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Longitudinal and depth variation of bacterioplankton productivity and related factors in a temperate estuary

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ABSTRACT

Bacterioplankton productivity (BP) spatial variation was investigated in relation to potential resources, including primary productivity and dissolved organic matter, in the micro-tidal Neuse River–Pamlico Sound estuarine system, North Carolina, USA. Estuarine BP was predicted to correlate with the trophic gradient, decreasing along the salinity gradient in parallel with the decrease in organic matter and primary productivity. This prediction was tested over four years at spatial scales ranging from kilometers to meters along the riverine axis and with depth. The general pattern of BP across the salinity gradient was unimodal and matched the phytoplankton patterns in peak location and variability. Peak locations varied with discharge, especially in 2003 when above average discharge moved peaks downstream. Spatial coherence of BP with other variables was much less at short time scales. The effect of temperature, nutrients, and phytoplankton on BP varied by location, especially fresh versus brackish stations, although only temperature explained more than 20% of the BP variation. Depth variation of BP was as great as longitudinal variation and bottom samples were often higher than surface. BP was strongly correlated with particulate organic carbon at the pycnocline and bottom, highlighting the importance of particulate matter as a resource. Station-averaged BP and phytoplankton data corresponded well with two published meta-analyses, although the offset of the freshwater station suggested longitudinal differences in community composition or resource availability.

1. Introduction

An essential part of understanding microbial activity in any system is to determine the patterns of variation through space and time. Estuaries can be considered ecotonal ecosystems (Odum and Barrett, 2005), forming the transition between inland and oceanic waters, and are typically characterized by great spatiotemporal variability. In particular, the mixing of water masses forms strong chemical (i.e., salinity and nutrients) and biological gradients. Resident bacterioplankton exposed to these gradients will form varying patterns of activity and abundance through a combination of physical forces (e.g., tides, flushing, mixing), resource availability, and grazing or viral pressure.

Given that estuaries are considered some of the world's most productive ecosystems, there usually exists a trophic gradient that decreases as salinity increases from estuarine to oceanic systems (Day et al., 1989). Rates of bacterioplankton productivity (BP) have been shown to correlate positively with rates of primary productivity across many systems (Cole et al., 1988). Therefore, BP and bacterioplankton abundance (BA) would be predicted to show a decrease along the increasing salinity gradient in estuaries, either because of conservative mixing and loss of cells, or because of a parallel decrease in autochthonous or allochthonous resources along the salinity gradient.

Indeed, that is what many authors studying a range of systems have found. Palumbo and Ferguson (1978) found a linear decrease in BA with increasing salinity in the shallow, tidal Newport River estuary. This was also seen in the Fraser River (Bell and Albright, 1981), and for both BA and bacterial activity in the St. Lawrence River (Painchaud et al., 1987, 1996). A decrease in BP and BA along a seaward transect was also reported for the Schelde (Goosen et al., 1997), Urdaibai (Revilla et al., 2000), Rhone (Troussellier et al., 2002), and Roskilde Fjord (Jensen et al., 1990) estuaries. In the York River, BP showed the same pattern, but BA increased with increasing salinity (Schultz et al., 2003).

Another spatial pattern that researchers have frequently reported is a mid-estuarine peak of abundance and/or activity. Systems including the Essex River (Wright and Coffin, 1983),

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Chesapeake Bay (Ducklow et al., 2000), Delaware Bay (Kirchman and Hoch, 1988), and Ria de Aveiro (Cunha et al., 2000) estuaries and the Mississippi River plume (Chin-Leo and Benner, 1992) had peaks of BA and BP or activity at intermediate salinities relative to the estuarine gradient. Other systems have a positive correlation between bacterial measurements and salinity. This trend appeared in the lower Hudson River (Sañudo-Wilhelmy and Taylor, 1999) and periodically in Mobile Bay (McManus et al., 2004).

Christian et al. (1984) examined the Neuse River estuary (NRE), a shallow, micro-tidal, meso- to eutrophic coastal plain estuary, and found a similar increase in BP and BA with increasing salinity, although they did not cover the full salinity gradient. The Neuse River has been the subject of much research over the past several decades, in part because of a well-documented history of nuisance algal blooms, hypoxia/anoxia, and fish kill events thought to be symptoms of eutrophication driven by human activities in the watershed (Paerl et al., 1998; Paerl, 2006). Most of this research has focused on phytoplankton and water quality issues. The long-term monitoring program already in place in this estuary (ModMon; Luettich et al., 2000; Paerl, 2006) provided the opportunity to focus on the less-studied bacterioplankton community. Here, the results from a 4-year study of bacterioplankton in the Neuse River and Pamlico Sound (NRPS) estuarine system are used to describe and discuss the spatial patterns and potential controlling factors of BP along the full salinity gradient and across depth. In particular, the question of bacterioplankton–phytoplankton coupling at those particular spatial scales was addressed.

2. Methods

2.1. Study area, field measurements, and water collection

Most methodological details for this study are reported in Peierls et al. (2003) and Peierls and Paerl (2010) and will only be summarized here. From 2002 through 2005, eight stations were visited biweekly to monthly (four at any one time) along the central axis of the NRE and out into the Pamlico Sound (PS, Fig. 1). In addition to the long-term sampling, the NRE between stations NR0 and NR120 was sampled four times over two weeks in June 2005 as part of an exercise to track estuarine phytoplankton biomass at a smaller scale. The locations were chosen so that the station group at each time point was centered on the local surface chlorophyll *a* maximum (Paerl et al., 2007), with the upstream and downstream locations spaced between 5 and 10 km from the center.

Profiles of basic water quality characteristics were collected at each station visit using a YSI 6600 sonde (Yellow Springs, OH) configured to measure temperature, salinity, dissolved oxygen (DO), and *in vivo* chlorophyll fluorescence. Sensors were calibrated prior to the sampling date, except DO, which was calibrated in the field and checked throughout the run. Readings were collected at 0.5 m intervals starting at the surface and continuing until just off the bottom. River discharge data came from USGS Gage No. 02091814 near Ft. Barnwell, NC (waterdata.usgs.gov/nc/nwis) and annual averages were based on calendar year.

At each station, water was collected from surface and near bottom levels. Surface samples were collected by submerging cleaned (dilute acid and deionized water) and sample-rinsed polyethylene containers 10–20 cm below the water surface. Subsurface samples were collected with a horizontal Van Dorn collector at approximately 0.5 m above the sediment surface and, when required, to the approximate depth of the pycnocline determined from salinity profiles. Samples were transferred to cleaned and sample-rinsed polyethylene containers. All samples were kept covered during transport to the laboratory.

2.2. Lab and data analyses

Methods for organic matter, nutrients, chlorophyll *a*, primary productivity, and BP are summarized here. Water samples were divided into dissolved and particulate fractions by filtration

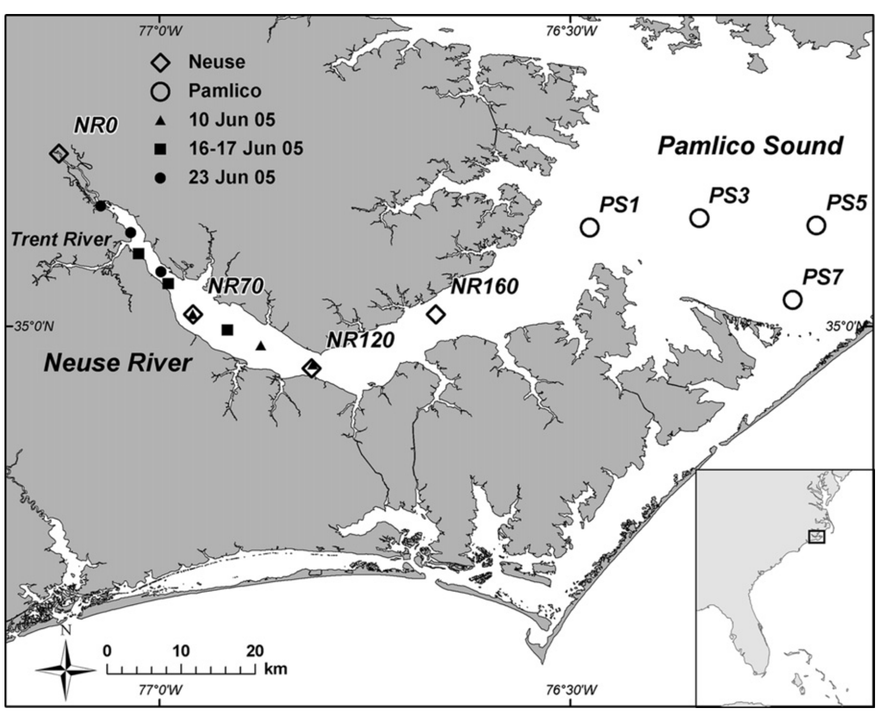

Fig. 1. Map of study site showing long-term sampling stations in the Neuse River and Pamlico Sound (open symbols) and three groups of stations used for smaller horizontal and vertical scale measurements (filled symbols).