



A River Water Quality Model for Chlorophyll and Dissolved Oxygen that Accommodates Zebra Mussel Metabolism

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Abstract. The development, testing and application of a dynamic two-dimensional (longitudinal-vertical) mass balance model for dissolved oxygen (DO) and chlorophyll (Chl) for rivers is documented that for the first time accommodates both the oxygen demand and filtering effects of zebra mussels. The test system is a phytoplankton-rich section (~ 15 km long) of the Seneca River, NY, that is believed to represent an upper bound of the impact of this exotic invader. Changes in common measures of water quality of the river brought about by the zebra mussel invasion are reviewed and related longitudinal patterns in DO, Chl, and Secchi disc transparency are documented. Model testing is supported by comprehensive measurements of DO, Chl, and various forcing conditions over a three-month period, and independent determinations of several model coefficients. Wide variations in the areal consumption rate of DO (ZOD; $\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) and filtering rate ($\text{m}^3\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) of zebra mussels, as determined through model calibration, occurred over the study period. Values of ZOD in areas with dense zebra mussel populations at times (e.g., $> 50 \text{ g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) were an order of magnitude greater than the sediment oxygen demand associated with organically enriched deposits. The value of determinations of these fluxes from model calibration procedures is evaluated within the context of the limitations of protocols presently available to support independent specification of these rates. Model analyses are conducted to evaluate the relative magnitude of source and sink processes for DO and Chl, the potential operation and implications of feedback from low DO levels on oxygen consumption by zebra mussels, and the sensitivity of model simulations to selected sources of uncertainty and variability. Model projections of oxygen resources of the river are presented in a probabilistic format in evaluating reductions in zebra mussel biomass that would be necessary to eliminate violations of standards and regain assimilative capacity.

Keywords: zebra mussels, modeling, water quality, Seneca River, dissolved oxygen

1. Introduction

Exotic bivalves have caused dramatic changes in the structure and function of invaded estuaries (Alpine and Cloern, 1992; Cohen et al., 1984), lakes (MacIsaac, 1996), and rivers (Strayer et al., 1999). Major related shifts in features of water quality have been reported where dense populations of these invaders have developed, associated with various aspects of their metabolism (Alpine and Cloern, 1992; Caraco et al., 1997; Effler et al., 2001; Howell et al., 1996). Water quality models developed before invasions occurred can be rendered essentially useless where dense populations have developed, because the effect of the invader's metabolism on the cycling and fate of key constituents was not accommodated. Model frameworks need to be modified to integrate key features of the

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

Feature (1)	Description/Comment: (2)
life span	2 to 5 years
adult shell size	25 to 35 mm long
Attachment to substrate	sessile organism; byssal threads to solid substrate
reproduction	2 to 5 spawnings·y ⁻¹ ; fertilization at 12 to 24° C
Dispersal	swimming larvac-veligers; in plankton 1 to 5 wks
feeding	filter feeder, particles >1 μm diameter
waste production	feces, pseudofeces [rejected (e.g., inorganic) particles], and enriched excretions
environmental requirements	salinity ≤ 4 ppt; pH ≥ 7.3; Ca ²⁺ conc. ≥ 20 mg·L ⁻¹ ; solid substrate; food particles (e.g., phytoplankton)

metabolism of these invaders if managers are to continue to have quantitative tools to guide related deliberations for these invaded ecosystems (Chapra, 1997; Thomann and Mueller, 1987). Further, an appropriately modified mass balance model, when supported by comprehensive monitoring and process information, represents a powerful analytical tool to quantify fluxes associated with the invader under field (e.g., versus laboratory) conditions.

The zebra mussel (*Dreissena polymorpha*, Pallus), a small bivalve native to Southern Russia, has been one of the most successful invaders of North America (Ludyanskiy et al., 1993). Selected features of the biology of this invader are summarized in Table 1. Since its introduction into the Laurentian Great Lakes in the mid-1980s this bivalve has spread rapidly throughout the Northeast and much of the Southeast and Midwest of the United States, and much of Canada (New York Sea Grant 2000). Zebra mussels require slightly alkaline waters with adequate Ca²⁺ concentration, solid substrate to support colonization, and food, mostly in the form of phytoplankton (Table 1) – conditions that are common to many surface water ecosystems. The rapid geographic expansion of this invader reflects its high reproductive and dispersal potential (Ramacharan et al., 1992) and the absence of effective predators and parasites (Ludyanskiy et al., 1993). Population densities of severely infested portions of the Great Lakes have exceeded 100,000 individual·m⁻² (e.g., Leach, 1993). Major changes in water quality have been documented where dense populations have developed, including: (1) decreases in phytoplankton and tripton concentrations and increases in transparency associated with filter feeding (e.g., Caraco et al., 1997; Effler et al., 2001; Fahnenstiel et al., 1995; Reeders and bij de Vaate, 1990), (2) depletion of dissolved oxygen (DO) from respiration (e.g., Caraco et al., 2000; Effler and Siegfried, 1994; 1998), and (3) increases in ambient nutrient concentrations from excretion (e.g., Arnott and Vanni, 1996; Effler et al., 2001; Effler and Siegfried, 1998; Johengen et al., 1995). Areal material fluxes (e.g., mg·m⁻²·d⁻¹) exerted at lake or river bottoms associated with dense populations, consistent with the sessile habitat of this bivalve, have been found to be large (e.g., 10 times greater) compared to those associated with enriched sediments (Effler et al., 1996; 1997; 1998a).

The generally simpler hydrodynamic regime of lotic versus lentic systems offers some advantages for initial development, testing and application of a water quality model framework modified to accommodate features of zebra mussel metabolism. First, rivers with dense populations can have rather stable and conspicuous longitudinal patterns in water quality parameters, (e.g., Caraco et al., 1997; Effler et al., 2001) that facilitates the modeling effort. The river setting also largely eliminates the hydrodynamic complexities of the extent/frequency of exposure of pelagic waters of lakes and estuaries to benthic areas (bivalve beds) that may cover only a limited portion of the bottom (Gerritsen and Irvine, 1994; Reed-Anderson et al., 2000). Further, the limited oxygen resources of many large rivers in developed areas, that have little or no assimilative capacity to lose to a new oxygen sink process (Gelda et al., 2000) because of inputs of oxygen-demanding wastes, represent a potentially acute problem requiring appropriate modifications in model frameworks. For example, oxygen depletion from zebra mussels has been reported 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 et al., 1996; Effler et al., 2000), and the Oswego River (Effler and Siegfried, 1998).

This paper documents the conspicuous longitudinal patterns in DO, Secchi disc transparency (SD), and concentration of chlorophyll *a* (Chl) imparted to a 15 km reach of the Seneca River, NY, by zebra mussels. A dynamic two-dimensional mass balance model for DO and Chl is developed, applied to determine patterns of oxygen demand [zebra mussel oxygen demand (ZOD; Effler et al., 1996); $\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$] and effective filtering rate [grazing (Caraco et al., 1997); $\text{m}^3\cdot\text{m}^{-2}\cdot\text{d}^{-1}$] associated with zebra mussels, and tested for conditions that prevailed for the reach before the invasion. Features of the monitoring program that supported the modeling effort are described. Model analyses are conducted to evaluate the relative magnitude of source and sink processes for DO and Chl, the potential operation of feedback from low DO levels on oxygen consumption by zebra mussels, and the sensitivity of model simulations to selected sources of uncertainty and variability. Model projections of DO for the downstream boundary of the study reach are provided as a function of zebra mussel biomass, to evaluate reductions in biomass that would be necessary to eliminate violations of standards and regain assimilative capacity for downstream sections of the river.

2. System Description

The study reach of the Seneca River extends from 1.3 km downstream of Cross Lake to Baldwinsville (Fig. 1). This is a nearly ideal system to support development and testing of a water quality model to accommodate and investigate zebra mussel metabolism because: (1) it has supported dense populations of zebra mussels that have been partially quantified by benthic surveys (Effler et al., 2001), (2) conspicuous signatures of water quality have been imparted by the invasion (Effler et al., 2001; and subsequently presented), (3) the reach receives no wastewater or tributary inputs that could complicate the analysis, (4)

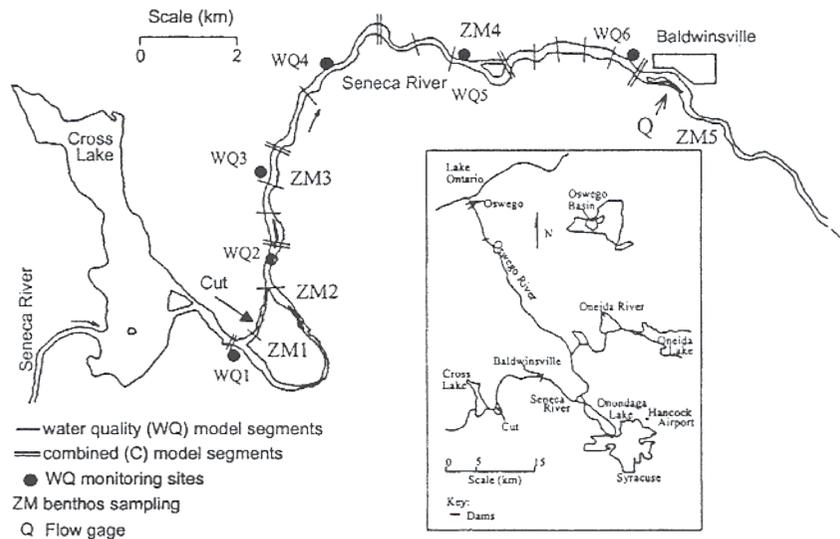


Figure 1. Study reach of the Seneca River, with model segments and monitoring sites, and its position in the larger river system.

morphology, hydrology and transport are well quantified, (5) water quality conditions are comprehensively specified by monitoring data, and (6) certain simplifying assumptions are appropriate for the system.

2.1. Setting

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). Oswego River, formed by the combination of the Seneca and Oneida Rivers, is the second largest inflow to Lake Ontario (Fig. 1), after Niagara River. Flow is gaged continuously at Baldwinsville by the U.S. Geological Survey. Values at this location are representative of the study reach (Coon, 1994). The annual average flow of the Seneca River at Baldwinsville for the 1951 to 1999 period was 97.5 m³·s⁻¹. The minimum average flow for a seven-day interval that occurs once in every ten years (7Q10) is 11.2 m³·s⁻¹; the 30Q10 is 15.8 m³·s⁻¹.

The river system is used for navigation (part of Barge Canal, minimum channel depth of 4.5 m), power generation, fishing, contact recreation, and waste disposal. The natural hydrodynamic features of the system have been greatly modified to support some of these uses, that has resulted in increased average water depth and reduced turbulent mixing and thereby diminished the reaeration capacity of the system (Canale et al., 1995). The domestic waste loads from the largest urban area in the watershed,

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Syracuse, are received by Onondaga Lake; the outflow from this lake enters the river 7.8 km downstream of Baldwinsville (Fig. 1). Onondaga Lake (surface area of 12 km² and mean depth of 10.9 m) is severely polluted as a result of the reception of this waste (Effler, 1996). The leading alternative for rehabilitation of Onondaga Lake before the zebra mussel invasion was diversion of Syracuse's domestic wastewater effluent (following treatment upgrade) from the lake to the Seneca River. Thus the assimilative capacity of this portion of the river, which is strongly influenced by DO levels at Baldwinsville (Canale et al., 1995), is an important management issue for the region. The rehabilitation plan for Onondaga Lake now specifies a continued discharge to the lake because of the systematic reductions in the assimilative capacity of the river brought about by the zebra mussel invasion (Effler et al., 1996; 2001).

Cross Lake (Fig. 1; surface area of 9 km², mean depth of 5.5 m, complete mixed flushing rate of ~ 50 times \cdot y⁻¹) and upstream inputs of domestic waste and agricultural runoff play important roles in supporting the zebra mussel population, and thereby water quality conditions, in the study reach (Effler et al., 2001). This intervening lake (Fig. 1) essentially acts to convert nutrient loading carried by upstream portions of the river to phytoplankton biomass (Effler et al., 2001). The lake is hypereutrophic (Effler and Carter, 1987) and infested with zebra mussels (Effler et al., 2001). Water exiting Cross Lake during summer low flow intervals largely reflects lake-wide epilimnetic conditions (e.g., Effler et al., 1989). However, during high runoff intervals substantial short-circuiting of the river inflow to the lake outlet occurs (Effler and Carter, 1987; Schindel et al., 1977). Cross Lake sustains dense zebra mussel populations, and related water quality impacts, downstream of its outflow by acting as a continuing source of veligers (Table 1) and suitable food for this bivalve (Effler et al., 2001). This lake functions in at least two important ways related to food supply for the invader (Effler et al., 2001): (1) by providing high concentrations of edible particles in the form of phytoplankton, and (2) by reducing the concentration of inorganic particles supplied from upstream portions of the river (through deposition), and thereby improving the quality of food delivered downstream (Madon et al., 1998).

The "State Ditch Cut" (Cut; Fig. 1), a 1.7 km channel, is one of a number of anthropogenic alterations of the river (e.g., channelized, dams, and locks) to support its multiple uses. The Cut carries more than 90% of the river flow (Coon, 1994), as the natural "horseshoe" river course (Fig. 1) is largely silted-in. Organic deposits occur between the lake outlet and the Cut and in certain shallow areas along the shores of the study reach, but are largely absent from the main channel of this reach. Rock, of cobble size or greater, covered most of the bottom of the Cut until after dense populations of zebra mussels were well established (Effler et al., 1997). Generally, cobble size rock makes progressively less of a contribution, and sand and gravel more, moving from the Cut towards Baldwinsville (Effler and Siegfried, 1994). The invasion has caused some change in substrate character, as empty zebra mussel shells now cover substantial portions of the bottom in certain sections, though there are no indications of progressive (e.g., from multiple years) accumulation of this debris (Effler et al., 2001).

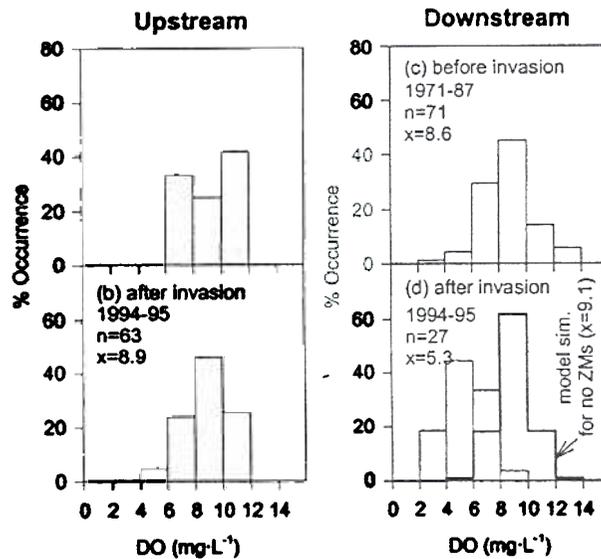


Figure 2. Comparison of distributions of DO concentrations at the bounds (upstream/downstream) of the study reach before and after the zebra mussel invasion: (a) upstream before invasion, observed, (b) upstream after invasion, observed, (c) downstream before invasion, observed, and (d) downstream after invasion, observed and simulated for case of no zebra mussels (n = number of observations, x = average concentration).

2.2. Zebra Mussel Invasion and Shifts in Water Quality

Zebra mussels had colonized the Seneca River both upstream and downstream of Cross Lake by late 1991 (New York Sea Grant, 1998). Bottom surveys (first with an Ekman dredge and subsequently by SCUBA) commenced in August 1993 in response to decreases in DO concentrations observed near Baldwinsville (Effler and Siegfried, 1994; Effler et al., 1996). Zebra mussels were found to occupy essentially all available solid (mostly rock) substrate > 3 cm in diameter along the bottom of the river from Cross Lake to Baldwinsville (Effler and Siegfried, 1994). The most dense populations of the bivalve were observed in the Cut, where densities ranged from 33,000 to 61,000 individuals·m⁻² (Effler and Siegfried, 1994). Continued colonization, growth, and loss of the bivalve have been reported in this portion of the study reach based on monitoring of the benthos conducted through 1998 (Effler et al., 2001). These results indicate this portion of the Seneca River represents an upper bound of infestation for rivers in North America with respect to population density and stability, conditions that are consistent with this reach's reception of productive lake water (Effler et al., 2001).

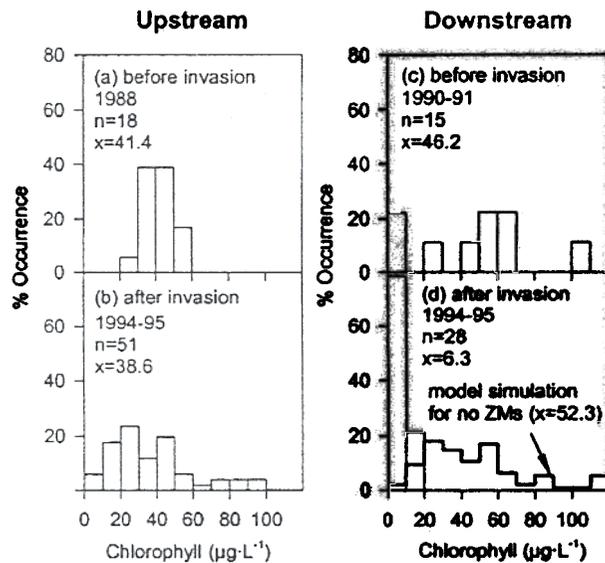


Figure 3. Comparison of distributions of Chl concentrations at the bounds (upstream/ downstream) of the study reach before and after the zebra mussel invasion: (a) upstream before invasion, observed, (b) upstream after invasion, observed, (c) downstream before invasion, observed, and (d) downstream after invasion, observed and simulated for case of no zebra mussels (n = number of observations, x = average concentration).

The available data establishes that commonly measured features of water quality, such as DO (Fig. 2), Chl (Fig. 3), SD, and nutrient [ammonia (T-NH_3), soluble reactive (SRP) and total phosphorus] concentrations remained largely unchanged between Cross Lake and Baldwinsville before the zebra mussel invasion (Effler et al., 2001). Further, these features of water quality in Cross Lake and immediately downstream of the lake have not changed since the invasion (Figs. 2 and 3). However, dramatic shifts in these common measures of water quality have been documented downstream near Baldwinsville (e.g., Figs. 2 and 3), as a result of the zebra mussel population in this reach (Effler et al., 1996; 2001). During summer low flow intervals, the invasion has converted this portion of the river from a low clarity, phytoplankton-rich, nutrient-depleted system, with nearly saturated oxygen concentrations, to a system with increased clarity, low phytoplankton levels, highly enriched in dissolved nutrients, with substantially undersaturated oxygen concentrations (e.g., Figs. 2 and 3; Effler et al., 1996; 2001). The degradation of oxygen resources has been severe enough to cause violations of New York State standards for daily minimum ($4 \text{ mg}\cdot\text{L}^{-1}$) and daily average ($5 \text{ mg}\cdot\text{L}^{-1}$) DO concentration (Effler et al., 1996). The water quality signature imparted by the invasion in the vicinity of Baldwinsville (e.g., Figs. 2 and 3) is the strongest reported to-date for a river in North America (Effler et al., 2001). Changes in

Table 2. Monitoring program supporting the DO and chlorophyll model testing for 1994 conditions.

Parameters (1)	Frequency (2)	Function (3)	Reference (4)
Field			
DO ^a	varied according to site	state variable	Effler et al. (1998)
temperature (T) ^a	varied according to site	state variable	Effler et al. (1997a)
Secchi disc (SD) ^b	1 - 3 times-wk ⁻¹	model input	-
incident irradiance	hourly	model input	UFT/NOAA ^d
air temperature ^{d,e}	hourly	model input	NOAA records
dew point temperature ^{d,e}	hourly	model input	NOAA records
wind speed ^{d,e}	hourly	model input	NOAA records
river flow	daily average	model input	USGS records
irradiance profiles ^f	5 times	model input	
Laboratory			
suspended solids	1 - 3 times-wk ⁻¹	ancillary	Effler et al. (1997a)
chlorophyll	1 - 3 times-wk ⁻¹	state variable	Effler et al. (1997a)
total ammonia	1 - 3 times-wk ⁻¹	ancillary	Effler et al. (1997a)
nitrate	1 - 3 times-wk ⁻¹	ancillary	Effler et al. (1997a)
soluble reactive P	1 - 3 times-wk ⁻¹	ancillary	Effler et al. (1997a)
zebra mussel biomass ^g	variable, by site	ancillary	Effler et al. (1997a)

^a HydroLab Sonde: hourly for WQ1 and WQ2, Hydrolab Surveyor II profiles weekly for WQ3 - WQ6 (Fig. 1); correspond to navigation buoy numbers 409, 397, 382, 372, 350 and 332.

^b To estimate attenuation coefficient.

^c Upstate Freshwater Institute - measurements in Syracuse.

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

^e Transport/temperature submodel inputs.

^f To determine attenuation coefficient.

^g ~ Monthly sampling for ZM1 and ZM2, 2 - 3 times for ZM3, ZM4, and ZM5.

summer average conditions since the invasion include (Effler et al., 2001): (1) ~ 40% decrease in DO (Fig. 2), (2) 8-fold decrease in Chl (Fig. 3), (3) > 2-fold increase in SD, (4) 10-fold increase in soluble reactive phosphorus, and (5) 4-fold increase in ammonia.

3. Supporting Measurements

3.1. Monitoring Program

A comprehensive program of field measurements, sampling, and laboratory analyses conducted in 1994 (Table 2) supported model development and calibration. The array of monitored parameters included the model state variables, model inputs, and a number of related auxiliary measurements, such as enumeration and size distribution data for the zebra mussel population. Features of this program have been described previously (Table 2; Effler and Siegfried, 1998; Effler et al., 2001). Water quality measurements were made at 6 longitudinal positions within the study reach (Fig. 1)

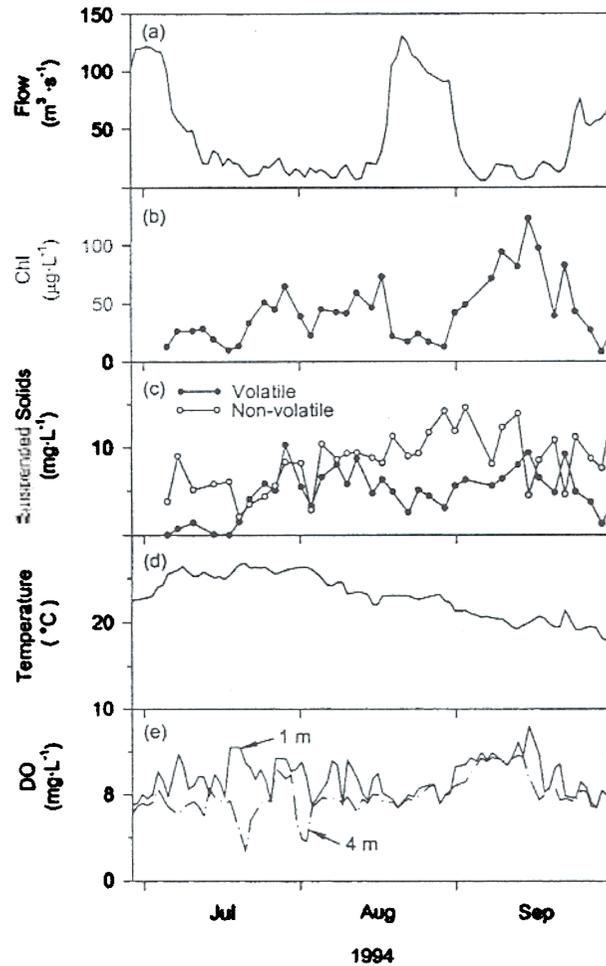


Figure 4. Dynamics of selected environmental conditions in the Seneca River, at the upstream boundary of the study reach, July–September, 1994: (a) flow, (b) Chl, (c) suspended solids, volatile and non-volatile, (d) average watercolumn T, and (e) daily average DO concentrations at depths of 1 and 4 m.

over the June–September interval. Measurements of DO and T at the two most upstream sites were made hourly. Longitudinal profiles for the entire reach were collected approximately weekly and were completed in about 3 hours. Meteorological measurements were made at Syracuse Hancock Airport, except incident irradiance that was measured near the southern end of Onondaga Lake (Fig. 1).

3.2. *Upstream Boundary/Ambient Conditions*

Rather strong dynamics in potential drivers of water quality and boundary conditions for model state variables occurred over the modeling interval of 1994 (Fig. 4). A review of historic conditions (Effler et al., 2001) indicates that such variability has been common for this location. Major variations in flow occurred over the June–September interval of 1994 (Fig. 4a). There were two intervals of low flow, from mid-July through mid-August and much of September, that separated three intervals of high flow, in early July, late August, and late September. Flows dropped below the 7Q10 on a number of days and were below the 30Q10 for intervals of several days. The levels and dynamics of Chl that entered the study reach (Fig. 4b) were consistent with the hypereutrophic conditions of Cross Lake (Effler and Carter, 1987; Effler et al., 1989), and indicate a potentially rich food supply for resident zebra mussels of the study reach. The dynamics of Chl (Fig. 4b) and suspended solids (Fig. 4c) were apparently influenced by variations in flow (Fig. 4a). The contribution of inorganic (non-volatile) solids to the total was greater during high flow intervals, and the concentrations of volatile solids and Chl were lower. This is consistent with short-circuited flow from the river upstream of the lake, as that portion of the river is enriched with inorganic solids and has lower Chl compared to the lake (Effler et al., 2001). Higher Chl levels were observed during lower flow intervals (Fig. 4a and b), when short-circuited flow contributions to the study reach were reduced. The variations in relative contributions of inorganic and organic solids (and Chl) indicate changes in food quality (Effler et al., 2001; Madon et al., 1998) occurred in the monitored interval.

The temporal pattern of T in 1994 (Fig. 4d) demonstrated a seasonality that is typical for the region (Effler, 1996). The DO signal received from Cross Lake was complex with respect to temporal patterns (e.g., Fig. 4e) and vertical differences (Gelda et al., 2000). The concentration of DO (and saturation conditions) varied strongly at time scales of within a day, day-to-day, and seasonally, and differed with depth in the water column of the river during low flow intervals (Fig. 4e; Gelda et al., 2001). These characteristics were the justification for the particularly intensive time/depth monitoring at the upstream boundary of the study reach (Table 2). Such features are commonly observed in the epilimnia of hypereutrophic lakes such as Cross Lake (e.g., Effler, 1996; Effler and Carter, 1987), driven by the timing of primary production and wind driven turbulence.

3.3. *Zebra Mussel Population*

The benthic survey data for the study reach available for 1994 (Table 3) are unusually comprehensive compared to many other study sites reported in the literature. Upstream portions of the reach (sites ZM1 and ZM2; Fig. 1) were sampled approximately monthly. At least six sub-sites/replicates (from a sampling grid; Effler et al., 1997a) were sampled at each of the two upstream sites. Sampling was less comprehensive downstream. Triplicate samples were collected at ZM3 and ZM4 on three occasions, and at ZM5 on two dates (Fig. 1).

Table 3. Zebra mussel (*Dreissena polymorpha*) population densities and biomass (average) for the Seneca River downstream of Cross Lake, 1994.

Site ^a	Density (individuals·m ⁻²)/Biomass ^b (g·m ⁻²)		
	August–October (1)	June–July (3)	September–October (4)
		60,000/1030 17,600/725	
	12,200/570 2180/140 330 ^c /12 ^c		

^a Locations appear in Fig. 1.

^b Dry weight, from shell lengths according to relationship of Effler et al. (1997a).

^c September only.

The average population density in the Cut in June and July was $\sim 60,000$ individuals·m⁻² (Table 3), however, the variability (spatial heterogeneity and temporal contributions) associated with this estimate was quite substantial (coefficient of variation (CV) = 75%). The population decreased to $\sim 15,500$ individuals·m⁻² (CV = 83%) in late summer and early fall (Table 3). At least a portion of the zebra mussels lost from the Cut over this interval was removed in the form of nearly spherical (e.g., < 15 cm diameter) colonies described as druses (Botts et al., 1996), observed in samples collected below the Cut (Effler et al., 1997a). Distinctly lower densities were reported for the downstream sites (Table 3), but such levels have been described as substantial and causing distinct shifts in water quality in other lotic systems (e.g., Caraco et al., 1997; 2000).

3.4. Longitudinal Patterns

Longitudinal profiles of (water column average) DO, Chl, and SD are presented (Fig. 5) for the study reach for 9 of the monitoring dates that represent much of the ranges encountered for flow ($8 - 101$ m³·s⁻¹) and boundary conditions for DO ($5 - 11$ mg·L⁻¹) and Chl ($13 - 125$ µg·L⁻¹). Patterns were generally progressive through the reach; DO and Chl concentrations decreased and clarity increased (Fig. 5). Decreases in DO of ~ 3 to 5 mg·L⁻¹ were observed for river flows ≤ 30 m³·s⁻¹ (Fig. 5c, e, g, i, m, and o). The depletion effect was diminished for flows ≥ 55 m³·s⁻¹ (Fig. 5a, k and q). A "leveling-off" in DO occurred in downstream portions of the reach during low flows, indicating a balance between source and sink processes (Fig. 5). Water column concentrations corresponding to < 25% saturation values were not observed. Approximately 15% of the observations at the most downstream of the study reach sites were in the range of 25 to 35% saturation during the 1994 study interval. Vertical differences in DO decreased abruptly downstream of the upstream boundary, particularly at higher flows (Fig. 5). Some return of vertical structure was observed mid-way down the study reach during low flows (e.g., Fig. 5m).

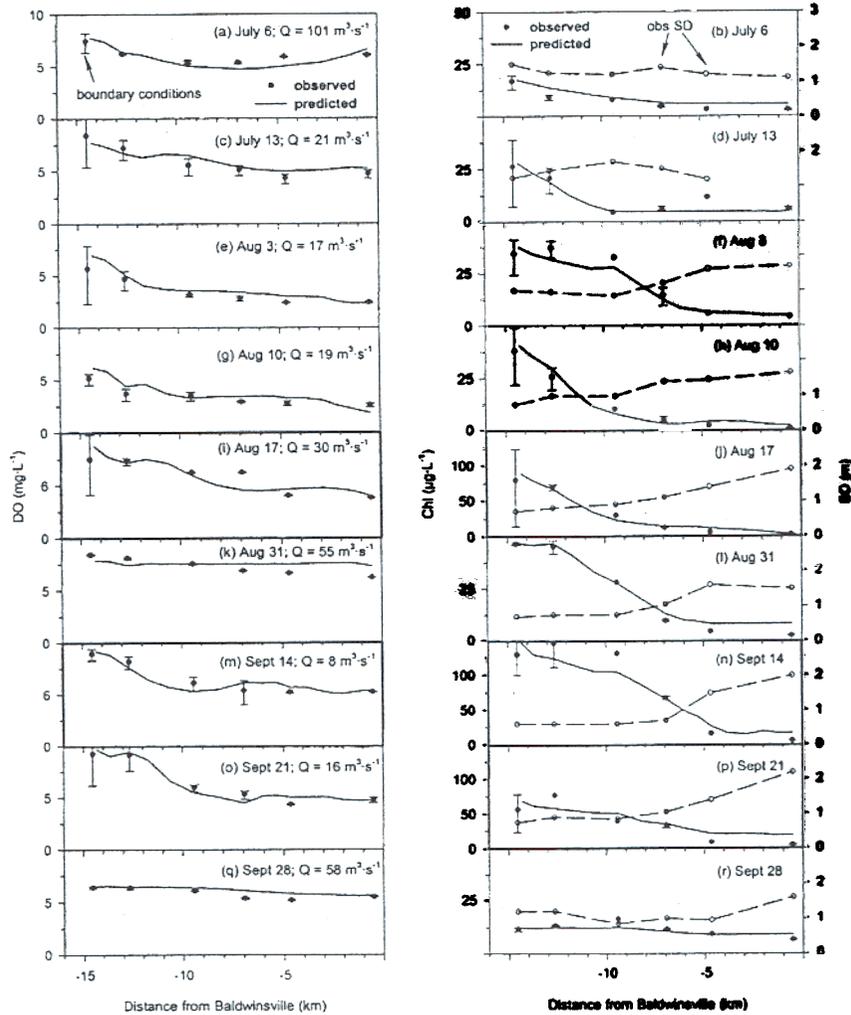


Figure 5. Longitudinal profiles for the study reach in 1994, dimensions of vertical bars correspond to range of observations over the upper 4 m of the watercolumn: (a) DO, July 6, (b) Chl and SD, July 6, (c) DO, July 13, (d) Chl and SD, July 13, (e) DO, August 3, (f) Chl and SD, August 3, (g) DO, August 10, (h) Chl and SD, August 10, (i) DO, August 17 (note scale change), (j) Chl and SD, August 17 (note scale change for Chl), (k) DO, August 31, (l) Chl and SD, August 31, (m) DO, September 14 (note scale change), (n) Chl and SD, September 14 (note scale change for Chl), (o) DO, September 21, (p) Chl and SD, September 21 (note scale change for Chl), (q) DO, September 28, and (r) Chl and SD, September 28. Calibration fits for DO and Chl profiles included.

Concentrations of Chl at the downstream boundary decreased to $\leq 10 \mu\text{g}\cdot\text{L}^{-1}$ and in several instances were $< 3 \mu\text{g}\cdot\text{L}^{-1}$. Reductions in Chl appeared to be less influenced by the magnitude of river flow than DO depletion. For example, substantial decreases in Chl were observed on July 6 (Fig. 5b) and August 31 (Fig. 5d) despite rather elevated flows. The greatest reductions in Chl occurred either between the second and third, or third and fourth, sampling sites for most of the profiles (Fig. 5). The total depletions of DO and Chl across the bounds of the study reach were poorly correlated.

An inverse relationship was generally observed between Chl and SD for the individual profiles (Fig. 5) that is widely reported for productive systems (e.g., Megard et al., 1979). However, in this case the relationship is casual, not causative. The dominant light attenuating material was instead tripton (Effler et al., 1988; 2001). Chlorophyll and SD (1/SD; Effler, 1996) were correlated for individual profiles because phytoplankton were part of an array of particles filtered from the water by the zebra mussels. Chlorophyll apparently acts as an indicator of the total particle pool, including tripton, for individual profiles. However, Chl fails as a surrogate measure of SD through time (e.g., seasonally), apparently because of uncoupled temporal variations in tripton (e.g., Effler et al., 1988).

4. Water Quality Model

4.1. Transport/Temperature Submodel

The transport/temperature submodel is a modified version of CE-QUAL-W2 (Cole and Buchak, 1995). This two-dimensional framework consists of longitudinal (16; Fig. 1) and vertical (0.5 m thick; i.e., laterally averaged conditions) segments. Design of the segmentation was supported by a bathymetric survey. Vertical segmentation in water quality models for inland rivers is somewhat unusual. However, it is important for this system because it can accommodate: (1) the limited turbulence that prevails under low flow conditions associated with anthropogenic modifications of the river (Canale et al., 1995), (2) the strong vertical differences in water quality that occur at the upstream boundary that persist for a portion of the study reach (Gelda et al., 2001), (3) the localization of the effects of the zebra mussel at the river bottom associated with its sessile habitat (Effler et al., 1996), and (4) the salinity-based density stratification that prevails downstream of the study reach (Effler et al., 1997b), as the water quality model is expanded to include downstream portions of the river system (Fig. 1).

The vertical mixing component of the transport framework of CE-QUAL was modified for this river application. The vertical eddy diffusion coefficient (D_z ; $\text{m}^2\cdot\text{s}^{-1}$) was calculated according to the expression (Martin and McCutcheon, 1999)

$$D_z = K_D \frac{D_{zo}}{(1 + \beta Ri)^\alpha} \quad (1)$$

where K_D = a calibration coefficient; D_{zo} = vertical eddy diffusivity coefficient for unstratified conditions ($\text{m}^2\cdot\text{s}^{-1}$); Ri = Richardson number; and α and β = dimensionless

coefficients. The protocol for the calculation of D_{zo} was described by Gelda et al. (2001). Values of K_D , α , and β , were determined by calibration (Gelda et al., 2001). The value of D_z increases as Q increases.

The heat budget that supports T simulations by the submodel 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, and wind speed, and incident solar radiation (Table 2).

4.2. Phytoplankton (Chl) kinetics

A generalized mass balance expression for Chl in the river is

$$\begin{aligned} \text{accumulation of Chl} = & \text{growth} - \text{respiration} - \text{zooplankton grazing} - \text{deposition} \\ & - \text{zebra mussel grazing} + \text{Chl inputs} \pm \text{Chl transport} \quad (2) \end{aligned}$$

Two of the four loss processes are assumed to be insignificant in this system, deposition (remains suspended from turbulence) and zooplankton grazing. Small zooplankton are removed by zebra mussels (e.g., Strayer et al., 1999). Further, cyanobacteria are the dominant component of Cross Lake's phytoplankton for much of the summer (Effler et al., 1989), a generally undesirable form of food for the more efficient grazers of the zooplankton community (e.g., Gliwicz and Siedlar, 1980). An appropriate kinetic expression for these conditions is

$$\frac{d\text{Chl}}{dt} = (\mu - r) \cdot \text{Chl} - k_f \cdot \text{Chl} \left(\frac{A - A_{+1}}{V} \right) \quad (3)$$

where $\frac{d\text{Chl}}{dt}$ = rate of change of Chl due to kinetic processes ($\text{g} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$); μ = specific growth rate for phytoplankton (d^{-1}); r = specific respiration rate for phytoplankton (d^{-1}); k_f = zebra mussel grazing rate ($\text{m}^3 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$); A = surface area of model cell (m^2); A_{+1} = surface area of next cell below (m^2); and V = volume of model cell (m^3). Grazing (filtering) by the zebra mussel occurs at the river bottom, consistent with the sessile habitat of this bivalve.

Phytoplankton growth is limited by temperature, light, and nutrient availability, described here according to (e.g., Chapra, 1997)

$$\mu = \mu_{\max} f(T) \cdot f(I) \cdot f(N) \quad (4)$$

where μ_{\max} = maximum specific growth rate for phytoplankton (d^{-1}); 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 saturated growth (i.e., $f(N) = 1$) is supported by the high concentrations of SRP and T-NH₃ that

prevailed over the study reach, driven largely by excretions from the resident zebra mussel population (Effler et al., 1996; 1997a; 2001). Light limitation is represented by

$$f(I) = \frac{I}{K_f + I} \quad (5)$$

where I = photosynthetically available solar radiation (PAR; $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$); and K_f = light half-saturation constant ($\mu\text{E}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$). Light at depth in the water column was calculated according to Beer's Law

$$I = I_0 e^{-k_d z} \quad (6)$$

where I_0 = PAR just below the water surface ($\mu\text{E}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$); k_d = attenuation coefficient for PAR (m^{-1}); and z = depth (m).

The phytoplankton respiration 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 relationship (Laws and Chalup, 1990)

$$k_b + \phi \cdot \mu \quad (7)$$

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

4.3. DO Kinetics

The generalized mass balance expression for DO in the river is

$$\begin{aligned} \text{accumulation of DO} = & \text{reaeration} + [\text{photosynthesis} - \text{plant respiration}] \\ & - \text{oxidation of CBOD} - \text{nitrification} \\ & - \text{sediment oxygen demand} \\ & - \text{zebra mussel oxygen demand} \\ & + \text{oxygen inputs} \pm \text{oxygen transport} \quad (8) \end{aligned}$$

where CBOD = carbonaceous biochemical oxygen demand. Sources of DO include photosynthesis and reaeration (for undersaturated conditions), and sinks include plant respiration, the oxidation of CBOD and nitrification, sediment oxygen demand (SOD) and zebra mussel oxygen demand (ZOD). Two of these sinks can be assumed to be insignificant for this study reach. The CBOD sink can be ignored here, as the concentration of labile organic carbon in the epilimnia of productive labels is low (Wetzel, 1992), particularly within the context of potential oxygen demand. There is no substantial

exertion of SOD, as there are no noteworthy organic deposits in the channel of the study reach. An appropriate kinetic expression for DO for this system is

$$\frac{dDO}{dt} = K_L \cdot (DO_{sat} - DO_s) / H_s + (P - R) - (k_n \cdot a_{ON} \cdot [T - NH_3]) - ZOD \left(\frac{A - A_{+1}}{V} \right) \quad (9)$$

where dDO/dt = rate of change of DO due to kinetic processes ($g \cdot m^{-3} \cdot d^{-1}$); K_L = oxygen transfer coefficient ($m \cdot d^{-1}$); 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 ($gO_2 \cdot m^{-3} \cdot d^{-1}$); R = uptake of oxygen due to endogenous respiration of phytoplankton ($gO_2 \cdot m^{-3} \cdot d^{-1}$); k_n = nitrification rate constant (d^{-1}); a_{ON} = oxygen to nitrogen ratio in the nitrification process (= 4.57, mass basis); ZOD = zebra mussel oxygen demand rate ($g \cdot m^{-2} \cdot d^{-1}$). ZOD is exerted at the river bottom, in a manner analogous to SOD [Eq. (9); Effler et al., 1996; 1997a; Gelda et al., 2001], because of the sessile habitat of zebra mussels (Table 1). It 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; Table 1). Respiration is the dominant component (e.g., Gelda et al., 2001; Schneider, 1992).

Gross photosynthetic production of oxygen (P) was calculated from the simulations of μ , according to (Chapra, 1997)

$$P = \mu \cdot Chl \cdot a_{CP} \cdot a_{OC} \quad (10)$$

where a_{CP} = carbon to Chl ratio (mass basis); and a_{OC} = oxygen to carbon ratio (mass basis). Loss of oxygen associated with phytoplankton respiration (R) was calculated from the simulations of r , according to

$$R = r \cdot Chl \cdot a_{CP} \cdot a_{OC} \quad (11)$$

Temperature effects on kinetic processes, other than ZOD and k_f , were made according to the Arrhenius format

$$k_{x,T} = k_{x,20} \theta_x^{T-20} \quad (12)$$

where $k_{x,T}$ and $k_{x,20}$ = values of kinetic coefficient x at temperatures T and 20° C; and θ_x = dimensionless temperature coefficient.

4.4. Model Coefficients

Values need to be specified for a number of coefficients to implement this model (Table 4). It is widely acknowledged that model credibility is enhanced through system-specific

Table 4. Specification of model coefficients.

	Coefficient (2)	Value/Description (3)	References (4)
		0.6; model calibration, upstream segments 1.0; model calibration, upstream segments 10.0; model calibration, upstream segments	
phytoplankton/growth and respiration	M_{max} K_L k_d ϕ k_b a_{CP} a_{OC}	1.5 d ⁻¹ ; from literature 180 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$; experiments with Seneca River phytoplankton specified from SD measurements, $k_d\text{SD}=1.9$ 0.15; from literature 0.1 d ⁻¹ ; from literature 75; from literature 2.67; stoichiometry of photosynthesis	Auer and Forrer (1998) Canale et al. (1995) Effler (1985) e.g., Cloem et al. (1995); Auer and Forrer (1998) e.g., Cloem et al. (1995); Auer and Forrer (1998) Chapra (1997) e.g., Chapra (1997)
other oxygen source/sink processes	K_L k_n a_{ON}	0.8 m·d ⁻¹ ; from <i>in situ</i> tracer gas (SF ₆) experiments 0.11 d ⁻¹ ; from experiments 4.57; stoichiometry of nitrification	Canale et al. (1995) Pauer and Auer (2000) e.g., Chapra (1997)
temperature effects on kinetics	θ_x values for μ R K_L k_n	see Eq. (12), values used for earlier Seneca River model 1.03 1.05 1.024 1.08	Canale et al. (1995) Canale et al. (1995) Canale et al. (1995) Canale et al. (1995)

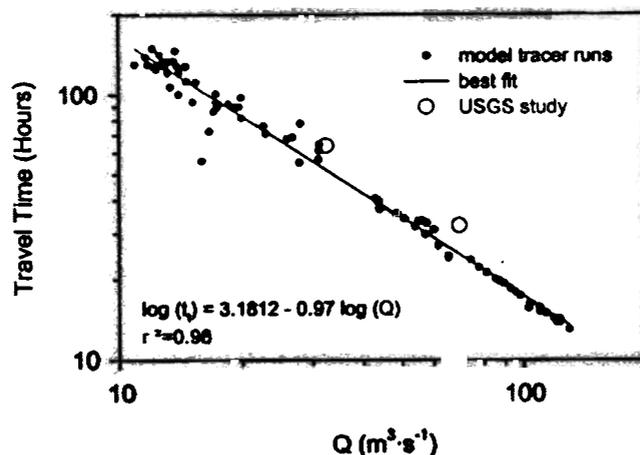


Figure 6. Time-of-travel (t_t) for the study reach as a function of river flow rate (average for t_t interval), from model tracer projections and two dye studies.

determination of model coefficient values; e.g., outcome of appropriately designed kinetic experiments and comprehensive measurements (e.g., Canale et al., 1995; Auer and Forrer, 1998). This inherently constrains the model calibration process, limiting the extent of "tuning" of multiple coefficients to match observations. It is particularly critical in cases such as this modeling analysis, where the model is to be applied as an analytical tool to estimate metabolism-based material fluxes through the calibration process. Such an approach is valid only if the magnitude of the uncertainty associated with the specified model coefficients is modest compared to that of the flux determined through the calibration process (demonstrated subsequently).

Values for the coefficients of this model are unusually well defined for this river based on a combination of earlier system-specific process and modeling studies (Canale et al., 1995; Gelda et al., 2001; Pauer and Auer, 2000) and accepted stoichiometry (a_{OC} , a_{ON}). Three coefficients for the transport model's vertical mixing relationship [Eq. (1)] were determined by calibration (Table 4). These values are within the range reported for stratified estuaries (Martin and McCutcheon, 1999). Further, Gelda et al. (2001) demonstrated this feature of the transport submodel performed well in simulating the strong dynamics in the vertical distribution of DO observed in the upstream portion of the study reach. Transport features of the submodel were supported by the closure of time-of-travel (t_t) predictions of the model, based on tracer inputs (instantaneous throughout the water column) at the upstream boundary for the flow conditions of the study interval, with the results of two dye studies (Fig. 6). The submodel also performed well in simulating T at time scales of within a day to seasonal (Gelda et al., 2001). However, the success of these simulations was largely assured by the frequent update of boundary conditions (Fig. 4d).

The values of K_L , k_n , and K_f are based on the results of system-specific experiments (Table 4) conducted in a reach of the Seneca River downstream of Baldwinsville. Experiments to determine K_L were conducted *in situ* (continuous injection) with the insoluble gas SF₆ (Canale et al., 1995), a tracer gas that has been used successfully to directly assess gas exchange for a range of surface water systems (Wanninkhof et al., 1987; 1990). Experiments to determine k_n were conducted in the laboratory with river bottom collections (Pauer and Auer, 2000). Further, the specified value of k_n , selected from the rather narrow range of observations (Pauer and Auer, 2000), performed well in matching longitudinal profiles of NO₃⁻ (calculations conducted outside of this water quality model). The value of K_f was determined in laboratory experiments with the natural phytoplankton assemblage of the river and verified in field incubations at several depths in the river (Canale et al., 1995).

Values of μ_{max} , θ_x , a_{CP} , and k_b are all consistent with the related scientific literature (Table 4). The values of θ_x [Eq. (12)] specified (Table 4) correspond to those used in an earlier (pre-zebra mussel invasion) water quality model developed for the reach of the river downstream of Baldwinsville (Canale et al., 1995). All of these values are well within the rather narrow limits of values reported in the modeling literature (Bowie et al., 1985). Moreover, the temperature of the river remained in a relatively narrow range (e.g., Fig. 4d) during the study period. The value adopted for a_{CP} (75, Table 4) is midway in the commonly observed range (50 – 100; Chapra, 1997).

4.5. Modeling Protocol

Initial conditions were set based on measurements made on June 29, 1994 at all six monitoring sites (Table 2, Fig. 1). Observations were linearly interpolated vertically and longitudinally to fill in the "grid" of the transport model. Upstream boundary conditions (WQ1, Fig. 1) were updated hourly for flow, T, DO, and Chl; interpolations were conducted in time (flow and Chl) and vertically to meet the time step (hourly) and vertical (0.5 m intervals) resolution requirements for the model inputs. Values of T-NH₃ (to drive nitrification sink for DO) and k_d (part of specification of I available to support phytoplankton growth) were specified in time and space throughout the grid based on measurements (Table 2) and interpolation of these observations. Meteorological conditions were updated hourly. The model's auto-stepping 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 specified range of time-steps was 1 sec to 1 hour. Model simulations and calibration were conducted for the conditions of June 29 – September 30, 1994.

All model coefficient values were kept constant (as specified in Table 4) except k_f [see Eq. (3)] and ZOD [see Eq. (9)], which were varied in time (increments ≥ 1 day) and space to approximately match the approximately weekly profiles of Chl and DO. Longitudinal structure for k_f and ZOD within the study reach was resolved according to five "combined" model segments (Fig. 1). Greater spatial resolution in calibration of these fluxes was deemed inconsistent with the spatial resolution of the measurements of

the state variables (Fig. 5) and information concerning the distribution of the zebra mussel population in the reach (Table 3). The most upstream of the "combined" segments (C1, includes three model segments; Fig. 1) corresponds to the limits of the earlier DO model analysis of Gelda et al. (2001) for the Cut. The time-series of ZOD values reported for this "combined" segment, based on similar model calibration protocols (Gelda et al., 2001), has been retained/specified here. Calibration to Chl observations was conducted first, because this variable is also part of the DO mass balance [P/R terms, Eqs. (9 – 11)].

5. Model Performance and Applications

5.1. *The No-Zebra Mussel Case*

One test of the representativeness of the water quality model is the character of predictions for downstream portions of the study reach for the case of no zebra mussels (Figs. 2d and 3d). The predicted distributions were formed from noontime simulations for the study interval of 1994. A value of $k_d = 1.9 \text{ m}^{-1}$ was assumed throughout the reach, and the T-NH₃ concentration was assumed equal to the upstream boundary value, conditions that were generally consistent with observations before the invasion (e.g., Effler et al., 1988; 1996). The predicted distributions are similar to those formed from observations from before the invasion (e.g., Figs. 2 and 3), thereby supporting the representativeness of the model for the no zebra mussel (i.e., pre-invasion) case and the position that on average these conditions did not change substantively from the Cut to Baldwinsville before the zebra mussel invasion. In particular, these simulations indicate the effects of phytoplankton production and respiration, that were dominant processes before the zebra mussel invasion, are being represented realistically in the model. The high value of k_d (limited light) prevented major imbalances in μ and r , and thereby major changes in Chl and DO, over the study reach. Modest differences in values from the upstream to downstream boundaries on a day-to-day basis, and in the character of the distributions (Fig. 2 and 3), could occur from such effects as variations in incident light. Moreover, the model predictions for this case support the position that the differences in observations from before and after the invasion at the downstream boundary of the reach (e.g., Figs. 2c and d, 3c and d) are a fair representation of the impact of zebra mussel invasion (Effler et al., 1996).

5.2. *Calibration Values of ZOD and k_f*

Dissimilar spatial distributions of ZOD and k_f were obtained through model calibration, and substantial temporal variations occurred, as indicated by the relatively large standard deviation values (Fig. 7a and b). The mean value of ZOD decreased in a generally progressive manner along the study reach (Fig. 7b), from values about 10× greater to levels corresponding to SOD values for organic enriched sediments ($\sim 5 \text{ g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$; Bowie et al., 1985). This pattern qualitatively tracks the available monitoring data for

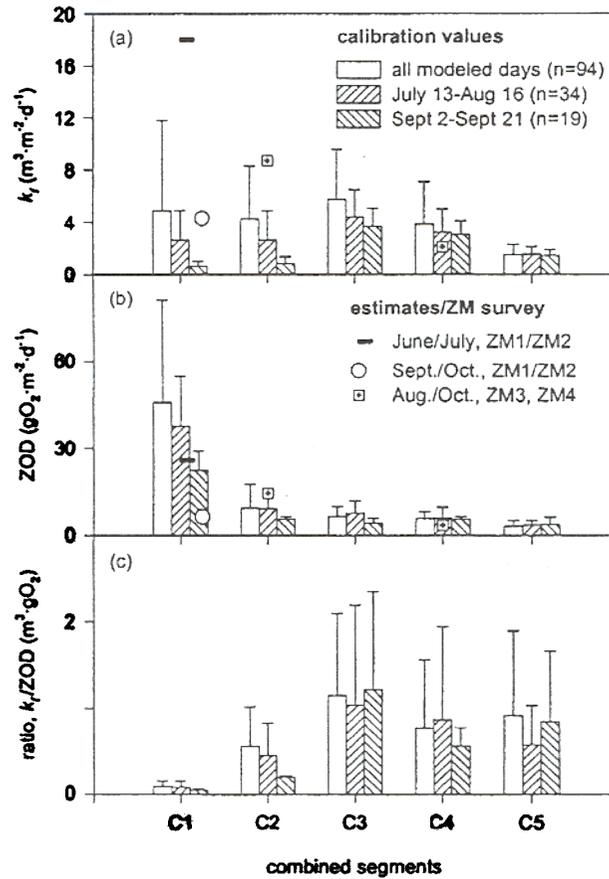


Figure 7. Rates of zebra mussel processes for the combined segments of the study reach, for selected intervals of 1994: (a) k_f , (b) ZOD, and (c) ratio of k_f/ZOD . Dimensions of vertical bars are one standard deviation.

zebra mussels (Table 3). In contrast, the highest average value of k_f occurred approximately mid-way along the study reach (Fig. 7a). Coefficient values are presented for three intervals, the entire study interval (94 d) and the two low flow intervals (Fig. 4a, and 7). Average values for the monitored days ($n = 14$, entire reach) were in general similar to those determined daily for the entire interval, supporting the use of values for all the modeled days to depict conditions in the shorter intervals (Fig. 7). Values of ZOD during low flow intervals are of particular interest for projections considered critical for river oxygen resources (e.g., Chapra, 1997). Mean values of ZOD and k_f were significantly (1% level) lower during the low flow interval of September than in the

preceding mid-July to mid-August interval for the upstream combined segment(s) (Fig. 7a and b). These decreases followed, and were consistent with, the documented (Effler et al., 2001; Table 3) major decrease in the zebra mussel population in the upstream portion of the reach between these two low flow intervals. The similarities of the fluxes determined for the two low flow intervals in the downstream portions of the study reach suggest zebra mussel biomass remained essentially unchanged in these areas over this period.

The wide variations in ZOD (Gelda et al., 2001) and k_f over intervals of relatively uniform biomass probably reflect responses to the dynamics of ambient conditions as well as the reproductive cycle. Potential environmental drivers include variations in size, concentration, and composition of food particles (Berg et al., 1996; Lei et al., 1996; Baker et al., 1998), concentration of non-food particles (Alexander et al., 1994; Summers et al., 1996; Madon et al., 1998), turbulence (Aldridge et al., 1987; Strayer et al., 1994), temperature (Aldridge et al., 1995), and reproductive state (Stoeckmann and Garton, 1997). Gelda et al. (2001) evaluated potential drivers for the variability in ZOD in combined segment C1 before the loss of biomass through empirical analyses. A strong positive relationship between ZOD and river flow was found ($R^2 = 0.82$, significant at 1% level). However, they suggested other factors that accompanied increased flow were the direct stimulus for higher respiration rates, rather than increased velocity and turbulence. Other analyses indicated the degradation in food quality (increased contribution of inorganic particles to total suspended solids) that accompanied the high flows might have contributed to increases in ZOD (Gelda et al., 2001).

The extent of the coupling of the effects of filtering and respiration by the zebra mussel population is characterized here by the ratio k_f/ZOD (Fig. 7c). The ratio values for the mid- and downstream portions of the reach (C3–C5) were similar, while much lower values occurred in the most upstream section (C1), where the most dense populations prevailed (Fig. 7c; Table 3). This suggests the most dense populations were the least effective in grazing (i.e., reducing) phytoplankton biomass from the river's water column. It is hypothesized that the colonial configuration of the zebra mussel population in this portion of the study reach contributed substantially to this spatial pattern. Dense populations such as observed in this portion of the reach ($\sim 60,000$ individuals $\cdot m^{-2}$) occurred as multiple layers of individual mussels as thick as 10 cm, that were held together rather tightly with their byssal threads (Table 1). This configuration doubtless inhibits circulation of the water column to individuals located below the surfaces of the colonies and reduces concentrations of phytoplankton available to them, thereby reducing their grazing effectiveness. This effect may contribute to self-regulation of the upper bound of the population that could be sustained. For example, lack of adequate food for older individuals at the bottom of the colonies could have contributed to the loss of much of the population at ZM1 (Fig. 1) after July in 1994 (Table 3). This configuration for dense zebra mussel colonies would not influence DO depletion from respiration in the same manner, as this demand from the entire thickness of the colony would be readily transmitted to the watercolumn. Such differences in the effects of the configuration of dense colonies on grazing and DO depletion are consistent with the observed longitudinal pattern of the ratio k_f/ZOD (Fig. 7c).

5.3. *The Alternative of Independent Specification of ZOD and k_f*

It is important to consider the potential value of the fluxes of k_f and ZOD determined here by model calibration (Fig. 7) within the context of approaches adopted for coefficients for other source/sink processes [Eqs. (3) and (9)] and alternatives presently available for this invader. Specification of key model coefficients (i.e., those that substantively influence the values of predictions) is a central concern for the modeling process and an issue with regards to model credibility (Canale et al., 1995; Chapra, 1997; Thomann and Mueller, 1987). Independent specification of kinetic coefficients through separate experiments is widely supported by the modeling community as an attribute that enhances model credibility (e.g., Auer et al., 1997; Canale et al., 1993; 1995; Doerr et al., 1996; 1998). However, the benefits of such an approach are compromised if the credibility/representativeness of kinetic experiments is in question. There are two important aspects of this credibility/representativeness issue that are of particular concern within the context of zebra mussels: (1) the extent to which collected samples for experiments are representative of the overall system, and (2) the extent to which the experimental design faithfully represents the actual ecosystem. It is valuable to consider this in the context of other kinetic processes that have been incorporated in water quality models as these quantitative tools have evolved (Chapra, 1997). For example, sample quality (e.g., undisturbed core sample, for laboratory experiments) and sampling effort (number and distribution of collection sites) are major issues in specifying SOD in systems where this sink is important. An important question for this DO sink is – to what portion of the lake or river bottom should the results be applied (Erickson and Auer, 1998; Gardiner et al., 1984)? Such spatial resolution (e.g., number of samples analyzed) issues are often influenced by project resources. Broadly acceptable experimental designs have emerged in several instances for certain kinetic processes such as SOD (Erickson and Auer, 1998) and K_L (Wanninkhof et al., 1987; 1990), but only after many years of the established need for such capabilities. There are other cases where debate continues concerning appropriate experimental protocols and inherent uncertainties after many years of research; e.g., phytoplankton kinetic studies (e.g., Auer and Forrer, 1998).

The addition of the influences of zebra mussel metabolism to water quality models represents a major challenge for independent specification of related constituent fluxes. Ideally, independent specification could be based on the following steps: (1) accurate spatial representation of the zebra mussel population, and (2) application of representative relationships from the scientific literature that quantify material fluxes as a function of the resident biomass, and mediating conditions. However, there are a number of shortcomings in the understanding and methods for quantification of zebra mussel metabolism, that at this time introduce major uncertainty for such an approach for this or any other system. Despite the fact that the benthic survey data of 1994 for Seneca River were unusually comprehensive within the context of observations for other river systems (e.g., Caraco et al., 1997), there remains substantial uncertainty concerning the magnitude and spatial distribution of the resident population of zebra mussels. The first aspect of this is a generally ubiquitous problem. High variability is encountered over rather small spatial scales for many benthic organisms associated with the heterogenous distribution of substrate

(e.g., Chutter, 1972; Needham and Usinger, 1956; Resh, 1979). For example, the average coefficient of variation (CV) for 10 samples collected in the Cut in 1994 (5 collections over the study interval of 1994) was nearly 90%. Similar variability has been manifested at this site in longer-term monitoring (Effler et al., 2001). The second feature that compromises accurate specification of biomass in this case is the limited sampling in downstream portions of the reach (Fig. 1) that may have failed to resolve important longitudinal structure in the zebra mussel populations. Substantial improvements in specification of biomass in these areas could only be attained at great cost. Additionally, the standing crop of zebra mussels may change in time (e.g., increases from growth) and space [e.g., rather abrupt reduction in upstream segments in 1994 (Effler et al., 1997a)] during the summertime interval of water quality concern, thereby requiring comprehensive seasonal monitoring at many sites.

There is a rich scientific literature documenting the development of relationships from which the grazing effects and oxygen consumption of zebra mussels can be calculated, based on population density/size distribution data. However, a wide range of flux estimates results (particularly for clearance rates/grazing; e.g., 10-fold) from the application of these expressions, as noted by several authors (Aldridge et al., 1995; Bunt et al., 1993; Fanslow et al., 1995; Kryger and Riisgård, 1988; Mellina et al., 1995; Reeders et al., 1993). The extensive differences in clearance rates reported for laboratory experiments have been attributed to differences in temperature (Reeders and bij de Vaate, 1990), food type and concentration (Berg et al., 1996; Bunt et al., 1993; Reeders et al., 1993), artifacts of experiment designs (Fanslow et al., 1995; Reeders et al., 1993), and extent of acclimation of the specimen animals (Reeders et al., 1993). Substantial variability in the results of replicate experiments is commonly observed in these laboratory experiments (e.g., CV \sim 25% for oxygen consumption, CV \geq 50% for filtration; Aldridge et al., 1995). Further, many laboratory experiments are conducted with actively filtering specimens, though in natural ecosystems zebra mussels do not filter 100% of the time (Horgan and Mills, 1997). Thus laboratory rates have been adjusted downward, somewhat arbitrarily (e.g., Padilla et al., 1996), to support more realistic estimates of *in situ* rates. Representing the effects of colonial/druse configurations encountered in densely populated systems, offers a particular challenge for laboratory experiments, that has yet to be comprehensively addressed. Failure to fairly reflect the effects of these configurations on rate processes (e.g., per unit biomass) may compromise the applicability of results from various experimental designs. Moreover, experiments apparently need to be conducted seasonally, as the metabolic activity of this bivalve has been observed to vary greatly during the summer (e.g., Stoeckmann and Garton, 1997; Quigley et al., 1993).

Included here for reference are independent estimates of k_f (Fig. 7a) and zebra mussel respiration (\sim ZOD; Fig. 7b). These were calculated from the available population data (Table 3) and expressions for filtering (Reeders and bij de Vaate, 1990) and respiration (Schneider, 1992) reported in the scientific literature that have been applied previously to this river (Effler et al., 1996; Effler and Siegfried, 1994; 1998). The theoretical estimates of filtering for the most densely populated section were about 5 to 6 times greater than that determined through model calibration, while the values converged more with model results at downstream locations (Fig. 7a) where population densities were much lower (Table 3). This spatial pattern is consistent with the position presented previously that the effective-

ness of grazing was particularly reduced in the most densely populated portion of the reach (e.g., Fig. 7c). Deviations of the independent respiration estimates and the calibrated ZOD values were in general smaller, and the estimated values were instead lower than the mean of the calibration results in the most densely populated section (Fig. 7b). The possibility that local oxygen consumption processes that operate in the colonies other than respiration, such as decomposition of feces and pseudofeces, were responsible for ZOD being greater than the independent respiration estimate cannot be discounted. However, it is more likely that the differences can be attributed mostly to respiration rates that were higher than the average calculated from relationships presented by Schneider (1992). The means of the model determinations of ZOD (Fig. 7b) were well within the bounds reported by Aldridge et al. (1995) for maintenance of a positive "scope of growth" (i.e., energy income > expended energy) for zebra mussels. The independent estimates of k_f and ZOD (from population data and literature relationships) included here have served to bring some level (e.g., order of magnitude) of closure to the values determined through calibration (Fig. 7a and b).

The determinations of ZOD and k_f from model calibration (Fig. 7) presented here are considered representative of these fluxes in this river system, as they are based on conspicuous signatures of the metabolism of the invader (Figs. 2, 3, and 5) and integrate the effects of prevailing environmental conditions. We favor such values over those that could be estimated independently from a combination of population (benthic) surveys and biomass-specific rates reported in the literature, because of the great uncertainty that presently attends these protocols. The long-term impacts imparted to surface waters of North America from the invasion (Effler et al., 2000; Strayer et al., 1999) dictate the credible accommodation of the effects of zebra mussel metabolism in water quality models. The credibility of models that incorporate zebra mussel metabolism, and thereby their utility for management applications, will be greatly enhanced by achieving closure between fluxes determined by model calibration and independent experiments; e.g., input of the results of benthic surveys and experiments into the model produces simulations that match observations (i.e., model validation). Thus there is a need to conduct an integrated program of monitoring (water quality, zebra mussels and environmental forcing conditions), kinetic experiments, and modeling over an extended interval to establish credibility for the modified model frameworks [e.g., Eqs. (2) and (8)] as well as experimental protocols. The conspicuous signatures manifested in this study reach (Figs. 2, 3, and 5) and their long tenure (since 1993; Effler et al., 2001) make this an ideal test system to pursue such goals.

5.4. Model Analyses

Sensitivity: Analyses were conducted with the model to depict the sensitivity of predictions to variations in k_f and ZOD and reasonable levels of uncertainty/variation in other model coefficients. The central issue for these analyses was the extent to which the apparent temporal variability indicated for k_f and ZOD based on calibration (Fig. 7) could instead be explained by uncertainty and variation in other coefficients. A number of rate processes were assumed to operate uniformly through the study period for calibration (Table 4), though variability doubtless occurred. Noteworthy examples include the coefficients used to represent phytoplankton metabolism (e.g., μ_{max} , K_I , ϕ , k_b , and a_{CP}). These values in reality

are subject to temporal changes in response to the seasonal succession of the phytoplankton community and its response to variations in mediating environmental conditions (Harris, 1986). Only a portion of the study period was addressed for the sensitivity analyses, and model output was averaged, to facilitate resolution of relative effects. These analyses were conducted for the first half of the study interval when the highest levels of zebra mussel biomass were present (particularly in the upstream portions of the study reach; Effler et al., 2001) and wide variations in river flow occurred (Fig. 4a). Predictions of Chl and DO have been averaged over depth of the segment, over daily intervals, and for the multiple water quality model segments within each of three combined segments (C1, C3, and C5). Sensitivity runs for k_f and ZOD were conducted with values that corresponded to the averages for the late June to mid-August interval, and compared to time series (daily) of Chl and DO that resulted from model calibration. Sensitivity simulations were made for a number of other model coefficients (μ_{max} , K_f , ϕ , k_b , a_{CP} , K_L and k_n) at limits of 25%; reasonable limits, based on the extent of system-specific information (e.g., Canale et al., 1995; Pauer and Auer, 2000) and the literature (Auer and Forrer, 1998; Bowie et al., 1985).

Failure to accommodate the apparent dynamics of k_f compromised substantially the model's performance in simulating the temporal and spatial distribution of Chl in the study reach (Fig. 8a - c). The least relative effect was observed for the upstream combined segment (C1; Fig. 8a), where use of the average k_f value caused noteworthy underpredictions (e.g., compared to the calibration case) for late July and early August. Overpredictions occurred for early July and major underpredictions were observed for late July and early August for the other two combined segments (Fig. 8b and c). The extent of overprediction in the early portion of the interval did not match the subsequent underprediction because of the dilution effects of the high flows through early July (Fig. 4a). The effects of uncertainties in the phytoplankton kinetic coefficients, such as μ_{max} were minor by comparison (Fig. 8d - f). Uncertainties in Chl predictions are transmitted to DO simulations through the dependence of P and R on phytoplankton biomass [Eqs. (10) and (11)]. However, the relative impact of not accommodating the dynamics of k_f on simulations of DO is minor (Fig. 8g - i) compared to the effect on Chl predictions (Fig. 8a - c). Failure to accommodate the apparent dynamics of ZOD had the greatest impact on the model's performance in simulating the temporal and spatial distribution of DO in the study reach (Fig. 8j - l). Substantial underpredictions of DO in late July and early August in the upstream combined segment resulted from the use of an average ZOD value (Fig. 8j). Even greater underpredictions occurred in that interval for the other two combined segments, and noteworthy overpredictions were observed in early July (Fig. 8k and l). The effects of uncertainties in the other coefficients on DO simulations, including μ_{max} (Fig. 8m - o) and K_L (Fig. 8p - r), were minor by comparison. The results of the sensitivity analyses (Fig. 8) support the position that much of the variability in k_f and ZOD determined through model calibration was real, reflecting mostly variations in zebra mussel metabolism rather than being an artifact of the calibration process.

Depleted DO, Implications for Feedback and Carrying Capacity: It is not well recognized by North American investigators that zebra mussels are tolerant (i.e., capable of sustaining metabolic activities) of substantially undersaturated oxygen levels. In their review of the related scientific literature of the former Soviet Union (FSU), Karatayev

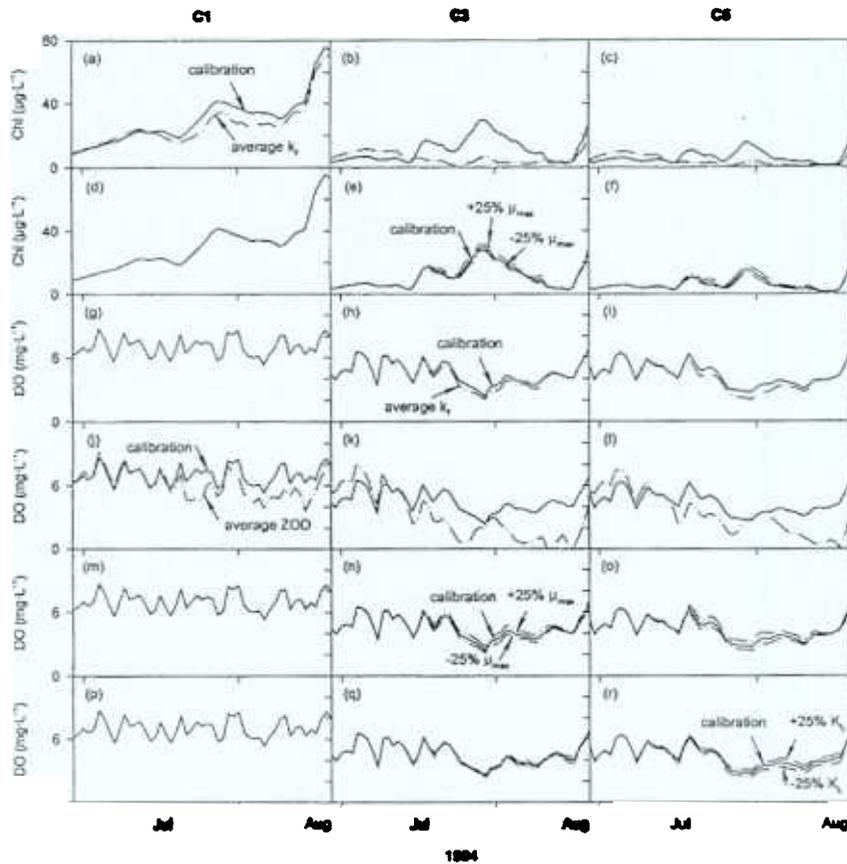


Figure 8. Model sensitivity analyses: (a – c) chlorophyll simulations, average k_t value versus calibration time series for upstream (C1), mid-reach (C3), and downstream (C5) combined segments, respectively, (d – f) chlorophyll simulations, $\mu_{max} \pm 25\%$ for C1, C3 and C5, respectively, (g – i) DO simulations, average k_t value versus calibration time series for C1, C3, and C5, respectively, (j – l) DO simulations, average ZOD value versus calibration time series for C1, C3, and C5, respectively, (m – o) DO simulations, $\mu_{max} \pm 25\%$ for C1, C3, and C5, respectively, and (p – r) DO simulations, $\pm 25\% K_L$ for C1, C3, and C5, respectively.

et al. (1998) identified 25% saturation as the critical threshold for sustained survival of the zebra mussel. The findings of at least two laboratory studies reported in English with North American specimens are generally consistent with this level. McMahon (1996) reported the chronic lower lethal percent saturation for North American zebra mussels was 21–26% at 25° C. Sprung (1987) reported a minimum of 21% saturation was required for larval development at 18–20° C. Field observations for Seneca River are generally

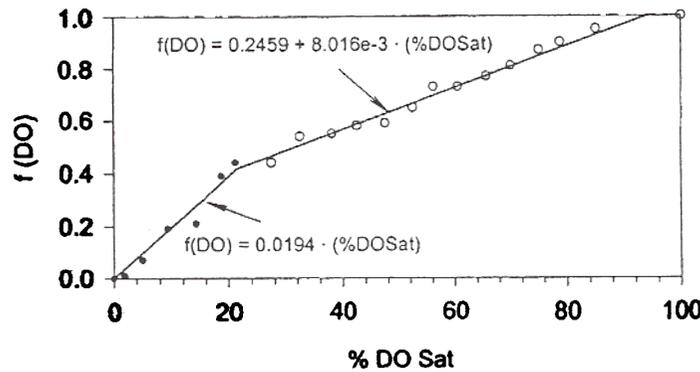


Figure 9. Relationship between oxygen consumption rate of zebra mussels and percent DO saturation, at 25 °C (acclimation and testing), as reported by McMahon (1996). Consumption rate normalized by value for 100% DO saturation [$f(\text{DO})$], two part linear regression expression included.

consistent with the threshold value reported from the FSU and the laboratory experiments with the North American zebra mussels. The DO levels reported for the Seneca River appear to be the lowest reported to date in North America for a system that sustains a zebra mussel population.

Most freshwater bivalves are capable of a high degree of "regulation" of DO consumption under depleted conditions, thereby maintaining consumption rates observed for saturation conditions even at highly undersaturated levels (McMahon, 1996). However, zebra mussels are poor regulators of consumption rates, demonstrating progressive marked decreases in consumption as percent saturation decreases (Fig. 9). The relationship has been quantified here by a two-part linear regression fit of McMahon's (1996) data (Fig. 9) from experiments (and acclimation) conducted at 25 °C, and is adopted in subsequent management applications with the model. The "slow down" of microbially-mediated oxygen demanding processes such as nitrification (Charley et al., 1980) and SOD (Lam et al., 1984; Snodgrass and Ng, 1985) is a widely acknowledged and modeled phenomenon, though these feedback processes are usually simulated by a Monod-type formulation (Bowie et al., 1985; Gelda and Auer, 1996). A multiplicative format has been adopted here to represent the dependence of ZOD on the levels of DO depletion and all other environmental conditions (X_i)

$$\text{ZOD} = \text{ZOD}_{\text{max}} \cdot f(\text{DO}) \cdot f(X_i) \quad (14)$$

where ZOD_{max} = maximum ZOD ($\text{g} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$); $f(\text{DO})$ = multiplier with a maximum value of 1 that depends on the status with respect to oxygen saturation (according to Fig. 9; dimensionless); and $f(X_i)$ = multiplier with a maximum value of 1 that depends on all other mediating conditions.

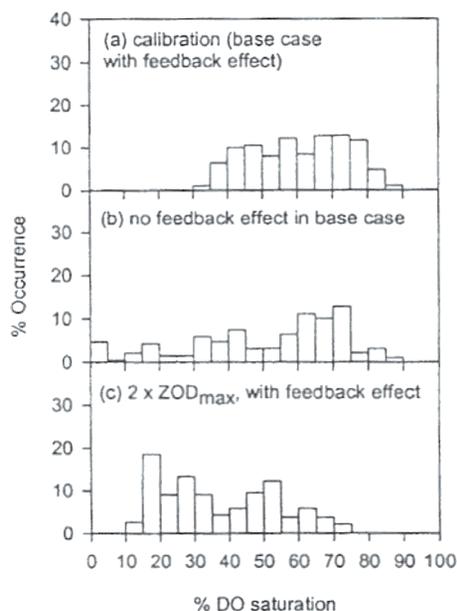


Figure 10. Model analyses of implications of feedback from low DO concentrations and increased zebra mussel biomass, predicted distributions of percent DO saturation for daily average values for the study interval of 1994: (a) calibration (base case; feedback assumed operative), (b) no feedback operative, and (c) zebra mussel biomass doubled (i.e., $2 \times ZOD_{max}$), with feedback operative.

The potential implications of this form of feedback from DO depletion (Fig. 9) are demonstrated by comparing the distributions of daily average values from the calibration simulations (the "base" case) for the furthestmost downstream water quality model segment to simulations that eliminate the feedback effect [$f(\text{DO}) = 1$; i.e., efficient regulation of DO consumption (McMahon, 1996); Fig. 10a and b]. According to the relationship of McMahon (1996; Fig. 9), DO concentrations would have been shifted substantially lower in the absence of feedback (Fig. 10b); daily average DO levels < 25% saturation would have prevailed ~ 15% of the interval. Yet more stressful conditions would occur during night-time intervals associated with diurnal variations. These conditions are inconsistent with the established tolerance of the zebra mussel (e.g., Karatayev et al., 1998; McMahon, 1996; Sprung, 1987). Thus, if the feedback relationship of McMahon (1996) is representative of the actual behavior of the invader, it was operative in the Seneca River during the study period of 1994, and it was critical to sustaining the population in the downstream portion of the study reach.

The implications of increased zebra mussel biomass in the study reach were investigated for the case of $2 \times$ the zebra mussel biomass by multiplying the calibrated time-series of

ZOD_{max} by two. Even with the operation of the feedback from low DO levels, a substantial shift to lower DO concentrations is predicted for this case (Fig. 10c). Zebra mussels could not have been sustained in this downstream segment under these severely depleted conditions. This suggests that the zebra mussel population in the study reach during 1994 was close to the system's carrying capacity with respect to the available oxygen resources. In other words, the infestation and related water quality impacts (Effler et al., 2001) in 1994 were about as bad as they could get for this system. Low DO levels may not have been the only condition limiting the zebra mussel population in that portion of the river. Low concentrations of potential food (e.g., Chl; Fig. 5) and less suitable substrate (Effler and Siegfried, 1994) may also act to limit further increases in the zebra mussel population in this portion of the river.

Resolution of Sources and Sinks of Chl and DO: The model was used to resolve the source and sink processes that contributed to the observed study average patterns of Chl (Fig. 11) and DO (Fig. 12) for the study reach and three selected combined segments within the reach. The selected segments correspond to the uppermost (C1), middle (C3), and lowermost (C5) portions of the reach (Figs. 11 and 12). The magnitudes of the processes have been normalized for the length of the river represented, to support comparisons among different portions of the reach. The new Chl sink associated with zebra mussel grazing was demonstrated to be essentially completely responsible for the observed decrease in Chl over the study reach (Fig. 11a). The net loss rate was demonstrated to be the greatest in the mid-reach area (Fig. 11c) followed by the upstream (Fig. 11b) and downstream (Fig. 11d) segments, respectively. These features were generally consistent with the longitudinal patterns observed for Chl for most of the surveys (Fig. 5). For example, the predicted minor imbalance in favor of Chl sinks in the downstream portion of the reach (Fig. 11d) were reflected in the modest decreases observed in Chl (e.g., Fig. 5b, f, j, and p).

The new DO sink associated with the consumption of DO by zebra mussels was predicted to be responsible for the observed decrease in DO (Fig. 12a). The much smaller nitrification sink can also be attributed to zebra mussel metabolism (e.g., indirectly), as the increases in T-NH₃ concentrations from excretion (Effler et al., 2001) were largely responsible for the nitrification. The reaeration source (Fig. 12a) reflects the prevalence of undersaturated conditions, particularly in downstream portions of the study reach. The net sink for DO was demonstrated to be the greatest in the most densely populated upstream portion of the reach, decreasing in downstream sections (Fig. 12b - d), consistent with the available zebra mussel population data (Table 3). Reaeration was minor in the upstream sections because of the limited extent of undersaturation (Fig. 12a). Net photosynthesis (P-R) represented a small net source throughout the reach. The longitudinal trends in Chl and light penetration (SD) had somewhat compensating effects in this regard, resulting in relatively uniform P and R levels through the study reach (Fig. 12), despite the reductions in Chl (Fig. 5). The DO sources (photosynthesis and reaeration) were on average in balance with the sinks (phytoplankton respiration, zebra mussel oxygen consumption, and nitrification) in the lower portion of the reach (Fig. 12d), as manifested by the "leveling-out" in DO observed in those sections (Fig. 5). The nitrification sink was greater in the downstream

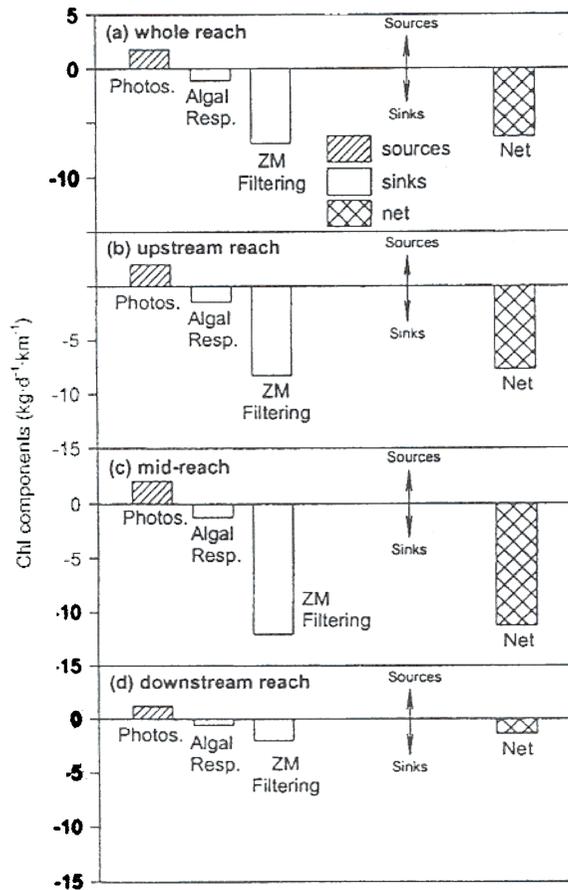


Figure 11. Resolution of sources and sinks of chlorophyll for the study reach, averages for the entire study interval of 1994, normalized for river length [units of kg per day per km of river length]: (a) entire study reach, (b) C1, (c) C3, and (d) C5.

sections (Fig. 12c and d) than in upstream sections (Fig. 12b) because of the higher concentrations of T-NH₃.

5.5. Model Applications

The calibrated model is used here to investigate the oxygen resources of the river near Baldwinsville as a function of zebra mussel biomass (Fig. 13). This type of simulation has management utility for this system, and other rivers where oxygen resources have been

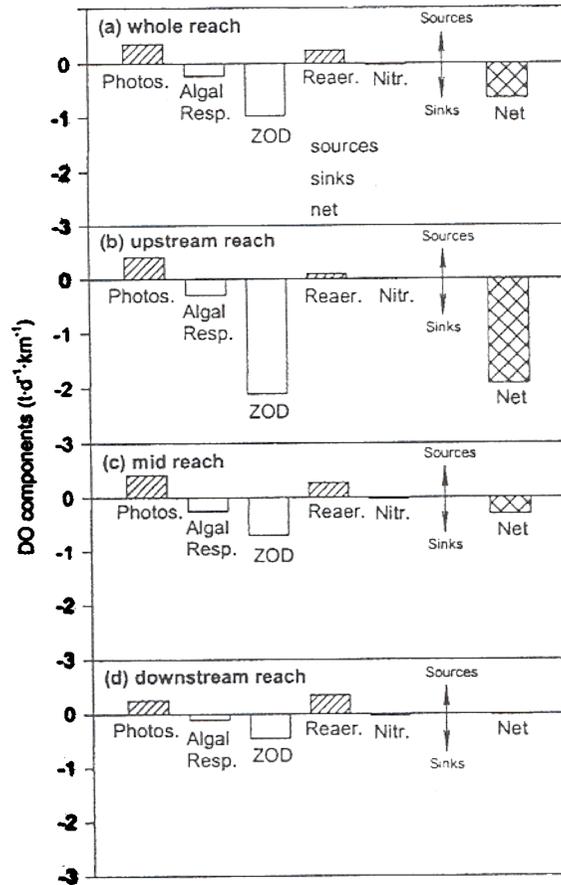


Figure 12. Resolution of sources and sinks of DO for the study reach, averages for the entire study interval of 1994, normalized for river length [units of metric tons (t) per day per km of river length]: (a) entire study reach, (b) C1, (c) C3, and (d) C5.

impacted by the invasion, with respect to the occurrence of violations of related water quality standards and assimilative capacity available to accommodate discharges of oxygen demanding effluents. The specification of environmental conditions is always a critical factor that influences the outcome of such projections (Chapra, 1997; Thomann and Mueller, 1987). Scenario projections are usually driven either by specified "critical" conditions (Chapra, 1997) or large data sets of actual measurements (e.g., Effler and Owens, 1985; Gelda et al., 2001; Owens and Effler, 1989; Owens et al., 1998). The later approach supports probabilistic representation of model output (Fig. 11), that is intended to

reduction in zebra mussel biomass is predicted to decrease the occurrence of violation of the daily minimum standard by one-half, from about 30% to 15% occurrence (Fig. 13). Nearly a 30% reduction of biomass would be required to reduce the occurrences of violation of the daily average standard by one-half (Fig. 13). A 50% reduction in biomass is predicted to essentially eliminate occurrences of violations of either standard (Fig. 13). An 80% decrease in zebra mussel biomass would be necessary to maintain daily average DO concentrations of $\geq 7 \text{ mg}\cdot\text{L}^{-1}$ for 90% of the days (i.e., $\sim 10\%$ occurrence of less than $7 \text{ mg}\cdot\text{L}^{-1}$; Fig. 13).

6. Summary and Recommendations

The conspicuous decreases in Chl and DO and increases in SD that occurred over a 15 km reach of the Seneca River over the summer of 1994 as a result of zebra mussel metabolism were documented. These signatures were important in supporting estimates of filtering (k_f) and oxygen consumption rates (ZOD) of the resident zebra mussel population based on calibration protocols with a mass balance water quality model. Historic Chl and DO data were reviewed that depict the major reductions brought about at the downstream boundary of the reach by the invasion, in the absence of changes at the upstream boundary.

A dynamic two-dimensional mass balance model for Chl and DO was developed that accommodates the oxygen demand (ZOD) and filtering (grazing, k_f) effects of zebra mussels. These fluxes were represented as river bottom-based processes, consistent with the sessile habitat of the invader. The transport submodel accurately simulated time-of-travel. The credibility of the non-zebra mussel components of the model was supported by the similarity of distributions of Chl and DO predictions for the downstream section of the reach, for the case of the absence of the invader, to historic observations.

According to the results of model calibration to the observed longitudinal patterns of Chl and DO, the values of k_f and ZOD varied substantially in time and space within the study reach in 1994. Values of k_f were generally the highest mid-way in the reach, while ZOD decreased progressively from upstream to downstream sections. The dissimilar spatial distributions of k_f and ZOD indicated a decoupling of the processes of effective filtration (grazing) and respiration for the zebra mussel population. In particular, the effectiveness of grazing was apparently reduced in the most densely populated portion of the study reach, probably associated with the thickness/configuration of the colonies. The temporal variations had two components, a systematic decrease in upstream sections associated with a major decrease in biomass, and variations over intervals of relatively uniform biomass that were apparently driven by dynamics in various ambient environmental conditions. Sensitivity analyses support the position that these variations in rate processes of the zebra mussel population were largely real, rather than being an artifact of uncertainty or variations in the other source/sink processes described by the model. Independent estimates of k_f and ZOD based on the available zebra mussel population data and biomass-specific rates available in the literature provided some closure to values obtained through model calibration. The substantial uncertainties associated with such independent estimates were reviewed.

The low DO levels documented for the downstream portion of the study reach appear to be the lowest reported to date in North America for a system that sustains a zebra mussel population, corresponding closely to the limit ($\sim 25\%$ saturated) reported in the former Soviet Union. A slow down of oxygen consumption in response to depleted (undersaturated) oxygen concentrations (e.g., feedback) has been reported in the scientific literature (McMahon, 1996), that has been incorporated in the model. Model simulations indicate that if this feedback relationship is representative, it was operative in the Seneca River during the study period of 1994, and it was critical to sustaining the zebra mussel population in the downstream portion of the reach. The results of additional simulations suggest the zebra mussel population in the study reach in 1994 was close to the system's carrying capacity with respect to the available oxygen resources. The model was also used to resolve the source and sink processes that were responsible for the observed longitudinal patterns of Chl and DO. The new sink for Chl and DO associated with the dense populations of this invader was demonstrated to be essentially completely responsible for the major decreases documented for these constituents in the Seneca River.

The model was used to make probabilistic predictions of the reductions in zebra mussel biomass that would be necessary to reduce or eliminate violations of water quality standards caused by the invasion and to provide waste assimilative capacity for downstream sections of the river. A 50% decrease in biomass from the 1994 levels was predicted to be necessary to eliminate violations of standards for the conditions of that year. An 80% decrease in biomass would be necessary to maintain daily average DO concentrations of $\geq 7 \text{ mg}\cdot\text{L}^{-1}$ for 90% of the days.

An integrated research program is recommended for a severely infested test river with conspicuous water quality signatures, such as Seneca River, that would have the following components: (1) detailed monitoring in time and space of water quality, the zebra mussel population, and environmental forcing conditions, (2) comprehensive kinetic experiments to independently determine biomass-specific filtering and oxygen consumption rates, seasonally, on specimens collected from the test system, and (3) mass balance modeling over extended intervals to establish the credibility of the framework and to obtain independent estimates of k_f and ZOD through calibration. A primary goal of this research should be to achieve a closure between the mass balance model and the kinetic experiments and benthic surveys; i.e., input of the results of benthic surveys and experiments into the model that produces simulations that match observations of water quality state variables (model validation). The successful model framework, modeling, experimental, and monitoring protocols could then be transferred to other impacted systems.

Acknowledgments

C.M Matthews directed and conducted laboratory analyses. B.A Wagner collected samples and made field measurements. This is contribution No. 206 of the Upstate Freshwater Institute.

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