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Bacterioplankton dynamics and organic carbon partitioning in the lower Hudson River estuary

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ABSTRACT: Surface water samples collected at 10 stations in April 1996 along the entire salinity gradient of the Hudson River estuary were fractionated into particulate (POC), dissolved (DOC; <0.45 µm), high molecular weight (HMWOC; 10 kDa – 0.45µm), and low molecular weight (LMWOC; <10 kDa) organic carbon. Bacterial concentrations, production and specific growth rates were also determined at each location. While HMWOC (6 to 26 µM) exhibited nonconservative removal relative to ideal dilution of river and seawater along the estuary, DOC (176 to 324 µM) showed a nonconservative excess along this salinity gradient. These contrasting distributions suggest that the majority of DOC was exported to the ocean and consisted of low lability material, while a reactive fraction of HMWOC was removed during estuarine mixing. Bacterial abundances (5 to 16 × 10^8 cells l^{-1}), production (3.4 to 28.7 µg C l^{-1} d^{-1}), and specific growth rates (0.09 to 0.66 d^{-1}) varied significantly along the salinity gradient. These variables were positively correlated with algal standing stocks (chlorophyll *a*) and even more coherent with HMWOC distributions. In contrast, bacterial metabolism varied independently of POC, DOC, and LMWOC concentrations. Therefore, while HMWOC accounted for <10% of the DOC, this pool appeared to be very dynamic, possibly due to bacterial degradation. However, mass balance estimates indicate that bacterial uptake could remove at most 30% of the HMWOC, suggesting that abiotic processes such as flocculation are probably the major removal mechanism of HMW organic matter within the estuary. Lastly, contrary to previous results from the tidal freshwater section of the Hudson, strong coherence between primary and secondary production and the nonconservative excesses of DOC found in the lower estuary suggest that carbon and bacterial dynamics can vary qualitatively along different reaches of this river.

KEY WORDS: Bacterioplankton · Organic carbon · Hudson River estuary

INTRODUCTION

The cycling of terrigenous organic carbon in rivers and its subsequent export to oceans are determined by heterogeneous estuarine processes (e.g. flocculation, precipitation, photolysis, microbial degradation, food web interactions, etc.). However, the conservative distributions and/or nonconservative excess of dissolved organic carbon (DOC) observed in estuaries (Mantoura & Woodward 1983, Aminot et al. 1990, Findlay et al. 1991a, 1992, Howarth et al. 1992, Dai et al. 1995, Powell et al. 1996) suggest that the bulk of allochthonous carbon is not involved in those processes and is mainly composed of relatively unreactive and biologically recalcitrant materials. In order to understand processes affecting regional and global carbon budgets, it is necessary to determine the fates of different organic carbon fractions in natural waters. For example, Fox (1983) showed that, while salt-induced flocculation is a major mechanism of removal of humic acids during estuarine mixing, this removal is not reflected in the DOC pool because humic compounds represent only a small fraction of the DOC.

One large uncertainty in the study of carbon cycling is the identity of the pool(s) supporting the high bacterial biomass and activity observed in estuaries (Coffin & Sharp 1987, Howarth et al. 1992, Hoch & Kirchman 1993, Connolly & Coffin 1995). Clearly, in severely light-limited estuaries, the observed low levels

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of *in situ* primary production are insufficient to support bacterial energy demands through fluxes driven by exudation and mortality. In fact, some estuaries, such as the tidal freshwater section of the Hudson River estuary and the Amazon River (Richey et al. 1990, Findlay et al. 1991b, 1992, Howarth et al. 1992, Benner et al. 1995), are net heterotrophic, i.e. respiration and bacterial net production (BNP) always exceed *in situ* primary production. Therefore, microbial metabolism must be subsidized by allochthonous carbon sources.

Microheterotrophic carbon demand has the potential to greatly influence the composition and amount of organic carbon delivered to the ocean. Results from a few laboratory studies have suggested that high molecular weight organic carbon (HMWOC; >10 kDa) in natural DOC pools can be more available to bacteria than the low molecular weight (LMWOC; <10 kDa) fraction (e.g. Tranvik 1990). The bioreactivity of HMWOC over LMWOC pools has also been observed in field studies of the Amazon River system and the Gulf of Mexico (Benner et al. 1995, Amon & Benner 1996). If this is the general case, then HMWOC may play a more important role in supporting bacterial metabolism and in subsequent trophic transfer than previously believed. Considering its small contribution to the total carbon pool (<20% of the total dissolved; Whitehouse et al. 1989, Guo et al. 1994, Dai et al. 1995), the HMWOC pool is potentially far more dynamic than particulate or dissolved pools. However, even if bacterial decomposition removes all HMWOC, this removal will not necessarily be apparent in the distribution of the much larger DOC pool.

To better understand bacterial interactions with native pools of organic carbon, we examined size-fractionated (particulate, dissolved, LMW, and HMW) organic carbon concentrations and bacterioplankton dynamics (abundance, production and growth rates) at 10 locations across the entire salinity gradient of the Hudson River estuary. The area of study included the rural, forested catchments in the tidal, freshwater region of the estuary as well as the marine end-member in the heavily populated upper bay. This sampling scheme was designed to allow us to determine the relative importance of different types and sources of DOM to bacterial metabolism.

The Hudson River estuary presents ideal conditions to establish the relationship between bacterial activity and HMWOC. It is known that the tidal, freshwater section of the Hudson River is net heterotrophic, and bacterial biomass and production appear to be decoupled from primary production (Findlay et al. 1991b). Therefore, BNP must be subsidized, in large part, by allochthonous input of organic matter into the system (Findlay et al. 1991a, 1992, Howarth et al. 1992). The conservative distribution of DOC during transport along this reach of the Hudson River further suggests that the majority of organic matter is refractory and that high bacterial abundance and production is supported by a relatively small, and 'unidentified' labile organic carbon pool (Findlay et al. 1992, Howarth et al. 1992). Results presented here suggest that, indeed, preferential bacterial utilization of HMWOC over the abundant LMWOC fraction is apparent along the estuarine reach of this river. However, contrary to previous results obtained upriver, we found a nonconservative excess of DOC with respect to ideal dilution of river and seawater, and a strong coherence between primary and secondary production in the lower estuary. These findings suggest that carbon and bacterial dynamics can vary qualitatively among different reaches of large rivers.

MATERIALS AND METHODS

Sampling. Surface water samples were collected during the period April 3 to 5, 1996 at 10 locations in the Hudson River estuary, under high river discharge conditions. The geographical distribution of the sampling sites covered the tidal, freshwater section of the river (Newburgh, New York, USA) to the Atlantic Ocean (Sandy Hook, New Jersey; about 120 km) (Fig. 1). Because bacterial activity varies as a function of water temperature, samples were collected in the spring when this effect should be minimal, due to uniformly low water temperatures typically observed (Ashizawa & Cole 1994). Surface waters, in fact, only varied from 5.1 to 6.4°C during this study. In contrast, allochthonous inputs of HMW organic matter from the watershed are expected to be greatest under high flow conditions during spring (Findlay et al. 1991a, Howarth et al. 1992).

Organic carbon inventories. Three independent samples were collected from a depth of 1 m at each location for POC and DOC analysis by a trace metal-clean pumping system. POC was analyzed on suspended matter retained on precombusted, 13 mm GF/F glass-fiber filters, and total DOC was determined in filtered (<0.45 µm; polypropylene capsule filters; MSI Inc.) samples. A 20 l water sample was also collected at each location and filtered (<0.45 µm) for size fractionation by ultrafiltration. This sample was stored in acid-cleaned 20 l dark Teflon bag containers, refrigerated immediately, and ultrafiltered within 24 h of collection in an acid-cleaned Filtron cross-flow filtration system (10 kDa) modified for trace metals analysis (Sañudo-Wilhelmy et al. 1996). In order to avoid breakthrough and/or diffusion of organic carbon from the retentate to the ultrafiltrate (Buesseler et al. 1996, Wen et al. 1996), samples were preconcentrated only to a factor of 7.5. Similar concentration factors (7 to 10) have also been used to isolate HMWOC in other estuaries (Powell et al. 1996).

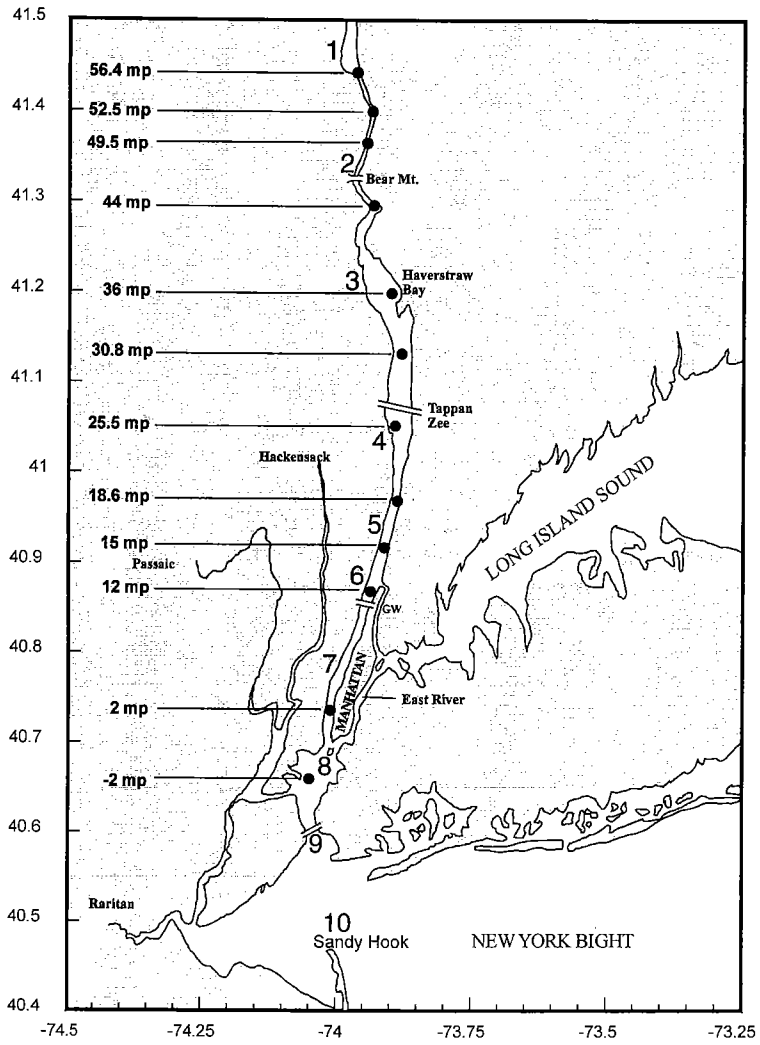

Fig. 1. Map of the Hudson River estuary showing the area of study and sampling locations

Ultrafiltration cleaning and operating protocols have been reported elsewhere (e.g. Whitehouse et al. 1990, Sañudo-Wilhelmy et al. 1996). The consistency of the ultrafiltration protocols is indicated by the high ultrafiltration recoveries (from 80 to 108%) (Table 1). The efficiency of the cleaning protocols was also demonstrated by the analysis of ultrafiltration blanks. Organic carbon blanks for the ultrafiltration system were obtained by ultrafiltering water from a combined Milli-RO/Milli-Q Plus System (Millipore) equipped with sand, carbon and polygard prefilters. The ultrafiltration blanks were 38 ± 22 µM for the retentate and 35 ± 21 µM for the ultrafiltrate (n = 3, mean ±1 SD).

The concentrations of organic carbon in the dissolved fractions were determined by high temperature catalytic oxidation using a Shimadzu TOC-5000 Total Organic Carbon Analyzer. POC was measured in a Carlo Erba NA1500 NCS system . Dissolved phosphate, salinity, suspended particulate matter, and chlorophyll *a* were determined using standard methods (Strickland & Parsons 1972).

Bacterial abundances. At each station, whole water samples (100 ml) were preserved with 2% borate-buffered formaldehyde (final conc.) for bacterial abundance and biomass determinations. In the laboratory, standard DAPI-stained slides were prepared on dark 0.2 µm Poretics polycarbonate membranes for enumeration by epifluorescence microscopy (Porter & Feig 1980). Bacterial biomass was determined

Table 1. Dissolved (DOC), low molecular weight (LMW), high molecular weight (HMW), and particulate (POC) organic carbon concentrations (µM) measured in surface waters of the Hudson River estuary in April 1996. DOC and POC are reported as the mean ±1 SD of 3 independent samples. LMWOC is reported as the mean ±1 SD of multiple analyses of the same sample

Location	DOC (<0.45 µm)	LMW (<10 kDa)	HMW[a] (10 kDa – 0.45 µm)	POC	HMW/DOC (%)	Mass balance[b] (%)
1. Newburgh Bridge	261 ± 15	247 ± 18	17	56 ± 12	6.5	101.2
2. Foundry Cove	294 ± 21	291 ± 6	26	52 ± 4	8.9	107.8
3. Haverstraw Bay	295 ± 28	289 ± 5	6	48 ± 2	2.0	100.0
4. Piermont	306 ± 30	244 ± 4	10	63 ± 1	3.3	83.0
5. Yonkers	324 ± 32	263 ± 5	11	77 ± 9	3.4	85.0
6. G.W. Bridge	281 ± 5	242	10	101 ± 8	3.6	89.7
7. Grant's Tomb	254 ± 26	237 ± 3	11	294 ± 8	4.3	97.6
8. Governor's Island	239 ± 26	228 ± 2	11	92 ± 8	4.6	100.0
9. Verrazano Bridge	206 ± 17	196 ± 2	11	65 ± 2	5.6	100.5
10. Sandy Hook	176 ± 26	171 ± 10	8	107 ± 3	4.6	101.7

[a]HMW = (retentate–filtrate)/concentration factor; [b][(HMW + LMW) × 100/DOC]

indirectly in each DAPI-stained sample by measuring 200 randomly selected cells with an ocular micrometer and placing them in 1 of 7 size classes. Mean cell volume was calculated from dimensions and simple geometry and carbon biomass was estimated using a conversion factor of 3.50×10^{-13} g C m^{-3} (Bratbak 1993).

Bacterial production. BNP was determined by measuring ^{3}H-leucine incorporation into protein (Kirchman 1993). Briefly, at each station 100 ml whole water samples were placed in acid-washed 125 ml polyethylene bottles and immediately spiked with ^{3}H-leucine (10 nM final conc.; L-(4,5-^{3}H(N))-leu; 52 Ci $mmol^{-1}$; NET 135H, Dupont NEN Products). Samples were placed in an on-deck water bath for 8 h and maintained at ambient temperature in total darkness, then fixed with cold trichloroacetic acid (TCA; 5% final conc.). Acid-fixed samples were refrigerated until processing for radiotracer incorporation into protein immediately after the cruise. After heating triplicate 20 ml subsamples at 80°C for 15 min, protein precipitates were captured on 0.22 µm cellulosic filters (Micron Separations, Inc., Westboro, MA, USA), rinsed with cold 5% TCA twice, and followed by 3 cold 80% ethyl alcohol (EtOH) rinses according to standard protocols (Kirchman 1993). Filters were dissolved with 0.5 ml ethyl acetate in scintillation vials and then radioassayed in Hionic-fluor (Packard Co.). Filter blanks were determined from samples that were fixed with 5% TCA (final conc.) immediately after ^{3}H-leucine was added. BNP was calculated as described by Kirchman (1993) using a conversion factor of 3.1 kg C mol^{-1} of leucine incorporated and specific growth rates (μ) were derived using biomass (B) estimates described above and the logistic growth equation (μ = ln(B + BNP/B)/t), where t = time.

Time courses of bacterial incorporation of ^{3}H-leucine were carried out in the laboratory immediately after the cruise with samples from Stns 1 and 10 (salinity end-members). Whole water samples (2.5 l) were maintained at ambient temperature (~5°C) and returned to the laboratory. Time courses (0 to 24 h) were performed at 5°C using the protocols described above, withdrawing duplicate 20 ml subsamples at each timepoint from initial samples of 220 ml.

RESULTS AND DISCUSSION

Size-fractionated organic carbon concentrations

Concentrations of organic carbon in the different size-fractions, as well as salinities, chlorophyll *a*, water temperature and suspended particulate matter, are presented in Tables 1 & 2. Concentrations of total DOC varied from 176 to 306 µM, similar to levels reported for other temperate estuaries, such as the Delaware Estuary (166 to 450 µM; Sharp et al. 1993), the Peconic River estuary (90 to 520 µM; Breuer et al. 1999) and the Mississippi River system (88 to 345 µM; Gardner et al. 1994). However, DOC levels measured along the salinity gradient of the Hudson River estuary were considerably lower than those measured in other estuarine systems in which the rivers drain a more forested watershed, such as the Amazon River system (250 to 1000 µM; Richey et al. 1990, Benner & Hedges 1993) and the Ochlockonee River estuary (200 to 1500 µM; Powell et al. 1996).

The distribution of organic carbon among the operationally defined size classes indicated that HMW (>10 kDa) carbon accounted for <10% of the total dissolved carbon in the estuary during our sampling (Table 1). The predominance of LMWOC has also been reported in other studies using the same (10 kDa) molecular weight cut-off (Whitehouse et al. 1989, Guo et al. 1994, Dai et al. 1995, Powell et al. 1996).

Table 2. Concentrations of suspended particulate matter (SPM), phytoplankton biomass (chl *a*), salinity, and temperature measured in surface waters along the Hudson River estuary during April 3 to 5, 1996

Location	SPM (mg l^{-1})	Chl *a* (µg l^{-1})	Salinity (ppt)	Temperature (°C)
1. Newburgh Bridge	27.7	0.50	0.12	5.29
2. Foundry Cove	18.8	0.45	0.82	5.11
3. Haverstraw Bay	13.2	0.30	4.03	5.38
4. Piermont	23.3	0.43	5.95	5.50
5. Yonkers	30.7	0.96	8.18	5.70
6. G.W. Bridge	40.4	1.70	10.51	6.40
7. Grant's Tomb	219	1.03	11.12	6.10
8. Governor's Island	26.1	7.73	22.97	5.80
9. Verrazano Bridge	5.23	9.12	23.52	5.60
10. Sandy Hook	4.50	28.8	26.53	5.30

Nonconservative distributions of size-fractionated organic carbon

The contrasting distributions of the particulate, dissolved, LMW and HMW organic carbon as a function of salinity suggest that these fractions are cycled differently in the lower Hudson River estuary (Fig. 2). For example, the nonconservative excess, relative to ideal dilution of river and seawater, observed for the DOC and LMW fractions (Fig. 2a,b) contrasts with extensive removal in the HMWOC pool detected in the low salinity region of the estuary (Fig. 2c). Estuarine mixing appears to have no effect on the distribution of POC

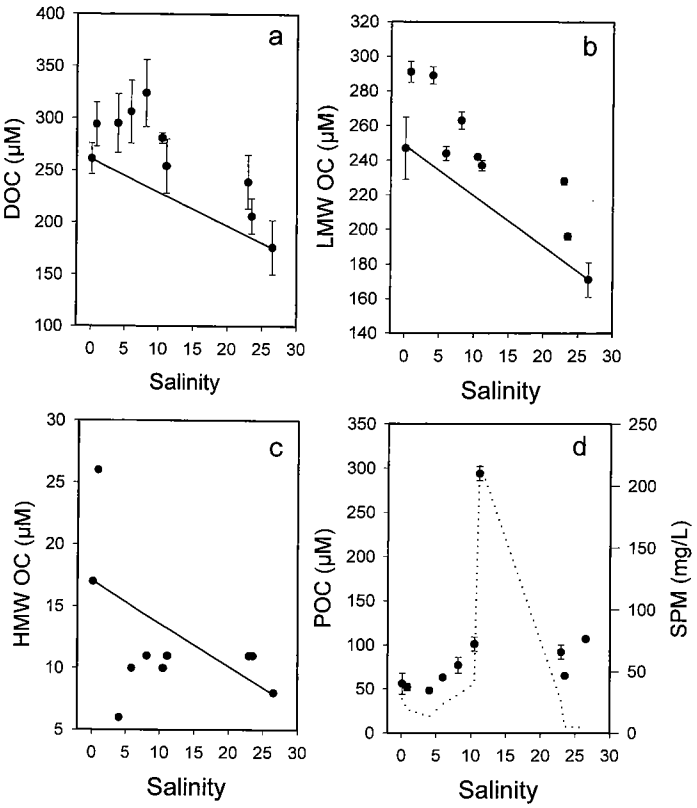

Fig. 2. Total dissolved (a) (DOC) (<0.45 µm), (b) LMWOC (<10 kDa), (c) HMWOC (10 kDa – 0.45 µm) and (d) particulate organic carbon (POC) concentrations versus salinity in the Hudson River estuary. Error bars represent ±1 SD of the mean of triplicate analyses. The solid line represents conservative mixing of river water with seawater and the dotted line indicates the total suspended solid distribution

(Fig. 2d). This fraction covaries with the concentrations of total suspended particulate matter (Fig. 2d), as reported for upriver (Findlay et al. 1991a) and for the Mississippi River system (Trefry et al. 1994). The turbidity maximum observed at Stn 7 (salinity = 11) is commonly observed in that part of the estuary (Bokuniewicz 1996). The sediment resuspension in this region is the result of a salt-water front, tidally modulated and bathymetrically controlled (Bokuniewicz 1996).

The nonconservative removal of HMWOC in the low (<12) salinity region of the Hudson (Fig. 2c) is also similar to that reported for humic acids in other estuaries (Fox 1983), suggesting that the HMWOC behaves like humic acids, even if not predominantly composed of those substances. However, the distribution of the HMWOC in the high (>22) salinity region of the estuary appears to be conservative (Fig. 2c). These 2 contrasting behaviors of the HMWOC pool observed along the salinity gradient of the estuary indicate that the sources and/or types of riverine and marine HMWOC may be distinct. The high levels of chlorophyll *a* (8 to 29 µg l^{-1}; Table 2) measured in the marine region of the estuary suggest that the HMWOC could be derived from phytoplankton through a variety of processes. This hypothesis is consistent with the documented release of HMW exudates by phytoplankton in coastal environments (Kepkay et al. 1993, Niven et al. 1995).

In contrast to the coupling of DOC and HMWOC observed elsewhere in coastal waters (Guo et al. 1995), the distinct distributions of HMWOC, DOC and POC pools (Fig. 2), i.e. absence of any correlation among these pools along the Hudson River estuary, suggest that the amount of HMWOC is not simply a function of the amount of DOC or POC but probably relates to the quality of these materials. The high proportion of LMWOC indicates that this pool is responsible for the nonconservative excess in the DOC fraction. Moreover, any additional non-POC inputs to the estuary were either primarily LMWOC or rapidly transformed into LMWOC through degradative processes. This nonconservative DOC distribution contrasts with the conservative behavior of riverine DOM reported in other estuaries (Mantoura & Woodward 1983, Dai et al. 1995) and even reported for the tidal freshwater reach of the Hudson River (Findlay et al. 1991a).

The obvious explanation for DOC excesses at intermediate salinities is the anthropogenic contributions from the heavily urbanized New York-New Jersey watershed, such as sewage and surface run-off. However, the geographical distribution of DOC indicates that deviation from the theoretical 2 end-member mixing relationship (Fig. 2a) might be due to additional processes. Although this estuary receives approximately 100 m^3 s^{-1} of sewage (Brosnan & O'Shea 1996), DOC levels were highest about 15 km upriver from the largest Manhattan sewage treatment plant (STP) outfall in the Hudson (North River STP). Furthermore, DOC levels were consistently high at all stations upriver, and steadily diminished from Stn 5 to NY Harbor (Fig. 3).

In contrast, dissolved phosphate, which is considered a tracer of sewage in the Hudson River estuary (Clark et al. 1992), was consistently high from the station with the highest DOC levels (Stn 5) down to the confluence of the East River and the NY Harbor (Stn 8) which exhibited only moderate DOC levels (Fig. 3). Differences in distributions of phosphate and DOC suggest that DOC levels were not strongly controlled by sewage input at this time of year. Obviously, this and other anthropogenic sources of DOC cannot be totally discounted. Because sampling was conducted in April 1996 after a winter of record snow accumulation, the DOC excesses could be related to the high run-off volume of melt waters, rich in terrigenous carbon. The importance of external loadings of organic matter from tributaries to the carbon budget of the upper Hudson

River has been suggested previously (Howarth et al. 1992). However, the nonconservative behavior of DOC observed in our area of study compared to the conservative mixing reported upriver by Findlay et al. (1991a) suggests that biogeochemical processes controlling the cycling of organic matter vary in different reaches of the same river. This is further demonstrated by observations on bacterial dynamics presented below.

Bacterial abundance and production

Bacterial abundances along the Hudson River estuary varied from 5 to 16 × 10^8 cells l^{-1} (Table 3). This range was consistent with the low end of ranges reported in other U.S. east coast estuaries, such as the Rhode River estuary (3.0 × 10^8 cells l^{-1}; Rublee et al. 1984), the Delaware River estuary (6.5 to 10 × 10^8 cells l^{-1}; Coffin & Sharp 1987, Hoch & Kirchman 1993) and in Massachusetts, USA, salt marsh estuaries (7 × 10^8 cells l^{-1}; Wright & Coffin 1983). The average cell density in the Hudson River estuary (8.6 × 10^8 cells l^{-1}) was also consistent with minimum cell counts (10 × 10^8 cells l^{-1}; Findlay et al. 1991b) measured in the tidal freshwater Hudson River in early spring.

Bacterial carbon production varied from 3.7 to 28.7 µg C l^{-1} d^{-1} (Table 3). The average BNP measured within the estuary (14.6 µg C l^{-1} d^{-1}) was between the high annual average reported for the freshwater section of Hudson River (246 µg C l^{-1} d^{-1}; Findlay et al. 1991b) and the relatively low production detected in the Hudson River plume through the New York Bight (1.6 to 2.4 µg C l^{-1} d^{-1}; Ducklow & Kirchman 1983). Because bacterial abundances and production are usually positively correlated with temperature (Wright & Coffin 1983, Findlay et al. 1991a), our relatively low bacterial abundance and productivity estimates were presumably depressed due to the low water temperatures (range = 5.1 to 6.4°C) prevailing during our sampling. Higher bacterial concentrations and production are likely to occur in the summer months in the Hudson River when water temperatures can reach 25°C (Findlay et al. 1991b, Ashizawa & Cole 1994).

Spatial gradients in bacterial dynamics

While previous studies in the freshwater tidal region of the Hudson River estuary did not find any spatial trends in bacterial concentrations or production (Findlay et al. 1991b), our results showed a strong spatial gradient for both variables within the lower portion of the estuary (Fig. 4A,B). Both bacterial abundances and production increased with salinity, being lowest at the riverine end-member and highest in the upper Bay/NY Harbor region. With the exception of 1 station in the upper Bay (Stn 8), bacterial concentrations increased linearly with salinity, suggesting conservative mixing of bacteria and/or their growth substrates (Fig. 4A). The highest bacterial abundances and production were measured at Stn 8, near the confluence of the East River and the NY Harbor, suggesting additional input of cells or labile OC from the East River. Higher bacterial activity at this station is consistent with the facts that the East River's shorelines are more densely urbanized than those of the Hudson and it receives waters from numerous STP outfalls and western Long Island Sound. The conservative bacterial distribution rela-

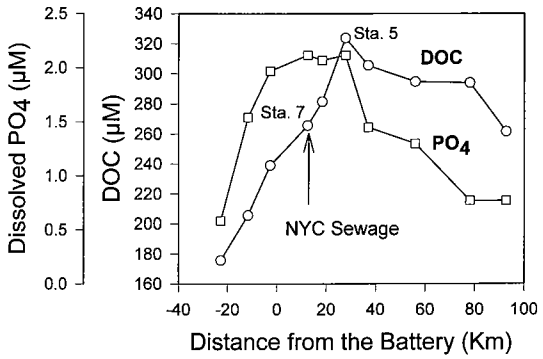

Fig. 3. Geographical distribution of DOC (○) and phosphate (□) along the Hudson River estuary. Locations are referred to by the axial distance, kilometers upstream (+) and downstream (–) from the Battery at the southern tip of Manhattan Island. The arrow indicates the location of the North River sewage treatment plant

Table 3. Bacterial abundances, production and specific growth rate measured in surface waters of the Hudson River estuary in April 1996. Bacterial abundances reported as the mean ±1 SD of counts from 10 fields on a single filter. Bacterial production and growth reported as the mean ±1 SD of triplicate analyses

Location	Bacterial abundance (10^8 cell l^{-1})	Bacterial production (µg C l^{-1} d^{-1})	Specific growth rate (d^{-1})
1. Newburgh Bridge	5.35 ± 0.36	4.04 ± 0.95	0.12 ± 0.033
2. Foundry Cove	5.03 ± 0.37	5.38 ± 0.45	0.16 ± 0.011
3. Haverstraw Bay	6.68 ± 0.66	3.37 ± 0.03	0.09 ± 0.00
4. Piermont	6.71 ± 0.40	8.01 ± 0.13	0.24 ± 0.00
5. Yonkers	7.12 ± 0.43	17.28 ± 1.90	0.61 ± 0.07
6. G.W. Bridge	7.98 ± 0.37	10.06 ± 0.75	0.35 ± 0.03
7. Grant's Tomb	6.63 ± 0.28	19.85 ± 1.56	0.66 ± 0.05
8. Governor's Island	16.00 ± 0.68	28.68 ± 0.79	0.54 ± 0.02
9. Verrazano Bridge	12.25 ± 0.70	26.05 ± 0.45	0.43 ± 0.01
10. Sandy Hook	11.69 ± 0.60	23.03 ± 1.70	0.28 ± 0.02

tive to salinity in the Hudson River estuary reported here is consistent with the distribution pattern observed in several other estuaries (e.g. Palumbo & Ferguson 1978, Wright & Coffin 1983). Even though a conservative distribution might be interpreted as indicating that bacterial communities are only affected by mixing, we demonstrate below that this is not the case for our observations.

Evidence for differential responses of freshwater and estuarine bacterial communities among stations is provided by examining BNP normalized to bacterial abundance or community-specific growth rates. The underlying assumption of this calculation is that all cells utilized the radiotracer and grew at the same rate, which is certainly untrue. As observed elsewhere, probably only a subset of populations were actively growing on available substrates while other populations were relatively dormant (Karner & Fuhrman 1997). Consequently, this approach provides a conservative estimate of bacterial growth rates. Even though total BNP was relatively coherent with salinity (Fig. 4B), specific growth rates varied unpredictably ($r^2 = 0.47$, $p < 0.17$) with salinity (Fig. 5). Growth rates at the riverine end tended to be lower than at the marine end, but were highest at 2 intermediate salinities, Stns 5 and 7, which coincided with the DOC maximum (Fig. 3) and the North River STP outfall, respectively. These observations demonstrate that controls on bacterial production are heterogeneous along the salinity gradient and may depend on the interplay of *in situ* primary production, allochthonous input of labile OM (watershed and point sources), temperature and salinity as it affects OM partitioning. These controls are evaluated below.

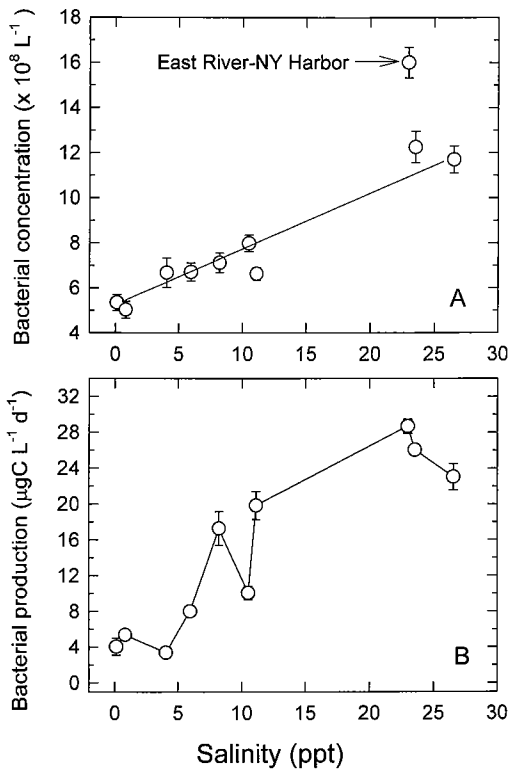

Fig. 4. Bacterial (A) abundance and (B) production as functions of salinity in the Hudson River estuary. Error bars represent ±1 SD of the mean; absence indicates error is smaller than symbol

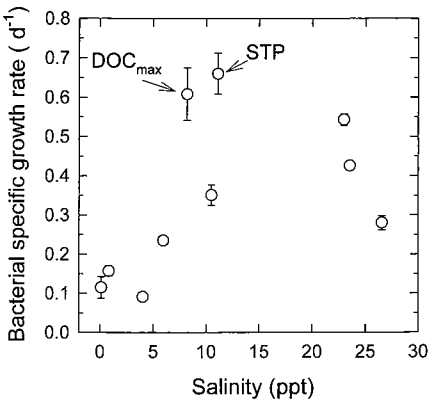

Fig. 5. Variance in bacterial specific growth rates along the salinity gradient. DOC_{max} and STP represent stations coinciding with highest observed DOC concentration and the North River sewage treatment plant (STP) outfall

Factors controlling bacterial dynamics in the lower Hudson River estuary

Phytoplankton biomass

Unlike Chin-Leo & Benner's (1992) study of the Mississippi River, few estuarine and riverine studies have reported discernible coupling between bacterioplankton and phytoplankton dynamics, presumably as a consequence of the high allochthonous loadings of bacterial substrates and strong light attenuations in these systems. In the present study, however, bacterial abundances within the lower Hudson River estuary were positively correlated ($r^2 = 0.70$; Fig. 6a) with algal standing stocks during this April cruise (chlorophyll *a* [chl *a*]; Fig. 6a). The potential importance of phytoplankton to bacterial dynamics is further supported by the covariance of BNP and chl *a* ($r^2 = 0.75$; Fig. 6b). These trends are in stark contrast to the absence of any discernible relationship between BNP and phytoplankton biomass distributions reported previously for the tidal freshwater reach of the Hudson (Findlay et al. 1991b), the Hudson River plume in the New York Bight (Ducklow & Kirchman 1983), the Chesapeake Bay (Ducklow & Shiah 1993), and the Delaware River estu-

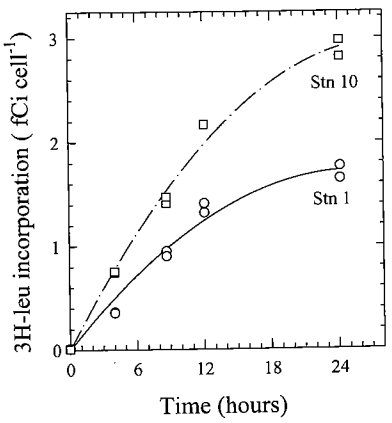

Fig. 8. Time course of ^{3}H-leucine incorporation into protein, normalized by cell concentration, n. At Stn 1, n = 5.4×10^8 cells l^{-1}, community uptake rate constant, $k = 0.12$ d^{-1}, and the leucine half-life, $t_{1/2}$ = 6.1 d. At Stn 10, n = 12.0×10^8 cells l^{-1}, $k = 0.46$ d^{-1}, and $t_{1/2}$ = 1.5 d

nous materials, e.g. humic and fulvic acids, which may flocculate out as salinities increase, whereas downstream HMWOC may originate from autochthonous or other allochthonous sources, such as sewage, and be less refractory in composition. The composition and lability of HMWOC along this reach of the Hudson estuary can not be assessed with existing data nor are there any direct methods for such determinations. However, while carbon and bacterial dynamics in this estuary must certainly vary seasonally with flow conditions, nutrient inputs, and temperature, our results indicate that HMWOC is a very important component of the DOC despite its small contribution to the total carbon budget. Therefore, our ongoing research is employing a variety of indirect methods (e.g. hydrolytic enzyme activity, bacterial oxygen demand, and radiotracer studies) to better assess the importance of HMW material in carbon cycling throughout the year. Finally, our results also suggest that trophic relationships and organic carbon cycling may vary significantly in different reaches of this river. Specifically, that, unlike the upper reaches of the Hudson River, bacterioplankton production in the estuarine portion may be coupled to *in situ* primary production for at least some portion of the year.

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