Distribution of large benthic foraminifers around a populated reef island:

Fongafale Island, Funafuti Atoll, Tuvalu

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Abstract

Low-lying, small reef islands on Pacific atolls are vulnerable to coastal erosion and flooding, mainly due to rises in sea level, as well as local stresses associated with overpopulation. Because reef island sediments on Pacific atolls are composed mostly of shells of large benthic foraminifers (LBFs), their future stability depends on understanding foraminiferal shell sources and their production rates around the islands. Here, we report on the distribution and population density of LBFs around Fongafale Island, the main populated island of Tuvalu in the South Pacific, where coastal erosion and inundation have occurred. We discuss their controlling factors, in particular, anthropogenic influences on foraminiferal distribution. The results based on multivariate analyses (canonical correlation analysis and multiple regression analysis) demonstrated that *Baculogypsina sphaerulata* and *Amphistegina lobifera* were more common on the high-energy, intertidal ocean reef flats ($\leq 10^6$ and $\leq 10^4$ individuals m^{-2} , respectively), and *B. sphaerulata* was less common around the populated area of the island. On the relatively low-energy subtidal lagoon reef flats, *Amphistegina lessonii* was the most common species, particularly in the dry (leeward) season, with an increasing density in deeper offshore zones ($\leq 10^4$ individuals m^{-2}). *Sorites orbiculus* was less common than the other species, but was found on both sides of the reef flats ($\leq 10^3$ individuals m^{-2}). Macroalgal $\delta^{15}N$ values indicated that upwelling nutrient-rich deep water could be the source of nitrogen for oceanic waters, whereas nutrients in lagoon seawater could be partly derived from groundwater mixing with domestic wastewater, especially near the populated area. These results suggest that the distribution and population density of LBFs in the study area are influenced by spatial differences in water energy and water quality, and that *B. sphaerulata* is less tolerant

49 of nutrient loading than other species. Comparison of distributions between living
50 individuals and empty shells indicated that ocean reef flats are the primary source of
51 foraminiferal shells for reef islands and lagoon beaches.

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53 **Keywords:** atolls, distribution, foraminifera, South Pacific (Tuvalu, Funafuti Atoll,
54 Fongafale Island), water quality

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1. Introduction

Small, low-lying reef islands with elevations of only a few meters are located around the equatorial Pacific atolls. Sediments underlying these reef islands are composed of unconsolidated bioclasts derived from the skeletons and shells of reef calcifying organisms (e.g., Chapman, 1902; Cushman et al., 1954; Emery et al., 1954; Hallock, 1981c; Yamano et al., 2005; Perry et al., 2011). These topographical and sedimentological features make reef islands highly vulnerable to increases in sea level and extreme events, such as the erosion of shorelines, flooding of low-lying areas, and saline intrusion into freshwater lenses (Mimura et al., 2007; Woodroffe, 2008). Furthermore, some reef islands have become so urbanized and overpopulated that anthropogenic impacts are now serious issues.

Tuvalu, located near the equatorial South Pacific, is a reef-island nation that is threatened by sea-level rise and overpopulation. It is known as one of the “sinking countries” (Patel, 2006). On Fongafale Island, the capital island of Tuvalu, flooding and inundation occur during spring high tides, known as “King Tides”. However, the phenomenon is partly related to increases in the human population and land-use changes since the 1970s (Yamano et al., 2007). Half of the central part of the island was constructed by infilling the original swamp using porous, highly permeable coral blocks (Nakada et al., 2012). Furthermore, 35% of the land area is made up of borrow pits, which were excavated during World War II to provide sedimentary materials for military construction, and in particular for airports (Collen and Garton, 2004).

Approximately 40% of the land and beach sediments on Fongafale Island are composed of shells of large benthic foraminifers (LBFs), including at least 10 species (Chapman, 1902; Collen and Garton, 2004). However, to date, the distribution and

population density of living LBFs have not been studied in detail. Living LBF populations were briefly reported in the 1990s (Collen, 1995, 1996; Collen and Garton, 2004). The ocean reef flats had large living populations of *Baculogypsina sphaerulata*, with lower numbers of *Amphistegina lessonii*, *Amphistegina lobifera*, *Marginopora vertebralis*, and smaller foraminifers. In the lagoon, no living individuals were found close to the shore in populated areas (Collen, 1995). Such knowledge on living LBFs is crucial to fully understanding current sources and production rates of foraminiferal shells, and for the future stability of the reef islands in the face of sea-level rise and coastal erosion. LBF production is also of interest for their potential use in restoration, including filling the borrow pits and porous infilled areas.

The distribution and abundance of foraminifers in atoll sediments have been examined at many Pacific atolls (Chapman, 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). However, detailed distribution and sediment production of living LBFs have been only reported for Majuro Atoll, in the Marshall Islands (Fujita et al., 2009). LBFs such as *Calcarina gaudichaudii* and *Amphistegina lobifera* were abundant on turf algae on windward ocean reef flats and in channels between the islands. The population density of LBFs was negatively correlated with human population density. Deterioration of water quality due to sewage discharge and infilling of the channels may have caused the decline of those LBF populations near populated areas (Osawa et al., 2010).

Other foraminiferal studies on the Pacific atolls and islands have also reported declines in LBF populations near populated areas. Hirshfield et al. (1968) first reported the rarity of LBFs in reef-flat sediments compared to heterotrophic small foraminifers

(miliolids) in the vicinity of a sewage outfall on the populated Eniwetok Atoll island. Ebrahim (2000) reported that living LBFs were absent from lagoons and ocean reef flats near densely populated areas of the South Tarawa Atoll. Carilli and Walsh (2012) reported that the proportion of mixotrophic LBFs in surface sediments decreased significantly over time at all sites on Kiritimati Island, with the largest decreases observed at sites with high fishing pressure. These changes in benthic foraminiferal assemblages on Kiritimati indicate that nutrification has occurred over several decades, possibly due to changes in trophic structure and nutrient cycling caused by fishing.

Water pollution has been reported along the lagoon coasts near the populated area of Fongafale Island, as evidenced by negative redox potentials, high numbers of coliform bacteria and heavy metal contamination in the lagoon water (Fujita et al., 2013, 2014). We hypothesized that the distribution and population densities of living LBFs around Fongafale Island were adversely affected by human activity, as observed in other islands. Here, we report the distribution and population densities of LBFs around Fongafale Island on Funafuti Atoll in Tuvalu, and discuss the controlling factors, with particular attention to the effects of water quality on foraminiferal ecology.

2. Study area

Funafuti Atoll is located in the tropical south Pacific at 8°31'S, 179°13'E, and it is the capital of Tuvalu, consisting of about 40 small islands surrounding a lagoon approximately 50 m deep (Fig. 1A, B). The air temperature is stable throughout the year (28–31°C). Precipitation is ~ 3,000 mm annually, with higher rainfall from December to March (300–400 mm); however, the difference in precipitation between the dry season from April to September and the rainy season from October to March is

small (data from World Weather and Climate Information; <http://www.weather-and-climate.com/average-monthly-precipitation-Rainfall.Funafuti.Tuvalu>). Southeastern (SE) trade winds are predominant in the dry season, whereas northwestern (NW) winds are predominant in the rainy season. The average water temperature in the lagoon is 29.4°C with a variation of $\pm 1^\circ\text{C}$ throughout the year (air temperature, wind direction, and water temperature data from the South Pacific Sea Level and Climate Monitoring Project; <http://www.bom.gov.au/pacificsealevel/index.shtml>).

Fongafale Island is located at the southeast edge of Funafuti Atoll, and is bordered by narrow reef flats (Fig. 1C). This capital island has the largest population in Tuvalu, with over 4000 people. This population has increased since the 1970s due to migration and centralization after Tuvalu gained independence, and with the decline in overseas mining operations (Yamano et al., 2007). The populated area is located on the lagoon side of the central part of the island, with residences decreasing toward the northern and southern tips of the island (Fujita et al., 2014). Approximately 70% of the Fongafale population is concentrated in this area (data from Census of Population and Housing and Sample Surveys, 2002, Basic Tables; http://www.spc.int/prism/country/tv/stats/Publication/Pub_index.htm). Half of the central part of the island was originally swamp, which was infilled with porous, highly permeable coral blocks (Yamano et al., 2007; Nakada et al., 2012). Sediments for infilling were excavated from pits, known as borrow pits, on the northern and southern parts of the island (Collen and Garton, 2004). A causeway was constructed by filling inter-reef channels to form a bridge between Fongafale Island and Tengako Island. There is a dumpsite on Tengako Island.

A total of seven line transects were set perpendicular to the shoreline on

Tengako and Fongafale Islands (Fig. 1C), and were arranged to capture data from both the populated and unpopulated areas. For each transect, reef flats on both the ocean and lagoon sides of the island were investigated. An ocean reef flat close to the dumpsite in Tengako Island was also investigated.

3. Materials and methods

3.1. Line-transect survey

Line-transect surveys were conducted on reef flats on both the ocean and lagoon sides along three transects (TN, CW, and SM) and at a dumpsite in March 2009. On the basis of results obtained from these transects, an additional four transects (ocean and lagoon sides of L2, L3, L4 and L5) were surveyed in September 2009. Because shallow-water LBFs are mostly phytal (*i.e.*, attached to algal substrates) and these environments are similar between the dry and rainy seasons, foraminiferal distributions do not differ greatly between seasons. A line transect was set perpendicular to the shoreline using a 100-m measuring tape. The topography was measured using an auto level with a staff. Depth and elevation data were corrected for tidal effects using tide tables for Funafuti obtained from the South Pacific Sea Level and Climate Monitoring Project. The substrata and benthic community were recorded at 10-m intervals to determine ecological zones and their boundaries.

3.2. Sampling

In ecological zones where macroalgae were present, typical macroalgae were collected for foraminiferal analysis. A circular plastic vial (~ 3 cm diameter) was placed over the 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 ten replicate samples were randomly taken from the macroalgae-dominated zone. The samples were immediately fixed with 5% formalin in seawater.

Reef-flat water samples were collected to measure nutrient concentrations. Filtered (using a 0.45- μ m cellulose acetate filter) surface seawater samples were taken in duplicate from near- and offshore zones along the line transects in March 2009, and again from the near-shore zone in September 2009. The seawater samples were taken during low tide when nutrient concentrations were expected to represent the maximum values due to groundwater discharge and lower mixing rates (dilution) with offshore seawater. These water samples were transferred to 10-mL acrylic tubes, capped, and stored in a freezer for later analysis.

To evaluate the nutrient sources in the near-shore zones, dominant macroalgal species were collected from the near-shore zones of both ocean and lagoon reef flats for $\delta^{15}\text{N}$ analysis. These algal samples were kept cool during transport to the laboratory.

3.3. Analytical methods

Each foraminiferal sample was washed on a 63- μ m sieve, and algae were removed and air-dried. The dried substratum was examined under a binocular microscope to remove any foraminifers that had remained attached. Macroalgae were identified to the lower taxonomic level 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 and all stained foraminiferal specimens were isolated in > 0.5-mm size fractions, identified to the species level, and counted. The resulting count data were converted to the number of individuals per m² of bottom

surface. We focused on four large species of algal symbiont-bearing benthic foraminifers (*Baculogypsina sphaerulata* [Parker and Jones], *Amphistegina lobifera* Larsen, *Amphistegina lessonii* d'Orbigny, and *Sorites orbiculus* Forskål; Fig. A.1), which together are the primary contributors to the land and reef-flat sediments (Chapman, 1902; Collen and Garton, 2004). The < 0.5-mm size fraction was not analyzed because large benthic foraminifers (> 0.5 mm diameter) predominantly constitute the reef-island sediments (Collen and Garton, 2004). However, since rapidly growing and reproducing foraminifers, in particular *Amphistegina*, can spend up to a third of their life span growing to 0.5 mm (Hallock et al., 1986), their population density may be underestimated in this study.

Nutrient analysis in the seawater samples and $\delta^{15}\text{N}$ analysis in the macroalgae samples were carried out as described in Osawa et al. (2010). Nutrient concentrations (NO_3^- , NO_2^- , NH_4^+ , and PO_4^{3-}) in the seawater samples were colorimetrically measured using an autoanalyzer (SWAAT; BLTEC, Osaka, Japan). Homogeneously ground macroalgae samples (2.5–12 mg) were placed in silver cups and treated with a few drops of 1 N HCl to remove inorganic carbon (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 1112-ConFloIII-DELTA^{PLUS} XP; Thermo Fisher Scientific Inc., Bremen, Germany). Instrument precision was checked with phenylalanine after every five samples (SD < 0.11‰ for $\delta^{15}\text{N}$ and < 0.10‰ for $\delta^{13}\text{C}$). Differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in replicate samples were < 0.2‰ and < 0.3‰ ($n = 2$ or 3), respectively, within and across all analysis periods.

3.5. Data analysis

Canonical correlation analysis (CCA) was performed to visualize associations between environmental variables and foraminiferal data. The composition and population densities of four foraminiferal species from all 78 sampling sites were analyzed. The raw count data (the number of individuals per sample) for each species were used. Environmental variables were as follows: a distance from the populated area to the transect line (referred to as “distance”; km), sampling season (as “season”; dry or wet), the location of a sampling site relative to the island (as “side”; ocean side or lagoon side), a water depth relative to mean sea level at each sampling site (as “depth”; cm), the mean nutrient concentration in the near-shore zone of each transect (as “nutrient”, a predominant DIN species, NO_3^- , μM). The center of the populated area was set as zero point for the “distance” (Fig. 1C). All the data used in the CCA were standardized.

A multiple regression analysis was performed to test if the population density of each foraminiferal species could be explained by the combination of environmental variables. The raw count foraminiferal data (the number of individuals per sample) were used as a predictor variable. The same environmental variables as for the CCA were used as explanatory variables. For “side” and “season”, negative values are indicated for the lagoon side and the dry season, respectively.

All statistical analyses were conducted in R 2.14 software and “CCA” package (R Development Core Team, 2011).

4. Results

4.1. Distribution along transects

Distribution of LBFs along transects in the rainy season (March 2009) showed that *Baculogypsina sphaerulata* was more abundant on the ocean reef flats (as much as 10^5 – 10^6 individuals m^{-2}) than the lagoon reef flats (Fig. 2, Table A.1). It was found primarily on turf algae (*Gelidiopsis intricata* and *Hypnea pannosa*) and macroalgae (*Turbinaria conoides* and *Valonia aegagropila*) on the reef rocks. On the lagoon reef flats, *Baculogypsina sphaerulata* was found along the northern parts near an inter-island channel (transect TN). *Amphistegina lobifera* was predominantly found in the near-shore algal zone of the ocean reef flats, at population densities (10^3 – 10^4 individuals m^{-2}) generally much lower than those of *B. sphaerulata*. *Amphistegina lessonii* was more common on lagoon reef flats than ocean reef flats, and tended to increase with distance from the shore (up to 10^4 individuals m^{-2}). *Sorites orbiculus* was found on both sides of the reef flats, but at lower population densities than the other species ($\leq 10^3$ individuals m^{-2}).

4.2. Comparisons among transects and between seasons

The mean population densities of LBFs were compared among transects and between seasons (Fig. 3). On the ocean reef flats, living individuals of *B. sphaerulata* were more common at the northern part of the study area (transects TN, DS and CW) in the rainy season (March 2009), and less common at transects near the populated area (transects L3, L4, and SM). The highest mean population density was observed in the rainy season at transect TN ($5.6 \pm 4.8 \times 10^5$ individuals m^{-2}). *Amphistegina lobifera* individuals were more abundant towards the southern part of the study area. The

highest mean population density was observed in the dry season (September 2009) at transect L5 ($3.4 \pm 1.1 \times 10^4$ individuals m^{-2}). Population density of *S. orbiculus* was similar among transects, but relatively high in the dry season.

On the lagoon reef flats, *B. sphaerulata* individuals were only found in the rainy season at transects TN ($7.6 \pm 5.3 \times 10^3$ individuals m^{-2}) and CW. *Amphistegina lessonii* was abundant throughout the lagoon reef flats, except for at transect TN, and was more common in samples collected during the dry season. The highest population density was observed at transect L5 ($1.2 \pm 1.4 \times 10^5$ individuals m^{-2}). Except for at transect TN, the mean population density of *S. orbiculus* was similar among transects and between seasons.

4.3. Relationships of LBF compositions and population densities with environmental variables

Canonical correlation analysis (Fig. 4A, Table A.2) revealed that vectors of the main three foraminiferal species were directed into different directions in the two-dimensional ordination, and characterized by vectors of environmental variables (“side”, “distance”, “season” and “depth”). The *B. sphaerulata* vector was mainly related to “side”, “season” and “distance”. The *A. lobifera* vector was mainly related to “side”. The *A. lessonii* vector was mainly related to “depth”. Biplots of canonical scores for all sampling sites (Fig. 4B) clearly showed environmental gradients within and among transects. Ordinations of transects were determined mainly by “distance”, “side” and “season”. Ocean and lagoon sides of each transect were placed in the second and third quadrants and the first and fourth quadrants, respectively. Transects distant from the populated area were placed toward the second quadrant, while transects investigated in the dry season were relatively placed toward the fourth quadrant. Within each

transect, sampling sites were arranged in lower-left to upper-right directions, which were mostly determined by “depth”.

Since vectors of the main three species are located toward different quadrants in the CCA, multiple regression analysis can be applicable for each species. The results (Table 1) revealed that the “distance” and “side” had a positive correlation with the population density of *B. sphaerulata*. The population density increased on ocean reef flats with increasing distances from the populated area. Only “side” had a positive correlation with the population density of *A. lobifera*, indicating the predominance of *A. lobifera* on the ocean reef flats. “Side” and “season” had a negative correlation with the population density of *A. lessonii*, indicating that the population density was most abundant on the lagoon reef flats in the dry season. No significant explanatory variable was found for the population density of *S. orbiculus*.

4.4. $\delta^{15}\text{N}$ of macroalgae

Most of the macroalgae sampled from the ocean reef flats had similar $\delta^{15}\text{N}$ values (5–8‰), whereas the $\delta^{15}\text{N}$ values of macroalgae sampled from the lagoon reef flats were in the range of 2–4‰ (Table 2). On the lagoon reef flats, the $\delta^{15}\text{N}$ values of these same algae (*Caulerpa*, *Padina*, *Cladophora*, and *Dictyota*) were higher on transects close to the populated area (transects L3, L4, and SM) than on transects in unpopulated areas (transects TN, L2, and CW).

5. Discussion

5.1. Factors controlling distribution of LBFs

Baculogypsina sphaerulata and *A. lobifera* predominantly live on the ocean

reef flats. Living individuals of *B. sphaerulata* were relatively common in the rainy season, and uncommon near the populated area. *Amphistegina lobifera* individuals were relatively abundant towards the southern part of ocean reef flats. *Amphistegina lessonii* commonly lives on the lagoon reef flats in the dry season, with the population density increasing with water depth. *Sorites orbiculus* was rare except on the TN-lagoon site, but was found on both sides of the reef flats.

These distribution trends were demonstrated by multivariate analyses. The distribution and population density of each LBF species were explained by environmental variables such as “distance”, “side” and “season”. The “distance” from the populated area is mainly related to the degree to anthropogenic influences (Fujita et al., 2013, 2014). “Side” is related to locations relative to ocean currents and waves. Shores of the ocean reef flats are subject to higher water energy than lagoon reef flats, in particular during high tides. “Season” is related to precipitation and prevailing wind directions in the sampling period. The lagoon side becomes leeward and relatively calm conditions in the dry season when SE trade winds predominate, while it becomes windward and relatively rough conditions in the rainy season when NW winds predominate.

Baculogypsina sphaerulata is highly adapted to intertidal, high-light, high-energy environments. This species is able to attach to substrates under strong hydrodynamic conditions by the extrusion of organic elastic flexible plugs from the tops of its spines, which stick to the substrate (Röttger and Krüger, 1990; Hohenegger, 2004). This species has a thick lenticular shell with a crystal orientation of 45° on the shell surface to reduce transparency (Hohenegger, 2004). These morphological and physiological adaptations to light and water energy likely explain why *B. sphaerulata*

is more abundant on intertidal ocean reef flats.

Morphological and physiological adaptations of *Amphistegina* spp. to light and water energy slightly differ from those of *B. sphaerulata*. *Amphistegina* individuals can be phototactic, and are commonly found in shaded microhabitats at shallow depths (Hallock, 1999), as demonstrated in a shallow-water species, *Marginopora vertebralis* (Sinutok et al., 2013). *Amphistegina lobifera* and *A. lessonii* had similar growth rates in 30–80% of full sunlight, and sharply decreasing rates at lower light intensities. However, *A. lessonii* was photoinhibited in full sunlight, whereas *A. lobifera* required higher light intensities to reproduce in culture (Hallock, 1981b). *Amphistegina* individuals attach to substrates by reticulopodia and can be easily dislodged by strong water motion. In water-motion experiments (Hallock et al., 1986), *Amphistegina* individuals subjected to water motion grew significantly thicker shells. *Amphistegina lobifera* increased in diameter and mass at a faster rate in moving water than did *A. lessonii*. These morphological and physiological adaptations to light and water energy likely explain why *A. lobifera* are found predominantly on the higher energy, intertidal ocean reef flats, but less common than *B. sphaerulata*, and why *A. lessonii* predominates on the lower energy, sub-tidal lagoon reef flats. Abundance of *A. lessonii* in the dry season, when the lagoon side becomes leeward, may also be related to relatively low-energy conditions.

5.2. Anthropogenic influences

On the ocean reef flats, the population density of *B. sphaerulata* tended to decrease near the populated area. Similar trends have been observed on other Pacific islands (Hirshfield et al., 1968; Ebrahim, 2000; Fujita et al., 2009; Osawa et al., 2010;

Carilli and Walsh, 2012). These declines in foraminifers have been attributed to a sewage outfall (Hirshfield et al., 1968), high nutrient inputs into the ambient seawater (Osawa et al., 2010), and changes in the trophic structure and nutrient cycling caused by fishing (Carilli and Walsh, 2012).

The decline in *B. sphaerulata* populations near the populated area is likely related to the deterioration of water quality. Water quality is a critical factor affecting the distribution and population density of LBFs (Hallock, 1981a, 2000). All LBFs need some nutrient sources, but if excess nutrient loading occurs, microalgae, heterotrophic smaller foraminifers and other microorganisms will overgrow or outgrow the LBFs (Hallock, 1985).

Nutrient concentrations in the reef-flat seawater were highly variable in the study area, but tended to be higher in seawater near the populated area in the same season (Table A.3). These values were similar to those around Majuro Atoll ($< 1 \mu\text{M}$); the highest values on Tuvalu ($4.8 \pm 0.3 \mu\text{M}$) were higher than those on Majuro ($1.77 \pm 0.87 \mu\text{M}$) (Osawa et al., 2010). Nitrogen fixation and nitrification play important roles in the nitrogen cycle of atoll reefs (Webb et al., 1975). However, relatively high nutrient concentrations in the near-shore seawater, especially near the populated area, suggest that some nutrients are derived from the land, either directly or indirectly through groundwater.

$\delta^{15}\text{N}$ values of macroalgae along the ocean reef flats were relatively stable (around 6‰), showing no differences between algal taxa, seasons, or anthropogenic influences. Although $\delta^{15}\text{N}$ values for wastewater generally range from 4 to 22 ‰ (Kendall, 1998), the stable values throughout the ocean reef flats can not be explained only by anthropogenic nutrient sources (wastewater). $\delta^{15}\text{N}$ values of around 6‰ have

been reported from tissue extracts of *Porites* corals offshore of the Great Barrier Reef (Sammarco et al., 1999), where upwelling supplies nutrients along the shelf edge of the barrier reef. This nutrient source is relatively enriched in ^{15}N , resulting in similar $\delta^{15}\text{N}$ values to those for nitrates from terrestrial sources. Thus, nutrient-rich deep water carried by upwelling may also be a potential source of nitrogen for atoll reefs. Nutrient enrichment in the surface water due to the turbulent vertical mixing of oceanic waters along outer slopes of the atoll, called “atoll-mass effect”, has also been reported in Tikehau Atoll, Tuamotu Archipelago, French Polynesia (Charpy-Roubaud et al., 1990).

Along the lagoon coasts, generally lower $\delta^{15}\text{N}$ values than those along the ocean side indicate nitrogen fixation as a major nutrient source. However, relatively high $\delta^{15}\text{N}$ values were observed for macroalgae at sites close to the populated area compared to those from unpopulated areas, suggesting nutrient input from domestic wastewater into the lagoon waters. Residences are concentrated along the lagoon coasts of Fongafale Island (Yamano et al., 2007). Fujita et al. (2013) reported negative redox potentials and high numbers of coliform bacteria in the lagoon waters around the populated area of Fongafale Island, particularly during ebb and low tides, suggesting that domestic wastewater from bottomless septic tanks and pit toilets were the primary sources of water pollution, controlled by groundwater dynamics due to tidal changes (Nakada et al., 2012). These nutrient inputs into the lagoon water are likely related to the absence of LBFs close to lagoon shores, particularly around the populated area.

Nutrient loading into ambient seawater may have both direct and indirect negative effects on LBFs through habitat changes and/or the collapse of algal symbiosis. Laboratory experiments have raised a controversy on the effects of nutrient loading on

LBFs. Lee et al. (1991) demonstrated that dinoflagellate symbiont-bearing *Marginopora* spp. grew well in enriched seawater, whereas other studies showed that growth and mortality of *Marginopora* spp. were negatively affected by nitrate addition (Reymond et al., 2011; Uthicke et al., 2012; Reymond et al., 2013). Enrichment with nitrate or phosphate did not stimulate growth of diatom symbiont-bearing *A. lobifera* (Lee et al., 1991), *Amphistegina radiata*, *Heterostegina depressa*, or *Calcarina mayori* (Schmidt et al., 2011). In field studies, increased exposure to nutrients derived from terrestrial runoff negatively affected the growth rates of *M. vertebralis* (Reymond et al., 2011), *A. radiata*, and *H. depressa* (Uthicke and Altenrath, 2010). Many studies have shown that low values of Foraminifera in Reef Assessment and Monitoring (FORAM) Index (Hallock and Lidz, 2003), resulting from low relative abundances of mixotrophic LBF taxa in surface sediments, are correlated with turbidity (Fabricius et al., 2012), finer grain size, and high organic contents (Uthicke and Altenrath, 2010), as well as sewage pollution (Koukousioura et al., 2011), and high total suspended solids and water column chlorophyll concentrations (Uthicke and Nobes, 2008). Although the threshold of nutrient loading may differ by species and by environments, this study suggests that *B. sphaerulata* is less tolerant of nutrient loading than other species.

5.3. Sediment source around Fongafale Island

Dead, empty LBF shells from *A. lobifera*, *B. sphaerulata*, and Soritinae (*Sorites* and *Marginopora*) comprise more than 35% and 67% of sediments of the lagoon beach and land, respectively (Collen and Garton, 2004). This study showed that living individuals of *B. sphaerulata* and *A. lobifera* were common on the ocean reef flats, and were rare or absent on the lagoon reef flats. This suggests that the shells, which originated from the

ocean reef flats, were transported after death by ocean waves onto the land, or by tidal currents into the lagoons through the inter-island channels, and deposited along the lagoon coasts by shore currents. In these sediments, empty *A. lobifera* shells are as numerous as *B. sphaerulata*, despite the lower population density of the former compared to the latter. This may be explained by the shorter life span and higher turnover rate (Hallock, 1981c), high preservation potential due to high resistance to abrasion (Kotler et al., 1992; Wetmore and Plotnick, 1992; Resig, 2004), and wider depth distributions (Hohenegger, 1994; Hallock, 1999) of *A. lobifera*.

In the shallow lagoon sediments, the relative abundance of empty *A. lobifera* and *B. sphaerulata* shells decreased from shore to offshore, whereas that of *A. lessonii* increased with the distance from shore (Collen and Garton, 2004). These distribution patterns of empty shells are consistent with their main sources as revealed in this study. However, the low percentages of empty *A. lessonii* shells on the lagoon beach and in land sediments suggest that, in spite of its high population density on the lagoon reef flats, *A. lessonii* does not contribute to beach and land sediments. Thus, the ocean reef flats, in particular near unpopulated areas, are the primary source of foraminiferal sediments for the land and lagoon beaches around Fongafale Island.

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Figure Captions

Fig. 1. Maps of the study area. A: map of the western and central Pacific showing locations of Funafuti Atoll (F), Tarawa Atoll (T), Majuro Atoll (M), and Kiritimati Island (K). B: Map of Funafuti Atoll, Tuvalu, showing location of the study area. C: Map of Fongafale and Tengako Islands, showing locations of transect lines for foraminiferal, water-quality, and $\delta^{15}\text{N}$ analyses. Abbreviations for transect lines: TN = Tengako, DS = dumpsite, CW = causeway, SM = Saramata.

Fig. 2. Topography (water depth or elevation relative to mean sea level), ecological zones, and population density of large benthic foraminifers on ocean and lagoon reef flats in the rainy season (March 2009). A: transect TN, B: transect CW, C: transect SM. Abbreviations for ecological zones: S&R = sand and rubble, RR = reef rock, R = rubble.

Fig. 3. Variations in the population density of large benthic foraminifers among transects in the study area. Value represents means $\pm$ standard deviation (SD).

Fig. 4. Canonical correlation analysis. A: canonical loading for four species of large benthic foraminifers and five environmental variables shown by vectors. B: canonical scores of 78 sampling sites around Fongafale Island, Funafuti, Tuvalu. CA1: the first canonical axis, CA2: the second canonical axis.

Fig. A.1. Living large benthic foraminifers commonly found in the study area. 1: *Baculogypsina sphaerulata* (Parker and Jones) from transect L5-ocean, 2: *Amphistegina lobifera* Larsen from transect L5-ocean, 3: *Amphistegina lessonii* d'Orbigny from transect L5-lagoon, 4: *Sorites orbiculus* (Forskål) from transect L5-ocean. Scale bar = 1 mm.

Figure 1

Figure 2

Figure 3

Figure 4

Table 1

Table 1 Coefficients and the significance for the variables in multiple regression. Negative values for "side" and "season" indicate lagoon side and dry season, respectively.

Species	Intercept	Variables				
		Distance	Side	Depth	Season	Nutrients
<i>Baculogypsina sphaerulata</i>	-144.4	20.46***	124.9***	0.38	66.14	-6.42
<i>Amphistegina lobifera</i>	4.60	-0.55	5.37***	-0.01	-0.49	-0.57
<i>Amphistegina lessonii</i>	7.23	1.06	-22.34**	0.37	-17.7*	-6.92
<i>Sorites orbiculus</i>	1.37	0.12	0.71	0.00	-1.04	-0.077

***: p<0.0001, **: p<0.01, *: p<0.05

Table 2

Table 2 $\delta^{15}\text{N}$ values (mean and SD) of macroalgal tissues.

Side	Transect	Algae	mean $\pm$ SD (‰)
Ocean	TN	<i>Cladophora</i>	7.0 $\pm$ 0.1
		<i>Turbinaria ornata</i>	7.3 $\pm$ 0.0
	DS	<i>Boergesenia</i>	5.8 $\pm$ 0.5
	L2	<i>Cladophora</i>	6.1
	CW	<i>Cladophora</i>	7.1 $\pm$ 0.1
		<i>Turbinaria ornata</i>	6.5 $\pm$ 0.2
		Gelidiaceae	7.2 $\pm$ 0.2
	L3	<i>Cladophora</i>	5.7 $\pm$ 0.4
	L4	<i>Cladophora</i>	6.9 $\pm$ 0.1
	SM	<i>Cladophora</i>	7.1 $\pm$ 0.1
		<i>Hypnea</i>	8.3 $\pm$ 0.1
		<i>Sargassum</i>	7.5 $\pm$ 0.2
Lagoon	TN	<i>Caulerpa</i>	2.8 $\pm$ 0.5
		Gelidiaceae	3.0 $\pm$ 0.1
		<i>Turbinaria ornata</i>	3.5 $\pm$ 0.4
	L2	<i>Cladophora</i>	2.0 $\pm$ 0.2
	CW	<i>Padina</i>	2.6 $\pm$ 0.2
		<i>Dictyota</i>	3.4 $\pm$ 0.3
		<i>Laurencia</i>	2.7 $\pm$ 0.1
		Gelidiaceae	2.5 $\pm$ 0.4
		<i>Boergesenia</i>	1.4 $\pm$ 0.1
	L3	<i>Cladophora</i>	3.9 $\pm$ 0.2
	L4	Phaeophyceae	10.9 $\pm$ 0.4
	SM	<i>Padina</i>	3.8 $\pm$ 0.3
		<i>Dictyota</i>	4.7 $\pm$ 0.0
		<i>Caulerpa</i>	6.9 $\pm$ 0.2
	L5	<i>Padina</i>	5.2 $\pm$ 0.1