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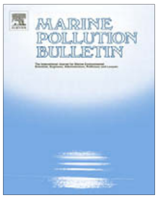

Human impacts on large benthic foraminifers near a densely populated area of Majuro Atoll, Marshall Islands

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ABSTRACT

Human impacts on sand-producing, large benthic foraminifers were investigated on ocean reef flats at the northeast Majuro Atoll, Marshall Islands, along a human population gradient. The densities of dominant foraminifers *Calcarina* and *Amphistegina* declined with distance from densely populated islands. Macrophyte composition on ocean reef flats differed between locations near sparsely or densely populated islands. Nutrient concentrations in reef-flat seawater and groundwater were high near or on densely populated islands. δ^{15}N values in macroalgal tissues indicated that macroalgae in nearshore lagoons assimilate wastewater-derived nitrogen, whereas those on nearshore ocean reef flats assimilate nitrogen from other sources. These results suggest that increases in the human population result in high nutrient loading in groundwater and possibly into nearshore waters. High nutrient inputs into ambient seawater may have both direct and indirect negative effects on sand-producing foraminifers through habitat changes and/or the collapse of algal symbiosis.

1. Introduction

Reef islands on atolls (motu and sand cays) are generally low, flat, and small, with a maximum elevation of up to a few meters above mean sea level. These islands are composed of unconsolidated carbonate sand and gravel (e.g., Woodroffe, 2008). Reef islands are thus highly subject to inundation, coastal erosion, catastrophic storms, and other coastal hazards caused by climate change, increases in sea level, and other extreme events (e.g., Mimura et al., 2007). In addition, some tropical island countries are either fully or predominantly located on atolls, and the main islands of these countries are densely populated and urbanized (e.g., Kiribati, Marshall Islands, Tuvalu). As a result, reef islands and adjacent coral reefs that are near population centers are now affected by 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 carbonate sediments of reef islands are derived from the skeletons and shells of calcifying organisms that live in adjacent reefs, such as corals, coralline algae, mollusks, and large benthic foraminifers (reviewed in Yamano et al. (2005)). In the western and central Pacific atolls, shells of large benthic foraminifers are the primary components of sand-sized sediments. Large benthic foraminifers are shelled protists (>1 mm in mature diameter) that are host to algal endosymbionts (Hallock, 1999). On Majuro Atoll, Marshall Islands, the chief foraminiferal constituents in reef-island sediments are *Calcarina* and *Amphistegina* (Yamano et al., 2002; Yasukochi, 2007). Living individuals of these foraminifers attach primarily to macrophytes, particularly turf-forming algae, and are abundant on ocean reef flats and in inter-island channels near windward reef islands (Fujita et al., 2009).

The distributions and densities of large living benthic foraminifers on the reef flats of Pacific atolls are largely influenced by a combination of natural environmental and human factors. Fujita et al. (2009) reported that large benthic foraminifers were rare or absent on an ocean reef flat located near densely populated islands on Majuro Atoll. Similarly, large living benthic foraminifers were absent from lagoons and ocean reef flats near densely populated areas of the south Tarawa Atoll (a population of about 27,000 persons; Ebrahim, 2000). At the Eniwetok Atoll, large benthic foraminifers were rare in the vicinity of sewage outfalls on a populated island (Hirshfield et al., 1968). Declines in populations of large benthic foraminifers will reduce the rate of sediment supply to reef islands, which will pose serious problems for the maintenance of these islands.

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However, it is not yet clear if foraminiferal density will decline near populated islands. The above results were based on field observations (Ebrahim, 2000) or field surveys of a single populated island (Hirshfield et al., 1968) or a single line transect (Fujita et al., 2009). Many foraminiferal researches in nearshore environments have demonstrated that abundances of benthic foraminifers either increased or decreased in areas polluted by sewage, fertilizers, and aquacultures (reviewed by Yanko et al. (1999)). Foraminiferal density should be investigated along a human population gradient occurring within a relatively constant physical environmental setting. In addition, human impacts such as the deterioration of water quality via sewage effluents and limited water circulation due to the reclamation of reef flats and inter-island channels have been suspected as possible causes for foraminiferal declines near populated islands (Hirshfield et al., 1968; Ebrahim, 2000; Fujita et al., 2009). However, no supporting evidence for this has been obtained.

In this paper, we present detailed field data on the density of large benthic foraminifers along a human population gradient on Majuro Atoll, Marshall Islands, and elucidate relationships between foraminiferal density and environmental conditions in the study area. Along with population density, we investigated foraminiferal habitats (macrophyte compositions) and water quality (nutrient concentrations and δ^{15}N analysis) as possible environmental factors influencing foraminiferal density. δ^{15}N values in macroalgal tissues can provide a useful indicator of nutrient sources in nearshore zones (Umezawa et al., 2002a).

2. Materials and methods

2.1. Study area

The study area was the northeast part of Majuro Atoll, southern Marshall Islands (Fig. 1). The climate at Majuro Atoll is tropical, with northeast trade winds prevailing throughout the year. The average annual temperature is ~27 °C, and annual precipitation is ~3500 mm. The area experiences distinct wet (May–November) and dry (December–April) seasons. Because Majuro is not situated in the typhoon belt, tropical storms are rare.

The study focused on the windward side of the atoll. Wind-induced waves originate predominantly 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). The tide is semidiurnal and has a range of ~1.8 m.

The topography of the study area included primarily reef islands and reef flats. Reef islands are generally low and flat, with an average elevation of only a few meters above mean sea level. The islands were composed of bioclastic carbonate sediments (mainly fragments of corals and coralline algae, *Halimeda* segments, and foraminiferal and mollusk shells) derived from adjacent reef flats; foraminiferal shells composed >50% of sands in surface and subsurface sediments throughout the reef islands (Yamano et al., 2002; Yasukochi, 2007). The ocean reef flats were generally less than 200 m wide from the shoreline to the reef edge and inclined slightly toward the reef edge (Fig. 2). Most portions of the reef flats were intertidal and subaerially exposed at low tide.

The study area stretched from Eneko Island at the northwest end to Delap Island at the southeast end (Fig. 1d). Reef islands in the northwest region were generally small and mostly covered with palm trees. These islands were sparsely populated (<10 persons per island; 24–174 persons km^{-2}), but the number of humans increased gradually toward the southeast region (Fig. 3). The reef islands in the southeast area are known as the Darrit–Uliga–Delap (DUD) area (Fig. 1d). This area is partially reclaimed, consisting of a series of connected islands, and is primarily composed of business, commercial, residential, and government-owned land. The DUD area has a human population of ~15,000, which is ~70% of the total population of the Majuro Atoll (Fig. 3); the population density is

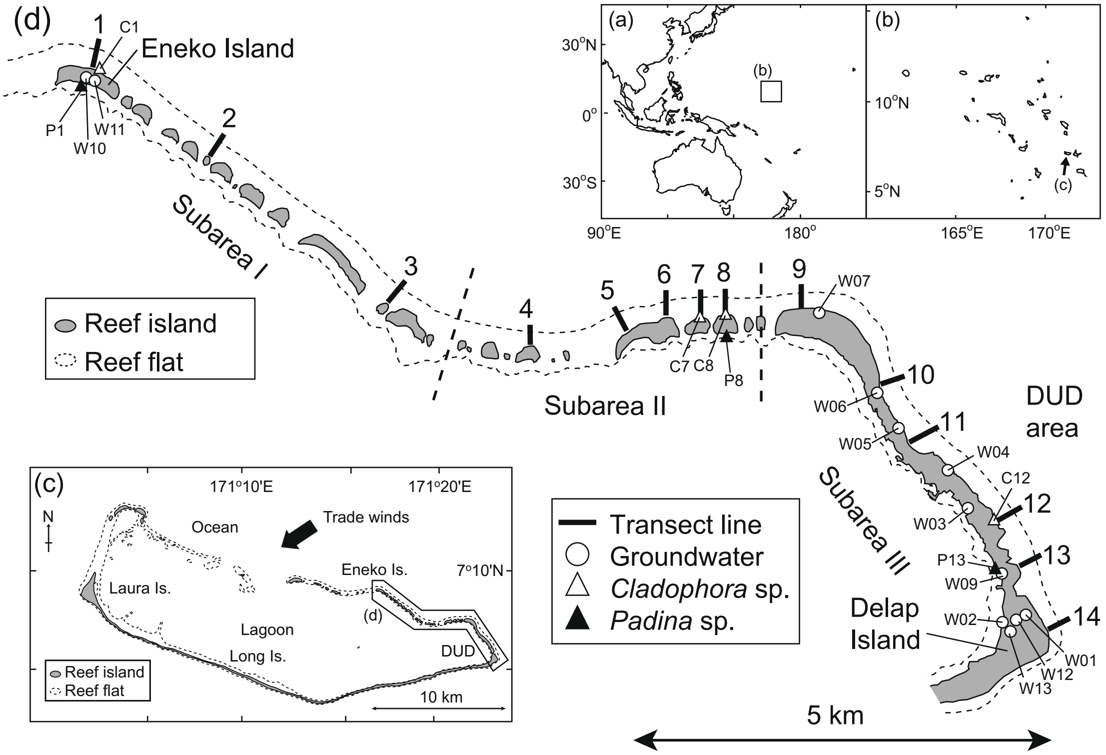

Fig. 1. Map of the study area. (a) Western Pacific, (b) Marshall Islands, (c) Majuro Atoll, (d) the northeast part of the Majuro Atoll, showing the locations of transect lines for foraminiferal and seawater nutrient analyses, macroalgal samples for δ^{15}N analysis, and well sites for groundwater nutrient analysis. Boundaries of three subareas with similar ecological zones are also shown.

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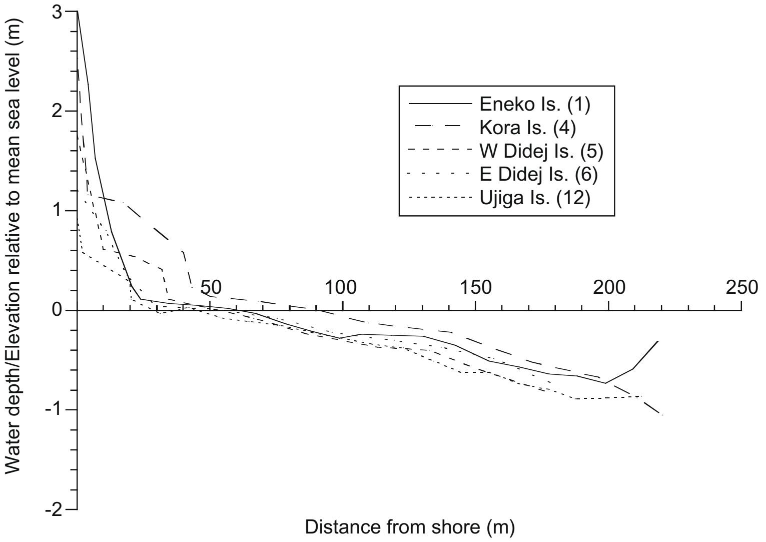

Fig. 2. Topographic profiles of selected transect lines.

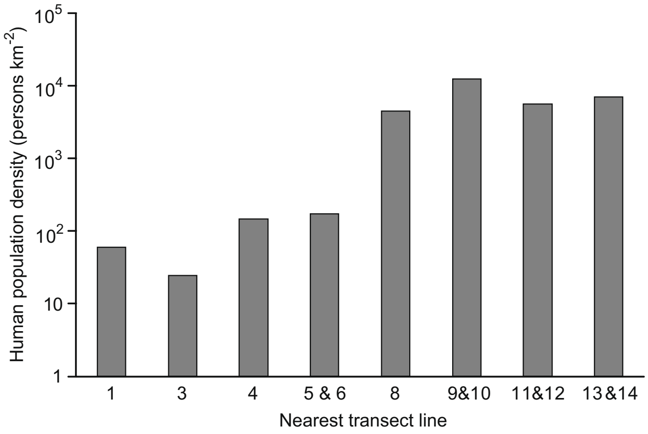

Fig. 3. Human population densities in reef islands near transect lines (population data from Economic Policy, Planning and Statistics Office (2007)).

11,724 persons km^{-2} (Economic Policy, Planning and Statistics Office, 2007). The population of the DUD area increased in the late 20th century (Spennemann, 1992).

2.2. Sampling

Field surveys were conducted in August 2006 and 2007. A total of 14 line transects were set across ocean reef flats to measure topography, identify substrata, and collect samples for foraminiferal analysis and water quality analysis (Fig. 1d). A line transect was established perpendicular to the shoreline using a 100-m measuring tape. At several line transects, 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 characterized at 10-m intervals to determine ecological zones and the boundaries thereof. Ecological zones were classified based on dominant substratum cover and the composition of the benthic community. In each ecological zone, except for offshore coral and coralline algae zones, typical macroalgae were collected in duplicate at regular intervals for foraminiferal analysis. A circular plastic vial (~3 cm in diameter) was placed over algal specimens, and the algae were subsequently detached from the substratum by sliding a steel plate under the vial; the vial was then capped with a plastic lid. Four to six samples were taken for each line transect. Samples were preserved in 5% formalin-seawater.

Water samples were collected to measure water quality (nutrient concentrations) in the groundwater and reef-flat seawater. Filtered (0.45-μm cellulose-acetate filter) surface seawater samples were taken in triplicate from the midpoint of a nearshore zone and an algal turf zone along most line transects. The seawater samples were taken at low tide when nutrient concentrations were expected to represent maximum values because of groundwater discharge and lower mixing rates (dilution) with seawater. Filtered (0.45-μm cellulose-acetate filter) groundwater samples were collected in triplicate from wells in sparsely populated (Eneko Island) and densely populated (DUD area) islands. These water samples were transferred to capped 10-mL acrylic tubes and stored in a freezer for later analysis.

To evaluate nutrient sources in nearshore zones, we collected dominant macroalgae species from the nearshore zones of ocean and lagoon reef flats (*Cladophora* sp. and *Padina* sp., respectively) for $\delta^{15}N$ analysis. These algal samples were kept cool during transport to the laboratory. Some groundwater samples were also used for $\delta^{15}N$ analysis for NO^{3-}, which was a major DIN component.

2.3. Analytical methods

2.3.1. Foraminifera

In the laboratory (about one month after sampling and preservation), each foraminiferal sample was washed on a 63-μm sieve, stained with rose Bengal (1 g per 1 L 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). All stained foraminiferal specimens were isolated from the 0.5–1-, 1–2-, and >2-mm size fractions; specimens were identified to the species level and enumerated. The <0.5-mm size fraction was not processed or analyzed because large specimens (>0.5 mm in diameter) of benthic foraminifers are the predominant constituents of living assemblages found in ocean reef flats. High-density samples were divided using a micro-splitter until a subsample of each size fraction contained at least 100 live foraminifers. Because large

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living benthic foraminiferal assemblages on reef flats of Majuro Atoll are characterized by very low taxon diversity (Fujita et al., 2009), subsamples of a minimum of 100 individuals are sufficient to reflect the original composition of the low-diversity foraminiferal assemblages (e.g., Fujita et al., 2006; Uthicke and Nobes, 2008). The resulting count data were converted to the number of individuals per square meter of bottom surface.

Because the resulting density data were not normally distributed, rank nonparametric statistical methods were applied. To compare foraminiferal densities among transects, we analyzed the density data for each species using a Kruskal–Wallis (KW) test. When a significant difference was found in a multiple-comparison data set, pairwise differences among treatments were analyzed using Nemenyi Joint-Rank (NJR) tests. In addition, regression analysis was conducted to determine the relationship between the mean foraminiferal density at each transect and the human population density in the nearest island. This study targeted the algal symbiont-bearing species *Calcarina gaudichaudii* (hereafter referred to as *Calcarina*), *Amphistegina lobifera* (hereafter referred to as *Amphistegina*), and *Sorites orbiculus* (hereafter referred to as *Sorites*), all of which are common species in both living and sediment assemblages on reef flats in the Majuro Atoll (Yamano et al., 2002; Yasukochi, 2007; Fujita et al., 2009).

2.3.2. Macroalgae

Macroalgae collected for foraminiferal analysis were identified to the lowest possible taxonomic level. Common taxa in each ecological zone were defined as those found in more than half of the sample sites.

2.3.3. Nutrients

Nutrient concentrations (NO_3^-, NO_2^-, NH_4^+, and PO_4^{3-}) were colorimetrically measured with an autoanalyzer (SWAAT: BL Tec KK, Osaka, Japan). Seawater nutrient data were analyzed by two-way analysis of variance (ANOVA) testing for differences among zones and transects and their interaction. Groundwater nutrient data were analyzed by one-way ANOVA testing for differences among well sites. When significant differences were observed within a data set, the difference between each pair of means was analyzed using Fisher's least significant difference (LSD) method.

2.3.4. $\delta^{15}N$

2.3.4.1. $\delta^{15}N$ of macroalgal tissues. Algal samples (5–10 mg) were placed in silver cups and treated with a few drops of 1 N HCl to remove inorganic C (HCO_3^- and precipitated $CaCO_3$); any remaining HCl was evaporated on a hotplate at 60 °C. The C and N contents and their stable isotope ratios were determined with an elemental analyzer and an isotope-ratio mass spectrometer (FLASH EA-Conflo III-DELTA^{PLUS} XP; Thermo Electron Co., Bremen, Germany). Instrument precision was checked with phenylalanine after every five samples (SD < 0.11‰ for $\delta^{15}N$ and <0.10‰ for $\delta^{13}C$). Differences in $\delta^{15}N$ and $\delta^{13}C$ in replicate samples were less than 0.2‰ and 0.3‰ (n = 2 or 3), respectively, within and across analysis periods.

2.3.4.2. $\delta^{15}N$ of nitrate in groundwater. Extraction of groundwater NO_3^- for $\delta^{15}N$ analysis occurred in three steps: (i) the sample was concentrated to remove preexisting NH_4^+, (ii) NO_3^- was converted to NH_3 using Devarda's alloy, and (iii) gas-phase diffusion of NH_3 was performed in high-pH water onto an acidified glass fiber disk (Sigman et al., 1997; Umezawa et al., 2002a). The $\delta^{15}N$ values of duplicate filter samples were measured using the same procedure as outlined for the algal samples. Slight N contamination, probably due to diffusion of atmospheric NH_3 into phosphoric acid on the GF/D filter or initially into the applied phosphoric acid, was accounted for by using distilled water blanks. Differences in $\delta^{15}N$ values between duplicate samples were 0.28‰ on average and 0.44‰ at maximum.

3. Results

3.1. Variation in ecological zones

Ocean reef flats from the shore to the reef edge could be generally divided into cyanobacteria–filamentous green algae mat (CGM) zones, algal turf (AT) zones, *Turbinaria* (Phaeophyceae) zones, and coral and coralline algae (CCA) zones. Furthermore, these flats could be qualitatively classified into three subareas based on the species composition of algal turfs and the presence/absence of nearshore CGM and offshore *Turbinaria* zones (Table 1, Figs. 1 and 4). Near sparsely populated northwest islands (subarea I; transects 1–3), ocean reef flats were divided into AT, *Turbinaria*,

Table 1

Classification of ecological zones in the study area based on the distribution and type of dominant substratum and benthic community.

Subarea	Transect line	Ecological zone (from left to right: from nearshore to offshore)			
I	1–3	Cyanobacteria–filamentous green algae mat zone (present only on transect 1) Width: ∼70 m Common taxa: *Lyngbya* spp. (Cy), *Cladophora* spp. (Ch), *Herposiphonia* sp. (Rh)	Algal turf zone Width: ∼50 m Common taxa: *Jania* sp. (Rh), Gelidiaceae (Rh)	*Turbinaria* zone Width: ∼70 m Common taxa: *Turbinaria ornata* (Ph), *Jania* sp. (Rh), *Laurencia* sp. (Rh)	Coral and coralline algae zone Width: ∼20 m
II	4–8	Cyanobacteria–filamentous green algae mat zone Width: ∼60 m Common taxa: *Cladophora* spp. (Ch), Phormidiaceae (Cy), Rivulariaceae (Cy), *Jania* sp. (Rh), *Anotrichium tenue* (Rh)	Algal turf zone Width: ∼100 m Common taxa: *Jania* sp. (Rh), Gelidiaceae (Rh)	*Turbinaria* zone (absent on transect 8) Width: ∼30 m Common taxa: *Turbinaria ornata* (Ph), *Jania* sp. (Rh), *Laurencia* sp. (Rh), Gelidiaceae (Rh)	Coral and coralline algae zone Width: ∼30 m
III	9–14	Cyanobacteria–filamentous green algae mat zone (absent on transect 14) Width: ∼60 m Common taxa: *Cladophora* spp. (Ch), Phormidiaceae (Cy), *Lyngbya* spp. (Cy), *Valonia macrophysa* (Ch)	Algal turf zone Width: ∼100 m Common taxa: *Valonia macrophysa* (Ch), *Padina* sp. (Ph), *Gelidiopsis intricata* (Rh), *Jania* spp. (Rh), *Lomentaria* sp. (Rh), *Chondria* spp. (Rh), *Laurencia* sp. (Rh), Gelidiaceae (Rh), Phormidiaceae (Cy), *Lyngbya* spp. (Cy)		Coral and coralline algae zone Width: ∼50 m

Cy: Cyanophyta, Ch: Chlorophyta, Rh: Rhodophyta, Ph: Phaeophyta.

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and CCA zones from the shore to the reef edge (Fig. 4a–d). A CGM zone only occurred in a nearshore zone of transect 1. In the intermediate area (between the northwest and southeast islands; subarea II; transects 4–8), ocean reef flats were divided into CGM, AT, *Turbinaria*, and CCA zones from the shore to the reef edge (Fig. 4e–h). In densely populated southeast islands (subarea III; transects 9–14), ocean reef flats were divided into CGM, AT, and CCA zones from the shore to the reef edge (Fig. 4i–l). CGM zones, which were composed primarily of *Cladophora* spp. and filamentous cyanobacteria (e.g., *Lyngbya* spp.; Fig. 4f and j), were widespread in the nearshore zones of subareas II and III. The AT zones in subareas I and II (Fig. 4b and g) were composed of *Jania* and Gelidiaceae, whereas the AT zone in subarea III (Fig. 4k) contained those two taxa and a variety of macroalgae and cyanobacteria, such as *Valonia macrophysa*, *Padina* sp., *Gelidiopsis intricata*, *Lomentaria* sp., *Chondria* spp., *Laurencia* sp., Phormidiaceae, and *Lyngbya* spp. The offshore *Turbinaria* zone (Fig. 4c) disappeared in subarea II (transect 8).

3.2. Variation in foraminiferal density

The densities of *Calcarina* and *Amphistegina* on ocean reef flats tended to decrease toward populated islands (Fig. 5). *Calcarina* was generally more abundant than *Amphistegina* and *Sorites* on ocean reef flats near sparsely populated northwest islands (subarea I). *Calcarina* was very rare in densely populated southeast islands (subarea III), whereas *Amphistegina* and *Sorites* were common near populated islands (subareas II and III).

The density of *Calcarina* varied substantially from 10^6 individuals m^{-2} in subarea I to 0 individuals m^{-2} in subarea III (Fig. 5a). A significant difference in density was observed among transects (KW test, $P < 0.0001$). Post hoc tests indicated that densities on some transects in subarea I (transects 2 and 3) were significantly higher than in subarea III (transects 9–14; NJR test, $P < 0.05$). The density of *Amphistegina* ranged from $>10^5$ individuals m^{-2} in subarea I to 10^2 individual m^{-2} in subarea III (Fig. 5b). There was a significant difference in density among transects (KW test,

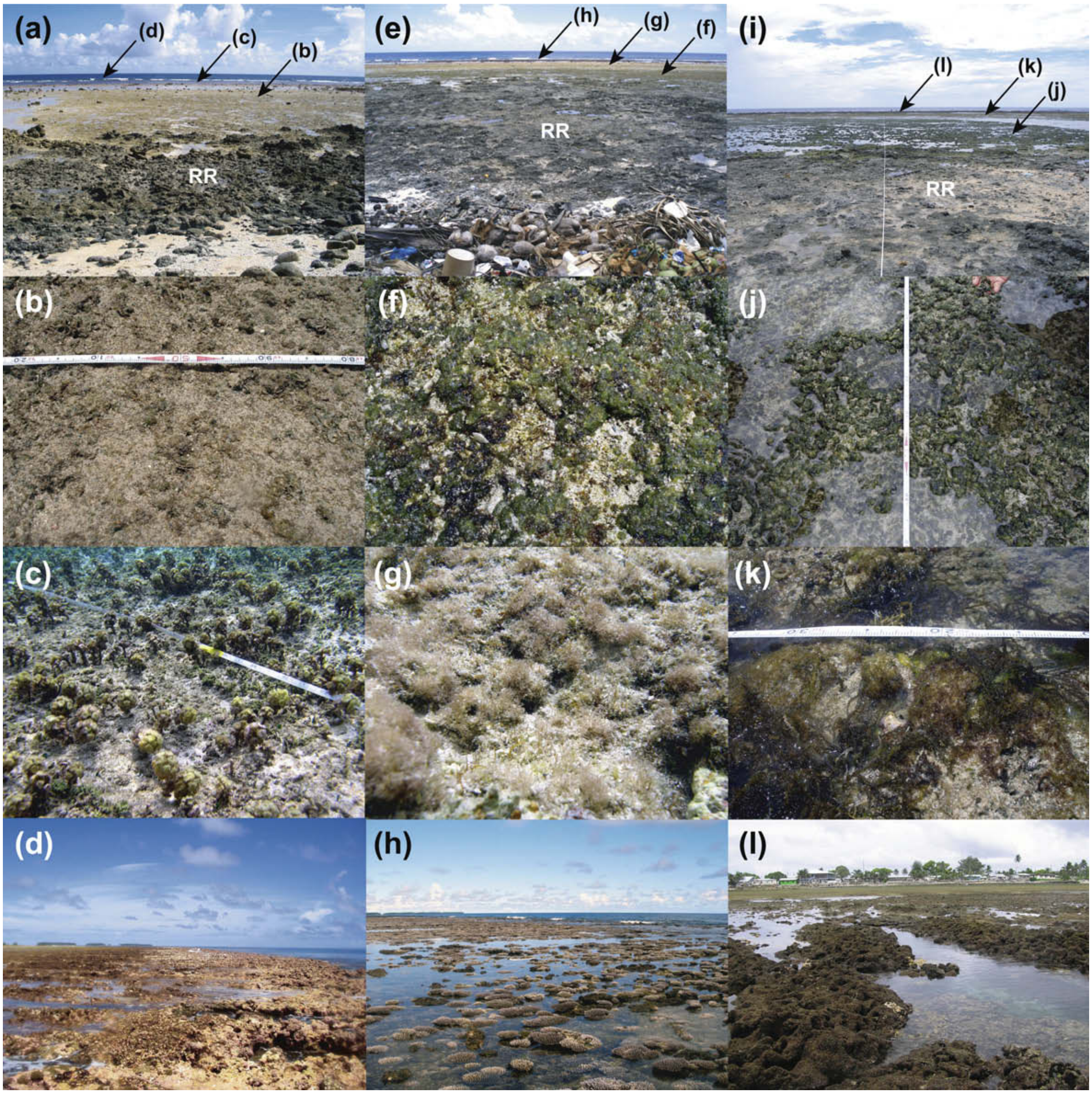

Fig. 4. Photographs showing typical transects and substratum. (a–d) transect 1 (Eneko Island), (a) view from the shoreline, RR: consolidated reef rock, (b) algal turf zone, (c) *Turbinaria* zone, (d) coral and coralline algae zone, covered with acroporiid corals and encrusting coralline algae, (e–h) transect 8 (Ejit Island), (e) view from the shoreline, (f) cyanobacteria–filamentous green algae mat zone, (g) algal turf zone dominated by *Jania* sp. and Gelidiaceae, (h) coral and coralline algae zone dominated by acroporiid corals, (i–l) transect 12 (the DUD area), (i) view from the shoreline, (j) cyanobacteria–filamentous green algae mat zone, (k) algal turf zone dominated by various fleshy macroalgae, (l) coral and coralline algae zone with low coral and coralline algal cover.

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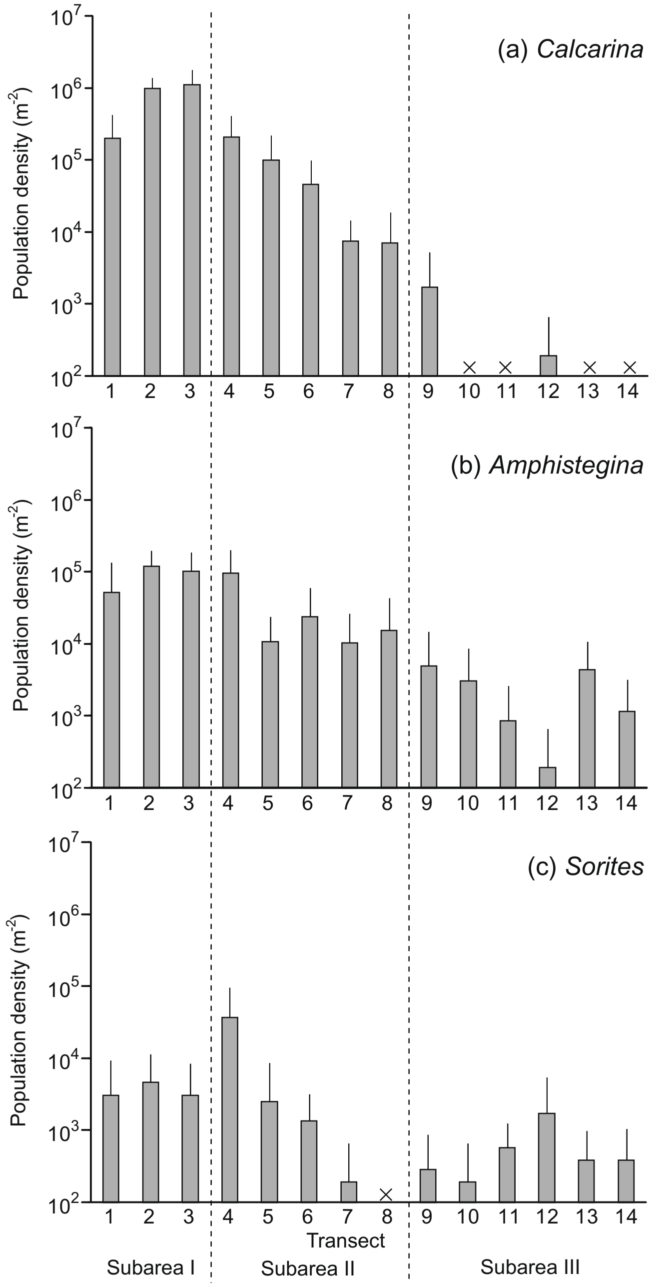

Fig. 5. Changes in the density of large benthic foraminifers on ocean reef flats. Values represent mean with 1SD (error bar). ×: absence of a foraminifer.

$P < 0.0001$). Densities on some transects in subarea I (transects 2 and 3) were significantly higher than on transect 12 in subarea III (NJR test, $P < 0.05$). In contrast to the results for *Calcarina* and *Amphistegina*, no significant differences were observed in *Sorites* densities in the study area (KW test), although the highest mean density was found in subarea II (transect 4; Fig. 5c).

3.3. Nutrients

Nitrate concentrations in reef-flat seawater were generally less than 1 μM (Fig. 6). Two-way ANOVA indicated that there were significant differences in nitrate concentrations among transects ($P < 0.01$), and there was a significant zone × transect interaction ($P < 0.01$). However, no significant differences were found among zones (i.e., nearshore zone vs. algal turf zone). A significant zone × transect interaction suggests that nitrate concentrations in the nearshore zone were not consistently higher than in the algal turf zone. Post hoc analysis among transects indicated that reef-flat seawater from two transects in subarea III (transects 12 and 14) had significantly higher nitrate concentrations than other transects (Fisher's LSD, $P < 0.01$).

Average phosphate concentrations in reef-flat seawater were 0.64 ± 0.74 μM. Two-way ANOVA indicated significant differences in phosphate concentrations among zones and transects and revealed a significant zone × transect interaction ($P < 0.01$). Phosphate concentrations in nearshore zones (0.85 ± 0.88 μM) were significantly higher than in algal turf zones (0.43 ± 0.37 μM; Fisher's LSD, $P < 0.01$). Maximum concentrations were recorded in subarea III (transect 10; 1.89 ± 1.84 μM).

Average ammonium concentrations in reef-flat seawater were 0.34 ± 0.15 μM. Two-way ANOVA found significant differences in ammonium concentrations among zones ($P < 0.05$) and transects and revealed a zone × transect interaction ($P < 0.01$). Ammonium concentrations in nearshore zones (0.37 ± 0.18 μM) were significantly higher than in algal turf zones (0.30 ± 0.11 μM; Fisher's LSD, $P < 0.05$).

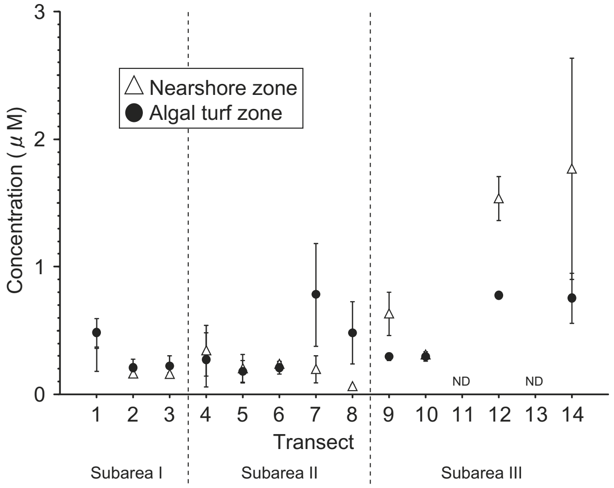

Fig. 6. Nitrate concentrations in reef-flat seawater. Values represent mean with 1SD (error bar). ND: no data.

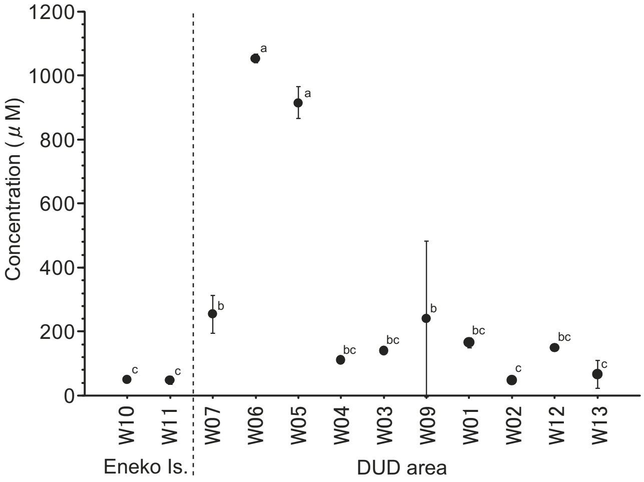

Fig. 7. Nitrate concentrations in groundwater. Values represent mean with 1SD (error bar). Different letters indicate significant differences between each pair of means.

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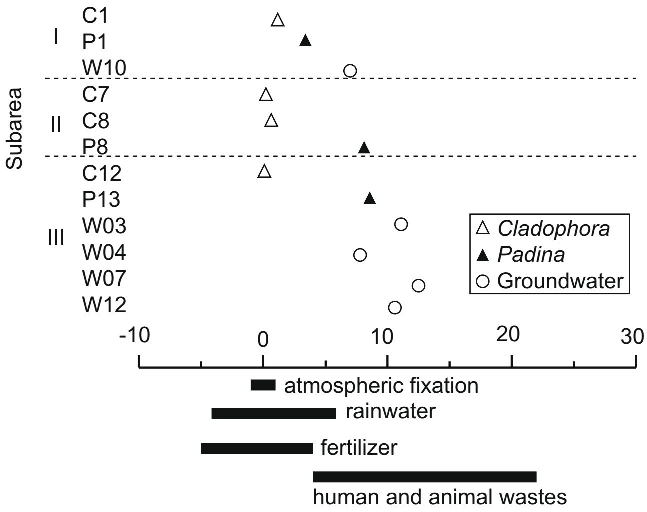

Fig. 8. δ^{15}N values in groundwater and macroalgal tissues compared with δ^{15}N ranges for major nutrient sources (data from Kendall (1998)).

In contrast, average nitrate concentrations were much higher in groundwater (250 ± 320 μM; Fig. 7) than in reef-flat seawater (0.45 ± 0.45 μM; $P < 0.01$, t-test). Nitrate concentrations in groundwater ranged from 49 to 1060 μM. One-way ANOVA indicated a significant difference in nitrate concentrations among wells ($P < 0.01$). Groundwater from 4 of 10 wells sampled in the DUD area had significantly higher nitrate concentrations than two wells on the sparsely populated Eneko Island (Fisher's LSD, $P < 0.05$). Groundwater nitrate concentrations from two wells in the DUD area (well sites W06 and W05) were considerably higher than those for other wells (Fisher's LSD, $P < 0.05$). Ammonium and phosphate concentrations in the groundwater were extremely low compared to concentrations of nitrate. Average ammonium and phosphate concentrations ranged from 2.4 to 16.9 μM and from 0.2 to 22.1 μM, respectively. Maximum concentrations were found in the DUD area (W09 for ammonium and W06 for phosphate).

δ^{15}N values for *Padina* sp. from nearshore lagoons ranged from 3.4‰ to 8.3‰, whereas those of *Cladophora* sp. from ocean reef flats ranged from 0.1‰ to 1.7‰ (Fig. 8). δ^{15}N values for nitrate in groundwater ranged from 7.0‰ to 12.5‰ in the study area.

4. Discussion

The densities of *Calcarina* and *Amphistegina* declined with distance from densely populated southeast islands (the DUD area; subarea III), whereas the density of *Sorites* did not differ significantly between sparsely and densely populated areas. In addition, mean foraminiferal densities of the three species at each transect were negatively correlated with the human population density in the nearest island along the northeast Majuro Atoll (Fig. 9). Thus, this study partially confirms the declines in densities of large living benthic foraminifers near populated islands as reported by Fujita et al. (2009) for the same study area, from Eniwetok Atoll (Hirshfield et al., 1968), and from south Tarawa Atoll (Ebrahim, 2000). These decreases in foraminiferal densities near populated areas are similar to azoic or low-density zones observed near outfalls in many nearshore environments, although the responses of foraminifers to sewage pollution are influenced by sewage type, geographical location, hydrodynamic regime, salinity, temperature, and effluent outfall rates (Yanko et al., 1999). Declining trends in the relative abundance of large benthic foraminiferal shells have been observed in surface sediment samples from regions where nutrification was suspected (Cockey et al., 1996; Hallock et al., 2003; Schueth and Frank, 2008) and in regions where water quality (in particular, total suspended solids and water column chlorophyll-a concentrations) declined with distance from the mainland (Uthicke and Nobes, 2008).

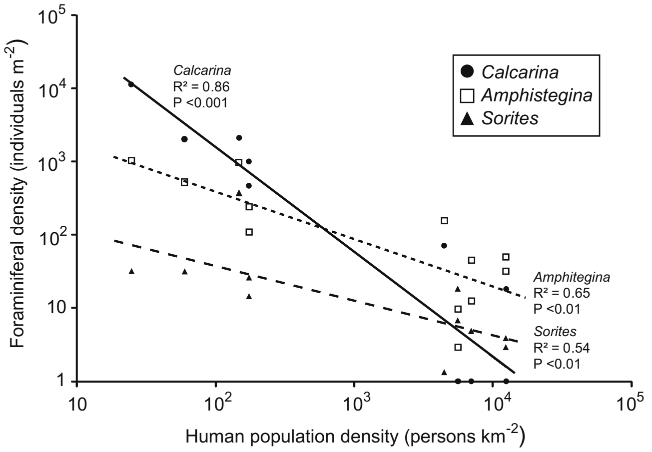

Fig. 9. Regression analysis of mean densities of large benthic foraminifers at each transect as a function to the population density in the nearest island.

Along with declining foraminiferal densities, macrophyte composition and water quality varied within the study area. However, the physical environment did not change notably. Ocean reef-flat topography (e.g., elevation/water depth relative to mean sea level, slope inclination) was similar among transects (Fig. 2). In the study area, ocean reef flats are influenced by similar wind-induced waves and ocean swells (Shimazaki et al., 2005). One of the major differences between sparsely populated islands and densely populated islands (the DUD area) is that ocean reef flats and inter-island channels in the DUD area are now reclaimed, connecting islands and expanding the land area. Thus, no surface water exchange occurs between lagoons and the ocean through inter-island channels. The reclamation of reef flats and channels would result in the loss of foraminiferal habitats and produce changes in water circulation patterns.

Foraminiferal habitats on ocean reef flats differed between sparsely and densely populated islands. Three main differences in ecological zones were observed in the study area. First, a CGM zone was widespread in the nearshore zone near densely populated islands, which may have resulted from nutrient overload from those islands. *Cladophora* blooms have been reported in reefs influenced by land-based nutrients around Hawaii (Smith et al., 2005) and tropical pond-based aquaculture systems (de Paula Silva et al., 2008). Experimental studies have demonstrated that *Cladophora* growth is enhanced by high nutrient levels (Smith et al., 2005; de Paula Silva et al., 2008). In particular, it is notable that *Cladophora* growth rates increase as a result of enrichment with commercial fertilizer (Smith et al., 2005). Second, the species composition of algal turf zones shifted from the dominance of turf-forming algae (*Jania* sp. and Gelidiaceae) near sparsely populated islands to the dominance of various fleshy macroalgae near densely populated islands. Fleshy macroalgae are often found in abundance in degraded reefs where anthropogenic influences are suspected (e.g., Hughes, 1994). These macroalgal changes are similar to observations from inshore coral reefs of the Great Barrier Reef, where Rhodophyta and Chlorophyta abundances increase with nutrients (Fabricius et al., 2005). Third, the disappearance of the offshore *Turbinaria* zone near densely populated islands may have also been related to human impacts. The density of *Turbinaria* changes with season and the degree of wave influence (Prathep et al., 2007). Because the tropical climate of Majuro lacks seasonality, except for changes in rainfall (wet and dry seasons), the distribution and density of

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Turbinaria would not vary significantly throughout the year. The disappearance of *Turbinaria* in the study area cannot be explained by differences in wave influence because all of the ocean reef flats examined were subject to similar wind-induced waves and ocean swells (Shimazaki et al., 2005). Increasing abundances of fleshy macroalgae may have inhibited the settlement and growth of *Turbinaria* near densely populated islands. Therefore, all three macroalgal changes may be related to human impacts, particularly nutrient overloading and/or low herbivory due to over-fishing on reef flats around densely populated islands (e.g., McCook, 1999).

Although the causes of the observed macroalgal changes are not fully understood, changes in macrophyte composition may lead to partial declines in *Calcarina* and *Amphistegina*. Experimental field studies have shown that both species prefer dense, three-dimensional surface configurations, such as algal turfs, which provide many entangled attachment sites, and both species are less abundant on substrates with smooth surfaces (Fujita, 2008). The two species can resist water motion by attaching to algal thalli using either adhesive elastic plugs secreted at the ends of spines (*Calcarina*; Röttger and Krüger, 1990) or weak reticulopodia extruded from an aperture (*Amphistegina*). *Sorites* individuals, however, become semi-permanently attached to flat algal surfaces and fix their shells using an organic pellicle (Kloos, 1980). Thus, soft, waving fleshy algae with smooth surfaces would provide unfavorable substrates for the attachment of *Calcarina* and *Amphistegina*, whereas *Sorites* could become firmly attached and reside on those substrates.

Our nutrient concentration results generally support the hypothesis that there are nutrient overloads near densely populated islands. Although seawater nutrient concentrations in the study area ranged within the values reported for other reef environments (Umezawa et al., 2002b; Lapointe et al., 2004; Smith et al., 2005; Lin et al., 2007), nutrient concentrations in reef-flat seawater were relatively high in the DUD area compared to other islands. This may have resulted, at least partially, from the relatively long residence time of reef-flat seawater due to reduced tidal flows through inter-island channels after reclamation in the DUD area. However, groundwater from some wells in the DUD area had significantly higher nutrient concentrations than wells on Eneko Island. Some groundwater nutrient values from the DUD area were considerably higher than those reported from Ishigaki Island (Okinawa, Japan), where many human populations, fields, and pastures are concentrated on a flat limestone-based watershed (Umezawa et al., 2002b). These results suggest that the nutrients in reef-flat seawater are derived from relatively high nutrient concentrations in the groundwater in the DUD area.

These inferences are partially supported by our δ^{15}N results for macroalgal tissues. The δ^{15}N values of *Padina* sp. from nearshore lagoons ranged from 3.4‰ to 8.3‰, whereas those of *Cladophora* sp. from ocean reef flats ranged from 0.1‰ to 1.7‰. The δ^{15}N values of nitrate in the groundwater ranged from 7.0‰ to 12.5‰ in the study area (Fig. 8). According to Kendall (1998), δ^{15}N values for nitrate in rainwater are generally −5‰ to +6‰, and δ^{15}N values for nitrogen in reef ecosystems supplied by nitrogen fixation by eiphytic cyanobacteria are ~0‰. In addition, the δ^{15}N values for nitrate in fertilizer and human/animal wastes are generally −5‰ to +4‰ and +4‰ to +22‰, respectively. Considering these values, the results of the present study indicate that macroalgae in nearshore lagoons assimilated primarily wastewater-derived nitrogen, whereas algae in nearshore ocean reef flats assimilated primarily nitrogen from other sources (e.g., rainwater, nitrogen fixation, oceanic seawater). In addition, groundwater nutrients were generally derived from human/animal wastes. In the Majuro Atoll, 80% of urban households (the DUD area) and 50% of rural households (Eneko Island) have improved toilet facilities. However, ~20% and 50% of the households in the urban and rural areas, respectively, have non-improved toilet facilities (Economic Policy, Planning and Statistics Office, 2007).

Our δ^{15}N results are consistent with the flow pattern of a groundwater body in reef islands called a freshwater lens. A freshwater lens is generally centered toward the lagoon side of a reef island. Thus, groundwater generally flows toward and seeps into the lagoon (Anthony et al., 1989; Presley, 2005). However, because the reef islands in the study area are very narrow (up to several 100 m from the ocean side to the lagoon side), groundwater may also flow and seep into the ocean side (Griggs and Peterson, 1993). In the DUD area, ~2840 m^3 of water is pumped daily from the rainfall catchment system near the urban area and supplied to residents (Presley, 2005), suggesting that seepage rates for groundwater in the DUD area are higher than in sparsely populated islands. Many houses are located along the coasts of ocean reef flats; therefore, sewage may mix with seawater during high tides or discharge directly into ocean reef flats. Although no supporting evidence for nutrient inputs into ocean reef flats was obtained from the δ^{15}N data, other data suggest that groundwater with high nutrient pulses can flow into nearshore waters in the DUD area.

High nutrient concentrations may influence large benthic foraminifers with algal symbionts. Algal symbiosis is energetically advantageous when dissolved nutrients and particulate food resources are scarce (Hallock, 1981). Hallock (2000) postulated that host foraminifers control the supply of nutrients to algal endosymbionts. However, when algal endosymbionts have access to abundant dissolved nutrients, they retain photosynthate for their own growth and reproduction, potentially creating physiological stress for their hosts. *Calcarina* and *Amphistegina* are more energetically dependent than *Sorites* on photosynthate from algal endosymbionts (Hallock, 1999). Thus, high nutrient levels may have direct adverse influences on the physiology of *Calcarina* and *Amphistegina*, which may result in declines in density near densely populated islands. However, high nutrient levels may be preferable for feeding-dependent *Sorites* individuals, because the enhanced nutrient supply can lead to higher microalgal biomass and increased phytodetritus for food. Future experimental studies are needed to determine threshold values for nutrient concentrations against the collapse of foraminiferal–algal symbiosis for each species. Paulay and Benayahu (1999) reported that coral mortality from bleaching in the Majuro lagoon in 1992 increased from west to east and peaked in the metropolitan area in the east (i.e., the DUD area), indicating that coral–algal symbiosis also suffered severe damage near populated areas.

In summary, this study shows that large human populations and human activities have resulted in high nutrient loadings in groundwater and possibly into nearshore water. Relatively high nutrient concentrations in reef-flat seawater near densely populated islands may have both direct and indirect negative effects on some large benthic foraminifer species through habitat changes (macrophyte composition) or the collapse of algal symbiosis. The reclamation of reef flats and channels in populated areas may result in the loss of foraminiferal habitats as well as produce changes in water circulation patterns and protract the residence time of seawater on reef flats. All this can adversely affect water quality in the surrounding seawater.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.marpolbul.2010.03.014.

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