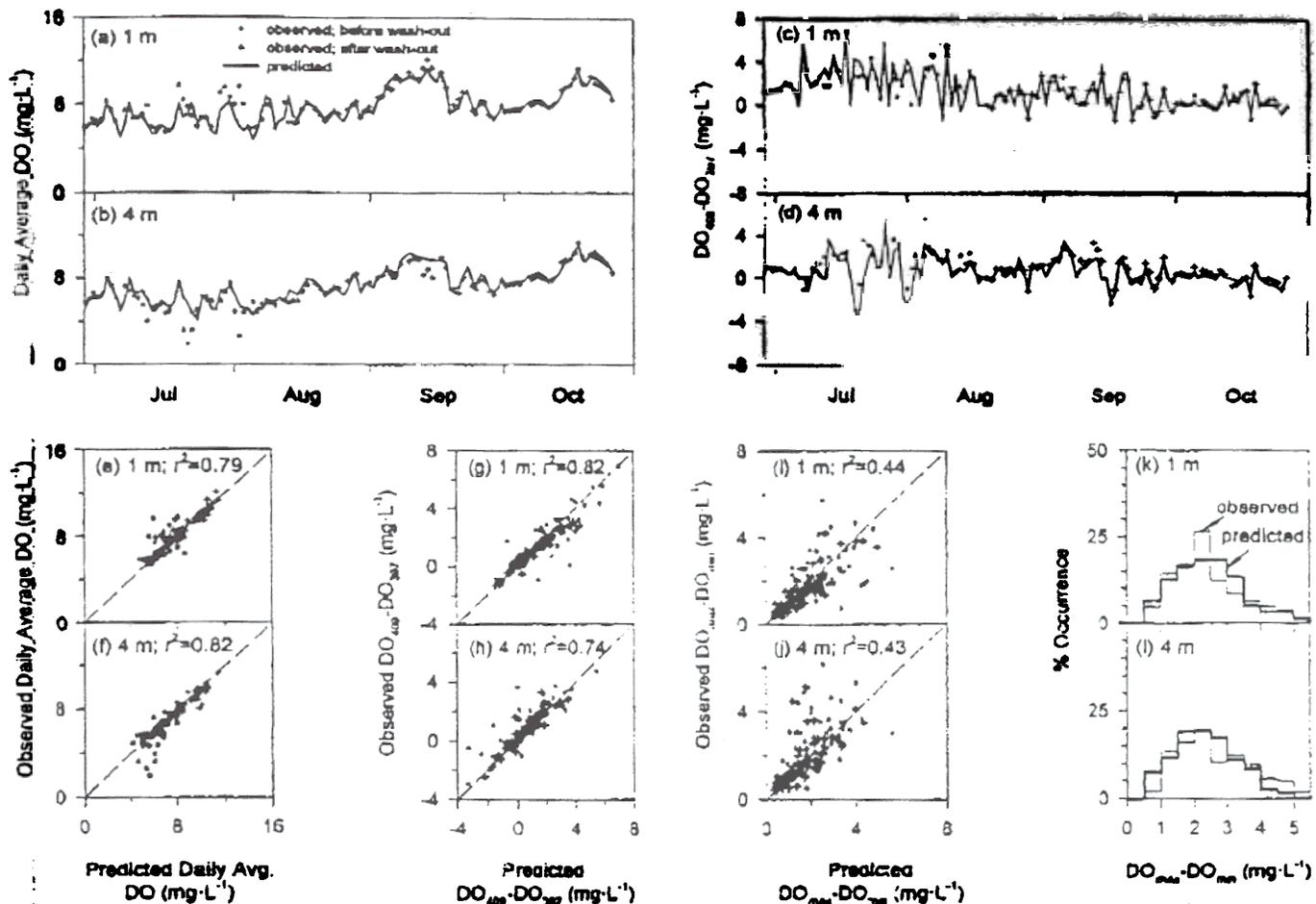


FIG. 4. Features of Model Performance at Buoy 397: (a) Daily Average DO at 1 m; (b) Daily Average DO at 4 m; (c) Differences in Daily Average DO between the Upstream and Downstream Sites at 1 m; (d) Differences in Daily Average DO between the Upstream and Downstream Sites at 4 m; (e) Observed versus Predicted Daily Average DO at 1 m; (f) Observed versus Predicted Daily Average DO at 4 m; (g) Observed versus Predicted DO Differences between the Upstream and Downstream Sites at 1 m; (h) Observed versus Predicted DO Differences between the Upstream and Downstream Sites at 4 m; (i) Observed versus Predicted Diurnal Range in DO ($DO_{max} - DO_{min}$) at 1 m; (j) Observed versus Predicted Diurnal Range in DO ($DO_{max} - DO_{min}$) at 4 m; (k) Comparisons of Observed and Predicted Distributions of the Diurnal Range in DO ($DO_{max} - DO_{min}$) at 1 m

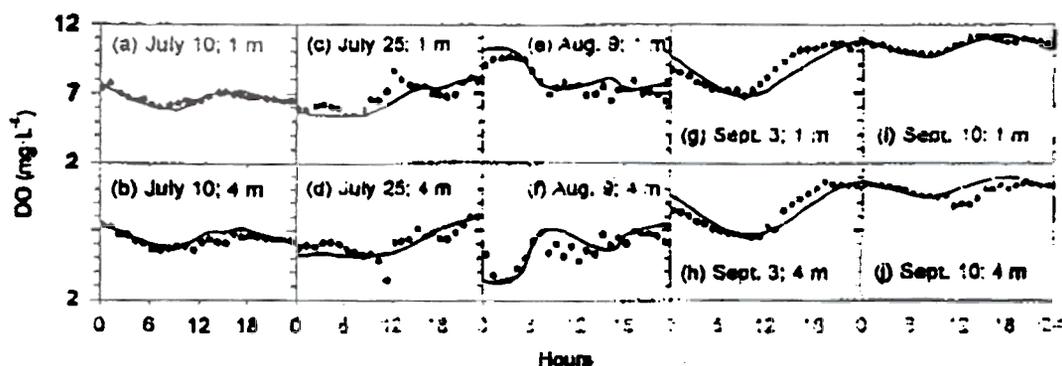


FIG. 5. Performance of Model in Simulating Diurnal Variations in DO for Selected Days: (a) July 10, 1 m; (b) July 10, 4 m; (c) July 25, 1 m; (d) July 25, 4 m; (e) August 9, 1 m; (f) August 9, 4 m; (g) September 3, 1 m; (h) September 3, 4 m; (i) September 10, 1 m; (j) September 10, 4 m

The performance of the model in simulating diurnal variations in DO, driven largely by phytoplankton activity, was somewhat less impressive than for daily average DO and DO depletion across the cut. However, this feature of model performance is considered quite good in light of the difficulties of such simulations (Thomann and Mueller 1987) and the complexities of the biochemical processes involved (e.g., influence of phytoplankton composition on kinetic coefficients) (Bolin et al. 1985). Predictions and observations of diurnal

ranges tended toward an equivalency, but substantial scatter in performance (between different days) was observed for this metric [Figs. 4(i) and 4(j)]. The observed and predicted distributions of diurnal variations in DO for both the upper and the lower depths matched reasonably well [Figs. 4(k) and 4(l)]. Simulations of the detailed temporal patterns of DO concentrations within individual days varied from good at both depths [Figs. 5(a)–(d) and 5(g)–(j)] to fair for both depths [Figs. 5(e) and 5(f)].

of course
its knob-tuning!

ZOD

The temporal pattern of ZOD in the cut determined by calibration (Fig. 6) depicts wide variations in the level of respiration by the resident zebra mussel population. Several factors support the position that the primary features of this pattern are real; i.e., the pattern is not an artifact of "knob-tuning" in model calibration, attributable to limitations in the measurements of the state variable, model inputs, or the model framework. Effler et al. (1998) reviewed several potential sources of error in these measurements and concluded they were minor. The pattern of ZOD determined here matched closely the distribution reported by Effler et al. (1998) (Fig. 6) that was based on a simplified DO budget calculation (conducted on daily average concentrations). The population of ZOD values was shifted lower following the washout (Fig. 6), consistent with the dependence of respiration on population density (Schneider 1992; Effler et al. 1996) and temperature (Aldridge et al. 1995). Further, the ZOD values reported here, when normalized for estimates of resident zebra mussel biomass (Effler et al. 1997a), demonstrate reasonable consistency with laboratory rates (Table 3). The average biomass-specific ZOD value for the low Q interval of mid-July to mid-August (average $T = 25^{\circ}\text{C}$) compares favorably with the laboratory rate(s) reported by Aldridge et al. (1995) (Table 3) for similar temperatures for specimens collected from the nearby Niagara River. Further, the results of laboratory experiments on single (Aldridge et al. 1995), as well as seasonal (Stoockmann and Garton 1997), collections establish that the metabolic rates of this invader are subject to substantial variation, as depicted by the ZOD pattern obtained for the cut (Fig. 6 and Table 3).

The magnitude of ZOD should be expected to vary not only with changes in biomass and size distribution of the population of the bivalve, but also in response to changes in ambient conditions and related stresses to the invader. The average ZOD in the cut for the July 1–15 interval, when flow was much higher and variable [Fig. 3(a)], was substantially greater

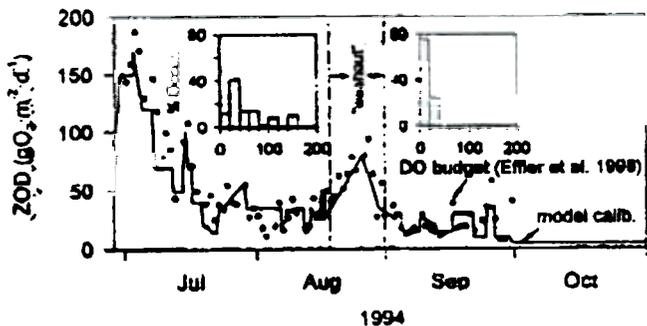


FIG. 6. Temporal Distribution of ZOD in the Cut Determined by Model Calibration; Values Based on Simple Budget Calculations (Effler et al. 1998) Included for Comparison

TABLE
Cut of
Conqui

Study/condition	Rate
	(mean \pm standard deviation) ($\text{mg O}_2 \cdot \text{g}^{-1} \cdot \text{zm} \cdot \text{day}^{-1}$)
(a) Cut, Seneca River	
July 1–July 15, 1994	116.2 \pm 40.2
July 16–August 15, 1994	39.2 \pm 17.7
(b) Laboratory (Aldridge et al. 1995)	
20°C	38.9 \pm 9.6
24°C	58.8 \pm 11.5
28°C	101.0 \pm 33.4
32°C	142.1 \pm 54.5

Why does
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than that found for the mid-July to mid-August interval (Fig. 6), but was well within the range of average laboratory rates reported for higher temperatures (Aldridge et al. 1995) (Table 3). Resuspension of feces and pseudofeces from the zebra mussel beds may have contributed to the increased oxygen demand during this high flow interval, but the contribution is believed to have been minor, as it is unlikely it would exceed the magnitude of a high SOD value (e.g., $5\text{--}10 \text{ g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) (Fig. 6). The laboratory rates for $T \geq 28^{\circ}\text{C}$ (Table 3) depict stress, as the expenditure of energy by the mussels (respiration) exceeded the capacity to compensate by feeding (Aldridge et al. 1995). The more likely reason for higher ZOD values (Fig. 6) and normalized oxygen demand values during this interval is stressful conditions for the invader. Potential environmental sources of variation in zebra mussel respiration (and stress) include variations in size, composition, and concentration of potential food particles (Lei et al. 1996; Baker et al. 1998), concentration of nonfood particles (e.g., inorganic turbidity) (Aldridge et al. 1995; Summers et al. 1996; Madon et al. 1998), turbulence (Strayer et al. 1994), temperature (Aldridge et al. 1995), and reproductive state (Stoockmann and Garton 1997).

Various empirical relationships were evaluated for potential drivers of the variability in ZOD in the cut over the July to mid-August interval, the period of the highest zebra mussel population density [Fig. 3(e)]. No relationships were observed over this interval for Chl or T . However, a strong positive relationship between ZOD and Q was observed ($\text{ZOD} = 1.0Q - 21.56$; $R^2 = 0.82$; significant at the 1% level). It is unlikely that increased Q , and the attendant increased velocity and turbulence, were the direct cause for higher ZOD values. It is more likely that other changes that accompanied increased flow were the direct stimulus for higher respiration rates. In particular, the quality of food supplied to the cut, as measured by the fraction of total suspended solids (TSS) as VSS (Madon et al. 1998), was lower during the high flow interval of early July (Fig. 3(c)), when the water was more riverine in character, associated with short-circuited flow through Cross Lake (Effler et al. 1989). Under these conditions the zebra mussels must work harder (increased pseudofeces production in response to higher concentrations of inorganic particles) to acquire the same amount of food. This potential interaction was supported by the negative relationship between ZOD and the ratio VSS/TSS before the washout interval ($\text{ZOD} = -102.2 \cdot \text{VSS}/\text{TSS} + 81.26$; $R^2 = 0.52$; significant at the 10% level).

The oxygen demand associated with the zebra mussel population of the cut was extremely high over the study period. Comparison with a value for SOD for organic-rich deposits (e.g., $5 \text{ g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) (Bowie et al. 1985) provides an appropriate perspective to consider the magnitude of ZOD reported for the cut. The average value of ZOD over the low flow interval of mid-July to mid-August ($\sim 40 \text{ g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, Fig. 6) was nearly an order of magnitude greater. Even after the washout the average value of ZOD during the low flow interval of early September (Fig. 6) was about twice as great as an upper bound value of SOD.

Model Analyses

Sensitivity

Analyses were conducted with the model to depict the sensitivity of predictions to variations and reasonable levels of uncertainty in inputs. Failure to accommodate the dynamics in ZOD (Fig. 6) over the study period (i.e., uniform values invoked, corresponding to the averages before and after washout) compromised substantially the model's performance in predicting the seasonality of DO depletion across the cut [Fig. 7(a)]. The effect was greatest during the low Q interval before

the washout. Reasonable changes in the rates of the other source and sink processes [(5)] resulted in relatively minor differences in this feature of model performance. Simulation of the short-term (e.g., diurnal) dynamics associated with phytoplankton activity remains a complex problem (Thomann and Mueller 1987; Chapra 1997) with a number of sources of variability and uncertainty. The effects of four potential sources of variability in simulating the diurnal range of DO are depicted here as follows: (1) detailed specification of incident light patterns within individual days, versus a typical (e.g., average) diurnal pattern [Fig. 7(b)]; (2) uncertainty in specification of k_d ($\pm 25\%$) from Secchi disk measurements (Effler 1985) [Fig. 7(c)]; (3) uncertainty in the stoichiometry of phytoplankton cells [$a_{CP} = 50-100$, Fig. 7(d)] (Chapra 1997); and (4) combined effects of differences in the treatment of phytoplankton respiration and the magnitude of μ_{max} [compared to kinetics of Canale et al. (1995)] [Fig. 7(e)]. The effects of

these sources of variability were generally the greatest in early September [Figs. 7(b)-(e)] when the highest Chl values were observed [Fig. 3(b)]. These effects ranged from modest to substantial, and together contributed to the observed variability in performance in simulating the diurnal range of DO [Figs. 4(i) and 4(j)]. Success in simulating the observed vertical structure in DO at the downstream site (Fig. 4) was critically dependent on the magnitude of D_v [Fig. 7(f)]. Stratified concentrations of DO were eliminated at magnitudes of five times greater than the calibration values, while the predicted vertical differences increased substantially beyond observations at 0.5 times the calibration values [Fig. 7(f)].

Resolution of Regulating Processes

The model was used to investigate the processes that contributed to the observed patterns in DO at the study site. The new DO sink associated with the zebra mussel invasion (ZOD) was essentially completely responsible for the substantial average DO depletion across the cut of $2.1 \text{ mg} \cdot \text{L}^{-1}$ for the study period (Fig. 8). This outcome is not substantively influenced by reasonable changes in the other source/sink processes associated with uncertainties in their kinetics. The other source and sink processes were nearly in balance (Fig. 3), supporting the assumption invoked by Effler et al. (1998) in estimating ZOD for this stream reach with a simple budget calculation approach (no predictive capability for DO). Further, this near balance of the processes other than ZOD is consistent with the position that DO concentrations remained relatively uniform downstream of Cross Lake before the zebra mussel invasion.

Features contributing to the pronounced diurnal and vertical signatures were resolved on a study-average basis by sequential inclusion of forcing conditions (Fig. 9). Invoking the daily average DO uniformly at the upstream boundary and eliminating phytoplankton kinetics essentially eliminated diurnal variations in DO [run number 1, Fig. 9(a)]. Approximately 65% of the average diurnal variation was attributable to phytoplankton activity [P/R; run number 3, Fig. 9(a)], while about 35% was associated with the diurnal pattern that entered the study reach at the upstream boundary [run number 4, Fig. 9(a)]. About two-thirds of the overall P/R effect was associated with the inclusion of the related kinetics [run number 2, Fig. 9(a)]; the remainder was attributable to accommodating the diurnal incident light pattern [run number 3, Fig. 9(a)]. About 25% of the vertical difference in DO on average, was attributable to limited vertical mixing [low D_v , Fig. 9(b)]. The remainder of the DO stratification at the downstream buoy was associated with the localization of the large DO sink at the river bottom [Fig. 9(b)].

Longitudinal Extension

A preliminary simulation is presented for the cut to Baldwinsville reach (Fig. 10) to demonstrate the utility of the

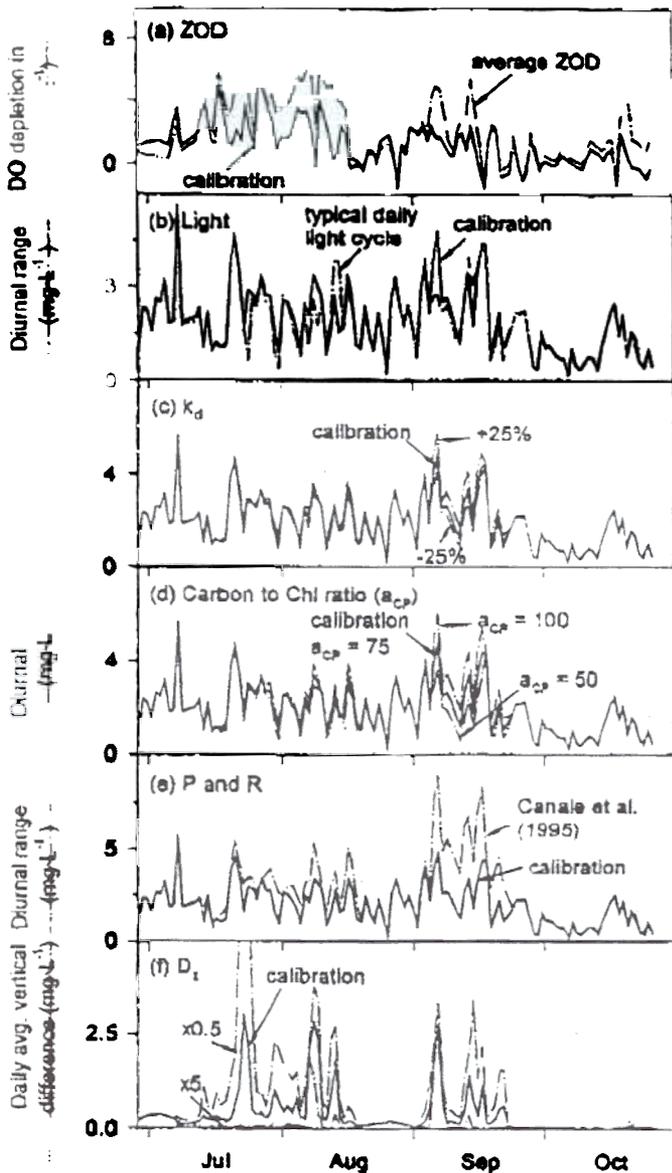


FIG. 7. Model Sensitivity Analyses: (a) ZOD for DO Depletion in the Cut. Use of Average Values for Two Time Intervals (e.g., Fig. 3(e)), July to Mid-August, and Mid-August through October; (b) Light for Diurnal Range in DO, Use of a Typical Day's Light Cycle for Entire Study Period; (c) $k_d = \pm 25\%$ for Diurnal Range in DO; (d) Carbon to Chl Ratio for Diurnal Range in DO; (e) P and R for Diurnal Range in DO, Use of Submodel Described by Canale et al. (1995); (f) D_v , for Systematically Higher and Lower Values

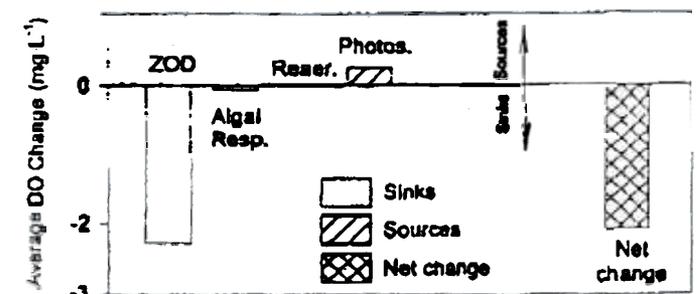


FIG. 8. Model Simulated Components (Sinks and Sources) of the DO Budget for the Cut of the Seneca River for the Study Interval of 1994

Diurnal inputs

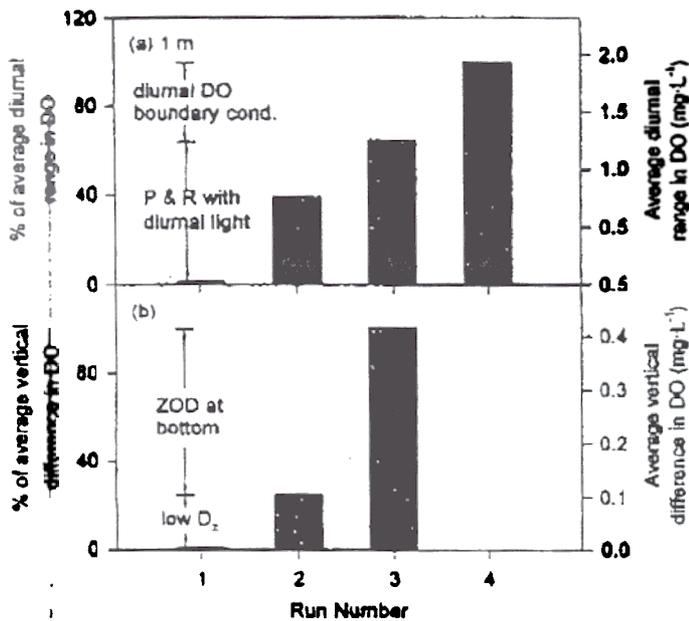


FIG. 9. Model Analyses to Partition Factors Contributing to Conditions at Buoy 397: (a) Average Diurnal Range in DO; (b) Average Vertical Difference in DO

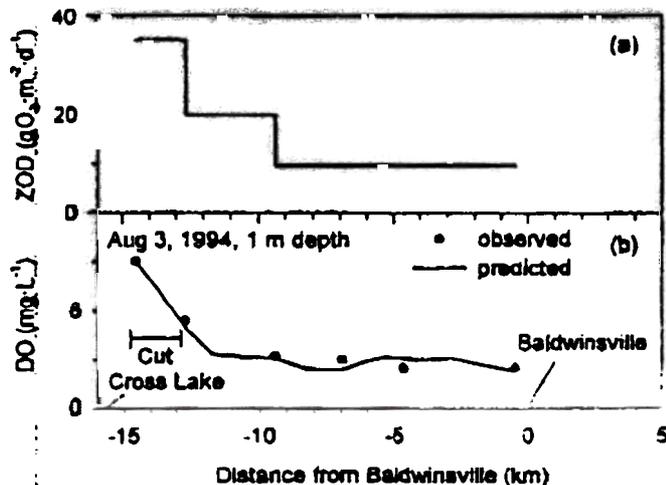


FIG. 10. Preliminary Application of DO Model for Seneca River Reach from the Upstream Boundary of the Cut (Buoy 407) to Baldwinsville, for the Conditions of August 3, 1994, Depth of 1 m: (a) Specified Longitudinal Distribution of ZOD [Fig. 6 and Effler and Siegfried (1998)]; (b) Comparison of Predictions of DO to Observations

framework for longer portions of the river. The specified longitudinal distribution of ZOD [Fig. 10(a)] has rather uneven support from biological monitoring. The resident zebra mussel population in the cut was reasonably well defined by spatially intensive surveys (Effler et al. 1997a), and the related oxygen demand was intensively evaluated (Fig. 6). However, the benthic surveys that supported the remainder of the longitudinal ZOD pattern were substantially more spatially limited (two sites over the remainder of the reach) (Effler and Siegfried 1998). The distribution of appropriate substrate, and therefore zebra mussels, was more "patchy" in these river sections, thereby introducing substantial uncertainty in the representativeness of estimated population densities and coupled estimates of ZOD [Fig. 7(a)].

The presented simulation is for a depth of 1 m [Fig. 10(b)]. The predictions for sites downstream of the cut are generally representative of the entire (vertical) water column of the river, as there was substantially less stratification in DO. The pre-

dictions for the various model cells correspond to the time of day of the DO measurements (Upstate Freshwater Institute, Syracuse, N.Y., unpublished data). The model performed well in matching the conspicuous DO depletion observed on this day over a 15 km reach of the river [Fig. 10(b)]. The substantially lower ZOD in the downstream portions of this reach, associated with the lower population densities (Effler and Siegfried 1998), apparently was a large enough sink for DO to prevent recovery from the major depletion affected by the more dense populations of the cut [Fig. 10(b)].

SYNTHESIS AND SUMMARY

The findings of this modeling effort have demonstrated that the zebra mussel invasion has resulted in substantial reductions in DO in the cut, and major depletions that extend at least 15 km downstream in the Seneca River, during summer low flow periods. The invasion has effectively resulted in the addition of a new oxygen sink to this river system, as well as for other rivers with substantial population densities (Caraco et al. 2000). This prompts questions concerning the source(s) of energy that drives ZOD and why this new DO sink has been manifested for this exotic invader instead of indigenous fauna. The zebra mussel is effectively converting upstream nutrient loading to an oxygen demand through feeding on the produced phytoplankton biomass. Phytoplankton growth is further promoted in this particular river system by an intervening lake. Previously, river eutrophication was primarily a concern for oxygen resources related to attendant diurnal swings in DO levels (Thomann and Mueller 1987). The potential oxygen demand of phytoplankton biomass (e.g., consider the results of a BOD test conducted on an unfiltered phytoplankton rich sample) was not exerted. The zebra mussel, through its rapid reproduction and growth, is out-competing indigenous fauna in the consumption of phytoplankton and more completely using this source of food. This new oxygen sink is expected to be decidedly smaller in most invaded rivers than that reported here (Madon et al. 1998), as the density of zebra mussels in the cut likely approaches an upper bound (e.g., worst case for rivers). However, even at 10% of the population density (and ZOD) of the cut (e.g., Hudson River; Caraco et al. 2000), this new oxygen sink would represent a major concern for the oxygen resources of rivers in many developed areas, corresponding in a high SOD such as that observed in systems with rich organic deposits (Bowie et al. 1985).

Reduction of upstream nutrient loading to decrease phytoplankton growth represents an appropriate management approach to limit the magnitude of this DO sink in affected rivers. However, the large number of relatively small discharges of treated domestic waste and diffuse agricultural inputs upstream of Cross Lake makes the feasibility of reducing the phytoplankton concentration in this lake's outflow, and thus downstream zebra mussel population densities, uncertain.

A two-dimensional dynamic mass balance DO model for rivers, that for the first time accommodates the sink associated with ZOD has been developed and successfully tested against the particularly complex patterns observed for the severely infested cut of the Seneca River. The model performed well in simulating important features of the DO patterns, including DO depletion across the cut, DO stratification, and diurnal variations. Model testing was rigorous in that simulations were compared to comprehensive measurements that documented detailed vertical and temporal patterns in DO over a four-month period. In particular, this one of the largest sets of diurnal DO data against which related simulation capabilities have been tested. Evaluations of model results were supported by comprehensive measurements of forcing conditions.

Wide variations in ZOD in the cut were determined over the study period through model calibration. Substantial reduc-

tions occurred following an abrupt reduction in biomass. The ZOD determinations were supported by closure with earlier estimates based on simple DO budget calculations (Effler et al. 1998), and with laboratory biomass-specific oxygen consumption rates (Aldridge et al. 1995) (Table 3). Higher ZOD values were obtained at elevated river flows—conditions that are generally not critical for the oxygen resources of rivers. The substantial variations determined for ZOD, even during low flow intervals, indicate that this variability needs to be considered in the development/specification of critical conditions for management applications of this DO model for infested systems.

Model analyses demonstrated that (1) ZOD was the dominant sink process within the cut responsible for the observed DO depletion; (2) the other source/sink processes were approximately in balance, on average; (3) the pronounced diurnal signature within the cut was driven largely by features of phytoplankton production and respiration (*P/R*), and secondarily by diurnal dynamics in DO input at the upstream boundary; (4) several sources of uncertainty and variability in inputs that drive the model's simulation of *P/R* contributed to the deviations between predicted and observed diurnal variations; and (5) the localization of ZOD at the river bottom, in combination with limited vertical mixing, was responsible for the substantial DO stratification observed during low *Q* intervals.

The DO model performed well in a preliminary simulation of the strong depletion observed over a 15 km reach of the Seneca River. Research is ongoing to further extend the DO model through the river system and to integrate other features of the invader's metabolism that have important ecological and water quality implications, including grazing and excretion. The complex predictive framework developed here, and future enhancements, will have great utility for managers for this and other invaded river systems in quantifying the potentially profound water quality impacts of this invader and in evaluating related management strategies.

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NOTATION

The following symbols are used in this paper:

- A = cross-sectional area of segment (m^2);
- a_{CP} = carbon to chlorophyll ratio ($mg \cdot mg^{-1}$);
- a_{OC} = oxygen to carbon ratio ($mg \cdot mg^{-1}$);
- CBOD = concentration of carbonaceous biochemical oxygen demand ($g \cdot m^{-3}$);
- CBOD_u = concentration of ultimate CBOD ($g \cdot m^{-3}$);
- Chl = chlorophyll concentration ($g \cdot m^{-3}$);
- D_z = vertical eddy diffusivity coefficient ($m^2 \cdot s^{-1}$);
- DO_s = surface layer DO concentration ($g \cdot m^{-3}$);
- DO_{sat} = DO concentration at saturation ($g \cdot m^{-3}$);

- $f(I)$ = light limitation factor (dimensionless);
- $f(N)$ = nutrient limitation factors (dimensionless);
- $f(T)$ = temperature limitation factor (dimensionless);
- H_s = surface layer height (m);
- I = photosynthetically available solar radiation ($\mu E \cdot m^{-2} \cdot day^{-1}$);
- K_L = light half-saturation constant ($\mu E \cdot m^{-2} \cdot day^{-1}$);
- K_L = oxygen transfer coefficient ($m \cdot day^{-1}$);
- k_b = basal component of phytoplankton respiration (day^{-1});
- k_c = CBOD decay rate (day^{-1});
- k_d = light attenuation coefficient (m^{-1});
- k_r = NBOD decay rate (day^{-1});
- NBOD = concentration of nitrogenous biochemical oxygen demand ($g \cdot m^{-3}$);
- P = gross photosynthetic production of oxygen ($gO_2 \cdot m^{-3} \cdot day^{-1}$);
- Q = flow ($m^3 \cdot s^{-1}$);
- R = uptake of oxygen due to phytoplankton respiration ($gO_2 \cdot m^{-3} \cdot day^{-1}$);
- r = phytoplankton respiration rate (day^{-1});
- SOD = sediment oxygen demand ($g \cdot m^{-2} \cdot day^{-1}$);
- T = temperature ($^{\circ}C$);
- t = time of travel (h);
- W_b = width of channel cross section at bottom of segment (m);
- W_t = width of channel cross section at top of segment (m);
- ZOD = zebra mussel oxygen demand rate ($g \cdot m^{-2} \cdot day^{-1}$);
- μ = growth rate of phytoplankton (day^{-1});
- μ_{max} = maximum growth rate of phytoplankton at 20 $^{\circ}C$; and
- ϕ = coefficient for active component of phytoplankton respiration (dimensionless).