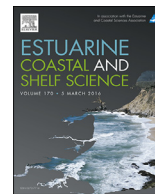




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Diet shifts and population dynamics of estuarine foraminifera during ecosystem recovery after experimentally induced hypoxia crises

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ABSTRACT

This study shows foraminiferal dynamics after experimentally induced hypoxia within the wider context of ecosystem recovery. ¹³C-labeled bicarbonate and glucose were added to the sediments to examine foraminiferal diet shifts during ecosystem recovery and test-size measurements were used to deduce population dynamics. Hypoxia-treated and undisturbed patches were compared to distinguish natural (seasonal) fluctuations from hypoxia-induced responses. The effect of timing of disturbance and duration of recovery were investigated. The foraminiferal diets and population dynamics showed higher fluctuations in the recovering patches compared to the controls. The foraminiferal diet and population structure of *Haynesina germanica* and *Ammonia beccarii* responded differentially and generally inversely to progressive stages of ecosystem recovery. Tracer inferred diet estimates in April and June and the two distinctly visible cohorts in the test-size distribution, discussed to reflect reproduction in June, strongly suggest that the ample availability of diatoms during the first month of ecosystem recovery after the winter hypoxia was likely profitable to *A. beccarii*. Enhanced reproduction itself was strongly linked to the subsequent dietary shift to bacteria. The distribution of the test dimensions of *H. germanica* indicated that this species had less fluctuation in population structure during ecosystem recovery but possibly reproduced in response to the induced winter hypoxia. Bacteria seemed to consistently contribute more to the diet of *H. germanica* than diatoms. For the diet and test-size distribution of both species, the timing of disturbance seemed to have a higher impact than the duration of the subsequent recovery period.

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1. Introduction

Coastal areas provide many resources and services beneficial to human settlement. These favorable conditions in near-coastal zones have led to human population densities nearly three times higher than the global average (Small and Nicholls, 2003). High population densities in coastal zones make these areas more prone to anthropogenic perturbations (Diaz et al., 2009 and references

therein). Consequences of such perturbations, as for example instances of low-oxygen concentrations in bottom waters, cause a loss of ecosystem services (Diaz and Rosenberg, 2008 and references therein). Hypoxia induced stress may alter species behavior and provoke mortality of sensitive species (as reviewed by e.g. Gray et al., 2002; Zhang et al., 2009; Diaz et al., 2009). These alterations affect food–web interactions and the functioning of estuarine communities (Conley et al., 2007; Diaz et al., 2009).

In order to be able to protect and restore complex coastal ecosystems, explicit knowledge on their functioning is required. The use of selected species as indicator for ecosystem functioning can be very helpful to more easily monitor ecosystem development. Among the benthic fauna in estuarine ecosystems, foraminiferal species are increasingly recognized as efficient ecological indicators

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(Debenay et al., 2006; Schönfeld et al., 2012; Bouchet et al., 2012; Brouwer et al., 2015; Strotz, 2015).

Foraminifera are common marine heterotrophic unicellular bikont eukaryotes from the supergroup Rhizaria; several characteristics favor their applicability as indicator species. Foraminifera have a small sized test and are densely present in most marine sediments. Hence, limited volumes of relatively easily collectable sediment suffice for an accurate study of foraminiferal dynamics. Furthermore, foraminifera generally possess a high ability to survive perturbations, so they may record the higher end of the disturbance spectrum, long after macrofauna have succumbed (Josefson and Widbom, 1988; Langlet et al., 2014). Notwithstanding their high potential to survive disturbance, foraminiferal populations commonly respond fast to changes in their environment (e.g. Jorissen et al., 1995; Debenay et al., 2006; Denoyelle et al., 2010). Especially fluctuations in the availability of oxygen and food are considered to structure benthic foraminiferal communities and their spatial distribution (Jorissen et al., 1995; Van der Zwaan et al., 1999).

Within the food web, foraminifera reside in an intermediate position in-between microbes and macrofauna and occupy a variety of trophic niches. Several foraminiferal feeding strategies have been described (e.g. Lipps, 1983). Some species have been reported to graze on diatoms or other algae, while others use their pseudopodia to trap detritus or even metazoans. Besides parasitism, carnivory, bacterivory and cannibalism, foraminiferal symbiotic trophic relationships with bacteria and algae have been observed (Goldstein 1999 and references therein). Hypoxic disturbance may alter the availability and composition of food resources and influence foraminiferal carbon utilization (e.g. Gustafsson and Nordberg, 2000).

Pulses of organic matter and oxygen depletion affect foraminiferal densities and migratory behavior; these responses are species-specific (Ernst et al., 2005) and variable effects can be observed in different foraminiferal size classes because of altered population dynamics and life-history strategies (Duijnsteet et al., 2005). Duijnsteet et al. (2005) observed that a pulse of organic matter, provoking anoxic conditions, inhibited foraminiferal growth, but enhanced fecundity and likely triggered reproduction at a very early stage. The foraminiferal test size and the foraminiferal fecundity are also related to the availability of specific food sources (e.g., Muller and Lee, 1969; Parfrey and Katz, 2010). For instance, Muller and Lee (1969) reported that some foraminifera require bacteria to sustain reproduction. Parfrey and Katz (2010) discovered that specimens of the foraminifer *Allogromia laticollaris* that foraged on a mixture of algae and bacteria had a higher number of offspring compared to specimens feeding on bacteria only. In consequence, hypoxia can alter foraminiferal assemblages because of their species-specific tolerance for oxygen depletion, as well as assemblage composition through its impact on food availability and food web interactions.

The main question addressed in this study is how ecosystem recovery after hypoxia influences the dynamics of foraminiferal species; i.e. their population structures (e.g. size distribution, survival, growth and reproduction) and feeding strategies. By disentangling the impact of ecosystem properties, such as food availability and macro- and meiofaunal presence, on foraminiferal feeding and population dynamics in disturbed and undisturbed ecosystems, the accurate use of foraminifera as indicator species for monitoring ecosystem functioning can be improved. To address these objectives, sediments of an intertidal flat in the Scheldt Estuary on the Dutch coast were *in situ* exposed to human-induced hypoxia in winter or late spring. To study the carbon flow from micro-organisms at the base of the food web – such as diatoms and heterotrophic bacteria – to the dominant foraminiferal species

Ammonia beccarii and *Haynesina germanica*, ¹³C-labeled glucose and bicarbonate were introduced in these *in situ* experiments to enrich heterotrophic bacteria and benthic algae, respectively (Rossi et al., 2009). To investigate the effect of ecosystem recovery following hypoxia on foraminiferal population dynamics, we analyzed the distribution of test sizes combined with food consumption patterns of foraminifera at different times in a 5-month period of ecosystem recovery. These observations were compared to simultaneous observations from undisturbed (control) sediments where no hypoxia occurred. Comparing foraminiferal dynamics (e.g., population dynamics and diet shifts) among hypoxia-disturbed and undisturbed sediments provide the opportunity to discriminate between the natural, seasonal development of the ecosystem (due to e.g. variations in temperature, day length, larval availability etc.) and the influence of ecosystem recovery following hypoxia.

Previous work on the same set of field experiments has shown that the timing of experimentally-induced disturbance lead to differential responses in ecosystem properties that are subsequently assumed to directly or indirectly influence foraminifera – e.g. via differential alterations of food availability (Brouwer et al., 2015), or differences in predation pressure and disturbance effects of recovering nematodes and macrofauna (see Montserrat et al., 2008, 2009; Van Colen et al., 2008, 2009, 2010a, b, 2012; Rossi et al., 2008, 2009; Rossi and Middelburg 2011). These hypoxia-related changes in ecosystem properties and the direct impact of hypoxia on foraminifera determine the net impact of hypoxia on foraminifera. Hence, our results will be discussed in the context of findings published in these parallel studies.

2. Material and methods

The field experiments took place on a tidal flat bordering the Paulina Polder on the southern bank of the Scheldt Estuary in the Netherlands (51°21'23"N, 3°42'49"E, Fig. 1). The mudflat covers an area of around 1.0 km², it has a mean tidal range of 3.9 m with a semidiurnal regime and a yearly average salinity of 24 (Van Colen et al., 2012). Under natural conditions, the macrofaunal community is dominated by polychaetes (*Heteromastus filiformis*, *Arenicola marina*, *Pygospio elegans*) and mollusks (*Macoma balthica*, *Cerastoderma edule*, *Hydrobia ulvae*) (Rossi et al., 2009). For food supply, this community of macrofaunal invertebrates relies of phytodetritus and autotrophs within the sediments such as microphytobenthos and chemo-autotrophic bacteria. This carbon can be transferred to the meiofaunal community of (predominantly) nematodes (e.g., *Daptonema* spp., *Chromadora* spp., *Anoplostoma viviparum*, *Oncholaimellus* sp.1., *Viscosia* spp. and *Ptycholaimellus ponticus*; Van Colen et al., 2009), foraminifera (*H. germanica*, *A. beccarii* and *Elphidium excavatum*; Brouwer et al., 2015) and macrofauna (Rossi et al., 2009). Heterotrophic bacteria utilize carbon from each trophic level and may return carbon to the system as food source especially for the meiofaunal part of the system.

2.1. Experimental set-up: labeling and sampling

Hypoxic conditions were experimentally induced twice: once in winter and once in late spring. To this end, two large patches (4 × 4 meter) within a 50 × 50 m location (Figs. 1 and 2) were covered for two months with black waterproof polyethylene sheets – both stopping oxygenic photosynthesis and effectively preventing the replenishment of oxygen that was consumed during decomposition of the ample organic matter content of the sediment, and thus rendering the sediment hypoxic. The first hypoxic period lasted from January 30th until March 30th 2005 and the second from May 9th until July 6th 2005 (Fig. 3). During both periods, two

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