Bacterial Dynamics in Large and Small Estuaries

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ABSTRACT

We have been investigating bacterioplankton biomass and production in Chesapeake Bay for the past decade. More recently we initiated a system-level study of bacterial and DOM dynamics in the York River, Virginia, a small (100 km) subestuary of the Chesapeake Bay. In Chesapeake Bay, where water residence times are long (months), bacterial biomass and production show maxima in the middle, mesohaline reaches of the estuary. In contrast, in the York River bacterial rates and biomass consistently show opposing monotonic trends, with biomass increasing, and activity decreasing, to the seaward. Dissolved organic carbon (DOC) utilization experiments and natural carbon isotopic abundance data suggest that terrestrial DOC supplied in the freshwater inflow is used preferentially and may structure the bacterial community. The contrasting patterns within and between estuaries were analyzed with respect to the DOM supply hypothesis and other environmental controls, and compared to oceanic patterns.

Introduction

Patterns in the distribution of organisms in space, and their fluctuations in time, provide useful clues about the ecological dynamics of populations [3, 9]. In many cases, production and removal processes governing the dynamics of microbial populations are closely coupled, masking temporal variations, and leading to the perception that populations are static. In such cases it is possible that spatial or geographical patterns in abundance might still provide information on the underlying dynamics. These same considerations might also be applied to the distributions of chemical compounds and geochemical tracers, especially labile and short-lived chemical species that are the chemical analogs of fast-growing microbes. Finally, simultaneous investigation of the distribution of organic compounds and the populations utilizing them should be a powerful tool for elucidating biogeochemical processes of carbon cycling. Geochemical tracers also provide rigorous constraints on biological rate processes.

Plankton populations in flowing water are a special case in geographical microbial ecology. It has long been understood that plankton can only accumulate if their net growth rate (production minus removal processes) exceeds dispersive forces (i.e., diffusion, turbulence and advection [7]. The same concept should apply to geochemical species as well as biotic ones. Thus if we can specify the spatial distribution of particular populations and rates of physical advection and dispersion, we should be able to constrain the net rates of turnover. The joint use of physical and biological rate processes is especially valuable for bacterial populations because our ability to accurately measure growth and removal rates is still quite limited [4]. Here we consider some aspects of this approach as it relates to the total heterotrophic bacterial assemblage and labile organic carbon compounds

Microbial Biosystems: New Frontiers
Proceedings of the 8th International Symposium on Microbial Ecology
Bell CR, Brylinsky M, Johnson-Green P (ed)
Atlantic Canada Society for Microbial Ecology, Halifax, Canada, 1999.

supporting bacterial production rates in estuaries. One final consideration concerns the spatial scales of processes and habitats. Since biotic populations and physical processes have characteristic time and space scales, the balance among physical and biological processes may differ in estuaries of different size. Therefore we examine biogeochemical and physical dynamics of several estuaries scaled according to flushing rates.

Bacterial Dynamics and Distribution

Chesapeake Bay is a large estuary (12,500 km^2) with a very large drainage basin and consequently a high ratio (ca. 28) of drainage area to water surface indicating the potential for great enrichment and, at least potentially, a large flux of terrestrially-derived organics into the estuary itself. Although the Bay is intensely monitored by local, state and federal water quality programs, none of the routine monitoring programs includes sampling of bacterial properties. Our group has been investigating bacterial dynamics in the Bay periodically since 1984 [5, 16]. We have consistently observed peaks of bacterial abundance and production rates in the mesohaline, mid-Bay region (Fig.1A). Although the location and amplitude of the peak varies seasonally and interannually, it is apparent even in annually averaged data and corresponds to the axial distribution of chlorophyll. Surprisingly, although chlorophyll is only weakly correlated with bacterial properties seasonally, there is a strong correlation between annual mean chlorophyll and thymidine incorporation rates ($r^2 = 0.97$, n=12). This pattern suggests a strong reliance of bacterial production in the mid-Bay region on *in situ* plankton metabolism. Bacteria can only accumulate in this hydrographic regime if the net growth rate (growth minus removal) exceeds the local dilution rate. Earlier we suggested that growth rates exceeded dilution rates in the mid-Bay surface layer [5], at least in summer, allowing net accumulation as seen in Fig. 1. The mesohaline abundance peak has also been observed during 1984-89.

Mid-estuarine maxima of abundance and production have also been observed in the Delaware Estuary [8], but the annual means suggest no up or down stream gradients [6]. The Essex Estuary, Massachusetts is about one tidal excursion in length and exhibited spatial variations over tidal to seasonal scales [17]. In the Newport River, North Carolina [11] and Upper St. Lawrence, Quebec [10] estuaries there were strong downstream declines in bacterial abundance. More recently we have carried out intensive bacteriological and geochemical investigations of the York River, a subestuary of Chesapeake Bay. The dynamics of the York are governed largely by tidal forces [1, 2]. The annual mean residence time of water in the surface layer is ca. 12 days [15]. Bacterial abundance shows a persistent monotonic trend of increasing abundance from freshwater downstream to the mouth where surface waters enter Chesapeake Bay (Fig 1B); 14], with no indication of a mid-estuarine maximum. Thymidine incorporation showed exactly the opposite pattern, increasing upstream from the mouth to the source waters. The opposing patterns of bacterial abundance and production suggest much faster specific growth rates (i.e., P/B ratios) and removal in the upper reaches of the estuary.

To investigate this pattern further, we applied a steady state box model [10] to our monthly, seasonally and annually averaged data sets. Painchaud [10] showed that down stream decreases in bacterial stocks in the St. Lawrence River (a large estuary) were due to a very slight excess of removal processes (principally grazing) over growth. In general however, they concluded that the bacteria in the estuary were in or very near trophodynamic equilibrium. Biological and physical processes generating the bacterial

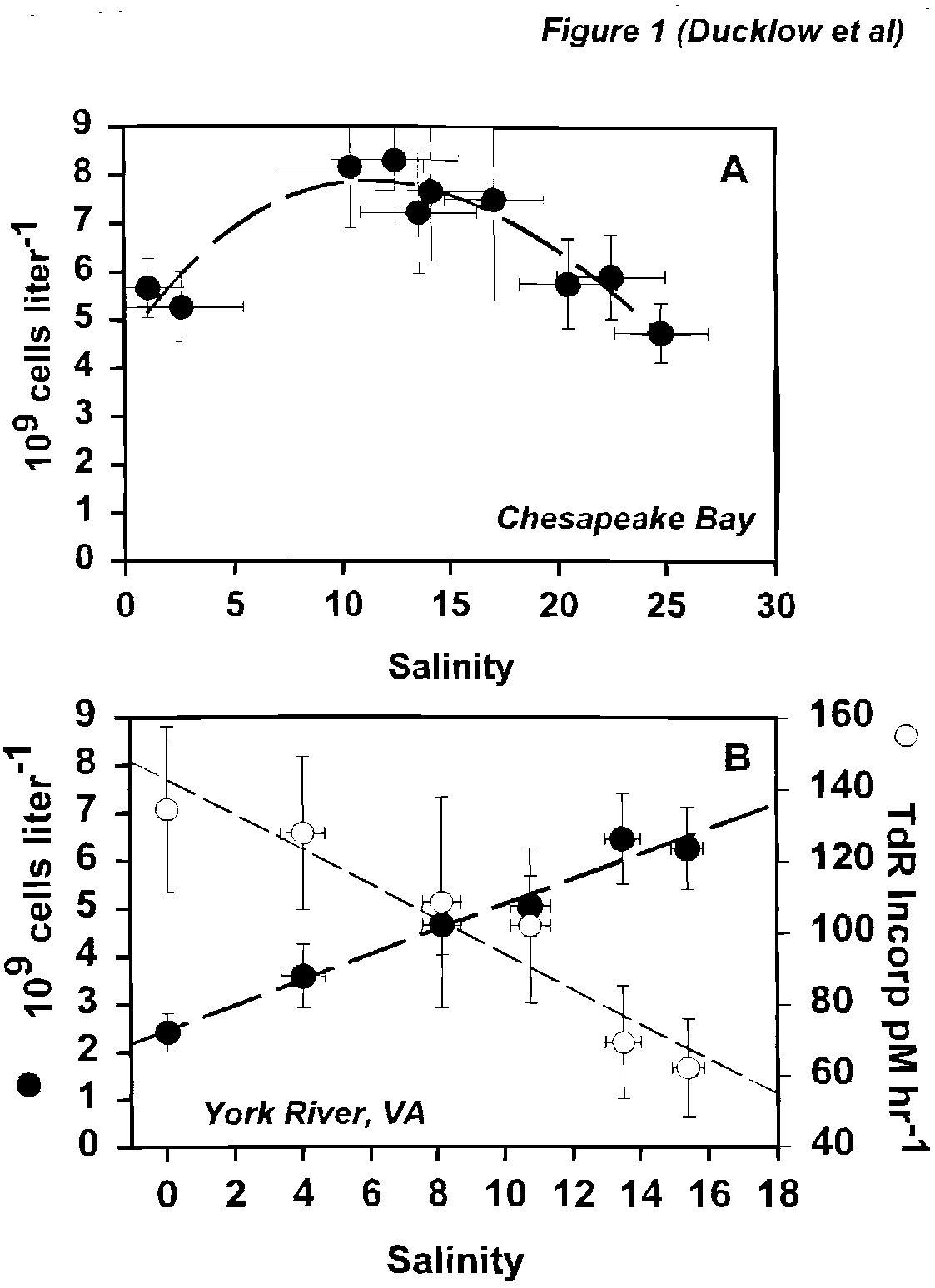

Fig. 1. A: Annual mean surface layer (2 m) bacterial abundance at principal sampling stations along the main stem of Chesapeake Bay during 1990-1991. Each point is the mean of 7 to 9 monthly samples [16]. **B:** Annual mean surface layer (2 m) bacterial abundance and thymidine incorporation rates at principal sampling stations in the York River, VA during 1996-97. Each point is the mean of 12 monthly samples [14,15]. (Error bars are one standard error of the mean.)

gradient had closely similar time scales. All segments of the St. Lawrence were shown to be a net sink for bacteria as a result of excess grazing at the time of sampling. Our analysis also suggests persistently close couplings of production and loss throughout the York estuary, but in this case the balance results in a gradient opposite to that in the St. Lawrence [15]. Also, in the York, the source-sink balances in different reaches along the salinity gradient vary seasonally. Overall, high bacterial growth rates in the upper reaches fuel the downstream gradient of bacterial abundance.

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Organic Carbon Dynamics

Estuaries have at least two distinct pools of dissolved organic carbon potentially utilized by bacteria: terrestrial carbon supplied by the fresh water input, and locally produced carbon from *in situ* plankton metabolism. Measurements of the isotopic composition of the DOC in the river and in experimental seawater culture incubations reveal patterns of bacterial utilization [12, 13]. Mixing curves reveal anomalies in the distribution of DOC on salinity (Fig. 2) as well as $\delta^{13}C$ and $\Delta^{14}C$ (data not shown), which can be explained by preferential utilization of freshwater DOC in the estuary. Further support for preferential utilization of freshwater DOC comes from incubation experiments which show that isotopically "light" ^{13}C, characteristic of terrestrial or freshwater DOC, is utilized even in intermediate salinity waters (Table 1). During the incubations $DO^{13}C$ becomes heavier (i.e., less negative) at salinities up to 12 PSU in September, indicating the preferential removal of terrestrial (light) DOC. A similar pattern is found for $DO^{14}C$ [13, data not shown]. Significant utilization of "marine" DOC was only found at salinities above 12 PSU.

Conclusions

The York River is anomalous in having a persistent *downstream* gradient of increasing bacterial abundance. Bacteriological and geochemical observations support the conclusion that this gradient is generated by high growth rates supported by utilization of terrestrial DOC in the upper reaches of the estuary. A box model analysis of circulation indicated that bacterial growth and removal are closely balanced, but that source-sink relationships in the York are more complicated than in the St. Lawrence. A simple excess of net growth over dilution alone cannot explain the distribution of bacteria in this estuary. For further insight we will be constructing numerical models of bacterial and tracer dynamics in the estuary.

Figure 2 (Ducklow et al.)

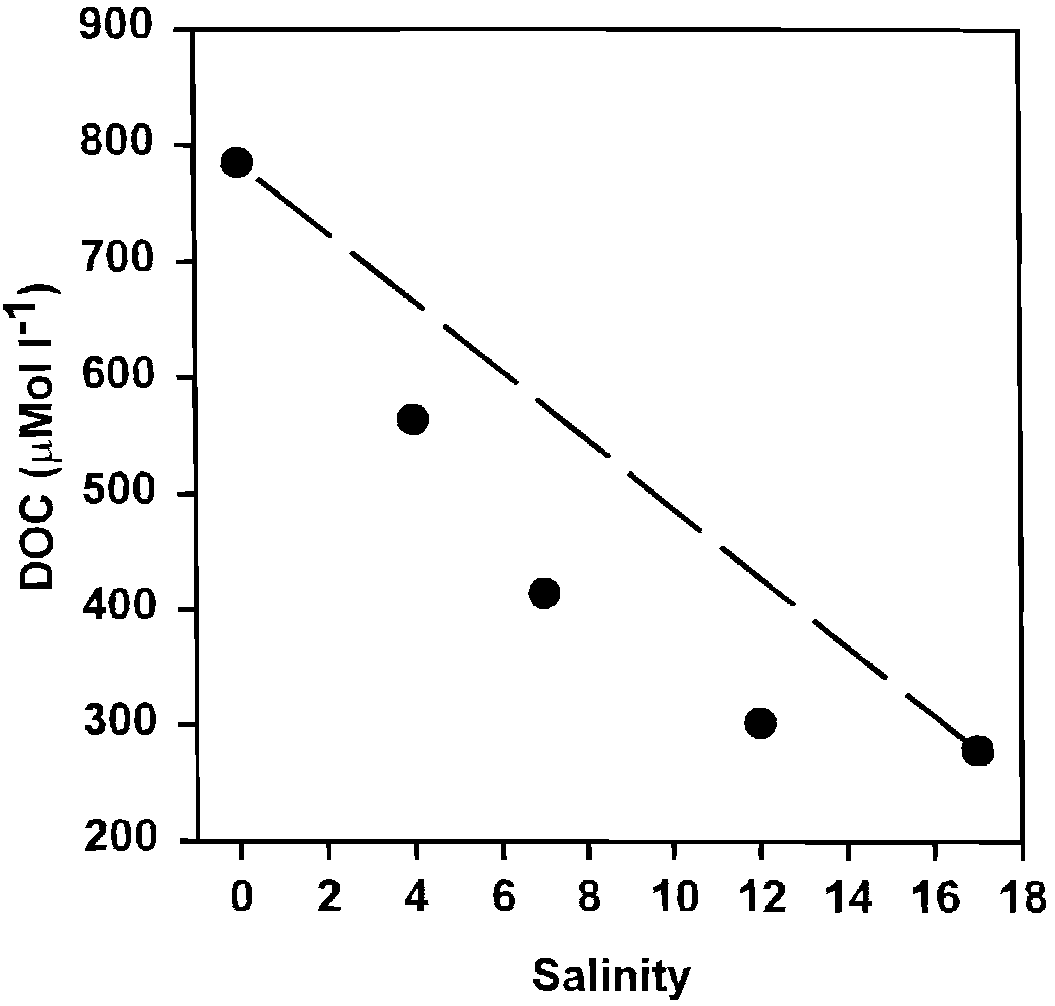

Fig. 2. Distribution of DOC in the York River in September, 1996. The line connecting the fresh- and saltwater endmembers shows the predicted concentrations if DOC behaved conservatively. The departure of the observed points indicates net removal during estuarine transit.

Table 1. Utilization of $DO^{13}C$ during seawater culture incubations. Incubations conducted in the dark over 6-8 weeks at *in situ* temperature using 07 μm filtrates.

Sample Salinity	$DO^{13}C$ t = 0	$DO^{13}C$ t = 6 weeks	Change
	March Sampling		
14.5	-24.21	-24.66	-0.45
12	-24.68	-25.29	-0.61
7.8	-25.49	-25.56	-0.07
3.4	-27.30	-26.63	0.67
0.1	-28.76	-28.67	0.09
	September Sampling		
17	-24.33	-24.53	-0.20
12	-25.40	-25.35	0.05
7	-26.36	-26.26	0.09
4	-28.68	-27.71	0.97
0	-28.02	-27.76	0.26

Acknowledgements

Research on bacteria in the York River will form part of G. Schultz's Ph. D. thesis and has been supported by ONR Contract N00014-93-1-0986. Research on carbon in the York River will form part of P. Raymond's Ph. D. thesis and has been supported by US DOE Contract DE-FG05-94ER61833. Chesapeake Bay data from F-K. Shiah's Ph. D. thesis supported by the University of MD Sea Grant and the NSF-LMER Program. The authors thank J. T. Hollibaugh for the invitation to present this work.

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