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Response of Heterotrophic Planktonic Bacteria to the Zebra Mussel Invasion of the Tidal Freshwater Hudson River

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ABSTRACT

Invasions of aquatic ecosystems by exotic bivalves are known to cause dramatic changes in phytoplankton and some other groups, but their effect on the microbial component is unknown. The invasion of the tidal freshwater Hudson River by the exotic zebra mussel (*Dreissena polymorpha*) has caused large changes in several components of the Hudson's food web. Planktonic bacteria in the tidal freshwater Hudson are a major part of the food web, and mediate important processes in the carbon budget. We used a long-term data set, spanning four years prior to the zebra mussel (ZM) invasion and four years post-invasion, to describe ZM effects on planktonic bacteria. Small and meso-scale experiments were conducted to specifically examine direct consumption of bacteria by ZM, as well as effects on protozoans. Bacterial abundances in the Hudson have increased roughly 2× since the ZM arrived, making it clear that direct consumption by *Dreissena* is a minor process. Experiments show that ZM do not remove bacteria from Hudson River water, but are very effective at clearing flagellated protozoans, the major predator of bacteria. The observed changes in bacterial abundance have not been accompanied by equally large changes in bacterial productivity, suggesting growth is primarily limited by carbon supply. Bacterial production has not declined despite a dramatic decline of phytoplankton, confirming previous suggestions that bacteria and phytoplankton are not strongly linked in the Hudson. As a result of the increase in bacterial abundance and removal of phytoplankton, the absolute and relative contributions of bacterial carbon to living particulate organic carbon (POC) standing stocks have increased dramatically. The maintenance of the bacterial component of the Hudson River's food web may be one mechanism whereby consumers are ''insulated'' from effects of zebra mussel consumption of phytoplankton carbon.

Introduction

Invasion of ecosystems by exotic species can have a wide range of effects, including competitive exclusion of native species and alteration of biogeochemical processes [23]. Many aquatic ecosystems seem particularly suspectible to dramatic changes following invasions or declines in benthic bivalve filter-feeders [3, 10], because these organisms have the capacity to filter a large fraction of the water column on a daily basis. The zebra mussel (*Dreissena polymorpha*) has

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spread rapidly over eastern North America over the past decade. It reaches abundances sufficient to cause significant changes in phytoplankton, and, ultimately, other ecosystem components [11, 16]. In the tidal freshwater Hudson River, zebra mussels have caused massive declines in chlorophyll *a* concentrations, with post-invasion summer averages only 20% of pre-invasion values [2]. Our 10-y record of bacterial abundance and productivity provides an excellent opportunity to explore whether zebra mussels (ZM) can, directly or indirectly, alter the microbial component of the Hudson River food web.

Planktonic bacteria are a major biomass component in the water column of the Hudson [6, 15]. They are almost certainly responsible for the bulk of water column respiration in the Hudson, where planktonic respiration metabolizes at least 25% of incoming allochthonous carbon [12]. Therefore, if an invasive, benthic filter-feeding animal can cause changes in planktonic bacteria, we would predict such alterations to spread to over ecosystem-level processes.

The direction of change in bacteria following ZM invasion depends on which of the three mechanisms is presumed to be the primary control on bacterial abundance. The simplest prediction is that ZM will filter bacteria from the water column, leading to an obvious reduction in cell numbers. Several lab experiments, and at least one field study, have shown that ZM can harvest large bacterial cells [4]. Most of this work, however, has used cultured bacteria, which are much larger (~1 to 3 µm in length) than most native bacteria (<1 µm). The range in size is critical for determining whether direct removal will occur, because ZM filtration efficiency drops sharply in the range 0.5 to 3 µm [20].

The second plausible mechanism controlling bacterial biomass is the carbon sources supporting heterotrophic bacterial growth. In many aquatic systems, bacterial production is tightly linked to phytoplankton carbon fixation, presumably because bacteria depend on phytoplankton exudation of fixed carbon as a growth substrate [14]. In the Hudson, the high rates of bacterial secondary production actually exceed phytoplankton primary production. There is only a weak correlation between bacterial and algal abundance or productivity [5]. Based on these inferences, we concluded, previously, that there was no strong link between planktonic bacteria and algae in the Hudson. However, we had no direct, supporting experimental evidence. The sharp decline in phytoplankton biomass caused by ZM provides a unique, whole-system manipulation directly relevant to examining the strength of the bacterial–algal linkage in the Hudson. Since ZM are capable of removing organic particles found in the Hudson River [19], and bacteria are at least potentially reliant on allochthonous carbon, ZM removal of detrital POC provides another whole-system manipulation of carbon resources. If either phytoplankton or detrital POC are critical to bacterial metabolism, we would expect bacterial abundance and production to decline following ZM invasion.

Lastly, planktonic bacteria are often controlled by protozoan grazers [8, 17], so ZM effects on grazers may well affect bacterial abundances. Based on previous studies in the Hudson [22], we know that flagellated protozoans are often, but not exclusively, the major consumers of planktonic bacteria. If grazing pressure on bacteria has declined due to direct or indirect ZM effects on protozoan or other grazers, we would predict an increase in bacterial abundance.

The ZM invasion of the Hudson provides (1) a real world test of various factors that might be controlling bacteria, and (2) a quantitatively significant shift in carbon flows as the bacterial community undergoes changes in activity or abundance. In this paper, we use a 10-year record (four before, one transitional, and five after ZM) of bacterial abundance, production and ancillary data, together with a series of manipulative experiments, to examine changes in bacteria and draw inferences about underlying mechanisms.

Methods

Site Description

The tidal freshwater portion of the Hudson River estuary reaches from the Federal Dam at Troy, NY, to approximately the Tappan Zee (Fig. 1), a distance of ~150 km. field sampling has two components: bi-weekly collections at a site near Kingston, NY, and a series of six stations (Fig. 1) sampled bi-monthly. All sampling is restricted to the ice-free season, roughly April to December. In the field, oxygen and temperature are measured with a Yellow Springs Inst. (YSI) meter and water samples are collected for seston, chlorophyll, DOC, bacterial abundance and production, and micro- and macrozooplankton abundances, using previously published methods [6, 18].

The ZM was first detected in the Hudson in the spring of 1991, near Catskill, NY [21], and spread rapidly up- and downriver, aided by a secondary invasion via the Mohawk River in 1992. River wide densities had increased to 4,000 individuals/m^2 by fall of 1992, with accumulations on hard substrate as high as 17,000/m^2. Abundances vary substantially along the river, primarily as a function of hard substrate availability. Highest densities are found between Kingston, NY (RKM = 152), and Castleton (RKM = 228) [21].

Experiments

Two scales of experimental manipulation were conducted to examine, in detail, the effects of varying ZM densities on the micro-

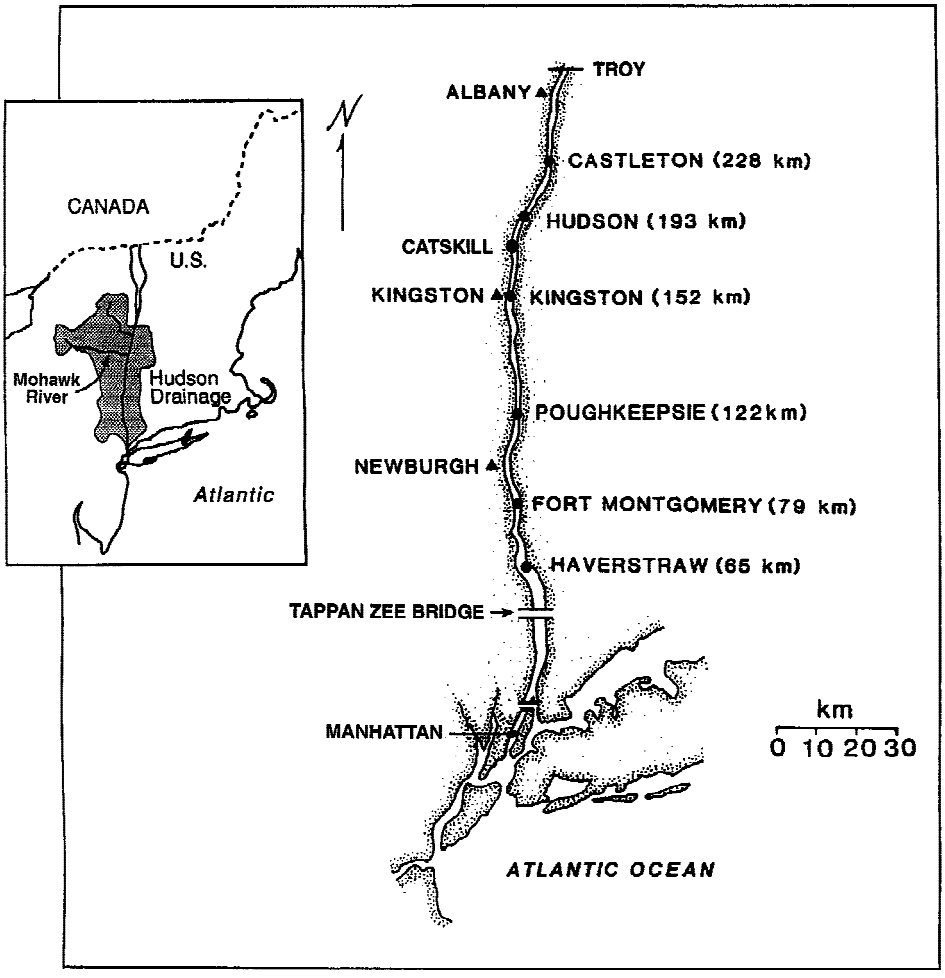

Fig. 1. Map of Hudson River sampling stations in the tidal freshwater portion of the estuary. Numbers in parentheses are km north of Battery Park in New York City.

bial community. Small, re-circulating chambers [19] with ZM densities sufficient to clear the volume once 1 were used to examine very short-term (<4 h) effects on bacterial and protozoan abundances. Experiments included freshly-collected Hudson River water, with ambient concentrations of particles, and were conducted in the dark at room temperature (~22°C). These experiments were intended to look only at direct effects, because there is insufficient time for significant growth of either bacteria or grazers. The potential grazing pressure by ZM on planktonic microbes was intentionally much higher than in the river (clearance approximately once day^{-1} versus once h^{-1} in microcosms), to maximize the likelihood that we could observe direct removal of bacterial cells if this occurred.

A longer-term, meso-scale experiment, using 100-l containers and various ZM densities, was conducted to look at potentially important, indirect ZM effects on planktonic microbes, phytoplankton, and zooplankton. ZM abundances on plastic (PVC) plates suspended in the tanks were either zero or about 30 animals $tank^{-1}$, which provides a filtration capacity of 0 to 100% day^{-1}. Tanks monitored for microbial processes were covered with shade cloth so that light levels were ~10% of ambient. There were three replicate tanks in each treatment. Tanks were filled with Hudson River water collected near Poughkeepsie, NY, in late June, 1996, and tanks were mixed manually 3× day^{-1} to mimic tidal resuspension.

Sample Analyses

Total suspended matter was collected on ashed, preweighed, glass-fiber filters (Whatman 934AH, 1.5 µm pore size). Three filters were prepared from each of three replicate water bottles. Dry mass was determined after drying at 70°C overnight, and ash-free dry mass after burning at 450°C for 4 h. Particulate organic matter was estimated as loss on ignition. Carbon was assumed to constitute 45% of organic matter.

Water samples for bacterial abundance were fixed in the field, using a buffered, 1% formaldehyde solution. Bacterial abundance was estimated from two filters for each sampling using acridine orange direct counts. Bacterial production was estimated from the rate at which [methyl-^{3}H]thymidine ([^{3}H]TdR) was incorporated into DNA, using techniques and assumptions described in Findlay et al. [5]. Heterotrophic flagellate abundance was estimated from direct counts of proflavine-stained samples collected on 1.0 µm Nuclepore filters. Two filters from each sampling were prepared upon arrival at the lab. The samples were stained with proflavine

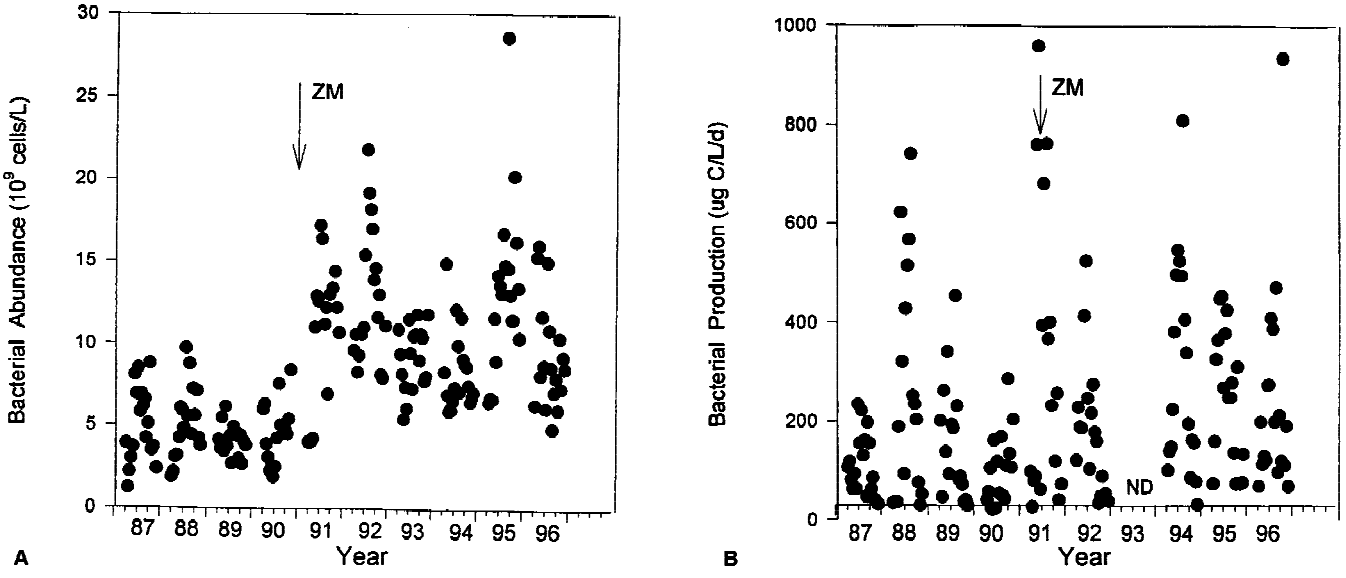

Fig. 2. Time series (bi-weekly) of bacterial abundance **(A)** and production **(B)** at a station near Kingston, NY. Arrow indicates first detection of ZM in the Hudson River.

(0.033%, 4 µl ml^{-1} sample) for two min, fixed with 1% glutaraldehyde for 2 minutes, then filtered under low vacuum pressure.

Results

Field Studies

Bacterial abundances were roughly 2× higher (Fig. 2) at the station near Kingston, NY, in the 5 y (1992 through 1996) after the ZM reached peak density. Annual average abundances prior to ZM (1987 through 1990) were 4.7×10^9 cells L^{-1}; densities since 1992 have averaged 10.7×10^9 cells L^{-1}. We treat 1987 through 1990 as pre-ZM years for all subsequent analyses. The period 1992 through 1996 served as the post-ZM data set. Based on the decline in chlorophyll *a* and the peak in river wide ZM density [21], both of which occurred in 1992, we treat 1991 as a ''transition'' year. Annual mean bacterial abundances differ significantly between the pre-ZM and post-ZM periods ($t = 5.0$, $p = 0.0015$). Even if we very conservatively include 1991 in the pre-ZM period, annual means still differ significantly ($t = 3.0$, $p = 0.017$).

The spatial patterns in the magnitude of change in bacterial abundance are consistent with regions known to have high vs low ZM densities [21]. Prior to ZM, there were no significant differences in bacterial abundance among stations (ANOVA, $p = 0.8$). Since 1992, overall densities have increased, and there is a strong and significant north–south gradient in abundance. For all stations, there has been a significant increase in cell densities (paired *t*-tests, $p < 0.05$), but the magnitude of change differs markedly. The four northernmost stations (Fig. 1) show, on average, a 100% increase in bacterial abundance, station 5 shows an 80% increase, and shows 20% the southernmost station (Fig. 3). The northern stations have the highest numbers of ZM, and have shown the greatest reduction in chlorophyll *a* [2]. The increases observed at the two southernmost stations could be due to cells from upriver rather than an *in situ* ZM effect.

Annual average production was 158 µg C^{-1} d^{-1} in y prior to 1991. It averaged 241 µg C^{-1} d^{-1} for the period 1992–1996. Consequently, the average turnover time for bacterial biomass has increased from 1.7 d prior to 1991 to 2.6 d since the ZM invasion. Moreover, the relationship between biomass and production has changed from a highly significant, although not very powerful, regression prior to 1991, to an insignificant relationship since the ZM invasion (Figs. 4A,B). The major change was an increase in standing stock accompanied by a relatively small increase in productivity. Low biomass values (<200 µg C^{-1}) are not evidence in the post-ZM pattern, although the seasonal cold temperatures are identical.

The contribution of bacterial carbon to standing stocks has changed markedly since the ZM invasion. Prior to ZM, bacterial carbon averaged ~100 µg C^{-1} (Fig. 5A). This was 10–20% of living microbial POC (bacterial plus algal car-

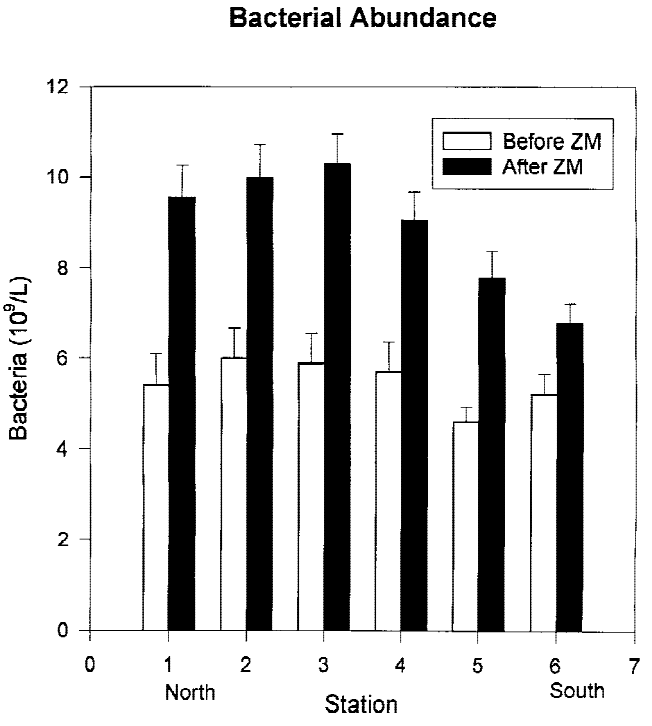

Fig. 3. Average bacterial abundance at stations ranging from north (RKM 228) to south (RKM 64) in years prior to ZM (1988 through 1990), compared to years since 1992. Station 3 is near Kingston, NY. Error bars are 1 SE. All pre–post comparisons are significant ($p < 0.05$).

bon). Since 1992, annual average bacterial carbon has ranged from 200 to 350 µg C^{-1}. This makes up as much as 75% of living POC (Fig. 5B). There was no significant relationship between bacterial abundance and chlorophyll *a* for either the period before or after the ZM invasion (r^2 = 1.6% pre-ZM, r^2 = 3.3% post-ZM). Relationships between bacterial production and particulate or dissolved organic carbon were not significant prior to or after the ZM invasion with r^2 less than 2% and *p* values greater than 0.25 in all cases.

Microcosm Experiments

Consistent with the increased abundances observed in the river, we found no evidence for direct removal of bacterial cells by ZM in either short- (intense grazing pressure) or medium-term experiments. Bacterial abundance at the start of two separate microcosm experiments was approximately 8 × 10^6 cells mL^{-1}, and did not decline significantly (Fig. 6) over a 4 h exposure to ZM filtration, even though the ZM abundance was such that the entire volume of the microcosm had been cleared 4×. Concurrent measures of chlorophyll *a* showed a 75% decline, indicating the ZM were actively filtering [1]. Our measures of abundance represent net changes, and there is some growth during microcosm experiments. Field estimates of turnover times averaged 0.7 d during water collection for microcosms. Therefore, during a 4 h microcosm experiment, there could have been ~25% increase in bacterial abundance. If we assume that a 25% increase was balanced by filtration (i.e., no net change in abundance), keeping in mind that our microcosm grazing pressures were 20× greater than ambient (once h^{-1} instead of once d^{-1}), we would conclude that, at most 1–2% of bacteria could be removed by direct filtration during a 4 h period, at realistic ZM densities.

In contrast to the stability in bacterial populations observed in both experiments, flagellate abundances declined to <10% of initial densities during the 4 h, indicating that they were efficiently removed by ZM filtering activity (Fig. 6).

Mesocosm experiments showed similar patterns: After 4 days, bacterial abundances were just as high in tanks with ZM as zero ZM controls (Fig. 7A), even though the populations of ZM were capable of clearing the entire volume in one day. The marked difference in chlorophyll *a* among treatments with and without ZM (means on day 4 were 0.1 µg L^{-1} ± 0.15 with ZM; 2.0 ± 1.2 without ZM) indicated high filtration rates. As before, direct consumption of native bacteria by ZM appears to have been minimal. Similar to the microcosm results, flagellate abundances, after 4 days, were almost an order of magnitude lower in ZM tanks, compared to controls (Fig. 7B). By day 8, bacterial abundances in ZM tanks were almost 2× higher consistent with the increase observed in the field, and may be explained by the lower population of heterotrophic flagellates. Flagellate abundances had converged by day 8, perhaps because increased macrozooplankton populations, in the absence of ZM, were reducing flagellate populations.

Both the micro- and mesocosm experiments show that Hudson River bacteria escaped direct ZM grazing, probably as a consequence of their small size, while their main grazers were highly susceptible to direct consumption by ZM. Our field data on flagellate abundances in the Hudson, itself, are inadequate to confirm or refute our hypothesis that ZM removal of flagellates has allowed bacterial abundance to increase. We have data on flagellate abundances for 1990, 1991, 1992, and 1996: Flagellate abundances in 1992 were only 15% lower (not statistically significant) than in 1990 or

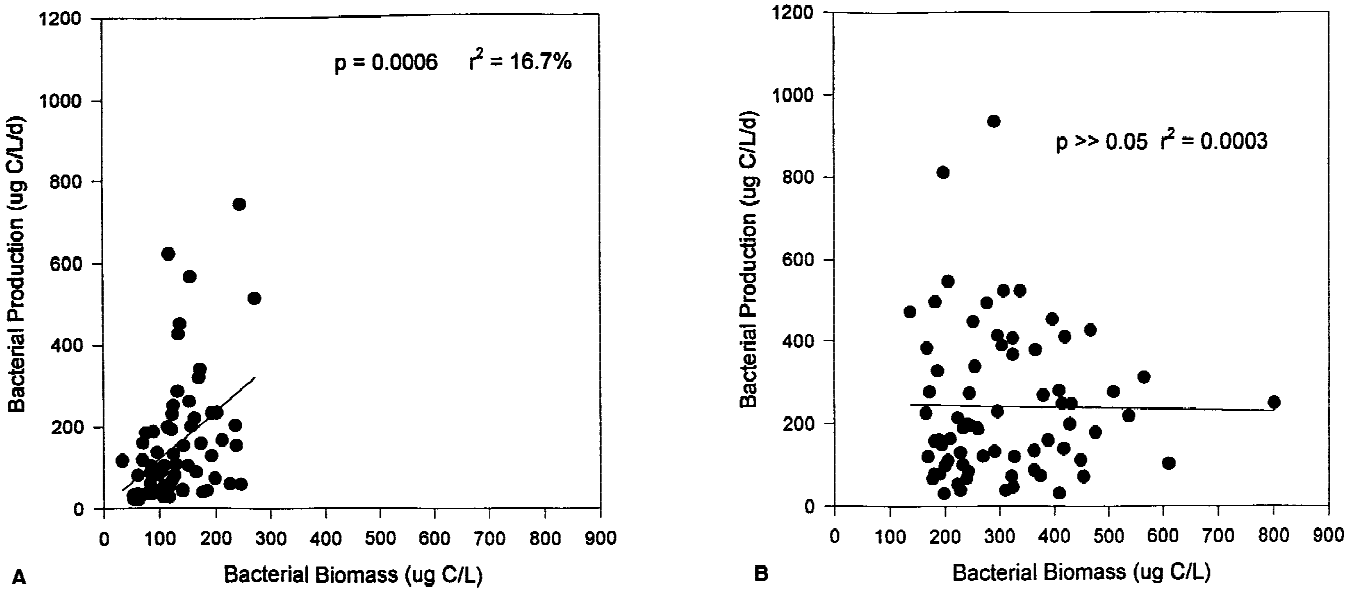

Fig. 4. Relationship between bacterial biomass and production in years before **(A)** and after **(B)** the ZM invasion.

1991; abundances in 1996 were actually slightly higher than 1990–1992. We do not, however, have a continuous record.

Discussion

Causative Factors

The large increase in bacterial abundance since the arrival of *Dreissena* could have been due to a wide range of environmental or methodological factors, including changes in temperature, organic carbon availability, grazing pressure, or enumeration techniques. We discount methodological explanations for two reasons: (1) the procedure and individual responsible for counting have not changed since 1987; and (2) bacterial abundances have not changed dramatically at the southernmost stations, where zebra mussels are absent, indicating there has been no change in counting efficiency.

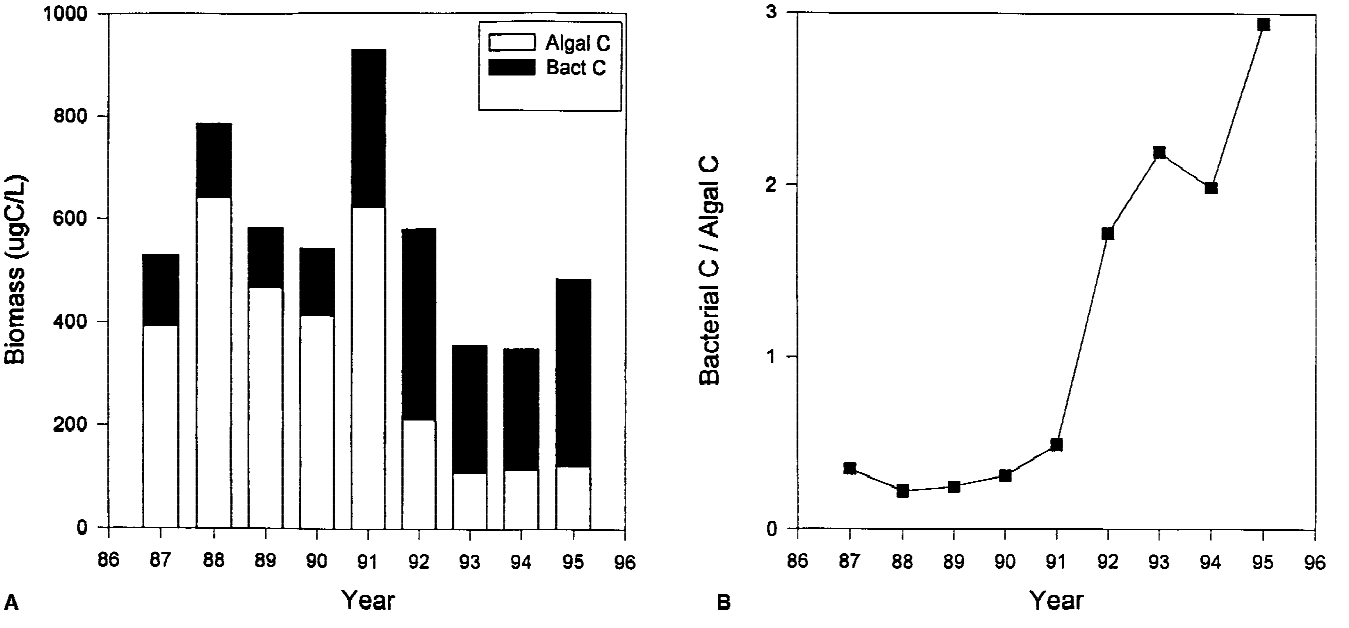

Fig. 5. Absolute **(A)** (μg C L^{-1}) and relative **(B)** standing stocks of planktonic bacteria and algae near Kingston, NY. Values are annual means for each year.

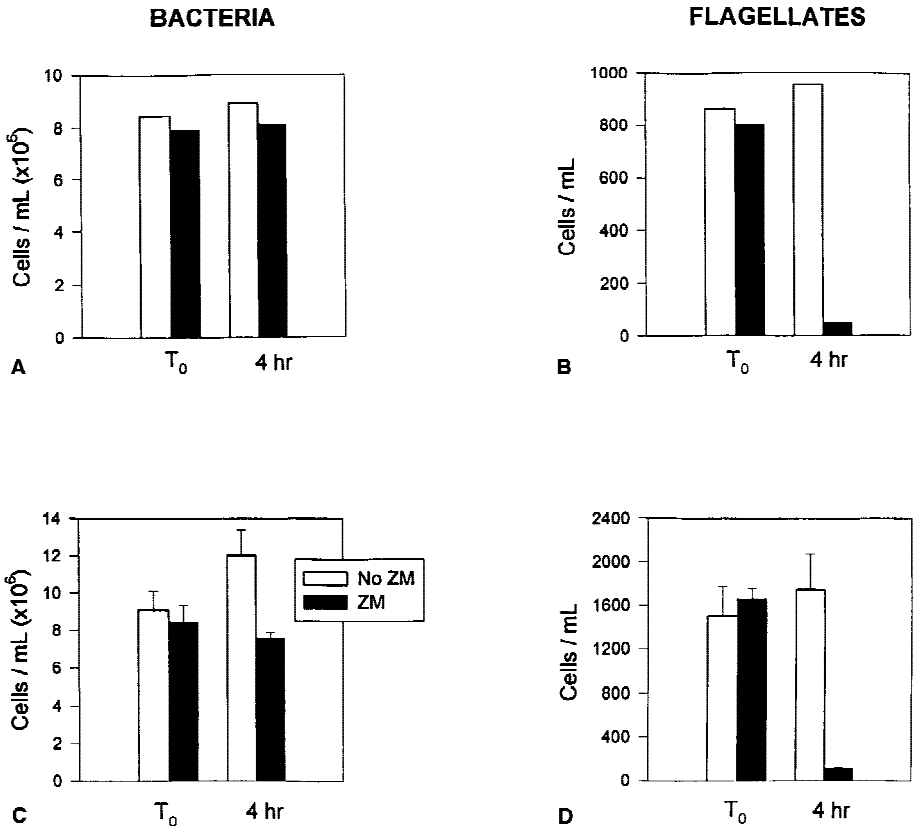

Fig. 6. Average abundances of bacteria **(A, C)** and flagellates **(B, D)** in microcosms with and without ZM. The top two panels represent unreplicated microcosms (August 1, 1996). Variability among subsamples within a microcosm were always <20% of the mean. Values in the bottom panels (C,D) are means (±1 SD) derived from duplicate microcosms (August 21, 1996).

We recognize the possibility that the 2× increase in cell abundance observed throughout much of the river may be counterbalanced by a 50% decrease in cell size. Unfortunately, the change in dimensions required to reduce cell biovolume by 50% is so small as to be undetectable using available technology. In 1987, we measured cell volumes monthly at our long-term station near Kingston, NY. We measured 100 cells month^{-1} over an annual cycle, totaling

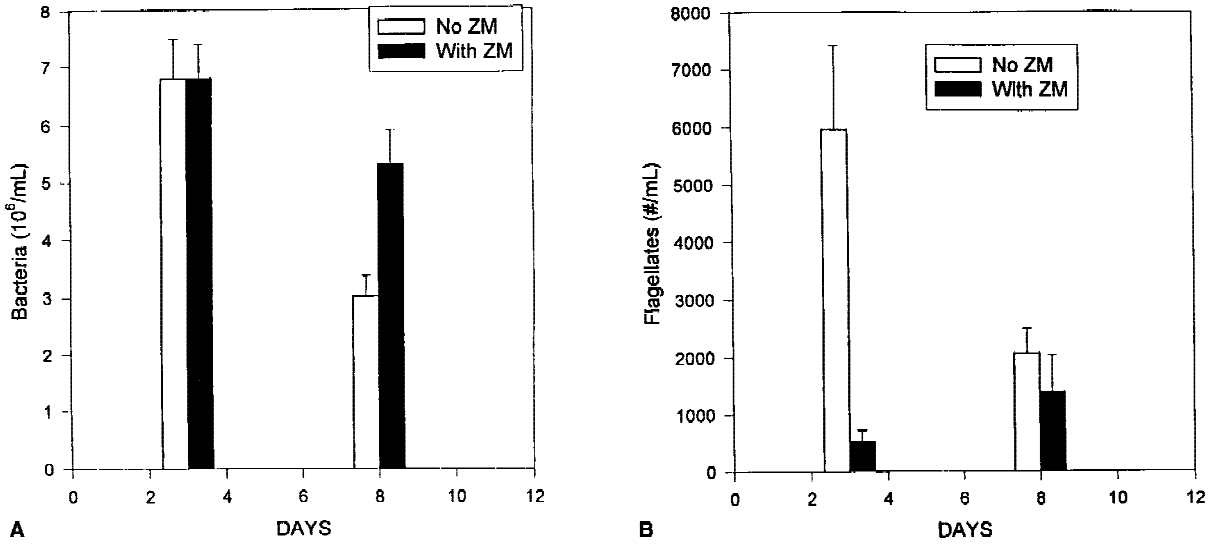

Fig. 7. Mesocosm bacteria **(A)** and heterotrophic flagellate **(B)** abundances after 3 and 8 d in the presence or absence of ZM. Values are means of triplicate mesocosms, with duplicate samples for each microcosm at each time point.

almost 1,000 cells. The resulting estimate of 0.14 μm^3 $cell^{-1}$ [5], is equivalent to a spherical diameter of 0.3 µm. A change in radius of 0.06 µm would decrease our estimated biovolumes and biomass by 50%, but such a change would have been undetectable by our experiments. We have assumed that cell volumes have remained unchanged, although we keep in mind the possibility that our post-ZM C $cell^{-1}$ conversions may be too high. In fact, since C $biovolume^{-1}$ conversions tend to increase for smaller cells, any undetected decrease in cell size will be partially compensated for by higher carbon:cell volume factors. Therefore, we do not believe we are badly overestimating bacterial biomass and carbon production by using the same conversion factors as we have in the past.

Simple physical factors, such as warmer temperatures or differences in freshwater flow, cannot be the explanation for the increase in bacterial numbers, since there was no consistent change in any of these variables in the years after 1991. Mean annual temperature and discharge were similar for the periods before and after ZM (*t*-tests, $p = 0.9$ for temperature, $p = 0.8$ for discharge).

Controls on Bacterial Dynamics

Of the three potential factors causing a change in bacterial abundance after the ZM invasion (direct consumption, carbon removal, or release from grazers), only a decline in grazing pressure could explain the observed increase in bacterial density. If direct consumption of bacterial cells or lower carrying capacity, due to removal of phytoplankton carbon, were important in affecting bacterial dynamic, we would expect decreases in abundance and production (not the increases actually observed). Moreover, both micro- and mesocosm results clearly show that direct removal of bacteria by ZM was negligible, even under artificially high filtration rates of once h^{-1}. These experiments confirm our hypothesis, based on body size: Hudson bacteria are not cleared by ZM, while flagellates are. In fact, densities of flagellates in realistic ZM filtration rates in the mesocosm experiments were only 10% of densities in the absence of ZM. The major consumers of planktonic bacteria in the Hudson River are heterotrophic nanoflagellates [22]. These organisms are well within the size class (1–3 µm) of particles ZM can remove at efficiencies approaching 100% [20].

Studies in the Great Lakes have also shown that small bacteria are relatively immune to clearance by ZM, although large bacteria suffer considerable mortality [4]. Experiments conducted with water and ZM collected from Lake Huron showed as much as 100% removal of large heterotrophic flagellates [13].

In contrast to the sketchy records for protozoans, we have a continuous and consistent record of rotifer and tintinnid abundance (two other likely bacterial grazers). Rotifer and tintinnid abundances in the Hudson have declined precipitously since arrival of ZM [18]. We estimate that rotifer grazing on bacteria can account for as much as 15% of total bacterial mortality d^{-1} [22]. These organisms are also in the size range we would expect to be susceptible to ZM filtration, and their well-documented decline in the Hudson adds credence to our belief that bacterial grazing pressure post-ZM is lower than prior to the invasion. The bulk of the field and experimental evidence, therefore, suggests that grazer release has been the major contributor to the increase in bacterial abundances observed in the Hudson.

The increase in bacterial populations and slight increase (certainly not a drop) in bacterial production concurrent with the decline in phytoplankton confirms our previous conclusion that bacteria in the Hudson are not strongly linked to planktonic primary production. Rates of phytoplanktonic C fixation are currently 20% lower than pre-ZM years [2], indicating that availability of carbon derived from planktonic algae has decreased (although not as sharply as chlorophyll *a* concentrations). These observations argue, convincingly, that bacteria rely on non-phytoplankton carbon.

The largest carbon source for the tidal freshwater Hudson is DOC and POC transported from above the head, at Troy, NY [12]. Concentrations of DOC show significant variability within and among years [6], but there has been no consistent change since 1991. Variations in POC loadings are strongly related to freshwater inputs, which show considerable interannual variability, but, again, there has been no consistent change since 1991. Non-phytoplankton POC (detrital POC estimated as total POC minus 30× chl *a* [6] has not changed since 1991, even though it is clear that ZM can filter, and deposit as pseudofeces, the predominant size class of seston in the Hudson [19]. Some sort of compensatory mechanism maintains concentrations of suspended particles, despite high clearance by ZM. Continuous measurements of turbidity over two-week time spans at three locations within the tidal freshwater Hudson show that resuspension occurs at every change of tide (data not shown). Deposited particulate matter is thus returned to the water column several times day^{-1}. Therefore, the physical conditions of the Hudson provide the mechanism to maintain detrital POC in the water column, counterbalancing the rapid deposition of par-

ticles by ZM filtering activity. Moreover, bioassays show that Hudson bacteria grow at roughly equal rates on DOC derived from a variety of sources [7], indicating that allochthonous DOC could maintain bacterial populations following decreases in phytoplankton-derived carbon. It seems quite likely that bacterial production and populations are maintained by allochthonous carbon, and removal of phytoplankton by *Dreissena* filtering has not affected the carbon actually used by planktonic bacteria.

It also seems likely that ZM effects on the microbial component of diverse aquatic ecosystems will depend strongly on the size distribution of planktonic bacteria. If cells are fairly large, direct consumption will be significant; overall abundances and productivity will decline, even if flagellate grazers are also depressed by ZM feeding. If bacterial cells are relatively small, as in the Hudson, direct consumption by ZM will be slight. Abundances may remain steady or even increase. The indirect effects of ZM removal of bacterial carbon resources will also vary among systems, and may act to either exacerbate or compensate for direct effects. If bacteria rely on phytoplankton exudates, and ZM are efficient in depressing phytoplankton, then the indirect ZM effect will be negative. In contrast, microbial communities receiving large inputs of available allochthonous carbon not consumed by ZM will be buffered against change, and may increase if grazers are preferentially removed. The response of growth rate is more difficult to predict, because there is a positive relationship between cell size and activity [9]. If large cells are removed, overall production might be depressed unless smaller cells can increase their growth rates to compensate. At this point, we cannot construct a quantitative model of how bacteria in any system will respond to changes in abundance of benthic filter-feeders. The important variables, though, are likely to include cell size and the relative importance of control by grazers vs carbon supply.

Effects on Carbon Stocks

Bacterial abundance has increased while phytoplankton biomass has declined, leading to a substantial shift in availability of algal vs bacterial particles for consumer organisms. Prior to *Dreissena*, bacteria were a major component of the living biomass in the water column only at the northernmost stations, where phytoplankton abundance was low [6]. Near Kingston, bacterial carbon averaged about 100 μg C L^{-1} prior to 1992, and represented less than 50% of the total bacterial + phytoplankton carbon (Fig. 4A,B). Presently, the biomass distribution is such that bacterial carbon is 1.5 to almost 3× greater than phytoplankton carbon at the Kingston site. For consumers reliant on one or the other type of microbial particle, the composition of the food resource has shifted quite dramatically. Moreover, the total standing stock of microbial particles (bacteria plus algae) is lower than in the pre-ZM years. One would predict that these shifts in availability and composition might lead to changes in planktonic consumers. Many taxa of zooplankton have decreased in abundance, but at least some of these shifts were probably due to direct consumption by *Dreissena*, rather than mediated by changes in food availability [18]. The complexity of interactions is further evidence of the diversity and extent of effects possible when bivalve grazers undergo drastic changes in abundance. We believe the availability of bacterial carbon to planktonic consumers may have buffered some of the zooplankton against loss of the phytoplankton resource.

Our results show that bacterial abundance and production may be only loosely coupled to, and are actually subject to, different controlling factors. Bacterial populations have increased, but overall bacterial secondary productivity has not increased in proportion. We conclude that biomass is under predatory control by flagellates and other grazers, but production is carbon-limited, and cannot simply increase in direct proportion to abundance. Apparently, decreased predation results in an accumulation of cells which, on average, grow more slowly than in years prior to ZM (an increase in doubling times of about 1 d). The overall productivity is related to the carbon supply, which has not been greatly altered by the small decline in phytoplankton primary production. An alternative explanation is that a small proportion of the community may have always been responsible for the bulk of productivity, with most cells growing at very slow rates. If this active component had always been immune to predator control, then the release from grazers would allow the ''slow growth'' component of the predator control, then the release from grazers would allow the ''slow growth'' component of the community to accumulate. Productivity, however, would not be changed greatly.

Overall, the invasion of the Hudson River by the ZM has resulted in both predicted and unpredicted changes in several components of the ecosystem, and most of the unpredicted changes have led to new understandings of ecosystem function. Invasive species will continue to be an important policy issue as humans accelerate the movement of indigenous plants and animals to new areas of the globe. Since microbial communities are generally responsible for the majority of carbon and nutrient transformations, we must in-

clude their responses when assessing effects of exotic species on ecosystems.

Acknowledgments

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