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Weak coupling of bacterial and algal production in a heterotrophic ecosystem: The Hudson River estuary

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Abstract

Bacterial abundances, biomass, and production were measured over a 3-yr period at stations along a 158-km reach of the tidal, freshwater Hudson River. Bacterial abundances ranged from 1 to 10 × 10^6 cells ml^{-1} with maximal values in summer. Abundance and production averaged over all stations for the ice-free season (April through December) were 4.9 and 9.1 × 10^9 cells $liter^{-1}$ d^{-1}, respectively, and both were significantly correlated with temperature. Neither bacterial abundance nor production showed significant spatial variability over the study reach. In contrast to the results from many autotrophic ecosystems, annual average bacterial abundances from different stations were not significantly correlated with algal standing stocks, and bacterial production was only weakly related to rates of primary production.

Absolute rates of bacterial C production were greater than phytoplankton primary production, indicating that much of the bacterial secondary production in this portion of the river must be supported by nonphytoplanktonic organic C.

In the past decade, information on rates of heterotrophic bacterial production in aquatic ecosystems has proliferated and contributed greatly to knowledge of C fluxes and nutrient mineralization (Ducklow et al. 1986; Pomeroy and Wiebe 1988). In general, these studies have shown that planktonic bacterial production is broadly related to primary production, implying that phytoplankton contribute the organic C required to support bacterial growth (Cole et al. 1988). The vast majority of studies showing this pattern have been conducted in lakes, the open ocean, or areas of phytoplankton blooms where sources of C other than phytoplankton fixation are relatively small, so one would expect such a relationship to emerge. In contrast, studies in the upper reaches of some estuaries (Coffin and Sharp 1987; Painchaud and Therriault 1989) have suggested that the algal-bacterial link is weaker in these systems. Additionally, dissolved organic matter from *Spartina* was inferred to be an important source of C for estuarine bacteria in the Parker River estuary (Coffin et al. 1989), although the general importance of non-*Spartina* sources of C in salt marshes has perhaps been underestimated (Peterson and Howarth 1987).

Many aquatic ecosystems, ranging from headwater streams (Fisher and Likens 1973) to the nearshore continental shelf (Hopkinson 1985), are heterotrophic (respiration > primary production) because they receive large quantities of allochthonous organic matter. These systems have distinctly different patterns of biogeochemical cycling (Smith et al. 1989), and food webs tend to be based on detritus. In these systems, bacteria are probably significant in mineralizing C and nutrients from organic matter rather than acting as sinks for nutrients as occurs in many autotrophic ecosystems (primary production > respiration) (Vadstein and Olsen 1989). Despite the widespread occurrence of heterotrophic ecosystems, there is considerably less information on bacterial standing stocks or rates of production in these systems. Views on the role of bacteria as links between primary producers and higher trophic levels may be biased by the preponderance of information from phytoplankton-dominated systems.

Before one can obtain a general picture of the role of bacteria in planktonic food webs, one must also consider systems that offer the opportunity to examine the contribution of various sources of C. It is likely

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that the importance of bacteria in supporting higher trophic levels will vary, depending on the source of C for the bacteria. For instance, the growth efficiency of bacteria is critical in determining whether bacteria are a link or a sink (Ducklow et al. 1986), and it is well accepted that growth efficiency may vary significantly with growth substrate (Linley and Newell 1984). Specifically, if allochthonous inputs of vascular plant detritus are important in streams, rivers, estuaries, and the nearshore zone, then one would predict lower conversion efficiencies for bacteria growing on these substrates relative to bacteria growing on algal exudates. Lower conversion efficiencies make it likely that bacteria are more important as mineralizers of organic matter rather than as a direct contribution to higher trophic levels.

Large rivers represent an important class of ecosystems, and a prevalent paradigm in lotic ecology—the river continuum concept (Vannote et al. 1980)—suggests that large streams and rivers should be dependent on loadings of organic C from upstream. Large river systems in general have not received a great deal of study but are recognized as major sites of material transport and transformation (Lewis and Saunders 1989). Additionally, large rivers are particularly susceptible to human impacts and management efforts, but fundamental knowledge of these systems is not well developed.

In this paper we present data on bacterial biomass and production in the tidal, freshwater Hudson River with the intent of describing and interpreting the spatial and temporal variability. We show that the Hudson is a heterotrophic ecosystem and, as a consequence, does not fit the general relationship derived from phytoplankton-dominated systems. These differences are due to alternative sources of C and the importance of turbidity in limiting algal growth.

Materials and methods

Site description and field sampling—This study was conducted in the mid-Hudson between Castleton, New York, and Haverstraw Bay, a distance of 158 km (Fig. 1). The tidal amplitude is ~1 m over this entire distance, and the intrusion of the salt front (0.1 g Cl liter^{-1}) ranges into the lower reaches of our study area in summer. Mean annual freshwater discharge from the upper Hudson into the tidal river is 384 m^3 s^{-1} (U.S. Geol. Surv. 1983). The mean width and depth change substantially along stretches of the river, so there are broad, shallow regions (avg depth, 5–10 m) interspersed with deep, narrow sections (avg depth, >10 m). Nutrient concentrations and alkalinity are high, with NO_3^- averaging 50 μM, total dissolved P (TDP) 1 μM, and dissolved inorganic C (DIC) ~1 mM. Seasonal fluctuations in total dissolved N (TDN) and TDP were minor, but PO_4^{3-}-P showed strong seasonality, with lowest values of 0.1 μM in late summer.

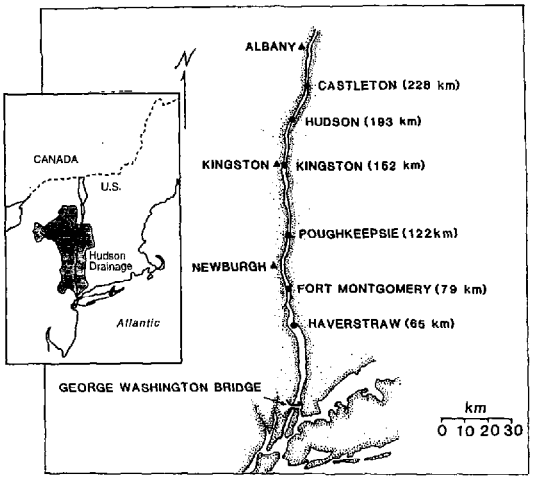


Fig. 1. Map of lower Hudson River showing sampling stations (●).

Sampling effort was divided between biweekly visits to stations near Kingston and Poughkeepsie to provide a detailed time series at two locations and less frequent, along-river transects from Castleton to Haverstraw Bay to assess spatial variability (Fig. 1). Over a 3-yr period (1987–1989), there were 51 sampling dates for the Kingston station and 14 along-river transects. Sampling was restricted to the ice-free season, roughly April through November. At each station, samples were collected for bacterial abundance and production ([^{3}H]thymidine incorporation), suspended matter, dissolved organic C (DOC), Chl *a*, and ^{14}C primary production (1987 and 1988 only). Three replicate water samples were collect-

ed from each sampling depth with a peristaltic pump and stored in the dark in polyethylene bottles. Incubations with [^{3}H]thymidine or $H^{14}CO_3^-$ were begun within 3 h of sample collection. Samples for bacterial direct counts were preserved with buffered Formalin in the field. Temperature and conductivity were determined with YSI meters.

Lab analyses—Total suspended matter was collected on ashed, preweighed glass-fiber filters (Whatman 934AH, nominal pore size, 1.5 μm). Three filters were prepared from each of the three replicate water bottles. Dry mass was determined after drying at 70°C overnight, and ash-free dry mass after combusting at 450°C for 4 h. Particulate organic matter was estimated as loss on ignition at 450°C for 4 h. C was assumed to constitute 45% of organic matter. DOC was determined with an Astro 2001 TOC analyzer.

Chl *a* was measured after methanol extraction and grinding of samples collected on Gelman AE glass-fiber filters. Chl concentrations were determined on a fluorometer, corrected for pheopigments and calibrated against Chl *a* from Sigma. C fixation was measured on 30-ml samples incubated with 2 μCi of $H^{14}CO_3^-$ for 2 h. Duplicate samples were incubated at in situ temperature, under twin 500-W quartz-halogen lights at seven different light levels (0–2,000 μEinst m^{-2} s^{-1}) that spanned the observed light levels in vertical profiles in the river. After incubation, samples were filtered (Gelman GN6), the filters dissolved in ethylene glycol monomethyl ether, and radioassayed in a Beckman LS1801 scintillation counter. DIC was measured with a Shimadzu gas chromatograph following the procedure of Stainton (1973). To compute daylight rates from short-term incubations, we calculated C fixation with photosynthetic parameters derived from production vs. intensity curves (Jassby and Platt 1976) and computer-generated estimates of solar radiation, assuming a cloudless sky. Therefore, these daylight estimates must be considered maximal. Complete details of techniques and photosynthetic parameters are given elsewhere (Cole et al. in press).

Bacterial abundance was estimated for two filters from each depth sampled, using acridine orange direct counts (Hobbie et al. 1977). There were two filters for each depth sampled. Bacterial biovolumes for surface-water samples were estimated with an image analysis system. In order to increase the magnification of individual bacteria on the image analyzer, we photographed cells and projected them on the analyzer with a video camera equipped with a 50-mm macro lens and 2× enlarger. Individual cells were isolated and contrast was enhanced with Image Analysis software (Olympus CUE-2, version 1.5). For each cell, we recorded cell area and perimeter and calculated volumes with the formula of Björnsen (1986). Cell sizes were calibrated against 0.6- and 1.0-μm-diameter fluorescent latex beads.

Bacterial production was estimated from the rate of incorporation of [*methyl*-^{3}H]thymidine ([^{3}H]TdR) into DNA (Findlay et al. 1984). Water samples (10 ml) (composite from the three replicate bottles) were incubated with 40 μCi of [^{3}H]TdR (80 Ci $mmol^{-1}$, NEN) at in situ temperature for 30 min. Incorporation was linear for at least 1 h at 24.5°C. Incubations were ended by adding 2 ml of 5% Formalin. Zero-time controls were fixed with Formalin immediately after adding labeled TdR. After incubation, bacteria were collected on 0.2-μm polycarbonate filters, washed twice with cold 5% TCA, and frozen for later DNA extraction. Isotope dilution was determined with a series of unlabeled TdR additions ranging from 6 to 24 times the concentration of labeled TdR added (50 nM). There were four replicates with zero-time cold-TdR addition, two zero-time controls, and three replicates for each of four levels of cold-TdR addition.

Isotope dilution was estimated at every sampling of the Kingston station in all 3 yr, and at every sampling of the Poughkeepsie station in 1987 and 1988. The *X*-intercept of isotope dilution plots gives an estimate of the effective pool size, i.e. the concentration of labeled and unlabeled TdR participating in DNA synthesis. DNA was extracted under alkaline conditions, precipitated with cold TCA, and collected and washed with centrifugation (Findlay et al. 1984). DNA was hydrolyzed in hot TCA and subsamples of the final hydrolysate were ra-

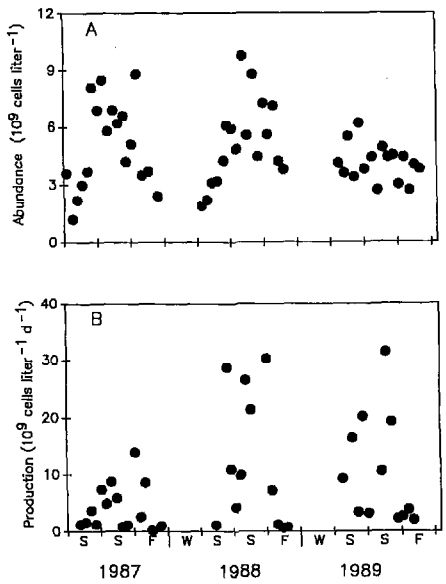


Fig. 2. Seasonal pattern of bacterial abundance and production in surface waters of the station near Kingston.

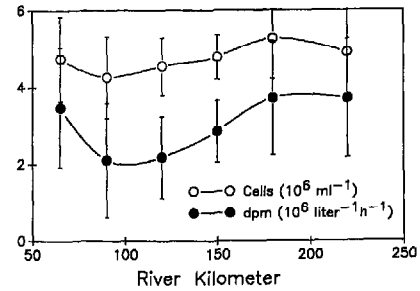


Fig. 3. Average bacterial abundance and TdR incorporation at stations along a north–south transect in the Hudson. Values are means ±95% C.I. over 3 yr. Kilometer zero is at the Battery in New York City.

dioassayed in a Beckman LS1801. Ethanol washes of the DNA-protein pellet did not remove significant amounts of radioactivity (cf. Robarts and Wicks 1989), indicating minimal interference from ^{3}H-labeled lipids. Quench was determined from the relationship between H number and counting efficiency (Horrocks 1977).

Bacterial production (BP) was calculated from the disintegrations per minute (dpm) incorporated into DNA and the effective pool size of TdR:

$$\mathrm{BP} = \left(\frac{\mathrm{dpm}}{\mathrm{liter} \times \mathrm{h}}\right) \times \left(\frac{\mathrm{nmolTdR}}{\mathrm{dpm\ added}}\right) \times \left(\frac{1 \times 10^9\ \mathrm{cells}}{\mathrm{nmol}}\right).$$

The actual value of the conversion factor from TdR incorporated to cells produced has been reported to vary considerably (Cole et al. 1989). A dilution growth experiment (Kirchman et al. 1982) was conducted in May 1988 to examine whether a conversion factor of 1×10^9 cells nmol^{-1} was appropriate for the river. Bacterial cell counts and TdR incorporation were followed for 39 h in three replicate flasks containing 1-μm-filtered Hudson River water.

Results

Bacterial abundance and biovolume—Bacterial cell counts at Kingston showed marked seasonal changes with maxima of $\sim 9 \times 10^9$ cells liter^{-1} in July and August of all years and minima of 1×10^9 in early spring (Fig. 2), with no significant difference among years (ANOVA $P > 0.05$). Seasonal patterns at other stations were similar (data not shown), and there were no significant differences among stations (ANOVA $P \gg 0.05$, Fig. 3). We did not use repeated-measures ANOVA because the minimum 2-week interval between samplings made it unlikely that we repeatedly sampled the same population.

Cell abundances were significantly correlated with both temperature and Chl *a* concentration (Table 1), and multiple regression showed both independent variables to be significant. Because both bacterial numbers and Chl concentrations correlate with temperature, we calculated partial correlation coefficients. The partial correlation of bacterial numbers with temperature ($r = 0.33$) was not significantly different from the partial correlation with Chl concentration ($r = 0.23$).

Mean cell volumes at Kingston during 1987 ranged from 0.07 to 0.19 μm^3 (Fig. 4). Cell volumes for individual samples tend to be lognormally distributed. We tested for seasonal variation in cell volume after log-transforming the data to satisfy the normality assumptions of ANOVA. There was

Table 1. Correlation matrix for Hudson River data set. Values are Spearman rank correlation coefficients, *n*, and significance level.

	POC	DOC	Alg prod.	Chl *a*	Bact N	Temp.	TdR
POC	X	0.1558 (146) 0.12	0.1475 (146) 0.18	0.3016 (146) 0.0003	0.1278 (146) 0.125	0.2601 (146) 0.0002	0.2188 (146) 0.009
DOC		X	−0.0307 (102) 0.84	−0.0416 (102) 0.68	−0.0006 (102) 0.99	−0.2043 (102) 0.04	−0.1479 (102) 0.14
Alg prod.			X	0.792 (146) 10^{-4}	0.2655 (83) 0.016	0.5743 (83) 10^{-4}	0.5156 (83) 10^{-4}
Chl *a*				X	0.3333 (146) 10^{-4}	0.4997 (146) 10^{-4}	0.4310 (146) 10^{-4}
Bact N					X	0.5406 (146) 10^{-4}	0.5177 (145) 10^{-4}
Temp.						X	0.6678 (146) 10^{-4}
TdR							X

a significant difference in cell volume among months ($P < 0.0001$, df = 8), but months explained only 4% of the variance in cell volume. Duncan's multiple range test ($\alpha = 0.05$) identified three broadly overlapping groups for the log-transformed means. The weighted mean for all the bacteria we measured in 1987 was (0.14 μm^3) ($n = 936$). We used a carbon-to-volume conversion factor of 0.2 pg C μm^{-3} to convert cell biovolumes to C units because this factor is appropriate for cells in the 0.1–0.2-μm^3 size range (Simon and Azam 1989). Thus, we estimate the average C content of Hudson bacteria to be 28 fg C $cell^{-1}$, and this value was used to convert cell abundances or production rates into C units.

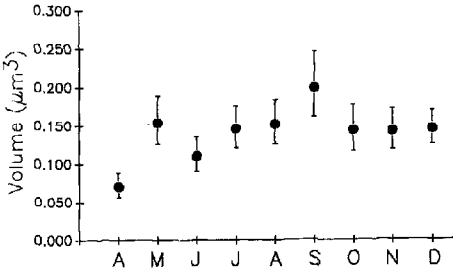


Fig. 4. Monthly mean bacterial biovolume determined at Kingston for the ice-free season in 1987. Each point is the mean of roughly 100 cells. The 95% C.I. are asymmetrical because the data were lognormally distributed.

Bacterial abundance showed significant increases with depth at both the Kingston and Poughkeepsie stations ($P < 0.05$, Fig. 5A). Total suspended matter and POC also increased with depth ($P < 0.01$, data not shown), indicating the potential for resuspension of bottom sediments and possibly bacteria. The water column at these two stations did not show any vertical variation in temperature or conductivity, indicating that density stratification was probably not the cause of vertical variations in bacteria and suspended matter.

Thymidine incorporation—Rates of TdR incorporation uncorrected for isotope dilution ranged from 2 to 70 pmol $liter^{-1}$ h^{-1} and were positively correlated with temperature ($P < 0.0001$, Table 1). There were no significant differences (ANOVA, $P \sim 0.34$) in TdR incorporation among stations along the longitudinal axis of the river (Fig. 3). The power of this analysis is fairly low ($\beta = 0.6$) because the range in station means is only 50% of the grand mean. Considering only the two stations (Poughkeepsie and Kingston) with the longest records shows that the rate of TdR incorporation was higher in 1988 than in 1987 or 1989 ($P < 0.05$).

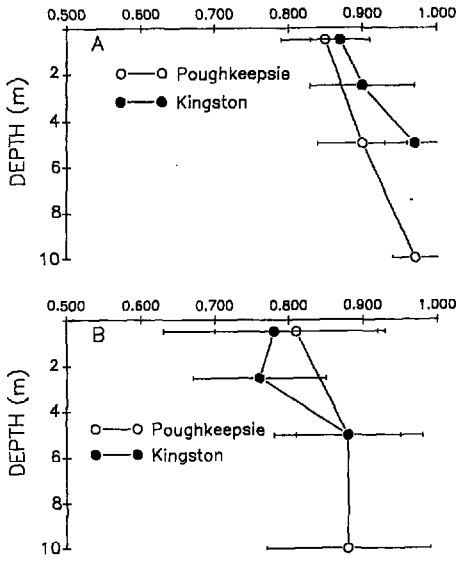


Fig. 5. Vertical profiles of bacterial abundance (A) and TdR incorporation (B) for stations near Kingston and Poughkeepsie. Data were normalized to the maximum value observed in a profile on a particular date to remove seasonal variation. Points represent means ±95% C.I. from all sampling dates.

Rates of TdR incorporation did not vary with depth at the Kingston and Poughkeepsie stations (Fig. 5B). TdR incorporation was positively correlated with POC, Chl *a* concentration, and surface primary production (Table 1). Because spurious correlations are possible in long time series, and all these parameters covary with temperature (Table 1), simple interpretation of these relationships is not possible.

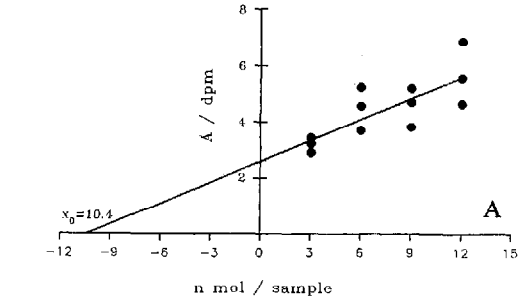
A multiple regression relating TdR incorporation to both temperature and algal production showed that both independent variables were significant. Precise estimates of the variance explained by each independent variable in the multiple regression is not possible because of the correlation between independent variables. Partial correlation showed that the partial correlation of TdR with algal production ($r = 0.62$) was significantly greater ($P = 0.02$) than that of TdR with temperature ($r = 0.28$). We argue below that using annual average values from different stations simplifies the examination of bacterial-algal relationships by removing the potential confounding effects of covariation with temperature.

Bacterial production—In order to convert rates of thymidine incorporation into bacterial production, we must estimate the conversion factor (cells produced per nmol TdR incorporated). This overall conversion factor is made up of two separate components—an isotope dilution factor and a factor based on the DNA content of bacterial cells and the thymine content of bacterial DNA. The isotope dilution factor was routinely estimated at the Kingston and Poughkeepsie stations and showed that the "effective pool size" (averaged over both stations and years) was 10.0 nmol per sample [±0.9 (SE), $n = 39$]. This value is the sum of the concentration of labeled and unlabeled TdR participating in DNA synthesis and is estimated from the X-intercept of reciprocal plots of labeled TdR incorporation vs. TdR concentration (Fig. 6A) (Moriarty and Pollard 1981; Findlay et al. 1984). Our samples contained 0.5 nmol of labeled TdR, so it is clear that unlabeled TdR, derived from exogenous or endogenous sources, contributes the bulk of TdR used in DNA synthesis.

There was no seasonal pattern in the degree of isotope dilution nor was it correlated with temperature or the actual rate of [^{3}H]TdR incorporation. The degree of isotope dilution was not related to total suspended matter, POC, DOC, or algal abundance or growth. There were no significant differences among years or stations (Fig. 6B).

Because isotope dilution was obviously a large factor in estimating bacterial production, we wanted to independently estimate the total conversion factor (also called the empirical conversion factor, Cole et al. 1989) with the dilution growth approach of Kirchman et al. (1982). The increases in cell counts and TdR incorporation were exponential and parallel (Fig. 7). The empirical conversion factor calculated for Kingston in the spring 1988 experiment was 10.6×10^9 cells nmol^{-1}. The empirical conversion factor may be separated into a "dilution" correction factor and a "biochemical" conversion factor.

The dilution correction factor is the ratio of the effective pool size (in nmol per sample) to the amount of labeled TdR (0.5 nmol per sample). The average effective pool size



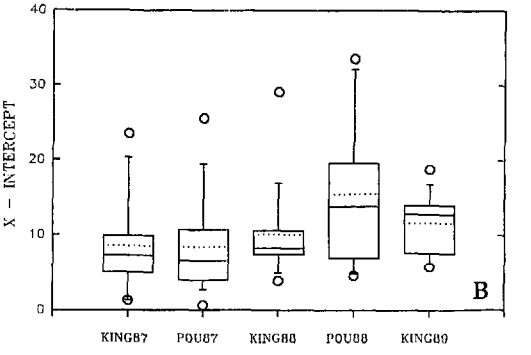


Fig. 6. A. Sample isotope dilution plot showing estimate of the X-intercept. Values plotted on the Y-axis are a constant divided by the radioactivity recovered in DNA from samples receiving different levels of unlabeled TdR. B. Summary statistics for the value of X-intercepts from the Kingston (3 yr) and Poughkeepsie (2 yr) stations. The dashed and solid horizontal lines show the mean and median, the box encloses 25th–75th quartile, error bars show the 10th and 90th percentiles, and circles represent the range.

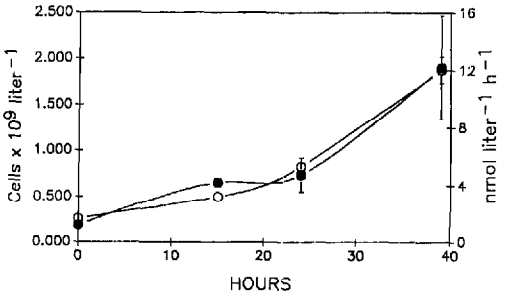


Fig. 7. Simultaneous determination of increases in bacterial cell abundance (O) and [^{3}H]TdR incorporation (●) in 1-μm-filtered Hudson River water used to calculate the empirical conversion factor. Some SE bars (n = 3) are smaller than the symbols.

for Kingston in 1988 was 10.1 nmol per sample, so the dilution correction factor would be 20.2 (10.1 ÷ 0.5). Therefore, the biochemical conversion factor, calculated as the empirical conversion factor (10.6×10^9) divided by the dilution correction factor (20.2), would be 0.52×10^9 cells nmol^{-1}. This value for the biochemical conversion factor is well within the range reported from theoretical calculations (Moriarty 1986) and has been reported from studies where isotope dilution was negligible (Servais 1989). If our estimates of isotope dilution were much too high, this estimate of the biochemical factor would have been unreasonably low. We routinely used a value of 1×10^9 cells nmol^{-1} to convert rates of TdR incorporation (corrected for isotope dilution) to cell production. None of our conclusions would be affected by a twofold change in the value selected for this biochemical conversion factor.

If we had not measured isotope dilution, we would have incorrectly concluded that a large proportion of bacteria in the river were either incapable of using exogenous TdR or had an extremely low thymine content of their DNA. The empirical conversion factor experiment supports our finding of large isotope dilution correction factors, and we show below that the resulting estimates of bacterial C production are within the bounds set by total planktonic respiration.

To examine whether this large isotope dilution factor could be related to adsorption of TdR to suspended matter, thereby reducing the effective concentration of added TdR, we measured the amount of [^{3}H]TdR retained on a 0.2-μm filter in zero-time controls. In one set of samples, unlabeled TdR (6 nmol per sample) was added first to saturate binding sites on particles, and in a second set, labeled TdR (0.5 nmol per sample) was added before unlabeled TdR. The amount of [^{3}H]TdR recovered in the filtrates was not different. If adsorption of TdR were occurring, we should have observed greater recovery of label in the first set of samples where binding sites had been saturated.

Bacterial production at Kingston showed strong seasonal variability (Fig. 2B) with an average, over the ice-free season of all 3 yr, of 8.8×10^9 cells liter^{-1} d^{-1}. All the significant correlations found between TdR incorporation and environmental variables

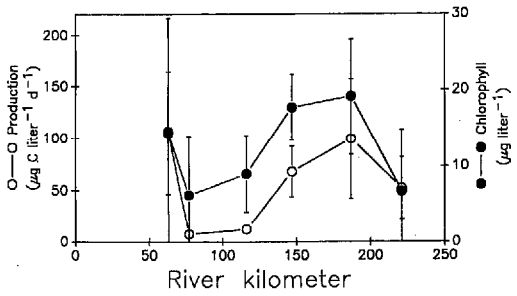


Fig. 8. Spatial patterns in Chl *a* concentration and primary production along a north–south transect. Values are means ±95% C.I. over 2 yr. Kilometer zero is at the Battery in New York City.

(Table 1) appear as significant correlations between bacterial production and environmental variables. To calculate bacterial C production at stations where isotope dilution was not routinely measured, we applied the overall average isotope dilution factor determined at the stations near Kingston and Poughkeepsie. We are confident in this extrapolation because there were no significant differences in dilution factors between the two intensively studied stations or between years (Fig. 6B).

Chlorophyll and primary production—Chl *a* concentrations and light-saturated ^{14}C incorporation showed strong seasonality at all stations, with peaks in June–July of each year (Cole et al. in press). Chl concentration, averaged over the ice-free season of 1986, 1987, and 1988 at all stations, was 11 μg liter^{-1} ($n = 106$), which is in the mid– upper range for estuaries and large rivers; rates of C fixation (200 mg C m^{-2} d^{-1}, $n = 106$) were nearer the low end of the range (Cole et al. in press). Due to rapid light extinction with depth (average extinction coefficient = 1.5 m^{-1}), ^{14}C fixation decreased strongly with depth so that the compensation depth was usually <2 m and depth-integrated net primary production was positive only at the shallow stations (Cole et al. in press). There were large differences in both Chl and C fixation among stations (ANOVA, $P = 0.01$ and $P < 0.001$, respectively, Fig. 8).

Discussion

We use two lines of argument to show that the phytoplankton-bacterial link in the tidal, freshwater Hudson River is substantially different from the linkages observed in more frequently studied autotrophic ecosystems. The simplest argument is that the magnitude of planktonic bacterial production is much too large to be supported solely by autochthonous planktonic primary production. Bacterial production at the Kingston station, averaged over the ice-free season, was 246 μg C liter^{-1} d^{-1} in the photic zone. Rates of TdR incorporation did not decrease in the deeper waters (Fig. 5B), so bacterial production integrated over a 5-m water column would be ~1.2 g C m^{-2} d^{-1}. This production is 4 times the value for depth-integrated phytoplankton production averaged over the ice-free season (0.3 g C m^{-2} d^{-1}) (Cole et al. in press). Ratios of bacterial to algal production would be even greater in deeper portions of the river. Clearly, sources of C other than phytoplankton primary production are necessary to support the observed rates of bacterial production. Several of these alternative sources represent allochthonous loadings, indicating the heterotrophic nature of the tidal freshwater portion of the Hudson estuary.

The second line of argument relies less on the absolute magnitude of bacterial production and more on the relationship between bacterial and algal parameters. In our data, as is often the case, both bacterial and algal abundances were correlated with temperature, so we used the station averages for the ice-free season for different years rather than individual data points to explore relationships. Bacterial abundance in the river was not correlated with standing stocks of Chl *a* (station means, $P > 0.05$, Fig. 9A), in contrast to the strong relationship reported for autotrophic systems such as the epilimnion of lakes (Bird and Kalff 1984, Fig. 9A). The power of this analysis is high ($\beta = 0.1$, assuming $H_1 : r^2 = 0.5$), indicating that there is only a 10% probability that we are committing a type 2 error if the correlation coefficient is as high as 0.7. Apparently, bacterial abundance is not directly related to algal abundance, and whatever parameters regulate algal abundance do not have the same influence on bacterial abundance. It is possible that intense grazing pressure on bacteria prevents a buildup of bacterial populations in regions (times) of

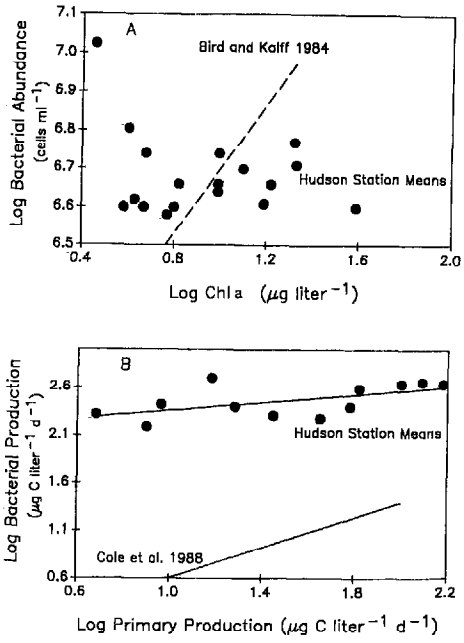


Fig. 9. Relationship between bacterial abundance and Chl *a* concentration with average values for different stations and years. The relationship has a slope not significantly different from zero. Shown for comparison is the relationship reported by Bird and Kalff (1984) for the epilimnion of lakes. B. Relationship between bacterial production and primary production with average values for different stations and years. The regression for Hudson data is significant ($P < 0.05$), but the slope is significantly less than that found by Cole et al. (1988) in a cross-system study.

high algal abundance, obscuring a correlation.

Bacterial production was positively correlated with both algal biomass and primary production (station means, $P < 0.05$, Fig. 9B), and either independent variable could explain ~40% of the variability in bacterial production. There is a tight correlation between Chl *a* and primary production (Table 1), so the similarity between relationships with these two independent variables is to be expected. The important point is that the slope of the bacterial-algal line in the Hudson [slope = 0.21 ± 0.09 (SE) $n = 12$] is significantly less (based on nonoverlapping 90% C.I.) than the slope (0.81) generated from a cross-system analysis of bacterial and algal production (Cole et al. 1988). Cole et al. (1988) found bacterial production to be a consistent 30% of primary production, so a 10× increase in primary production would lead to a 10× increase in bacterial production. If bacterial production was a constant proportion of primary production in the river, one would expect a >10-fold range in TdR incorporation, given the 20-fold range in primary production (Fig. 9B). The observed range in bacterial production was only about threefold. The relationship between phytoplankton primary production and heterotrophic bacteria in the Hudson is fundamentally different from relationships observed in the more frequently studied autotrophic ecosystems.

Our data clearly indicate that other sources of C are required to support heterotrophic bacterial production in the Hudson. If planktonic primary production were actually supporting a small fraction of bacterial production, one would expect to see what we observed: bacterial production exceeds primary production and there is only a weak relationship between bacterial and algal production. Nonphytoplanktonic autochthonous sources of C include macrophytes and resuspended sediments. There are extensive submerged macrophyte beds in the northern reaches of the tidal, freshwater Hudson, and evidence from photopigment distributions indicates that macrophyte debris may be a significant component of suspended POC (T. S. Bianchi pers. comm.). Also, DOC released from macrophytes is a good growth substrate for planktonic bacteria (Findlay et al. 1986) and is important in supporting bacterial production in the upper Mississippi River (Henebry and Gordon 1989). Resuspended benthic organic matter stimulates heterotrophic production in coastal waters (Wainwright 1987) and could be contributing organic matter to the water column of the shallower portions of the Hudson.

Allochthonous loadings of organic C from tributaries represent a major source of organic matter for the tidal, freshwater Hudson (Howarth et al. 1991). Export of detritus from fringing wetlands is one additional source of C, and export of mangrove C has been shown to be important to bacteria in the Gambia River (Healey et al. 1988). There is inferential evidence that a *Typha* marsh upstream of our Kingston sta-

tion is exporting detritus to the main-stem river (Findlay et al. 1990).

To examine possible relationships between bacteria and these sources of detrital material, we estimated detrital POC as total POC minus algal POC (Chl $a \times 30$). We did not, however, find a significant relationship between detrital POC and bacterial growth, possibly because our measures of detrital POC do not adequately describe the quality of the organic matter or because of time lags between detrital POC abundance and availability to bacteria.

The values for bacterial production that we have determined are higher than most of those reported in the literature (cf. Cole et al. 1988; Coffin and Sharp 1987). We can independently estimate the upper bound on bacterial production in the river from measurements of whole-system metabolism. Estimates of whole-system O_2 consumption during June and July 1988 in a shallow area a few kilometers downstream of our Kingston station ranged from 4.2 to 11.4 g O_2 m^{-2} d^{-1} (H. Garritt unpubl. data). Sediment oxygen consumption in a similar area was estimated to be 1.3 g O_2 m^{-2} d^{-1} (Findlay unpubl. data), so water-column respiration was 3–10 g O_2 m^{-2} d^{-1}, which corresponds to 1–4 g C m^{-2} d^{-1}, assuming a RQ of 1. Algal respiration for the entire growing season (May–October) was estimated to be 0.8 g C m^{-2} d^{-1} (Cole et al. in press) and ~1.3 g C m^{-2} d^{-1} during the June–August period.

Our bacterial production estimates for this same interval (June–August 1988) averaged 2.3 g C m^{-2} d^{-1} (± 0.2 SE $n = 5$), so water-column bacterial respiration would be on the order of 2.3 g C m^{-2} d^{-1}, assuming a growth efficiency of 50%. Because bacterial respiration estimated from our growth measurements was within the range of total water-column respiration, this comparison lends validity to our bacterial production estimates. If our production estimates were much too high, our production-based estimates of bacterial respiration would be much greater than the direct measurements of water-column respiration.

Large river ecosystems have been understudied, at least in part because they are viewed as overly complex and difficult to characterize. Bacterial abundance and production showed surprisingly little variation among the stations we examined, despite large longitudinal heterogeneity in salinity, algal abundance, primary production, and nutrient concentrations. Apparently, bacterial biomass and production do not respond to physiographic or other changes along the axis of the Hudson. In any case, lack of spatial variation facilitates large-scale study of bacterial processes in the Hudson ecosystem.

The significance of bacteria in the heterotrophic Hudson ecosystem offers a contrast to understanding of bacteria in the more frequently studied autotrophic systems. Bacterial production exceeds phytoplankton primary production in the river, implying that the role of bacteria in system respiration as well as nutrient cycling will be greater than in autotrophic ecosystems. Bacteria should be a source of nutrients in heterotrophic ecosystems rather than a sink, as appears to be the case in autotrophic systems (Vadstein and Olsen 1989). In addition, if one assumes that allochthonous sources of C are of lower quality than autochthonous phytoplankton production, then the efficiency of bacterial substrate utilization (production/incorporation) is likely to be lower in heterotrophic ecosystems. Consequently, the transfer of bacterial production to higher trophic levels will occur with a lower efficiency. This lower efficiency might, however, be compensated for by the overall higher rates of bacterial productivity. Testing these hypotheses will require broad-scale comparative studies of bacteria in heterotrophic and autotrophic ecosystems.

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