

ZEBRA MUSSEL INVASION IN A LARGE, TURBID RIVER: PHYTOPLANKTON RESPONSE TO INCREASED GRAZING

NINA F. CARACO, JONATHAN J. COLE, PETER A. RAYMOND, DAVID L. STRAYER, MICHAEL L. PACE,
STUART E. G. FINDLAY, AND DAVID T. FISCHER

Institute of Ecosystem Studies, Box AB, Millbrook New York 12545 USA

Abstract. Changes in the biomass of benthic bivalves can cause dramatic changes in total grazing pressure in aquatic systems, but few studies document ecosystem-level impacts of these changes. This study documents a massive decline in phytoplankton biomass concurrent with the invasion of an exotic benthic bivalve, the zebra mussel (*Dreissena polymorpha*), and demonstrates that the zebra mussel actually caused this decline. In the fall of 1992 the zebra mussel became established at high biomass in the Hudson River Estuary, and biomass of mussels remained high during 1993 and 1994. During these 2 yr, grazing pressure on phytoplankton was over 10-fold greater than it had been prior to the zebra mussel invasion. This increased grazing was associated with an 85% decline in phytoplankton biomass. Between 1987 and 1991 (pre-invasion), summertime chlorophyll averaged 30 mg/m³; during 1993 and 1994 summertime concentrations were <5 mg/m³. Over this same period, light availability increased, phosphate concentrations doubled, some planktonic grazers declined, and average flow was not different from the pre-invasion period. Thus, changes in these other factors were not responsible for phytoplankton declines.

We developed a mechanistic model that reproduces the spatial and temporal dynamics of phytoplankton prior to the invasion of the zebra mussel (1987–1991). The model accurately predicts extreme declines in phytoplankton biomass after the invasion (1993–1994). The model demonstrates that zebra mussel grazing was sufficient to cause the observed phytoplankton decline. The model also allows us to test which features make the Hudson River sensitive to the impact of benthic grazers. The model suggests that the fate of light-scattering inorganic particles (turbidity) is a key feature determining the impact of benthic grazers in aquatic systems.

Key words: *benthic grazing on phytoplankton; Dreissena polymorpha; Hudson River Estuary (USA); modelling phytoplankton production and biomass; phytoplankton decline; primary production; species invasion; turbidity and compensation to grazing; zebra mussel invasion of a large river.*

INTRODUCTION

Dramatic changes in bivalve abundance are an increasingly frequent phenomenon. In many estuaries and rivers, overharvesting, pollution, or disease have led to bivalve declines (Dame 1993). On the other hand, shipping, canal building, and recreational boating have resulted in the introduction and expansion of several exotic species of bivalves (Carlton 1992). These bivalve introductions or eliminations can potentially have consequences to other components of the ecosystem including benthos, zooplankton, and phytoplankton (Dame 1993, Ludyanskiy et al. 1993, Nalepa and Schloesser 1993, Kimmerer et al. 1994). Of particular interest is the dramatic change in grazing rates on phytoplankton that occurs when bivalve biomass expands or contracts (MacIsaac et al. 1992). Since phytoplankton form one base of the aquatic food web, changes in phytoplankton biomass can have ramifications throughout the ecosystem (Ulanowicz and Tuttle 1992).

Relatively detailed models constructed for several

estuaries point to the importance of benthic grazing in controlling phytoplankton biomass. For example, one model for Chesapeake Bay clearly suggests that decreases in oyster stocks during the past century were sufficient to cause substantial increases in phytoplankton biomass (Ulanowicz and Tuttle 1992). Thus, part of the eutrophication problem in the Chesapeake may be the result of overharvesting oysters. Another model for the Chesapeake confirms the general importance of benthic grazers but also points out that their ability to control phytoplankton will vary with location (Gerritsen et al. 1994). For San Francisco Bay, a simulation model was constructed that also includes phytoplankton losses by advection and zooplankton grazing (Cloern 1982). This model demonstrates that benthic grazing is the most important fate of primary production during the summer and fall, and without benthic grazing phytoplankton biomass would be far greater during this time period.

A few empirical studies also exist that demonstrate the importance of benthic grazers. These studies have documented changes in phytoplankton biomass that have occurred simultaneously with changes in biomass

of benthic grazers. In some stretches of the Potomac River, declines in phytoplankton of about five-fold were correlated with the introduction and establishment of the exotic bivalve *Corbicula fluminea* (Cohen et al. 1984). In western Lake Erie, a decline in diatom abundance coincided with the arrival and establishment of the zebra mussel, *Dreissena polymorpha* (Holland 1993). Similarly, in Saginaw Bay, Lake Huron, establishment of the zebra mussel was associated with a 60% decline in chlorophyll concentrations and a 60% increase in water clarity (Fahnenstiel et al. 1995). Lastly, in San Francisco Bay, severe declines in phytoplankton abundance were coincident with the invasion of the exotic bivalve, *Potamocorbula amurensis* (Alpine and Cloern 1992). Additionally, this study used ancillary data on nutrients and hydrology to eliminate other likely causes for the observed decline in phytoplankton.

These few field observations, in agreement with some of the ecosystem models, show substantial changes in phytoplankton biomass in association with increased grazing pressure by bivalves. Further, we know of no published field observations that document a large change in bivalves without a concomitant change in phytoplankton. Does this mean that all systems respond similarly to changes in benthic grazing pressure? That is, do bivalve invasions always lead to substantial phytoplankton declines, while bivalve reductions due to disease or overharvesting always lead to increased phytoplankton biomass?

A body of both experimental and theoretical literature exists suggesting that increased grazing may not necessarily result in declines in phytoplankton biomass, and that different systems may show vastly differing responses to similar benthic grazing pressure. For example, phytoplankton can compensate for direct grazing losses by increasing growth rates, due to increased nutrient supply (Doering et al. 1986, Sterner 1986). Further, the depth of the water column and degree of vertical mixing control the probability that phytoplankton will come into contact with benthic grazers, and these vary tremendously among systems (Cloern 1982, Sullivan et al. 1991, Koseff et al. 1993). These considerations and many others (Bianchi and Jones 1991) suggest that we should not expect a uniform response to expansions or contractions of bivalve populations.

Clearly, we need well-documented cases of bivalve invasions in systems with differing physical and chemical characteristics before we will fully appreciate the factors that make one system more sensitive than another to a change in bivalve populations. One way to rapidly gain insight towards this understanding is through the use of models. A model that is validated under conditions of both low and high bivalve abundance can be an extremely useful tool to test the importance of various features of a system that make it sensitive or not to the invasion. In this study we take advantage of a long-term data base in the Hudson River

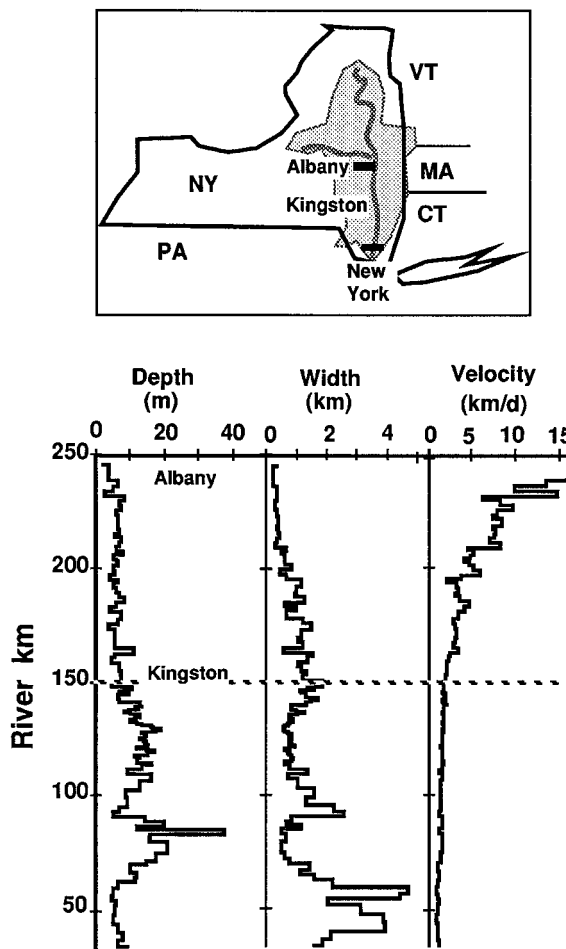


FIG. 1. Geographical and physical features of the Hudson River. The upper panel shows the location of the river and its watershed (stippled) within the boundaries of New York State. The horizontal bars represent the end points of the 200-km reach under study. The lower panel depicts some physical features of the river along its length from Albany (river km 247) towards Manhattan (New York, river km 0). Velocity is based on average flow for the summer period (1 June–10 Sept.). In this diagram, as in our model, the study region is divided into 126 1.5-km-scale boxes. The dashed line at river km 150 represents our intensively sampled station (Kingston) for the time-series data.

that spans periods of both low and high benthic grazing. The data set is used to demonstrate changes in phytoplankton biomass that occurred due to benthic grazing increases, and to validate a model of phytoplankton dynamics in the river. The validated model is then used to run scenarios that test phytoplankton sensitivity to grazers.

STUDY SITE

The Hudson River is a large river located in eastern New York, USA. The lower 247-km stretch, extending from Albany (river kilometer 247) to Lower Manhattan (km 0), is tidal (Fig. 1). The upper >200 km of this

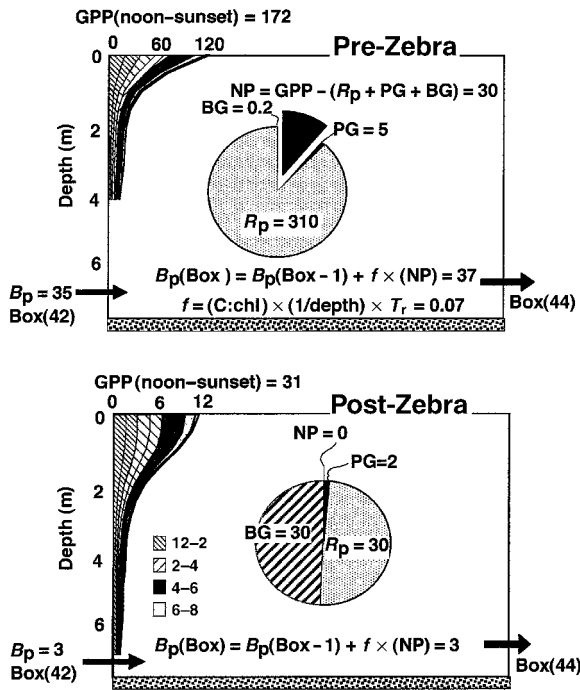


FIG. 2. Structure of one box of the phytoplankton box model under conditions prior to (upper) and during (lower) the zebra mussel invasion for the same day of the year (210) and location (river km 156, Box 43). Phytoplankton biomass (B_p) is imported into Box 43 from the box immediately upstream (Box 42). Within the box, biomass is increased by light-dependent gross primary production (GPP), and diminished by algal respiration (R_p), zooplankton grazing (PG), and benthic grazing (BG). Net production (nP), which is the difference between GPP and the sum of loss terms, is converted into yield of phytoplankton biomass ($B_p(\text{box})$) in each box by a units-conversion factor (f ; see Appendix for all units). R_p , PG, and BG are calculated at daily times steps. GPP is calculated at 1-h intervals between noon and sunset but depicted in 2-h time blocks during this period (1200–1400, 1400–1600, 1600–1800, 1800–2000). GPP for the day (sunrise to sunset) is 2 times the integrated production from noon to sunset.

tidal river (km 247 to 40) has been the focus of a great deal of work on food-web dynamics (Findlay et al. 1991, Cole et al. 1992, Pace et al. 1992). This area is deep (average ≈ 9.5 m), well mixed, turbid, and nutrient rich (Limburg et al. 1986). These conditions combine to make phytoplankton in the river extremely light-limited, and constrain positive net production to relatively shallow reaches (Cole et al. 1992).

The 200-km study reach of the Hudson River is hard water; pH values are between 7.5 and 8.3 throughout the tidal section, and alkalinities and Ca^{2+} are both greater than 700 micromoles of charge per liter (700 $\mu\text{eq/L}$, Limburg et al. 1986). A large part of the 200-km study reach is completely fresh (km 247–km 125) or only mildly brackish (km 125–km 75). Further, although the bottom sediments are primarily soft (silts, sands, and clays), hard substrate, which is required by zebra mussels, exists throughout the length of the river

(Strayer et al. 1996). Thus, the low saline section of the Hudson has chemical and physical features suggesting it should be susceptible to the invasion by the zebra mussel (Simpson et al. 1986, Strayer 1991, Nalepa and Schloesser 1993). In 1991 the zebra mussel was first documented to be present in low numbers in the Hudson. By 1993 numbers had increased to nearly 2000 mussels/ m^2 in the freshwater tidal portion of the river (km 75–km 247, Strayer et al. 1996).

METHODS

Hudson River sampling

Studies of phytoplankton dynamics were ongoing before and during the invasion of the zebra mussel. Thus, we have data on photosynthetic parameters and light availability in the Hudson (Cole et al. 1991, Cole et al. 1992, J. J. Cole and N. F. Caraco, unpublished data). Data on planktonic grazers are available for 1987–1994 based on the sampling procedure reported in Pace et al. (1992). Finally, surveys of benthic organisms were being carried out before and during the invasion of the zebra mussel (Strayer et al. 1996).

Phytoplankton biomass (B_p) was measured as chlorophyll *a* in both temporal and spatial surveys. At Kingston (km 150) we have a continuous 9-yr record of over 320 measurements of chlorophyll *a*. Additionally, the entire study reach (km 247–km 40, Fig. 1) was sampled extensively: 5–6 spatial transects were taken per year from 1991 through 1994. A total of 1700 chlorophyll measurements were made from these transects, with samples taken every 2–3 km. Spatial and temporal measurements of light extinction and nutrient concentrations were also made from 1986 through 1994.

Chlorophyll *a* was determined by fluorometry after extraction in methanol (Holm-Hansen and Riemann 1978). Light extinction (K_d) was calculated from in situ profiles of light (using a LI-COR model LI-1935A 4 π sensor and a LI-1000 data logger). NO_3^- , NH_4^+ , and PO_4^{3-} were analyzed colorimetrically on an ALPKEM model 3590 autoanalyzer or a Shimadzu UV-160 spectrophotometer (Murphy and Riley 1962, Wood et al. 1967, Solorzano 1977).

Phytoplankton modelling

Our box-flow model uses a simple mass-balance approach to predict phytoplankton biomass as chlorophyll-*a* concentration (Fig. 2). Phytoplankton biomass in each box is a function of inputs from the previous upstream box ($B_p(\text{box} - 1)$) and net production (nP). nP is equal to gross primary production (GPP) less the sum of phytoplankton respiration (R_p), planktonic grazing by zooplankton (PG), and benthic grazing (BG); thus

$$B_p(\text{box}) = B_p(\text{box} - 1) + (f \times \text{nP}) \quad (1)$$

and

$$nP = GPP - (R_p + PG + BG) \quad (2)$$

where nP and GPP are measured in units of $\text{mmol C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, biomass gain is measured as mg/m^3 of chlorophyll *a* (chl *a*), and *f* is a conversion factor that allows biomass gain per box to be calculated from production. This factor (*f*) is a product of residence time of box (T_r), in days; average depth of box (*z*), in metres; and a C-to-chl conversion factor. In all our conversions we use a conversion factor of 50 C:chl by mass. This value is consistent with average ratios found in many natural systems (Steele and Baird 1965, McBride et al. 1993). Additionally, a recent review of C:chl ratios suggests that, for the summer temperature, light, and nutrient conditions in the Hudson, 50:1 is very close to expected values (Cloern et al. 1995).

In all model runs, simulations start at box 1 (river km 247, near Albany [Fig. 1]) where initial biomass is input at $3 \text{ mg chl } a/\text{m}^3$. This value corresponds to the average measured value in this section of the river. In order to simulate seasonal cycles at any one location, or spatial simulations, we do multiple runs of the model. The parameters used in the model are shown in the Appendix; the use and origin of these parameters are described below.

Morphometry and hydrology.—Depth is needed to change volume-dependent parameters (zooplankton grazing and respiration) into area-based estimates of carbon loss. Further, depth, width, and length of each box are used to calculate the volume of each box (see Appendix). Residence time in each box (calculated from volume and flow) is needed to change daily calculated phytoplankton changes into absolute changes occurring in a given box and to calculate the day of the year that phytoplankton reach the next box.

Water flow in box 1 is from the United States Geological Service Gauging station at Green Island. The water entering at box 1 is 70% of the water flow in box 126; Abood et al. 1992). The additional 30% of water is added at four major inlets located at river kms 186, 147, 118, and 84 (Abood et al. 1992).

Light regime.—In order to calculate photosynthesis over depth, estimates of light at depth (L_z) are needed. This light depends on the light at surface waters (L_0), the degree of light extinction in the water column (K_d), and the depth (*z*); thus

$$L_z = L_0 e^{-z \times K_d} \quad (3)$$

Potential light (PL, cloudless conditions) reaching surface waters for any day of the year or time of day was calculated as a latitude-dependent sine-cosine function (Iqbal 1983). Actual light was diminished by 40% due to cloud cover (CF), based on meteorological data for this area (Kelly 1993). Light is additionally diminished by reflectance at the water surface (albedo [A]). In the Hudson measurements of light taken in air immediately above the water surface and immediately

below suggest that about 10% of the light reaching the water is reflected. Thus, surface light is

$$L_0 = (CF \times PL) - A. \quad (4)$$

Light attenuation in any water column can be divided into several components. Here we divide it into that due to phytoplankton (K_p) and a residual (K_{res}) that includes extinction from non-phytoplankton (nP) suspended sediments, dissolved organics, and water itself. Thus,

$$K_d = K_{res} + K_p. \quad (5)$$

In the Hudson, K_{res} is due primarily to nP (Stross and Sokol 1989). The light extinction by phytoplankton in a water column depends on phytoplankton biomass and the extinction of light per unit biomass (EC). Thus,

$$K_p = EC \times B_p. \quad (6)$$

Phytoplankton biomass (B_p) is an output term from the model. The extinction coefficient (EC) can vary with phytoplankton size and shape. For the green algae and diatoms found in the Hudson, an EC of ≈ 0.02 would be expected (McBride et al. 1993). We used this value for all runs. Having estimates of K_p , we estimated K_{res} by fitting a curve to average annual measured K_d with K_p subtracted. The calculated best-fit K_{res} for this period varies from 1.2 per meter in the summer and fall to 3 per meter during high flow in March (Fig. 3). If we apply the average seasonally calculated K_{res} values to all years we can model year-to-year variation in K_d as a function of year-to-year variation in phytoplankton biomass. The results for the summer season show a good correspondence between modelled and measured values of K_d (Fig. 4). This correspondence, which implies that there has been little change in nP due to zebra mussels, is in agreement with measurements of suspended sediment in the Hudson River (Fig. 4).

Algal growth.—The photosynthesis parameters ($P_{b,max}$ and α) determine phytoplankton growth response to light regime. $P_{b,max}$ is the light-saturated photosynthetic rate per unit B_p (as chlorophyll), and α is the photosynthesis efficiency and represents the initial slope of the production vs. irradiance relationship (Appendix). These parameters were determined for the Hudson from $^{14}\text{C}-\text{HCO}_3$ uptake vs. irradiance curves (Cole et al. 1991). These parameters are assumed to represent the algal net response in the light. That is, they are not corrected for respiration (see Peterson 1980; Eq. 7).

In the Hudson, both $P_{b,max}$ and α vary seasonally but not spatially (Cole et al. 1992). Before invasion by the zebra mussel, $P_{b,max}$ varied from a high of $0.4 \text{ mmol C}\cdot(\text{mg chl})^{-1}\cdot\text{h}^{-1}$ in summer to a low of $0.05 \text{ mmol C}\cdot(\text{mg chl})^{-1}\cdot\text{h}^{-1}$ in winter. The values of α before the invasion varied from 0.0013 to 0.0006 $\text{mmol C}\cdot(\text{mg chl})^{-1}\cdot\text{h}^{-1}$ ($\mu\text{mol of photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) in summer and winter, respectively. Measurements taken after the invasion show only a 5% increase in $P_{b,max}$ and a 40%

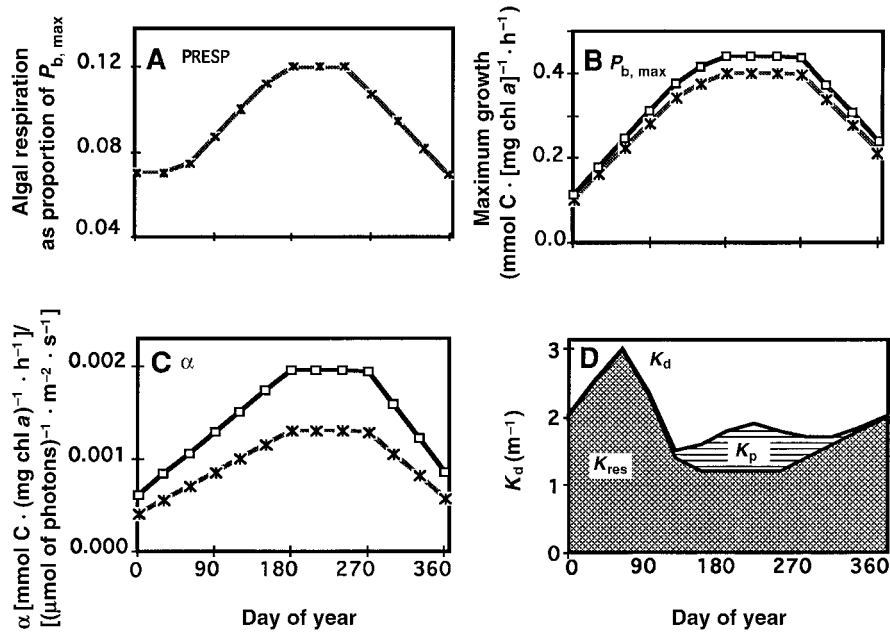


FIG. 3. Seasonal variation in modelled input parameters in the phytoplankton growth sub-models. (A) Algal respiration (R_p) is expressed as a fraction (PRESP) of $P_{b,max}$, and is assumed not to have changed with the invasion. (B) and (C) For $P_{b,max}$ (B) and α (C), which changed when the zebra mussel invaded, we show both pre-invasion (\times) and post-invasion (\square) values. (D) Modelled values of light extinction (K_d), which we calculate as the sum of extinction due to phytoplankton (K_p ; hatched) and non-phytoplankton (K_{res} ; dark stippling) components. K_p values shown are average pre-zebra-mussel values at river km 150. K_p is calculated from B_p and, therefore, varies from year to year and with location in the model (see Fig. 4).

increase in α (J. J. Cole, N. F. Caraco, R. J. Stevenson, and T. Smith, *unpublished data*). These changes in photosynthesis parameters are similar to those found in San Francisco Bay concurrent with a bivalve invasion (Alpine and Cloern 1992).

Using these photosynthesis parameters and light, gross primary production (GPP) is calculated at any depth–time. The areal production (GPP) is the integral of production estimates from depth = 0 to the bottom of the photic zone. Likewise, production over the day is the sum of production from sunrise to sunset ([noon to sunset] \times 2, Fig. 2). Steps of 0.5 m and 1 h were used for depth and time integrations, respectively. The actual formulation for production at depth is given by

$$GPP_z = R_p + [P_{b,max} \tanh(\alpha \times L_z / P_{b,max})] \quad (7)$$

where R_p is phytoplankton respiration (PRESP; see next paragraph). The expression within the brackets is net primary production in the light (see above). Respiration (R_p) must be added to this term to calculate gross primary production (Peterson 1980).

Loss terms.—Several studies have shown that algal respiration (R_p) varies with photosynthesis potential ($P_{b,max}$), and can be represented as

$$R_p = (\text{PRESP}) \times (P_{b,max}) \quad (8)$$

where PRESP is a fraction that varies between 0.05 and 0.25 with species composition (Geider and Os-

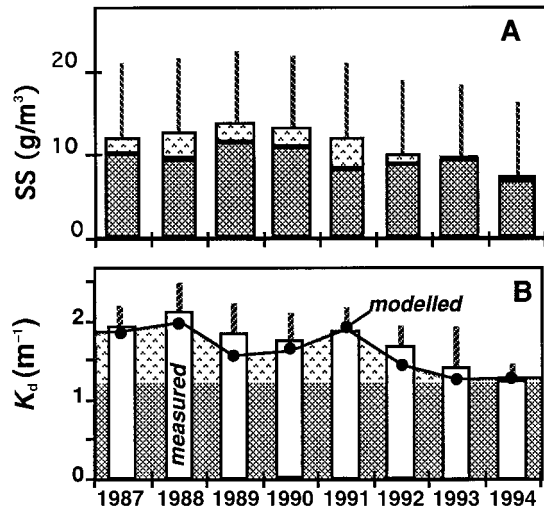


FIG. 4. (A) Suspended sediments (SS; dry mass) and (B) light extinction (K_d) in the Hudson River at river km 150 for the 1987–1994 period. Zebra mussel biomass was high during the last 3 yr (1992–1994). Summer mean values and 90% confidence intervals are shown for each year. (A) Total measured SS mass is divided into a phytoplankton component (light stippling) and non-phytoplankton (dark stippling). The phytoplankton mass is calculated as chlorophyll *a* times 100. This conversion assumes a C:chl of 50 and a dry mass:C of 2. (B) Measured (open bars) and modelled (\bullet) light extinction. Modelled K_d is the sum of extinction due to phytoplankton (light stippling) and a residual component (K_{res}). Note that as K_d increases, light decreases.

borne 1989, Beardal and Raven 1990). Direct measurements of PRESP in the Hudson suggest values between 0.07 to 0.12 (J. J. Cole, N. F. Caraco, R. J. Stevenson, and T. Smith, *unpublished data*). These relatively low values of PRESP are typical of diatoms and chlorophytes that make up the bulk of the phytoplankton in the Hudson (Geider and Osborne 1989, Beardal and Raven 1990). In the model, algal respiration occurs evenly throughout the water column and over the day and night.

The two major groups of pelagic grazers of phytoplankton are cladocerans (primarily *Bosmina*) and copepods. The total grazing of these zooplankton (PG) is the product of the individual grazing rate and abundance (BOSDEN and COPDEN, see Appendix). Thus,

$$PG = (BOSDEN \times BOSRATE) + (COPDEN \times COPRATE). \quad (9)$$

To estimate abundance at any given day-box we use linear interpolation of measured abundance at six stations (Pace et al. 1992). The individual grazing rate of *Bosmina* and copepods (BOSRATE and COPRATE, respectively) is based on a curvilinear relationship between consumption and phytoplankton concentrations such that

$$BOSRATE = GMAX_B \times (B_p)/(B_p + B_{p0.5}) \quad (10a)$$

and

$$COPRATE = GMAX_C \times (B_p)/(B_p + B_{p0.5}) \quad (10b)$$

where $B_{p0.5}$ is the half-saturation value. In our model, 5 mg chl *a*/m³ was used as the $B_{p0.5}$ for both *Bosmina* and copepods. This value corresponds to a half-saturation value of ≈ 250 mg/m³ in terms of C. GMAX values of 5×10^{-5} and 5×10^{-4} mmol C·ind⁻¹·d⁻¹ were used for *Bosmina* and copepods, respectively (DeMott 1982, Adrian 1991). Grazing in the model occurs evenly over the water column and time of day.

The biomass of native bivalves (unionids) and exotic zebra mussels varied dramatically over the length of the river. In the model we consider three different stretches of the river: km 250–214, km 214–150, and km 150–75. For each of these stretches bivalve size and abundance were coupled with individual grazing rates to get an areal clearance rate (Strayer et al. 1996). These clearance rates (CR) are expressed as cubic metre of water filtered per square metre of sediment per day. This expression simplifies to m/d and can be thought of as a piston velocity into the sediment. If the depth of the water column is known, the fraction of the water column filtered per day is simply depth of water column divided by CR. CRs shown in Table 1 are optimal (warm temperature) rates; at lower temperatures (below 20°C) CR was calculated using a Q_{10} of 2. Benthic grazing (BG), in mmol C·m⁻²·d⁻¹, was calculated from CR and phytoplankton biomass (B_p), such that

$$BG = (50/12) \times B_p \times CR, \quad (11)$$

TABLE 1. Spatial distribution and characteristics of benthic grazers (unionids and zebra mussels) for each of three stretches in the Hudson River, as well as area-weighted average for the entire stretch. Average density includes hard substrate with extremely high densities and soft substrates with no mussels.

River section (river km to river km)	Density (no./m ²)	Biomass [†] (g dry mass/m ²)	Clearance rate, [‡] Mid (Low–High) (m/d)
Zebra mussel, 1993			
250–213	590	5.3	1.2 (0.4–3.6)
213–150	5000	51	7.2 (2.4–21.6)
150–75	61	0.8	0.6 (0.2–1.8)
Entire, 250–75	2000	20	6.0 (2–18)
Unionid, 1991–1993			
250–213	73	64	1.9
213–150	3.1	0.03	0.001
150–75	2.3	2.7	0.1
Entire, 250–75	6.7	5.1	0.2

[†] Biomass includes mass of soft tissue only (no shell).

[‡] Clearance rates are given as a piston velocity. A range of clearance rates [mid (low–high)] is given for each stretch in the river; this range is associated with calculated errors of zebra mussel biomass, which were found to be nine-fold (\pm three-fold; Strayer et al. 1996).

where 50:12 converts millimoles of C into grams of chl *a*.

Our formulation of benthic grazing assumes phytoplankton biomass is mixed evenly throughout a box. Potential errors generated from this assumption are discussed in the *Results*.

RESULTS

Phytoplankton dynamics before zebra mussels

Before the invasion and establishment of the zebra mussel, phytoplankton biomass (measured as chlorophyll *a*) in the mid-estuary was relatively high (1987–1991, Fig. 5) and averaged 17 mg/m³. Variability among years (13–21 mg/m³) was small and was associated with variation in hydrology (Fig. 5). Between 1987 and 1991 biomass showed extreme seasonal variation and was lowest throughout the winter and spring (Fig. 6A). In late May biomass increased dramatically and, after a slight decline in June due to grazing by dense populations of *Bosmina* (Pace et al. 1992), reached its peak from July to September. At river km 150, our station of most intensive sampling (Figs. 1 and 6A), these peaks in phytoplankton biomasses were high and averaged 30 mg chl *a*/m³ during summer months. The spatial extent of high summer biomass was limited to two reaches: a mid-upper section (\approx km 200–140) and a lower section (\approx km 60–40; Figs. 1 and 7B). Both the extreme upper portion of the tidal Hudson (km 250–200) and the middle section (km 120–70) tended to have lower biomass. In the upper section both hydrology (short residence time) and grazing by native benthic grazers appear to play a role in keeping biomass low. In the mid-section severe light

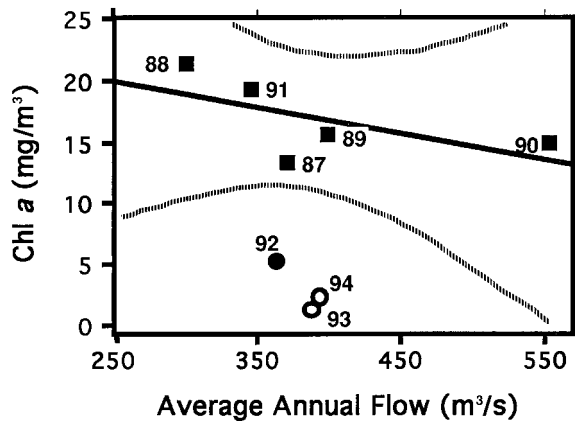


FIG. 5. Relationship between hydrology and phytoplankton biomass (B_p , measured as chlorophyll a) at river km 150 in the Hudson River. Data are mean annual values. Years both prior to (1987–1991, ■) and after (1992–1994, ○) the establishment of the zebra mussel are shown; 1992 (●) is a transitional year in terms of impact. For 1987–1991 B_p was related to flow such that $B_p = 25 - 0.03(\text{flow})$; this regression line and 95% confidence bands on this line are shown.

limitation due to deep and turbid conditions contributed to low biomass throughout the year.

Benthic grazing and the zebra mussel invasion

Data taken between 1991 and 1994 suggest that before 1992 unionids were the only significant benthic grazer in the river. These bivalves were abundant in the upper reaches of the river (Table 1). During 1992 and 1993, after the invasion and establishment by the zebra mussel, unionid biomass remained the same as pre-zebra-mussel values. However, during 1994, unionid biomass and clearance rate declined by 50%.

The zebra mussel was first observed in the Hudson in 1991 near river km 200 (Strayer et al. 1996). Population densities of adult zebra mussels remained extremely sparse until late summer 1992. Numbers peaked during autumn 1992 and remained high through 1993 (Strayer et al. 1996). During 1994 densities declined over 1993 values and estimated clearance rates (CR) were 30% lower than in 1994.

The zebra mussel abundance was not uniform over the length of the river (Table 1, Fig. 7A). In the lower brackish reaches, zebra mussels were absent due to salt intolerance (Walton 1993). Within the freshwater section, mussel density was highest between km 213 and 150. In this section the clearance rate was between 2.4 and 21.6 m/d. Because the depth of this section is about 7 m in this area, this means that the entire water column is filtered in 0.3–3 d.

Estimates of benthic grazing may have large errors associated with them. These errors come from both uncertainties in the number of zebra mussels present (Strayer et al. 1996; Table 1) and the calculation of grazing per mussel. In many systems a large source of grazing-rate uncertainty is generated from translating

clearance rate (CR; in meters per day) of benthic bivalves into amount of phytoplankton biomass filtered (BG). This error is particularly severe in temporarily stratified systems, like San Francisco Bay, where a detailed knowledge of mixing regime is needed to accurately predict phytoplankton grazing (Koseff et al. 1993). Even in systems like the Hudson that are vertically well mixed, however, phytoplankton depletion over bivalve beds can occur (Gerritsen et al. 1994). For the relatively low bivalve biomass and high tidal currents found in the Hudson, these errors are not likely to be severe (Butman et al. 1994). Therefore, we believe that the major source of error in estimating bivalve grazing in the Hudson is estimating bivalve abundance.

There is roughly a nine-fold uncertainty in estimates of bivalve abundance (Table 1: CR column, Fig. 7A). In modelling the impact of the zebra mussel invasion on phytoplankton, we explicitly consider this error by running grazing scenarios using high, middle, and low estimates of grazing derived from estimates of variability in zebra mussel abundance.

Phytoplankton dynamics after zebra mussel

The establishment of the zebra mussel (ZM) was associated with severe reductions in phytoplankton biomass. During summer 1993, the average biomass was only 10% of the pre-ZM values at river km 150 (Figs. 6A and 7B). The massive decline in biomass extended

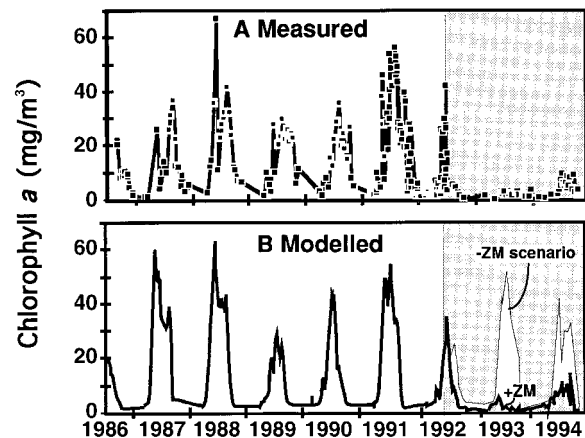


FIG. 6. Temporal trends in measured (A) and modelled (B) phytoplankton biomass in the Hudson River. (A) Weekly to every-two-week measurements of chlorophyll a at river km 150 for the period prior to the zebra mussel (ZM) invasion (1986–1991); the transitional year of the invasion (1992); and two years of full invasion (1993 and 1994; stippled). (B) Modelled output for the same period. For the post-invasion period, we show two modelled scenarios. The heavy line (labeled “+ZM”) represents modelled chlorophyll a using our low estimates of zebra mussel density in the river (Tables 2 and 3). The light line (labeled “-ZM”) represents what chlorophyll a would have been in 1992–1994 had the zebra mussel not invaded. The white area between these two simulations represents the drop in phytoplankton biomass due to zebra mussel grazing.

throughout much of the freshwater tidal portions of the river but did not extend into the brackish regions of the river (Fig. 7B). Patterns during the summer of 1994 were similar to 1993 but the decline was not as severe, and phytoplankton averaged 18% of pre-ZM values.

Elimination of other causes of phytoplankton decline

Changes in hydrology, nutrient concentration, light regime, or biomass of planktonic grazers are potential alternative explanations for the 1993 and 1994 declines in phytoplankton biomass (Figs. 6A and 7B, Table 2). Nitrate, the dominant form of dissolved inorganic nitrogen in the Hudson (Limburg et al. 1986), was not substantially different in 1993–1994 than in the pre-ZM period (Table 2). Phosphate concentrations, on the other hand, actually showed significant increases during the summers of 1993–1994 compared to pre-ZM years (Table 2). This increase in phosphate concentrations is possibly due to decreased uptake by phytoplankton during summer months. Regardless of the cause, however, the change in phosphate concentration is in the wrong direction to have caused a decline in phytoplankton biomass.

Light is an extremely important variable in controlling phytoplankton production and biomass in the Hudson River (Cole et al. 1992). A decline in summertime light levels could, therefore, have caused severe declines in phytoplankton biomass. Such declines in light, however, did not occur. Conversely, during the summer growing season, light levels in the Hudson increased in the period after zebra mussel invasion (Table 2). Thus, as with phosphate, the change in light is in the wrong direction to have caused a decrease in phytoplankton in the river.

Increases in planktonic grazers have been associated with decreases in the abundance of primary producers in many systems (Shapiro and Wright 1984). In the Hudson River there was no increase in abundance of planktonic grazers in 1993. Depending on the group, abundance of planktonic grazers showed either no change from previous values or showed possible declines after the invasion of the zebra mussel (Table 2; M. L. Pace, *unpublished data*). Thus, changes in planktonic grazers could not have been responsible for the decline in phytoplankton biomass in the Hudson.

In estuaries and rivers, interannual variation in flow can be responsible for year-to-year variation observed in phytoplankton. For San Francisco Bay, a strong negative relationship was observed between hydrologic flow and phytoplankton biomass (Alpine and Cloern 1992). The impact of benthic grazers could only be evaluated by demonstrating that phytoplankton biomass in years with high grazer biomass were “outliers” in the flow–biomass relationship. We repeated this type of analysis for the Hudson and found that during the zebra mussel years (1992–1994), phytoplankton biomass clearly falls below the hydrologic trend line (Fig. 5). While this analysis is very suggestive, it could be

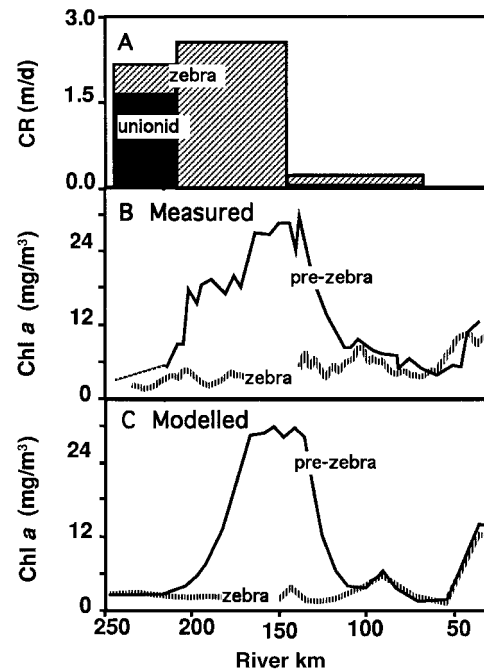


FIG. 7. Spatial trends in benthic grazing pressure (A) and measured (B) and modelled (C) phytoplankton biomass during 1991 (prior to the invasion, labeled “pre-zebra”) and in 1993 (during the invasion, labeled “zebra”). (A) Clearance rate (CR) of benthic grazers. In 1993 grazing is the sum of unionid (black bar) and zebra mussel (hatched area) grazing. Clearance rates for zebra mussels are our low estimate (see Table 1). In 1991 there were no zebra mussels, so total benthic grazing was due to unionids alone (Table 1). (B) Measured values of chlorophyll *a* before (pre-zebra; solid line) and during (zebra; slashed line) the invasion. For both years we show the average of four transects taken between 1 June and 10 September, with samples taken at 2-km intervals spanning the 200-km reach. (C) Modelled values of chlorophyll *a*; time periods and labels as in (B). The “zebra” modelled output uses the low estimate of zebra mussels for 1993 (Tables 1 and 3).

argued that the impact of hydrology on phytoplankton may be fairly complicated, involving optimal biomass at mid-flow, or time lags. We address these complexities using our model of phytoplankton production below.

Modelling phytoplankton biomass and production

Before invasion of the zebra mussel, the model reproduces both the spatial and temporal variation in phytoplankton biomass in the Hudson River. For the years 1987–1991 the model predicts summertime chlorophyll values to peak at 60 mg/m³ and average 30–40 mg/m³ at our station near river km 150 (Fig. 6B). Further, the complex spatial pattern of biomass in the Hudson is well captured by the model (Fig. 7C), with low biomass in the uppermost reaches of the estuary (above km 200) and again in the lower-middle reaches. Conversely, high summertime biomass is predicted both in the lowermost reaches (40–60 km) and the upper-middle

TABLE 2. Characteristics of the Hudson River that could potentially influence phytoplankton biomass and production. All values are divided into three time periods: pre-zebra (prior to establishment of zebra mussel in the river); transition (a year when mussels were increasing dramatically); and post-zebra (two years where high biomass of mussels was maintained). Values are for the summer growing season (\approx 1 June–7 September) and include means and 1 SD in parentheses. Samples were taken at weekly to every-other-week intervals for all variables except flow where daily values were available.

Year	NO ₃ ⁻ (μ mol/L)	PO ₄ ⁻ (μ mol/L)	K _d (m ⁻¹)	Flow (m ³ /s)	Density (10 ⁻³ ind./m ³)	
					Copepod	Cladocera
Pre-zebra						
1987	42 (21)	0.4 (0.2)	1.94 (0.16)	170 (57)	10.1 (9.0)	55 (130)
1988	26 (9)	0.3 (0.1)	2.12 (0.24)	160 (80)	4.3 (2.6)	67 (144)
1989	nd	nd	1.82 (0.27)	320 (190)	3.5 (2.0)	14 (22)
1990	nd	nd	1.75 (0.21)	253 (123)	5.9 (4.1)	11 (24)
1991	nd	nd	1.88 (0.17)	147 (35)	5.7 (4.2)	4 (7)
Transition						
1992	27 (6)	0.5 (0.4)	1.68 (0.19)	277 (155)	4.0 (2.9)	4 (4)
Post-zebra						
1993	41 (16)	0.8 (0.4)	1.41 (0.34)	163 (145)	5.3 (3.5)	5 (7)
1994	28 (12)	1.0 (0.4)	1.22 (0.14)	232 (94)	4.8 (4.2)	8 (17)
Pre vs. Post†						
Change (%)	+1	+150	-39	-6	-14	-78
<i>P</i> value	0.97	0.04*	0.01*	0.96	0.68	0.32

* $P < 0.05$; nd = no data for this year.

† Percentage change from pre- to post-zebra values and *P* values for a significant change (unpaired *t* test).

reaches (170–130 km). These modelled patterns are consistent with our observations.

For the post-zebra mussel (ZM) period we ran our model considering several scenarios (Table 3). We discuss here our scenarios of different grazing intensity, but review spatial and compensation scenarios in the discussion section. The first scenario run is a “no ZM” scenario. This scenario was run to calculate directly zebra mussel impact during 1993 and 1994 (Fig. 6B: light line). Model results suggest that during 1993, a year with a dry summer (i.e., long residence time), chlorophyll would have peaked at 50 mg/m³ and averaged 40 mg/m³ had the zebra mussel been absent. During 1994 we estimate that in the absence of zebra mussel grazing chlorophyll would have peaked at 40 mg/m³ and averaged 30 mg/m³. The actual measured average chlorophyll during summer 1993 (3 mg/m³) and 1994 (5.5 mg/m³) were 8% and 18%, respectively, of that predicted in the absence of ZM grazing. Thus, the model values for actual impacted years agree well with our conclusions from comparing pre- and post-ZM periods. That is, zebra mussels caused severe declines in phytoplankton biomass.

The next three scenarios of the model simulate different grazing pressure by the zebra mussel (Table 1: low, mid, high). These runs tell us about the grazing pressure required to cause phytoplankton declines and allow us to evaluate conclusions about grazer impact given a nine-fold error in estimates of this grazing. Mid and high runs both predicted complete crash of phytoplankton (Table 3). The total decline predicted by these model runs occurs even though phytoplankton

turnover time (growth per unit biomass) increases due to increases in light and α values. Using the low estimate of grazing by zebra mussels, model predictions agree well with the actual response of phytoplankton to ZM grazing (Figs. 6B, Table 3).

The detailed spatial view of the “low biomass” scenario is shown in Fig. 7C. The model predicts maximum decreases in phytoplankton biomass occur from river km 190–140 with only minimal impact of the zebra mussel in the lower reaches of the river (Fig. 7C). Measurements demonstrate similar dramatic declines in phytoplankton biomass between river km 200 and 140, and little impact in the lower reaches of the river. Thus, both the magnitude and spatial extent of the phytoplankton decline is consistent with that modelled with a low estimate of grazing (Table 3).

In addition to changes in phytoplankton biomass, we can examine modelled changes in production (Fig. 2). Before the invasion of the zebra mussel, our model suggests gross production was 100–400 mmol·m⁻²·d⁻¹ for the middle part of the Hudson River (near km 150) during the summer growing period. In contrast, after the invasion of the zebra mussel, our model (Table 3 “low-density scenario”) suggests a decline in gross production to 20–80 mmol·m⁻²·d⁻¹ for the same section of the river, which is heavily impacted by ZM grazing (Fig. 2). In addition to major changes in production, the model suggests changes in the fate of primary production. Before the invasion of the zebra mussel the major fate of production was respiration by phytoplankton themselves (Fig. 2; Cole et al. 1992). Little of the gross production was consumed by grazers (Fig.

TABLE 3. Modelled scenarios of phytoplankton biomass (measured as chlorophyll *a*) in the middle (river km 180–130) and lower (km 100–50) reaches of the Hudson River. Scenario runs include: different zebra mussel (ZM) density (and clearance rate, CR); location of ZM in the river; and compensation that is greater or less than that actually measured to occur. Also included are measured values for post-ZM (1993–1994) and pre-ZM periods.

Compensation can occur through changes in light availability (differences in light extinction, K_d) or changes in photosynthetic efficiency (primarily α changes; Fig. 3). In all model runs $K_d = K_{res} + K_p$ and $K_p = 0.02 B_p$; K_p is the light-extinction coefficient due to phytoplankton, and K_{res} is the residual extinction due to non-phytoplankton (nP) suspended matter, dissolved organics, and water itself.

Scenarios	Chlorophyll <i>a</i>					
	Middle reach	Lower reach	CR† (m/d)	α ‡	K_{res} §	
Modelled						
ZM density	Zero	25	3	Zero	0.0018	1.2
	Low	3	3	Low	0.0018	1.2
	Mid	1	1	Mid	0.0018	1.2
	High	1	1	High	0.0018	1.2
Location	Shallow	2	3	2.5	0.0018	1.2
	Deep	20	1	2.5	0.0018	1.2
Compensation	None	1	1	Low	0.0013	1.2
	No nP	50	50	Low	0.0018	0.2
Measured	Post-ZM	4	4	Low–high	0.0018	1.2
	Pre-ZM	26	4	Zero	0.0013	1.2

† Clearance rate entries “low, mid, high” refer to Table 1; CR column values: mid (low–high).

‡ Biomass-specific growth at limiting light. The values 0.0018 and 0.0013 are based on measurements made after and before ZM invasion, respectively.

§ Values used in the model are shown. The value of 0.2 used in the “no nP (non-phytoplankton) scenario is derived from the zero intercept of the regression “suspended sediment vs. K_d ” and represents the K_{res} , 1.2, is estimated as measured $K_d - 0.02B_p$ (see *Methods: Phytoplankton modelling: Light regime* and Fig. 4).

|| Shallow = river km 200–150; deep = km 150–75. ZM grazing was assumed to occur at the same rate in both locations.

2). Following the ZM invasion roughly 50% of gross primary production, or essentially all of phytoplankton net primary production, was consumed by zebra mussels (Fig. 2).

DISCUSSION

We have shown that concomitant with establishment of the zebra mussel, phytoplankton biomass in the tidal-freshwater Hudson experienced a massive decline and has not recovered (Figs. 6A and 7B). Gross primary production of phytoplankton also declined dramatically following the invasion of the zebra mussel (Fig. 2). Our simulation model suggests that biomass decline was consistent with that expected from increased grazing pressure by the zebra mussel (Figs. 6B and 7C). Further, we have ruled out the possibility that this decline could have been caused by other factors, including changes in light, nutrients, or hydrology (Table 2).

What factors caused the Hudson to be so responsive to the zebra mussel invasion, and do we expect most aquatic systems to have a nearly 10-fold reduction in phytoplankton biomass when the zebra mussel invades? As the zebra mussel has recently invaded or is in the process of invading numerous rivers, reservoirs, and lakes in North America (Ludyanskiy et al. 1993), this question is becoming increasingly important. Additionally, many other bivalve species invasions are

occurring and will continue to occur (Carlton 1992). Thus the question of phytoplankton response to bivalve invasion is of broad significance. Finally, the general question of sensitivity of primary producers to grazing pressure is of considerable ecological interest (Bianchi and Jones 1991).

Phytoplankton response to grazing will depend upon both the grazing pressure and system sensitivity to a given amount of grazing. This sensitivity is, in turn, determined by both the fixed characteristics of the system (e.g., factors not alterable by the organisms) and compensatory changes that are associated with increased grazing pressure (e.g., factors that organisms do alter). Using our data from the Hudson River, literature information from other aquatic systems, and model scenarios, we now explore how grazing pressure of zebra mussels and system characteristics came together to cause the extreme phytoplankton declines in the Hudson. We further discuss key characteristics of systems that will impact their sensitivity to changes in grazing pressure.

Our first assessment considers benthic grazing pressure in the Hudson as compared to other systems that have been or will be invaded by zebra mussels. This comparison suggests that the grazing pressure (as indicated by zebra mussel density) by the zebra mussel in the Hudson was not particularly high. For the entire

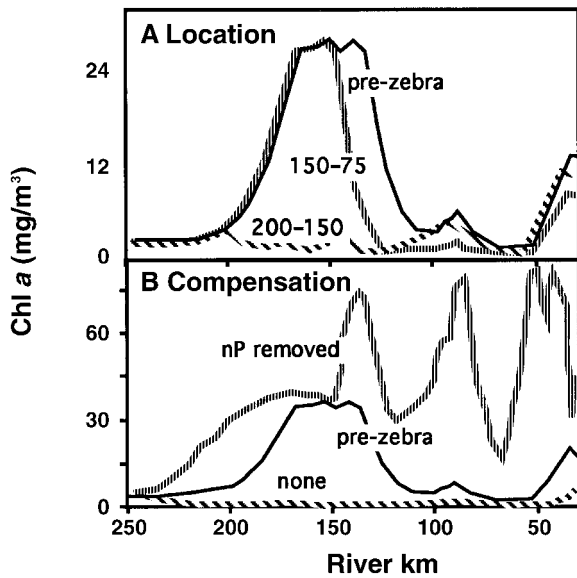


FIG. 8. Model scenarios to look at impact of varying location of zebra mussel (A) and system compensation (B). In both (A) and (B) the solid line ("pre-zebra") is the modelled response of phytoplankton biomass (measured as chlorophyll *a*) in the absence of zebra mussels (as in Fig. 7C), and is shown for comparison. (A) The slashed line (labeled 200–150) and the heavy lines (labeled 150–75) are modelled phytoplankton response if zebra mussels occurred only between river km 200 and 150 (shallow site) or 150 and 75 (deep site), respectively. (B) The thick line (labeled "nP removed") shows modelled phytoplankton biomass response if turbidity (excluding phytoplankton) were removed and $K_{res} = 0.2$ instead of 1.2. The slashed line (labeled "none") is the no-compensation scenario and represents modelled output in the absence of the compensation due to change in phytoplankton growth parameters.

tidal–freshwater Hudson, mussel densities peaked at about 600–6000 individuals/m² (Table 1). If we use the low estimate of abundance as closest to correct (see Tables 1 and 3), we can state that many rivers have densities much higher than those of the Hudson (Melina and Rasmussen 1993), and lakes often exceed these densities by up to 30-fold (Ramcharen et al. 1992, Melina and Rasmussen 1993). Further, even if mussel densities in the Hudson were as high as 6000 individuals/m², there would be many systems with comparable mussel densities. Clearly, if other systems are as sensitive to the impacts of benthic grazing as is the Hudson, we would expect widespread, large decreases in phytoplankton biomass to be occurring as the zebra mussel becomes established in aquatic systems throughout North America.

Next, we explore system sensitivity, first in terms of fixed system characteristics and then in terms of compensatory characteristics. Two fixed characteristics of aquatic systems that determine sensitivity of phytoplankton to benthic grazing are the average depth of the water column and the degree of vertical stratification (Sullivan et al. 1991, Dame 1993). When sys-

tems are completely mixed there is no refuge within the system, and grazer impact is likely to be greater. The importance of water depth can be appreciated by considering the following example: for a clearance rate of 2 m/d, water bodies of 1 and 10 m depth would have water turnover times of 0.5 and 5 d, respectively. That is, in the shallower system, the entire water mass would pass through benthic grazers every 12 h. Maximal phytoplankton turnover rates (production occurring at $B_{P,max}$) are near 1–2 d⁻¹ (McBride et al. 1993). Thus, even with optimal light and nutrient, filtration times faster than 1–2 d will cause phytoplankton to crash.

The depth of a system is of course not constant in space, and in large systems like the Hudson depth varies over river length. For these systems the impact of benthic grazers can vary depending on whether the invaders settle at primarily shallow or deep sites. In the Hudson, zebra mussels settled primarily in a relatively shallow section (river km 200 to 150). Model scenarios suggest that this fact enhanced the impact of the zebra mussel. If the zebra mussel had settled primarily between km 150 and 75 (a deeper stretch), the impact on phytoplankton biomass and production in the river would have been far less (Table 3, Fig. 8A).

The Hudson is relatively well mixed and, although on average quite deep (≈ 9.5 m), has many relatively shallow reaches (Fig. 1). These factors make phytoplankton potentially sensitive to the impact of benthic grazing. Many other rivers and estuaries are also well mixed and may be shallow throughout or have many shallow reaches (Sullivan et al. 1991). Some of these physically similar systems may not, however, show the same sensitivity as the Hudson. Differences could come about not only from the location that bivalves settle but also from between-system variation in compensation to grazing.

In both aquatic and terrestrial ecosystems, a large body of literature suggests that primary producers can compensate for increases in grazing loss by increasing growth rate (McNaughton 1985, Berquist and Carpenter 1986, Bianchi and Jones 1991). In many aquatic systems primary production is severely limited by available nutrient supply (Caraco et al. 1987), and enhanced release of nutrients by grazers can lead to increased growth rates (Fig. 9; Bianchi and Jones 1991). These enhanced growth rates may be large enough that, despite greatly increased grazing losses, little or no decline in phytoplankton biomass occurs and production actually increases (Berquist and Carpenter 1986, Doering et al. 1986, Sterner 1986). In contrast to these low-nutrient systems, the Hudson, like many turbid systems, has relatively high levels of dissolved nutrients (Wofsy 1983, Cole et al. 1992). Thus, increases in dissolved nutrients would have a smaller impact on total phytoplankton production. For example, for the Hudson there was an increase in photosynthetic efficiency (as indicated by increase in α) that was possibly due in part to increases in dissolved P (Fig. 9). Our

model suggests that this increased efficiency did lower zebra mussel impact somewhat (Table 3). The compensation was, however, far less than the complete compensation observed in systems with low nutrients.

Another compensatory change to increased grazing that occurs in both terrestrial and aquatic systems is species shifts. Species resistant to grazing or that grow faster when grazed are favored at high grazing pressures (Porter 1977, Power et al. 1988). There is preliminary evidence that in some systems inedible cyanobacteria may be selected for by heavy bivalve grazing (Vanderploeg and Nalepa 1995). In these systems this compensatory mechanism can completely alter the outcome of zebra mussel grazing. In the Hudson, instead of seeing a switch to inedible species, we actually saw a decline in the abundance of genera thought to be inedible (*Microcystis* in particular, T. Smith, *personal communication*). Although species shifts in the Hudson did not lead to inedible groups, the shifts could have resulted in some compensation by selecting for faster growing species. That is, the increase in *alpha* values may have been in part the result of an altered assemblage of phytoplankton in the river (Fig. 9). As stated above, this change was only enough to diminish the impact of the zebra mussel grazing moderately (Table 3).

Increases in light can also allow phytoplankton to compensate for increased removal by grazers (Fig. 9). Grazers remove particles, including phytoplankton and non-phytoplankton, both of which extinguish light (increase K_d ; Figs. 4 and 9). In many non-turbid systems the major light attenuating particle is phytoplankton and there is a good relationship between phytoplankton biomass and light attenuation (Carlson 1977). In many turbid rivers, reservoirs, and shallow lakes on the other hand, light attenuation is associated largely with suspended sediments other than phytoplankton (nP) (Phlips et al. 1995). In these turbid systems, phytoplankton removal in itself does not lead to large increases in light and it is necessary to remove nP to increase greatly light availability. For example, in the Hudson (where only 30% of light attenuation is due to phytoplankton), if 100% of the phytoplankton had been removed light attenuation would not drop below 1.2 m^{-1} without the removal of nP. If nP were removed, light attenuation could be $<0.6 \text{ m}^{-1}$ even if no phytoplankton had been removed.

In turbid systems, like the Hudson, the fate of nP is critical to determining the degree to which light changes under a regime of increased grazing pressure. Thus, the fate of nP is also critical to determining the impact on phytoplankton. In the Hudson the zebra mussel invasion resulted in only a small decrease in suspended sediments (see Fig. 4). Interestingly, the zebra mussel can filter these kinds of particles from the water column in the Hudson (Roditi et al. 1996), and without resuspension the river would be completely clear of these particles during the summer growing season. Ev-

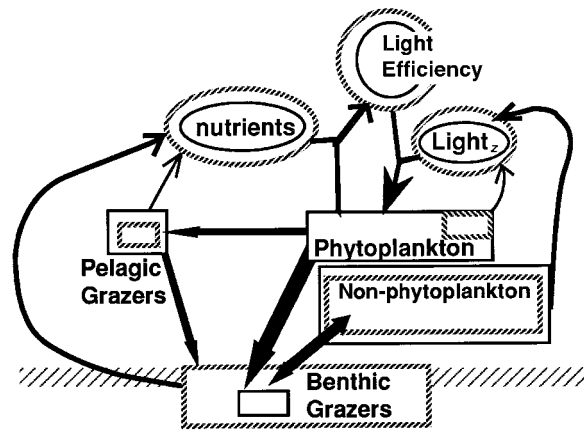


FIG. 9. Diagram showing direct and indirect effects of the invasion of zebra mussel on phytoplankton in the Hudson River. The area of each component is meant to represent its magnitude prior to (solid boundary) and during (stippled boundary) the zebra mussel invasion. For example, benthic grazers increased greatly and phytoplankton decreased greatly while non-phytoplankton suspended sediment showed only a slight decline. The arrows represent interactions between components. Some interactions are complex. For example, changes in efficiency of carbon fixation (light efficiency, as described by B_{pmax} and α) could be the result of changes in the algal species present and/or the greater availability of phosphate following the zebra mussel invasion. Changes in available light act in concert with changes in photosynthetic efficiency to alter growth rates of phytoplankton.

idently, however, due to the high turbulence in the Hudson, there is rapid resuspension of removed particles. What would have happened to phytoplankton if the Hudson were less turbulent and nP had declined dramatically? Although we have no empirical data that address this question, we can use our model to suggest what the impact may be. We ran a model scenario in which nP was completely removed by the zebra mussel (Fig. 8B). When this was done we found a dramatic difference in grazer impact. That is, rather than phytoplankton declining severely after the invasion of the mussel, phytoplankton was actually higher than pre-invasion levels despite greatly enhanced grazing rates (Table 3, Fig. 8B). This difference was particularly evident in lower reaches of the river (Fig. 8B).

The response of different systems to increased grazing pressure from invading bivalves will depend strongly on the degree to which phytoplankton compensate for increased grazing losses. Our work in the Hudson indicates that for turbid systems a critical feature determining compensation is the fate of turbidity. Potential fates include: (1) no removal of material by benthic grazers to sediments, (2) removal by benthic grazers but rapid resuspension to the water column (Hudson case), and (3) removal and slow resuspension. If conditions 1 or 2 are true, there will be little net removal of turbidity associated with increased benthic grazing, and systems will likely compensate poorly and show substantial decreases in phytoplankton biomass.

If condition 3 occurs, increased benthic grazing may actually result in increased phytoplankton biomass. The fate of turbidity will likely vary with several features. The type of grazer and the size range of particles will determine if grazers remove turbidity (condition 1 vs. 2 or 3). The amount of turbulence at the sediment-water interface and sediment stability will be critical if sediments are removed by grazers (condition 2 vs. 3). Turbulence varies tremendously between different systems due to differences in wind and tidal features. Sediment stability can vary tremendously with changes in benthic microbial, algal, and macrofauna communities.

Understanding how turbid systems will respond to increased benthic grazing pressure is critical. Many reservoirs, rivers, and estuaries that will experience or have experienced dramatic changes in benthic grazing have high turbidity (Alpine and Cloern 1992, Cohen et al. 1984). In the past, work on phytoplankton compensation to grazing has focused on nutrient cycling (Bianchi and Jones 1991, Doering et al. 1986). This work may not be relevant to turbid systems that are not strongly nutrient limited (Wofsy 1983). Our work suggests that in these systems the fate of suspended silts and clays may be the most important predictor of phytoplankton response to changes in benthic grazing pressure. Empirical and experimental studies are needed to document the importance of turbidity as a key control of phytoplankton response to benthic grazing.

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APPENDIX

Variables used in the phytoplankton model. Equations using these variables are given in the text and in Fig. 2.

Variable	Description	Units
Morphometry and Hydrology		
UP (<i>i</i>)	Upstream km of box <i>i</i>	km
DN (<i>i</i>)	Downstream km of box <i>i</i>	km
Z (<i>i</i>)	Mean depth of box <i>i</i>	m
W (<i>i</i>)	Mean width of box <i>i</i>	km
V (<i>i</i>)	Volume of box <i>i</i>	m ³
Q (<i>i, t</i>)	Flow at km <i>i</i> and time <i>t</i>	m ³ /s
T _r (<i>i, t</i>)	Residence time in box <i>i</i> at time <i>t</i>	d
Light regime and Hydrology		
K _d (<i>i, t</i>)	Total light extinction for box <i>i</i> at time <i>t</i>	m ⁻¹
K _p (<i>i, t</i>)	Light extinction due to phytoplankton for box <i>i</i> at time <i>t</i>	m ⁻¹
K _{nP} (<i>i, t</i>)	Light extinction due to non-phytoplankton (nP) for box <i>i</i> at time <i>t</i>	m ⁻¹
PL (<i>t</i>)	Potential surface irradiance (moles of photons) at time <i>t</i>	(μmol of photons)·m ⁻² ·s ⁻¹
A	Albedo	Dimensionless
CF	Cloud factor	Dimensionless
L ₀ (<i>t</i>)	Surface irradiance at time <i>t</i>	(μmol of photons)·m ⁻² ·s ⁻¹
L _c (<i>i, t, z</i>)	Irradiance at depth <i>z</i> for box <i>i</i> at time <i>t</i>	(μmol of photons)·m ⁻² ·s ⁻¹
EC	Extinction coefficient for chlorophyll	m ² /(mg chl <i>a</i>)
B _p	Algal (phytoplankton) biomass	mg chl <i>a</i> /m ³
Algal growth		
P _{b,max} (<i>t</i>)	Biomass-specific growth at saturating light for box <i>i</i> at time <i>t</i>	mmol C·(mg chl <i>a</i>) ⁻¹ ·h ⁻¹
α <i>t</i>	Biomass-specific growth at limiting light for box <i>i</i> at time <i>t</i>	mmol C·(mg chl <i>a</i>) ⁻¹ ·h ⁻¹ [(μmol of photons)·m ⁻² ·s ⁻¹] ⁻¹
GPP _z (<i>i, t, z</i>)	Gross primary production at depth <i>z</i> for box <i>i</i> and time <i>t</i>	mmol C·m ⁻³ ·h ⁻¹
GPP (<i>i, t</i>)	Integrated gross primary production for box <i>i</i> and time <i>t</i>	mmol C·m ⁻² ·d ⁻¹
Loss		
PRESP (<i>t</i>)	Fraction of B _{p,max} to calculate algal respiration at time <i>t</i>	Dimensionless
R _p (<i>i, t</i>)	Algal respiration for box <i>i</i> at time <i>t</i>	mmol C·m ⁻² ·d ⁻¹
BOSRATE (<i>i, t</i>)	<i>Bosmina</i> grazing	mmol C·ind. ⁻¹ ·d ⁻¹
COPRATE (<i>i, t</i>)	Copepod grazing	mmol C·ind. ⁻¹ ·d ⁻¹
GMAX _B	Maximum grazing rate for <i>Bosmina</i>	mmol C·ind. ⁻¹ ·d ⁻¹
GMAX _C	Maximum grazing rate for copepods	mmol C·ind. ⁻¹ ·d ⁻¹
B _{p0.5}	Half-saturation chlorophyll <i>a</i> concentration	(mg chl <i>a</i>)/m ³
BOSDEN (<i>i, t</i>)	<i>Bosmina</i> density for box <i>i</i> at time <i>t</i>	no./m ²
COPDEN (<i>i, t</i>)	Copepod density for box <i>i</i> at time <i>t</i>	no./m ²
PG (<i>i, t</i>)	Total planktonic grazing by zooplankton	mmol C·m ⁻² ·d ⁻¹
CR _{ZM} (<i>i, t</i>)	Zebra mussel clearance rate for box <i>i</i> at time <i>t</i>	m/d
CR _U (<i>i, t</i>)	Unionid clearance rate for box <i>i</i> at time <i>t</i>	m/d
ZG (<i>i, t</i>)	Zebra mussel grazing rate for box <i>i</i> at time <i>t</i>	mmol C·m ⁻² ·d ⁻¹
UG (<i>i, t</i>)	Unionid grazing rate for box <i>i</i> at time <i>t</i>	mmol C·m ⁻² ·d ⁻¹
BG (<i>i, t</i>)	Total benthic grazing rate for box <i>i</i> at time <i>t</i>	mmol C·m ⁻² ·d ⁻¹