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Original article

Diverse thermotolerant assemblages of benthic foraminiferal biotas from tropical tide and rock pools of eastern Africa

Anna E. Weinmann *, Martin R. Langer

Steinmann Institut für Geologie, Mineralogie und Paläontologie, Universität Bonn, Nussallee 8, 53115 Bonn, Germany

Abstract

Tropical tide and rock pools are extreme environments with regard to temperature. They undergo diurnal heating and constitute natural laboratories to assess the fate of marine calcifiers under scenarios of global change. This study focuses on benthic foraminiferal assemblages from tide and rock pool sites from eastern Africa as "natural" laboratories to document the diverse spectrum of foraminiferal biotas potentially capable to succeed under conditions of future global warming. To date, the majority of foraminiferal thermal tolerance data have been compiled from laboratory experiments, anthropogenically heat-polluted or extreme hydrothermal vent areas. A total of 111 species of benthic foraminifera were recorded within the tide pool samples. Perforate species were most abundant (up to 84%), followed by porcellaneous taxa (up to 45%), while agglutinated species were only rare (up to 5%). Larger benthic foraminifera represented between 30 and 75% of the total assemblages with 8 observed genera. Species richness varied between 23 and 63 species per sample. The foraminiferal communities of most sites were dominated by larger perforate taxa such as *Neorotalia calcar* and *Amphistegina* spp., followed by a variety of small miliolid taxa (54 species) and small rotaliids (27 species). The surprisingly high foraminiferal species richness suggests that a large range of shallow-water benthic taxa appear to be capable to tolerate exposure to diurnally occurring temperature extremes (35°–> 40 °C). The large spectrum of benthic taxa recorded provides insight into potential acclimatization capacities of foraminiferal assemblages with regard to ongoing ocean warming and projected temperature changes. We infer that calcification in heat-tolerant benthic foraminifera, a group of productive carbonate producers, is more widespread than previously thought and will continue in future decades when water temperatures are significantly elevated. Tolerance to thermal stress is imperative for intertidal foraminifera and assemblages from tropical rock and tide pools appear to be less susceptible to future change. This capacity is central to the resilience to rising ocean temperatures and dictates how warming affects these delicate environments. Intertidal foraminiferal assemblages could potentially act as source populations for restocking and to mitigate detrimental effects of global change.

Keywords: Foraminifera; LBF; Tide pools; Global warming; Heat tolerance; Diversity

1. Introduction

Benthic foraminifera, and especially the group of larger symbiont-bearing foraminifera, are prolific producers of calcium carbonate and contribute substantially to the tropical carbonate budget of nearshore coastal ecosystems. The ability of foraminifera to survive under conditions of rapidly rising sea surface temperatures depends largely on their capability to tolerate increased temperature extremes. Recent studies have indicated that tolerance levels to thermal stress greatly varied among foraminifera.

Intertidal rock and tide pool environments are highly dynamic and impose a variety of physical stresses on benthic foraminifera including strong wave action, light, and significant temperature and salinity fluctuations. Along the tropical eastern coast of Africa, tide pool environments can occasionally reach temperatures close to 40 °C or above in peak summer. Temperature is a major constraint for the distribution of foraminifera (Murray, 1973; Langer and Hottinger, 2000; Langer et al., 2013a) and the most pervasive climate-related influence on biological function (Johnston and Bennett, 1996; Halpern et al., 2008). Nonetheless, diverse assemblages of foraminifera flourish under harsh intertidal conditions and heat-tolerant assemblages may serve

* Corresponding author.
E-mail address: a.weinmann@uni-bonn.de (A.E. Weinmann).

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as model systems to understand resilience to global warming and future climate change (Pereira, 1979; Neagu, 1982; Pignatti et al., 2012; Langer et al., 2013a; Dimiza et al., 2016; Fajemila and Langer, 2016; Thissen and Langer, 2017).

Benthic foraminifera are prolific producers of carbonate in tropical reef ecosystems and perform vital ecosystem functions (Langer et al., 1997; Hallock, 2000; Langer, 2008; Fujita et al., 2011; Doo et al., 2014). Previous studies on thermal tolerance of foraminifera revealed considerable differences and species-specific resistance levels to elevated temperatures. This is especially true for larger, symbiont-bearing foraminifera (LBF), which can react to ecological stress by expelling their symbionts, a phenomenon commonly known as bleaching (Hallock et al., 1992; Schmidt et al., 2011). Schmidt et al. (2011) showed that specimens of *Amphistegina radiata*, *Heterostegina depressa* and *Calcarina hispida* showed signs of heat-stressed bleaching at temperatures above 30 °C. Other studies also showed negative effects of increased temperatures on LBF, with many of them also combining nutrient effects or ocean acidification (e.g. Uthicke et al., 2012; Sinutok et al., 2014). However, in recent years, several studies also showed more ambivalent responses of some LBF to higher temperatures (Fujita et al., 2014; Engel et al., 2015; Prazeres and Pandolfi, 2016; Prazeres et al., 2016; Titelboim et al., 2016; Schmidt et al., 2016a, 2016b; Stuhr et al., 2017). Reasons for potentially higher temperature tolerances could be the presence of more heat-tolerant symbionts (Fujita et al., 2014; Titelboim et al., 2016; Schmidt et al., 2016a, 2016b) or a constant exposure to more “stressful” environments with regard to overall temperature (Prazeres and Pandolfi, 2016; Prazeres et al., 2016). *In situ* experiments at extremely heated sites around hydrothermal vents also showed high survival rates of locally sourced specimens of various LBF (Engel et al., 2015).

To date, most of the thermal tolerance studies conducted on foraminifera were performed as laboratory experiments. They provide valuable physiological information but it remains yet to be determined how they apply to natural environmental settings. This study provides field evidence for thermotolerant foraminiferal populations by studying assemblages from “naturally” heated sites that are largely unaffected by anthropogenic or volcanic sources. We analyzed the benthic foraminifera from tide and rock pools in eastern Africa, which are subject to a diurnal tidal cycle that exposes the remaining water to heating due to solar radiation. The tide and rock pools act as a natural laboratory for heat-involved studies since they retain all other factors to a very natural level of tropical nearshore coral reef environments and are not affected by anthropogenic influences such as industrial effluents around power plants (Friedlander et al., 1996) or by submarine volcanic exhalations (Engel et al., 2015) that might otherwise impact the local communities of foraminifera.

All of our study sites are situated within the biogeographic region of the East African Coral Coast ecoregion (EACC), which extends from central Kenya to the Primeiro and Segundo Archipelagos in central Mozambique (Marine ecoregions of the world, MEOW; Spalding et al., 2007). The area includes the largest coral reef environments of eastern Africa with a generally high diversity (Spalding et al., 2001). The coastal areas of the EACC are situated on a narrow continental shelf with barrier or fringing reef environments and associated lagoons (Obura et al., 2002; Arthurton, 2003; Ngusaru, 2011). An important and characteristic feature of the region are extensive “beach rock” formations, which are limestone cliffs originating from fossil coral reef structures that were built during the Pleistocene, when sea-level was up to 15 m higher than today (Ngusaru, 2011). With falling sea-level during the Holocene, the reefs were gradually exposed and eroded, building extensive limestone platforms along the coast (Arthurton, 2003; Ngusaru, 2011). With rising sea-level after the Last Glacial Maximum, these platforms were gradually flooded and constitute the present-day coastal lagoons, which, in turn, are bordered by modern fringing reef bars, generally about 1 m above the platform itself (Arthurton, 2003). The settings of the modern structures constitute sheltered conditions on the platforms characterized by a variety of smaller nearshore rock and tide pools that are exposed during low-tide.

The intertidal zone between coast and fringing reefs can be quite extensive (Ochieng and Erftemeijer, 2003). The tidal range during spring tide varies between 3 and 4 m within the study area (Ngusaru, 2011). The mean time for low water during spring tides is generally late morning to mid-day (Ngusaru, 2011), thus exposing the intertidal areas at the peak of daily solar radiation. This leads to increased evaporation and possibly to a reduction in oxygen content (Ngusaru, 2011). Most importantly, temperatures in the restricted tidal pools can rise to over 40 °C (Coppejans et al., 1992; Hamisi et al., 2004). Normal monthly average coastal temperatures of Kenya and Tanzania vary between 24.3–24.7 °C in August and 30.1–30.5 °C in March and April (data retrieved from seatemperature.org; accessed 07/09/2017). Other studies have shown that water temperatures in tide and rock pools of this area often range between 25 and 40 °C, with average values around lowest water stands of about 35 °C (Hamisi et al., 2004; Msuya and Porter, 2014). Nevertheless, a variety of seagrasses grow in those tidal pools, with *Thalassodendron ciliatum* (Forskål) and *Thalassia hemprichii* (Ehrenberg) being most dominant (Ochieng and Erftemeijer, 2003; Bandeira, 2011; Ngusaru, 2011). They are generally associated with algae of the genus *Ulva*, *Boodlea*, *Padina*, *Cystoseira*, *Enteromorpha* and coralline algae, among others (Leliaert et al., 2011). Invertebrate faunal associations include sponges and anemones as well as various crustaceans, mollusks and echinoderms.

Previous studies have indicated that thermal filtering appears to severely constrain the number of thermotolerant benthic foraminifera implying that the limited resilience to future warming has severe consequences for benthic biotas and ecosystem functioning. This study analyses the species richness of heat-tolerant benthic foraminifera from intertidal rock and tide pools of eastern Africa to assess possible resiliences of foraminiferal biotas to future warming.

2. Material and methods

2.1. Sampling sites

Tide and rock pools from eight sites along the coast of eastern Africa were sampled between February 2011 and May 2012: