NOTE



Shifts in species abundance of large benthic foraminifera Amphistegina: the possible effects of Tropical Cyclone Ita

Martina Prazeres^{1,3} · T. Edward Roberts² · John M. Pandolfi¹

Received: 30 March 2016/Accepted: 26 August 2016/Published online: 2 September 2016 © Springer-Verlag Berlin Heidelberg 2016

Abstract On the Great Barrier Reef (GBR), the large benthic foraminifera Amphistegina lobifera, A. lessonii and A. radiata occur in shallow (<30 m) areas and have a clear distribution gradient. In April 2014, Severe Tropical Cyclone (TC) Ita impacted the northern region of the GBR. We surveyed the leeward slope of Yonge Reef at 6 and 18 m, in August 2013 and 2014. Results showed an overall decline in abundance of Amphistegina and a shift in proportion at both depths between 2013 and 2014. The shallow-dweller A. lobifera was severely affected; however, the deep-dweller A. radiata and the generalist A. lessonii only declined at 6 m and increased in abundance at 18 m. Patterns observed are likely linked to the occurrence of TC Ita. We propose that differing population-level source-sink dynamics should be considered when exploring persistence and recovery patterns over depth in foraminiferal communities.

Communicated by Geology Editor Prof. Eberhard Gischler

Electronic supplementary material The online version of this article (doi:10.1007/s00338-016-1497-x) contains supplementary material, which is available to authorized users.

Martina Prazeres martina.defreitasprazeres@jcu.edu.au

- ¹ ARC Centre of Excellence for Coral Reef Studies and School of Biological Sciences, The University of Queensland, St. Lucia, QLD 4072, Australia
- ² ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia
- ³ Present Address: College of Public Health, Medical and Veterinary Sciences, James Cook University, Townsville, QLD 4811, Australia

Keywords Great Barrier Reef · Symbiont-bearing foraminifera · Depth distribution · Community structure

Introduction

Large benthic foraminifera (LBF) are important elements of benthic communities in carbonate sediments of reef environments (Langer 2008). They are restricted to the photic zone and house symbiotic algae (Hallock 1999). Temperature, sediment structure, light intensity and wave energy are some of the main factors responsible for the local distributions of these organisms on the reef (Hollaus and Hottiger 1988; Hohenegger et al. 1999). The interaction of these factors, coupled with specific physiological and morphological traits of each species, define their distribution (Hohenegger 2006).

Amphistegina is the most widely distributed and abundant genus of LBF in reef environments (Langer and Hottinger 2000). Amphistegina is able to live over a wide depth range (<1 m to ~100 m; Hallock 2011), using a reticulopodial network to move across the substrate, allowing them to regulate light exposure (Hallock 2011). Globally, Amphistegina community structure over depth is well documented (Hallock and Hansen 1978; Hohenegger 2006), and species-specific traits reflect the distribution of each species along gradients of light and hydrodynamic energy (Hohenegger et al. 1999; Renema 2006). Three Amphistegina species are common on the shallow reef slopes (<30 m) of the Great Barrier Reef (GBR): A. lobifera, A. lessonii and A. radiata. Amphistegina lobifera is a shallow-dwelling species, commonly found between 0 and 6 m; A. lessonii is the most generalist of the three species, being found at depths ranging between 0 and 60 m. Both A. lobifera and A. lessonii have thick tests and large apertural

faces, resulting in a strong reticulopodial attachment, and are well adapted to shallow, high-energy environments (Hallock and Hansen 1978). In contrast, *A. radiata* is a deep dweller, and although adapted to live below 18 m (Hallock 1999; Hohenegger et al. 1999), some individuals can occasionally be found at shallower depths (8–12 m; Renema et al. 2013), overlapping with *A. lessonii*, although in lower relative abundances (Renema 2008). *Amphistegina radiata* produces thin test walls, and their apertural faces are smaller, resulting in a weaker substrate attachment than the *A. lobifera/lessonii* group (Hohenegger 2006).

In August 2013, preliminary sampling at 6 and 18 m on the leeward slope of Yonge Reef, located on the outer shelf of the GBR, revealed a community structure consistent with the expected depth distribution, where A. lobifera and A. lessonii dominated shallow areas (6-m samples), and A. radiata specimens were abundant at 18 m. In April 2014, Severe Tropical Cyclone (TC) Ita impacted the northeast coast of Australia and moved across the northern region of the GBR (Munksgaard et al. 2015), affecting the reef region surrounding Yonge Reef. Subsequent sampling at the same site and depths in August 2014 revealed a community structure different to previously reported depth zonation patterns. An extreme disturbance event such as TC Ita provides a natural experiment on the impact of acute events on the community structure of reef organisms, including benthic foraminifera (Hughes and Connell 1999; Strotz et al. 2016). It allows further insight into how potential factors other than light intensity, such as hydrodynamic energy and space competition, might affect organisms' distributions (Strotz et al. 2016). However, the impact of cyclones on foraminifera populations at different depths remains to be tested. Therefore, the goal of this study was to describe the shifts in Amphistegina species abundances at 6 and 18 m at Yonge Reef between 2013 and 2014 as a result of cyclonic activity.

Methods

Sampling design and processing

Sampling was carried out in 2013 and 2014, before and after the impact of TC Ita. On 7 August 2013, 12 replicate samples were collected at each sampling depth (6 and 18 m) along two transects, ~20 m apart. On 6 August 2014, a total of four replicate samples were collected at each depth, each along a single transect. Each sample comprised ten pieces of dead branching *Acropora* corals of approximately 80–100 cm³. Most coral pieces (~80%) were covered in turf algae or bare; a substantial increase in coral rubble was observed in 2014. Samples were of a

consistent morphology, to ensure a consistent surface area for a given volume among samples. All samples were handpicked by SCUBA divers from the leeward slope of Yonge Reef (14°35.81'S, 148°37.44'E). In the laboratory, coral fragments were scrubbed using a toothbrush and washed through a 125-µm mesh sieve. Sediment samples were dried in a Lavoisier oven at 50 °C for 24 h. In some cases, samples were fractionated using a sediment splitter. Since live specimens of Amphistegina preserve symbiont color after being dried, all colored specimens were removed from the residue, identified to species and counted. Volume of rubble pieces of each sample was estimated by volumetric assay. For the calculation of species density, the expression $T \times 2^n/V$ was used, where T represents total number of specimens found in the sample, n refers to the fraction number (i.e., number of times sediment samples were split) and V refers to the volume of the fragment (in cm³). We calculated the proportions of A. lobifera, A. lessonii and A. radiata in each replicate sample and measured the diameter of all specimens in each sample. To allow comparison, the variable volume of coral fragments was standardized to 1 cm^3 .

Statistical analyses

Differences between each depth and year were tested using a two-way analysis of similarity (ANOSIM) based on the density of each species in each replicate sample using the Bray–Curtis similarity index. Before statistical analyses, density values were square-root transformed. Similarity percentages (SIMPER) were used to identify the species that most discriminated among sample clusters. Analyses were conducted using Primer 6 (Clarke and Gorley 2006). Size frequency distributions of each species population were examined using generalized linear models (GLM), and pairwise comparisons were performed using a Tukey's test through the '*multcomp*' package in R (R Core Team 2013).

Results and discussion

Abundance of *Amphistegina* species changed significantly between 2013 and 2014, at 6 and 18 m (ANOSIM, global R = 0.643, P = 0.01). Total density of *Amphistegina* individuals declined at 6 m, but increased at 18 m (Fig. 1). In 2013, the relative abundance of each species was consistent with the community expected at that depth. However, in 2014 samples at 6 m revealed a 92% decline in *A. lobifera* and a 67% decline in *A. lessonii*, whereas *A. radiata* showed the least change (Fig. 1; Table 1; Electronic Supplementary Material Table S1). At the 18-m site, only *A. lobifera* showed a substantial decline in abundance,



Fig. 1 Average (\pm SD) density of **a** *Amphistegina lobifera*, **b** *A*. *lessonii*, **c** *A*. *radiata* and **d** all *Amphistegina* collected from Yonge Reef at 6 and 18 m in 2013 (*blue*) and 2014 (*orange*)

Table 1Changes in average
absolute abundance and
percentage of Amphistegina
lobifera, A. lessonii and A.
radiata and total Amphistegina
(total) between 2013 and 2014
at 6 and 18 m, and relative
contribution to dissimilarity
according to SIMPER

		Depth (m)	A. lobifera	A. lessonii	A. radiata	Total
Abundance	(ind.cm ⁻³)	6	- 1.68	-0.70	- 0.01	- 2.39
		18	- 0.32	+ 0.52	+ 0.51	+ 0.71
	(%)	6	- 92	- 67	- 13	- 81
		18	- 60	+31	+ 76	+ 25
Contribution		6	68.79	27.49	3.73	100
(SIMPER)	<i>70)</i>	18	16.55	52.27	31.18	100

Red and green colors signify decline and increase in absolute abundance/percentages, respectively

whereas *A. lessonii* and *A. radiata* abundances increased by 31 and 76%, respectively. SIMPER analysis revealed that 68.79% of the dissimilarity between 6-m samples collected in 2013 and 2014 was due to the decline in *A. lobifera*, while the decline of this species at 18 m contributed only 16.55% (Table 1).

Average test size of each *Amphistegina* population at 6-m sites for all species was significantly larger in 2013 than in 2014. Additionally, the *A. radiata* population at 18 m showed a significant decrease in test size between 2013 and 2014, a trend that was not observed for the other two species (GLM; P > 0.001; Fig. 2).

Cyclone events produce extreme wave and current forces, resulting in mechanical destruction such as dislodgement of corals, rubble and sand, stripping off the superficial reef framework and transporting material to deeper regions (Done 1992; Larcombe and Carter 2004). All levels of reef organization are affected by cyclones (Fabricius et al. 2008), and temporary increases in turbidity can be observed due to re-suspension of reef sediments (Harmelin-Vivien 1994). Cyclones can significantly affect benthic foraminifera communities on the GBR (Strotz et al. 2016), but the relative impacts at different depths remain poorly studied. Our results showed a depth-dependent decline in total abundance of



Fig. 2 Test size of a Amphistegina lobifera, b A. lessonii and c A. radiata at 6 and 18 m depth in 2013 (blue) and 2014 (orange). Solid line, box limits and bars represent mean test size, quartiles and 95% confidence intervals, respectively

Amphistegina between 2013 and 2014 and a shift in species proportions and test sizes likely associated with TC Ita.

Sites at 6 m were exposed to a greater impact than 18-m sites and would be expected to show selective removal of species less adapted to hydrodynamic stress (Madin et al. 2014). While the physical removal of individuals was reflected in the overall decline in abundance (Fig. 1; Table 1), it is possible that the removal was not selective. *Amphistegina lobifera* did not fare better than other species, suggesting that an impact such as TC Ita is capable of removing even well-adapted and robust species. The deeper sites (18 m) showed little change in overall species abundance, consistent with a reduced impact with depth (Roberts et al. 2015).

Another consequence of severe cyclones is the movement of sediment downslope (Harmelin-Vivien 1994). Sediment disturbance could have buried many resident and newly transported individuals (Harmelin-Vivien 1994). In this case, species with the ability to move through the sediment and a greater tolerance to low light could have an advantage. *Amphistegina* are negatively geotaxic and will climb up through the sediment onto the surface (Hallock et al. 2006). The ability to move and survive low light could enable some to persist in shallow waters and gain a foothold to increase in numbers following the disturbance, as observed for *A. lessonii* and *A. radiata*.

Lastly, light is a crucial structuring factor, and the expected increase in turbidity immediately following TC Ita likely changed local conditions temporarily. Deeper sites would have had reduced light, possibly overstressing any species already living at the edge of their tolerance, such as A. lobifera (Fig. 1). In contrast, turbidity at shallow sites could enable the colonization of species usually unable to thrive in high light, such as A. radiata. The higher relative abundance of A. lessonii and A. radiata at 6 m in 2014 compared to A. lobifera may reflect an increase in post-disturbance colonization success for these species. This is further supported by the proportional increase in younger individuals of A. radiata at 6 m (Fig. 2). Yonge Reef is located ~ 50 km from the coast and is little influenced by terrestrial runoff (Brodie et al. 2007). Consequently, it is very likely that normal light levels would have returned within days. Any benefit gained by species taking advantage of lower light levels (such as A. lessonii and A. radiata) would quickly disappear, but whether a population established under altered conditions has the ability to persist remains to be tested.

The non-selective removal of species at 6 m, coupled with the large decrease in total *Amphistegina* abundance, potentially provides a chance for re-colonization from other adjacent areas. This may be reflected in the changed relative abundance and average test size in 2014 for *A*.

radiata and A. lobifera. There was a clear downward shift in average test size and an increase in relative abundance of A. radiata at 6 m from 2013 to 2014. In contrast, A. lobifera had low relative abundance and a narrow test size range at 18 m in 2014. At 6 m, the range of test sizes remained wide, with smaller individuals entering the population despite a significant drop in absolute and relative abundance after TC Ita. These results suggest that these species have differing source-sink dynamics over depth, with a shallow and deep source for A. lobifera and A. radiata, respectively. Amphistegina lessonii fills a more generalist role, with moderate abundance at both depths and no significant change in test sizes between 2013 and 2014. As long as there are populations surviving nearby and substrate is available, foraminifera can re-establish themselves within a short period (i.e., within a few years; Strotz et al. 2016). Our data suggest that A. lessonii populations, with shorter life spans (6-9 months) and a higher reproductive rate, have the potential to recover faster than A. lobifera/radiata (Hallock 1999). However, due to the restrictions of this study, the hypothesis remains to be tested. We hypothesize that the source pools for A. lessonii and A. radiata at 18 m could influence the re-colonization and recovery of populations at 6 m. The lack of a refuge for A. lobifera would potentially make it more vulnerable to a disturbance of this nature.

Acknowledgments This study was funded by the ARC Centre of Excellence for Coral Reef Studies and the Ian Potter Doctoral Fellowship at Lizard Island. We also thank the field assistance of Australia Museum's Lizard Island Research Station staff.

References

- Brodie J, De'ath G, Devlin M, Furnas M, Wright M (2007) Spatial and temporal patterns of near-surface chlorophyll *a* in the Great Barrier Reef. Mar Freshw Res 58:342–353
- Clarke KR, Gorley RN (2006) Primer v6: User Manual/ Tutorial. PRIMER-E, Plymouth
- Done TJ (1992) Effects of tropical cyclone waves on ecological and geomorphological structures on the Great Barrier Reef. Cont Shelf Res 12:859–872
- Fabricius KE, De'ath G, Puotinen ML, Done T, Cooper TF, Burgess SC (2008) Disturbance gradients on inshore and offshore coral reefs by a severe tropical cyclone. Limnol Oceanogr 53:690–704
- Hallock P (1999) Symbiont-bearing foraminifera. In: Sen Gupta BK (ed.) Modern foraminifera. Kluwer, Amsterdam, pp 123–149
- Hallock P (2011) Modern coral reefs under global change: new opportunities to understand carbonate depositional hiatuses. In:

Stanley GD Jr (ed.) Coral and reefs crises, collapse and change. Paleontological Society papers volume 17, Geological Society of America, Minneapolis, pp 121-130

- Hallock P, Hansen HJ (1978) Depth adaptation in *Amphistegina*: change in lamellar thickness. Bulletin of the Geological Society of Denmark 27:99–104
- Hallock P, Williams DE, Fisher EM, Toler SK (2006) Bleaching in Foraminifera with algal symbionts: implications for reef monitoring and risk assessment. Anuario do Instituto de Geociencias 29:108–128
- Harmelin-Vivien ML (1994) The effects of storms and cyclones on coral reefs: a review. J Coast Res 12:211–231
- Hohenegger J (2006) Morphocoenoclines, character combination, and environmental gradients: a case study using symbiont-bearing benthic foraminifera. Paleobiology 32:70–99
- 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 56:109–168
- Hollaus SS, Hottiger L (1988) Temperature dependence of endosymbiontic relationships? Evidence from the depth range of Mediterranean Amphistegina lessonii (Foraminiferida) truncated by the thermocline. Eclogae Geologicae Helvetiae 90:591–597
- Hughes TP, Connell JH (1999) Multiple stressors on coral reefs: a long-term perspective. Limnol Oceanogr 44:932–940
- Langer MR (2008) Assessing the contribution of foraminiferan protists to global ocean carbonate production. J Eukaryot Microbiol 55:163–169
- Langer MR, Hottinger L (2000) Biogeography of selected "larger" foraminifera. Micropaleontology 46:105–126
- Larcombe P, Carter RM (2004) Cyclone pumping, sediment partitioning and the development of the Great Barrier Reef shelf system: a review. Quat Sci Rev 23:107–135
- Madin JS, Baird AH, Dornelas M, Connolly SR (2014) Mechanical vulnerability explains size-dependent mortality of reef corals. Ecol Lett 17:1008–1015
- Munksgaard NC, Zwart C, Kurita N, Bass A, Nott J, Bird MI (2015) Stable isotope anatomy of Tropical Cyclone Ita, north-eastern Australia, April 2014. PLoS One 10:e0119728
- R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Renema W (2006) Habitat variables determining the occurrence of large benthic foraminifera in the Berau area (East Kalimantan, Indonesia). Coral Reefs 25:351–359
- Renema W (2008) Habitat selective factors influencing the distribution of larger benthic foraminiferal assemblages over the Kepulauan Seribu. Mar Micropaleontol 68:286–298
- Renema W, Beaman RJ, Webster JM (2013) Mixing of relict and modern tests of larger benthic foraminifera on the Great Barrier Reef shelf margin. Mar Micropaleontol 101:68–75
- Roberts TE, Moloney JM, Sweatman HPA, Bridge TLC (2015) Benthic community composition on submerged reefs in the central Great Barrier Reef. Coral Reefs 34:569–580
- Strotz LC, Mamo BL, Dominey-Howes D (2016) Effects of cyclone generated disturbance on a tropical reef foraminifera assemblage. Sci Rep 6:24846