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Nitrogen uptake and primary productivity rates in the Mid-Atlantic Bight (MAB)

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ABSTRACT

Nutrient concentrations, primary productivity, and nitrogen uptake rates were measured in coastal waters of the Mid-Atlantic Bight over a two-year period that included measurements from all four seasons. In order to assess carbon productivity and nitrogen demand within the context of the physical environment, the region was divided into three distinct hydrographic regimes: the Chesapeake and Delaware Bay outflow plumes (PL), the southern Mid-Atlantic shelf influenced by the Gulf Stream (SS), and the mid-shelf area to the north of the Chesapeake Bay mouth (MS). Annual areal rates of total nitrogen (N) uptake were similar across all regions (10.9 ± 2.1 mol N m^{-2} y^{-1}). However, annual areal rates of net primary productivity were higher in the outflow plume region (43 mol C m^{-2} y^{-1}), than along the Mid-Atlantic shelf and in areas influenced by the Gulf Stream (41 and 34 mol C m^{-2} y^{-1}, respectively). Rates of net primary productivity were not well correlated with Chl *a* concentrations and were uncoupled with net N uptake rates. Seasonally averaged annual areal rates of net primary productivity for the Mid-Atlantic Bight measured in this study were higher than those calculated in previous decades and provide important validation information for biogeochemical models and satellite remote sensing algorithms developed for the region.

1. Introduction

While the global coastal ocean (<200 m) comprises less than 10% of the world's oceans, these highly productive regions are thought to account for more than 21% of total oceanic productivity (Gattuso et al., 1998; Jahnke, 2007). Primary production in most coastal and shelf systems is thought to be limited by nitrogen (N) (Dugdale and Goering, 1967; Ryther and Dunstan, 1971; Howarth and Marino, 2006), however these areas are impacted by adjacent landmasses and receive anthropogenic N inputs that can potentially alleviate this limitation. Consequently, productivity in these areas is often controlled by "new" N inputs [sensu Eppley and Peterson, 1979] from terrestrial sources such as rivers, overland and groundwater discharge, and from atmospheric deposition (Duce et al., 2008). Denitrification in freshwater, terrestrial, and estuarine sediments removes a substantial amount of reactive N (globally, between 80 and 90%) before it even enters the coastal zone and it is thought that most of the remainder is denitrified in continental shelf sediments (Galloway et al., 2008). In the Mid-Atlantic Bight (MAB), denitrification is thought to remove 90% of the total N entering the region by advection from the north and riverine sources (Fennel et al., 2006).

Because high denitrification rates in freshwater and estuarine systems effectively removes N before it is delivered to coastal systems, riverine and terrestrial run-off has less of an effect on primary productivity in the coastal zone than would otherwise be expected (Seitzinger et al., 2006). However, riverine N loading to the coastal U.S. has almost doubled over the past forty years and it is projected that these inputs will increase by another 30% over the next 30 years (Howarth et al., 1996, 2002). If denitrification in freshwater and estuarine sediments does not increase concomitantly with increasing N loads, the system may become saturated with reactive N and become a source of N to otherwise N-limited coastal systems off-shore (Galloway et al., 2008).

The N budget in the MAB is an important driver of primary production in this N-limited area, and therefore is tightly coupled to the carbon (C) budget (Howarth, 2004; Gruber and Galloway, 2008). Increases in primary productivity have been related to increases in anthropogenic N inputs into the coastal zone (Howarth et al., 2002; Paerl and Piehler, 2008; Conley et al., 2009). In particular, models used to predict algal growth and C draw down from nutrient loading often use simple conversion factors such as the Redfield ratio to estimate primary productivity from N uptake and vice versa (Fennel et al., 2006, 2008). Ratios of standing stocks of N and C may not be appropriate for relating N uptake to C productivity or turnover. In eutrophic environments, there may be shifts in the absolute amount and dominant source or form of N delivered to the coastal ocean from terrestrial sources (Cloern, 2001; Galloway et al., 2008), which

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in turn could effect photosynthetic activity and metabolism (Syrett, 1981; Syrett and Peplinska, 1988). For example, a shift from inorganic N to organic N loading may alter a community structure which could then affect net system trophic status or fuel algal blooms (Glibert et al., 1991, 2001). Mixotrophy also appears to be common in eutrophic environments (Burkholder et al., 2008; Heisler et al., 2008; Anderson et al., 2008) and both grazing and osmotrophic C uptake by phytoplankton mixotrophs can result in bicarbonate:N uptake rates that deviate from Redfield.

Large-scale shifts in circulation patterns and nutrient delivery to coastal regions due to sea level rise and changes in storm activity under projected climate change scenarios are likely to have great consequences for N delivery to coastal systems and coastal productivity (Stevenson et al., 2002; Alley et al., 2007). Physical processes controlling mixing are an important control on N availability and primary productivity and seasonal stratification/destratification; upwelling can dominate the annual cycle of productivity in the MAB (Flagg et al., 2002; Lentz, 2003; Rasmussen et al., 2005). Specifically, interactions between the flow of the cold Labrador current from the north and the warm oligotrophic Gulf Stream current from the south creates a complicated pattern of seasonal stratification and destratification that is highly dependent on wind speed, direction, duration, and eddy development (Flagg et al., 2002). In the Summer months, along the southern near shore section of the North American Mid-Atlantic coast, the water column is highly stratified, thus limiting vertical transport of nutrients to surface waters from depth and primary productivity is greater near the bottom of this shallow water column rather than in surface waters (O'Reilly and Zetlin, 1998; Flagg et al., 2002). Intrusions of saltier deep water from the slope increases during the Summer in the along-shelf direction (from north to south), thus leading to higher salinity surface waters, nutrient upwelling and increased biomass concentrations in subsurface waters (about 20–25 m) during this time (O'Reilly and Zetlin, 1998; Flagg et al., 2002; Lentz, 2003). In the Fall, surface waters cool and the water column turns over, due to wind-driven mixing, and there is higher productivity in the near shore surface waters and along the shelf (O'Reilly and Zetlin, 1998). The water column is usually well-mixed with generally low productivity during the Winter (Wright and Parker, 1976; Rasmussen et al., 2005). In the Spring, increased light availability leads to higher productivity in relatively nutrient enriched surface waters (O'Reilly and Zetlin, 1998).

In addition to physical forcing and anthropogenic N inputs, primary productivity in the MAB and other coastal areas may be affected by increasing atmospheric carbon dioxide (CO_2) concentrations and/or projected temperature rises in the future, as has been observed in the oligotrophic North Atlantic and in mesocosm experiments (Hein and Sand-Jensen, 1997; Riebesell et al., 2007). The sensitivity of coastal regions to increasing CO_2 and water temperature is largely unknown and so the future of these systems as sources or sinks of atmospheric CO_2 is in question (Riebesell et al., 2007). While ocean margins, including those associated with the MAB, are currently thought to be net sinks for atmospheric CO_2, it is unclear whether the MAB will be a net source or sink of atmospheric CO_2 in the future given the complex interactions affecting productivity in the region (Chavez et al., 2007). How N availability will affect primary production and the ocean's ability to continue to take up C is centered on understanding 'nitrogen-carbon-climate interactions' (Gruber and Galloway, 2008). Quantifying regional N dynamics at present will not only help resolve N budgets and primary productivity in coastal regions under present day climatic conditions, but will allow us to begin to project what the future might hold under evolving climate change scenarios (Howarth, 2004).

Like most oceanic systems, the MAB is under-sampled and so the N budget is poorly constrained. There are few measurements of N uptake in this coastal system and most models estimate N demand for primary productivity from nitrate (NO_3^-) and ammonium (NH_4^+) uptake (Fennel et al., 2006). However, uptake of these compounds is often lower than that of other N compounds such as nitrite (NO_2^-), urea, and dissolved free amino acid N (DFAA N) and uptake of these compounds can be particularly important in coastal regions where recycling is rapid (Lipschultz, 2008; Filippino et al., 2009). Multiple N forms are present at any given time, including inorganic and organic compounds, and phytoplankton and bacteria can compete for these N compounds, complicating our interpretation of uptake data (Mulholland and Lomas, 2008). In addition, many phytoplankton are mixotrophic and so the relationship between N uptake and photosynthetic C fixation can be complicated, particularly in coastal regions enriched in organic and inorganic N compounds. In this study we quantified ambient N concentrations, N uptake using a broad range of inorganic and organic N compounds, and photosynthetic C uptake with respect to the hydrographic regime. This information is essential for constructing and testing models, developing accurate algorithms to estimate productivity from ocean color, and predicting present day and future uptake of atmospheric CO_2 in this highly productive region.

2. Materials and methods

Five cruises were undertaken over two years (30 March–2 April 2005; 26–30 July 2005; 9–12 May 2006; 2–5 July 2006; 30 October–2 November 2006). Primary productivity rates, N uptake rates, and nutrient concentrations were measured during these 3–5 day sampling excursions. Stations included locations in the Chesapeake Bay mouth and its outflow plume [see also Filippino et al., 2009], the Delaware Bay outflow plume, waters influenced by the Gulf Stream, and the non-estuarine influenced continental shelf between the Delaware Bay and Chesapeake Bay (Fig. 1). Exact station locations varied between cruises due to meteorological,

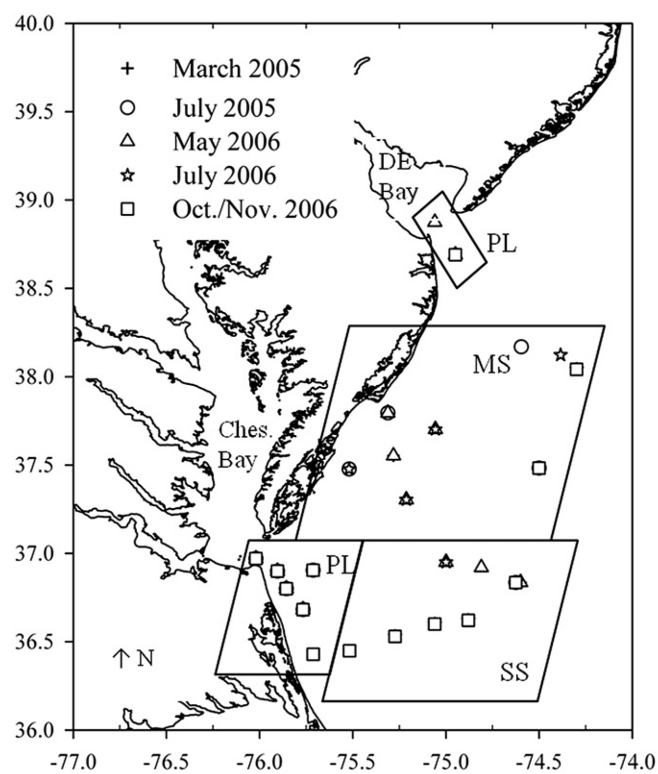

Fig. 1. Station locations for cruises conducted during March 2005 (plus signs), July 2005 (circles), May 2006 (triangles), July 2006 (stars), and October/November 2006 (squares).