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Microphytobenthos along the Louisiana continental shelf during mid-summer hypoxia

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ABSTRACT

Microphytobenthos may influence benthic processes, such as the oxygen dynamics in the bottom-water of the hypoxic area of the northern Gulf of Mexico. We collected sediment along the Louisiana continental shelf ~14–20 m isobath from the Mississippi River to Lake Calcasieu, LA, during periods of extensive bottom-water hypoxia in July 2006–2008 to estimate microphytobenthos biomass (chlorophyll a) and community composition. Typical sediment chlorophyll a concentrations were < 1.0 μg g dry sed^{-1}, with the highest mean concentration at a sandier mid-shelf area, and the lowest mean concentration at a station near the Mississippi River. Microphytobenthos abundances in the size fraction > 3 μm ranged from 0.7×10^1 to 1×10^5 cells g dry sed^{-1}. Benthic cells represented on average 67% of total cell abundance, varying from 1 to 99%, while pelagic and tychopelagic phytoplankton cells contributed to the remainder. Microphytobenthos were composed of diatoms (*Nitzschia*, *Gyrosigma*, *Pleurosigma* and *Bacillaria)* and cyanobacteria (filamentous and colonial). Our results indicate that environmental variables, mainly seafloor PAR and bottom-water nutrient concentrations correlated the most with the spatial distribution of microphytobenthos biomass and composition. Microphytobenthos along the Louisiana continental shelf, in turn, could influence benthic processes, such as secondary production, nutrient fluxes and oxygen dynamics.

1. Introduction

An area of bottom-water hypoxia (≤ 2.0 mg l^{-1}; a.k.a. 'Dead Zone') typically occurs from March to October off Terrebonne Bay located ~100 km west of the Mississippi River delta. It forms a continuous band of low-oxygen water along the Louisiana continental shelf and parts of the Texas shelf in mid-summer (Rabalais et al., 2002, 2007). The high spring discharge from the Mississippi and Atchafalaya rivers, which mostly flows westward with the Louisiana Coastal Current in winter and spring, provides the nutrient enrichment and stratification that promotes high primary productivity (> 300 g C m^{-2} y^{-1}) along the inner and mid continental shelf (Sklar and Turner, 1981; Lohrenz et al., 1990; Lehrter et al., 2009). Beginning in late winter, and especially spring (Redalje et al., 1994), the surface organic matter settles to the seafloor and fuels the microbially-mediated decomposition and mineralization of organic carbon resulting in the persistent oxygen depletion below the pycnocline (Turner and Allen, 1982; Murrell and Lehrter, 2011; Turner et al., 2012). Hypoxia is commonly found between the depths of 5–30 m on the Louisiana continental shelf (Rabalais and Turner, 2001), and its areal extent in mid to late-July averaged 18,800 km^2 since 1993, unless the area was perturbed by tropical storms or unusual shelf circulation patterns (Rabalais et al., 2007; http://www.gulfhypoxia.net, 19 December 2011).

Microphytobenthos are common on continental shelves (Cahoon, 1999; Underwood and Kromkamp, 1999), including in the western Atlantic (Cahoon et al., 1990; Nelson et al., 1999), Dogger Bank, North Sea (Reiss et al., 2007), Kattegat (Sundbäck and Jönsson, 1988), and the northern Adriatic Sea (Totti, 2003), which also experiences summer stratification and hypoxia (Justić et al., 1995). Photosynthetically available radiation (PAR) is a main factor limiting their abundance and production (MacIntyre et al., 1996; Blackford, 2002; Baustian et al., 2011).

Microphytobenthos are important food resources for micro- and macroheterotrophs, including deposit-feeding infauna (Marsh et al., 1989; Reiss et al., 2007) and may contribute to benthic secondary production in the northern Gulf of Mexico (Wells et al., 2008; Grippo et al., 2011). They also contribute to the total primary production of marine systems, which may exceed the integrated water column primary production (Cahoon and Cooke, 1992; Nelson et al., 1999;

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Totti, 2003; Grippo et al., 2009). Microphytobenthos can decrease the benthic inorganic nutrient fluxes out of the sediment (Sundbäck et al., 1991) and potentially reduce Si fluxes by >80% during daylight hours (Sigmon and Cahoon, 1997). They also may produce enough oxygen in the bottom water to affect hypoxia formation and maintenance (Jahnke et al., 2000; Justić et al., 2007).

Microphytobenthos were common with high abundances and biomass in the late summer/early fall off the central coast of Louisiana among sandy shoals and deeper muddier sites (Grippo et al., 2009, 2010; Baustian et al., 2011). The seasonal abundance and biomass of microphytobenthos along one frequently-hypoxic transect ~100 km west of the Mississippi River delta were correlated with relatively higher PAR levels, warmer temperatures, and the higher salinity of the bottom water. They co-occurred with summer hypoxia, typically following peak discharge in spring and during reduced wave activity (Baustian et al., 2011).

The null hypothesis for our research was that the microphytobenthos community in terms of abundance and biomass (as chlorophyll a) would be similar across the continental shelf within similar low oxygen conditions characteristic of mid-summer. The alternative hypothesis was that microphytobenthic abundances and biomass (estimated by chlorophyll a) would vary because of variations in seafloor PAR, sediment characteristics, or bottom-water nutrient concentrations. Here we describe the estimated biomass, abundance, and composition of microphytobenthos along the Louisiana continental shelf where hypoxia is typically present in mid-summer. We also verify that most of the primary producers on the sediment surface are benthic cells, and not the settled phytoplankton which are common in this highly productive area (Dortch et al., 1994, 2001; Baustian et al., 2011). This study is the first to document the broader distribution of microphytobenthos and related environmental conditions along the Louisiana continental shelf in the area of frequent hypoxia.

2. Methods

2.1. Field collections

We collected sediment for microphytobenthos on the annual, mid-summer shelfwide cruises that map hypoxia and related environmental variables (Rabalais et al., 2007). Sampling occurred from the Mississippi River to Lake Calcasieu, LA, along a 14 to 20 m depth contour in late-July of 2006–2008.

Water column environmental parameters were measured with a SeaBird CTD deployed within 1–2 m of the seafloor. A Hydrolab Surveyor 3 or YSI 6820 was used to obtain data as close to the seafloor as possible (0.1 to 0.5 m). The bottom waters for the 2006 stations I4, J4 and K4 were sampled only with the SeaBird CTD. We used data from a Biospherical Instruments Inc. profiling natural fluorometer (PNF-300) to determine the photosynthetically available radiation (PAR) at the seafloor and on the research vessel (reference PAR). The percent surface PAR reaching the seafloor was calculated from the reference PAR (mean $\approx$1600 μmol photons m^{-2} s^{-1}, $n=12$). The percent PAR calculations were used to normalize readings at different sampling times. Attenuation coefficients using the reference and bottom PAR were also calculated.

We sampled the surface water with a bucket and the bottom water with a 5-l Niskin bottle at 0.5 m above the seafloor. Water samples for phytopigments were filtered on 47 mm diameter Whatman GF/F filters (porosity of 0.7 μm) and stored in liquid nitrogen. Surface and bottom water for microscopic analyses were preserved in a nalgene bottle containing 1 ml glutaraldehyde (50%) and filled to 100 ml. Bottom-water samples were analyzed for nitrate+nitrite (BWNO3+NO2), ammonium (BWNH4), silicate (BWSi) and phosphate (BWPO4) using EPA methodology (353.2, 350.1, and 365.2) and a Lachat auto-analyzer II system (8000 series) equipped with an autosampler (ASX-400 series).

At each station we collected sediment from five GOMEX box cores (0.5 m high, 0.3 m long, 0.3 m wide, surface area 0.09 m^2, Boland and Rowe, 1991) that retained the overlying water and had an undisturbed sediment surface. Subsamples were taken using two acrylic core tubes (7.6 cm diameter) and the top 0.5 cm was removed from each subcore with a precision core extruder (Fuller and Butman, 1988) to obtain the depth of sediment most likely to be affected by light (MacIntyre et al., 1996). The first subcore sediment slice from each box core was homogenized in a Petri dish to fill two cyrovials (1.8 ml each, stored in liquid nitrogen) for pigment analysis and two cryovials (1.25 ml each, stored at 4 °C) for total organic carbon (TOC) analysis. Five replicates were analyzed for sediment pigments and three replicates for sediment grain size and TOC. The remaining sediment (~17 ml of slurry) from the first subcore (of one box core) was preserved for microscopy analysis in a 125 ml nalgene bottle with 1 ml of glutaraldehyde (50%) and filled with filtered sea water (0.02 μm) to 100 ml.

The percent total organic carbon by weight in sediment was determined using a Perkin Elmer CHN Model 2400 elemental analyzer after drying and grinding the sediment and acidifying to remove calcium carbonates (Hedges and Stern, 1984). We removed organics with 6% hydrogen peroxide, dispersed the sediments in hexametaphosphate, wet sieved (63 μm) to separate the sand from the mud, and determined sediment grain size by weight (Folk, 1974).

Bottom-water salinity, temperature, and dissolved oxygen concentrations were measured at station C6C (about 2.2 km from station C6B) south of Terrebonne Bay in 20 m water depth (28.8686°N, −90.4903°W) from June to August in 2006–2008 at 15 min intervals by a YSI 6600 EDS sonde located 1 m above the seafloor. We calculated the daily means of bottom-water parameters to help identify mixing events before, during, and after the shelfwide cruises.

2.2. Laboratory analyses

2.2.1. Phytopigments

Phytopigments were extracted in a dark room by sonication in cold HPLC-grade 100% methanol for water samples and sonicated with cold HPLC-grade 100% acetone for sediment samples. The filtered (0.2 μm) extract was injected into a Waters® high-performance liquid chromatography (HPLC) system equipped with a 600 controller, 600 pump, 996 photodiode array detector and 474 fluorescence detector based on the methods of Wright et al. (1991). The water content of the sediment samples was minimized during sample collection by carefully pipetting water from the core sediment surface before extruding and considered to have a minimal effect on calculating the concentration. We found high levels of pigment degradation products in the sediment and used three columns (Waters Nova-pak C_{18} 3.9 × 150 mm, a Rainin Microsorb C_{18} and a Vydac Reverse-Phase C_{18}) to separate and identify pigments. Sediment samples were run for 75 min with an elution gradient of 80:20 methanol:ammonium acetate, 90:10 of acetonitrile:water, and 100 percent ethyl acetate. Only one column (Waters Nova-pak C_{18} 3.9 × 150 mm) was needed for phytopigment analysis of the water samples, and they were run for 30 min on the same elution gradient. We used retention times and visible absorption spectra from DHI Lab standards as well as data and graphic sheets from Jeffrey et al. (1997) to help identify the pigments present. Some phytopigments were left out of the water and sediment analysis because the concentrations were zero or minimal for the majority of the samples. These pigments