Marine Environmental Research 108 (2015) 14–23

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Seasonal changes in infaunal community structure in a hypertrophic brackish canal: Effects of hypoxia, sulfide, and predator–prey interaction

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ARTICLE INFO

Article history:
Received 2 February 2015
Received in revised form
16 April 2015
Accepted 19 April 2015
Available online 20 April 2015

Keywords:
Eutrophication
Oxygen depletion
Macrozoobenthos
Trophic interaction
Stable isotopes
Succession
Sulphide

ABSTRACT

We conducted a one-year survey of macrozoobenthic community structure at 5 stations in a eutrophic canal in inner Tokyo Bay, focusing on the impacts of hypoxia, sediment H_2S, and species interaction in the littoral soft-bottom habitats. Complete defaunation or decreasing density of less-tolerant taxa occurred under hypoxia during warmer months, especially at subtidal or sulfidic stations; this was followed by rapid recolonization by opportunistic polychaetes in fall–winter. Sedimentary H_2S increased the mortality of macroinvertebrates under hypoxia or delayed population recovery during recolonization. The density of several polychaetes (e.g., *Pseudopolydora reticulata*) declined in winter, coincident with immigration of the predator *Armandia lanceolata*. This suggests that absence of *A. lanceolata* under moderate hypoxia enabled the proliferation of prey taxa. We conclude that oxygen concentration, sediment H_2S, and hypoxia-induced changes in species interactions are potential drivers for spatio-temporal changes in macrozoobenthic assemblage structure in hypoxia-prone soft-bottom communities.

1. Introduction

Degradation of marine soft-bottom habitats often leads to an overall decrease in biodiversity and ecosystem functions, constituting a major global environmental problem (Diaz and Rosenberg, 2008). During the past 100 years, anthropogenic environmental modifications such as reclamation and eutrophication have increasingly disturbed estuaries in the world (Lotze et al., 2006). These disturbances can induce partial, or even complete, loss of macrobenthic assemblages on the seafloor. In soft-bottom communities, macrozoobenthos plays key roles in biogeochemical cycles (Levin et al., 2001). Accordingly, we need to ensure colonization by benthic invertebrates to maintain its ecosystem functions in the habitat; these functions include nutrient flux, benthic–pelagic coupling, and food-web transfer (Altieri and Witman, 2006; Sturdivant et al., 2013; Villnäs et al., 2012).

The incidence of bottom-water hypoxia (defined as dissolved oxygen [DO] <2.0 mg l^{-1} in this study, see Gray et al., 2002) has increased exponentially since the 1960s because of increasing nutrient loads from anthropogenic activities in catchment areas (Diaz and Rosenberg, 2008). Increasing organic loading from the water column to the sediment surface enhances oxygen consumption at the sediment–water interface, leading to the development of hypoxic water bodies (Pearson and Rosenberg, 1978). Furthermore, excess organic loading on the seafloor often modifies the sediment characteristics. In eutrophic marine sediments, hydrogen sulfide (H_2S; $\Sigma H_2S + HS^- + S^{2-}$) is created during the anaerobic decomposition of organic matter by sulfate-reducing bacteria (see Hargrave et al., 2008). H_2S is highly toxic to most benthic invertebrates, even at low concentrations (but see Llansó, 1991), and toxicity is accelerated under hypoxia (Gamenick et al., 1996; Vaquer-Sunyer and Duarte, 2010). Accordingly, H_2S accumulation associated with bottom water hypoxia often causes seasonal or even more long-term defaunation.

Shallow coastal habitats, including tidal flats, are characterized by highly fluctuant environmental conditions that are potential stressors for macrozoobenthos (Dauer, 1984; Sturdivant et al., 2013). They often cause mass mortalities of the less tolerant taxa

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http://dx.doi.org/10.1016/j.marenvres.2015.04.006
0141-1136/

within a community, resulting in the spatial or temporal heterogeneity in the assemblage structure along environmental gradients (Como and Magni, 2009; Kanaya et al., 2011). In natural, undisturbed estuaries, the community structure of macrozoobenthos are generally altered by factors such as salinity, tidal level, and sediment grain size (Kanaya et al., 2011; Ritter et al., 2005; Ysebaert and Herman, 2002). In some cases, species interaction has been suggested to be an additional factor (Tamaki, 1985a; Van Colen et al., 2008, 2010). In contrast, in eutrophic and urbanized estuaries, anthropogenic stressors such as hypoxia, organic enrichment, and sediment deterioration have often become more important than the above-mentioned factors as determinants (Gamenick et al., 1996; Kodama et al., 2012; Villnäs et al., 2012). For better understanding the ecological consequences of ongoing environmental degradation, we should know what factors determine the spatiotemporal changes in macrozoobenthic community structure in highly urbanized estuarine habitats.

Tokyo Bay is a semi-enclosed and highly eutrophic bay located on the Pacific Coast of central Japan. In inner Tokyo Bay, bottom-water hypoxia frequently occurs in the warmer months on a broad scale, leading to complete defaunation or alteration of the community structure of macrozoobenthos in the subtidal area (see Kodama et al., 2010, 2012 and references therein). In the bay system, hypoxia in the bottom water had firstly been observed in 1955 in its inner portion, and increased in its spatial extent and duration (Ishii et al., 2008). However, our knowledge of the impacts of environmental degradation on shallow littoral habitats remains limited. Recently, Yuhara et al. (2013) showed that small tidal flats and salt marshes along the tidal canals of inner Tokyo Bay are substantial habitats for endangered macrozoobenthos species. Restoration of these intertidal habitats is necessary to conserve the biodiversity of tidal-flat macrozoobenthos in inner Tokyo Bay (Yuhara et al., 2013). It is therefore important to determine the responses of the macrozoobenthic community in these fragmented and isolated intertidal habitats to seasonal fluctuations in environmental quality.

We selected a shallow (<4 m water depth) canal system in inner Tokyo Bay as the site for a one-year survey of spatiotemporal variations in the macrozoobenthic assemblage structure. Stations were assigned along a steep gradient in DO and sediment H_2S contents within a small spatial scale in the littoral zone. We specifically focused on (1) the intensity and extent of hypoxia in the shallow littoral habitat; (2) the response of macrozoobenthos to seasonal hypoxia and sedimentary H_2S accumulation at both population and community levels; and (3) the possible biotic interactions between early and late colonists during post-hypoxia population recovery.

2. Materials and methods

2.1. Study area

The field survey was conducted in a shallow eutrophic canal (water depth <4 m, Keihin Canal) in inner Tokyo Bay (Fig. 1). The cement-lined canal was constructed in the mid-20th century through reclamation in the surrounding area (Endoh, 2004). Dissolved inorganic nitrogen $(NO_3^- + NO_2^- + NH_4^+)$ was considerably high (226 ± 82 μM in 2010–2011, n = 17, monthly measurement by the authors) and red tides often occurred in warmer months. The canal was characterized by hypoxia (DO < 2.0 mg l^{-1}) in the warmer months and by organic pollution of the sediments (Ando, 2009; Kodama et al., 2012). The salinity ranges from 20 to 30 but sometimes falls below 10 (Nakamura et al., 2009). Tides are semi-diurnal, with a spring tidal range of 1.9 m. Contents of chemical pollutants in the canal sediment (e.g., PCB, Cd, Cr, Hg) had decreased significantly during the past 40 years, and the contents were much lower than ERM level (Effects Range Median; NS and T Program, NOAA, USA) (Ando, 2009).

Macrozoobenthos and sediment parameters were monitored monthly from May 2010 to May 2011 at 5 stations on an artificial tidal flat (Oi tidal flat, area: 1.38 ha in spring low tide) and in an adjacent subtidal zone. The tidal flat was constructed in the Oi Central Seaside Park by the government of Tokyo Metropolis during 1970s. Five stations with different sediment types and elevations (see Table 1) were defined. St. A to D were located on the tidal flat, which was characterized by spatially heterogeneous sediment texture. Differences in sediment type were possibly formed by the degree of wave exposure at each location. St. A and B were in the middle tide zone and St. C and D were in the low tide zone. St. A and C were located in muddy sand and muddy patches characterized by sulfide accumulation (silt–clay content before March 2011, 11 ± 3% and 35 ± 11%, n = 10, respectively), whereas St. B and D were located on a sandy non-sulfidic flat (silt–clay content before March 2011, 3.7 ± 0.5% and 4.1 ± 1.6%, n = 10, respectively). St. E was located in the subtidal zone (2.7 m below mean low water spring [MLWS]) and was characterized by sulfidic mud (silt–clay content before March 2011, 89 ± 3%, n = 10).

During the study period, sediment liquefaction occurred in March 2011 as a result of the Great East Japan Earthquake, resulting in an overall increase in the silt–clay fraction on the tidal flat (see Table 1). The earthquake induced a slight drop in total density in the intertidal zone, while not in species richness (see Results in Figs. 4 and 5). Only *Streblospio benedicti japonica* at St. C and D exhibited declining density after the earthquake, probably due to physical disturbance. Overall, the impacts of this liquefaction on the macrozoobenthos seemed not conspicuous at a whole-community level. Therefore we considered that the post-earthquake data were valid and included them in our analysis.

2.2. Water quality measurements

Water temperature, salinity, and DO in the canal were measured at St. E by using a water quality meter (Quanta, Hydrolab). From April 2010 to June 2011, daytime measurements were conducted at 2- or 4-week intervals on spring low tides on the water surface (10 cm deep) and in the bottom water layer (10 cm above the sediment). The salinity and DO sensors were calibrated before each measurement, and the accuracy was 0.01 and 0.01 mg l^{-1}, respectively. Loggers for salinity and DO (Compact-CT and Compact-TD, JFE Advantech) were set up with a float on the water surface near St. C to calculate daily mean and minimum values from the data obtained every 30 min. The sensors were cleaned and calibrated with a 2- or 4-weeks intervals. Since canal water flowed through the 2 measuring sites with tidal currents (G. Kanaya, pers. obs.), we regarded that water quality at the 2 locations were comparable. In this study, we defined “hypoxia” as DO < 2.0 mg l^{-1} and “moderate hypoxia” as DO between 4 and 2 mg l^{-1} since metabolism of aquatic organism is affected at oxygen concentration between 4 and 2 mg l^{-1} and mortality occurs where concentrations are below 2.0 to 0.5 mg l^{-1} (Gray et al., 2002).

2.3. Sediment characteristics

Sediments were sampled monthly at the stations from May 2010 to May 2011. Sediment parameters, including redox potential (Eh) and the contents of silt–clay, H_2S, and total organic carbon (TOC), were measured. Four sediment cores (φ 10 cm by 30 cm deep) were collected from each station by using a core sampler (φ 10 cm by 50 cm length). In the subtidal zone (St. E) we used an acrylic suspended core sampler (HR type, Rigo-sha), whereas at the intertidal