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Microbial activities and organic matter degradation at three sites in the coastal North Atlantic: Variations in DOC turnover times and potential for export off the shelf

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ABSTRACT

The Mid-Atlantic Bight is a highly productive region where considerable quantities of organic matter are processed, transformed, and respired. Much of this organic matter is in the form of dissolved organic carbon (DOC). We investigated the activities of heterotrophic microbial communities responsible for DOC processing at three sites in the coastal Mid-Atlantic Bight/northern end of the South Atlantic Bight: near the Chesapeake Bay mouth, off Cape Hatteras, and near Cape Lookout, NC. Activities of endo- and exo-acting extracellular enzymes (polysaccharide hydrolases, and glucosidase and peptidases, respectively), and bacterial protein production were measured in surface and subsurface waters at the three stations. Total suspended material, cell counts, and particle-associated enzyme activities were also quantified. Water masses at each station showed distinct physical characteristics (temperature, salinity, total suspended material), and differed notably in rates and spectrum of enzyme activities, as well as in the fraction of particle-associated activities. Despite similar cell counts, bacterial productivity differed by a factor of ca. 30 among depths and stations. Glucosidase and peptidase activities differed by a factor of ca. 40 among stations, but the differences in enzyme activities among stations did not scale with the differences in bacterial productivity. Theoretical turnover times of dissolved carbohydrates – calculated from total dissolved carbohydrate concentrations and polysaccharide hydrolase activities – range from weeks to months, suggesting that dissolved carbohydrates may be among the components of DOC that can be advected from the Mid-Atlantic Bight into the open ocean, connecting the carbon cycle in the ocean margin with the ocean's interior.

1. Introduction

Coastal and continental margin environments typically are sites of active carbon cycling, where autochthonous and allochthonous organic matter is transported, transformed, respired, and buried in sediments (Hedges and Keil, 1995). The Mid-Atlantic Bight, extending from George's Bank to Cape Hatteras, NC, is one such region that has been intensively studied in order to quantify organic matter burial as well as export to the open ocean. Net transport in the Mid-Atlantic Bight is generally in a southward direction towards Cape Hatteras; the northward flow along the South Atlantic Bight (Cape Canaveral FL to Cape Hatteras) also exits the shelf near Cape Hatteras (Lohrenz et al., 2002). The continental slope off Cape Hatteras has therefore been regarded as a potential 'depocenter' for organic carbon produced on and transported from the shelf, and initial studies focused on characterizing and quantifying particulate organic carbon (POC) transport and burial along the continental slope (e.g. Anderson et al., 1994; Biscaye et al., 1994).

The dissolved organic carbon (DOC) pool in this region, however, is estimated to be one to three orders of magnitude greater than the POC pool (Bauer et al., 2001). Sources of DOC to the Mid-Atlantic Bight include input via the Chesapeake and Delaware estuaries, fluxes from shelf sediments, and primary productivity on the shelf (Vlahos et al., 2002). Variations in primary productivity in these waters are associated in part with the relative influence of the Chesapeake and Delaware outflow, compared to shelf waters that have been influenced by the Gulf Stream (Filippino et al., 2011). Considerable spatial and seasonal differences in DOC dynamics have consequently been observed within the Mid-Atlantic Bight (e.g. Bauer et al., 2001; Hopkinson et al., 2002; Vlahos et al., 2002).

Some of these differences are likely due to spatial and seasonal variations in the composition and activities of the heterotrophic microbial communities that drive much of DOC cycling in the ocean (Baltar et al., 2007; Carlson et al., 2004). These communities repackage, respire, and recycle a considerable fraction of DOC, regenerating nutrients and releasing CO_2 to the surrounding waters. The initial step in microbial processing of high molecular weight DOC is carried out by the activities of extracellular enzymes, which hydrolyze substrates outside the cell to sizes sufficiently small to permit uptake. Within a heterotrophic

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microbial community, some member(s) of the community must produce enzymes of the correct structural specificity to hydrolyze the substrate at hand (see Arnosti (2011) for a recent review). Differences in enzymatic capabilities have been demonstrated among isolated bacteria and individual organisms (Martinez et al., 1996; Wegner et al., 2013; Xing et al., 2014) and among communities at different locations and depths in the ocean (Arnosti et al., 2011, 2012; Steen et al., 2012), including the Delaware and Chesapeake River and Bay, and the Blake Ridge, off North Carolina (Keith and Arnosti, 2001; Steen et al., 2008; Ziervogel and Arnosti, 2009; D'Ambrosio et al., 2014). These differences suggest that the nature and quantity of organic matter available for heterotrophic processing is also a function of the enzymatic capabilities of the microbial community in a given location.

In the current investigation, we focus on microbial heterotrophic activities at three near-shore stations of the Mid-Atlantic Bight and the northern edge of the South Atlantic Bight, sites that have distinct physical and chemical characteristics. Our previous investigations of extracellular enzymatic activities have focused primarily on the activities of polysaccharide hydrolases, but did not typically encompass measurements of bacterial protein production or biomass. Previous studies of carbon dynamics at the Mid-Atlantic Bight have focused on dynamics of water masses, DOC inventories, characteristics, and bulk consumption (Bauer et al., 2001; Hopkinson et al., 2002; Vlahos et al., 2002), but detailed investigations of the carbon-degrading capabilities of microbial communities have been lacking. In the present study, we measured bacterial protein production, cell counts, and the activities of a range of extracellular enzymes that initiate organic matter remineralization. These enzymes included endo-acting (mid-chain cleaving) enzymes that hydrolyze specific polysaccharides as well as exo-acting enzymes that hydrolyze glucose and leucine from terminal ends of polysaccharides and proteins, respectively. Since freshwater input to the Mid-Atlantic Bight also can include particles and sediments that likely harbor active microbial communities, we measured total suspended material, and determined the contribution of large-particle-associated (>3 μm) enzymes to the total activities measured. Our objective was to measure the heterotrophic turnover of organic matter, as indicated by the activities of extracellular enzymes, and to estimate variations in DOC turnover times by depth and location.

2. Methods

2.1. Study sites and sample collection

Water samples were collected between November 1st and 5th 2010 from three stations in the coastal North Atlantic, in southern portion of the Mid-Atlantic Bight and the northern edge of the South Atlantic Bight (Fig. 1). A Niskin bottle rosette sampler equipped with a conductivity-temperature-depth (CTD) sensor was deployed from the R/V *Cape Hatteras* to collect surface water samples as well as samples from subsurface waters at or near the particle maximum depth, as determined by beam attenuation recorded by the CTD (Fig. 2). At the mouth of the Chesapeake Bay (Station CBM; 36° 57.72 N, 75° 59.85 W; water column depth 22 m) samples were collected at depths of 1 m and 14 m. Offshore Cape Hatteras, North Carolina, samples were collected at 1 m and 58 m (Station CHO; 35° 24.08 N, 74° 55.65 W; water column depth 64 m). Station CLN (34° 36.15 N, 76°36.23 W; water column depth 14 m) was a near-shore station just south of Cape Lookout, North Carolina. Only surface water (1 m) was collected at Stn. CLN. Processing of water began immediately aboard ship after collection.

2.2. Sample filtration for activities of particle-associated microbial communities

Triplicate water samples from surface (Stns. CBM, CHO, CLN) and subsurface depths (Stns. CBM and CHO) were gravity-filtered for several hours through 3 μm Isopore membrane filters (Millipore USA) immediately after the CTD rosette was retrieved to capture the particle-associated microbial communities. The specific volume of water filtered through each of the replicate filters ranged from 1.5 to 6 L; rates reported are normalized in each case to volume filtered. The filters were

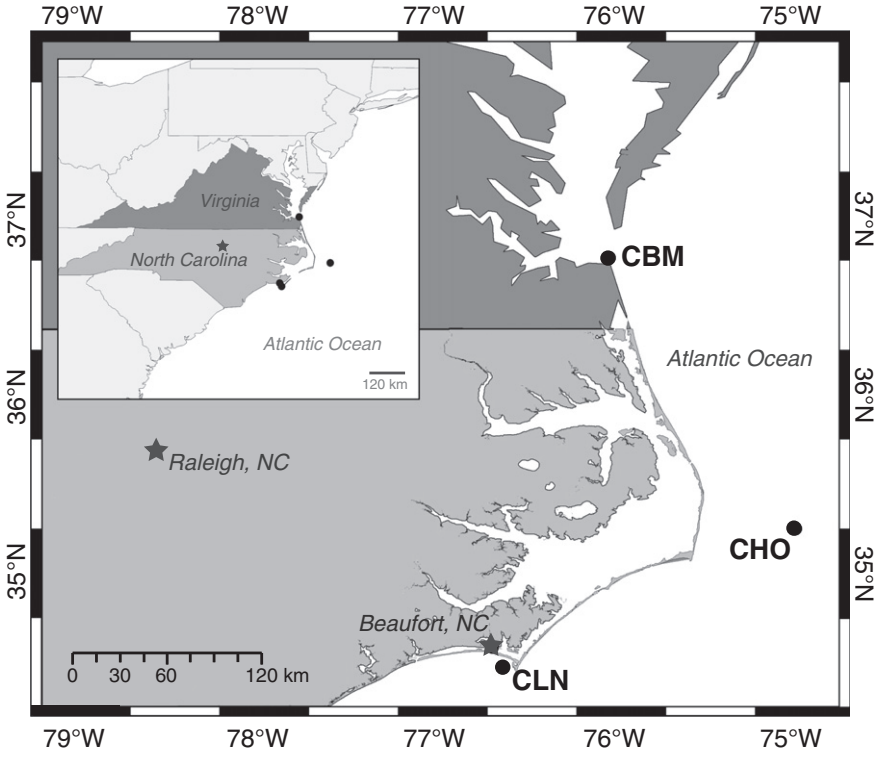

Fig. 1. Map of station locations: CBM (Chesapeake Bay mouth), CHO (Cape Hatteras offshore), and CLN (Cape Lookout nearshore).