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Influence of hypoxia on biogenic structure in sediments on the Louisiana continental shelf

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ABSTRACT

As part of a study of the effects of seasonal hypoxia on sediment properties, samples were collected during the spring and late summer of 2009 from four sites of similar sediment type and water depth (30–39 m), but different recent history of bottom water oxygen concentration on the continental shelf of Louisiana. Sediment profile imaging (SPI), box coring, X-radiography, and computed tomography (CT) imaging were employed to characterize the biogenic structural differences in surficial sediments among a normoxic control site and three sites subjected to hypoxic events varying in frequency of occurrence. Results of the CT imagery indicated that macrobenthic biogenic structures were the most numerous at the H7 site that had experienced the least hypoxia in the past 23 years. The E4 site that had experienced hypoxia seasonally with a frequency between 50% and 75% of the time had the fewest biogenic structures in spring 2009, but exhibited recovery in terms of their abundance and diameter in summer 2009. E4 also exhibited high rates of bioturbation during the late-summer sampling as determined from excess ^{234}Th. This suggests that the macrobenthos community at this site was in an active phase of recovery from hypoxia. At the A6 site, exposed to hypoxia with an annual frequency ≥75%, biogenic structures were numerous but dimensionally small, correlating with the average individual size of macrobenthos found there. The total volume maxima occupied by biogenic structures in the sediment occurred below the uppermost sediment intervals, with the exception of the spring sample from the D5 site that experienced hypoxia between 25% and 50% of the time. CT-imagery indicating effects of seasonal hypoxia on biogenic structure in the top 10 cm of sediments detected more structures than SPI, X-radiographic imagery, or macrobenthos census data. The presence of relict burrows probably inflated estimates of biogenic structures in the subcores, rendering an integrated result that included creation, destruction, and preservation of burrows and voids over time.

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1. Introduction

Seasonal hypoxia is present in coastal bottom waters around the world and over the past 60 years it has become more prevalent, especially in the northern Gulf of Mexico, Chesapeake Bay, and the East China and Baltic Seas (Conley et al., 2011; Díaz and Rosenberg, 2008; Lim et al., 2006). On the Louisiana continental shelf, hypoxia has been a recurring seasonal phenomenon since the 1970s, starting in spring, intensifying through summer, and declining in autumn (Rabalais et al., 1991, 1994). When bottom waters become hypoxic (<2 mg $O_2 \cdot L^{-1}$), pelagic and benthic fauna are adversely affected (Díaz and Rosenberg, 1995). Formation of seasonal hypoxia affects macrobenthic communities in the Gulf of Mexico, with declines in benthic species richness, abundance, and biomass (Rabalais et al., 2001; Baustian et al., 2009). Hypoxia also affects bioturbation activities of benthic infauna, through behavioral effects such as decreased movement and feeding (Tyson and Pearson,

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1991), decreased burrowing depth (Díaz et al., 1992), and emergence from the sediment (Nilsson and Rosenberg, 1994).

Bioturbation and creation of biogenic structures by macrobenthos have important consequences for sedimentary processes. The consequences of selective mortality and altered behavior of macrobenthos due to hypoxia will manifest as changes in faunal activities. When macrobenthos move, feed, excavate sediment, or construct and irrigate burrows, they can obliterate sedimentary structures (D'Andrea and Lopez, 1997), change sediment physical properties (Meadows and Meadows, 1991), redox profiles (Weissberger et al., 2009), and biogeochemistry (Aller, 1982). Biogenic activity also has various effects on the surrounding environment, and can affect larval and juvenile recruitment (Woodin et al., 1998), diagenetic properties of surficial sediments through dilation and compaction (Meadows and Tait, 1989; Jones and Jago, 1993; Rowden et al., 1998), and acoustic signal absorption and reflection (Briggs and Richardson, 1997).

Because of the close connection between eutrophication and hypoxia, the influence of hypoxia on benthic fauna closely follows the Pearson–Rosenberg organic gradient model (Pearson and Rosenberg, 1978), which defines patterns of abundance and biomass of equilibrium and opportunist faunal species that occur along a gradient of increasing organic matter. According to the model, as eutrophication proceeds with an increased uptake of oxygen by heterotrophic activity, the environment shifts from more aerobic to more anaerobic. The redox potential discontinuity (RPD) layer deep in the sediment becomes shallower and in extreme instances of anoxia the RPD can be at the sediment surface or extend into the water column (Rosenberg et al., 2001). Well oxygenated areas typically have abundant, diverse benthic communities that include larger, deeper burrowing fauna dominated by infaunal deposit-feeders, such as "head-down" conveyor-belt feeders and tubicolous polychaetes. These abundant, diverse, deep-burrowing benthic fauna help to create and maintain a deeper RPD through sediment reworking. A normoxic environment involving intensive particle mixing should be characterized by homogenized sediments, void spaces produced by feeding, and a rough sediment–-water interface covered with feeding pits and fecal or excavation mounds. Conversely, a hypoxic environment should be characterized by sediment mixing restricted to surficial depths as a consequence of fewer, smaller fauna consisting of fewer species that represent a more limited range of burrowing/feeding activities. The niche emptied by the mortality of hypoxia-sensitive fauna encourages colonization by small-sized, opportunistic species that have high reproduction rates. These opportunistic species can thrive under stressful conditions like hypoxia due to abundant food supply and deceased competition, which results in increased abundance and decreased species diversity and biomass.

Louisiana continental shelf hypoxia varies spatially and temporally. Since 1985, annual systematic bottom water dissolved oxygen surveys from the Birdfoot Delta to the Louisiana–Texas border (Rabalais et al., 1991, 2002) found the total hypoxic area has varied from approximately 8000 km^2 in 1985 to a low of 40 km^2 in 1988, and to an estimated 22,000 km^2 maximum in 2002 (Rabalais et al., 2007). More recent hypoxic events in 2007, 2008, and 2010 on the Louisiana shelf have been on the order of 20,000 km^2, with a five-year (2008–12) average of 14,000 km^2 (N. Rabalais, pers. comm.). Data from long-term moorings deployed off Terrebonne Bay in 1990 (15-min interval oxygen measurements) indicated that bottom-water oxygen concentrations varied within and between years. In general, concentrations gradually declined through the summer, with periodic re-oxygenation from wind-mixing events that broke down water column stratification and allowed vertical mixing. Furthermore, water column oxygen can oscillate hourly, as demonstrated by a time series in spring 2005 off Atchafalaya Bay in 20 m water depth (Bianchi et al., 2010). Dissolved oxygen concentrations 7 m above the bottom dipped below 2 mg $O_2 \cdot L^{-1}$ six times in 24 d. Thus, hypoxia exposure varying in frequency, severity, or duration may affect communities that are sensitive to low oxygen in a discontinuous manner. Depending on the benthic community's intolerance to hypoxia, equilibrium species may be removed and opportunists may replace them.

With the large amount of historical data on the occurrence of hypoxia on the Louisiana shelf, we undertook an integrated study of the interactions of hypoxia, macrobenthos, bioturbation, and sedimentary properties to assess the potential effects of frequent hypoxia on sediment physical and acoustic properties. Our results specifically concern the biogenic structural differences in surficial sediments among a normoxic control site and three sites subjected to hypoxic events varying in frequency of occurrence. Fine-scale biogenic features of surficial sediments were imaged with high-resolution Computed Tomography (CT) and these results were compared with larger-scale imagery that is traditionally employed to interpret biogenic structure. We intended to compare evaluations by various imaging methods of the biogenic structure of sediments exposed to hypoxia to discover whether the methodologies were complementary or divergent in revealing patterns and processes. Considering that many parameters could affect how the distribution and activity of burrowing infauna varied due to hypoxia, we made supporting measurements of sediment grain size, low-oxygen-tolerant benthic foraminifers, bottom-water oxygen, bioturbation, sedimentation, sedimentary organic carbon and nitrogen, and macrobenthos. We expect that the greater the long-term frequency of hypoxia, the greater the deleterious effects on the numbers and size of burrows, the depth of the mixed surficial layer, and the rates of biogenic mixing.

2. Materials and methods

2.1. Experimental design and study area

Four sites were chosen using historical bottom-water oxygen concentration data from mid-summer shelf-wide surveys (Rabalais et al., 2002; Baustian et al., 2011) from the Louisiana Universities Marine Consortium (LUMCON). The site designations in Fig. 1 are derived from the LUMCON survey station along the H, E, D, and A transects nearest the 30-m depth contour. Each site had a different frequency of hypoxia occurrence over the 23 years between 1985 and 2008. The four study sites were located at 30 m water depth to avoid differences in benthic communities due to variation in sediment types and shallow areas subject to intense, episodic sediment reworking. The westernmost site (H7) was exposed to hypoxia <25% of the time, D5 between 25% and 50% of the time, E4 between 50% and 75% of the time, and A6 $\geq$75% of the time. Station C6B, which is traditionally hypoxic in the summer months (exposed to hypoxia $\geq$75% of the time), is shown as a benchmark in Fig. 1. Because highly resolved bottom-water oxygen measurements as a function of time are sparse for the study area, interpretation of the abundance and characteristics of biogenic structures and associated macrobenthic assemblages should rely on cumulative effects of hypoxia integrated over multiple seasons. We do not expect the effects of high-frequency oscillations of hypoxic bottom water within a season to be resolvable in our data.

2.2. Field methods

Samples were collected in early spring (30 March–6 April, 2009) and late summer (5–11 September, 2009) aboard the R/V *Pelican*. Spring sampling represented baseline conditions and established macrobenthos densities and sediment properties before