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REPORT

Distribution and sediment production of large benthic foraminifers on reef flats of the Majuro Atoll, Marshall Islands

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Abstract The distributions and population densities of large benthic foraminifers (LBFs) were investigated on reef flats of the Majuro Atoll, Marshall Islands. Annual sediment production by foraminifers was estimated based on population density data. Predominant LBFs were *Calcarina* and *Amphistegina*, and the population densities of these foraminifers varied with location and substratum type on reef flats. Both foraminifers primarily attached to macrophytes, particularly turf-forming algae, and were most abundant on an ocean reef flat (ORF) and in an inter-island channel near windward, sparsely populated islands. *Calcarina* density was higher on windward compared to leeward sides of ORFs, whereas *Amphistegina* density was similar on both sides of ORFs. These foraminifers were more common on the ocean side relative to the lagoon side of reef flats around a windward reef island, and both were rare or absent in nearshore zones around reef islands and on an ORF near windward, densely populated islands. Foraminiferal production rates varied with the degree to which habitats were subject to water motion and human influences. Highly productive sites ($>10^3$ g $CaCO_3$ m^{-2} $year^{-1}$) included an ORF and an inter-island channel near windward, sparsely populated islands, and a seaward area of a reef flat with no reef islands. Low-productivity sites (<10 g $CaCO_3$ m^{-2} $year^{-1}$) included generally nearshore zones of lagoonal reef flats, leeward ORFs, and a windward ORF near densely populated islands. These results suggest that the distribution and production of LBFs were largely influenced by a combination of natural environmental factors, including water motion, water depth, elevation relative to the lowest tidal level at spring tide, and the distribution of suitable substratum. The presence of reef islands may limit the distribution and production of foraminifers by altering water circulation in nearshore environments. Furthermore, increased anthropogenic factors (population and activities) may adversely affect foraminiferal distribution and production.

Keywords Distribution · Foraminifer · Production · Reef islands · Sediments

Introduction

Approximately 500 atolls are distributed in and near the equatorial, circum-tropical climate zone of the world's oceans. On the rim (reef flats) of atolls form generally low-lying, flat, small islands, termed reef islands (motu and sand cays; Woodroffe et al. 1999). The elevations of these reef islands reach up to a few metres above the mean sea level (e.g. Kayanne et al. 2005; Woodroffe 2008), and the islands are largely composed of unconsolidated bioclastic sands and gravels (e.g. Woodroffe and Morrison 2001). Reef islands are thus highly subject to inundation, coastal

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erosion, catastrophic storms, and other coastal hazards, which are caused by climate change, increases in the sea level, and extreme events (e.g. Mimura et al. 2007). In addition, some tropical island countries are situated either fully or mostly on atolls, and the main islands in these countries are densely populated and urbanised (e.g. Spennemann 1992; Kayanne et al. 2005). As a result, reef islands and adjacent coral reefs near population centres now suffer from anthropogenic disturbances such as water pollution, waste disposal, dredging, construction, and land reclamation (Richmond et al. 2002; Abraham et al. 2004; Vieux et al. 2004).

The bioclastic sediments of reef islands are primarily composed of fragments and shells produced by calcifying organisms that live in the adjacent reefs such as corals, coralline algae, molluscs, and large benthic foraminifers (Woodroffe 2002). In the western and central Pacific atolls, the sand-sized sediments are dominated by shells of large benthic foraminifers (reviewed in Yamano et al. 2005). Large benthic foraminifers (LBFs), which belong to several families and subfamilies, are shelled protists (>1 mm in mature diameter) and are host to algal endosymbionts (Lee 1998; Hallock 1999). Thus, LBFs with algal symbionts have physiological analogy with reef-building symbiotic corals (Hallock 2000a). Living individuals of LBFs are found in great abundance on reef flats (Hallock 1984; Hohenegger 1994), and their distribution and abundance are mainly influenced by light, temperature, water energy, substratum type, and water quality (Hohenegger 2004; Renema 2006). These organisms live for several months to several years (Hallock et al. 1986b; Hallock 1999) and reproduce both sexually and asexually (Lee et al. 1991). These features result in high production rates of their calcareous shells (Hallock 1981; Langer et al. 1997; Fujita et al. 2000; Hohenegger 2006). After death, the empty shells are very robust and resistant to abrasion and breakage (Kotler et al. 1992; Wetmore and Plotnick 1992; Yordanova and Hohenegger 2002) and thus remain in the system as sediments. Because these robust shells typically range from coarse-grained sand to granules in size, various hydrodynamic forces (e.g. wind-waves, tides, and storms) transport and accumulate them in shoreline environments (e.g. Hohenegger 2006). Therefore, the shells of LBFs are the chief components of the sand-sized sediments of reef islands on many Pacific atolls (Tudhope et al. 1985; Ebrahim 2000; Woodroffe and Morrison 2001; Collen and Garton 2004).

Studies of the distribution and production of living LBFs are necessary to elucidate the sources and rates of sediment production by foraminifers around reef islands. Such research has broad implications for understanding the formation process of reef islands and the responses of these vulnerable systems to future environmental changes. The distribution and abundance of foraminifers in atoll sediments have been examined in many Pacific atolls (e.g. Chapman 1900, 1901, 1902; Cushman et al. 1954; Todd 1961; Tudhope et al. 1985; Ebrahim 2000; Woodroffe and Morrison 2001; Bicchi et al. 2002; Yamano et al. 2002; Collen and Garton 2004). These studies have revealed that foraminiferal shells are the main components of surface sediments on reef flats and in lagoons, and that foraminiferal assemblages in reef-flat sediments are primarily composed of *Baculogypsina*, *Calcarina*, *Amphistegina*, and *Marginopora* in central and western Pacific atolls, although the species composition varies with region, environment, and substratum type. However, several questions are yet to be answered. First, most previous studies only examined dead specimens in sediments; thus, the distribution and abundance of living specimens on atolls remain unclear. Only Todd (1961) studied both dead and live specimens from surface sediment samples that originally contained only a few living specimens (e.g. Hallock 1984; Hohenegger 1994). Second, previous studies have reported that living foraminifers are abundant on windward reef-flats (Collen 1995; Ebrahim 2000), implying that the distribution of foraminifers may be influenced by the wave energy experienced within a particular habitat. Third, Collen (1995) and Ebrahim (2000) also reported that LBFs have recently become absent on reef flats near densely populated islands, indicating that the population densities and sediment production rates of these foraminifers may decline in response to anthropogenic effects.

The goals of this study were to determine the distribution patterns and sediment production rates of large benthic foraminifers on the reef flats of a Pacific atoll and to more generally understand the factors that control foraminiferal distribution and production in atoll environments. In particular, this study focused on natural environmental variables such as water energy, water depth, and substratum type, as well as the effects of human populations and activities, as potential factors affecting foraminiferal distribution and production.

Materials and methods

Study area

The field survey was conducted in the Majuro Atoll, which is representative of central north Pacific atolls. The Majuro Atoll (7°10′ N, 171°10′ E) is located in the southern Marshall Islands (Fig. 1) and is elongated in shape, spanning approximately 40 km from east to west and approximately 10 km from north to south. A wide, deep lagoon is enclosed by the atoll rim, on which lie the reef flats and reef islands. Most portions of the reef flats are

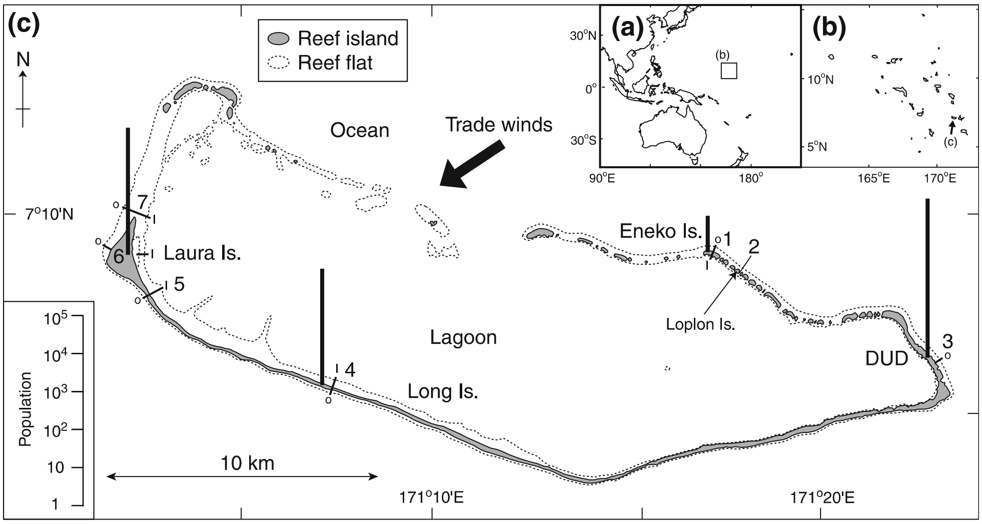

Fig. 1 Maps of the study area. **a** Western Pacific, **b** Marshall Islands, and **c** the Majuro Atoll, indicating the locations of line transects 1–7. o: ocean side, l: lagoon side. *Vertical bars* indicate the size of the human population in each island/area

intertidal and subaerially exposed at low tide. The reef islands are generally low lying and flat, with an average elevation of only a few metres above the mean sea level. The islands are composed of bioclastic carbonate sediments (mainly fragments of corals and coralline algae, *Halimeda* segments, and foraminiferal and mollusc shells) derived from adjacent reef flats. Foraminiferal shells comprise >50% of sands in surface and subsurface sediments throughout the reef islands. Other components (corals, coralline algae, *Halimeda*, and molluscs) are relatively minor in the sand fractions, but are predominant in the gravel fractions (Anthony et al. 1989; Yasukochi 2007).

The climate at the Majuro Atoll is tropical, with north-east trade winds prevailing throughout the year. The average annual temperature is approximately 27°C, and the annual precipitation is approximately 3,500 mm. The area experiences distinct wet (May–November) and dry (December–April) seasons; however, because Majuro is not situated in the typhoon belt, tropical storms are rare.

Sea-surface temperatures around the Majuro Atoll are approximately 30°C, and the salinity of the oceanic water is approximately 34 psu (Suzuki et al. 1997). Water exchange between the lagoon and the open ocean is primarily caused by radiation-stress-induced flows over windward reef flats and in part by tidal flushing and wind-stress-induced mixing (Kraines et al. 1999). Wind-induced waves predominantly originate from the east-northeast throughout the year; ocean swells approach from the northeast, but shift to come from the east between May and September (Shimazaki et al. 2005). Wind waves and ocean swells break at oceanward reef edges, raise water levels, and convert to cross-reef currents. The ocean side of reef islands suffers from strong water motion during high tides, but protects the lagoon from the direct influence of cross-reef currents. The tide is semidiurnal and has a range of approximately 1.8 m. During rising and ebb tides, lagoon and oceanic water exchange through the main channel located in the centre of the northern atoll rim and also through inter-island channels between reef islands.

At present, reef islands to the east, south, and west of the atoll are connected, resulting in a long continuous island, whereas reef islands to the north are separated by passages (inter-island channels; Fig. 1c). Reef islands in the eastern part of the atoll, known as the Darrit-Uliga-Delap (DUD) area, are situated on the windward side of the atoll. The DUD area has a human population of approximately 15,000, which is approximately 70% of the total population of the Majuro Atoll (Spennemann 1992). This area is partially reclaimed and is primarily composed of business, commercial, residential, and government-owned land. Compared to the early 1900s, the population of the DUD area dramatically increased in the late 1900s (Spennemann 1992).

Reef islands in the southern part of the atoll are elongated in the east–west direction, narrow from north to south ($\sim$100 m in width), and are situated on the leeward side of the atoll. The population of this area is sparse (approximately 1,000) and decreases with distance from the DUD area. The land is primarily covered with palm trees and is used in part as agricultural and residential areas. Laura Island has the largest area on the atoll (total land area of 1.8 km^2) and is located at the southwestern tip of the atoll. The population of Laura Island is approximately 2,000, and the land is mainly used as agricultural and residential areas. Situated on the windward side of the atoll, the reef islands in the northern region are generally small in area, and mostly covered with palm trees. These islands are sparsely populated (<10 persons per island), but populations gradually increase with proximity to the DUD area.

Several line transects were established across the reef flats and islands of the Majuro Atoll (Fig. 1). The reef flats near a windward reef island (Eneko Island; Transect 1) and a leeward reef island (Long Island; Transect 4) were studied to compare the foraminiferal distribution and production under different wave-energy settings. Three transects around Laura Island (offshore of the northern area, the central region, and the southern tip of the island; Transects 5–7) and an inter-island channel between windward reef islands (the east channel of Loplon Island; Transect 2) were also examined to characterise the influence of reef islands on the foraminiferal distribution and production. These variables were also compared between reef flats near a sparsely populated island (Eneko Island; Transect 1) and near a densely populated area (the DUD area; Transect 3) to examine anthropogenic influences on the foraminiferal distribution and production.

Field survey

On ocean and lagoonal reef flats at each transect, a line-transect survey was conducted in August 2005 and 2006 to measure topography, identify substrata, and collect samples for foraminiferal analysis. A line transect was established perpendicular to the shoreline using a 100-m measuring tape. The water depth (within <5 cm) was measured at 10-m intervals along the line transect using measuring tape. At several line transects (Transect 3 and a nearshore zone of a lagoonal reef flat at Transect 4), the topography was measured using an auto level with a staff. The depth and elevation data were corrected for tidal effects using tide tables at Majuro obtained from the South Pacific Sea Level and Climate Monitoring Project (http://www.bom.gov.au/pacificsealevel/). The substrata and benthic community were characterised at 10-m intervals to determine ecological zones and the boundaries thereof. Each ecological zone was classified based on the dominant substratum cover and benthic community.

Within each ecological zone, sampling sites were established at regular intervals. At each site, the typical substratum (such as macrophytes and reef rubble) was collected for foraminiferal analysis. For turf-forming algae and sediments, a circular plastic vial (approximately 3 cm in diameter) was placed over algae or inserted into surface sediment (the upper 2–3 cm). Algae or sediment was subsequently detached from the substratum from below by sliding a steel plate under the vial, which was then capped with a plastic lid. For other macrophytes and reef rubble, a sample area of 100 cm^2 was collected by hand and carefully placed into a plastic bag. Samples were then preserved in 5% formalin-seawater.

Laboratory procedures

In the laboratory, each sample was washed on a 63-μm sieve, and algae or gravel were then removed and air-dried. The dried substratum was examined under a binocular microscope to remove any foraminifers that had remained attached; if the substratum was algae, they were identified to as specific a taxonomic level as possible. The residue remaining in the sieve was stained with rose Bengal (1 g l^{-1} of water), washed three times to remove surplus stain, and dried at 60°C. The dried residue was sieved into four size fractions (<0.5, 0.5–1, 1–2, and >2 mm). From the 0.5–1-, 1–2-, and >2-mm size fractions, all stained foraminiferal specimens were isolated, identified to species level, and enumerated. The <0.5-mm size fraction was not processed or analysed because large-sized specimens (>0.5 mm in diameter) of benthic foraminifers are the predominant constituents of reef-island sediments. High-density samples were divided using a micro-splitter until a subsample of each size fraction contained at least 100 individuals of live foraminifers. The resulting count data were converted to the number of individuals m^{-2} of bottom surface. Population densities are expressed as the mean (±SD) for each ecological zone. The number of replicates for each ecological zone is 4 ($n = 4$), except for being mentioned in the text.

Because the resulting density data were not normally distributed, rank non-parametric statistical methods were applied. To compare foraminiferal densities between ecological zones on each reef flat or between different transects, the population density data of each species were analysed using Mann–Whitney *U*-tests for pairwise comparisons and Kruskal–Wallis (KW) tests for multiple comparisons. To compare foraminiferal densities between different transects, the population density in the ecological zone at which each species was dominant was chosen at each transect. When a significant difference was found in a multiple-comparison data set, pairwise differences among treatments were analysed using Nemenyi Joint-Rank (NJR) tests.

Large benthic foraminiferal assemblages (>0.5 mm in diameter) on reef flats of the Majuro Atoll were characterised by both very low taxon diversity and very high abundance. The dominant species were *Calcarina gaudichaudii* d'Orbigny in Ehrenberg 1840 and *Amphistegina lobifera* Larsen 1976. Both species are also major foraminiferal components of reef-island sediments on the Majuro Atoll (Yamano et al. 2002; Yasukochi 2007). *Calcarina gaudichaudii* (hereafter referred to as *Calcarina*) has a thick, low trochoid shell characterised by many radial thick spines. *Amphistegina lobifera* (hereafter referred to as *Amphistegina*) has a thick, bilenticular trochoid shell. Both species are host to diatom endosymbionts (Lee 1998). Other minor species included *Peneroplis* spp., *Cymbaloporetta* spp., *Planorbulina* spp., *Amphisorus* sp., and *Sorites* sp. *Calcarina* and *Amphistegina*, the two dominant species in both living and sediment assemblages on reef flats of the Majuro Atoll, were targeted for distribution and production estimates.

Estimates of production rates

Based on population density data, gross shell production rates (GP; i.e. the number of shells produced m^{-2} $year^{-1}$) were calculated for each species as

$$\mathrm{GP} = \sum (N_i \times \tau) \tag{1}$$

where N_i is the population density of size-fraction i (individuals m^{-2}), and τ is the turnover rate ($year^{-1}$). Turnover rates for *Calcarina* (11 $year^{-1}$) and *Amphistegina* (13 $year^{-1}$) in Majuro were assumed to be the same as those estimated for the same or similar species in Palau by Hallock (1981).

Gross carbonate production rates (CP; g $CaCO_3$ m^{-2} $year^{-1}$) were then calculated for each species using a simple method presented by Hallock (1981):

$$\mathrm{CP} = \sum (N_i \times \tau \times W_i) \tag{2}$$

where W_i is the mass (g) of an intermediate-sized individual in size-fraction i, calculated using the mass–diameter relationship described in Hallock (1981). Production by the smallest size fraction (<0.5 mm) was not included in this estimate, but can reach up to 10–20% of estimated production (Hallock 1981).

Gross sediment production rates by volume (SP; m^3 $year^{-1}$ m^{-2}) were also determined for each species using the formula

$$\mathrm{SP} = \sum (N_i \times \tau / V_i) \tag{3}$$

where V_i is the mean number of foraminiferal specimens per unit of volume (number cm^{-3}) in size-fraction i, which was estimated by counting the number of foraminiferal specimens in each size fraction in a known volume of a metre-cylinder; values of V_i for *Calcarina* were 300 (>2 mm), 600 (1–2 mm), and 1,200 (0.5–1 mm), and values of V_i for *Amphistegina* were 1,000 (1–2 mm) and 2,000 (0.5–1 mm).

Results

Distribution and population density

Windward reef islands (Transects 1–3)

On an ocean reef flat (ORF) at Transect 1 (Fig. 2a), *Calcarina* increased in abundance with distance from shore on the oceanward side, and its population density was significantly higher in an algal turf (AT) zone ($1.5 \pm 0.9 \times 10^6$ individuals m^{-2}) than in a nearshore cyanobacterial and filamentous algal mat (C&A Mat) zone (NJR test, $P < 0.05$). *Amphistegina* was most abundant in macrophytes (*Cladophora* and *Jania*) growing on the side walls of small, shallow tide pools (~50 cm in diameter and ~10 cm in depth) in the C&A Mat zone ($2.02 \pm 0.32 \times 10^5$ individuals m^{-2}). The population density of *Amphistegina* at this site was significantly higher than in an offshore *Turbinaria* zone (NJR test, $P < 0.05$).

On a lagoonal reef flat (LRF) at Transect 1, live individuals of *Calcarina* and *Amphistegina* were very rare. Few individuals of either species (100 individuals m^{-2}) were found on reef rubble on sand and gravel bottom surfaces. Thus, the population density of neither species was significantly different among ecological zones (KW test, *ns*).

In an inter-island channel between windward reef islands (water depth of ~50 cm below mean sea level; Transect 2), both *Calcarina* and *Amphistegina* were abundant on surfaces of *Halimeda* (Table 1). The population densities of *Calcarina* and *Amphistegina* were $1.1 \pm 1.0 \times 10^6$ and $1.9 \pm 1.7 \times 10^5$ individuals m^{-2}, respectively, which were of the same order of magnitude as densities in the AT zone for *Calcarina* and in the C&A Mat zone for *Amphistegina* on the windward ORF (Transect 1; Mann–Whitney *U*-test, *ns*).

On an ORF near a densely populated area (Transect 3; Fig. 2b), *Calcarina* was only found at one site in the AT zone (1,156 individuals m^{-2}). *Amphistegina* was rarely found in offshore zones (AT zone and corals, coralline algae, and reef rubble zone), and its population density in the AT zone was $1.4 \pm 2.9 \times 10^3$ individuals m^{-2}. Therefore, the population density of neither species was significantly different across ecological zones (KW test, *ns*).

Leeward reef island (Transect 4)

On an ORF of a leeward reef island (Transect 4; Fig. 3), *Calcarina* was found at only one site in the AT zone (1.2×10^3 individuals m^{-2}). The population density of *Calcarina* did not vary significantly across ecological zones (KW test, *ns*). *Amphistegina* was more common than *Calcarina* on the reef flat, except in a nearshore filamentous green algal zone. The population density of *Amphistegina* was highest in the AT zone ($1.2 \pm 1.3 \times 10^4$ individuals m^{-2}); however, its population density did not differ significantly between ecological zones (KW test, *ns*).

On a LRF along Transect 4, *Calcarina* was absent, and *Amphistegina* was also limited in its distribution among offshore coral and reef rubble zones. The population

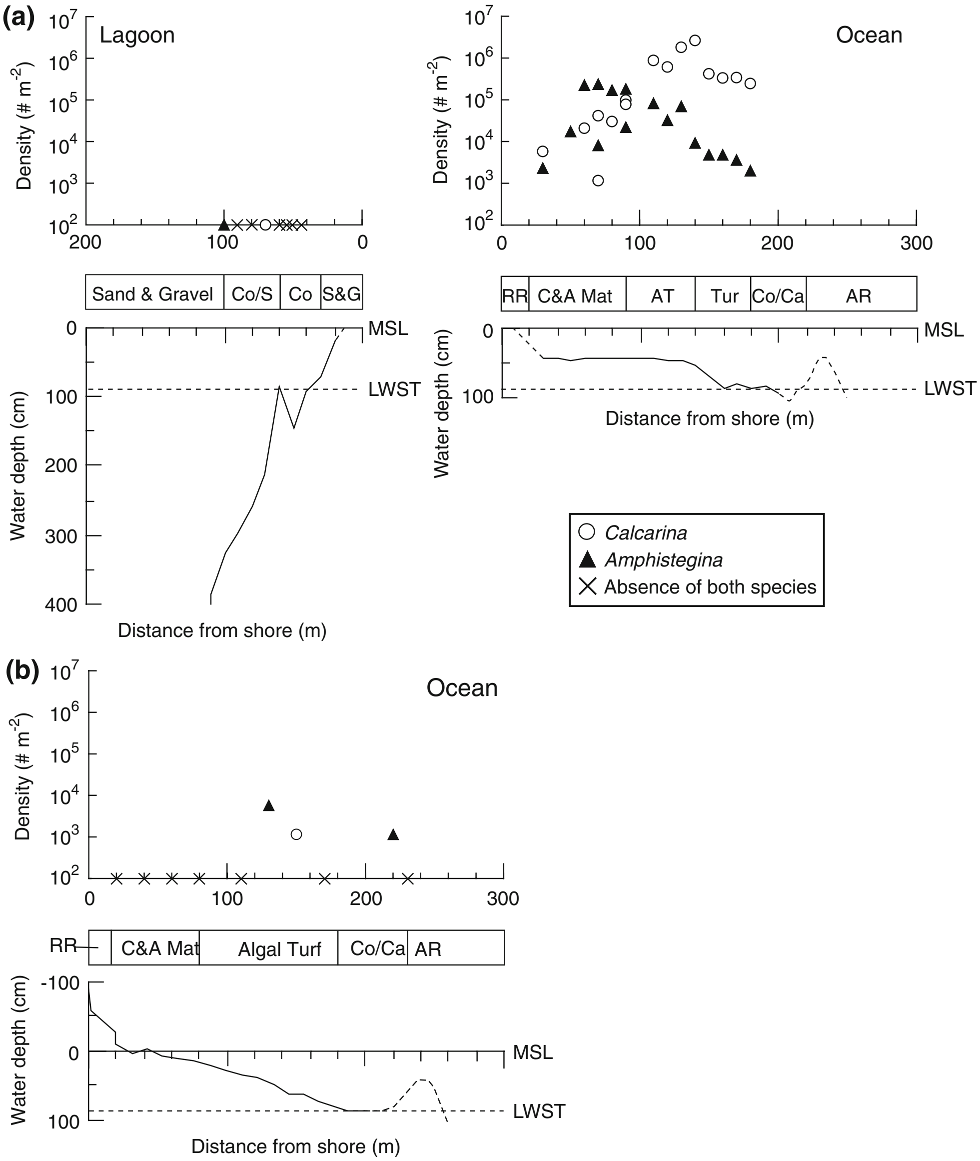

Fig. 2 Topography, ecological zones, and population densities of large benthic foraminifers on reef flats of windward reef islands. **a** Ocean and lagoonal reef flats of a windward, sparsely populated island (Transect 1). **b** An ocean reef flat near a densely populated area (Transect 3). MSL: mean sea level, LWST: the lowest water level at spring tide. Abbreviations for ecological zones: S&G: sand and gravel; Co: coral; Co/S: coral on sand bottom; RR: reef rock; C&A Mat: cyanobacterial and filamentous algal mat; AT: algal turf; Tur: *Turbinaria*; Co/Ca: corals and coralline algae; AR: algal ridge

density of *Amphistegina* in the coral and reef rubble zone was 2.2 ± 2.3 × 10^3 individuals m^{-2} ($n = 8$). The population density of *Amphistegina* differed significantly among ecological zones (KW test, $P < 0.01$); however, a post hoc test did not indicate any differences in the population density of *Amphistegina* between any pair of ecological zones, which was likely caused by high variability in the data.

Laura island (Transects 5–7)

Both species of foraminifers were common throughout a reef flat offshore of the northern area of Laura Island (Transect 7; Fig. 4a). Thus, the population density of neither species differed significantly across ecological zones (KW test, *ns*). The population densities of *Calcarina* and *Amphistegina* on the reef flat were 5.0 ± 8.3 × 10^4 and 1.9 ± 1.6 × 10^4 individuals m^{-2}, respectively ($n = 13$ for each species).

Moving southward, the ocean sides of reef flats around Laura Island become narrower (Fig. 1). On an ORF at the central part of the island (Transect 6; Fig. 4b), *Calcarina* and *Amphistegina* were more common in offshore zones (an AT zone and a *Laurencia* and *Halimeda* zone) than in a nearshore filamentous green algal zone (NJR test, $P < 0.05$). The population densities of *Calcarina* and *Amphistegina* in the *Laurencia* and *Halimeda* zone were 5.0 ± 1.7 × 10^4 and 2.4 ± 0.9 × 10^4 individuals m^{-2}, respectively. On an ORF at the southern tip of the island (Transect 5; Fig. 4c), *Calcarina* was patchy in the AT and *Turbinaria* and *Halimeda* zones, and its population densities in the two zones were 2.89 ± 5.78 × 10^2 and

Table 1 Population density and production rates (mean ± SD) of large benthic foraminifers in ecological zones on ocean and lagoonal reef flats of the Majuro Atoll

Transect	Island	Environment	Ecological zone	Distribution range (m)	Tidal level	# Samples	Population density ($\times 10^3$ m^{-2})			Shell production ($\times 10^3$ m^{-2} year^{-1})		
							Calcarina	*Amphistegina*	Total	*Calcarina*	*Amphistegina*	Total
1	Eneko Is.	Ocean reef flat	Reef rock	0–20	MSL							
			Cyanobacterial & microalgal mat (sand)	20–90	MSL-LWST	4	26 ± 48	12 ± 9	39 ± 54	290 ± 530	160 ± 120	500 ± 600
			Cyanobacterial & microalgal mat (algae)	20–90	MSL-LWST	4	42 ± 25	202 ± 32	245 ± 34	470 ± 270	2,630 ± 420	3,100 ± 420
			Algal turf (*Jania* & Gelidiaceae)	90–140	MSL-LWST	4	1,500 ± 900	48 ± 33	1,500 ± 900	16,000 ± 10,000	630 ± 440	17,000 ± 10,000
			Turbinaria	140–180	LWST	4	330 ± 70	3.8 ± 1.3	340 ± 70	3,700 ± 800	49 ± 17	3,700 ± 800
			Corals & coralline algae	180–220	LWST-ST							
		Lagoon reef flat	Sand & gravel	0–30	MSL							
			Corals (branching) & hard substratum	30–60	MSL-ST	4	0	0	0	0	0	0
			Corals (branching & massive) on sand & gravel bottom	60–100	ST	4	0.025 ± 0.050	0.025 ± 0.050	0.050 ± 0.060	0.28 ± 0.55	0.3 ± 0.7	0.6 ± 0.7
			Sand & gravel bottom	100–	ST							
2	Loplon Is.	Channel	*Halimeda* patch	0–220	ST	4	1,100 ± 1,000	190 ± 170	1,300 ± 1,200	12,000 ± 12,000	2,500 ± 2,300	15,000 ± 14,000
3	Uliga Is.	Ocean reef flat	Reef rock	0–15	Above MSL							
			Cyanobacterial & microalgal mat	15–80	MSL-LWST	4	0	0	0	0	0	0
			Algal turf (*Jania*, Gelidiaceae & *Gelidiopsis*)	80–180	MSL-LWST	4	0.29 ± 0.58	1.4 ± 2.9	1.7 ± 2.8	3 ± 6	19 ± 38	22 ± 36
			Corals (branching), coralline algae & rubble	180–230	LWST	2	0	0.6 ± 0.8	0.6 ± 0.8	0	8 ± 11	8 ± 11
4	Long Is.	Ocean reef flat	Sand & gravel	0–10	Above MSL							
			Filamentous green algae	10–40	MSL-LWST							
			Algal turf (*Jania* & *Gelidiopsis*)	40–100	MSL-LWST	4	0.29 ± 0.58	12 ± 13	12 ± 13	3 ± 6	150 ± 170	160 ± 170
			Laurencia	100–130	MSL-LWST	4	0	7.2 ± 3.9	7.2 ± 3.9	0	94 ± 51	94 ± 51
			Corals & coralline algae	130–145	LWST-ST							
		Lagoonal reef flat	Sand & gravel	0–20	Above MSL							
			Seagrass	20–50	LWST	4	0	0	0	0	0	0
			Sand & gravel bottom with coral patch	50–110	ST	4	0	0	0	0	0	0
			Padina	110–160	ST	4	0	0	0	0	0	0
			Reef rubble & *Dictyota*	160–290	LWST	4	0	0	0	0	0	0
			Coral (branching & massive) & reef rubble	290–410	LWST	8	0	2.2 ± 2.3	2.2 ± 2.3	0	28 ± 29	28 ± 29
			Coral (branching & massive)	410–440	LWST-ST							

Table 1 continued

Transect	Island	Environment	Ecological zone	Distribution range (m)	Tidal level	# Samples	Population density (×10³ m⁻²)			Shell production (×10³ m⁻² year⁻¹)		
							Calcarina	*Amphistegina*	Total	*Calcarina*	*Amphistegina*	Total
5	South Laura Is.	Ocean reef flat	Sand	0–10	Above MSL							
			Filamentous green algae	10–50	MSL-LWST	4	0	0	0	0	0	0
			Algal turf (*Hypnea* & Gelidiaceae)	50–100	MSL-LWST	4	0.29 ± 0.58	4.3 ± 4.9	4.6 ± 5.5	3 ± 6	60 ± 60	60 ± 70
			Turbinaria & *Halimeda*	100–120	LWST-ST	4	0.9 ± 1.1	4.3 ± 3.3	5.2 ± 3.6	10 ± 12	56 ± 43	66 ± 46
			Corals & coralline algae	120–160	ST							
		Lagoonal reef flat	Sand	0–10	Above MSL							
			Seagrass	10–90	LWST	4	0	0	0	0	0	0
			Caulerpa on sand & gravel bottom	90–140	ST	4	0	0	0	0	0	0
			Caulerpa	140–180	ST	4	0	0	0	0	0	0
			Coral (branching)	180–250	ST	2	18 ± 19	0	18 ± 19	200 ± 210	0	200 ± 210
			Sand & gravel bottom	250–350	ST	4	50 ± 70	0.6 ± 0.7	50 ± 70	500 ± 800	8 ± 9	500 ± 800
			Coral (branching & massive)	350–470	ST	4	11 ± 7	0	11 ± 7	120 ± 80	0	120 ± 80
6	Central Laura Is.	Ocean reef flat	Reef rock	0–20	Above MSL							
			Filamentous green algae	20–60	MSL-LWST	4	0	0	0	0	0	0
			Caulerpa & *Dictyosphaeria*	60–180	MSL-LWST	4	10 ± 13	16 ± 12	25 ± 22	100 ± 140	210 ± 160	310 ± 260
			Algala turf (*Jania* & *Caulerpa*)	180–270	MSL-LWST	4	14.7 ± 5.6	23 ± 9	38 ± 10	160 ± 60	300 ± 120	460 ± 130
			Laurencia & *Halimeda*	270–330	MSL-LWST	4	50 ± 17	24 ± 9	74 ± 11	550 ± 190	310 ± 110	860 ± 110
			Corals & coralline algae	330–375	LWST-ST							
		Lagoon Nearshore Zone	Sand	0–10	MSL-LWST							
			Seagrass	10–40	LWST	4	0	0	0	0	0	0
			Muddy sand	40–	ST							
		Lagoon Offshore Patch Reef	Muddy sand	0–10	ST							
			Coral & *Halimeda*	10–90	ST-LWST	8	0.55 ± 0.64	0.025 ± 0.071	0.58 ± 0.65	6 ± 7	0.3 ± 0.9	6 ± 7
			Reef rubble & *Halimeda*	90–110	LWST	4	4.1 ± 5.1	0.58 ± 0.57	4.6 ± 5.4	45 ± 56	7 ± 7	52 ± 59
			Reef rubble	110–130	LWST-MSL	4	0.13 ± 0.19	0.6 ± 0.8	0.7 ± 1.0	1.4 ± 2.1	7 ± 11	9 ± 13
			Dictyota & Coral (massive)	130–190	ST	4	1.7 ± 3.5	16 ± 10	18 ± 12	19 ± 38	210 ± 130	230 ± 150
7	North off Laura Is.	Submerged reef flat	Corals & coralline algae	0–20	ST							
			Laurencia & *Udotea*	20–40	LWST	2	210 ± 120	25 ± 24	240 ± 140	2,400 ± 1,300	320 ± 310	2,700 ± 1,600
			Algal turf (Gelidiaceae & *Microdictyon*)	40–170	LWST-MSL	2	64 ± 26	27 ± 18	90 ± 40	700 ± 290	350 ± 230	1,000 ± 500
			Rubble	170–220	LWST-MSL	1	7	18	25	76	240	317
			Halimeda Patch	220–670	LWST-MSL	4	10 ± 6	7 ± 7	17 ± 12	110 ± 70	90 ± 90	200 ± 140
			Sand & gravel bottom	670–870	LWST-MSL	1	10	37	47	114	481	595
			Halimeda Patch	870–970	LWST-MSL	1	12	12	23	127	150	277
			Coral (massive)	970–	ST	2	12 ± 11	26 ± 27	38 ± 38	130 ± 130	340 ± 350	500 ± 500

Table 1 continued

Transect	Island	Environment	Ecological zone	Distribution range (m)	Tidal level	# Samples	Carbonate production (g $CaCO_3$ m^{-2} $year^{-1}$)			Sediment production ($\times 10^{-3}$ m^3 $year^{-1}$ m^{-2})		
							Calcarina	*Amphistegina*	Total	*Calcarina*	*Amphistegina*	Total
1	Eneko Is.	Ocean reef flat	Reef rock	0–20	MSL							
			Cyanobacterial & microalgal mat (sand)	20–90	MSL-LWST	4	300 ± 600	27 ± 19	400 ± 600	0.5 ± 0.8	0.08 ± 0.06	0.5 ± 0.9
			Cyanobacterial & microalgal mat (algae)	20–90	MSL-LWST	4	270 ± 210	460 ± 60	730 ± 180	0.52 ± 0.34	1.33 ± 0.21	1.86 ± 0.30
			Algal turf (*Jania* & Gelidiaceae)	90–140	MSL-LWST	4	8,000 ± 4,900	110 ± 80	8,100 ± 4,800	17 ± 11	0.32 ± 0.22	18 ± 11
			Turbinaria	140–180	LWST	4	2,470 ± 420	8.1 ± 2.8	2,470 ± 420	4.37 ± 0.53	0.025 ± 0.009	4.39 ± 0.54
			Corals & coralline algae	180–220	LWST-ST							
		Lagoon reef flat	Sand & gravel	0–30	MSL							
			Corals (branching) & hard substratum	30–60	MSL-ST	4	0	0	0	0	0	0
			Corals (branching & massive) on sand & gravel bottom	60–100	ST	4	0	0	0	0	0	0
			Sand & gravel bottom	100–	ST							
2	Loplon Is.	Channel	*Halimeda* patch	0–220	ST	4	9,000 ± 1,0000	420 ± 380	10,000 ± 11,000	20 ± 20	1.3 ± 1.1	20 ± 20
3	Uliga Is.	Ocean reef flat	Reef rock	0–15	Above MSL							
			Cyanobacterial & microalgal mat	15–80	MSL-LWST	4	0	0	0	0	0	0
			Algal turf (*Jania*, Gelidiaceae & *Gelidiopsis*)	80–180	MSL-LWST	4	0.6 ± 1.2	17.5 ± 35.0	18.1 ± 34.6	0.003 ± 0.005	0.019 ± 0.038	0.021 ± 0.036
			Corals (branching), coralline algae & rubble	180–230	LWST	2	0	1.2 ± 1.8	1.2 ± 1.8	0	0.004 ± 0.005	0.004 ± 0.005
4	Long Is.	Ocean reef flat	Sand & gravel	0–10	Above MSL							
			Filamentous green algae	10–40	MSL-LWST							
			Algal turf (*Jania* & *Gelidiopsis*)	40–100	MSL-LWST	4	4 ± 8	25 ± 29	30 ± 28	0.005 ± 0.011	0.08 ± 0.09	0.08 ± 0.09
			Laurencia	100–130	MSL-LWST	4	0	18 ± 13	18 ± 13	0	0.050 ± 0.028	0.050 ± 0.028
			Corals & coralline algae	130–145	LWST-ST							
		Lagoonal reef flat	Sand & gravel	0–20	Above MSL							
			Seagrass	20–50	LWST	4	0	0	0	0	0	0
			Sand & gravel bottom with coral patch	50–110	ST	4	0	0	0	0	0	0
			Padina	110–160	ST	4	0	0	0	0	0	0
			Reef rubble & *Dictyota*	160–290	LWST	4	0	0	0	0	0	0
			Coral (branching & massive) & reef rubble	290–410	LWST	8	0	8 ± 9	8 ± 9	0	0.016 ± 0.017	0.016 ± 0.017
			Coral (branching & massive)	410–440	LWST-ST							
5	South Laura Is.	Ocean reef flat	Sand	0–10	Above MSL							
			Filamentous green algae	10–50	MSL-LWST	4	0	0	0	0	0	0

Table 1 continued

Transect	Island	Environment	Ecological zone	Distribution range (m)	Tidal level	# Samples	Carbonate production (g $CaCO_3$ m^{-2} $year^{-1}$)			Sediment production ($\times 10^{-3}$ m^3 $year^{-1}$ m^{-2})		
							Calcarina	*Amphistegina*	Total	*Calcarina*	*Amphistegina*	Total
			Algal turf (*Hypnea* & Gelidiaceae)	50–100	MSL-LWST	4	4 ± 8	12 ± 10	16 ± 17	0.005 ± 0.011	0.030 ± 0.031	0.035 ± 0.041
			Turbinaria & *Halimeda*	100–120	LWST-ST	4	13 ± 16	9 ± 7	22 ± 18	0.016 ± 0.020	0.028 ± 0.022	0.044 ± 0.031
			Corals & coralline algae	120–160	ST							
		Lagoonal reef flat	Sand	0–10	Above MSL							
			Seagrass	10–90	LWST	4	0	0	0	0	0	0
			Caulerpa on sand & gravel bottom	90–140	ST	4	0	0	0	0	0	0
			Caulerpa	140–180	ST	4	0	0	0	0	0	0
			Coral (branching)	180–250	ST	2	130 ± 150	0	130 ± 150	0.23 ± 0.26	0	0.23 ± 0.26
			Sand & gravel bottom	250–350	ST	4	340 ± 530	1.2 ± 1.4	340 ± 530	0.6 ± 0.9	0.004 ± 0.004	0.6 ± 0.9
			Coral (branching & massive)	350–470	ST	4	70 ± 60	0	70 ± 60	0.13 ± 0.10	0	0.13 ± 0.10
6	Central Laura Is.	Ocean reef flat	Reef rock	0–20	Above MSL							
			Filamentous green algae	20–60	MSL-LWST	4	0	0	0	0	0	0
			Caulerpa & *Dictyosphaeria*	60–180	MSL-LWST	4	70 ± 90	43 ± 36	120 ± 120	0.11 ± 0.14	0.11 ± 0.09	0.22 ± 0.20
			Algala turf (*Jania* & *Caulerpa*)	180–270	MSL-LWST	4	74 ± 27	55 ± 22	128 ± 26	0.17 ± 0.06	0.15 ± 0.06	0.32 ± 0.08
			Laurencia & *Halimeda*	270–330	MSL-LWST	4	370 ± 90	51 ± 18	420 ± 80	0.65 ± 0.20	0.156 ± 0.055	0.81 ± 0.16
			Corals & coralline algae	330–375	LWST-ST							
		Lagoon Nearshore Zone	Sand	0–10	MSL-LWST							
			Seagrass	10–40	LWST	4	0	0	0	0	0	0
			Muddy sand	40–	ST							
		Lagoon Offshore Patch Reef	Muddy sand	0–10	ST							
			Coral & *Halimeda*	10–90	ST-LWST	8	2.5 ± 3.8	0	2.6 ± 3.7	0.006 ± 0.008	0	0.006 ± 0.008
			Reef rubble & *Halimeda*	90–110	LWST	4	13 ± 17	1.5 ± 1.6	14 ± 17	0.040 ± 0.051	0.004 ± 0.004	0.044 ± 0.053
			Reef rubble	110–130	LWST-MSL	4	0.6 ± 1.0	1.2 ± 1.8	1.8 ± 2.8	0.0014 ± 0.0022	0.004 ± 0.005	0.005 ± 0.007
			Dictyota & Coral (massive)	130–190	ST	4	7 ± 14	43 ± 31	50 ± 41	0.019 ± 0.037	0.11 ± 0.07	0.13 ± 0.10
7	North off Laura Is.	Submerged reef flat	Corals & coralline algae	0–20	ST							
			Laurencia & *Udotea*	20–40	LWST	2	1,800 ± 800	50 ± 50	1,900 ± 800	3.0 ± 1.4	0.16 ± 0.15	3.1 ± 1.6
			Algal turf (Gelidiaceae & *Microdictyon*)	40–170	LWST-MSL	2	460 ± 220	57 ± 39	520 ± 260	0.83 ± 0.36	0.17 ± 0.12	1.0 ± 0.5
			Rubble	170–220	LWST-MSL	1	29	40	68	0.074	0.120	0.194
			Halimeda Patch	220–670	LWST-MSL	4	78 ± 49	15 ± 14	90 ± 60	0.13 ± 0.08	0.047 ± 0.043	0.18 ± 0.12
			Sand & gravel bottom	670–870	LWST-MSL	1	50	79	129	0.117	0.240	0.357
			Halimeda Patch	870–970	LWST-MSL	1	53	25	77	0.127	0.075	0.202
			Coral (massive)	970–	ST	2	53 ± 24	60 ± 60	110 ± 80	0.13 ± 0.11	0.17 ± 0.18	0.30 ± 0.28

Abbreviations for tidal level: *MSL* mean sea level, *LWST* the lowest water level at spring tide, *ST* subtidal

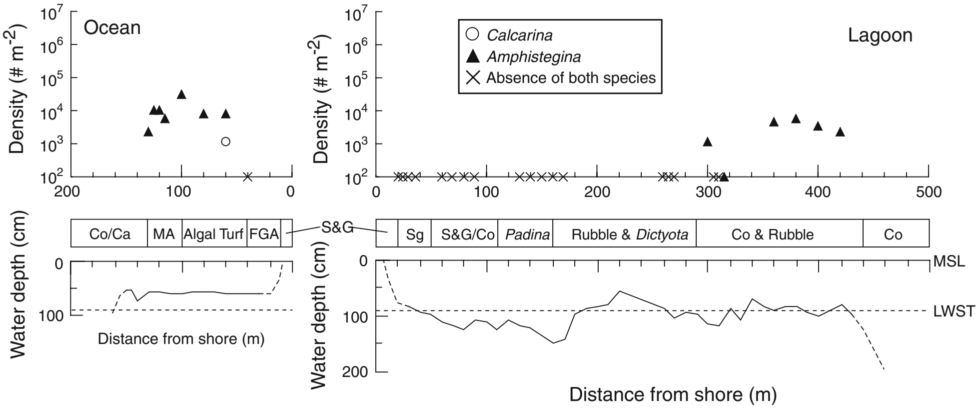

Fig. 3 Topography, ecological zones, and population densities of large benthic foraminifers on ocean and lagoonal reef flats of a leeward reef island (Transect 4). Abbreviations for ecological zones: FGA: filamentous green algae; MA: macroalgae; Sg: seagrass bed. Other abbreviations for ecological zones and sea-levels are the same as in Fig. 2

$8.67 \pm 11.07 \times 10^2$ individuals m^{-2}, respectively. Thus, the population density of *Calcarina* did not differ significantly among ecological zones (KW test, *ns*). Compared to *Calcarina*, *Amphistegina* was more common in the AT and *Turbinaria* and *Halimeda* zones and reached their highest population density in these two ecological zones ($4.3 \pm 3.3 \times 10^3$ and $4.3 \pm 4.9 \times 10^3$ individuals m^{-2}, respectively). The population density of *Amphistegina* differed significantly between ecological zones (KW test, $P < 0.05$); however, a post hoc test did not reveal any differences in population density between any pair of ecological zones, likely because of high variability in the data.

The lagoon sides of reef flats around Laura Island were separated from the island by a deep lagoon of ~10 m deep, but the reef flats were connected to the island on their southward sides (Fig. 1). On a lagoonal patch reef located off of the central part of the island (Transect 6; Fig. 4b), *Calcarina* was common on the flat top of the patch reef, and its highest population density occurred in the reef rubble and *Halimeda* zone ($4.0 \pm 5.1 \times 10^3$ individuals m^{-2}). However, the population density of *Calcarina* did not differ significantly among ecological zones (KW test, *ns*). *Amphistegina* increased in abundance from the flat top to the lagoonal edge, and its population density in a lagoonward *Dictyota* and coral zone ($1.6 \pm 1.0 \times 10^4$ individuals m^{-2}) was significantly higher than that in an islandward coral and *Halimeda* zone (NJR test, $P < 0.05$). On a LRF at the southern tip of the island (Transect 5; Fig. 4c), *Calcarina* and *Amphistegina* were absent in nearshore zones, although the former was more common in offshore coral and sand bottom zones ($5.0 \pm 7.0 \times 10^4$ individuals m^{-2}). The population density of *Calcarina* differed significantly across ecological zones (KW test, $P < 0.01$); however, a post hoc test did not reveal any differences in the population density between any pair of ecological zones, likely because of high variability in the data. *Amphistegina* was rare throughout the reef flat and was only found on surfaces of *Caulerpa* in the sand and gravel bottom zone ($5.78 \pm 6.67 \times 10^4$ individuals m^{-2}). Thus, the population density of *Amphistegina* did not differ significantly among ecological zones (KW test, *ns*).

Comparisons of population density among transects

Calcarina and *Amphistegina* were most abundant on an AT zone and nearshore tide pools on a windward ORF (Transect 1), respectively (Table 1). Both foraminifers were also abundant on *Halimeda* meadows in an inter-island channel (Transect 2). *Calcarina* was more common on the windward (Transect 1) than leeward side of ORFs (Transect 4; NJR test, $P < 0.05$), whereas the density of *Amphistegina* was similar on both sides of ORFs (NJR test, *ns*). Both species were more common on the ocean side than the lagoon side of reef flats around a windward reef island (Transect 1; NJR test, $P < 0.05$). The population densities of both species were significantly lower on an ORF near densely populated islands (Transect 3) than on an ORF near sparsely populated islands (Transect 1; NJR test, $P < 0.05$).

Production rates

The calculated carbonate production rates of the two foraminiferal species varied across physical environments and ecological zones (Table 1; Fig. 5). Production rates using other units exhibited similar variation to those measured in grams of carbonate (Table 1). The highest production rates of *Calcarina* (>10^3 g $CaCO_3$ m^{-2} $year^{-1}$) occurred in offshore zones of a windward ORF (Transect 1), an inter-island channel between windward reef islands (Transect 2), and an oceanward macroalgal zone off of the north shore of Laura

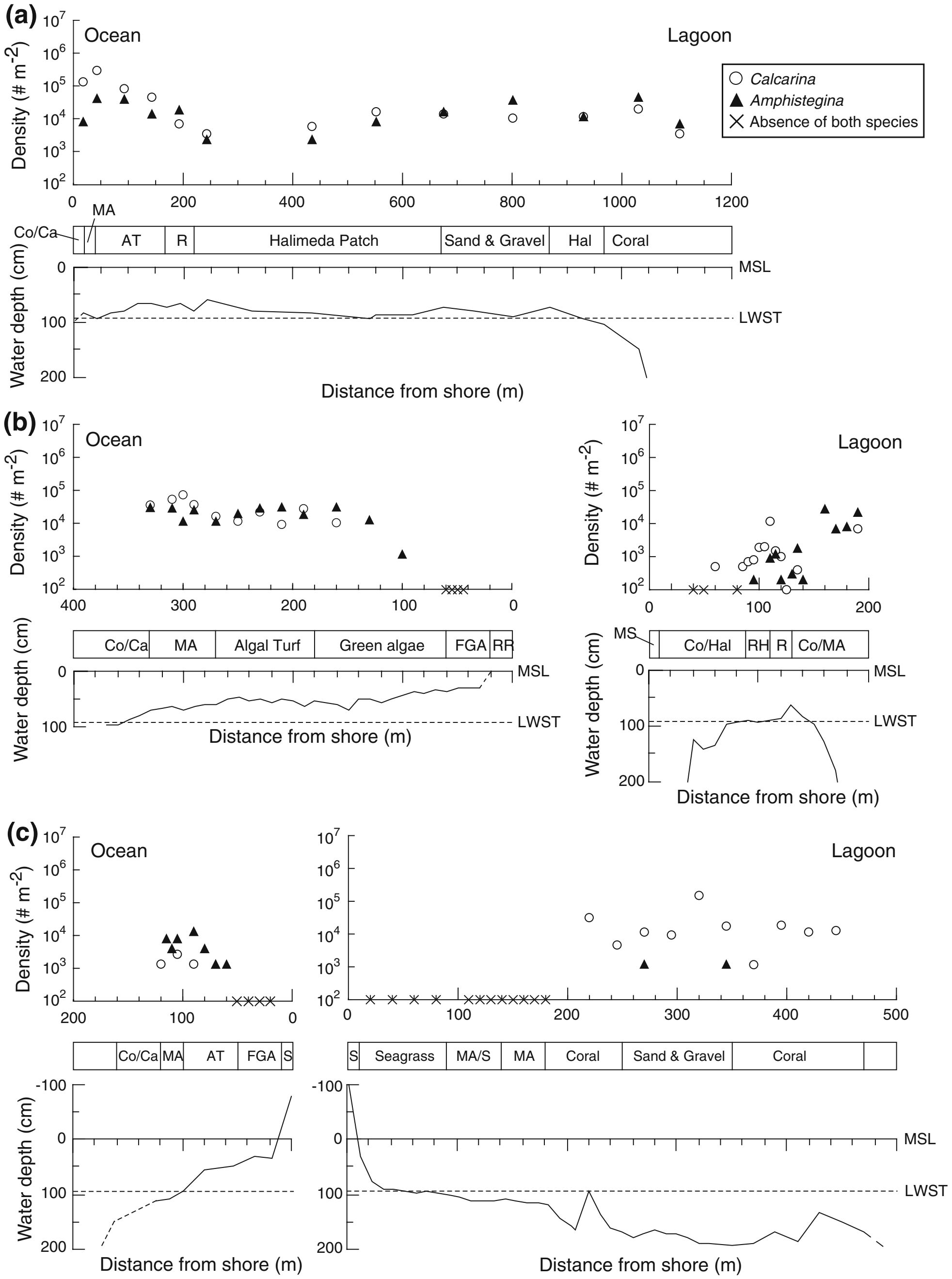

Fig. 4 Topography, ecological zones, and population densities of large benthic foraminifers on reef flats around Laura Island. **a** A reef flat off the north shore of Laura Island (Transect 7). **b** Ocean reef flat and lagoonal patch reef at the central part of Laura Island (Transect 6). **c** Ocean and lagoonal reef flats at the southern tip of Laura Island (Transect 5). Abbreviations for ecological zones: R: reef rubble; Hal: *Halimeda* patch; MS: muddy sand; RH: reef rubble and *Halimeda*. Other abbreviations are the same as in Figs. 2 and 3

Island (Transect 7). Low *Calcarina* production rates (<10 g $CaCO_3$ m^{-2} $year^{-1}$) occurred in a windward ORF near densely populated islands (Transect 3), a leeward ORF (Transects 4), LRFs of windward and leeward reef islands (Transects 1 and 4), nearshore zones around Laura Island (Transects 5 and 6), and a lagoonal patch reef off Laura Island (Transect 6).

The highest production rates of *Amphistegina* (>10^2 g $CaCO_3$ m^{-2} $year^{-1}$) occurred in macroalgae in nearshore tide pools (Transect 1), an AT zone of a windward ORF (Transect 1), and an inter-island channel between windward reef islands (Transect 2). Low *Amphistegina* production rates (<10 g $CaCO_3$ m^{-2} $year^{-1}$) occurred in an offshore *Turbinaria* zone on a windward ORF (Transect 1), most portions

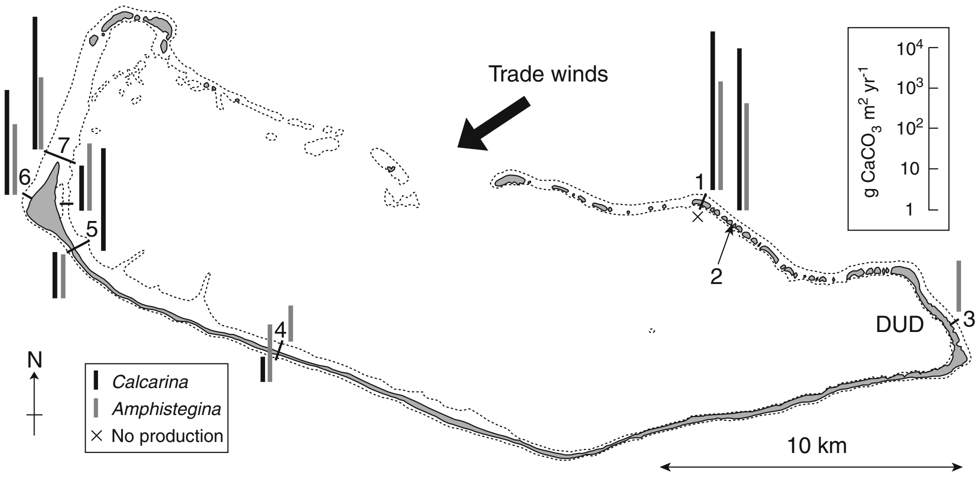

Fig. 5 Carbonate production rates (g CaCO$_3$ m^{-2} year^{-1}) of two species of large benthic foraminifers on reef flats of the Majuro Atoll. Mean rates are shown for the ecological zones at which each species dominated on each reef flat

of a windward ORF near a densely populated area (Transect 3), LRFs of windward and leeward reef islands (Transects 1, 4, and 5), nearshore zones around Laura Island (Transects 5 and 6), and most portions of a lagoonal patch reef off of Laura Island (Transect 6).

Discussion

Natural environmental factors that affect foraminiferal distribution and density

On the reef flats of the Majuro Atoll, the population density of LBFs differed across locations and substratum types, and the patterns of distribution varied between the two species. *Calcarina* and *Amphistegina* were most abundant on a windward ORF and in an inter-island channel (Fig. 2, Table 1). *Calcarina* density was higher on windward than leeward sides of ORFs, whereas *Amphistegina* density was similar on both sides of ORFs (Figs. 2, 3). Both species were more common on the ocean side than the lagoon side of reef flats around a windward reef island (Fig. 2). The observed foraminiferal distributions and abundances may be related to variation in water motion across sites. At the Majuro Atoll, cross-reef currents driven by wind-waves and ocean swells are stronger on the windward than the leeward side of ORFs, as well as on the ocean side than the lagoon side of reef flats around reef islands (Fig. 1). In inter-island channels, strong tidal currents occur during rising and ebb tides.

Water motion also affects the metabolism and growth of foraminifers. Measurements of photosynthesis and respiration using oxygen microsensors indicate that the average gross photosynthesis rates of symbiont-bearing foraminifers (*Amphistegina*) under flow conditions are significantly higher than gross rates measured under stagnant conditions (Köhler-Rink and Kürl 2000). The chemical microenvironment around the shells of symbiont-bearing foraminifers is largely controlled by the prevailing flow conditions (Köhler-Rink and Kürl 2000, 2001). Culture experiments under continuous water flow showed that *Amphistegina* individuals subjected to water motion grow significantly thicker shells than those that are not (Hallock et al. 1986a).

The two study foraminifers can resist water motion by attaching to the substratum using adhesive elastic plugs (*Calcarina*) or pseudopodia (*Amphistegina*). Macroalgae also provide highly efficient protection against wave and current action by forming dense tangles on reef surfaces (e.g. Langer 1993). A loose meshwork of filamentous or densely branched macroalgae enables *Calcarina* individuals to hook within the algal meshwork and to affix to algal thalli with elastic plugs that protrude from the tip of spines (Röttger and Krüger 1990). Species with weak pseudopodial attachment (*Amphistegina*) are also protected against transport by macroalgae. These observations, together with the distributions of these two species, suggest that *Calcarina* individuals require stronger water motion and are better able to stay attached than are *Amphistegina* individuals.

Calcarina and *Amphistegina* were rare or absent in nearshore zones on both ocean and lagoon sides of reef flats (Figs. 2–4). The nearshore zone is generally characterised by weak water motion compared to offshore zones. In addition, the nearshore zone of ORFs is subaerially exposed during low tide; therefore, this zone experiences large daily variation and extreme levels of physical and chemical variables (e.g. light, temperature, and salinity). Such nearshore environments may exceed the physiological tolerance levels of the two species, particularly during calm conditions or low tides. The substrata of nearshore zones were primarily composed of thin, soft mats of cyanobacteria and filamentous algae on ORFs and flat, smooth seagrass leaves on a sand and gravel bottom on LRFs. Neither substrate type may provide suitable habitat for the settlement of these foraminiferal species.

On ORFs where *Calcarina* individuals were relatively common (Transects 1 and 6; Figs. 2, 4), this species tended to be more abundant in offshore AT and macroalgal zones above the level of the lowest water at spring tide (LWST). The distribution of macroalgae appeared to be affected by water energy and water depth, particularly turf-forming algae (primarily *Jania* and Gelidiaceae) that flourished offshore and above the level of LWST. In more offshore subtidal zones with high levels of water energy, macroalgal cover decreased, whereas coral and coralline algal cover increased (Figs. 2–4). *Calcarina* generally exhibits peak abundance on reef edges, but can persist in water as deep as 20 m (Hohenegger et al. 1999). Therefore, the abundance of *Calcarina* in offshore AT and macroalgal zones may be explained in part by the presence of numerous attachment sites provided by algae, as well as protection from strong water motion.

Amphistegina was differentially distributed across windward and leeward reef flats, which is likely explained by its lower tolerance to water motion. On a windward ORF (Transect 1; Fig. 2), weakly attached *Amphistegina* individuals avoided offshore high-energy environments and instead preferred macroalgae in relatively calm nearshore tide pools. On leeward ORFs (Transects 4, 5, and 6; Figs. 3, 4), this species was more common in the offshore macroalgal zone. *Amphistegina* density was also significantly higher in a shallow lagoonal slope than on reef flats of patch reefs offshore of Laura Island (Transect 6; Fig. 4). These results suggest that *Amphistegina* requires areas with relatively moderate water motion.

Results from Laura Island and the inter-island channel indicate that the foraminiferal distribution is influenced by the presence of reef islands. On reef flats off of the north tip of Laura Island (Transect 7), at which no reef islands are present, *Calcarina* and *Amphistegina* were distributed throughout the reef flat. However, on reef flats around Laura Island (Transects 5 and 6), the two species were rare or absent in nearshore zones and common in offshore zones (Fig. 4). Furthermore, the population densities of the two species in an inter-island channel were comparable to those in ecological zones that were dominated by these two species on a windward ORF (Table 1). The presence of a reef island on reef flats likely results in weak water circulation in nearshore zones, which may affect the physiology of foraminifers and limit their distribution in nearshore zones around reef islands.

Anthropogenic factors that affect foraminiferal distribution and density

The population densities of the two species were much lower on an ORF near densely populated islands (Transect 3) than on that near sparsely populated islands (Transect 1), even though both transects were similar in physical environment (topography and wave influence; Figs. 1, 2). Foraminiferal habitat (primarily macrophytes) on reef flats also differed between sparsely and densely populated islands. Offshore *Turbinaria* zones were not found on reef flats near densely populated islands. Algal turfs near sparsely populated islands were composed primarily of *Jania* sp. and Gelidiaceae, whereas those near densely populated islands were composed of these two taxa, as well as cyanobacteria and various types of macroalgae (*Padina* sp., *Gelidiopsis* sp., *Chondria* sp., *Laurencia* sp., and *Lomentaria* sp.). Paulay and Benayahu (1999) reported that coral mortality due to bleaching in the Majuro lagoon in 1992 increased from west to east and peaked in the metropolitan area at the east end (i.e. the DUD area). As suggested by Paulay and Benayahu (1999), these ecological changes may be related to variation in the human population on reef islands (Fig. 1). Large amounts of sewage caused by large populations and human activity likely result in the deterioration of water quality (particularly nutrient concentrations) in ground water and surrounding waters. The reclamation of reef flats and channels to connect islands and expand land area may cause changes in water circulation patterns on reef flats, negatively affecting water quality.

The observed decline in foraminiferal densities near densely populated islands echoes several reports from other atolls and reefs in the Pacific. LBFs were rare compared to heterotrophic small foraminifers (Miliolids) in the vicinity of sewage outfall on a populated island at the Eniwetok Atoll (Hirshfield et al. 1968). Similarly, Collen (1995) and Ebrahim (2000) reported that living LBFs were absent from lagoons and ORFs near densely populated areas of the Majuro Atoll and the South Tarawa Atoll, respectively. In the 1970s in Hawaii, off the coast of Honolulu, the daily disposal of millions of gallons of sewage promoted macroalgal growth, resulting in *Amphistegina* densities that were approximately one order of magnitude lower than at healthy reef sites (Hallock 2000a). The declines in the abundance of living LBFs are also consistent with reported historical changes in foraminiferal assemblages in surface sediments, which shifted from a predominance of symbiont-bearing large taxa to that of heterotrophic small taxa in regions where nutrification was suspected (Cockey et al. 1996; Schueth and Frank 2008). Because algal symbiosis is energetically advantageous when dissolved nutrients and particulate food resources were scarce (Hallock 2000b), further studies should aim to confirm the deterioration of water quality as a possible cause of declines in symbiont-bearing LBFs on reef flats near densely populated areas. Outcome of these studies may imply that the distribution and density of symbiont-bearing LBFs is useful as an indicator of anthropogenic influence on reef flats, thus of coral-reef vitality as suggested by Hallock (2000a).

Sediment production rates of large benthic foraminifers on the Majuro Atoll

This study is the first estimate of sediment production by LBFs on reef flats of Pacific atolls, which contribute to the formation and maintenance of reef islands that are highly vulnerable to future environmental changes. Foraminiferal production rates primarily varied with the degree to which habitats were subject to water motion and human influences. Highly productive sites included a windward ORF, an inter-island channel, and a seaward portion of a reef flat (north of Laura Island; $>10^3$ g $CaCO_3$ m^{-2} $year^{-1}$). Low-productivity sites typically included the nearshore zones of LRFs, leeward ORFs, and a windward ORF near densely populated islands. The production rates at these sites were four orders of magnitude lower than those at the highest productivity sites. The ranges in production rates were generally similar to those in other tropical and subtropical reef environments (Hallock 1981; Hallock et al. 1986b; Langer et al. 1997; Harney et al. 1999; Yamano et al. 2000; Harney and Fletcher 2003; Hohenegger 2006; Hart and Kench 2007). In particular, the highest production rates of *Calcarina* and *Amphistegina* were comparable to those occurring at high-density sites on seaward reef flats in Palau (Hallock 1981).

Production rates are chiefly affected by population density and turnover rate (Hallock 1981). In particular, the high production rates on the windward ORF and the inter-island channel were likely caused by the predominance of *Calcarina* populations because the production rate of *Amphistegina* was similar to rates reported in other areas (Hallock 1981; Harney et al. 1999; Hohenegger 2006). As discussed above, the population density of *Calcarina* is affected by physical factors (water energy and water depth) and substratum type. The turnover rates of foraminifers in Majuro were assumed to be the same as those in Palau, which shares a similar climate zone. However, life history parameters (growth rate, mortality, fecundity) may vary in different physical settings (windward vs. leeward sites) and with the degree of human influence (polluted vs. unpolluted environments). To allow for more accurate estimates of production rates, further studies should characterise the temporal variation and life history of foraminiferal populations in various reef-flat environments on atolls. Nevertheless, the results in this study suggest that LBFs in suitable habitats have a strong potential to produce and supply carbonate sediments. These foraminiferal sediments are transported by waves and currents across reef flats and deposited along shores and the inner margin of lagoons (Yamano et al. 2002; Smith and Collen 2006).

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References

Abraham T, Beger M, Burdick D, Cochrane E, Craig P, Didonato G, Fenner D, Green A, Golbuu Y, Gutierrez J, Hasurmai M, Hawkins C, Houk P, Idip D, Jacobson D, Joseph E, Keju T, Kuartei J, Palik S, Penland L, Pinca S, Rikim K, Starmer J, Trianni M, Victor S, Whaylen L (2004) Status of the coral reefs in Micronesia and American Samoa. In: Wilkinson C (ed) Status of coral reefs of the world: 2004. Australian Institute of Marine Science, Townsville, pp 381–410

Anthony SS, Peterson FL, Mackenzie FT, Hamlin SN (1989) Geohydrology of the Laura fresh-water lens, Majuro Atoll: a hydrogeochemical approach. Geol Soc Am Bull 101:1066–1075

Bicchi E, Debenay J-P, Pages J (2002) Relationship between benthic foraminiferal assemblages and environmental factors in atoll lagoons of the central Tuamotu Archipelago (French Polynesia). Coral Reefs 21:275–290

Chapman F (1900) On some new and interesting foraminifera from the Funafuti Atoll, Ellice Islands. J Linn Soc Lond Zool 28:1–27

Chapman F (1901) Foraminifera from the lagoon at Funafuti. J Linn Soc Lond Zool 28:161–210

Chapman F (1902) On the Foraminifera collected round the Funafuiti Atoll from shallow and moderately deep water. J Linn Soc Lond Zool 28:379–417

Cockey E, Hallock P, Lidz BH (1996) Decadal-scale changes in benthic foraminiferal assemblages off Key Largo, Florida. Coral Reefs 15:237–248

Collen JD (1995) Preliminary comment on visit to Funafuti, Majuro and Tarawa Atolls June–July 1995. SOPAC Preliminary Report 81, South Pacific Applied Geoscience Commission, Suva

Collen JD, Garton DW (2004) Larger foraminifera and sedimentation around Fongafale Island, Funafuti Atoll, Tuvalu. Coral Reefs 23:445–454

Cushman JA, Todd R, Post RJ (1954) Recent Foraminifera of the Marshall Islands. Geol Surv Prof Pap 260-H:319–384

Ebrahim MT (2000) Impact of anthropogenic environmental change on larger foraminifera: Tarawa Atoll, Kiribati, South Pacific. In: Martin RE (ed) Environmental micropaleontology. Kluwer Academic/Plenum Publishers, New York, pp 105–119

Fujita K, Nishi H, Saito T (2000) Population dynamics of *Marginopora kudakajimensis* Gudmundsson (Foraminifera: Soritidae) in the Ryukyu Islands, the subtropical northwest Pacific. Mar Micropaleontol 38:267–284

Hallock P (1981) Production of carbonate sediments by selected large benthic foraminifera on two Pacific coral reefs. J Sediment Petrol 51:467–474

Hallock P (1984) Distribution of selected species of living algal symbiont-bearing foraminifera on two Pacific coral reefs. J Foraminifer Res 14:250–261

Hallock P (1999) Symbiont-bearing Foraminifera. In: Sen Gupta BK (ed) Modern Foraminifera. Kluwer Academic Publishers, Dordrecht, pp 123–139

Hallock P (2000a) Larger foraminifera as indicators of coral-reef vitality. In: Martin RE (ed) Environmental micropaleontology. Kluwer Academic/Plenum Publishers, New York, pp 121–150

Hallock P (2000b) Symbiont-bearing foraminifera: harbingers of global change? Micropaleontology 46:95–104

Hallock P, Forward LB, Hansen HJ (1986a) Influence of environment on the test shape of *Amphistegina*. J Foraminifer Res 16:224–231

Hallock P, Cottey TL, Forward LB, Halas J (1986b) Population biology and sediment production of *Archaias angulatus* (Foraminiferida) in Largo Sound, Florida. J Foraminifer Res 16:1–8

Harney JN, Fletcher CH III (2003) A budget of carbonate framework and sediment production, Kailua Bay, Oahu, Hawaii. J Sediment Res 73:856–868

Harney JN, Hallock P, Fletcher CH III, Richmond BM (1999) Standing crop and sediment production of reef-dwelling foraminifera on O'ahu, Hawai'i. Pac Sci 53:61–73

Hart DE, Kench PS (2007) Carbonate production of an emergent reef platform, Warraber Island, Torres Strait, Australia. Coral Reefs 26:53–68

Hirshfield HI, Charmatz R, Helson L (1968) Foraminifera in samples taken mainly from Eniwetok Atoll in 1956. J Protozool 15:497–502

Hohenegger J (1994) Distribution of living larger foraminifera NW of Sesoko-jima, Okinawa, Japan. PSZNI Mar Ecol 15:291–334

Hohenegger J (2004) Depth coenoclines and environmental considerations of western Pacific larger foraminifera. J Foraminifer Res 34:9–33

Hohenegger J (2006) The importance of symbiont-bearing benthic foraminifera for west Pacific carbonate beach environments. Mar Micropaleontol 61:4–39

Hohenegger J, Yordanova E, Nakano Y, Tatzreiter F (1999) Habitats of larger foraminifera on the upper reef slope of Sesoko Island, Okinawa, Japan. Mar Micropaleontol 36:109–168

Kayanne H, Chikamori M, Yamano H, Yamaguchi T, Yokoki H, Shimazaki H (2005) Interdisciplinary approach for sustainable land management of atoll islands. Global Environ Res 9:1–7

Köhler-Rink S, Kürl M (2000) Microsensor studies of photosynthesis and respiration in larger symbiotic foraminifera. I The physico-chemical microenvironment of *Marginopora vertebralis*, *Amphistegina lobifea* and *Amphisorus hemprichii*. Mar Biol 137:473–486

Köhler-Rink S, Kürl M (2001) Microsensor studies of photosynthesis and respiration in the larger symbiont bearing foraminifera *Amphistegina lobifera* and *Amphisorus hemprichii*. Ophelia 55:111–122

Kotler E, Martin RE, Liddell WD (1992) Experimental analysis of abrasion and dissolution resistance of modern reef-dwelling foraminifera: implications for the preservation of biogenic carbonate. Palaios 7:244–276

Kraines SB, Suzuki A, Yanagi T, Isobe M, Guo X, Komiyama H (1999) Rapid water exchange between the lagoon and the open ocean at Majuro Atoll due to wind, waves, and tide. J Geophys Res 104:15635–15653

Langer MR (1993) Epiphytic foraminifera. Mar Micropaleontol 20:235–265

Langer MR, Silk MT, Lipps JH (1997) Global ocean carbonate and carbon dioxide production: the role of reef foraminifera. J Foraminifer Res 27:271–277

Lee JJ (1998) "Living sands"-larger foraminifera and their endosymbiotic algae. Symbiosis 25:71–100

Lee JJ, Faber WW Jr, Anderson OR, Pawlowski J (1991) Life-cycles of foraminifera. In: Lee JJ, Anderson OR (eds) Biology of Foraminifera. Academic Press, London, pp 285–334

Mimura N, Nurse L, McLean RF, Agard J, Briguglio L, Lefale P, Payet R, Sem G (2007) Small islands. In: Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (eds) Climate change 2007: impacts. adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp 687–716

Paulay G, Benayahu Y (1999) Patterns and consequences of coral bleaching in Micronesia (Majuro and Guam) in 1992–1994. Micronesica 32:109–124

Renema W (2006) Habitat variables determining the occurrence of large benthic foraminifera in the Belau area (East Kalimantan, Indonesia). Coral Reefs 25:351–359

Richmond R, Kelty R, Craig P, Emaurois C, Green A, Birkeland C, Davis G, Edward A, Golbuu Y, Gutierrez J, Houk P, Idechong N, Maragos J, Paulay G, Starmer J, Tafileichig A, Trianni M, Velde NV (2002) Status of the coral reefs in Micronesia and American Samoa: US Affiliated and Freely Associated Islands in the Pacific. In: Wilkinson CR (ed) Status of coral reefs of the world: 2002, GCRMN Report. Australian Institute of Marine Science, Townsville, pp 217–236

Röttger R, Krüger R (1990) Observations on the biology of Calcarinidae (Foraminiferida). Mar Biol 106:419–425

Schueth JD, Frank TD (2008) Reef foraminifera as bioindicators of coral reef health: low isles reef, northern Great Barrier Reef, Australia. J Foraminifer Res 38:11–22

Shimazaki H, Yamano H, Yokoki H, Yamaguchi T, Chikamori M, Tamura M, Kayanne H (2005) Geographic database on the natural and socioeconomic conditions of reef islands. Global Environ Res 9:47–55

Smith R, Collen JD (2006) Three-dimensional imaging of lagoon aggregate extraction and resources: case study from Majuro Atoll, Marshall Islands. Environ Eng Geosci 12:93–102

Spennemann DHR (1992) Historic demography of Majuro Atoll, Republic of the Marshall Islands. J Pac Soc 15:132–152

Suzuki A, Kawahata H, Goto K (1997) Reef water CO_2 system and carbon cycle in Majuro Atoll, the Marshall Islands in the central Pacific. Proc 8th Int Coral Reef Symp 1: 971–976

Todd R (1961) Foraminifera from Onotoa Atoll, Gilbert Islands. Geol Surv Prof Pap 354-H:171–191

Tudhope AW, Scoffin TP, Stoddart DR, Woodroffe CD (1985) Sediments of Suwarrow Atoll. Proc 5th Int Coral Reef Congr 6: 611–616

Vieux C, Aubanel A, Axford J, Chancerelle Y, Fisk D, Holland P, Juncker M, Kirata T, Kronen M, Osenberg C, Pasisi B, Power M, Salvat B, Shima J, Vavia V (2004) A century of change in coral reef status in southeast and central Pacific: Polynesia Mana Node, Cook Islands, French Polynesia, Kiribati, Niue, Tokelau, Tonga, Wallis and Futuna. In: Wilkinson C (ed) Status of coral reefs of the world: 2004. Australian Institute of Marine Science, Townsville, pp 363–380

Wetmore KL, Plotnick RE (1992) Correlations between test morphology, crushing strength, and habitat in *Amphistegina gibbosa*, *Archaias angulatus*, and *Laevipeneroplis proteus* from Bermuda. J Foraminifer Res 22:1–12

Woodroffe CD (2002) Reef-island sedimentation on Indo-Pacific atolls and platform reefs. Proc 9th Int Coral Reef Symp 2: 1187–1192

Woodroffe CD (2008) Reef-island topography and the vulnerability of atolls to sea-level rise. Global Planet Change 62:77–96

Woodroffe CD, Morrison RJ (2001) Reef-island accretion and soil development on Makin, Kiribati, central Pacific. CATENA 44:245–261

Woodroffe CD, McLean RF, Smithers SG, Lawson EM (1999) Atoll reef-island formation and response to sea-level change: West Island, Cocos (Keeling) Islands. Mar Geol 160:85–104

Yamano H, Miyajima T, Koike I (2000) Importance of foraminifera for the formation and maintenance of a coral sand cay: Green Island, Australia. Coral Reefs 19:51–58

Yamano H, Kayanne H, Matsuda F, Tsuji Y (2002) Lagoonal facies, ages, and sedimentation in three atolls in the Pacific. Mar Geol 185:233–247

Yamano H, Kayanne H, Chikamori M (2005) An overview of the nature and dynamics of reef islands. Global Environ Res 9:9–20

Yasukochi T (2007) Ecological and physical factors of Holocene atoll-island formation in the Pacific. Ph. D. thesis, University of Tokyo, p 129

Yordanova EK, Hohenegger J (2002) Taphonomy of larger foraminifera: relationships between living individuals and empty tests on flat reef slopes (Sesoko Island, Japan). Facies 46:169–204