



Research paper

Changes in diversity and assemblages of foraminifera through the Holocene in an atoll from the Maldives, Indian Ocean

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ABSTRACT

This study presents the first high-resolution Holocene records of diversity and assemblages of benthic foraminifera from tropical reef environments in the Indian Ocean. Two 3.2 m and 4.4 m long cores from the lagoon of Rasdhoo Atoll (4°N/73°W) in the central Maldives, were sampled at ~250 yr intervals. Core #16 covers most of the Holocene (10.32–0 kyr BP) and was taken in the deep lagoon of the atoll (35 m water depth). Core #19 covers the time span 7.375–0 kyr BP and is from a sublagoon (14 m water depth) on the northern margin of the atoll. In Core #16, an early colonization phase during Holocene sea-level rise is characterized by an *Ammonia* sp. 1 dominated assemblage until ~7 kyr BP. The slowdown of sea-level rise in the Mid Holocene (~4 kyr BP) marks the onset of a phase of stable environmental conditions in the deep lagoon with high diversity. A shift toward lower diversity and the dominance of *Textularia foliacea* has occurred from ~4–1 kyr BP, which may be explained with the Intermediate Disturbance Hypothesis. An environmental change at ~1.4 kyr has caused a distinct faunal change, the decrease of *T. foliacea* and an increased recovery in diversity. In Core #19, a significant faunal change at ~4.0 kyr BP from an *Ammonia* sp. 2 dominated fauna to a fauna with *Ammonia* sp. 1, miliolid taxa and a higher diversity might be related to the formation of a sand spit that separates the sublagoon from the main lagoonal basin. The westward extension of the sand spit during the Late Holocene could have changed the restricted bottom water circulation in the main lagoon and caused longer residence times of water and the build-up of lower oxygen and higher nutrient concentrations. This study underlines the importance of the factor time on diversity and the significance of lagoon circulation and bottom water residence times on assemblages and diversity of benthic foraminifera.

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1. Introduction

A better understanding of temporal and spatial variations in natural biodiversity in the vulnerable tropical coral reef environment will be crucial when attempting to estimate future loss of biodiversity due to natural and anthropogenic environmental change (Hoegh-Guldberg, 2011). In present-day coral reefs, benthic foraminifera are the most important carbonate sediment producers besides corals and calcareous algae (Langer et al., 1997; Yamano et al., 2000). They have a great significance for ecological, sedimentological and stratigraphic studies (Scott et al., 2001; Yamano et al., 2001; Murray, 2006; Boudagher-Fadel, 2008; Langer, 2008). Numerous studies have used benthic foraminifera as facies indicators of fossil and modern carbonate depositional environments (Yamano et al., 2001; Langer and Lipps, 2003; Beavington-Penney and Racey, 2004), of Holocene sea level change (Horton, 2006), of environmental stress in modern reef environments (Alve, 1995; Cockey et al., 1996) and for the interpretation of storm deposits (Mamo et al., 2009). The investigation of differences between

foraminiferal assemblages and diversities in fossil and modern reef environments also contributes to a better understanding of the long-term influence of environmental factors on the biodiversity in modern coral reefs and associated faunas on glacial/interglacial scales (Mossadegh et al., 2012; Parker et al., 2012).

Studies on the distribution of modern benthic foraminifera in shallow-water reef and carbonate platform environments in the Indo-Pacific mainly focus on the central Indo-Pacific and the western Pacific (Langer and Hottinger, 2000; Bicchi et al., 2002; Langer and Lipps, 2003; Parker, 2009; Makled and Langer, 2011 and references within). Existing surveys of benthic foraminifera in surface sediments from the Western Indian Ocean region (including the Red Sea) show many differences in faunal composition, compared to those from the central Indo-Pacific (e.g. compare Heron-Allen and Earland, 1915; Chasens, 1981 and Hottinger et al., 1993 with Loeblich and Tappan, 1994; Parker, 2009). In the Maldives, Parker and Gischler (2011) identified taxa of Indo-Pacific provenance co-occurring with taxa recorded only from coastal regions in the Red Sea and western Indian Ocean.

These studies show that a variety of environmental and sedimentological parameters control the distribution, assemblages and diversity of benthic foraminifera in reef environments. Bicchi et al. (2002) and

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Gischler et al. (2003) found the highest foraminiferal diversity in the Pacific and Caribbean atoll lagoons that have open circulation. Habitat size can also influence diversity, by virtue of habitat diversity (Schultz et al., 2010). Schultz et al. (2010) also observed the highest diversity in an atoll lagoon with high levels of nutrient availability and abundant fine-grained substrate. Haig (1988, 1993) found diversity of miliolid and buliminid foraminifera in a Papuan lagoon related with mud content and depth. Parker and Gischler (2011) also showed water depth to have a significant influence on diversity and assemblages of benthic foraminifera in the Maldives. They found a positive correlation between water depth and diversity ($r = 0.63$; $p < 0.0001$; Shannon's H) and the highest diversity in water depths of 30–50 m. All these environmental factors have an impact on the number of available microhabitats in reef environments that influence diversity and distribution of benthic foraminifera in modern surface sediments (Langer and Lipps, 2003).

Few studies have examined changes in benthic foraminiferal assemblages and diversity through the Holocene in tropical reef environments (Schultz et al., 2010; Cheng et al., 2012). In the Indian Ocean, no such studies have been conducted. Cheng et al. (2012) studied Holocene and historical changes in species richness, diversity and assemblages of benthic foraminifera in Florida Bay to infer anthropogenic-induced environmental stress during the last 100 yr, and Late Holocene salinity and sea level changes.

Habitat age has been reported as a factor that could influence benthic foraminiferal diversity in atoll reefs and lagoons. Bicchi et al. (2002) found higher species richness in deeper lagoons that were flooded earlier during the post glacial transgression as compared to shallower lagoons that were inundated later. These authors suggested the longer colonization period as a possible cause, but could not rule out the influence of a greater variety of available biotopes in the deeper lagoons (Bicchi et al., 2002).

Over deep geological time, i.e., millions of years, factors such as plate tectonics and the opening/closing of seaways may explain species richness and diversity changes in certain biogeographical regions (Langer and Lipps, 2003). On smaller time frames, several hypotheses have been suggested to account for modern species richness in terrestrial and marine habitats (Sanders, 1969; Connell, 1978 and references therein). According to the Intermediate Disturbance Hypothesis (IDH) of Connell (1978), local diversity reaches its maximum, when ecological and/or physical disturbance is neither too rare, nor too frequent, or occurs neither too soon nor too long after a certain disturbance. The applicability of the IDH was tested for different communities in various environments (e.g., Aronson and Precht, 1995 for coral reefs) and its validity is subject of debate (e.g., Hughes, 2012 and references therein). This idea opposes older hypotheses such as theories that assume highest diversity in an equilibrium state of a community (i.e. the Time Stability Hypothesis of Sanders, 1969) suggesting that diversity is higher in less disturbed and older environments. Richardson-White and Walker (2011) found that the IDH could not explain all encountered diversity patterns in different environments of encrusting foraminifera. Schultz et al. (2010) suggested that an increase in foraminiferal diversity in Belizian atolls during the Holocene was a diversification phase. However, a higher temporal resolution was needed to analyze the effects of disturbance events on diversity and assemblages.

Complementary to the study of Parker and Gischler (2011) that investigated spatial patterns of distribution, diversity and assemblages in surface sediments from Rasdhoo and Ari Atolls at the Maldives, this study investigates the temporal variation of diversity and assemblages through the Holocene. Sediment cores from two different lagoon sites are chosen for this study. They are well suited for such a study: they offer continuous sedimentation records through the Holocene and enable high temporal resolution sampling. Both cores represent two lagoonal sites that experienced environmental changes during the Holocene sea-level rise (Lambeck, 1990; Gischler et al., 2008). To date, most research on effects of Holocene environmental change on biodiversity has been conducted in coastal environments, which is sensitive

to changes in sea level as compared to mid-oceanic reefal settings that are considered more stable. The aim of this study is to contribute to knowledge of the factors that forced Holocene changes in the distribution, assemblages and diversity of benthic foraminifera in the center of the Indian Ocean.

2. Study area

2.1. Geomorphology, sedimentology and benthic foraminifera

The Maldives archipelago consists of 1300 small sand islands on 21 atolls in the central Indian Ocean (Gischler et al., 2013). They extend from just below the equator about 1000 km north toward India. The archipelago is up to 150 km wide and encompasses an area of 107,500 km². The Maldives are among the largest carbonate platform areas in the world. Rasdhoo Atoll (4°N/73°W) is located in the western row of the Maldivian atolls (Fig. 1). It is almost circular with a maximum diameter of 9.25 km and an area of ~62 km². The reef rim is continuous and surface breaking and almost completely surrounds the 40 m deep lagoon that contains numerous coral patch reefs. Three channels through the marginal reef connect the interior lagoon to the ocean. The fore-reef slope is very narrow except on the western side of the atoll, and ends in a near vertical drop-off (Gischler, 2006). Coral grainstone dominates the reef crest facies. Carbonate facies in the lagoon include a hard bottom in the east, mollusk wackestone to packstone in the center, and mudstone in the west (Fig. 2a). This asymmetric distribution reflects the hydrodynamic gradient created by tidal currents, which enter and exit the lagoon through the channels. A further consequence of this gradient is the sand spit-like continuation of the northern reef margin westwards from the NE channel into the lagoon (Gischler, 2006).

Gischler et al. (2008) provided the first comprehensive data on Holocene reef anatomy and sea-level rise in the Maldives at Rasdhoo. They identified four Holocene reef facies: robust-branching coral facies, coralline algal facies, domal coral facies and detrital sand and rubble facies. The Holocene reefs started to grow at ~8.6 kyr BP and developed to a thickness of between 14.5 and >22 m. Marginal reefs accreted in the keep-up mode with high rates >15 m/kyr from 9–7 kyr BP. Due to sea-level slowdown, accretion-rates decreased significantly from 7–6 kyr BP to values of <1 m/kyr. Kench et al. (2009) suggested slightly (50 cm) higher than present sea levels from 4–0 kyr BP, while Gischler et al. (2008) found no evidence for such a highstand at Rasdhoo and suggested that the present day sea level was reached ~4.0 kyr BP (Gischler et al., 2008). Gischler et al. (2008) also showed that the Pleistocene atoll was asymmetrical in shape with a highly elevated rim in the western part and weakly developed or somewhat deeper water margins in the south and east.

Parker and Gischler (2011) conducted the first detailed study on benthic foraminifera in the Maldives, encompassing a variety of reef and lagoon environments. They analyzed surface sediment samples from the adjacent Rasdhoo and Ari atolls and characterized the lagoons by benthic foraminiferal assemblages including three reef crest and back reef assemblages, and five lagoonal assemblages. Their assemblages compare well with the sedimentological characteristics of the lagoons (Gischler, 2006), and their species compositions are largely controlled by depth. In this study, 270 species were identified, which is moderate compared to the central Indo-Pacific lagoons (e.g., Langer and Lipps, 2003; Parker, 2009) and Parker and Gischler (2011) interpreted this as a consequence of lower habitat diversity. Epiphytic species typical of algal and seagrass communities, such as *Cibicides*, are sparse in the Maldives and were found only as a minor component in the samples from Rasdhoo Atoll (Parker and Gischler, 2011). The existence of seagrass meadows is known from the Maldives, but their distribution is patchy (Miller and Sulka, 1999). Shallow reef assemblages in Rasdhoo are characterized by *Amphistegina* and *Calcarina*, while textularid and miliolid taxa are abundant in the lagoon.

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