Macrobenthos and megabenthos responses to long-term, large-scale hypoxia on the Louisiana continental shelf

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ARTICLE INFO

ABSTRACT

The macrobenthos and megabenthos responses to long-term, recurring hypoxia on the Louisiana continental shelf were compared at four locations with different historical (2000–2010) episodes of annual exposure to bottom-water hypoxia. Measurements of abundance, biomass, species diversity, and community composition of the two size classes of benthos suggested that the macrobenthic response is driven chiefly by tolerance to hypoxia, whereas the megabenthic response was affected by the ability to migrate and the availability/unavailability of macrobenthos prey at the sediment surface. The site exposed to the historically lowest average bottom-water dissolved oxygen (BWDO) concentration exhibited the lowest species diversity for macrobenthos and the highest species diversity for megabenthos, exemplifying the differential effects of hypoxia on different size classes. The high diversity and smaller average size of the megabenthos at the lowest DO site was due to high abundance of invertebrates and a preponderance of small, less vagile fishes that appeared to remain in the area after larger dominant sciaenids had presumably emigrated. The average size and the depth of habitation in the sediment of macrobenthos prey may have also influenced the abundance and biomass of megabenthos foragers.

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1. Introduction

Seasonal hypoxia has become a common problem in coastal ecosystems over the last 60 years (Lim et al., 2006; Diaz, 2001; Conley et al., 2011). Seasonal, summertime hypoxic (≤ 2.0 mg $O_2 \cdot L^{-1}$) bottom-waters recur on the northern Gulf of Mexico inner continental shelf (29–60 m water depth) on a yearly basis. Stratification of water masses and high inputs of nutrients and organic matter from the Mississippi-Atchafalaya river system promote the development of the second-largest zone of human-caused coastal hypoxia in the world (Rabalais et al., 2002b; Justić et al., 2005; Bianchi et al., 2010). The hypoxic area varies annually and has covered up to 22,000 km^2 of the Louisiana shelf according to yearly systematic bottom water dissolved oxygen (BWDO) surveys (Rabalais et al., 2007). Periodic exposure to bottom-water hypoxia

has been linked to alteration of sediment properties by benthos (Briggs et al., 2015a); declines in benthic species richness, abundance, biomass and biomass-size spectra (Diaz and Rosenberg, 1995; Rabalais et al., 2001; Baustian et al., 2009; Seitz et al., 2009; Shivarudrappa et al., 2011; Shivarudrappa, 2015; Qu et al., 2015; Rakocinski and Menke, 2016); reduction in movement and feeding activity of benthos (Tyson and Pearson, 1991; Diaz et al., 1992; Weissberger et al., 2009; Briggs et al., 2015b); movements and spatial distributions of large invertebrates and demersal fish (Pihl et al., 1991; Craig and Crowder, 2005; McAllen et al., 2009; Kodama et al., 2010; Craig et al., 2010; Craig, 2012; Craig and Bosman, 2013); and effects on the spatial distribution and landings of commercial fisheries (e.g., penaeid shrimp; Purcell et al., 2016; Zimmerman and Nance, 2001; O'Connor and Whitall, 2007).

The structure of benthic communities exposed to hypoxia may be controlled by a combination of recruitment, migration, predation, and hypoxia tolerance (Gaston, 1985; Harper et al., 1991; Powers et al., 2001, 2005; Rabalais et al., 2001; Rakocinski and Menke, 2016). Post-hypoxia recruitment of individuals can come from dispersal of larvae settling from the overlying normoxic water

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column (Powers et al., 2001) or migration from nearby areas unaffected by localized hypoxia (Pihl et al., 1991; Tyler and Targett, 2007). Some macrobenthos may enter resting states or find refuge by burrowing deeper into the sediment (Llansó, 1992; Sagasti et al., 2001; Baustian et al., 2009; Montagna and Froeschke, 2009). Other macrobenthos may leave their burrows and move to the sediment surface during hypoxic events. This vertical migration may subject the animals to increased predation by megabenthos (Diaz et al., 1992), though Montagna and Ritter (2006) found no evidence of increased predation during hypoxic episodes in Corpus Christi Bay, presumably due to avoidance of the area by hypoxia-intolerant megabenthos. Nevertheless, low-oxygen conditions can change predator-prey relationships and result in major alterations in trophic pathways and energy flow (Breitburg et al., 1997; Baird et al., 2004).

Studies of shelf and estuarine macrobenthos indicate that the most tolerant species to low BWDO concentrations are the polychaete annelids, typically members of the families Spionidae, Nereididae, Magelonidae, Pilargiidae, Lumbrineridae and Cossuridae (Harper et al., 1981; Van Colen et al., 2010; Kodama et al., 2012; Rakocinski and Menke, 2016). Hydroid cnidarians, burrowing anemones, and some epibenthic muricid gastropods have also been observed to be tolerant to hypoxic conditions (Sagasti et al., 2001; Riedel et al., 2008). Among demersal fishes, a number of species appear to tolerate conditions at or slightly below 2 mg $O_2 \cdot L^{-1}$ (Tallqvist et al., 1999; Eby and Crowder, 2002; Switzer et al., 2009; Craig, 2012). Typically, these tolerant species are the first to return in great abundance following the return of normoxic conditions at the seabed. Rapid recovery from a hypoxic event has been documented in some studies (Niermann et al., 1990; Boesch and Rabalais, 1991; Lu and Wu, 2000; Lim et al., 2006), but effects of hypoxia on benthic community structure has also been shown to linger for years (Josefson and Widbom, 1988; Harper et al., 1991; Gray et al., 2002; Van Colen et al., 2010).

The frequency and duration of hypoxia exposure and the duration of the interim recovery between successive hypoxic events can have important effects on benthic community structure. For instance, the structure of benthic communities is different for environments experiencing frequent hypoxic episodes or severe hypoxia than those environments experiencing brief episodes of hypoxia separated by months (Rabalais et al., 2001). Those areas subjected to sustained severe or frequent hypoxia have the greatest reduction in species richness and abundance and typically become dominated by a few short-lived species (Llansó, 1992). Even short-duration hypoxia (i.e., days) with long intervening periods of normoxia, however, can result in increased predation on macrobenthos that have migrated to the sediment surface by crustaceans and demersal fishes, causing changes in macrobenthos assemblages (Long and Seitz, 2008).

In general, severe hypoxia leads to mass mortality of non-mobile and weakly mobile benthos, which would reduce the transfer of secondary production to higher trophic levels. With sufficient resources (i.e., organic matter and small-size-class prey) to support the production of macrobenthos following a hypoxic episode, the growth and development of macrobenthos assemblages in post-hypoxic environments becomes an important linkage between hypoxia and the size structure and species composition of megabenthos assemblages. Of interest, therefore, is not only the response of the macrobenthos community to oxygen stress, but the response of the megabenthos community to oxygen stress and to the state of the macrobenthos community. System-level linkages between benthic production and demersal fisheries yields under the influence of eutrophication indicate a coincident fluctuation between the two standing crops (Caddy, 1993; Diaz, 2001), but the complexity of the interactions between these two size classes is not

well understood. We characterized macrobenthos assemblages at four sites in 2009 with differing 10-year average dissolved oxygen concentrations (Briggs et al., 2015a,b; Shivarudrappa, 2015). Results indicated that macrobenthos assemblage structure differed among sites differing in historical BWDO concentrations and these effects could not be explained by regional differences in sediment type (Briggs et al., 2015b). Our objective in this paper was to revisit the four sites one year later (i.e., summer 2010) and re-sample the macrobenthos as well as sample the megabenthos to address the following questions:

- Do macrobenthos and megabenthos assemblage structure (species and size composition) differ among stations with different histories of annual bottom-water hypoxia?
- Does vertical distribution of macrobenthos within the sediment differ among regions differing in long-term, summer dissolved oxygen concentrations and how does this potentially influence prey availability to megabenthos?
- How do the combined macrobenthos and megabenthos abundance, biomass and assemblage structure differ according to long-term, summer dissolved oxygen concentrations?

2. Methods

2.1. Site descriptions and experimental design

Four sites were chosen based on historical BWDO data from mid-summer (late July) shelf-wide surveys conducted by the Louisiana Universities Marine Consortium (LUMCON) (Fig. 1; Rabalais et al., 2002a; N. Rabalais, personal communication). The site designations H7, E4, D5, and A6 were derived from the nearest LUMCON survey station. Each site had a different history of dissolved $O_2 \leq 2$ mg L^{-1} over the period 2000–2010 as indicated by different average BWDO concentrations (Briggs et al., 2015a, b) (Table 1). H7 experienced no documented hypoxia during the eleven-year period; D5 experienced hypoxia in one year (2006); E4 experienced hypoxia in three years (2002, 2006, and 2008); and A6 experienced hypoxia in five years (2000, 2002, 2007, 2008, and 2009). All sites were located along the 30-m depth contour to avoid confounding effects due to variation in water depth that would present different hydrodynamic regimes that control distribution of sedimentary organic matter, occurrence of feeding types, and larval supply, and thus, affect benthic assemblage composition (Snelgrove and Butman, 1994). Critical to our sampling design was the occurrence of a normoxic site (H7) as well as sites exposed to various documented episodes of oxygen stress (E4, D5, and A6). Based on the occurrence of hypoxia-tolerant benthic forams (Osterman, 2003), the effects of long-term annual exposure to hypoxia at our sites appeared consistent with the BWDO concentrations from the LUMCON annual survey data (Briggs et al., 2015b). Notably, the site with the lowest average BWDO concentration (A6) had the greatest proportion of hypoxia-tolerant forams and was most similar in its foram assemblage to that of the LUMCON site C6B, which experiences near-annual hypoxia (Rabalais et al., 2001). Based on measurements made in 2009 (Briggs et al., 2015b), the sediments of the four sites are predominately silty clay, though the sediment at H7 contained more gravel-size material deeper than 12 cm. Because the coarsest sediments (sand and gravel) occur in thin storm laminations or lag layers below the sediment-water interface, the surficial 10 cm of interest for all four sites can be characterized as a mud facies. From 2009 measurements the sites are also relatively similar in terms of organic matter content (Table 1). Multivariate analysis of macrobenthos abundance and biomass at the four selected sites in 2009 indicated that sediment