



Seasonal hypoxia regulates macrobenthic function and structure in the Mississippi Bight



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ABSTRACT

Hypoxic conditions are escalating to the east of the Mississippi River within the Mississippi Bight. The objective of this study was to examine changes in macrobenthic function and structure relative to seasonal hypoxia over a 3.5 year period at the 10 m (Site 6) and 20 m (Site 8) isobaths within the Mississippi Bight. Seasonal hypoxia acted as a regular periodic disturbance during the study period, although the magnitude and duration of hypoxia varied inter-annually. Macrobenthic metrics revealed seasonal hypoxia effects on secondary production potential and community maturity, which agrees with previous studies. In addition, metrics were notably higher at the 20 m isobath during the latter half of the study period, following the Deepwater Horizon (DWH) oil spill. This study confirms hypoxia as a major driver affecting the function and structure of soft-bottom macrobenthos in the Mississippi Bight.

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1. Introduction

Hypoxia threatens coastal ecosystems on a global scale (Diaz and Rosenberg, 2008) due to anthropogenic activities related to expansion of coastal populations, agricultural runoff and climate change (Wu, 2002). Coastal ecosystems support goods and services in the form of seafood, human health and commerce, but the provision of these societal requirements depends directly or indirectly on proper ecosystem function. Hypoxia stifles proper functioning of coastal ecosystems by diverting the flow of energy and materials to microbial communities (Diaz and Rosenberg, 2008) as a consequence of defaunation and altered biogeochemical processes (Hansen and Kristensen, 1997; Levin et al., 2009; Villnäs et al., 2012). Consequently, hypoxia also impairs the functional capacity of the ecosystem to support secondary production (Xu et al., 1999; Baird et al., 2004; Sturdivant et al., 2014).

The Louisiana continental shelf of the northern Gulf of Mexico comprises the largest region of hypoxia (i.e., $\text{DO} \leq 2 \text{ mg O}_2 \text{ L}^{-1}$) in the United States (Rabalais and Turner, 2001), and the second largest hypoxic region in the world (Rabalais et al., 2002a). Located west of the Mississippi River outlet along the continental shelf from Louisiana to Texas, this region, colloquially known as the “Dead Zone” (Rabalais et al., 2002b), can cover up to 21,000 km² in any given year. Located within productive fishery waters known as the ‘fertile crescent’ — the “Dead Zone” has been extensively studied in terms of contributing factors and detrimental effects on the coastal ecosystem. Stratification due to freshwater runoff triggers the formation of bottom hypoxia in this region (Stow et al.,

2005). Moreover, for more than half a century hypoxia has been exacerbated within this region by fertilizer runoff from the US Great Plains via the Mississippi, Atchafalaya and Pearl Rivers. Heightened primary production in response to excess nutrients increases the supply of organic matter (OM) and biological oxygen demand (BOD) within the sediments (Paerl, 2004). Estuarine derived organic matter also contributes to the oxygen demand, and seasonal hypoxic conditions are set-up through stratification caused by the occlusion of the deeper cooler denser layers by overlaying warmer fresher surface waters (Bianchi et al., 2010). Resulting effects on the benthic fauna lead to diminished ecosystem function and reduced biodiversity (Rabalais and Turner, 2001; Baustian and Rabalais, 2009).

Hypoxic conditions are escalating to the east of the Mississippi River delta within the Mississippi Bight (Brunner et al., 2006), a region spanning the continental shelf seaward of the Mississippi-Alabama barrier islands (Keen, 2002). Thermohaline stratification during periods of freshwater runoff plays a critical role (Bianchi et al., 2010); and the Mississippi Bight has undoubtedly experienced increased nutrient loading since the advent of commercial fertilizer use. However, unlike the infamous “Dead Zone” of the Louisiana shelf, ecological effects of hypoxia have not been extensively studied within this region. Brunner et al. (2006) showed that the inner Mississippi Bight east of the delta has experienced intermittent seasonal hypoxia since the mid-20th century, based on foraminiferan indicator taxa within sedimentary cores. Recent frequent reports of low dissolved oxygen (DO) have raised concerns that seasonal hypoxia may now be forming regularly within this region (Moshogianis et al., 2013). Although continuous hypoxic periods of up to a month have been documented within this region over the past 20 years, it is not well known how regularly and extensively hypoxia

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occurs. Moreover, effects of hypoxia on macrobenthic function and biodiversity have not been examined within the Mississippi Bight.

Macrobenthic communities serve as ecological indicators because they comprise sedentary organisms living at the sediment–water interface, where stressors impinge on the aquatic environment (Engle and Summers, 1999). Effects of organic enrichment and hypoxia on macrobenthic communities are well known. A paradigm known as the Pearson–Rosenberg model of organic enrichment and hypoxia (P–R model) (Pearson and Rosenberg, 1978; Gray et al., 2002) identifies successional sequences in the traits and abundances of macrobenthic organisms along an organic enrichment gradient in time or space, spanning from unperturbed equilibrium communities consisting of relatively large-bodied and long lived taxa to more frequently disturbed communities comprising opportunistic small-bodied and short lived taxa. However, Gray et al. (2002) point out that the major detrimental effects of eutrophication on the benthic fauna reflect hypoxia as opposed to enrichment. Moreover, organic enrichment and hypoxia potentially have opposing effects on the biota (Rakocinski, 2012). An updated perspective views the stage of macrofaunal community maturity as a dynamic response modulated by the frequency and magnitude of hypoxia (Diaz and Rosenberg, 2008).

Effects of hypoxia on the macrobenthos have generally confirmed the P–R model in terms of changes in community structure and species-specific traits (Dauer et al., 1992; Rosenberg, 2001; Lim et al., 2006; Baustian and Rabalais, 2009). More recently, effects of hypoxia have been considered in terms of functional responses of the macrobenthos (Fleddum et al., 2011; Rakocinski, 2012; Villnäs et al., 2012; Sturdivant et al., 2013, 2014). Whereas structural metrics like diversity reflect responses in taxonomic composition (Niemi et al., 2004), functional metrics including secondary production, community turnover time (inverse P:B), and biomass-size spectra reflect ecological processes (Rakocinski, 2012). Because functional metrics focus on body size as a key trait, they should be mechanistically linked to the P–R model (Rakocinski, 2009). However, functional metrics have seldom been used to examine effects of hypoxia within the Mississippi Bight, or for other “Dead Zone” shelf regions in the Gulf of Mexico (but see Rabalais et al., 2001).

1.1. Objective

Herein, we examine macrobenthic function and structure in relation to hypoxia at the 10 m and 20 m isobaths of the Mississippi Bight over a 3.5 year period. Furthermore, we ask how the timing and magnitude of seasonal hypoxia varies relative to macrobenthic metrics. When recovering from hypoxia, relatively depauperate macrobenthic communities consisting of tolerant and small-bodied opportunists are expected to be functionally less productive, and structurally less numerous and diverse. The frequency and magnitude of hypoxia is expected to regulate macrobenthic function and structure in a manner analogous to how disturbance affects succession, as exemplified by the P–R model.

2. Materials and methods

2.1. Study area

Benthic field sampling was conducted concurrently with the NOAA NCI Monitoring and Assessment for Ecosystem Management Project (MAEMP) in the northern Gulf, which comprised a transect extending seaward from the mouth of the Bay of Saint Louis out to the western portion of the Mississippi Bight (Fig. 1). Benthic sampling occurred regularly at two transect locations on the inner shelf at the 10 m (site 6) (30° 08.0' N; 88° 54.5' W) and the 20 m (site 8) (30° 02.5' N; 88° 39.0' W) isobaths. All samples at the site 6 location fell within a 6.4 ha area, and all samples at the site 8 location fell within a 21.7 ha area. The study region experienced extreme, widespread and sustained hypoxia during the summer of 2008, as well as recurrent seasonal

hypoxia throughout the rest of the 3.5 year study period. Site 6 was centrally situated within the widespread 2008 hypoxic zone; while site 8 was more peripherally located within the 2008 hypoxic zone.

2.2. Field methods

A total of 25 benthic sampling events occurred between May 2008 and November 2011 within two areas on the Mississippi Bight; including 13 events at site 6 and 12 events at site 8. Sediments always consisted of silty-mud at both sites. Rough seas prevented sampling at site 8 during the first event in May 2008. Sampling included the spring, summer, and fall seasons. During each event, three macrobenthic samples were obtained using a 0.0413 m² modified Van Veen grab, yielding a total of 75 benthic samples for this study.

Usually, sediment from benthic samples was double bagged in 2 gal zip lock bags, placed on ice, and returned to the laboratory for processing the next morning. Alternatively, sediment was sieved on board a research vessel. Sediment was transferred to a large metal bowl and rinsed through a 0.5 mm sieve; coarse material and organisms retained on the sieve were transferred to a labeled sample jar, and preserved with buffered 10% Formalin.

Associated water quality and physical measurements were also made monthly. Using a computer linked in situ optical profiling package and sensor system enclosed within a metal cage, water column profiles of conductivity, temperature, dissolved oxygen, pH and turbidity were obtained. DO values were verified based on Winkler titrations and salinity independently confirmed from water samples.

2.3. Laboratory methods

In the laboratory, Rose Bengal stain was added to macrobenthic samples to facilitate sorting of the organisms. Sorted organisms were placed into labeled vials containing buffered 5% Formalin solution. Organisms were size fractionated by passing them through a series of nested sieves: 8.0, 5.6, 4.0, 2.8, 2.0, 1.4, 0.71, 0.5, and <0.5 mm (Edgar, 1990; Rakocinski and Zapfe, 2005). Size fractions were placed into separate labeled vials for further processing; organisms from each fraction were identified (taxon-size fraction) to the lowest practical taxonomic level (usually species). Fragments of organisms without heads were combined with the same type of organism within that taxon-size fraction; organisms were enumerated based on the number of heads within that taxon-size fraction. Each taxon-size fraction was placed into a separate labeled vial for which the information was entered on a data sheet.

Typically, volumes of taxon-size fractions were determined using calibrated squash plates and image analysis following Hellawell and Abel (1971) and Rakocinski and Zapfe (2005). Squash plates were calibrated with premeasured volumes of a KOH-glycerol solution using MetaVue® 5.0 imaging software on a PC attached to a Nikon® image analysis system consisting of a DMX 1200 digital camera mounted on a SMZ 1500 stereomicroscope. Image analysis was used to relate the areas to the known KOH-glycerol volumes, and conversion factors were obtained for each set of slides from regressions through zero of volume on area. Volumes of taxon-size fractions were estimated from digital images of their two-dimensional areas when compressed to a uniform thickness using calibrated squash plates (Hellawell and Abel, 1971). During squashing, taxon-size fractions were adjusted so that the organisms did not overlap, while still forming a uniform blotch. Digital squash images were traced twice to obtain duplicate measures of the blotch areas. Values for mollusks were based only on soft tissue. Organisms that were too large for the squash plate method were blotted and weighed to the nearest 10⁻⁵ g wet mass using an Ohaus® Analytical Plus microbalance. Volumes and wet weights were converted to dry mass values using conversion factors (Rakocinski and Zapfe, 2005). Wet mass values were obtained from volumes of squashed organisms using the conversion factor, 1.13 g cm⁻³ (i.e., specific gravity of 1.13) (Wieser, 1960; Gerlach

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