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Changes in phytoplankton community structure during the zebra mussel (*Dreissena polymorpha*) invasion of the Hudson River (New York)

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Abstract. We analyzed differences in the cell density and taxonomic composition of phytoplankton assemblages in the tidal, freshwater portion of the Hudson River to assess the impact of the recent zebra mussel invasion. In order to assess this change, phytoplankton genera were identified and counted during two representative periods, 1987–88 (before zebra mussel invasion) and 1993–94 (after invasion) and major groups in 1995 and 1996. Average cell density of phytoplankton declined ~17-fold from 25.6×10^6 cells l^{-1} before invasion to 1.5×10^6 cells l^{-1} after invasion. Dominance of the phytoplankton (by cell density, assessed on an annual scale) shifted from cyanobacteria before the invasion to diatoms during the invasion; cyanobacterial density decreased 778-fold and diatoms decreased by a factor of only 2.5. Samples from 1995 and 1996, counted only to class, confirm the patterns from the more detailed counts in 1993 and 1994: a major decline in cell numbers and a dramatic decline in cyanobacteria relative to diatoms. The taxonomic composition of assemblages based on relative abundances of both genera and divisions showed significant shifts from colonial and unicellular cyanobacteria to large, colonial or benthic diatoms. Also, the large decline in cyanobacteria and some diatom genera, which had been abundant in late summer, dampened the seasonal variation in the taxonomic composition of phytoplankton following the zebra mussel invasion.

Introduction

The zebra mussel (*Dreissena polymorpha*) is an exotic bivalve that was introduced into North America in 1986 and has been expanding its range since then (O'Neill and Dextrase, 1994). Predictions suggest that it will eventually spread throughout most of North America, except for areas with waters too soft or too saline to support its growth (Strayer, 1991). Because the mussel can attain very high densities, it is capable of filtering enormous quantities of water (Sprung, 1989; Nalepa and Schloesser, 1993; Nalepa, 1995). This high-volume filtration is capable of reducing plankton populations, and in many places where the zebra mussel has become established, phytoplankton biomass has declined (MacIsaac, 1996).

In addition to decreasing phytoplankton biomass, it has been suggested that the zebra mussel can cause changes in the species composition of the phytoplankton. This suggestion is supported by both laboratory studies and modeling which show that direct and indirect effects of filtration by zebra mussels may have selective effects on different phytoplankton taxa, leading to major changes in the phytoplankton community composition (Heath *et al.*, 1995; Vanderploeg *et al.*, 1996; Bastviken *et al.*, 1998). However, phytoplankton species composition has been examined in only a handful of invaded systems which allow comparison to pre-zebra mussel conditions and, to our knowledge, all of these are lakes (Nicholls and Hopkins, 1993; Fahnenstiel *et al.*, 1995; Nalepa, 1995; MacIsaac, 1996; Vanderploeg *et al.*, 1996). In some of these systems, phytoplankton species

composition has changed, while in others it has not (Holland, 1993; Nicholls and Hopkins, 1993; Lowe and Pillsbury, 1995).

The zebra mussel was first observed at low density in the Hudson River in 1991, and by late summer of 1992 adult populations had reached river-wide densities of 4000 individuals m^{-2} (Strayer and Smith, 1993; Strayer *et al.*, 1996, 1998). Prior to the zebra mussel invasion, the total volume of the Hudson River was filtered by organisms (zooplankton and benthic bivalves combined) about once every 50 days; the zebra mussel now filters the entire volume about once every 2–3 days (Figure 1; Caraco *et al.*, 1997). This 25-fold increase in biological filtration has had a dramatic effect on phytoplankton biomass. During the period of zebra mussel invasion, mean summertime phytoplankton chlorophyll *a* decreased from ~30 to <5 mg m^{-3} in the Hudson River (Figure 1). Using multiple lines of evidence and a continuous 8 year record of chlorophyll *a*, Caraco *et al.* (1997) demonstrated that zebra mussels were responsible for this massive decline in phytoplankton biomass (Figure 1). The objective of this study was to determine whether phytoplankton species composition changed concurrently with the arrival of the zebra mussel in the Hudson. We report here the first effort to document phytoplankton species compositional changes in a large river following an invasion of the zebra mussel.

Method

Study site

The Hudson River is a large river that has been used as a commercial thoroughfare for 200 years. Its watershed occupies about one-third of New York State and the river is ~315 miles long (Limburg *et al.*, 1986). The focus of this study is the tidal, freshwater portion of the river that extends from the dam at Troy, New York,

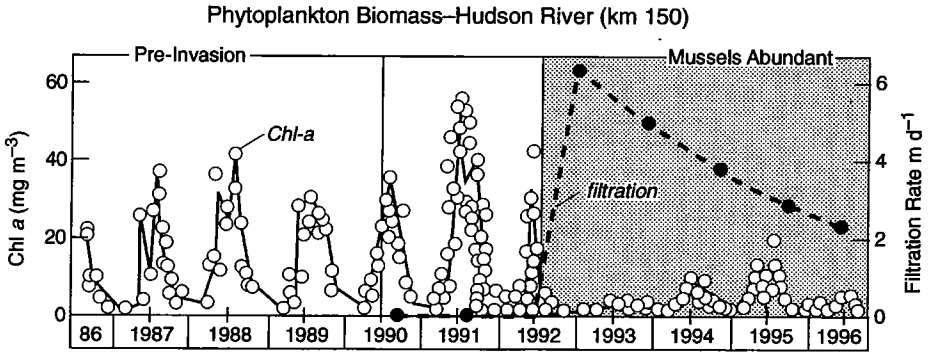

Fig. 1. Time series of chlorophyll *a* (open circles, solid line) and zebra mussel filtration rate (filled circles, slashed line, right axis) for the tidal, freshwater Hudson River. Data are for the Kingston–Rhinecliff area, the same area as the phytoplankton species counts. Data are from Caraco *et al.* (1997) and Strayer *et al.* (1996, 1998). The filtration rate is the product of zebra mussel density and individual filtration rate, and is expressed in m day^{-1}. The average depth of the tidal, freshwater river is ~9 m; at 6 m day^{-1}, the entire water column is filtered every 1.5 days.

~200 km south to the Tappan Zee Bridge. This section of river has been the subject of numerous investigations and is well described elsewhere (Findlay *et al.*, 1991; Cole *et al.*, 1992; Howarth *et al.*, 1996). The river is large (mean width ~1 km; mean depth ~10 m), well mixed, nutrient rich and turbid (Cole *et al.*, 1992; Raymond *et al.*, 1997); these conditions lead to persistent light limitation of the phytoplankton and continuous nutrient sufficiency (Cole *et al.*, 1992; Caraco *et al.*, 1997).

Sample collection and assay

Phytoplankton density and species composition in the Hudson River were characterized by Marshall (1988) in a study during 1986–1987, 6 years prior to the invasion. Additional historical information on phytoplankton in the Hudson comes from several sources (Howells and Weaver, 1969; Frederick *et al.*, 1976). We sampled phytoplankton in the Hudson River from 1993 to 1996 at the same locations of the earlier study to compare directly with Marshall's (1988) results, and to test the hypothesis that phytoplankton cell density and community composition changed in the Hudson River during the time that zebra mussels invaded. For the period 1993–1994, samples were identified to species and counted to genera; for 1995 and 1996, samples were counted only to major groups.

Fifty-six phytoplankton samples were collected during the 1993–94 period, seven samples from the Marist location (near Poughkeepsie, NY; 122 km from the mouth of the River) and 49 samples from the Rhinecliff location (near Kingston, NY; 152 km from the mouth). Whole-water samples (1 or 4 l) were collected biweekly at 1 m depths. They were preserved with M3 (American Public Health Association, 1992) and were concentrated by settling. The algae, both non-diatom and diatom, were identified using two different methods. A total of 500 cells of algae, whether non-diatom or diatom, were counted using a Palmer cell (×400) under a research-quality Nikon® light microscope. Diatoms were identified after digestion in H_2SO_4 and mounted in Naphrax®. Diatoms were counted until 500 valves or until 10 species with at least 10 valves were counted. Relative abundances of diatoms were calculated for each species and related to the total diatom counts in Palmer cells. In addition to the samples described above, we also counted 16 additional samples from the Rhinecliff location, eight in 1995 and eight in 1996, taken in July–August at peak algal abundance. These samples were enumerated only to major groups.

Marshall (1988) recorded the results of 97 sample assays from the same locations, near Poughkeepsie and Kingston, in 1986–1987. Marshall's samples were also collected every 2 weeks. His samples were whole-water samples, were concentrated by settling, and were preserved with acid Lugol's solution. Marshall's analysis of the algae was carried out with an inverted plankton microscope using the Utermöhl technique.

Data analyses

Data analyses were performed to determine whether phytoplankton density and taxonomic composition data sets were significantly different between the 1986–87 and the 1993–94 periods. Analysis of variance was used to test for differences in

mean phytoplankton densities during the two periods. TWINSPAN (Two Way Indicator Species Analysis) was used to cluster assemblages with the most similar species composition. Canonical discriminate analysis (SYSTAT®) was used to determine the statistical significance of differences between groups of assemblages identified with TWINSPAN. Detrended correspondence analysis (DCA) was used to illustrate the differences between clusters of species in two-dimensional ordination space (CANOCO v.3.1) (ter Braak, 1990). Analyses of changes in phytoplankton assemblages were assessed with both genera and divisions to account for possible differences in taxonomic identifications by Marshall (1988) and this study. TWINSPAN constructs a two-way table using correspondence analysis (CA) from the sites by species matrix. The two-way table clusters groups by sites and species data. The CA program uses a near block structure and similar data will be clustered closer together (dichotomy). TWINSPAN can generate a dichotomy of the sample by ordination. The clusters are first separated by positive and negative scores. Each respective group is further separated by using a simple discriminate analysis. To be conservative, DCA was used to eliminate any possible arching or horseshoe artifact. CA uses weighted average regression to develop a data score for the first axis. The reciprocals are used in another regression to get the second axis, and so on.

In these analyses, the data were not transformed. The analyses on total densities used raw cell counts; the data on species composition used relative abundance as percent of total counts.

Results

We will refer to the sampling period from 1986 to 1987 as the 'early period', and the sampling from 1993 to 1994 as the 'later period'. A total of 161 species were identified during the later period. Bacillariophyceae constituted the largest percentage, 78% of the species. Chlorophyceae (15%), Cyanobacteria (3%), Chrysophyceae (2.5%), Pyrrhophyceae (1%) and Cryptophyceae (0.6%) had successively lower proportions of species in the assemblages. For the period 1986–87, Marshall (1988) identified 137 species with Bacillariophyceae (43%), Chlorophyceae (27%), Cyanobacteria (15.3%), Cryptophyceae (2.2%), Chrysophyceae (2.2%) and Pyrrhophyceae (0.7%) having successively smaller proportions of species numbers.

Cell densities decreased significantly ($P < 0.05$): 17-fold from an average of 25.6×10^6 cells l^{-1} in the early period to 1.5×10^6 cells l^{-1} in the later period (Figure 2). From the early to the later period, diatoms decreased significantly ($P < 0.05$) by a factor of 2.5, from 3.3×10^6 to 1.3×10^6 cells l^{-1} (Figure 3a and b), and green algae decreased ($P > 0.05$) by a factor of 2.63, from 0.50×10^6 to 0.19×10^6 cells l^{-1} (Figure 3c and d). The most drastic change was the 778-fold decrease ($P < 0.05$) in cyanobacteria during the later period, from 10.12×10^6 to 0.13×10^6 cells l^{-1} in the early period (Figure 3e and f). A division of minor importance, Cryptophyta, also decreased significantly ($P < 0.05$) by a factor of 6 from 3.7×10^5 to 0.65×10^5 cells l^{-1}. Annual mean densities of other divisions did not decrease significantly between the two sampling periods ($P > 0.05$).

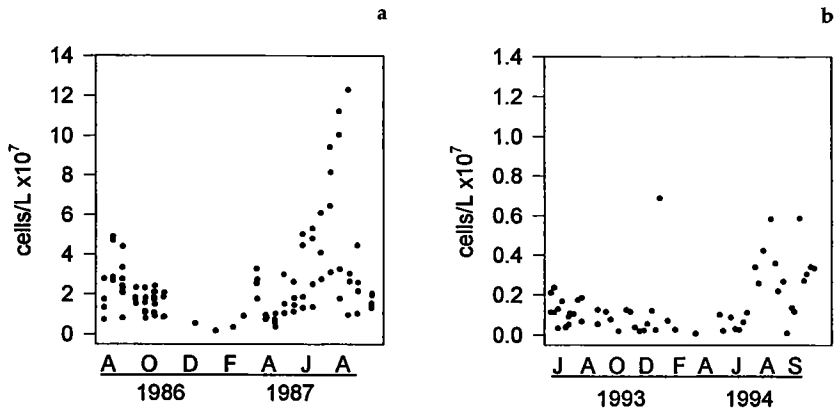

Fig. 2. Cell densities of phytoplankton in the Hudson River during periods before (**a**) and after (**b**) zebra mussel invasion.

Table I. Relative abundance (as percent of total cells) of selected major groups of phytoplankton in the Hudson River. The zebra mussel became established in 1992 (see the text)

Group	1986	1987	1993	1994	1995	1996
Cyanobacteria	24.6	46.7	1.0	0.7	11.4	0.9
Diatoms	18.3	10.3	78.2	86.1	42.3	96.2
Chlorophytes	1.9	2.0	11.4	2.2	2.2	2.3
Other	55.2	59.0	7.7	1.8	44.1	0.6

In addition to changes in density, community composition changed significantly between the two periods, whether generic or division-level classifications were assessed. The largest change was a dramatic increase in the fraction of total cells represented by diatoms, and a corresponding decline in the fraction represented by cyanobacteria. Expressed as a percent of total cells on an annual average basis and using the data for 1986–87 as the pre-period and 1993–1996 as the after-period, diatoms increased from 14.0 ± 5.6% (SD) prior to the invasion to 75.7 ± 23% following it (Table I). Cyanobacteria decreased from 35.7 ± 15.6% to 3.5 ± 5.3%.

At the level of genera, cluster analysis (TWINSPAN) and ordination (DCA) showed two distinct groups of assemblages based on the relative abundances in the assemblages (Figure 4). The first ordination axis explained 31% of the variation in genera among assemblages and separated the assemblages such that all assemblages from the later period were ordinated positively on the first axis and all assemblages from the early period were negatively ordinated. The difference between these two groups of assemblages, based on differences in relative abundances of genera, was highly significant (canonical discriminant analysis, $P < 0.001$).

The less intensive samples counted from 1995 and 1996 generally extend the patterns seen in 1993 and 1994. Total cell abundance was lower during 1995–96

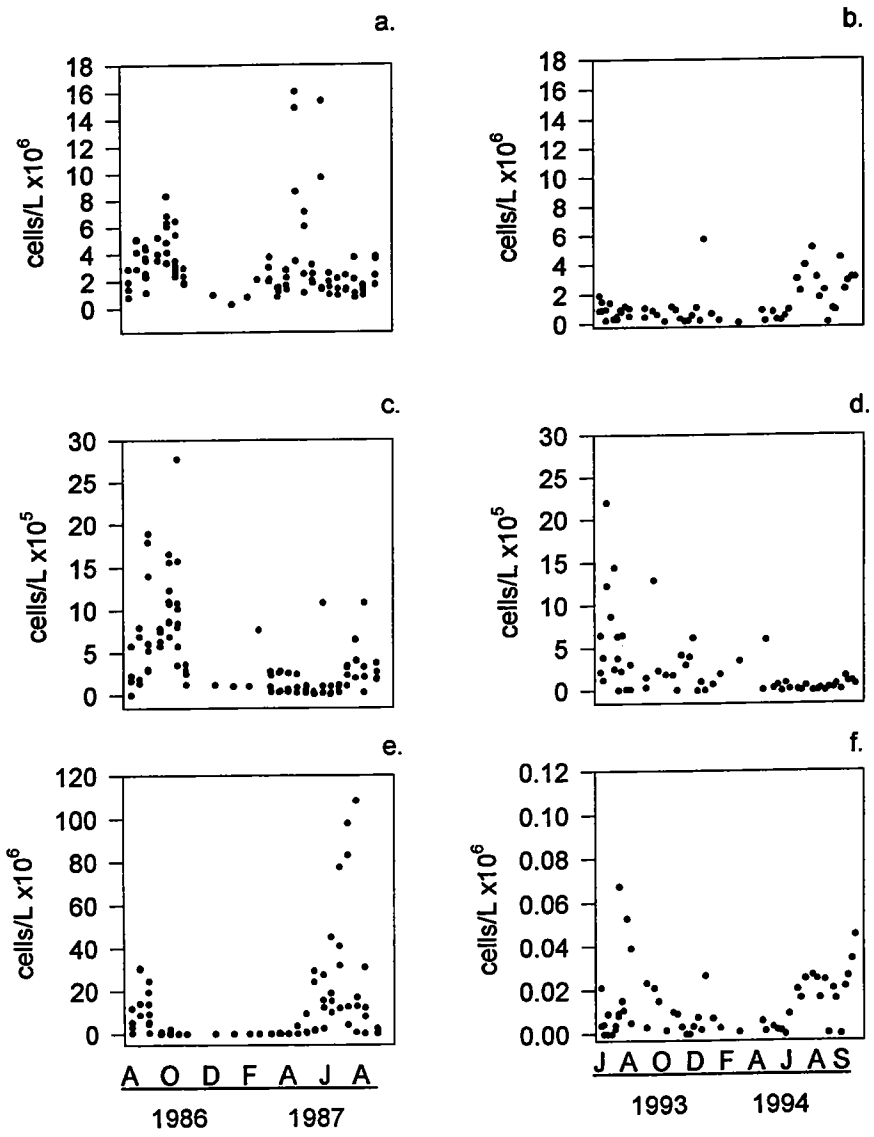

Fig. 3. Cell densities of diatoms (**a**, **b**), green algae (**c**, **d**) and cyanobacteria (**e**, **f**) in the phytoplankton of the Hudson River during periods before (1987–88) and after (1993–94) zebra mussle invasion. In each case, the panels on the left (a, c, e) are before, and the panels on the right (b, d, f) are after the zebra mussel invasion for each algal group.

than during the 1987–88 period, averaging 2.7×10^6 cells l^{-1} in 1995 and 0.8×10^6 cells l^{-1} in 1996. These total counts are 9.5- and 32-fold lower than the average counts during the 1987–88 period, and co-equal with the mean counts for the 1993–94 period. Like the 1993–94 period, cyanobacteria were low in 1995 and

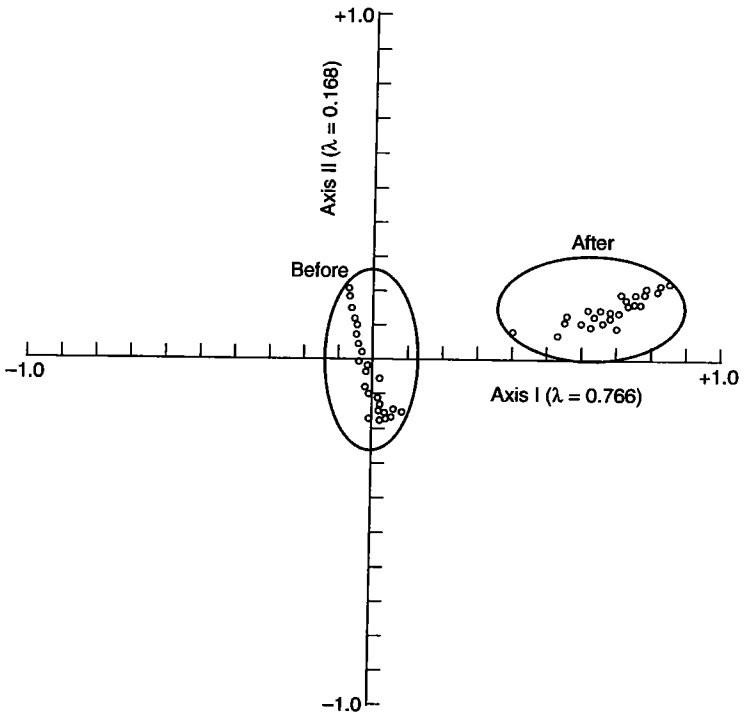

Fig. 4. Ordination (detrended correspondence analysis) of Hudson River phytoplankton assemblages based on relative abundances of phytoplankton genera during periods before and after zebra mussel invasion.

negligible in 1996 (Table I). Diatoms were relatively constant in the 1995–96 samples (0.5 and 0.7 × 10^6 cells l^{-1}, respectively), and comparable to the 1993–94 samples (Table I).

The genera could be classified into three categories according to occurrence in the two clusters (TWINSPAN): 'sensitive' (declined from early to late period), 'indifferent' (unchanged) and 'benefitted' (increased from early to late period) in relative abundance comparing the two sampling periods. In general, non-diatom genera decreased more than diatom genera from the early to later periods (Table II). Algae that declined tended to be small cells ranging from colonial to unicellular growth forms. Some fragile diatoms were also classified as declining between the periods. The indifferent genera tended to be the planktonic diatoms; however, some non-diatom algae also persisted throughout both periods: *Scenedesmus*, *Cryptomonas* and *Oscillatoria*. The genera that increased in concentration during the invasion were most commonly large, colonial, benthic or stalk-forming diatoms.

Assemblages from the early and later periods could also be discriminated when algae were only classified by division. Based on relative abundances of algal division in assemblages, assemblages before and after invasion were significantly

different (canonical discriminate analysis, $P < 0.001$) and the first ordination axis explained 55% of the variation in relative abundances of division among assemblages (Figure 5).

The second axis in the ordination with genera and division characteristics of assemblages explained a smaller percentage of the variation in relative abundances among assemblages and that variation was correlated to time of the year. The second ordination axis explained 7 and 17% of the variation in ordinations with genera and divisions, respectively. Ordination scores of assemblages were highly correlated to time of the year (Table III).

Seasonal variation in the species composition of phytoplankton in the Hudson River decreased during the period of zebra mussel invasion. Many of the taxa in the sensitive category had been present in only one season; the elimination of these taxa caused a dampening in seasonal variation. The decrease in seasonal variation during zebra mussel invasion is also evident in the decrease in variation in assemblage scores on DCA axis-2 in ordinations with both genera and division (Figures 4 and 5). Correlations between assemblage scores on the second ordination axis and time of year were particularly high for changes in genera both before and after zebra mussel invasion (Table III). Division changes, however,

Table II. Genera categorized as sensitive, indifferent or benefitted based on relative abundances. TWINSPAN grouped these genera in assemblages that were sampled before and after the zebra mussel invasion

Sensitive		Indifferent	Benefitted
Gonium	*Spirulina*	*Ankistrodesmus*	*Bacillaria*
Phacus	*Coelastrum*	*Asterionella*	*Diploneis*
Phormidium	*Cylindrotheca*	*Gyrosigma*	*Glenodinium*
Tetraedron	*Gymnodinium*	*Oscillatoria*	*Gomphonema*
Cosmarium	*Thalassionema*	*Scenedesmus*	Chrysophyceae sp.
Gomphosphaeria	*Biddulphia*	*Surirella*	*Cymbella*
Pandorina	*Coscinodiscus*	*Syndra*	*Diatoma*
Staurastrum	*Hantzchia*	Centric sp.	*Navicula*
Eudorina	*Pleurosigma*	*Cryptomonas*	*Nitzschia*
Kirchneriella	*Prorocentrum*	*Cyclotella*	*Eunotia*
Merismopedia	*Protoperidinium*	*Melosira*	*Dinobryon*
Nostoc	*Dactylococcopsis*	Pennate sp.	*Meridion*
Oocystis	*Skeletonema*	*Fragilaria*	
Chroomonas	*Trachelomonas*		
Euglena	*Amphiprora*		
Katodiuium	*Grammatophora*		
Lagerheimia	*Guinardia*		
Lauderia	*Gyrodinium*		
Leptocylindrun	*Pyramimonas*		
Schroederia	*Rhizosolenia*		
Actinastrum	*Micractinium*		
BG trichomes	*Pediastrum*		
Closterium	*Anabaena*		
Coelastrum	*Aphanocapsa*		
Crucigenia	*Ceratium*		
Microcystis	*Chroococcus*		
BG spheres			

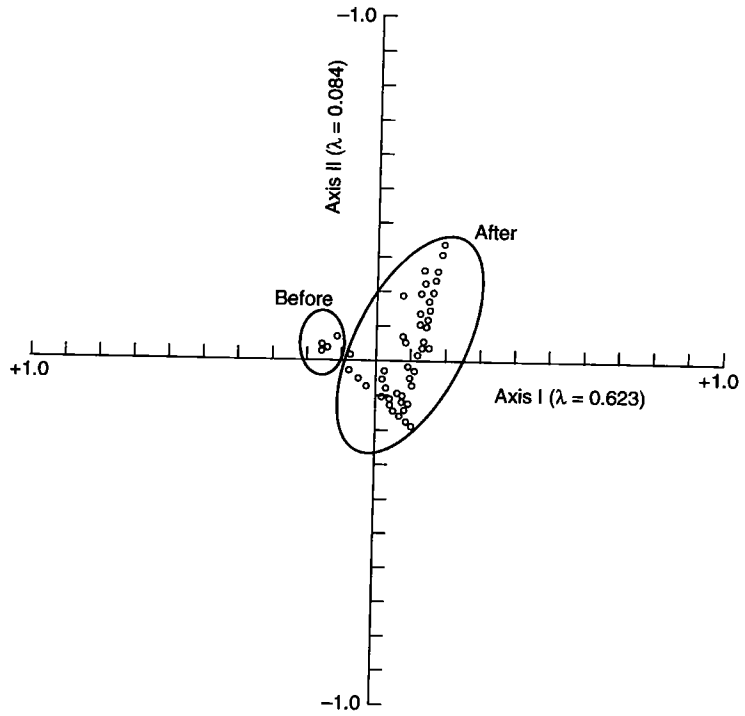

Fig. 5. Ordination (detrended correspondence analysis) of Hudson River phytoplankton assemblages based on relative abundances of phytoplankton divisions during periods before and after zebra mussel invasion.

were only highly correlated to season before zebra mussel invasion (Table III). The decrease in genus level diversity was also evident in the greater number of genera that declined in relative abundance during the zebra mussel invasion versus the smaller number of genera that increased (Table II).

Discussion

We found dramatic changes in both the total abundance and species composition of the phytoplankton of the tidal, freshwater portion of the Hudson River among samples analyzed in 1986–87 and 1993–6. Prior to the zebra mussel invasion, cell numbers averaged ~25.6 × 10^6 l^{-1} and cyanobacteria dominated cell numbers (36%). Following the invasion, cell numbers averaged 17-fold lower (1.5 × 10^6 l^{-1}) and diatoms were numerically dominant (76%). Major changes were also seen at the genus level as well, such that the phytoplankton community from 1993–94 was quite different from that of 1986–87. Clearly phytoplankton in the pair of years prior to the invasion of the zebra mussel differed substantially from those in the 4 years following the invasion, but how much of these differences represent a state change and how much could be random variation?

Table III. Correlation coefficients (r) for the relationship between ordination scores of assemblages on DCA axis-2 and time of the year. Correlation coefficients were determined separately for each year and for ordinations when taxa were classified by genera and by division. Attained significance (P) of the correlations was also determined

Year	Taxonomic level	r	P
1987	Genera	–0.699	<0.001
1987	Division	–0.667	<0.001
1988	Genera	0.397	0.002
1988	Division	0.482	<0.001
1993	Genera	–0.615	<0.001
1993	Division	–0.348	0.051
1994	Genera	0.851	<0.001
1994	Division	0.229	0.282

Although our record of phytoplankton counts is discontinuous, the record of chlorophyll *a* is continuous and extensive (Figure 1). The 10 year chlorophyll *a* record shows an 85% decline in summertime chlorophyll *a* that coincides with the establishment of the zebra mussel both temporally and spatially (Caraco *et al.*, 1997). That is, the chlorophyll *a* decline is very clearly a state change that occurred in the late summer of 1992, precisely when the first large year-class of zebra mussels became established. The dramatic decline in cell numbers is in good agreement with the more detailed, continuous, record of chlorophyll *a* and would, therefore, represent a state change that coincided with the invasion of the zebra mussel.

The more limited data on species composition require more caution in their interpretation. For the period following the invasion, the additional samples we examined in summer 1995 and 1996 for major groups confirmed the general pattern of the complete dominance by diatoms and a general absence of cyanobacteria. So, we can say with certainty that cyanobacteria were a very small proportion of the total phytoplankton from 1993 onwards. For the period prior to the invasion, the information is more anecdotal, except for the 1986–87 samples counted by Marshall (1988). For example, Frederick *et al.* (1976) recorded the presence of 36 species of cyanobacteria that occurred commonly in the tidal freshwater portion of the Hudson during the 1970s; Marshall (1988) reported 21 species of cyanobacteria prior to the zebra mussel invasion, and following the invasion of the zebra mussel we found only five. Howells and Weaver (1969) enumerated the larger phytoplankton from the intake water of the Indian Point power plant, located in the mesohaline part of the river. At this location (and in the netplankton fraction they counted), diatoms were dominant, but cyanobacteria were found in most samples. *Anabaena*, *Oscillatoria* and *Microcystis*, for example, occurred in 33, 46 and 31% of the samples counted. Howells and Weaver (1969) also refer to frequent blooms of *Microcystis* (no quantitative data) in the tidal freshwater region north of Poughkeepsie (the region we sampled).

Thus, although the earlier data are sparse, it appears that cyanobacteria were always abundant in the tidal freshwater portion of the river, as they were when

Marshall (1988) quantified them in 1986 and 1987. It is certainly clear that cyanobacteria were capable of reaching high numbers in the Hudson in the years prior to the zebra mussel. Since the establishment of the zebra mussel, cyanobacteria have been in very low abundance in every sample counted.

Very few systems have been analyzed for changes in either the abundance or structure of phytoplankton assemblages before and after an invasion of the zebra mussel, and the results have not been consistent among systems (MacIsaac, 1996). In general, declines in phytoplankton abundance have been observed, but these have varied from modest (Reeders and de Vaate, 1990; Leach, 1993) to severe (Holland, 1993; Nicholls and Hopkins, 1993; Fahnenstiel *et al.*, 1995; Caraco *et al.*, 1997). In some systems, blooms of cyanobacteria have increased following the introduction of the zebra mussel (western Lake Erie; Saginaw Bay; Oneida Lake), while in other systems these blooms have not occurred (small ponds; Reeders and de Vaate, 1990). Once it became established in the Hudson, the zebra mussel filtered the entire volume of the tidal, freshwater river every 2–3 days (Caraco *et al.*, 1997). Despite this intense amount of filtration, cyanobacteria have not been more than a few percent of total cell counts in the Hudson since the zebra mussel arrived.

We suspect that the mixing regime is an important factor in the outcome of the invasion to phytoplankton taxa. The water column of the Hudson is mixed rapidly enough so that temperature and oxygen gradients are rarely observed over the entire water column (Raymond *et al.*, 1997). This mixing brings phytoplankton into repeated contact with the mussels; in more quiescent systems, buoyant forms, such as some cyanobacteria, may escape grazing by remaining on the surface (Sullivan *et al.*, 1991). Another factor may be the high turbidity of the river which imparts severe light limitation on the phytoplankton. The much greater removal rates caused by the zebra mussel imply that only those taxa that either escape grazing or are replaced rapidly will persist in the system (Bastviken *et al.*, 1998). This replacement would have to come from either rapid growth for the planktonic species, or could come from either growth or resuspension in the case of benthic taxa.

The observed changes in phytoplankton community structure between the pre- and post-zebra mussel periods were not due to subtle differences in identification of the algae. The changes were evident at the species, genus and even major division levels. In the Hudson River, with great seasonal variability in the composition of assemblages, zebra mussel grazing appears to have constrained seasonal variation in phytoplankton assemblages. That is, rather than seeing a succession of algal groups from spring into summer, as occurred prior to the zebra mussel, we are now seeing dominance by a few genera of diatoms all season long. We do not yet know the full effects of the zebra mussel invasion on the entire food web of the Hudson, but it is possible that the selective effects on the phytoplankton have ramifications elsewhere. For example, despite the 9-fold decline in algal biomass, copepods did not show a discernible decline (Pace *et al.*, 1998). It is conceivable that diatoms are the major food of these copepods and diatoms declined by only 2.5-fold following the establishment of the zebra mussel.

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

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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/m^3; during 1993 and 1994 summertime concentrations were <5 mg/m^3. 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

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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 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.

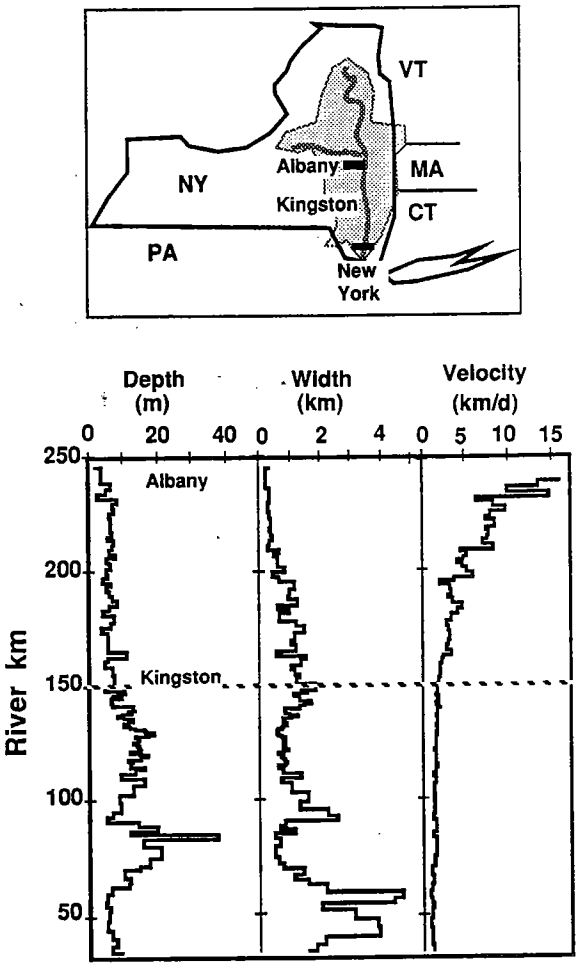

FIG. 1. Geographical and physical features of the Hudson River. The upper panel shows the location of the river and its watershed (stippled) within the boundaries of New York State. The horizontal bars represent the end points of the 200-km reach under study. The lower panel depicts some physical features 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.

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

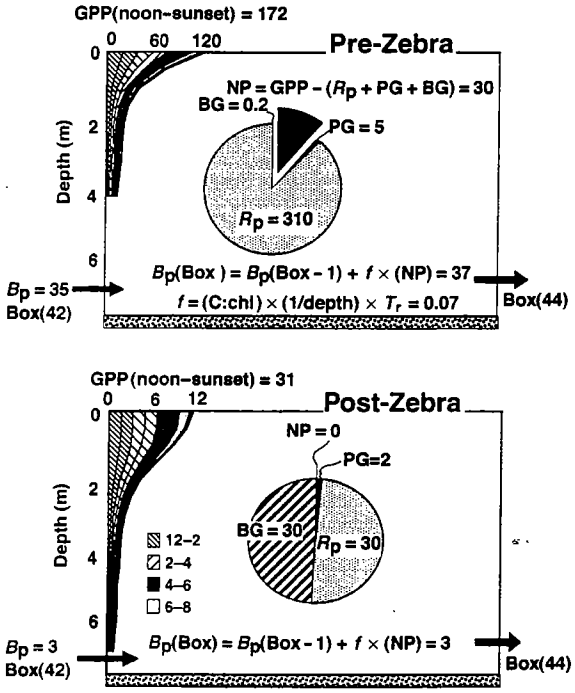

FIG. 2. Structure of one box of the phytoplankton box model under conditions prior to (upper) and during (lower) the zebra mussel invasion for the same day of the year (210) and location (river km 156, Box 43). Phytoplankton biomass (B_P) is imported into Box 43 from the box immediately upstream (Box 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(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 μeq/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/m² 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 4π 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(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

$$B_P(\text{box}) = B_P(\text{box} - 1) + (f \times \text{nP}) \qquad (1)$$

and

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

where nP and GPP are measured in units of mmol $C \cdot m^{-2} \cdot d^{-1}$, 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 mg chl a/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 $^{14}C-HCO_3$ 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 mmol $C \cdot (mg\ chl)^{-1} \cdot h^{-1}$ in summer to a low of 0.05 mmol $C \cdot (mg\ chl)^{-1} \cdot h^{-1}$ in winter. The values of α before the invasion varied from 0.0013 to 0.0006 mmol $C \cdot (mg\ chl)^{-1} \cdot h^{-1}$ (μmol of photons $\cdot m^{-2} \cdot s^{-1}$) in summer and winter, respectively. Measurements taken after the invasion show only a 5% increase in $P_{b,max}$ and a 40%

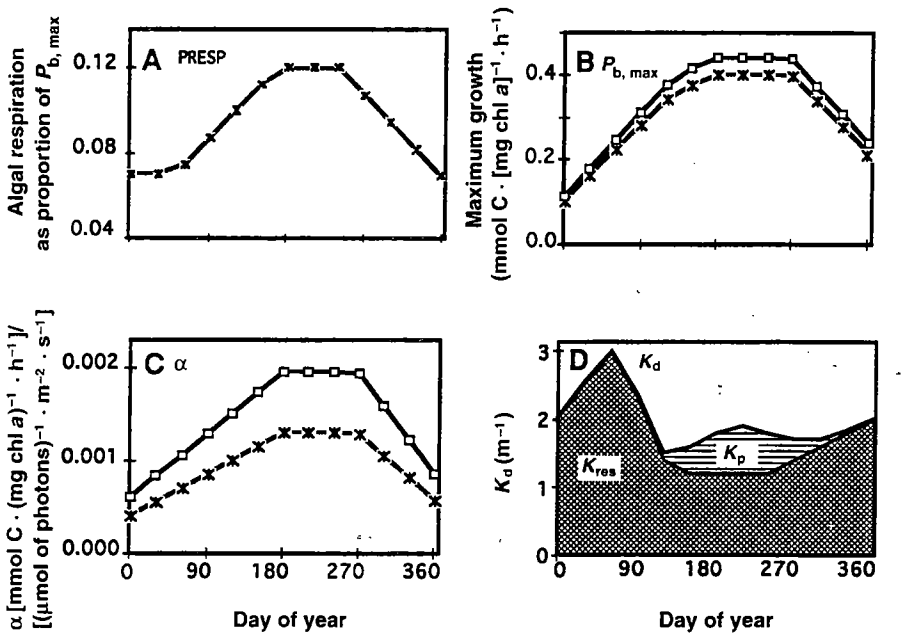

FIG. 3. Seasonal variation in modelled input parameters in the phytoplankton growth sub-models. (A) Algal respiration (R_P) is expressed as a fraction (PRESP) of $P_{b,max}$, and is assumed not to have changed with the invasion. (B) and (C) For $P_{b,max}$ (B) and α (C), which changed when the zebra mussel invaded, we show both pre-invasion (×) and post-invasion (□) 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] × 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-

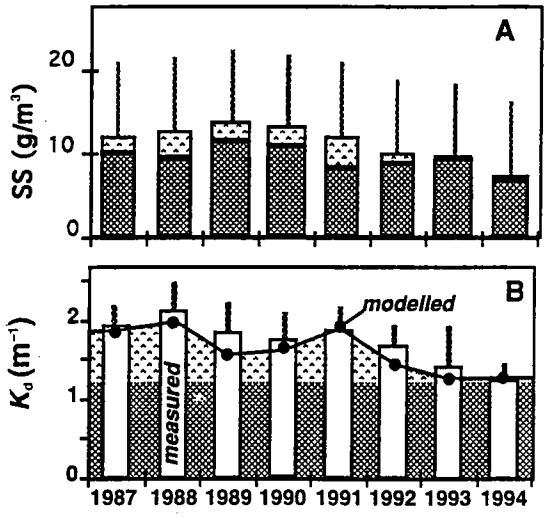

FIG. 4. (A) Suspended sediments (SS; dry mass) and (B) light extinction (K_d) in the Hudson River at river km 150 for the 1987–1994 period. Zebra mussel biomass was high during the last 3 yr (1992–1994). Summer mean values and 90% confidence intervals are shown for each year. (A) Total measured SS mass 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 (●) 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.