Dissolved Oxygen Declines in the Hudson River Associated with the Invasion of the Zebra Mussel (*Dreissena polymorpha*)

N I N A   F .   C A R A C O , *   J O N A T H A N   J .   C O L E ,
S T U A R T   E .   G .   F I N D L A Y ,
D A V I D   T .   F I S C H E R ,
G R E G O R Y   G .   L A M P M A N ,
M I C H A E L   L .   P A C E ,   A N D
D A V I D   L .   S T R A Y E R

Institute of Ecosystem Studies, Millbrook, New York 12545

Dissolved oxygen (DO) declines have serious implications for the health of aquatic systems. These declines are often attributed to changes in organic or nutrient loading but are not generally attributed to species invasions. We use an 11-year record of DO in the tidal Hudson River to describe the timing and spatial extent of the DO decline as compared to the timing and spatial extent of the zebra mussel establishment in the river. Furthermore, the system attributes that interact with zebra mussel respiration to moderate DO declines are explored using physical and biological budgets. Concurrent with the establishment of the zebra mussel, mean summertime DO declined from 8.3 to 7.3 mg L^{-1}. Because of moderate hydrologic inputs and atmospheric exchange, system respiration would have to increase by only about 0.5 g of O$_2$ m^{-2} d^{-1} to have caused this decline. Independently estimated zebra mussel respiration (1.1 g of O$_2$ m^{-2} d^{-1}) is about double this required respiration. Increased macrophyte photosynthesis, due to increased light penetration after the zebra mussel invasion, may have moderated the effect of zebra mussels on DO.

Introduction

In aquatic environments, dissolved oxygen (DO) is a critical variable that both affects and integrates numerous components of the ecosystem. Low DO, or hypoxic conditions, reduce or eliminate sensitive fish and invertebrate species (*1–3*); alter biogeochemical pathways; and reduce nutrient retention by sediments (*4–6*). For these reasons, water quality managers strive to maintain DO at acceptable levels (*7*).

The processes that combine to determine DO levels include the primary production and respiration of all components of the ecosystem as well as many physical aspects that affect stratification and gas exchange. This integrative aspect makes interpreting the cause of changes in DO potentially difficult. Nevertheless, declines in DO are generally thought to arise for three main reasons: (i) the discharge of organic compounds (such as sewage), the decomposition of which consumes DO (*8, 9*); (ii) the point or nonpoint input of plant-limiting nutrients, which leads to eutrophication of surface waters and hypoxia or anoxia in bottom waters (*2, 3*); and (iii) changes in physical mixing or isolation of bottom water (*10, 11*). For well-mixed systems, such as many rivers, organic loadings are usually considered the most likely explanation; changes in the aquatic food web are rarely invoked to explain changes in system metabolism or DO (but see refs *12–14*).

One way in which food webs can be altered is by the introduction of exotic species such as the zebra mussel (*Dreissena polymorpha*; refs *13–17*). The impact of the zebra mussel in North America has been better documented than many prior invasions as this introduction occurred relatively recently and was predicted to have large economic impacts. Commonly documented impacts of the zebra mussel are declines in phytoplankton and zooplankton (*13–15, 18–21*) as a direct result of water filtration by the mussel (*21, 22*). Other, less direct, changes include declines in other benthic animals, increases in water clarity, and increases in benthic primary production (*13, 15, 20, 23, 24*). The DO of aquatic systems could be affected directly by the direct impact of zebra mussel respiration or indirectly by one of the above changes. We know, however, of only two cases where such changes have been documented, a section of the Seneca River (*13*) with exceptionally high populations of zebra mussel and the nearby Oswego River (*14*).

In this study we document, using a long-term data set, DO changes in a large river with only moderate zebra mussel populations (*15, 21, 25*). Causes of the changes are assessed using DO budgets for this system.

Methods

Study Site. The Hudson River drains 34 000 km², primarily in eastern New York (*26*). A large (150-km) section of the river is tidal and freshwater (Figure 1A). Most of the water (85%) enters the tidal–freshwater Hudson (TF Hudson) at the confluence of the nontidal Hudson and Mohawk Rivers above the dam at Troy, below which there is a tidal range of 1 m (*26*). Average annual and summertime flows at the dam are 350 and 150 m³ s^{-1}, respectively (*27*). The river throughout much of the tidal–freshwater section is relatively wide (average = 0.8 km) and deep (average depth = 8 m). Despite this depth, the water column is well-mixed, showing little vertical stratification for major ions, nutrients, and DO (*28–30*).

In addition to the uniform vertical profiles, many chemical variables show little gradient along the 150-km TF Hudson (*26, 30, 31*). Biotic components can however be somewhat more variable. For example, strong spatial variation exists in macrophyte cover and phytoplankton biomass (*21, 32, 33*). Furthermore, the zebra mussel is not found uniformly throughout this section (*21*). Our intensively studied site near Kingston, NY (Figure 1, km 148 and km 144) is typical of much of the TF Hudson not only for chemical features but also for physical and biological characteristics (Figure 1B–D). Here the river is about 1.2 km wide and averages 7 m deep. Macrophytes (dominantly *Vallisneria)* cover about 15% of the river area (*33*). The Kingston site represents the lower edge of a large stretch of river where zebra mussels became well-established in 1992 and have maintained high population densities (Figures 1B and 2A).

The invasion of the zebra mussel and many of its effects on the Hudson ecosystem have been reported previously (*15*). The zebra mussel was first observed at very low numbers in the tidal Hudson River in 1991. By 1992, it had established relatively large populations averaging 2000 individuals m^{-2} with a biomass averaging 20 g dry mass m^{-2} (*25*). Due to the zebra mussel population increase, there was an increase in

* Corresponding author e-mail: Caracon@ecostudies.org; phone: (914)677-5343; fax: (914)677-5976.
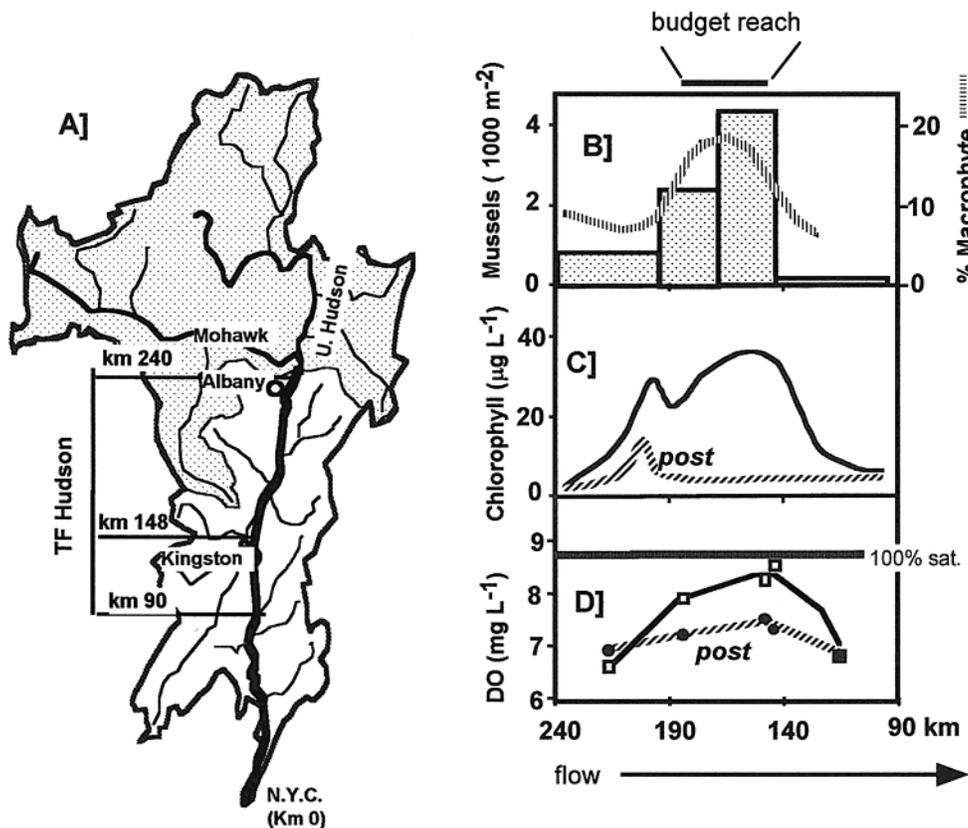
FIGURE 1. (A) Map of the Hudson River watershed showing the location of the tidal—freshwater (TF) section of the river. Below this, the river is brackish to saline. (B—D) Longitudinal variation in the TF Hudson. (B) Zebra mussel density considered in 4 subsections and macrophyte abundance (right-hand axis) as expressed in % coverage of the river area. (C) Summertime (June—September) phytoplankton abundance as expressed in μg L^{-1} chlorophyll *a* for periods pre- and post-zebra mussel invasion (see Figure 2). Values are averaged at 10-km intervals in both periods. (D) Summertime dissolved oxygen (DO) for pre- and post-zebra mussel periods at five key locations where long-term DO are available. The 100% saturation line shown reflects saturation at 22 °C, the average summertime temperature in the Hudson.
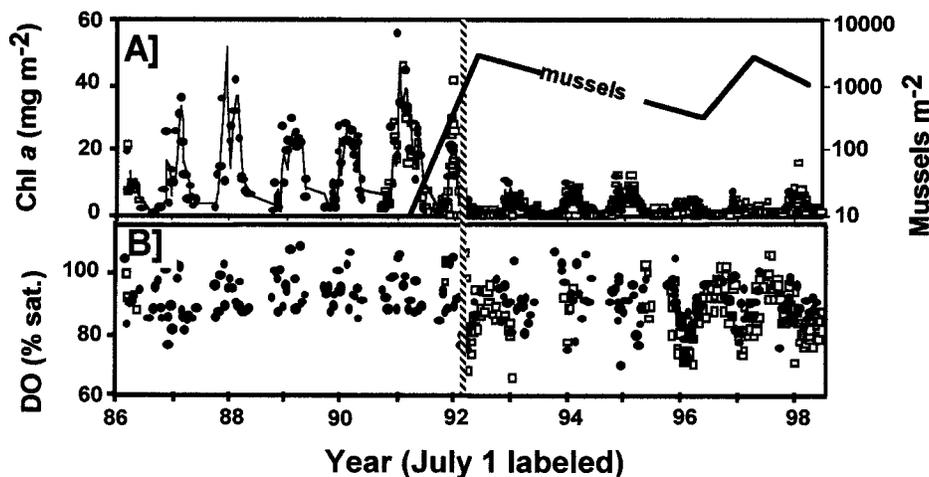

FIGURE 2. Hudson River phytoplankton biomass and zebra mussel biomass (A) and dissolved oxygen (DO) concentration (B) for an 11-year period. The DO decline, which began in 1992 at km 149 (closed circles) and km 144 (open squares), extended over a 50-km stretch of the river where zebra mussels established at moderately high densities.

total biomass of heterotrophs, which occurred despite some declines in zooplankton and other benthic invertebrates (*15, 25*). Additionally there was a dramatic increase in biological filtration of the system. Prior to the invasion of the zebra mussel, the water column was filtered every 50 days; after the invasion, filtration occurred approximately every 3 days (*15, 21*). This change in filtration was associated with a sharp decline in phytoplankton biomass (Figures 1C and 2A).

Water Sampling and Measurements. Between fall 1986 and fall 1998, surface water (0.5 m) was sampled at km 148

at biweekly intervals during spring—fall and at approximately monthly intervals in winter months (*28—32*). Samples were taken between 10:00 AM and 12 noon in both pre- and post-zebra mussel periods. During 1986 and 1992—1998, weekly to monthly measurements were also taken at river km 144. These measurements were generally taken between 8:00 and 10:00 AM. Recent diurnal DO measurements suggest that between 8:00 AM and 12 noon DO generally increases by less than 0.1 mg L^{-1}. Additionally, during the same time period, samples at approximately monthly intervals were taken at

TABLE 1. Calculated Summertime Net System Respiration (NSR) in the Pre- and Post-Zebra Mussel Establishment Periods and the Change in NSR between These Periods[a]

physical budget				biological budget			
	pre	post	change		pre	post	change
mass change	0.09	0.09	0.00	net primary production			
advective input	−0.12	−0.12	0.00	phytoplankton	0.70	0.70	0.00
atmospheric exchange	0.33	0.86	0.53	macrophyte	0.80	1.10	0.30
				heterotrophic respiration			
calcd NSR	0.30	0.83	0.53	microbial	1.55	1.55	0.00
				zooplankton	0.15	0.04	−0.11
				other macro benthos	0.12	0.04	−0.08
				zebra mussel	0.00	1.10	1.10
				calcd NSR	0.32	0.93	0.61

[a] Both physical and biological budgets are calculated for a 45-km budget stretch of the Hudson River (Figure 1). All components are in g of O_2 m^{-2} d^{-1}. NSR is calculated as heterotrophic respiration minus net primary production.

three additional study sites within the TF Hudson. The site at km 184 was toward the northern end of the area that experienced high zebra mussel establishment (Figure 1). The two other sites were outside the area that was heavily invaded by zebra mussels; an upstream sampling site (km 216) was north of the area of highest zebra mussel densities, and the other site (km 115) was south of the area of high zebra mussel abundance (Figure 1C,D). Last, summertime transects were made where surface waters were sampled at approximately 2-km intervals over the entire TF Hudson (*21, 31*). Chlorophyll and DO were sampled in these transects starting in 1991 and 1992, respectively.

DO and temperature were measured with a Yellow Springs Instruments meter (YSI model 580). Before DO measurements were taken, the meter was warmed for 15 min and air-calibrated. Measurements were checked in both pre- and post-zebra mussel periods against Winkler titrations (*34*). Saturation of DO with respect to the atmosphere was estimated from these DO measurements and temperature measured at the same time (*34, 35*). Water samples collected for chlorophyll were kept cool and in the dark until processed (*21, 28, 29*).

Differences in concentration of DO for pre- and post-zebra mussel periods or between sites were assessed by unpaired *t*-tests and by time intervention analysis (*23, 36*). Time series intervention analysis can account for possible artifacts of correlation between sampling events. For all statistics, significance was considered at $p < 0.05$.

During 1990−1998, zebra mussels were sampled on both soft and hard bottom substrates, and total numbers were estimated by multiplying the density on these substrates by the total areas of substrates (*25*).

DO Changes and Net System Respiration. Net system respiration (NSR) is the difference between biological consumption of DO by respiration and production by photosynthesis. This respiration can be estimated directly by summing estimates of respiration by consumers and microbes and subtracting estimates of net primary production (biological budget, below). Except in rare cases where inputs of reduced inorganics such as sulfides are high, NSR can also be calculated by a physical mass balance of DO in the system (physical budget) that considers change in mass of DO in the system and the supply of DO from the atmosphere and water inputs (*30*). For the Hudson we assembled a physical budget for a 36-km stretch of the river (km 184 to km 148) that was greatly impacted by the zebra mussel invasion (Figure 1). We consider the summer months only (June−September) when zebra mussels would be expected to be active due to higher temperatures. All terms are expressed on an areal basis in g of O_2 m^{-2} d^{-1}.

Physical Budget. In this budget, we considered NSR to be the sum of declines in the mass of DO in the system (ΔDO),

net supply from atmospheric exchange (DO_{flux}), and net advective supply from freshwater inputs (DO_{ad}). Since on time scales greater than one tidal cycle tidal flows do not directly bring new water into the freshwater section of the river being considered, these flows were not considered in the budget. All terms in the budget are calculated for each month and are expressed as mean summertime values (Table 1).

The decrease in mass of DO is the rate of change in concentration times the average depth of the water. Thus

$$\Delta DO = z(DO_x - DO_{x-1})/days \qquad (1)$$

where z is the average depth in meters; DO_x and DO_{x-1} are the monthly average DO concentrations (mg L^{-1} or g m^{-3}) for the month and previous month, respectively; and days are the number of days in the month.

The atmospheric exchange of DO was calculated as

$$DO_{flux} = k(DO_{wat} - DO_{sat}) \qquad (2)$$

where DO_{wat} and DO_{sat} are the measured DO and calculated DO value at 100% saturation, respectively. k is a surface water/gas exchange coefficient expressed as a piston velocity (in m d^{-1}). Studies in the Hudson based on additions of an inert gas (sulfur hexafluoride, SF_6) demonstrated an increase in k at 20 °C (*37*, k_{600}) with increasing wind speed. Furthermore, these data for the Hudson fit a power function of wind vs k_{600} that has been developed for a variety of aquatic systems (*38*). Wind speed was from the IES meteorological station, which measures wind continuously at a height 10 m above the ground, approximately 20 km from the Hudson River (*39*). These wind speeds were corrected up by 50% to wind speeds on the Hudson using a 720-measurement comparison between data taken at IES and wind measurements taken directly on the Hudson (*40*). We calculate k_{600} based on monthly average wind speed, but a 1-year comparison between these values and k_{600} values based on daily wind speeds show very little difference (1988 summertime k values were calculated as 0.82 and 0.83 for monthly based and daily based averages, respectively). The monthly k_{600} were corrected to k values using mean monthly temperatures, k_{600} values, and the Schmidt equation (*37*).

Net advective inputs of DO were calculated as

$$DO_{ad} = WL(DO_{184} - DO_{148}) \qquad (3)$$

where WL is the water load to the system in m d^{-1} and is calculated as the quotient of flow at km 148 and surface area of the river between km 184 and km 148 (*21*). Flow was based on measurements at the Troy Dam (*27*) corrected for tributary inputs between Troy and km 148 (*21, 27*). DO_{184} and DO_{148} are DO concentrations at these two sites.

Biological Budget. Net system respiration can be calculated directly as the difference between microbial and consumer respiration and net primary production. For the Hudson, we considered the following terms for which measurements were directly available in the Hudson:

  (i) watercolumn bacterial respiration
  (ii) zooplankton respiration
  (iii) zoobenthos respiration (excepting zebra mussels)
  (iv) zebra mussel respiration
  (v) phytoplankton net production
  (vi) macrophyte net production

The estimate of primary production was based on ^{14}C uptake measurements at an array of light levels (*P* vs *I* curves), measurements of light at depth in the Hudson, and phytoplankton standing stock (*21, 28, 29*). Similarly, macrophyte production was calculated from measured *P* vs *I* curves for macrophytes in the Hudson, macrophyte abundance with depth, and light at depth (*33, 41*). As macrophytes were not stripped of attached periphyton, these estimates represent a combination of macrophyte and periphyton production. Bacterial respiration was estimated from measurements of bacterial production (*42, 43*) and measurements of bacterial growth efficiency in the Hudson River (*43*). Zooplankton respiration was based on biweekly estimates of zooplankton biomass (*23*) and literature estimates of biomass specific respiration (*44*). Similarly, respiration of non-zebra mussel benthic organisms was estimated from estimates of abundance and biomass in the Hudson River (*15, 25*) along with literature-based relationships to respiration (*45*). Finally, zebra mussel biomass based on diver surveys was converted to respiration by fitting an empirical model to data collected in three different lab studies (*25*). Body mass and temperature were the only independent variables in the model, which fit the data well ($r^2 = 0.92$). All of these lab studies were run in filtered lake or river water and so provided no food to the zebra mussels. As high food levels may increase respiration of zebra mussels (*46*), our estimates could be somewhat of an underestimate of true zebra mussel respiration in the river. As phytoplankton concentrations in the Hudson are quite low for the post-zebra mussel period, this underestimate would however be expected to be quite low.

Results and Discussion

Spatial and Temporal Patterns of DO. DO in the TF Hudson is generally undersaturated with respect to the atmosphere (Figures 1D and 2B). At km 184, km 148, and km 144, all locations with high zebra mussel abundance, there was a decline in DO associated with the invasion of the zebra mussel (increase in the degree of undersaturation). The DO decline at km 148 is best documented. Considering the full annual data, both the times series analysis and an unpaired *t*-test demonstrated that this decline was significant ($p < 0.05$). The summertime decline drives this trend. There was no significant change for the winter period (when zebra mussel activity is low). For the summertime data, the reduction in DO associated with the zebra mussel was highly significant ($p < 0.01$). During pre-zebra mussel periods (1986–1991), DO averaged 95% saturation during summer months (June–September). After 1992, the DO averaged 85% saturation, thus the degree of undersaturation increased nearly 3-fold. Although few data at km 144 exist for the pre-zebra mussel period, the DO record at km 144 showed similar results to that of km 148. For both periods, these two sites were not significantly different from each other considering the data set as a whole or the summertime period only ($p > 0.2$, unpaired *t*-test).

The change in DO saturation was driven by changes in absolute measured DO and not by temperature changes that

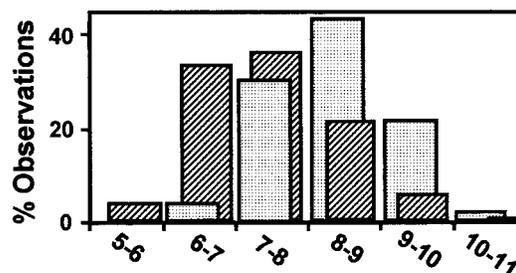FIGURE 3. Frequency distribution of summertime DO concentrations for pre- (stippled) and post-(hatched) zebra mussel periods. Distributions are expressed in percent of observations, and data are divided into concentrations at 1 mg L^{-1} intervals.
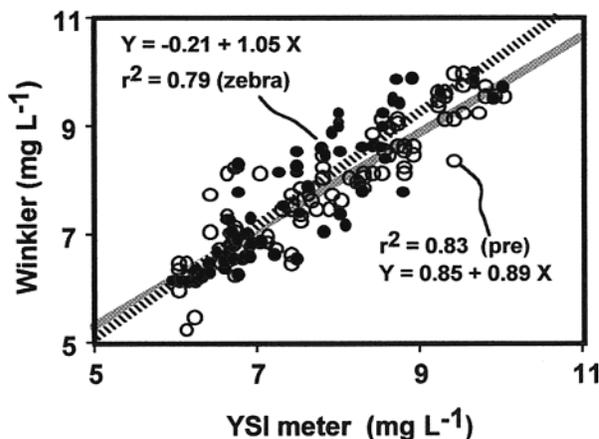

FIGURE 4. Comparison of DO measurements taken on a YSI meter and those calculated from Winkler titrations. Comparison are shown for both pre- (open circles) and post-zebra mussel periods (filled circles). Regressions for both periods (shown) are not significantly different from each other or a 1:1 relationship.

would impact saturation. Summertime temperature averaged 22.0 and 22.5 °C in the pre- and post-zebra mussel period, respectively, and this difference was not significant at $p < 0.05$. Considering data from km 148 and km 144 together, DO decreased from an average of 8.3 to 7.3 mg L^{-1}, a highly significant decline ($p < 0.01$). In addition to the decline in average DO, there was an increase in the frequency of low DO values. Prior to the invasion of the zebra mussel, DO concentrations were less than 7 mg L^{-1} only 4% of the time. After the invasion, concentrations were below 7 mg L^{-1} 37% of the time, and values below 6 mg L^{-1} were found 4% of the time (Figure 3). Thus, following the invasion concentrations declined to levels where sensitive fish species could be impacted (*1*).

Causes of DO Decline. The measured decline in DO in the Hudson is consistent in timing with the zebra mussel invasion, but other potential causes for the decline need to be examined. Measurement error is an unlikely explanation for the observed decline: (i) the DO decline is large enough to be easily detected by the YSI meter; (ii) the meter measurements were routinely calibrated to Winkler titrations and titrations agree well with meter measurements for both pre- and post-zebra mussel periods (Figure 4); (iii) different meters and operators were used for the two locations in the river (km 144 and km 148), and both of these sites show similar patterns for DO decline (Figure 2); (iv) despite the same methodology being used at all sampling sites, DO did not decline significantly at sites upstream (km 216) or downstream (km 116) of the area with highest zebra mussel density (Figure 1C,D); (v) measurements were primarily taken in late morning to noon in both the pre-and post-zebra mussel periods, a period of near average DO during both periods.

DO changes can be driven by changes in physical supply of DO (*10, 11*). In a well-mixed water column, like the TF Hudson, change in physical supply may be due to changes in advective input or changes in atmospheric exchange (*37*). In regard to advective changes, there was no significant difference in water load between the pre- and post-zebra mussel periods (*15, 21*). Changes in atmospheric exchange could occur with changes in wind speed (*37, 40*). Interestingly, in the Hudson there was a significant ($p < 0.05$) difference in summertime wind speed between the pre- and post-zebra mussel period. Summertime monthly average wind at IES was 2.0 and 1.7 m s^{-1} for the pre- and post-zebra mussel period, respectively. We estimate that this indicates average wind speeds of 3 and 2.5 m s^{-1} on the Hudson. This change would have decreased the summertime gas exchange constant for DO (*k*, eq 2) from 0.85 to 0.81 m d^{-1}. Without a change in system metabolism, this decline would only account for a 0.1 mg L^{-1} decline in DO. This decline is relatively small and is accounted for in the monthly DO balance (below).

One of the most often cited causes for increases in respiration and DO changes in rivers is changes in inputs of sewage or industrial waste. For the TF Hudson, sewage load averaged 0.16 g of C m^{-2} d^{-1} (*47, 48*). Thus, if this material were completely respired, it would consume only 0.3 g of O$_2$ m^{-2} d^{-1} (lower than the increased NSR calculated in our budget, below). Furthermore, data on sewage loads suggest declines since the 1980s rather than increases (*49*), and most of the sewage enters the TF Hudson near Albany, NY, approximately 100 km north of the study site. If completely respired, nonpoint organic loads from the watershed could consume approximately 2 g of O$_2$ m^{-2} d^{-1} (*47, 48*), and these inputs could vary from year to year with hydrologic flow. However, summertime and mean annual flows did not change significantly before and after the invasion of the zebra mussel (*15, 21*). Furthermore, two years in the post-zebra mussel period (1995 and 1996) represented the wettest and driest summers during the 1987−1998 period (*15, 21*). Both of these years had lower DO than the pre-zebra mussel period.

Considering the above evidence, the DO decline in the Hudson is not likely a measurement artifact. The decline is in large part due to an increase in net system respiration (NSR) and was augmented slightly by lower winds in recent years. Further, the 2-fold increase in NSR does not correspond to changes in organic load to the system. The change in NSR could be due to a decline in net summertime primary production or could be due to an increase in respiration of organic material within the system. We use physical and biological NSR budgets to assess how zebra mussels could have caused either one of these changes.

NSR Budgets. *Physical Budget.* The balance of DO includes change in mass of DO, advective inputs, and atmospheric exchange (eqs 1−3). Although the mass of DO declined in early summer due to temperature increases and respiration, these declines were nearly met by DO increases in late summer. For the entire summer, the change in the mass of DO (ΔDO, eq 1) averaged only 0.09 g of O$_2$ m^{-2} d^{-1} for both pre- and post-zebra mussel periods. Net advective inputs of water (WL) averaged near 0.4 m d^{-1} in the km 184−148 stretch for both pre- and post-zebra mussel periods, and the DO gradient over this stretch was also near 0.3 mg L^{-1} for both periods. Thus, the contribution of advection was approximately −0.12 g of O$_2$ m^{-2} d^{-1} in both periods with the negative sign indicating that advection was a negative source of DO due to the slightly higher DO concentration at km 148 as compared to km 184 (Figure 1D).

While the net summertime advective input of DO and the mass change of DO were unchanged with the zebra mussel invasion (Table 1), the atmospheric exchange of DO changed substantially between these periods due to a large increase

in DO undersaturation (Figure 2B). In the post-zebra mussel years, atmospheric inputs averaged 0.86 g of O$_2$ m^{-2} d^{-1}, and in the pre-zebra mussel years, it averaged 0.33 g of O$_2$ m^{-2} d^{-1}. Considering all components of the physical budget, we estimated that NSR increased from 0.30 to 0.83 g of O$_2$ m^{-2} d^{-1} after the zebra mussel invasion. Thus, according to the physical budget, NSR increased by 0.53 g of O$_2$ m^{-2} d^{-1} (Table 1).

Biological Budget. The biological budget is the balance between DO outputs from respiration and DO inputs from net primary production. With the invasion of the zebra mussel there was a decline in phytoplankton biomass (Figure 2A) and gross phytoplankton production (*21*). Interestingly, however, total net primary production appears to have actually increased substantially. First, after the zebra mussel invasion there was an increase in light penetration and phytoplankton growth efficiency associated with phytoplankton species shifts (*13, 21*). Thus, despite declines in phytoplankton biomass, summertime net phytoplankton production appears to have remained relatively constant at 0.7 g of O$_2$ m^{-2} d^{-1} (*21*). Second, biomass specific production of macrophytes has increased due to greater light penetration, and assuming constant macrophyte coverage (*33*), net macrophyte production should have increased from 0.8 to 1.1 g of O$_2$ m^{-2} d^{-1}. If macrophyte biomass or biomass of attached periphyton actually increased with the greater light availability, this production increase would be even greater. Thus, overall net primary production may have increased by more than 0.3 g of O$_2$ m^{-2} d^{-1} (Table 1), and this change should have increased rather than decreased DO in the system.

Because net primary production in the Hudson may well have increased with the zebra mussel invasion, loss of DO must have been caused by substantial increases in respiration. Microbial secondary production has not increased significantly between pre- and post-zebra mussel periods (*42*); thus, given no change in growth efficiency, microbial respiration would have remained at near 1.5 g of O$_2$ m^{-2} d^{-1} in both the pre- and post-zebra mussel periods (*43*). Zooplankton biomass declined by about 0.25 g of C m^{-2} after the invasion of the zebra mussel (*23*), and given a respiration rate for zooplankton of 0.43 g of O$_2$ (g of zooplankton C)$^{-1}$ d^{-1} (*44*), zooplankton respiration would have declined by 0.11 g of O$_2$ m^{-2} d^{-1} (Table 1). Similarly, the biomass of non-zebra mussel benthic organisms declined after the zebra mussel invasion (*15*) and considering biomass specific respiration of these organisms (*45*), respiration of these organisms should have decreased by 0.08 g of O$_2$ m^{-2} d^{-1} (Table 1). The respiration of zebra mussels themselves may, however, be large enough to more than offset increases in net primary production and slight declines in respiration by zooplankton and other zoobenthos in the Hudson.

Since 1992 the zebra mussel biomass in the Hudson River has been near 20 g dry matter (shell free) m^{-2}, and population respiration was estimated at near 200 g of O$_2$ m^{-2} yr^{-1} (*25*). Considering the relationship between temperature and zebra mussel respiration, summertime respiration of zebra mussels is calculated to be 1.1 g of O$_2$ m^{-2} d^{-1}. This respiration expressed on a per mussel weight basis is about 50 mg of O$_2$ g dry weight^{-1} d^{-1} and is consistent with summertime values found in the Seneca River (*50*). Using this value of zebra mussel respiration and considering the 0.3 g of O$_2$ m^{-2} d^{-1} increase in net primary production and the 0.19 g of O$_2$ m^{-2} d^{-1} decline in respiration by other heterotrophs, the zebra mussel respiration should have increased NSR in the Hudson by about 0.61 g of O$_2$ m^{-2} d^{-1} (Table 1). The physical budget of DO suggests NSR increases of 0.53 g of O$_2$ m^{-2} d^{-1}. These two estimates are in remarkably good agreement considering potential errors in estimates of the components of both budgets. For example, zebra mussel respiration is subject to errors in estimates of zebra mussel abundance (*26*) and to

potential errors in metabolism including the possible impact of food level or turbidity on respiration rates ([46]). Additionally, for the physical budget, substantial uncertainties exist in estimates of wind speed on the Hudson River and the exact relationship of wind speed to gas exchange coefficients (ks, [38]).

Comparison to Seneca Budget. The zebra mussel has invaded many lakes and rivers within the United States during the past 2 decades ([15]). The only other system, however, for which DO changes have been both well-documented and explained is a ca. 1.5-km stretch of the Seneca River ([13, 50]). As for the Hudson River, in the Seneca River the DO decline was budgeted from both physical and biological perspectives, and these two budgeting approaches agreed well. The Seneca River budgets were however quite different from those of the Hudson River. In terms of the physical supply budget, due to the high flows in the river (ca. 30 m d^{-1}, water load) and high DO gradient in the post-zebra mussel period, advective inputs of DO dominated the DO load, and atmospheric exchange and change in mass of DO could be ignored. In the Seneca River, zebra mussel respiration lowered the DO concentration and the advective loss of DO. Since the upstream concentration and advective input of DO were unaffected, the net advective input of DO increased by 44 g of O_2 m^{-2} d^{-1}. This physically budgeted increase in NSR agrees well with the increased system respiration due to zebra mussels (34 g of O_2 m^{-2} d^{-1}). The fact that the physical supply was not lower than the zebra mussel respiration suggests that NSR was not moderated substantially by increased photosynthesis or declines in respiration of other consumers following the mussel invasion.

By comparing the budget of the Seneca and Hudson Rivers, some major differences are apparent. First, in systems such as the Hudson, with moderate residence time, compensatory factors may play a greater role. That is, the DO drop can be buffered significantly by increases in net primary production and macrophytes, which are not eaten by zebra mussels but benefit from higher light, might be significant in this regard. Second, and more striking, is the greater relative zebra mussel impact on DO in systems with moderate as compared to rapid flows. Thus, in the Seneca River despite approximately 30-fold higher zebra mussel biomass than in the Hudson and 60-fold greater increase in NSR, the DO decline (1.7 mg L^{-1}) was less than 2-fold the decline observed in the Hudson River (1 mg L^{-1}). In systems with limited advective inputs of DO, as is true for lakes, reservoirs, and many larger rivers;,it would seem probable that even moderate numbers of zebra mussels could impact DO concentrations. DO declines may sharply impact food webs, biogeochemical cycles, and aesthetics of aquatic systems. Considering the case of the Hudson River and the Seneca River together suggests that a number of physical and biological features will interact with the zebra mussel introduction to determine their ultimate impact to DO in the aquatic system.

Acknowledgments

Literature Cited

(1) Alabaster, J. S.; Lloyd, R. *Water quality for freshwater fish*; Butterworth: Boston, 1982.
(2) D'Elia, C. F. *Environment* **1987**, *29*, 6–11 and 30–33.
(3) Rabalais, N. N.; Turner, R. E.; Justic, D.; Dortch, Q.; Wiseman, W. J., Jr.; Sen Gupta, B. K. *Estuaries* **1996**, *19*, 386-407.
(4) Caraco, N. F.; Cole, J. J.; Likens, G. E. *Nature* **1989**, *341*, 316–318.
(5) Kemp, W. M.; Sampou, P.; Caffrey, J.; Mayer, M.; Henriksen, K.; Boynton, W. R. *Limnol. Oceanogr.* **1991**, *35*, 1545–1563.
(6) Seitzinger, S. P.; Giblin, A. E. *Biogeochemistry* **1996**, *35*, 235–260.
(7) Cooke, G. D.; Welch, E. B.; Peterson, S. A.; Newroth, P. R. *Lake and Reservoir Restoration*; Butterworth: Boston, 1986; pp 1–392.
(8) O'Shea, M. L.; Brosnan, T. M. New York State Department of Environmental Protection, 1997.
(9) Officer, C. B.; et al. *Science* **1984**, *223*, 22–27.
(10) Fonselius, S. H. *Tellus* **1970**, *22*, 533–544.
(11) Wiseman, W. J.; Rabalais, N. N.; Turner, R. E.; Dinnel, S. P.; McNaughton, A. *J. Mar. Syst.* **1998**, *12*, 237–248.
(12) Schindler, D. E.; Carpenter, S. R.; Cole, J. J.; Kitchell, J. F.; Pace, M. L. *Science* **1997**, *277*, 248–251.
(13) Effler, S. W.; Siegfried, C. *Environ. Sci. Technol.* **1994**, *28*, 2216–2221.
(14) Effler, S. W.; Siegfried, C. *J. Great Lakes Res.* **1998**, *24*, 453–463.
(15) Strayer, D. L.; Caraco, N. F.; Cole, J. J.; Findlay, S.; Pace, M. L. *Bioscience* **1999**, *49*, 19–28.
(16) MacIsaac, H. J. *Am. Zool.* **1996**, *36*, 287–299.
(17) Mills, E. L.; Strayer, D. L.; Scheuerell, M. D.; Carlton, J. T. *Estuaries* **1996**, *19*, 814–823.
(18) Holland, R. E. *J. Great Lakes Res.* **1993**, *19*, 617–624.
(19) Padilla, D. K.; Adolph, S. C.; Cottingham, K. L.; Schneider, D. W. *Ecol. Modell.* **1996**, *85*, 129–144.
(20) Fahnenstiel, G. L.; Bridgeman, T. B.; Lang, G. A.; McCormick, M. J.; Nalepa, T. F. *J. Great Lakes Res.* **1995**, *21*, 465–475.
(21) Caraco, N. F.; Cole, J. J.; Raymond, P. A.; Strayer, D. L.; Pace, M. L.; Findlay, S. E. G.; Fischer, D. T. *Ecology* **1997**, *78*, 588–602.
(22) Bastviken, D. T. E.; Caraco, N. F.; Cole, J. J. *Freshwater Biol.* **1999**, *39*, 375–386.
(23) Pace, M. L.; Findlay, S. E. G.; Fischer, D. *Freshwater Biol.* **1998**, *39*, 103–116.
(24) Karateyev, A. L.; Butalakova, L. E.; Padilla, D. K. *J. Shellfish Res.* **1997**, *1*, 187–203.
(25) Strayer, D. L.; Powell, J.; Ambrose, P.; Smith, L. C.; Pace, M. L.; Fischer, D. T. *Can. J. Fish. Aquat. Sci.* **1996**, *53*, 1143–1149.
(26) Limburg, K. E.; Moran, M. A.; McDowell, W. H. *The Hudson River Ecosystem*; Springer-Verlag: New York, 1986; pp 331.
(27) Abood, K. A.; Apicella, G. A.; Wells, A. W. In *Estuarine Research in the 1980s*; Smith, L. C., Ed.; State University of New York Press: Albany, 1992; pp 3–28.
(28) Cole, J. J.; Caraco, N. F.; Peierls, B. *Verh. Internat. Verein. Limnol.* **1991**, *24*, 1715–1719.
(29) Cole, J. J.; Caraco, N. F.; Peierls, B. L. *Limnol. Oceanogr.* **1992**, *37*, 1608–1617.
(30) Raymond, P. A.; Caraco, N. F.; Cole, J. J. *Estuaries* **1997**, *20*, 381–390.
(31) Lampman, G.; Caraco, N.; Cole, J. *Estuaries* **1999**, *22*, 285–296.
(32) Findlay, S.; Pace, M.; Fischer, D. *Estuaries* **1996**, *19*, 866–873.
(33) Findlay, S.; Blair, E.; Nieder, W. C., Branaba, E.; Hoskins, S. *Distribution of Submerged Rooted Vegetation Beds of the Tidal Hudson River*; Report to the Hudson River Foundation; 1997.
(34) Wetzel, R. G.; Likens, G. E. *Limnological Analysis*; Sanders: Philadelphia, 1979; p 357.
(35) del Giorgio, P. A.; Cole, J. J.; Caraco, N. F.; Peters, R. H. *Ecology* **1999**, *80*, 1422–1431.
(36) SAS Institute. *SAS/ETS User's Guide*; SAS Institute Inc.: Cary, NC, 1993.
(37) Clark, J. F.; Waninkof, R.; Schlosser, P.; Simpson, H. J. *Tellus* **1994**, *46B*, 274–285.
(38) Cole, J. J.; Caraco, N. F. *Limnol. Oceanogr.* **1998**, *43*, 647–656.
(39) Kelly, V. R. *Occas. Publ. Inst. Ecosyst. Stud.* **1993**, *8*, 1–16.
(40) Consolidated Edison Danskammer Plant. Unpublished data.
(41) Harley, M. T.; Findlay, S. *Estuaries* **1994**, *17*, 200–205.
(42) Findlay, S. E. G.; Pace, M. L.; Fischer, D. T. *Microb. Ecol.* **1998**, *36*, 131–140.
(43) Roland, F.; Cole, J. J. *Aquat. Microb. Ecol.* **1999**, *20*, 31–38.
(44) Lampert, W. In *A Manual of Methods for the Assessment of Secondary Productivity in Fresh Waters*; Downing, J. A., Rigler, F. H., Eds.; Blackwell Scientific: Boston, 1984; pp 413–468.
(45) Strayer, D.; Likens, G. E. *Ecology* **1986**, *67*, 303–313.

(46) Madon, S. P.; Schneider, D. W.; Stoeckel, J. A.; Sparks, R. E. *Can. J. Fish. Aquat. Sci.* **1998**, *55*, 401−413.

(47) Howarth, R. W.; Marino, R.; Garritt, R.; Sherman, D. *Biogeochemistry* **1992**, *16*, 83−102.

(48) Howarth, R. W.; Schneider, R.; Swaney, D. *Estuaries* **1996**, *19*, 848−865.

(49) Johnson, C.; Hetling, L. A historic review of pollution loadings to the lower Hudson River. 1999, unpublished report.

(50) Effler, S. W.; Boone, S. R.; Siegfried, C.; Ashby, S. L. *Environ. Sci. Technol.* **1998**, *32*, 2216−2221.