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Top-down control from the bottom: Regulation of eutrophication in a large river by benthic grazing

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Abstract

We use a 15-yr record from a 100-km stretch of the tidal, freshwater Hudson River to examine the controls of phytoplankton biomass. Across years, seasonal mean chlorophyll *a* (Chl *a*) and maximum Chl *a* varied by approximately 15-fold, with mean growing-season Chl *a* as high as 24 μg L^{-1} and maximum Chl *a* as high as 120 μg L^{-1}. For 3 of the 15 yr the river would be classified as eutrophic on the basis of lake standards for Chl *a*. Year-to-year variation in Chl *a* was not closely related to either nutrients (phosphorus or nitrogen concentrations) or hydrologic flow. Annual variation in grazing by the invasive zebra mussel (*Dreissena polymorpha*) explained 90% of the variation in mean Chl *a*; however, the maximum Chl *a* reached during the growing season was not significantly related to grazing and, even with high grazing, blooms of phytoplankton that contained high proportions of potentially toxic cyanobacteria occurred. Further, zebra mussels decreased dissolved oxygen concentrations even while increasing production of submersed aquatic vegetation. The results from the Hudson add to a growing literature that suggests that ecosystem changes linked with high phytoplankton biomass depend on a diverse range of system characteristics as well as whether phytoplankton are controlled by top-down or bottom-up mechanisms.

For lakes, reservoirs, and estuaries it is well established that high N and P inputs frequently result in high phytoplankton biomass and to problems associated with this high biomass (Schindler 1978; Smith 2003). However, it is now recognized that resistance to eutrophication can vary greatly between systems (Cloern 2001). As a group, large rivers, which tend to have high N and P loads from both point and nonpoint sources, may show strong resistance to both high phytoplankton biomass and many of the associated consequences of high phytoplankton biomass. In large rivers biomass of phytoplankton can potentially be kept low by high advective losses associated with short residence times (Soballe and Kimmel 1987; Wetzel 2001) and strong light limitation resulting from the combination of a well-mixed water column and turbid conditions (Cole et al. 1992). Additionally, the well-mixed conditions may make river phytoplankton more susceptible to control by benthic grazers than are phytoplankton in stratified systems (Sullivan et al. 1991). Finally, because of turbulent conditions in most rivers, even bottom waters exchange relatively rapidly with the atmosphere (Caraco et al. 2000) and, thus, low oxygen conditions resulting from phytoplankton decomposition are less likely.

The potential resistance that rivers show to eutrophication could explain why there has been comparatively little research on the controls of phytoplankton biomass or consequences of high phytoplankton biomass in riverine systems (Smith 2003). At times, however, phytoplankton biomass can reach values well above 15 μg L^{-1} chlorophyll *a* (Chl *a*) (Basu and Pick 1996; Welker and Walz 1998; Smith 2003), which would be indicative of eutrophic conditions in lakes (Wetzel 2001) and estuaries (Nixon 1995). Further, phytoplankton in rivers can include significant proportions of potentially toxic cyanobacteria (Smith 2003). As these waters are often important sources of drinking water (van der Leeden et al. 1990), the consequences of eutrophication include not only deterioration of recreational value of the system but also potentially serious consequences to human health.

The past dogma that rivers uniformly have high resistance to eutrophication is being challenged by recent studies demonstrating high phytoplankton biomass in some riverine systems (Smith 2003). We hypothesize that large rivers, like estuaries and lakes, show strong variation in both eutrophication and resistance to eutrophication. We focus on phytoplankton biomass as a major indicator of eutrophication, but in addition analyze system characteristics thought to be linked to high phytoplankton biomass, including cyanobacterial abundance and bottom-water oxygen depletion. The work takes place in the tidal Hudson River, a site with long-term data on phytoplankton biomass as well as top-down and bottom-up factors that potentially control it.

Site description

The focus of this paper is a 100-km stretch of the tidal, freshwater Hudson River (TFW Hudson, Fig. 1). The mesohaline section of the Hudson River Estuary, downstream of the TFW section, may have very different controls on primary production and phytoplankton biomass (Howarth et al. 2000). This TFW stretch of river has several small cities and towns that use the Hudson for both drinking water and sewage disposal. However, most of the nutrients come from diffuse and point sources above this stretch of the river (Lampman et al. 1999). Annual nitrogen and phosphorus loads from combined point and nonpoint inputs coming in at the top of the study stretch are approximately 140×10^5 kg yr^{-1} and 9×10^5 kg yr^{-1}, respectively, whereas inputs

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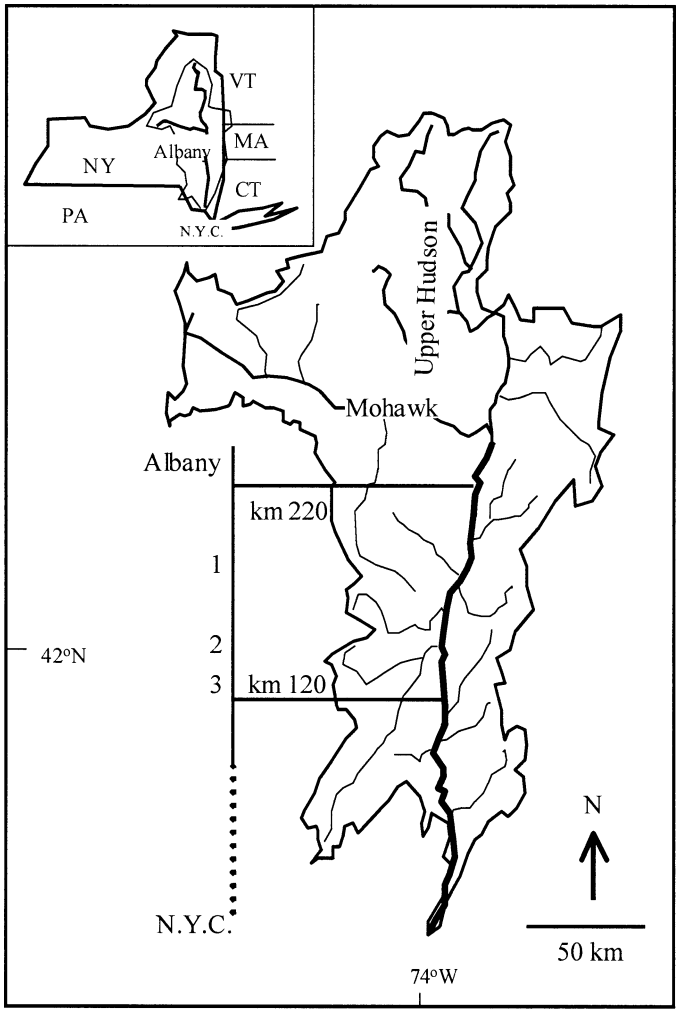

Fig. 1. Hudson River and its watershed and location of the watershed with respect to New York and adjoining states. The Hudson River is tidal for 250 km from New York City (km 0) to just north of Albany, New York. The tidal river receives water dominantly from the nontidal Mohawk and Upper Hudson Rivers. The upper 150-km stretch of the tidal Hudson is freshwater (TFW) and our study focuses on a 100-km stretch of the TFW Hudson (km 220–120). The three locations of spatiosampling for the 1987–1990 sampling are numbered 1–3.

from point and tributary loads within the 100-km study stretch are approximately 40×10^5 kg yr^{-1} and 2×10^5 kg yr^{-1}, respectively (Lampman et al. 1999).

The 100-km study reach of the TFW Hudson River is relatively wide (average 0.8 km) and deep (8 m), and this in combination with moderate freshwater inputs results in relatively long residence times (Caraco et al. 1997). At average growing-season flows of 200 m^3 s^{-1} the water residence time averages about 45 d. The entire TFW Hudson River has a mean tidal range of near 1 m and the currents generated by tides as well as freshwater runoff create a turbulent water column that results in well-mixed conditions (Cole et al. 1992). The high energy also keeps sediments in suspension, resulting in moderately turbid conditions (Cole et al. 1992; Lampman et al. 1999), and this coupled with the relatively deep water column results in low-light availability and depressed phytoplankton and submerged macrophyte production (Cole et al. 1992; Caraco and Cole 2002).

An additional factor affecting phytoplankton biomass and production is grazing. Although both zooplankton biomass and grazing are low in the Hudson (Pace et al. 1992), the grazing by benthic filter feeders is substantially greater (Strayer et al. 1996). This benthic filtration is dominated by one species, the invasive zebra mussel *Dreissena polymorpha* (Strayer et al. 1996). The zebra mussel invaded the river and became an important filter feeder in 1992. Before the invasion of the zebra mussel the water column of the Hudson was filtered about once every 30 d by a combination of zooplankton and benthic filter feeders; following the invasion the water column is filtered about every 2 d (Strayer et al. 1996).

Methods

We base our analysis primarily on a 15-yr period (1988–2002). During this period we have spatiotemporal coverage of phytoplankton biomass and physicochemical conditions for a 100-km stretch of the TFW Hudson (Fig. 1) during the 6-month growing season (May–October). During 1988–1990, sampling was based on three stations located at kms 193, 152, and 122, with samples taken at monthly intervals (Pace et al. 1992). For 1991 to 2002 we have more extensive spatial coverage, with samples taken during transects at ca. 3- to 5-km intervals over the study reach. During this period samples were taken at monthly to 1.5-month intervals, and for various years we have between 5 and 3 longitudinal transects per year (Lampman et al. 1999). Additionally, for the entire 15-yr period, weekly samples were taken from one station (sta. 2, Fig. 1). All samples were taken in the main channel of the river at ca. 0.2 m depth.

At all samplings we have measurement of Chl *a* as an estimate of phytoplankton biomass (Caraco et al. 1997). Nutrient analysis were made for all but a 3-yr period (1989–1991). Nutrient samples include dissolved inorganic N (DIN, or the sum of NH_4, NO_3, and NO_2), dissolved inorganic P (DIP), and total N and P (TN and TP) concentrations. Methods of storage, processing, and analysis are described elsewhere (Lampman et al. 1999). For 7 of the 15 years we additionally have direct measurements of turbidity (as NTU, nephelometric turbidity units) for transects (at 2- to 3-km intervals) and at station 2 (Fig. 1) at approximately weekly intervals (Lampman et al. 1999). Hydrologic inputs reported are for the top of the study stretch and are based either on direct U.S. Geologic Survey (USGS) monitoring at Green Island, New York or on correlative models calibrated to USGS monitoring at sites on the Upper Hudson and Mohawk (Caraco et al. 1997). In both cases daily hydrologic inputs are used to calculate seasonal averages for various years.

Estimates of zebra mussel filtration in the river were made by applying the regression of Kryger and Riisgard (1988) to measured population densities and body sizes of Hudson River zebra mussels (Strayer et al. 1996). Zebra mussel population density was estimated each year (1991–2003)

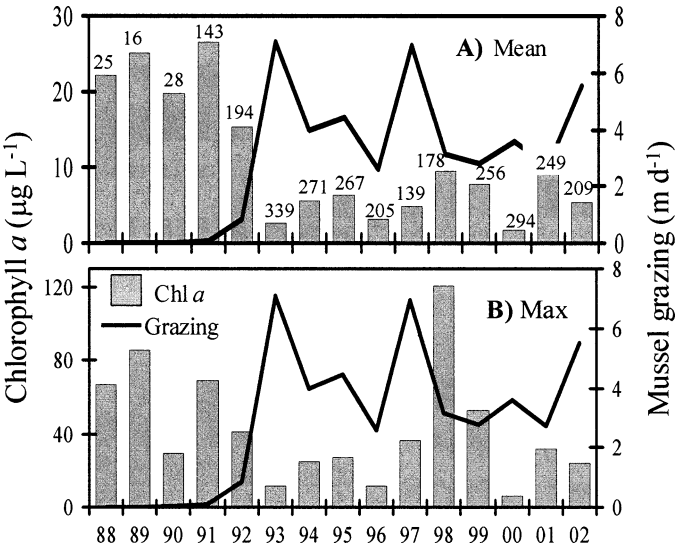

Fig. 2. Phytoplankton biomass as measured by chlorophyll *a* (Chl *a*) and zebra mussel grazing for the 15-yr study period. (A) Mean annual Chl *a* with the number of samples for which average values are calculated in each year. (B) Maximum Chl *a* in each year.

through a combination of grab samples (on sand and mud) and hand-collecting by divers (on rocky sediments). Estimates of zebra mussel size were made on a subset of collected mussels. Filtration rates estimated from the Kryger and Riisgard regression agreed well with measurements of filtration rates of Hudson River zebra mussels (Roditi et al. 1996).

Phytoplankton counts, taxonomic separation, and biomass estimates were made at one station in the middle of the study reach (Fig. 1, sta. 2) for 12 yr, 2 yr before the zebra mussel invasion and 10 yr after the invasion (Smith et al. 1998, unpubl. data). Counts are from 1-liter Lugol-preserved samples (Smith et al. 1998). Here we present information only on total and cyanobacterial biomass for the late summer period (20 July–20 September).

Dissolved oxygen (DO) was measured from 1987 to 2000 by Consolidated Edison (unpubl. data courtesy of J. Young). Measurements were made with a YSI oxygen meter calibrated to atmospheric concentrations. Oxygen measurements were made at ca. monthly throughout the growing season (May–October). Oxygen was measured at 10 stations in the 100-km study reach and at each station measurements were made from the surface to bottom of the water column at approximately 2-m intervals. We present DO values for three depth strata, which we define as: shallow waters (<2 m), mid-waters (2 to 8 m), and deep waters (>8 m). In total there are 4,134 measurements of DO for the 6-month growing season in the 100-km study reach.

Results

Considering the entire study reach of the Hudson there was a large variation in both seasonal mean and maximum Chl *a* (Fig. 2). During the 15-yr period mean Chl *a* varied between 1.5 and 27 μg L^{-1} and maximum Chl *a* ranged between 6.2 and 127 μg L^{-1}. The ratio of maximum to mean Chl *a* averaged 4.5 and varied from 1.5 to 13 among years. Overall there was a significant ($p = 0.02$) but relatively weak correlation between maximum and mean Chl *a* ($r^2 = 0.35$). Additionally, among years the timing of maximum Chl *a* varied by more than 120 d between June to October and the location of this peak varied by 60 km from km 200–140 (Fig. 3). This variation was not driven by inputs of phytoplankton above the study reach. At the top of the TFW Hudson (km 230–250, Fig. 1) Chl *a* averaged only 1.3 μg L^{-1} and the maximum Chl *a* reached over the entire 15-yr study period was only 6.4 μg L^{-1}.

In comparison to the large year-to-year variation in Chl *a*, the between-year variation in nutrient concentrations was relatively low. Year-to-year variation in average TP, TN, DIP, and DIN was 2.0-, 1.6-, 2.5-, and 1.7-fold, respectively. The between-year variation in nutrient concentrations was not significantly related to variation in mean or maximum Chl *a* (Table 1, Fig. 4A for TP). For both mean and maximum Chl *a*, the closest relationships to nutrients were for DIN and DIP, but these relationships were negative, opposite from that seen in lakes and estuaries (Table 1).

Between-years average growing season hydrologic flow varied by over threefold from 90 to 338 m^3 s^{-1}. For the 15-yr study period, annual variation in hydrologic flow was not significantly related to annual variation in TP, TN, DIN, or DIP concentrations ($p > 0.05$, linear regression), nor was flow significantly related to mean Chl *a* or maximum Chl *a* (Table 1). However, for the 7-yr period (1996–2002) for which we have turbidity data, turbidity and flow were significantly related to each other ($p < 0.01$, $r^2 = 0.81$, linear regression) and both were significantly related to variation in Chl *a* ($p < 0.05$, linear regression). This time period represents a period of relatively high and constant zebra mussel grazing (Fig. 2).

The filtration rate (m^3 m^{-2} d^{-1}) by the invasive zebra mussel can be expressed as a piston velocity (m d^{-1}) and this varied between 0 m d^{-1} (pre-1992) to near 7 m d^{-1} in 1993 and 1997. This filtration rate did not relate significantly to maximum Chl *a* (Table 1), but was significantly related to mean Chl *a* in a linear regression (Table 1). The relationship of Chl *a* to grazing was better described, however, by a negative exponential (Fig. 5A), and this relationship was highly predictive ($p < 0.001$, $r^2 = 0.90$). The residuals from the exponential relationship (ΔChl *a*) showed weak negative relations to hydrologic flow (Fig. 5B). The relationship was not significant considering the entire data set ($p = 0.08$) but was significant ($p = 0.01$) considering only the period after 1990 when more extensive data were available (Fig. 2, Fig. 5B, filled circles). There was not a significant relationship between ΔChl *a* and TN, TP, DIN, or DIP concentrations considering the entire data set or the period after 1990 ($p > 0.1$, linear regression).

Over the same time period that the average phytoplankton biomass was significantly reduced by zebra mussels grazing ($p < 0.001$, unpaired *t*-test, Fig. 6), cyanobacterial biomass was not reduced significantly ($p = 0.89$, unpaired *t*-test). This difference was driven by a tendency for, on average, higher relative abundance of cyanobacteria after the invasion of the zebra mussel (Fig. 6). The postzebra mussel period

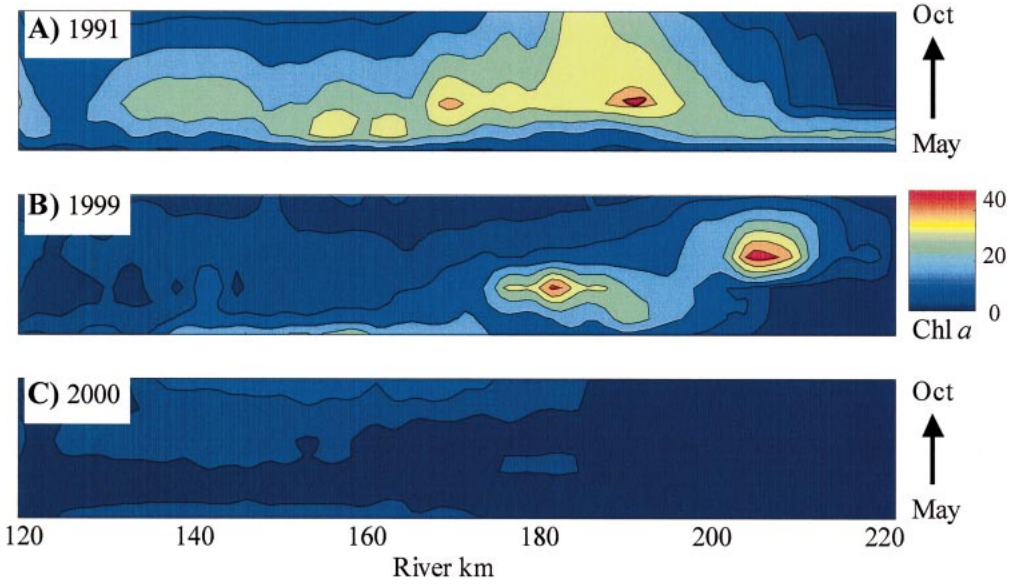

Fig. 3. Spatiotemporal variation in chlorophyll *a* (Chl *a*) in the tidal freshwater Hudson River for 3 yr (labeled on plots). 1991 is a year with low benthic grazing by the zebra mussel, whereas 1999 and 2000 have moderately high grazing rates but differ in hydrologic inputs. 2000 is a wet year and 1999 is a dry year. Note that in 1999, despite relatively low average biomass, ''hot spots'' of high biomass occur.

also differed from the prezebra mussel period in that in the postzebra mussel period there was a highly significant positive relationship between cyanobacterial and total phytoplankton biomass ($p < 0.001$, $r^2 = 0.41$, linear regression). Before the zebra mussel invasion there was no relationship between cyanobacterial and total phytoplankton biomass ($p = 0.84$, linear regression). Further, after the invasion of the zebra mussel the cyanobacteria biomass was up to 90% of total biomass, whereas prior to the invasion the highest percentage of cyanobacteria biomass was 10% of the total.

For the more than 4,000 DO measurements that covered more than a decade of time and ranged from surface to bottom waters, DO ranged between 2.9 and 12.8 mg L^{-1}. Surprisingly, depth was not significantly related to this variation in either the pre- or postzebra mussel period or considering the entire data set as a whole ($p > 0.05$, unpaired *t*-test). Further, the maximum average DO gradient, which occurred between surface and bottom waters in the prezebra mussel period, was only 0.1 mg L^{-1} (Fig. 7). The difference between DO in pre- and postzebra mussel periods was, on the other hand, highly significant ($p < 0.001$, unpaired *t*-test). On average, for the entire 100-km reach, DO was 0.5 mg L^{-1} lower after the invasion of the zebra mussel (Fig. 7).

Discussion

During a 15-yr study in the Hudson River there was a 15-fold range in average Chl *a*. On the basis of mean annual Chl *a* and eutrophication standards for lakes (Wetzel 2001), during the 15-yr period there would have been 3 yr classified as oligotrophic (≤ 3 μg L^{-1}, average chl-*a*), 5 yr as eutrophic (>11 μg L^{-1}), and 7 yr as mesotrophic. The variation in phytoplankton biomass did not relate significantly to variation in phosphorus or nitrogen (Table 1, Fig. 4); rather, it

Table 1. Relationship, based on linear regressions, between growing season mean chlorophyll *a* (Chl *a*) and maximum Chl *a* and six potential predictor variables. All predictor variables are mean values for the growing season. The columns are the regression outcomes between Chl *a* (in μg L^{-1}) and total phosphorus (TP), total nitrogen (TN), dissolved inorganic phosphorus (DIP), and dissolved inorganic nitrogen (DIN) (all expressed in μg L^{-1}). Hydrologic flow (flow) is in m^3 s^{-1} and zebra mussel grazing (ZMG) is in m d^{-1}. The number of years in the regression analysis for both the mean and maximum Chl *a*. All variables had distributions that were not significantly different from normal as judged by skewness and kurtosis criteria (Tabachnick and Fidell 1996).

	Mean Chl *a*					Max Chl *a*			
	p	r^2	slope	Int	*n*	*p*	r^2	slope	Int
TP	0.45	0.06	0.11	1.5	12	0.14	0.20	−1.11	101.0
TN	0.86	0.00	0.00	5.1	11	0.79	0.01	−0.03	59.0
DIP	0.18	0.17	−0.31	15.8	12	0.13	0.22	−1.86	86.0
DIN	0.09	0.21	−0.03	20.7	11	0.13	0.24	−0.20	139.0
flow	0.78	0.01	−0.01	12.9	15	0.78	0.01	−0.01	12.9
ZMG	<0.001	0.70	−2.94	19.6	15	0.10	0.20	−5.72	59.5

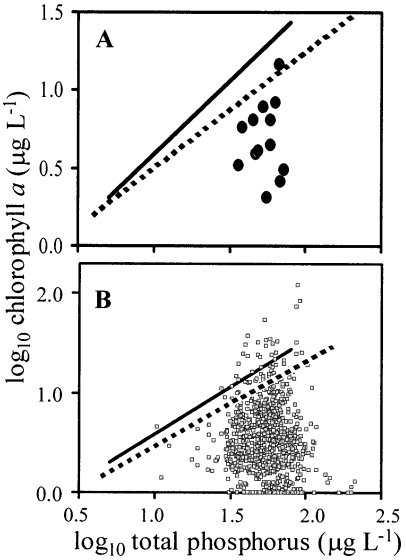

Fig. 4. (A) Log–log plot of total P vs. chlorophyll *a* based on mean seasonal values and (B) individual data points in the tidal, freshwater Hudson River. The lines shown for comparison are regressions derived for temperate lakes and reservoirs (solid line, Mazumder 1994) and Canadian Rivers (dashed line, Basu and Pick 1996).

was driven by variation in resistance to eutrophication across years. That is, while at times phytoplankton yield at a given TP concentration was equal to that found in nutrient-limited lakes, often the values were far lower (Fig. 4).

High flow and resulting low residence time has classically been an explanation for low phytoplankton biomass and, therefore, high resistance to eutrophication in flowing waters (Wetzel 2001). For example, Soballe and Kimmel (1987) compared phytoplankton biovolume–TP relationship in rivers and found that, as compared to lakes or reservoirs, there was on average lower phytoplankton biomass at a given TP

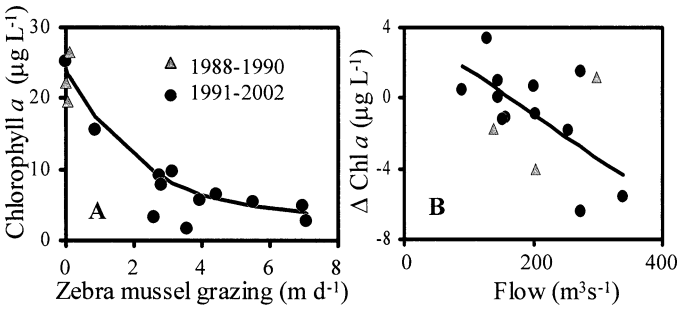

Fig. 5. (A) Chlorophyll *a* (Chl *a*) vs. zebra mussel grazing (ZMG) and (B) the residuals (ΔChl *a*) from the negative exponential relationship vs. flow. The equation for the negative exponential in panel A is: Chl $a = 21\ e^{-.45\ ZMG}$. ΔChl *a* is the actual values of Chl *a* at a given grazing rate minus those predicted from the negative exponential in panel A. Flow, Chl *a*, and mussel grazing are all mean growing season averages for the 100-km study reach (Fig. 1). In both panels the triangles are data from 1988–1990, during which time we had less spatiocoverage and fewer points to define the mean Chl *a* values; the dark circles are for the 1991–2002 period. The regression lines in both panels are for the entire study period.

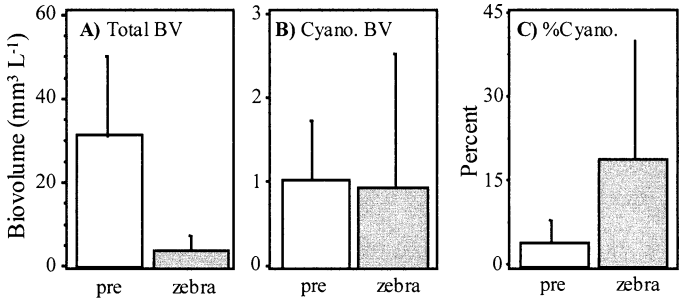

Fig. 6. (A) Total biovolume of phytoplankton (Total BV), (B) cyanobacterial biovolume (Cyanobacteria BV), and (C) relative contribution of cyanobacteria (% Cyanobacteria). All values are split into periods before the establishment of the zebra mussel (pre) and after the establishment in 1992 (zebra). Bars represent mean values and error bars are 95% confidence intervals on the mean. Total BV and cyanobacteria BV are both in $mm^3\ L^{-1}$.

value in rivers, and TP explained a smaller percentage of the variation in phytoplankton biomass than it did in lakes. The residual of the TP–phytoplankton biomass relationship was related negatively to residence time of waters, which decreases with increased flow in a given system. In the Hudson, however, flow is not strongly related to phytoplankton biomass across years (Table 1). The lack of a strong negative relationship to flow and phytoplankton biomass could be due to very high among-year variation in grazing. The lack of a strong relationship between phytoplankton biomass and flow is consistent, however, with results of Basu and Pick (1996) for Canadian Rivers.

Although flow and its associated higher turbidity and greater light limitation may not explain well the variation in mean summer Chl *a* in the Hudson, the overall high light limitation may influence the extent to which grazers can affect phytoplankton biomass. The Hudson River, and possibly rivers in general (Basu and Pick 1996), have relatively low biomass of zooplankton as compared to rivers and estuaries (Pace et al. 1992). For the Hudson the zooplankton clearance rates are only about 3% of the water column per day on average (Strayer et al. 1996). By comparison, for lakes, biomass of zooplankton at a given phytoplankton level is 10-fold greater, with resultant water-column clearance rates of

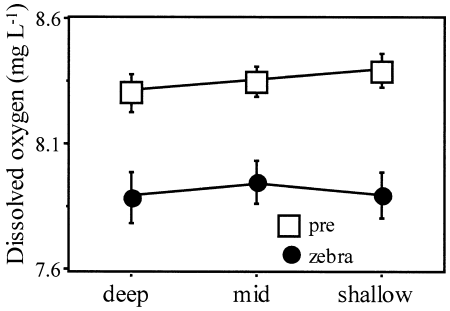

Fig. 7. Average dissolved oxygen concentrations for the pre- and postzebra mussel periods in the 100-km study reach of the Hudson. The values are divided by depth intervals of <2 m (shallow), 2–8 m (mid), and >8 m (deep). The error bars are 95% confidence intervals on the mean values.

near 30% per day (Sterner 1986; Cole et al. 1988). Further, before the invasion of the zebra mussel in the Hudson, grazing by benthic grazers was low (Strayer et al. 1996). With these low total grazing rates phytoplankton production could regularly outstrip removal even with very low phytoplankton turnover rates and on average, phytoplankton biomass was quite high (Fig. 2). With even moderately high grazing rates, however, phytoplankton biomass on average was kept quite low.

The relative importance of benthic grazers in controlling phytoplankton biomass in rivers or the extent to which light limitation interacts with this control is to date not well known. This control depends on both the growth rate of phytoplankton as well as grazing rates of the benthos (Schol et al. 2002). Interestingly, at present most riverine studies that suggest a substantial role of benthic grazers in controlling riverine phytoplankton are of invasive bivalves (e. g., Welker and Walz 1998; Akopian et al. 2001; Gelda and Effler 2002). For a large number of rivers it is possible that at present there is relatively low grazing by native populations of benthic grazers because of human-related reductions in bivalves (Strayer et al. 1999). Thus, historically many rivers may have had stronger control of phytoplankton biomass by benthic grazing than they do at present.

In systems where phytoplankton biomass is controlled by grazing, occasional outbreaks can occur, resulting in very high phytoplankton biomass (blooms). For the Hudson these blooms were evident in the postzebra mussel period; in this period there was a high ratio of maximum to mean Chl *a* and our highest observed phytoplankton biomass was found in a year with substantial zebra mussel grazing (1998, Fig. 2). The high phytoplankton biomass in the Hudson that occurs in spatiotemporal ''hot spots'' (Fig. 3) can lead to water quality problems including the increased abundance of potentially toxic cyanobacteria (Smith 2003). Although measurements of cyanobacterial abundance in the TFW Hudson are limited to one station (Fig. 1, sta. 2) and miss some of the highest biomass of phytoplankton in postzebra mussel years (Figs. 2, 3), the data indicate that for the 12 yr since the invasion of the zebra mussel the average and peak relative abundance of cyanobacteria has increased (Fig. 6C). This result is in contrast to sharp reductions in cyanobacteria in the TFW Hudson in the first 2 yr after the zebra mussel invasion (Smith et al. 1998). The results are consistent, however, with effects of strong top-down control in general (Carpenter et al. 1992) and with zebra mussel effects found in some lakes (e. g., Raikow et al. 2004). For the TFW Hudson the reason for the low cyanobacterial biomass 2 yr after the zebra mussel invasion (Smith et al. 1998) or the overall high variation in both cyanobacterial biomass and relative abundance after the invasion of the zebra mussel is not clear. Year-to-year variation in temperature, microstratification of the water column, phosphorus, or trace element concentrations could all play a role in controlling variation in cyanobacterial abundance.

In addition to potential blooms of toxic phytoplankton a frequent consequence of high phytoplankton biomass is low oxygen in bottom waters (Cloern 2001; Wetzel 2001). The response of DO in the Hudson to changes in phytoplankton biomass differs substantially from this expectation. First, because of high water-column mixing there was little difference in oxygen concentrations between surface and bottom waters. Second, there was on average lower oxygen concentration in both surface and bottom waters in years with zebra mussels when phytoplankton biomass was lower (Fig. 7). The DO decline throughout the water column can be explained by an increase in total system respiration that is only partially compensated by increased production of submerged aquatic vegetation associated with higher light penetration in postzebra mussel years (Caraco et al. 2000). Although in the Hudson DO did not decline to hypoxic levels in the water column with the invasion of the zebra mussel, in systems with greater biomass of benthic grazers or high inputs of BOD (biological oxygen demand) from sewage, hypoxia could occur along with decreased phytoplankton biomass (Gelda and Effler 2002). Further, it is possible that within the Hudson the zebra mussels caused substantially lower DO at the sediment–water interface, but we have no measurements to confirm or refute this.

For aquatic systems evidence is mounting that increased phytoplankton biomass and production (e.g., eutrophication) can cause a cascade of ecosystem changes (Cloern 2001). In many cases the factors linked with high phytoplankton biomass are of greater consequences than the phytoplankton biomass per se. To date, however, the specific ecosystem changes linked to high phytoplankton biomass, including bottom-water hypoxia and undesirable or toxic phytoplankton blooms, are based on a paradigm constructed for bottom-up controlled (nutrient-limited) stratified lakes and estuaries. The factors linked with high phytoplankton biomass can depend, however, not only on system characteristics but also on the mode of eutrophication control. For well-mixed and nutrient-rich rivers more studies are needed to determine not only the relative importance of top-down and bottom-up processes in controlling phytoplankton biomass but also on how the different control processes affect the system as a whole.

References

AKOPIAN, M., J. GARNIER, P. TESTARD, AND A. FICHT. 2001. Estimating the benthic population of *Dreissena polymorpha* and its impact in the lower Seine River, France. Estuaries **24:** 1015–1028.

BASU, B. K., AND F. R. PICK. 1996. Factors regulating phytoplankton and zooplankton biomass in temperate rivers. Limnol. Oceanogr. **41:** 1572–1577.

CARACO, N. F., AND J. J. COLE. 2002. Contrasting impacts of a native and alien macrophyte on dissolved oxygen in a large river. Ecol. Appl **12:** 1496–1509.

———, ———, S. E. G. FINDLAY, D. T. FISCHER, G. G. LAMPMAN, M. L. PACE, AND D. L. STRAYER. 2000. Dissolved oxygen declines in the Hudson River associated with the invasion of the zebra mussel (*Dreissena polymorpha*). Environ. Sci. Technol. **34:** 1204–1210.

———, ———, P. A. RAYMOND, D. L. STRAYER, M. L. PACE, S. E. G. FINDLAY, AND D. T. FISCHER. 1997. Zebra mussel invasion in a large, turbid river: Phytoplankton response to increased grazing. Ecology **78:** 588–602.

CARPENTER, S. R., J. F. KITCHELL, AND J. R. HODGSON. 1992. Cascading trophic interactions and lake productivity. Bioscience **35:** 634–639.

CLOERN, J. E. 2001. Our evolving conceptual model of the coastal eutrophication problem. Mar. Ecol. Prog. Ser. **210:** 223–253.

COLE, J. J., N. F. CARACO, AND B. L. PEIERLS. 1992. Can phytoplankton maintain a positive carbon balance in a turbid, freshwater, tidal estuary? Limnol. Oceanogr. **37:** 1608–1617.

———, S. FINDLAY, AND M. L. PACE. 1988. Bacterial production in fresh and saltwater ecosystems: A cross- system overview. Mar. Ecol. Prog. Ser. **43:** 1–10.

GELDA, R. K., AND S. W. EFFLER. 2002. A river water quality model for chlorophyll and dissolved oxygen that accommodates zebra mussel metabolism. Water Qual. Ecosyst. Model. **1:** 271–309.

HOWARTH, R. W., D. P. SWANEY, T. J. BUTLER, AND R. MARINO. 2000. Climatic control on eutrophication of the Hudson River Estuary. Ecosystems **3:** 210–215.

KRYGER, J., AND H. U. RIISGARD. 1988. Filtration rate capacities in 6 species of European freshwater bivalves. Hydrobiologie **140:** 207–219.

LAMPMAN, G., N. CARACO, AND J. COLE. 1999. Spatial and temporal patterns of nutrient concentration and export in the tidal Hudson River. Estuaries **22:** 285–29.

MAZUMDER, A. 1994. Phosphorus-chlorophyll relationships under contrasting herbivore and thermal stratification: Predictions and patterns. Can. J. Fish. Aquat. Sci. **51:** 390–399.

NIXON, S. W. 1995. Coastal marine eutrophication: A definition, social causes, and future concerns. Ophelia **41:** 199–219.

PACE, M. L., S. E. G. FINDLAY, AND D. LINTS. 1992. Zooplankton in advective environments: The Hudson River community and a comparative analysis. Can. J. Fish. Aquat. Sci. **49:** 1060–1069.

RAIKOW, D. E., O. SARNELLE, A. E. WILSON, AND S. K. HAMILTON. 2004. Dominance of the noxious cyanobacterium *Microcystis aeruginosa* in low nutrient lakes is associated with exotic zebra mussels. Limnol. Oceanogr. **49:** 437–481.

RODITI, H. A., N. F. CARACO, J. J. COLE, AND D. L. STRAYER. 1996. Filtration of Hudson River water by the zebra mussel (*Dreissena polymorpha*). Estuaries **19:** 824–832.

SCHINDLER, D. W. 1978. Factors regulating phytoplankton production and standing crop in the world's freshwaters. Limnol. Oceanogr. **23:** 478–486.

SCHOL, A., V. KIRCHESCH, T. BERGFELD, F. SCHOLL, J. BORCHERDING, AND D. MULLER. 2002. Modelling the chlorophyll a content of the River Rhine—interrelation between riverine algal production and population biomass of grazers, rotifers, and the zebra mussel, *Dreissena polymorpha*. Int. Rev. Hydrobio. **87:** 295–317.

SMITH, T. E., R. J. STEVENSON, N. F. CARACO, AND J. J. COLE. 1998. Changes in phytoplankton community structure during the zebra mussel (*Dreissena polymorpha*) invasion of the Hudson River (New York). J. Plankton Res. **20:** 1567–1579.

SMITH, V. H. 2003. Eutrophication of freshwater and coastal marine ecosystems: A global problem. Environ. Sci. Poll. Res. **10:** 1–14.

SOBALLE, D. M., AND B. L. KIMMEL. 1987. A large-scale comparison of factors influencing phytoplankton abundance in rivers, lakes and impoundments. Ecology **68:** 1943–1954.

STERNER, R.W. 1986. Herbivores direct and indirect effects on algal populations. Science **231:** 605–607.

STRAYER, D. L., N. F. CARACO, J. J. COLE, S. FINDLAY, AND M. L. PACE. 1999. Transformations of freshwater ecosystems by bivalves: A case study of zebra mussels in the Hudson River. Bioscience **49:** 19–28.

———, J. POWELL, P. AMBROSE, M. L. PACE, AND D. T. FISCHER. 1996. Arrival, spread, and early dynamics of a zebra mussel (*Dreissena polymorpha*) population in the Hudson River estuary. Can. J. Fish. Aquat. Sci. **53:** 1143–1149.

SULLIVAN, B. K., P. H. DOERING, C. A. OVIATT, A. A. KELLER, AND J. B. FRITHSEN. 1991. Interactions with the benthos alter pelagic food web structure in coastal waters. Can. J. Fish. Aquat. Sci. **48:** 2276–2284.

TABACHNICK, B.G., AND L.S. FIDELL. 1996. Using multivariate statistics, 3rd ed. Harper Collins.

VAN DER LEEDEN, F., F. L. TROISE, AND D. K. TODD. 1990. The water encyclopedia, 2nd ed. Lewis.

WELKER, M., AND N. WALZ. 1998. Can mussels control the plankton in rivers?—a planktological approach applying a Lagrangian sampling strategy. Limnol. Oceanogr. **43:** 753–762.

WETZEL, R. G. 2001. Limnology: Lake and river ecosystems, 3rd ed. Academic Press.

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