Estuaries and Coasts Vol. 30, No. 1, p. 163–170 February 2007

Changes in Cyanobacterial Dominance Following the Invasion of the Zebra Mussel *Dreissena polymorpha*: Long-term Results from the Hudson River Estuary

SARAH H. FERNALD*, NINA F. CARACO, and JONATHAN J. COLE

Institute of Ecosystem Studies, 65 Sharon Turnpike, Millbrook, New York 12545

ABSTRACT: The introduction of invasive bivalves such as the zebra mussel (*Dreissena polymorpha*) can have profound effects on aquatic ecosystems, including decreases in phytoplankton biomass and changes in the taxonomic composition of phytoplankton. Zebra mussel introductions have been associated with increased dominance of cyanobacteria, especially *Microcystis*, but this change may depend on interacting physical, chemical, or biotic conditions. We used a 12-yr record in the Hudson River to explore the relationship between phytoplankton composition and zebra mussel filtration. During this period (1993–2005), the mean July–September filtration rate of the zebra mussel (ZMF) varied by 8-fold, and the mean biovolume of cyanobacteria, which was dominated by *Microcystis*, varied from 0 to 4.2 $mm^3 l^{-1}$ and comprised up to 52% of total phytoplankton biovolume. There was a tendency for high cyanobacterial biomass to be associated with low rather than high ZMF. Neither the absolute nor the relative amounts of either total cyanobacteria or *Microcystis* were significantly correlated to ZMF alone or in combination with total phosphorus or any other physical or chemical parameters that we measured. Cyanobacterial dominance and abundance were both strongly correlated to temperature, and over 80% of the among year variance in cyanobacterial dominance could be explained by temperature in a linear model. Temperature in combination with dissolved SiO_3 explained 90% of the variation in cyanobacterial dominance. At higher temperatures and lower dissolved SiO_3, cyanobacterial abundance increased at the expense of diatoms that dominated at lower temperatures and in higher SiO_3 years. The high explanatory value of temperature is surprising as the variation in temperature among years was relatively low (24.0–26.8°C). The results suggest that even slightly increased temperatures could lead to higher biomass and dominance of cyanobacteria in some aquatic systems.

Introduction

Phytoplankton populations are often dramatically altered by invasions of grazers, such as the zebra mussel *Dreissena polymorpha*. Zebra mussel populations can filter large volumes of water and change phytoplankton biomass and species composition (MacIsaac 1996; Caraco et al. 1997), as well as other aspects of the food web and chemistry of the system (Strayer et al. 1999; Vanderploeg et al. 2002). As the base of the aquatic food web, such changes in phytoplankton abundance and composition can significantly affect the entire ecosystem (Ulanowicz and Tuttle 1992; Holland 1993; Thorp and Casper 2002). Major changes in phytoplankton species composition may be caused both directly and indirectly by zebra mussel filtration (Bastviken et al. 1998; Smith et al. 1998; Vanderploeg et al. 2001). Directly, zebra mussels may affect phytoplankton composition through selective removal from the water column, selective ingestion of particles from the mantle cavity, or selective digestion of phytoplankton species; filtration can have a greater effect on the bottom of the water column increasing removal of less buoyant phytoplankton species, or zebra mussel filtration can remove phytoplankton from the water column at such a high rate that only faster growing phytoplankton species survive (Bastviken et al. 1998; Baker and Levinton 2003). Indirectly, zebra mussel filtration can alter the light intensity, rendering it more favorable to a particular phytoplankton group (Bastviken et al. 1998), or they can change the rate and stoichiometry at which nutrients are recycled, creating a selective environment for further algal growth (Gardner et al. 1995; Heath et al. 1995; Johengen et al. 1995; Sarnelle et al. 2005).

In the case of cyanobacterial selection, a prevailing model is that selective grazing on readily edible phytoplankton causes a shift towards less edible forms, most often colonial cyanobacteria that may contain toxins (Lavrentyev et al. 1995; Vanderploeg et al. 2001). On the other hand, laboratory work has shown that zebra mussels readily consume cyanobacteria at least when colonies are small (Baker et al 1998; Bastviken et al. 1998; Pires et al. 2004), and in some systems, notably rivers, cyanobacteria have been reported to be strongly reduced by zebra mussel grazing (Caraco et al. 1997; Smith et al. 1998). Variation in vertical mixing, turbidity and

* Corresponding author; current address: Hudson River Research Reserve, Bard College Field Station, Annandale, New York 12504; tele: 845/758-7022; fax: 845/758-7033; e-mail: shfernal@gw.dec.state.ny.us

nutrient concentrations may all cause variable response of phytoplankton composition to zebra mussel grazing (Roditi et al. 1996; Effler and Siegfried 1998; Raikow et al. 2004). Long-term selective grazing may lower edibility of some phytoplankton groups and could change zebra mussel effects over time in the absence of other system changes. Long-term studies following the invasion of the zebra mussel can provide insights to the factors that interact to cause variation in effects on phytoplankton composition (Barbiero et al. 2006).

The Hudson River is a large tidal estuary extending 247 km from Albany to Lower Manhattan in eastern New York State. The northern 200 km of the river is freshwater, deep (average ca. 9.5 m), turbid, well mixed, and nutrient rich (Limburg et al. 1986; Cooper et al. 1988). The zebra mussel first appeared in the Hudson River Estuary in 1991 and rapidly spread to all freshwater and oligohaline parts of the estuary by 1992 (Strayer et al. 1996). Filtration by organisms in the Hudson River (zooplankton and benthic bivalves combined) increased 25-fold following the zebra mussel invasion. Prior to the invasion, the total volume of the river was biologically filtered approximately every 50 d, but as rapidly as every 2–3 d post invasion (Caraco et al. 1997; Smith et al. 1998). In the Hudson River 1 yr following the invasion (1993), the average summer phytoplankton biomass equaled only 10% of the pre-invasion values, and 18% of the pre-invasion values in the summer of 1994 (Caraco et al. 1997).

We previously reported the effects immediately following the invasion (Caraco et al. 1997; Smith et al. 1998), but have found the patterns have changed significantly over the longer time frame. In particular, the cyanobacteria that decreased 778-fold immediately following the invasion of the zebra mussel (Smith et al. 1998) appear to have staged an irregular recovery with populations being high in some years. Here, we analyze changes in summertime phytoplankton composition during the 1993–2005 period to determine the environmental correlates of variable phytoplankton composition in the presence of zebra mussels.

Materials and Methods

Phytoplankton biovolume and dominance based on percent biovolume of major taxonomic groups were analyzed for 1993–2005. In all years, this analysis was performed for the late July through early September period when cyanobacteria are most abundant (Marshall 1988; Smith et al. 1998). The methods and cell count data for the 1993–1996 period are reported in Smith et al. (1998). The 1995–1996 samples had cell counts only of major taxonomic groups. These samples were recounted so that the biovolume of each group could be calculated (see below).

During 1997–2005, surface water samples were collected weekly from Rhinecliff, located at river km 144 in the freshwater tidal section of the Hudson River (Cole and Caraco 2006). Five samples were taken, at approximately weekly intervals, during the late summer period in each year. Sampling and preservation techniques follow the procedure for the 1993–1996 period (Smith et al. 1998). Briefly, 1-l phytoplankton samples were preserved with 1% acid Lugol's solution within 2 h of collection (Wetzel and Likens 1991) and concentrated by settling. For the 1997–2005 cell counts, and 1995–1996 recounts, aliquots of concentrated samples were permanently mounted on microscope slides in Taft's (1978) syrup medium by the method of Stevenson (1984). Two replicate slides were made from a single 1-l sample from each of the 5 sampling dates, resulting in a total of 10 late summer phytoplankton sample slides. Variance in the sampling container was not found to be as significant as slide to slide differences (Marshall 1988). Cells were counted on an Olympus BH2 inverted microscope with Nomarski interference contrast. Rather than count a set number of taxa, we counted a set number of microscopic fields, as we were not concerned with the accuracy of densities of rare species. The phytoplankton from 10 fields were counted for each of the 10 slides, and then averaged for an annual late summer phytoplankton density value.

Algal biovolume was calculated as the product of cell numbers and cell volume for each taxon. For the dominant phytoplankton groups, which were counted to genus, we used the mean volume for each genus reported by Marshall (1988). For minor genera, most of which were diatoms, we used the mean sizes for four size classes: small pennate and centric diatoms ($< 12\ \mu m^2$) and large pennate and centric diatoms ($> 12\ \mu m^2$). For other minor taxa, including cholorophytes, there was little size differentiation within each major group, so we used the mean volumes reported by Marshall (1988). The dominant taxon of cyanobacteria was *Microcystis*, which we counted as colonies. We measured the area covered by each colony in each field counted using a stage micrometer. We observed that some *Microcystis* colonies had larger cells and some smaller, so we recognized two size classes. Small-celled colonies had on average 200 cells within a 12-μm^2 grid square, and large celled colonies had 100 cells within a 12-μm^2 grid square. These smaller and larger *Microcystis* cells were also described by Marshall (1988), though identified to species. We obtained cell volumes from mean values of Marshall's species groups. *Microcystis* biovolume was

TABLE 1. Mean (and SD) by year for selected physical characteristics for late-summer water samples, and the filtration rate of the zebra mussel expressed in m d^{-1} (ZMF, m^3 m^{-2} d^{-1}, with 90% CI shown). ZMF data are from Strayer and Malcom (2006) and Strayer (personal communication). Missing values are expressed as nd.

Year	Temperature (°C)	Flow (m^3 s^{-1})	Secchi (m)	ZMF (m d^{-1})	90% CI
1993	24.4 (1.07)	202 (101)	1.00 (0.10)	7.1	(nd)
1994	24.6 (2.16)	271 (150)	1.08 (0.15)	4.0	(2.1–6.2)
1995	25.7 (1.58)	99 (22)	1.28 (0.18)	4.4	(2.6–6.7)
1996	24.4 (0.80)	443 (390)	0.67 (0.19)	2.6	(0.3–6.1)
1997	24.2 (1.48)	246 (223)	0.96 (0.11)	7.0	(2.8–11.9)
1998	25.2 (0.53)	290 (171)	0.98 (0.13)	3.1	(1.4–5.0)
1999	25.2 (1.36)	166 (71)	1.09 (0.12)	2.8	(1.1–4.6)
2001	26.0 (0.84)	243 (152)	0.98 (0.21)	2.8	(1.1–4.6)
2002	25.8 (0.81)	297 (241)	1.26 (0.22)	5.5	(3.5–7.8)
2003	25.2 (1.92)	295 (84)	1.20 (0.27)	1.9	(0.5–4.0)
2004	24.0 (1.02)	324 (132)	1.06 (0.20)	2.1	(1.0–4.3)
2005	26.8 (1.14)	222 (44)	1.04 (0.17)	0.9	(0.4–1.8)

calculated as the product of the mean colony area (μm^2), cells per unit area (either 200 or 100 cells per 12 μm^2), and cell volume (μm^3).

Water samples were taken simultaneously with phytoplankton samples. Here we report only temperature and total and dissolved nutrients for the late summer period. Temperature was measured in the field using a YSI 3,000 T-L-C meter that was calibrated to a mercury thermometer. Water samples for dissolved nutrients (nitrate [NO_3], nitrite, ammonia, phosphate [PO_4], and silicate [SiO_3]) were filtered through Whatman GF/F filters within 2 h of collection and both total (nitrogen [TN] and phosphorus [TP]) and dissolved nutrients were preserved by acidification to pH 2 (Lampman et al. 1999). All nitrogen and phosphorus samples were measured on an Alpkem Autoanalyzer Flow III using standard Alpkem methods (Clakemas, Oregon). TN and TP were persulfate digested prior to analysis (Lampman et al. 1999). Dissolved silicate concentrations were measured colorimetrically using a Shimadzu UV-1601 UV-Visible Spectrophotometer (Wetzel and Likens 1991).

Each year during August, and also in June for some years, zebra mussel population counts were obtained from rocks, fine-grained sediments, and unionid mussels across a wide geographic range from river kilometers 99–248 (Strayer et al. 1996; Strayer and Malcom 2006). The vast majority of the population (> 95%) occurred upstream of our sampling station, although isolating zebra mussels upstream of our sites was not a major concern as the Hudson River is tidal with a rapid longitudinal coefficient of dispersion (Strayer et al. 1996; Strayer personal communication). To estimate per capita zebra mussel filtration rates (ZMF), the regression of Kryger and Riisgard (1988) was applied to zebra mussel counts and biomass for the Hudson River. Our filtration estimates assume a water temperature of 20°C to match published values (Strayer and Malcom 2006). In the temperature-filtration rate data for zebra mussels given by Lei et al. (1996), there is no statistical difference in filtration rate between zebra mussels adapted to 20°C and zebra mussels exposed to a range between 14°C and 26°C (Lei et al. 1996, Fig. 2). Since the mean temperatures for the period of analyses vary by a range of less than 3°C and fall within this optimal temperature range, temperature correction was unnecessary. Our calculated filtration rates agreed with direct measurements for Hudson River populations measured in the lab (Roditi et al. 1996) and field (Roditi et al. 1997).

River flow rates were obtained from daily water discharge values from the U.S. Geological Survey gauging station for Green Island, located immediately downstream of the confluence of the Mohawk and Hudson Rivers (Lampman et al. 1999), and average values from May 1 to September 30 were calculated.

Across years, the relationship of environmental variables to both the absolute phytoplankton biovolume and the relative abundance of phytoplankton groups were analyzed using Spearman Rank directional correlations. To further explore these relationships and compare to predictions from the literature we used both simple and multiple linear regressions. All analyses were performed in Stat View version 5.01.0 (SAS Institute, Inc.).

Results

A summary of key physical and chemical conditions, along with the ZMF for late summer at Rhinecliff during 1993–2005, are shown in Tables 1 and 2. Some variables remained in a narrow range among years. Mean temperature varied by only 12% from minimum to maximum, and TN varied by about 1.6-fold. Other variables showed larger variation. Freshwater flow varied nearly 5-fold among years, dissolved SiO_3 varied 10-fold, and ZMF varied 8.3-fold. At its highest rate (7.1 m d^{-1} in

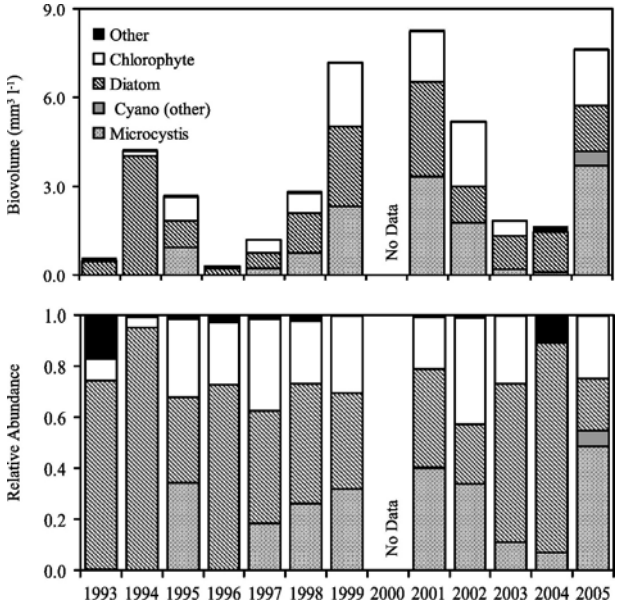

Fig. 1. Biovolume and percent of total phytoplankton biovolume for the late summer period from 1993 to 2005, by major taxonomic group.

1993) the entire water column would be filtered through zebra mussels every 1.1 d. At the slowest rate (0.85 m d^{-1} in 2005) this would take 9.4 d.

During the same time period (1993 through 2005), mean late-summer algal biovolume varied about 15-fold from 0.32 $mm^3\ l^{-1}$ in 1996 to 5.81 $mm^3\ l^{-1}$ in 2001 (Fig. 1). While biovolume for all years during the invasion were lower than preinvasion levels, during the invasion period biovolume was not trended in time (Spearman Rank; $p = 0.55$).

During 1993–2005, cyanobacteria comprised a highly variable fraction of total algal biovolume, from 52% in 2005 to 0% in three of the years (1993, 1994, and 1996; Fig. 1). In two additional years (2003 and 2004), cyanobacteria comprised less than 10% of total algal biovolume. The coefficient of variation (CV), as percent of biovolume, was 88%. The absolute biovolume of cyanobacteria was also highly variable and ranged from 0 to 2.6 $mm^3\ l^{-1}$ with a CV of 140% (Table 2). Diatoms have generally been the dominant in algal biovolume, averaging 58% of total over the 12 yr, and ranging from 25% (2005) to 97% (1994). Varying by less than 4-fold, diatoms have been the least variable major group. Chlorophytes, like cyanobacteria, averaged about 20% of the total and both ranged broadly among years. Chlorophytes were somewhat less variable than cyanobacteria. In only one year (2004) chlorophytes were not seen, and in only two additional years (1993 and 1994) they were less than 10% of total phytoplankton biovolume. The maximum (40%) was seen in 2002. Neither the percent composition nor the total biovolume of any of these groups showed a significant trend with time (Spearman Rank; $p > 0.05$).

Cyanobacteria were dominated by the genus *Microcystis*, which comprised 75–100% of cyanobacterial biomass in all years. Other genera observed included *Anabaena, Chroococcus*, and *Oscillatoria*. Centric and pennate forms of diatoms were about evenly represented, with most abundant centric genera including *Aulacoseira* and *Cyclotella*, and the most abundant pennate genera including *Navicula* and *Synedra*. Chlorophyte genera observed included *Coelastrum, Cosmarium, Crucigenia, Kirchneriella, Micractinium, Oocystis, Scenedesmus*, and *Staurastrum*. Cells designated as other included unidentifiable green spheres, *Cryptomonas* sp., and several types of dinoflagellates, the most abundant genera being *Glenodinium* and *Ceratium*.

The 8-fold variation in ZMF was not correlated with cyanobacterial dominance (Spearman Rank; $p = 0.69$), total cyanobacterial biovolume ($p = 0.56$), or the biovolume of *Microcystis* ($p = 0.2$). There is no evidence that cyanobacterial dominance increased with ZMF. Cyanobacterial dominance was highest in the year with the lowest ZMF and lowest in the year with the highest ZMF, and tends to

TABLE 2. Mean (and SD) for selected chemical variables for the same samples as in Table 1. All units are μM. Missing values are expressed as nd.

Year	NO_3	TN	PO_4	TP	SiO_3
1993	28.4 (22.6)	nd	0.76 (0.42)	2.73 (0.32)	26.8 (9.9)
1994	27.3 (14.6)	44.3 (5.0)	0.85 (0.31)	2.25 (0.69)	nd
1995	33.1 (3.6)	40.6 (12.7)	1.11 (0.10)	1.39 (0.44)	14.1 (8.5)
1996	36.5 (7.7)	59.8 (13.2)	1.12 (0.25)	1.71 (0.73)	70.5 (29.3)
1997	33.4 (4.8)	56.6 (2.6)	0.64 (0.13)	1.36 (0.27)	21.2 (6.5)
1998	22.5 (1.1)	56.8 (9.3)	0.59 (0.04)	1.32 (0.11)	11.7 (5.2)
1999	18.4 (0.8)	46.1 (1.9)	0.62 (0.07)	1.04 (0.05)	13.2 (3.8)
2001	19.5 (7.7)	39.0 (3.4)	0.65 (0.18)	1.90 (0.59)	11.3 (7.6)
2002	25.9 (4.9)	41.9 (2.0)	0.98 (0.12)	1.49 (0.10)	6.9 (0.8)
2003	34.7 (6.7)	44.7 (11.4)	0.60 (0.08)	1.50 (0.40)	47.0 (30.7)
2004	35.0 (8.1)	63.3 (9.3)	0.81 (0.23)	1.68 (0.25)	24.4 (18.9)
2005	14.9 (4.7)	39.8 (6.4)	0.61 (0.12)	1.38 (0.19)	8.3 (1.4)

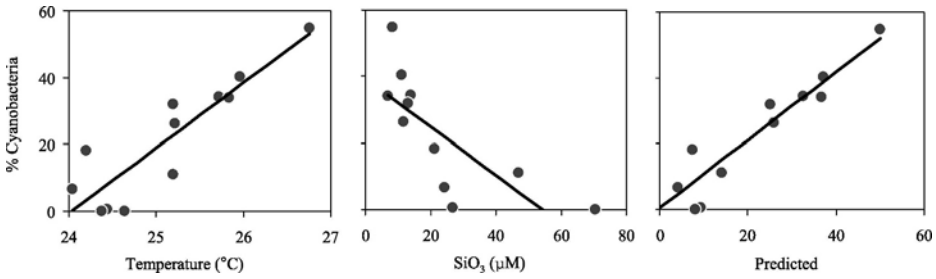

Fig. 2. Significant relationships between cyanobacterial biovolume as a percent of total phytoplankton (% cyanobacteria) and temperature (%Cyanobacteria = $-454 + 19.7 \times$ temp; $p < 0.0001$, $r^2 = 0.81$), dissolved silicate (%Cyanobacteria = $38 - 0.67 \times$ Si; $p = 0.0002$, $r^2 = 0.54$), and a multiple regressions with temperature and dissolved silicate predictors (%Cyanobacteria = $-348 + 15 \times$ temp $- 0.32 \times$ Si; $p < 0.0001$, $r^2 = 0.91$; adjusted $r^2 = 0.89$).

decrease with increasing ZMF. On the other hand, there are several years that fall off the apparent trend for which cyanobacterial dominance is low over a broad range of ZMF). *Microcystis* relative abundance and biovolume show nearly identical trends to total cyanobacteria, and neither is significant (Spearman Rank, $p > 0.1$).

There was a trend for higher cyanobacterial dominance with lower nutrient concentrations. These trends were significant for TN, NO_3, and SiO_3 using both Spearman Ranks ($p < 0.01$ for all) and linear regressions (TN $p < 0.03$, NO_3 $p < 0.005$, SiO_3 $p < 0.01$). Neither Spearman Rank nor linear regressions gave significant relationships ($p < 0.05$) between cyanobacterial dominance and either PO_4 or TP.

Over the wide range of observed hydrologic flows, neither cyanobacterial dominance, cyanobacterial biovolume, nor *Microcystis* biovolume was significantly related to flow (Spearman Rank, $p > 0.10$ for all). Cyanobacterial dominance, cyanobacterial biovolume, and *Microcystis* biovolume were all highly positively correlated with temperature (Spearman Rank, $p < 0.01$ for all) despite the small range in temperature among years. This relationship was linear (Fig. 2), and a simple regression between temperature and cyanobacterial dominance was highly explanatory and significant ($r^2 = 0.81$, $p < 0.001$). As diatoms make up most of the noncyanobacterial biovolume, diatom dominance was inversely correlated with temperature as well ($p < 0.01$). Temperature was also inversely related to TN (Spearman Rank, $p = 0.008$) and NO_3 (Spearman Rank, $p = 0.012$).

Interaction of Factors

Because our primary interest was in the possible effects of ZMF on cyanobacterial dominance, we also examined relationships using multiple linear regressions that combined ZMF with other factors. None of the nonsignificant correlations discussed above were improved by adding ZMF in a multiple regressions; e.g., the two independent variables, ZMF and TP, did not explain a significant amount of the variation on cyanobacterial dominance ($p = 0.24$; adjusted $r^2 = 0.11$).

For the variables that were significantly correlated with cyanobacterial dominance (TN, NO_3, SiO_3, temperature), adding ZMF as an additional independent variable did not in any case improve the adjusted r^2. In fact, for temperature, which explained only 80% of the variation in percent cyanobacteria in a linear regression, only SiO_3 improved the adjusted r^2 (Fig. 2).

Discussion

The invasion of the zebra mussel caused a massive phytoplankton decline in the Hudson River Estuary (Caraco et al. 1997). Following the zebra mussel invasion, phytoplankton biomass, based on year-round, weekly measurements of chlorophyll *a*, decreased and has generally remained low for a decade after invasion (Caraco et al. 2006; Cole and Caraco 2006), a result very similar with that for Lake Erie (Barbiero et al. 2006). The effect that the zebra mussel population has had on phytoplankton species composition is less certain. In the 2 yr immediately following the invasion, cyanobacteria were virtually eliminated from the Hudson River (Smith et al. 1998), a result consistent with laboratory studies that showed that the zebra mussel could both filter and remove several cyanobacterial taxa, including *Microcystis*, from the water column (Roditi et al. 1996; Bastviken et al. 1998; Baker and Levinton 2003). For the complete 12 yr period following the invasion, cyanobacteria has not consistently remained extremely low; rather, it has been highly variable in both total amount and as a fraction of phytoplankton biovolume. While there continue to be years where cyanobacteria have low biomass and represent less than 10% of the total algal biovolume (e.g., 1993–1994), during 2001 and 2005 cyanobacterial biomass was high and contributed over 45% of the total late summer algal

biomass. It is clear that in rivers as in lakes (Raikow et al. 2004) the presence of zebra mussels do not necessarily have a uniform effect on cyanobacterial dominance.

Although there was a tendency for increased cyanobacterial abundance with time (Fig. 1), this increase was not significant. Our data does not suggest that there was strong selection over time for less palatable cyanobacteria relative to other phytoplankton groups. The effect of zebra mussels also did not strongly depend on among year variation in the intensity of ZMF. ZMF in conjunction with time, physical variables, or nutrient conditions did not indicate a significant effect of grazing on phytoplankton composition.

We initially hypothesized that ZMF could have a large negative effect on cyanobacterial relative abundance (Smith et al. 1998), while others have indicated a potential positive effect (Vanderploeg et al. 1995). The lack of response of cyanobacterial abundance to ZMF might be expected based on the high TP in the Hudson (Table 2). In a study comparing zebra mussel effects in 61 Michigan lakes, Raikow et al. (2004) found that zebra mussels were associated with greater dominance of *Microcystis* only for lakes with TP < 0.8 μM. For lakes with TP equivalent to that found in the Hudson (> 0.8 μM), there was no significant relationship between the presence of zebra mussels and cyanobacterial dominance. On the other hand, in manipulative experiments of Sarnelle et al. (2005), higher zebra mussel abundance was associated with higher *Microcystis* dominance at moderate TP (0.3 μM) but not low TP (0.1 μM). The results in the Hudson are either inconsistent with this experimental result or suggest that zebra mussels cause a positive effect on *Microcystis* only at intermediate TP levels, but not at the high levels in the Hudson.

A somewhat unexpected result of our study is that temperature was highly correlated to the variation in cyanobacterial dominance among years (Fig. 2). This is surprising because mean late summer temperatures varied by only 3°C among years. It is hard to know if we are seeing a correlate of some factor related to temperature or a functional relationship; e.g., the lower nitrogen associated with high temperatures could have played a role in selecting against diatoms and for cyanobacteria with the capacity to fix nitrogen. On the other hand, the stronger relationship between cyanobacteria and temperature as compared to the relationship with TN, NO_3, or SiO_3 and the relatively high nutrient concentrations even in warm years as compared to half-saturation for phytoplankton uptake (Huszar and Caraco 1998) suggest that temperature could have a role independent of nutrients in controlling cyanobacterial dominance. Because in all years temperature was high and among year temperature differences were small, we do not believe temperature affected cyanobacteria dominance due to the direct effect of higher temperatures on cyanobacterial growth (e.g., Verspagen et al. 2006) or ZMF (Reeders and DeVaate 1990; Fanslow et al. 1995; Lei et al 1996). We hypothesize that the role of elevated temperature may be to cause greater frequency of transient microstratification. This microstratification could increase overall growth of phytoplankton in well mixed, light-limited systems like the Hudson (Cole et al. 1992; Howarth et al. 1996) and select for more buoyant groups of phytoplankton.

During transient, shallow stratification, phytoplankton in well mixed turbid systems can be relieved of light limitation and increase in growth substantially. This increased growth can deplete nutrients, and nitrogen and silicon depletion can play a role in decreasing diatom dominance and increasing cyanobacterial dominance. Large diatoms that dominate in the Hudson can rapidly sink out of surface waters making them subject to greater light limitation and, when zebra mussels are present, high benthic grazing. *Microcystis*, on the other hand, is highly buoyant. This high buoyancy could temporarily keep *Microcystis* colonies in surface waters where they could overcome intense light limitation and evade benthic grazers. The period of microstratification also could be long enough for *Microcystis* colonies to become large and render them resistant to grazing once the water column mixes again. Although we do not have the long-term high intensity temperature measurements to directly test this hypothesis, we have seen occasional, small (1–2°C) deflections in temperature profiles during warm low-wind weather (Raymond et al. 1997; MacIntyre et al. 2002). It is also true that some *Microcystis* blooms in the Hudson form visible surface slicks consisting of extremely large colonies. This hypothesis is consistent with the data and models of Huisman et al. (2004) and empirical work of Sullivan (1991).

Cyanobacterial blooms, especially of potentially toxic taxa such as *Microcystis*, can be associated with degradation of waters for recreation and drinking water supply. The regulation of cyanobacterial dominance and abundance are important questions for scientists and managers of water resources (Smith et al. 2002; Downing et al. 2001). For the Hudson, the large among year variation in the dominance and abundance of *Microcystis* is not correlated to phosphorus concentrations or to filtration by the zebra mussel. The strong association of cyanobacterial dominance and abundance with small increases in water temperature is intriguing. The temperature of the Hudson River has

increased over the past century (Ashizawa and Cole 1994), as have other water bodies including lakes and estuaries (Magnuson et al. 2000; Nixon et al. 2004), and these temperature increases are likely to occur into the next century. We believe that the effect of these temperature increases on cyanobacteria will vary greatly across systems with different nutrient, benthic grazing, and stratification regimes.

Acknowledgments

We thank David Fischer, Lane Smith, and Heather Malcom for technical support, and David Strayer and two anonymous reviewers for comments on the manuscript. We thank David Strayer also for the use of unpublished zebra mussel data. Financial support was provided in part by the National Science Foundation grant DEB-0075265 and grants from the Hudson River Foundation. This is a contribution to the Institute of Ecosystem Studies and to the Hudson River National Estuarine Research Reserve.

Literature Cited

Ashizawa, D. and J. J. Cole. 1994. Long-term temperature trends of the Hudson River: A study of historical data. *Estuaries* 17:166–171.

Baker, S. M. and J. S. Levinton. 2003. Selective feeding by three native North American freshwater mussels implies food competition with zebra mussels. *Hydrobiologia* 505:97–105.

Baker, S. M., J. S. Levinton, J. P. Kurdziel, and S. E. Shumway. 1998. Selective feeding and biodeposition by zebra mussels and their relation to changes in phytoplankton composition and seston load. *Journal of Shellfish Research* 17:1207–1213.

Barbiero, R. P., D. C. Rockwell, G. J. Warren, and M. L. Tuchman. 2006. Changes in spring phytoplankton communities and nutrient dynamics in the eastern basin of Lake Erie since the invasion of *Dreissena* spp. *Canadian Journal of Fisheries and Aquatic Sciences* 63:1549–1563.

Bastviken, D. T. E., N. F. Caraco, and J. J. Cole. 1998. Experimental measurements of zebra mussel (*Dreissena polymorpha*) impacts on phytoplankton community composition. *Freshwater Biology* 39:375–386.

Caraco, N. F., J. J. Cole, 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.

Caraco, N. F., J. J. Cole, and D. L. Strayer. 2006. Top down control from the bottom: Regulation of eutrophication in a large river by benthic grazing. *Limnology and Oceanography* 51: 664–670.

Cole, J. J. and N. F. Caraco. 2006. Primary production and its regulation in the tidal-freshwater Hudson River, p. 107–121. *In* J. Levinton and J. Waldman (eds.), The Hudson River Estuary. Cambridge University Press, New York.

Cole, J. J., N. F. Caraco, and B. L. Peierls. 1992. Can phytoplankton maintain a positive carbon balance in a turbid, fresh-water, tidal estuary? *Limnology and Oceanography* 37:1608–1617.

Cooper, J. C., F. R. Cantelmo, and C. E. Newton. 1988. Overview of the Hudson River estuary. *American Fisheries Society Monograph* 4:11–24.

Downing, J. A., S. B. Watson, and E. McCauley. 2001. Predicting cyanobacteria dominance in lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1905–1908.

Effler, S. W. and C. Siegfried. 1998. Tributary water quality feedback from the spread of zebra mussels: Oswego River, New York. *Journal of Great Lakes Research* 24:453–463.

Fanslow, D. L., T. F. Nalepa, and G. A. Lang. 1995. Filtration rates of the zebra mussel (*Dreissena polymorpha*) on natural seston from Saginaw Bay, Lake Huron. *Journal of Great Lakes Research* 21:489–500.

Gardner, W. S., J. F. Cavaletto, T. H. Johengen, J. R. Johnson, R. T. Heath, and J. B. Cotner. 1995. Effects of the zebra mussel, *Dreissena polymorpha*, on community nitrogen dynamics in Saginaw Bay, Lake Huron. *Journal of Great Lakes Research* 21: 529–544.

Heath, R. T., G. L. Fahnenstiel, W. S. Gardner, J. F. Cavaletto, and S. J. Hwang. 1995. Ecosystem-level effects of zebra mussels (*Dreissena polymorpha*): An enclosure experiment in Saginaw Bay, Lake Huron. *Journal of Great Lakes Research* 21:501–516.

Holland, R. E. 1993. Changes in planktonic diatoms and water transparency in Hatchery Bay, Bass-Island area, western Lake Erie since the establishment of the zebra mussel. *Journal of Great Lakes Research* 19:617–624.

Howarth, R. W., R. Schneider, and D. Swaney. 1996. Metabolism and organic carbon fluxes in the tidal freshwater Hudson River. *Estuaries* 19:848–865.

Huisman, J., J. Sharples, J. M. Stroom, P. M. Visser, W. E. A. Kardinaal, J. M. H. Verspagen, and B. Sommeijer. 2004. Changes in turbulent mixing shift competition for light between phytoplankton species. *Ecology* 85:2960–2970.

Huszar, V. and N. F. Caraco. 1998. The relationship between phytoplankton composition and physical chemical variables: A comparison of taxonomic and morphological approaches in six temperate lakes. *Freshwater Biology* 40:679–696.

Johengen, T. H., T. F. Nalepa, G. L. Fahnenstiel, and G. Goudy. 1995. Nutrient changes in Saginaw Bay, Lake Huron, after the establishment of the zebra mussel (*Dreissena polymorpha*). *Journal of Great Lakes Research* 21:449–464.

Kryger, J. and H. U. Riisgard. 1988. Filtration-rate capacities in 6 species of European fresh-water bivalves. *Oecologia* 77:34–38.

Lampman, G. C., N. F. Caraco, and J. J. Cole. 1999. Spatial and temporal patterns of nutrient concentration and export in the tidal Hudson River. *Estuaries* 22:285–296.

Lavrentyev, P. J., W. S. Gardner, J. F. Cavaletto, and J. R. Beaver. 1995. Effects of the zebra mussel (*Dreissena polymorpha* Pallas) on protozoa and phytoplankton from Saginaw Bay, Lake Huron. *Journal of Great Lakes Research* 21:545–557.

Lei, J., B. S. Payne, and S. Y. Wang. 1996. Filtration rates of the zebra mussel, *Dreissena polymorpha. Canadian Journal of Fisheries and Aquatic Sciences* 53:29–37.

Limburg, K. E., M. A. Moran, and W. H. McDowell. 1986. The Hudson River Ecosystem. Springer Verlag, New York.

MacIntyre, S., J. R. Romero, and G. W. Kling. 2002. Spatial-temporal variability in surface layer deepening and lateral advection in an embayment of Lake Victoria, East Africa. *Limnology and Oceanography* 47:656–671.

MacIsaac, H. J. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. *American Zoology* 36:287–299.

Magnuson, J. J., D. M. Robertson, B. J. Benson, R. H. Wynne, D. M. Livingstone, T. Arai, R. A. Assel, R. G. Barry, V. Card, E. Kuusisto, N. G. Granin, T. D. Prowse, K. M. Stewart, and V. S. Vuglinski. 2000. Historical trends in lake and river ice cover in the Northern Hemisphere. *Science* 289:1743–1746.

Marshall, G. 1988. Seasonal phytoplankton composition and concentration patterns within the Hudson River. Hudson River Foundation, Report No. 018/86b/011. New York.

Nixon, S. W., S. Granger, B. A. Buckley, M. Lamont, and B. Rowell. 2004. A one hundred and seventeen year coastal water temperature record from Woods Hole, Massachusetts. *Estuaries* 27:397–404.

Pires, L. M. D., R. R. Jonker, E. Van Donk, and H. J. Laanbroek. 2004. Selective grazing by adults and larvae on the zebra mussel (*Dreissena polymorpha*): Application of flow cytometry to natural seston. *Freshwater Biology* 49:116–126.

RAIKOW, D. F., 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. *Limnology and Oceanography* 49:482–487.

RAYMOND, P. A., N. F. CARACO, AND J. J. COLE. 1997. Carbon dioxide concentration and atmospheric flux in the Hudson River. *Estuaries* 20:381–390.

REEDERS, H. H. AND A. B. DEVAATE. 1990. Zebra mussels (*Dreissena polymorpha*) - a new perspective for water-quality management. *Hydrobiologia* 200:437–450.

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.

RODITI, H. A., D. L. STRAYER, AND S. FINDLAY. 1997. Characteristics of zebra mussel (*Dreissena polymorpha*) biodeposits in a tidal fresh water estuary. *Archiv für Hydrobiologie* 140:207–219.

SARNELLE, O., A. E. WILSON, S. K. HAMILTON, L. B. KNOLL, AND D. F. RAIKOW. 2005. Complex interactions between the zebra mussel, *Dreissena polymorpha*, and the harmful phytoplankton *Microcystis aeruginosa*. *Limnology and Oceanography* 50:896–904.

SMITH, V. H., J. SIEBER-DENLINGER, F DENOYELLES, S. CAMPBELL, S. PAN, S. J. RANDTKE, G. T. BLAIN, AND V. A. STRASSER. 2002. Managing taste and odor problems in a eutrophic drinking water reservoir. *Lake and Reservoir Management* 18:319–323.

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). *Journal of Plankton Research* 20:1567–1579.

STEVENSON, R. J. 1984. Procedures for mounting algae in a syrup medium. *Transactions of the American Microscopical Society* 103: 320–321.

STRAYER, D. L., N. F. CARACO, J. J. COLE, S. FINDLAY, AND M. L. PACE. 1999. Transformation of freshwater ecosystems by bivalves - A case study of zebra mussels in the Hudson River. *Bioscience* 49: 19–27.

STRAYER, D. L. AND H. M. MALCOM. 2006. Long-term demography of a zebra mussel (*Dreissena polymorpha*) population. *Freshwater Biology* 51:117–130.

STRAYER, D. L., J. POWELL, P. AMBROSE, L. C. SMITH, 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. *Canadian Journal of Fisheries and Aquatic Sciences* 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 costal waters. *Canadian Journal of Fisheries and Aquatic Sciences* 48:2276–2284.

TAFT, C. E. 1978. Mounting medium for freshwater plankton. *Transactions of the American Microscopical Society* 97:263–264.

THORP, J. H. AND A. F. CASPER. 2002. Potential effects on zooplankton from species shifts in planktivorous mussels: A field experiment in the St Lawrence River. *Freshwater Biology* 47: 107–119.

ULANOWICZ, R. E. AND J. H. TUTTLE. 1992. The trophic consequences of oyster stock rehabilitation in Chesapeake Bay. *Estuaries* 15:298–306.

VANDERPLOEG, H. A., J. R. LIEBIG, W. W. CARMICHAEL, M. A. AGY, T. H. JOHENGEN, G. L. FAHNENSTIEL, AND T. F. NALEPA. 2001. Zebra mussel (*Dreissena polymorpha*) selective filtration promoted toxic *Microcystis* blooms in Saginaw Bay (Lake Huron) and Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1208–1221.

VANDERPLOEG, H. A., T. F. NALEPA, D. J. JUDE, E. L. MILLS, K. T. HOLECK, J. R. LIEBIG, I. A. GRIGOROVICH, AND H. OJAVEER. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1209–1228.

VANDERPLOEG, H. A., J. R. STRICKLER, J. R. LIEBIG, T. F. NALEPA, G. L. FAHNENSTIEL, W. S. GARDNER, J. F. CAVALETTO, D. L. FANSLOW, AND T. H. JOHENGEN. 1995. Do zebra mussels promote blue-green and metaphyton blooms in Saginaw Bay, and do these blooms affect the mussels?, p. 131. *In* 38th Conference of the International Association for Great Lakes Research, East Lansing, Michigan.

VERSPAGEN, J. M. H., J. PASSARGE, K. D. JOHNK, P. M. VISSER, L. PEPERZAK, P. BOERS, H. J. LAANBROEK, AND J. HUISMAN. 2006. Water management strategies against toxic *Microcystis* blooms in the Dutch delta. *Ecological Applications* 16:313–327.

WETZEL, R. G. AND G. E. LIKENS. 1991. Limnological Analyses, 2nd edition. Springer-Verlag, New York.

SOURCE OF UNPUBLISHED MATERIALS

STRAYER, D. personal communication. Institute of Ecosystem Studies, 65 Sharon Turnpike, Millbrook, New York 12545.

Received, January 26, 2006
Revised, September 7, 2006
Accepted, September 20, 2006