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Mixing of relict and modern tests of larger benthic foraminifera on the Great Barrier Reef shelf margin

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ABSTRACT

The distribution of live, well preserved, and relict larger benthic foraminifera (LBF) in sediment samples collected off the shelf margin near Hydrographers Passage in the Great Barrier Reef, Australia, was studied to document taphonomic processes in this setting. In total, eight living species of LBF were found, mostly of the families Amphisteginidae and Nummulitidae, separated into a shallow (platform) assemblage and a deep (terrace) assemblage. The modern (well preserved) shells in the sediment revealed a good representation of this fauna, but differences in depth distribution were lost. The relict fauna is represented by a more diverse fauna, and is composed mostly of taxa occurring in much shallower conditions. We interpret this pattern as an initial downslope transport of the foraminifera from the shelf into deeper waters, and a mixing of foraminifera derived from nearby Pleistocene coral reef structures.

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1. Introduction

Symbiont-bearing larger foraminifera live within the photic zone, both on reefs and on carbonate platforms. The most important environmental parameters influencing the distribution of living larger foraminifera on modern day reefs are temperature, light intensity, substrate type, nutrient availability, and hydrodynamic energy all interrelated with depth (Hottinger, 1977; Hallock, 1984; Hohenegger et al., 1999, 2000; Renema and Troelstra, 2001; Jorry et al., 2006; Renema, 2006a,b). In modern day tropical marine environments, larger foraminifera are important carbonate producers (e.g., Hallock, 1981; Tudhope and Scoffin, 1988; Yamano et al., 2000). For example, Tudhope and Scoffin (1988) estimated that foraminifera contributed up to a third of the total carbonate on the Great Barrier Reef (GBR) shelf. Foraminifera were the most important contributors to Holocene carbonate, followed by the calcareous green algae *Halimeda*, and only in third place came reef building corals. In tropical Cenozoic settings, larger benthic foraminifera can contribute up to 80% of the carbonates (e.g., Wilson, 2012), as well as comprising significant proportions of marly sediments. In these environments foraminifera traditionally have been used for stratigraphical purposes. By definition, larger benthic foraminifera (LBF) are symbiont-bearing and larger than 0.5 mm. They are mixotrophic organisms that at least partly depend on the photo synthetic energy generated by their micro-algae symbionts. Hence, they are restricted to the photic zone.

Recently LBF have increasingly been used to asses environmental change in coral reef systems, either by documenting occurrence patterns in relation to environmental parameters over reef systems (e.g., Hottinger, 1977; Hallock, 1981; Hohenegger et al., 1999, 2000; Renema and Troelstra, 2001; Renema, 2006a), or using an experimental approach (e.g., Briguglio and Hohenegger, 2011; Uthicke et al., 2012b). The study of subsequent samples from the same area through time, or in sediment cores have demonstrated the potential use of LBF as an important monitoring tool (Hallock et al., 2003; Renema, 2010; Uthicke et al., 2012a). Furthermore, Yamano et al. (2000) and Lobegeier (2002) found that LBF were the single most important contributor to the sediment production that maintains sand cay reefs in the northern GBR. They found a high production of foraminifera associated with algae on the reef flat of the islands they investigated. The most important producers were *Calcarina hispida*, *Baculogypsina sphaerulata* and *Amphistegina lessonii*. Most of that work was directed at the most popular and easiest accessible (since they are within safe SCUBA diving depths) reef flat and upper reef slope of patch reefs on carbonate shelves. However, the surface area of reefs forms only 5–10% of the entire GBR shelf, and few studies have focused on the much larger shelf area between the reefs. This is at least in part since sampling is more difficult, since using (gravity) coring and grabs requires a vessel. On the GBR benthic foraminifera sands dominate the bulk of the inter-reef shelf area (Tudhope and Scoffin, 1988). Seven facies along a cross-shelf transect from the inner-shelf to outer-shelf were recognized. Larger benthic foraminifera of the family Nummulitidae were the most important contributors to the assemblages, with high densities of *Operculina* and *Cycloclypeus* especially in the outer part of the shelf (Tudhope and Scoffin, 1988). The distribution of LBF on the outer-shelf margin, or shelf edge, of the GBR has not been documented yet.

In this paper we explore the distribution of LBF tests on the shelf edge from the outer-shelf margin of the GBR. Contrary to other

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investigated areas within the Indo-West Pacific, this has a complex geomorphology, including (submerged) reefs, platforms, and terraces (Abbey et al., 2011; Beaman et al., 2012). We investigate the taphonomic processes acting on the assemblages, as well as potential sources of mixed assemblages.

2. Research area

Hydrographers Passage lies on the outer-shelf continental margin of the world's largest extant tropical siliciclastic/carbonate depositional system, the Great Barrier Reef (GBR) in north-eastern Australia (Fig. 1A, B). The research area includes the shelf edge, ranging from the outermost part of the shelf platform, the barrier reef, seaward terraces, and the upper slope to seaward of the shelf break at about 100 m. The following description is, unless otherwise stated, based on Beaman et al. (2012), who studied in detail the bathymetry and geomorphic features in the same area and using the same grab samples for their sediment composition analysis.

Beaman et al. (2012) recognized five distinct geomorphic features: platform, dunes, reef, terrace, and slope (Fig. 1B). The *platform* is the

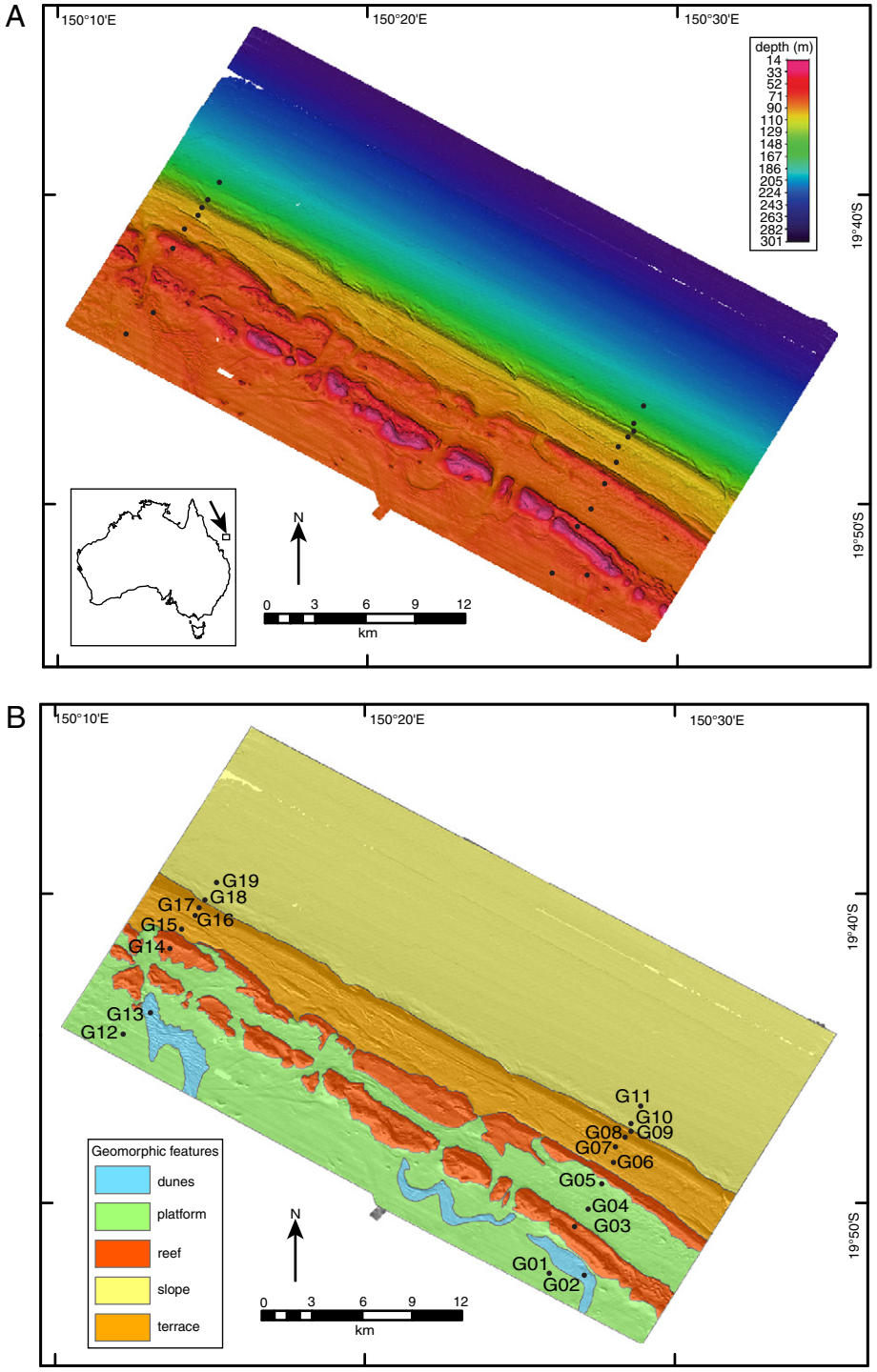


Fig. 1. (A) Multibeam sonar bathymetric map of Hydrographers Passage at a grid pixel resolution of 25 m. (B) Geomorphic features from Hydrographers Passage, including the locations of the grab samples.
Both after Beaman et al. (2012).

main GBR outer-shelf upon which the reefs and dune fields are located. The gradient is near flat or <0.5°. The platform broadly extends from the inter-reefal area between the middle- and outer-shelf patch reefs to landward of the study area, then to the seaward limit where it extends into the inter-reefal tidal channels between the reefs shown in Fig. 1B. Depths range from about 70 m along the south-western edge of the survey area to about 80 m within the deepest channels feeding into the adjacent terrace. Sediments range from poorly-sorted coarse sand and rubble to moderately-sorted medium to coarse sand. The coarse fraction is composed of 30% benthic forams, 15% *Halimeda*, 10% bryozoa, 5% mollusk fragments, and the remainder unidentifiable fragments (grabs G01, G04, G05, and G12; Beaman et al., 2012).

The *reef* constitutes two parallel lines of barrier reefs, which extend across the survey area. The inner line of reefs rises up to 50 m above the surrounding platform, with the shallowest parts of the reefs at 14 m. However, most reefs top at 20–30 m water depth. The outer line of reefs rises about 20 m above the surrounding platform, with reef tops generally at 50–60 m water depth. IODP drilling through these structures confirmed that these shelf edge features consist of older, Pleistocene reef deposits overlain by a last deglacial phase of reef growth (Webster et al., 2011; Yokoyama et al., 2011). Sediments are poorly-sorted sand to coarse gravel (grabs G03 and G14). The coarse fraction is composed of 60% benthic forams, 15% *Halimeda*, 10% mollusk fragments, 5% bryozoa, and the remainder unidentifiable fragments (grabs G03, G14; Beaman et al., 2012).

The *dune* mounds or ridges of unconsolidated sand are found on the landward side of the reefs. They are a response to the strong tidal streams through the inter-reefal tidal channels. Trough to crest heights range from 2 to 4 m, in water depths of 65 to 70 m. Sediments are well-sorted medium to coarse sand. Individual smaller sand wave crests are also observed right across the platform, as distinct from the three main fields of dunes mapped (grabs G02, G13; Beaman et al., 2012).

Between the reefs and the shelf break is a wide *terrace* feature with a gentle slope of ~1° in gradient. The seaward extent is marked by the steep step which is the shelf break, starting at about 100 m and dropping to 130 m at the upper limit of the continental slope. The landward extent abuts the bases of the numerous submerged reefs lying parallel to the shelf edge at about 90 m. Sediments are moderately- to poorly-sorted muddy sand to fine gravel. The coarse fraction is 30% benthic forams, 20% *Halimeda*, 20% mollusk, 10% bryozoans, 5% echinoderms, and the remainder coral fragments (grabs G06, G07, G08, G09, G15, G16, and G17; Beaman et al., 2012).

Seaward of the terrace is the upper part of the continental *slope*. Water depths range from 130 to 300 m to the deepest part of the surveyed area. The surface is relatively smooth and slopes about 1° to the north-east. Sediments are poorly-sorted, muddy, coarse sand, and gravel. The coarse fraction is generally ~30% *Halimeda* algae, 30% benthic forams, 10% bryozoa, 10% mollusks, and the remainder unidentifiable fragments (grabs G10, G11, G18, and G19; Beaman et al., 2012).

3. Methods

Foraminifera where counted in the >0.5 mm fraction of 19 grab samples taken in two transects perpendicular to the GBR margin at Hydrographers Passage. Eight additional grab samples from across the GBR region, from the inter-reef area and reef slope around Orpheus Island on the central GBR, and the inter-reef near Lizard Island in the far northern GBR, have been included for comparison with our assemblages. Orpheus Island is located close to the boundary between inshore and mid-shelf reefs. Here, the reef base samples (Pioneer 1 and 2) were collected at ~15 m on sand below the reef slope. The reef slope samples (Orpheus 1–3) were collected at 8–12 m on the reef slope. The Lizard Island samples were collected at 30–40 m depth in the mid-shelf inter-reef to the north of Lizard Island.

The LBF in the Hydrographers Passage grab samples were counted in three categories:

1) Live (Fig. 2A): Pristine tests colored by algal symbionts. In most cases, specimens living at the time of sampling displayed a dark green to brown coloration, which is most pronounced in the initial chambers of the test. Since the fraction of the total surface of the sediment grab was not recorded while subsampling, it is only possible to present the relative assemblage composition of the samples.
2) Modern (Fig. 2B): White pristine tests. The test is at most slightly milky in color, and hardly abraded or fractured. This compares to the moderate and good preservation classes of Hohenegger and Yordanova (2001).
3) Relict (Fig. 2C): Poorly preserved tests. Tests are milky and opaque, often broken and abraded. Some specimens are strongly iron stained. This compares to the poor preservation class of Hohenegger and Yordanova (2001).

Only the living foraminifera (rose Bengal stained) in the >0.5 mm in five samples from the inshore reefs around Orpheus Island (Palm Island group; Orpheus sl1–3, Pio1, 2) as well as three samples from the inter reef area around Lizard Island (JK023–025) were counted. Finally, the fossilized foraminifera in a rock dredge from Hydrographers Passage (D22) was analyzed as well.

Either all specimens from the entire >0.5 mm fraction, or a split of the sample containing at least 200 specimens were studied. A bootstrapping analysis has shown that a sample size of 50 specimens was enough to capture the variation in sample composition, and that only rare species were potentially missed.

We utilized three multivariate analytical approaches to investigate assemblage composition of large benthic foraminifera in the GBR margin samples: non-metrical multidimensional scaling (NMDS); Analysis of Similarities (ANOSIM); and hierarchical clustering combined with similarity profile (SIMPROF) analysis. Each analytical approach is performed on a log-transformed [$x_i = \log(\text{relative abundance}_i + 1)$] species × sample matrix using a Bray–Curtis similarity index. NMDS was used to graphically display the samples in a two dimensional plot. ANOSIM (Clarke, 1993) tests for differences in the assemblage

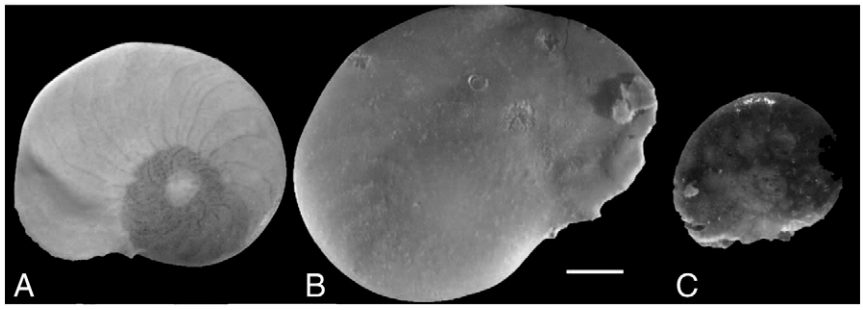


Fig. 2. (A) Live specimen of *Operculina* sp. 1 from G13. (B) *Operculina* sp. 1 in modern preservation style from G11. (C) Relict *Operculina ammonoides* from G11. Scale bars represent 1 mm.

composition between predefined groups, in our case the 'live', 'modern', and 'relict' assemblages. Cluster analysis (hierarchical clustering, Bray–Curtis similarity index) followed by a similarity profile (SIMPROF) test was used to test for significant sample groupings within the dataset. SIMPROF tests whether the coherence within a cluster is larger than expected than by randomly selecting the same number of samples from the entire dataset (maximum of 1000 runs, 0 = 0.05%; Clarke et al., 2008). Geomorphologic features were used to label the samples as platform, reef, dunes, terrace, and slope (Beaman et al., 2012). Live, modern, and relict factors were treated as three subsamples within each grab sample.

ANOSIM and SIMPER analyses were performed in Primer v6.1.6.

4. Results

In the entire dataset we found 21 species of LBF (including *Elphidium*). We observed 8 live, 13 modern, and 18 relict species of LBF in the 18 grab samples we examined (Tables 1–3). The composition of the reference samples is shown in Table 4. The deepest occurrence of living LBF was at 135 m water depth. In the four grab samples taken at the slope no living LBF was found. In the samples G02, G12, and G13, less than 40 living specimens were found and the live category of these samples has not been included in the analysis.

The faunal composition in the live, modern, and relict classes were significantly different (ANOSIM, $R = 0.717$, $p < 0.001$).

4.1. Live assemblages

The relative abundance of *Amphistegina bicirculata* contributed 10–56% in the live category (Table 1). *Amphistegina papillosa* was found in 9 (7 included in the analysis) samples, but was rare in the shallower samples, and the highest numbers occurred in the terrace samples. *Cycloclypeus carpenteri* had a very comparable distribution pattern as *A. papillosa*, but it was not found on the platform, and in higher abundance on the terrace. *Planostegina heterosteginoides* was the most abundant species in the deepest samples. *Operculina complanata* was found in highest numbers around the transition from the platform to the terrace. Finally, another species of *Operculina* from the *O. complanata*-group was observed. It differed from *O. complanata* by having a larger, more robust test. The test is at least partly involute, the chambers are longer, and the spire is opening more rapidly than in *O. complanata*. The marginal cord often appears to be thickened. This species is larger than *O. complanata*, the B-form can have a diameter of more than 2 cm. Due to these morphological differences it can be regarded as a separate species, but a more comprehensive study of this group (including molecular phylogenetic data) is needed before it can be named. Here it is referred to as *Operculina* sp. 1. No similar species are known to the authors from outside the GBR. In our samples *Operculina* sp.1 is especially abundant in the shallow (platform) samples. In total, 12 samples have been included in the cluster analysis for the live assemblages. Two significant clusters were observed, roughly comparing to the platform and terrace geomorphologic unit (Fig. 3). The average water depth in which samples from these two clusters have been collected differs significantly (t-test, $t = 5.4$, $p < 0.01$). The platform and reef cluster is taken on average in 68 ± 14 m depth, the terrace cluster in 103 ± 29 m.

4.2. Modern assemblages

In the 'modern' preservation data set we found 10 species of LBF and two species of *Elphidium* (Table 2). The dominant living species are also the most important (in terms of numbers) in the modern dataset. However, the order of these species differs slightly, and *A. papillosa* ranks third in the modern data set (Table 5) and sixth in the live fauna. Also the distribution in the samples is comparable to the live samples, although the differences between the samples are smaller. *Alveolinella quoyi*, *Amphistegina radiata*, *Calcarina mayori*, and *Peneroplis* spp. have not been observed in the live fauna. The SIMPROF analysis on the clustered assemblages did not result in any significant clusters.

4.3. Relict assemblages

The relict faunas are significantly different from both the modern and live fauna. None of the five most important species of the modern and live dataset is numerically abundant in the relict set (Table 5). Apart from the species in the modern data set, *Marginopora* sp., *A. lessonii*, *Baculogypsina sphaerulata*, and *Heterostegina depressa* have been found as well (Table 3). *P. heterosteginoides* is not found in the relict fauna at all, whereas *C. carpenteri* is represented by a single specimen only. Most remarkable is the high abundance of *Operculina ammonoides* and *A. radiata*, of which only a single specimen is found in the non-relict fauna. The SIMPROF analysis on the clustered assemblages did not result in any significant clusters.

The reference samples collected around Orpheus and Lizard Island show overlap in assemblage composition with the relict assemblages. In the inshore Orpheus Island samples both in the reef slope and reef base samples *A. lessonii*, *A. quoyi*, and *Peneroplis* spp. are important elements (Table 4). On the coral rubble substrate of the reef slope samples these are accompanied by *A. radiate*, *C. mayori*, and *H. depressa*, on the reef base by *Marginopora* sp. and *O. ammonoides*.

Table 1
The occurrence of 'Live' foraminifera in the Hydrographers Passage grab samples.

	Amphistegina bicirculata	*Amphistegina papilosa*	*Cycloclypeus carpenteri*	*Elphidium craticulatum*	*Operculina* sp. 1	*Operculina complanata*	*Parasorites* sp.	*Planostegina operculinoides*	Geomorphology	Depth
G01	25	1	0	1	31	3	0	0	Platform	71
G02	1	1	0	0	1	0	0	2	Dunes	63
G03	12	0	0	0	24	0	1	0	Reef	53
G04	19	0	0	0	41	6	0	0	Platform	74
G05	23	0	0	0	27	12	0	0	Platform	72
G06	44	0	12	0	2	22	0	3	Terrace	92
G07	25	1	14	0	0	12	0	46	Terrace	100
G08	34	9	25	0	1	0	0	22	Terrace	101
G09	4	2	1	0	0	0	0	34	Terrace	129
G12	6	0	0	0	0	0	0	4	Platform	78
G13	3	1	0	0	2	1	0	0	Dunes	74
G14	68	1	0	0	58	0	1	2	Reef	68
G15	46	1	23	0	0	12	0	0	Terrace	90
G16	44	0	34	0	0	29	0	24	Terrace	99
G17	23	5	27	0	0	23	0	22	Terrace	97

Table 2
The occurrence of 'Modern' foraminifera in the Hydrographers Passage grab samples.

	Alveolinella quoyii	*Amphistegina bicirculata*	*Amphistegina lessonii*	*Amphistegina papilosa*	*Cycloclypeus carpenteri*	*Elphidium craticulatum*	*Elphidium* sp.	*Operculina* sp. 1	*Operculina ammonoides*	*Operculina complanata*	*Peneroplis* spp.	*Planostegina operculinoides*	Geomorphology	Depth
G01	0	27	0	0	0	4	0	18	0	2	0	0	Platform	71
G02	0	40	0	0	1	0	1	43	0	0	0	2	Dunes	63
G03	0	20	0	2	0	1	0	39	0	0	0	1	Reef	53
G04	0	39	0	1	0	2	2	7	0	3	0	0	Platform	74
G05	0	44	0	7	1	5	0	5	0	7	0	2	Platform	72
G06	0	165	0	5	7	2	0	5	0	2	0	8	Terrace	92
G07	0	76	0	23	32	11	0	57	5	38	0	44	Terrace	100
G08	0	55	0	34	7	3	0	2	0	1	0	4	Terrace	101
G09	1	14	0	15	10	0	0	4	0	0	0	7	Terrace	129
G10	0	18	0	4	25	3	5	14	0	0	0	9	Slope	141
G11	0	15	0	30	3	1	0	18	0	1	1	1	Slope	166
G12	0	0	0	3	0	6	0	0	0	0	0	0	Platform	78
G13	0	29	0	2	0	0	0	14	0	0	0	14	Dunes	74
G14	0	196	0	1	0	5	0	178	3	0	0	16	Reef	68
G15	0	216	0	6	6	5	0	8	0	0	0	2	Terrace	90
G16	0	122	0	4	14	2	0	6	0	0	0	5	Terrace	99
G17	0	39	0	16	27	0	0	10	0	0	1	6	Terrace	97
G18	0	14	1	3	0	0	1	23	0	0	0	3	Slope	135
G19	0	47	0	49	6	2	0	12	0	0	0	2	Slope	161

Table 3
The occurrence of 'Relict' foraminifera in the Hydrographers Passage grab samples.

	Alveolinella quoyii	*Marginopora* sp.	*Amphistegina bicirculata*	*Amphistegina lessonii*	*Amphistegina papilosa*	*Amphistegina radiata*	*Baculogypsina sphaerulata*	*Calcarina mayori*	*Cycloclypeus carpenteri*	*Elphidium craticulatum*	*Elphidium* sp.	*Heterostegina depressa*	*Operculina* sp. 1	*Operculina ammonoides*	*Operculina complanata*	*Parasorites* sp.	*Peneroplis* spp.	*Sorites orbiculus*
G01	16	2	0	2	0	28	0	4	0	0	0	2	0	12	0	5	10	4
G02	0	4	0	7	0	0	0	1	0	0	0	0	0	24	0	12	0	5
G03	0	0	0	3	0	38	0	1	0	11	0	0	0	0	0	1	0	1
G04	5	1	0	1	0	0	0	0	0	2	0	0	0	35	2	3	4	0
G05	3	0	0	0	0	52	0	2	0	14	0	0	0	12	1	0	0	0
G06	0	0	9	0	1	10	0	2	0	2	0	0	0	18	5	1	0	0
G08	1	0	10	0	5	10	0	2	0	0	0	0	0	49	8	2	0	0
G09	1	0	0	0	0	27	0	9	0	1	1	0	6	39	2	0	0	0
G10	4	1	0	1	12	30	0	4	0	0	0	0	2	34	4	0	0	0
G11	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
G12	21	1	0	7	0	100	2	0	0	0	0	0	0	6	0	0	0	0
G13	0	2	0	1	0	0	1	1	0	0	0	0	0	5	0	22	3	0
G14	2	0	0	2	0	9	0	0	0	18	0	0	0	0	0	4	0	0
G15	3	1	0	2	0	11	0	10	1	5	0	1	0	11	0	0	0	0
G16	3	1	0	0	0	17	0	8	0	6	0	1	0	39	0	3	3	1
G18	4	0	0	0	0	57	0	0	0	0	6	0	0	34	0	0	0	0
G19	1	0	0	0	0	5	1	3	0	9	0	0	4	43	0	0	0	0

Table 4
Occurrence of larger benthic foraminifera in seven reference samples collected in the inshore-midshelf GBR shelf.

	Alveolinella quoyii	*Marginopora* sp.	*Amphistegina lessonii*	*Amphistegina radiata*	*Baculogypsina sphaerulata*	*Calcarina mayori*	*Elphidium craticulatum*	*Elphidium* sp.	*Heterostegina depressa*	*Operculina* sp. 1	*Operculina ammonoides*	*Operculina complanata*	*Parasorites* sp.	*Peneroplis* spp.	*Sorites orbiculus*	Depth	
JK023	10	9	2	6	0	0	12	0	0	0	10	2	0	0	1	34	Shelf near Lizard Island (GBR)
JK024	6	10	1	5	1	0	21	0	0	0	35	2	2	0	0	40	Shelf near Lizard Island (GBR)
JK025	15	10	1	12	0	0	3	0	0	0	67	2	0	0	0	37	Shelf near Lizard Island (GBR)
Orpheus-sl1	12	0	12	8	0	34	4	0	7	1	0	0	0	22	0	8	Orpheus Island reef slope
Orpheus-sl2	9	2	16	9	0	23	5	0	2	3	0	0	0	12	0	6	Orpheus Island reef slope
orpheus-sl3	16	0	23	5	0	22	6	0	8	2	0	0	0	24	0	9	Orpheus Island reef slope
Pio1	12	5	12	0	0	0	7	2	0	0	3	0	1	12	0	14	Pioneer Bay reef base
Pio2	7	6	11	0	0	0	12	2	0	0	2	0	2	13	0	15	Pioneer Bay reef base

The NMDS analysis (Fig. 4) corroborates these results. The live fauna clusters in two distinct clusters, whereas most of the modern fauna plots between these two clusters. The relict fauna plots in a separate, non-overlapping area of the NMDS plot compared to the other two datasets, but the reference (live) assemblages collected in the inter-reef and reef slope of Orpheus and Lizard Islands plot within or close to the relict samples.

5. Discussion

On the GBR continental shelf edge margin, large benthic foraminifera (LBF) occur until at least 129 m. This is comparable with the bathymetric distribution of LBF in other parts of the Indo West Pacific, such as East Kalimantan (Renema, 2006a) and Japan (Hohenegger et al., 1999). In more turbid environments, there is a shallower maximum depth limit. Compared to these other localities, the recorded number of seven species is lower compared to 13 species found in southern Japan (Hohenegger et al., 1999) and 11 in East Kalimantan (Renema, 2006a). There is a shallow assemblage characterized by *Operculina* sp. 1 and a deeper assemblage characterized by *Cycloclypeus* and *Planostegina*. Both the significant difference in the cluster with SIMPROF analysis (Fig. 3) and the separate position of the shallow and deep clusters in the NMDS plot (Fig. 4) indicate that these are separate assemblages and not artifacts as the result of the type of analysis we performed. Furthermore, the very low abundance of LBF in the unconsolidated sands of the dunes is a further indication that other parameters than depth play an important role in shaping LBF assemblage composition.

For a full appreciation of how the living assemblage is represented in surface sediments or even sediment cores, the processes during the transition from living (biocoenosis) to dead assemblage (thanatocoenosis) needs to be understood. The thanatocoenosis is the result of the processes accounting for the production and loss of shells in the system. Comprehensive models have been published showing all processes that affect the translation of the biocoenosis into the thanatocoenosis for molluscs (Kidwell, 1991; Kidwell and Flessa, 1996).

Life processes affecting the incongruence between the living and dead assemblages include differences in production rate between species (Murray, 1991). In the ideal dead assemblage, the proportion of all species is the same as in the living assemblage. However, due to differences in production rate between species, the dead assemblage differs from the living assemblage. Long-lived species will tend to produce fewer tests than short-lived species. Furthermore, major post-mortem sources of bias for foram assemblages are out of habitat transport, selective destruction of species at the accumulation site, and mixing with non-contemporaneous and/or out of habitat derived material (Kidwell and Flessa, 1996). Larger foraminifera are relatively small and light organisms that are prone to transport (Martin, 1999; Jorry et al., 2006; Briguglio and Hohenegger, 2011).

In reefal environments of the Spermonde Archipelago (Sulawesi, Indonesia), foraminiferal assemblages in the thanatocoenosis resembled those of the biocoenosis (Renema, 2002). The exceptions were samples from the exposed reef slope and sheltered reef slopes that were identical, whereas they differed in the living assemblage. However, all individual species were observed to have larger depth ranges as empty tests compared to the living foraminifera. Similar results were obtained by James et al. (1999) in Western Australia. Hohenegger and Yordanova (2001) concluded that on a gentle reef slope near Okinawa, Japan, three factors influenced the depth transport of larger foraminifera tests: 1) traction caused by storms and offshore currents; 2) slope steepness; and 3) differences in test buoyancy between species. Due to the depth position of living populations, the combination of these three factors leads to varying displacement intensities and mixing of empty tests (Hohenegger and Yordanova, 2001). The thanatofacies however, still had a bathymetric signal. Webster et al. (2012), however, found both representatives of reef flat, reef slope, and intra-reef LBF assemblages all mixed in submarine canyon turbidites offshore of the GBR

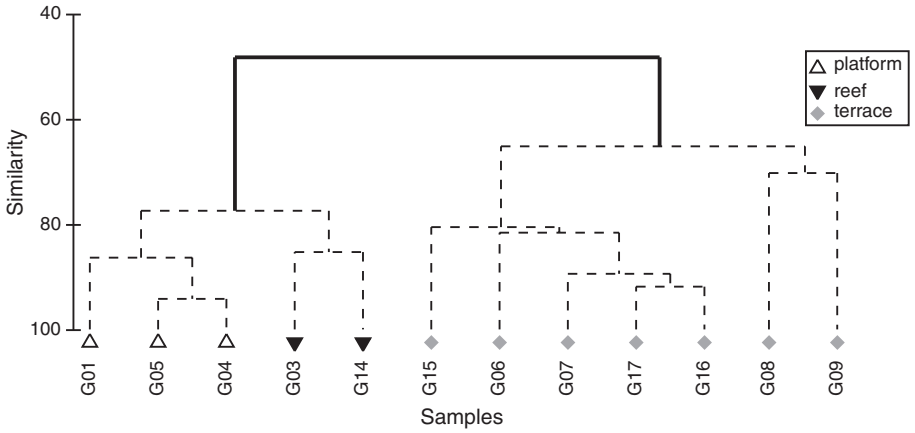


Fig. 3. Dendrogram for hierarchical clustering of the 13 samples containing more than 40 specimens, using group-average linking of Bray–Curtis similarities calculated on log-transformed data. Clusters showing significantly higher similarities than expected from a random subsample from the entire data set are indicated by the solid lines, while the dashed lines indicate clusters that do not show such a structure.

shelf, indicating the need to differentiate between 'regular' and mass flow transport modes.

In our study, the modern fauna is a good reflection of the live fauna, with only a single species that ranks differently in the five most important species of each. However, even though the last deglaciation double barrier reef (Abbey et al., 2011) could potentially serve as barriers to downslope transport the difference between the shallow and deep assemblage in the living fauna is not observed in the modern fauna. Likely, downslope transport obscured the bathymetric gradient in the modern thanatocoenoses.

Conversely, the relict fauna does not compare at all to either the modern or live fauna. All five most important species have hardly been recorded in either the live or modern data set. The additional species that were found mostly as iron-stained tests all occur in shallower reef slope and inter-reef assemblages elsewhere (e.g. Hohenegger et al., 1999; Renema and Troelstra, 2001; Renema, 2006b). This is well reflected in the position of the Orpheus and Lizard Island reference samples in Fig. 4A. Rather than being transported downslope and over long distances over the carbonate shelf, it is more likely that these relict faunas are erosional products from the submerged reef structures formed during the last deglaciation (Abbey et al., 2011; Webster et al., 2011) along the shelf edge. This interpretation is supported by the similarity of the LBF composition to a *Halimeda* grainstone in a dredge sample (D22) taken close to G15 and G16, which compares well with the relict fauna in these samples (Fig. 4A). It is further supported by the similarity of the relict fauna in G03 and G14, collected in the reef geomorphologic feature, that plot nearest to the samples collected at the reef slope around Orpheus Island. At the Lincoln shelf Li et al. (1996) also reported these iron-stained specimens as an indication of sea-level lowstand during the Last Glacial Maximum.

However, not the entire relict fauna will be derived from erosion of these structures. The samples from the dune geomorphologic feature (G02 and G13) plot markedly different, and are more affected by intense abrasion and breakage than iron staining. The terrace samples G06 and G08, have a much larger similarity to the modern and live fauna than all the other samples (Fig. 4A), indicating spatial heterogeneity in the relative importance of each of these processes. Next to downslope transportation (Hohenegger and Yordanova, 2001), mixing with erosion-derived foraminifera is an important factor to take into account when interpreting the depositional environment of continental slope deposits.

6. Conclusion

Along the GBR shelf, live LBF assemblages are roughly arranged along a depth gradient. The platform, reef, and terrace assemblages are most similar, showing both a distinct shallow and deep assemblage. *Operculina* sp. is the most characteristic species in the relatively shallow (50–80 m) assemblage, whereas *Planostegina operculinoides* and *C. carpenteri* are the dominant species in the deep assemblage. Dune assemblages are very poor in living LBF. However, the distribution of empty shells in the sediments does not reflect this distribution very well, and thus it is impossible to accurately infer depth from the LBF assemblages in the sediment. Finally, mixing with LBF derived from the fossil reef associated structures deposited in much shallower environments further altered the thanatocoenosis. When a total assemblage study from environments comparable to this complex shelf margin are used for (paleo)environmental interpretations, care should be taken to include the possibility of mixing of multiple faunas from different paleoenvironmental settings.

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Table 5
The five most abundant species in the Live, Modern, and Relict datasets, absolute numbers in brackets.

Live	Modern	Relict
Amphistegina bicirculata (377)	*Amphistegina bicirculata* (1176)	*Operculina ammonoides* (428)
Operculina sp. 1 (187)	*Operculina* sp. 1 (463)	*Amphistegina radiata* (425)
Planostegina operculinoides (159)	*Amphistegina papillosa* (205)	*Elphidium craticulatum* (72)
Cycloclypeus carpenteri (136)	*Cycloclypeus carpenteri* (139)	*Alveolinella quoyi* (66)
Operculina complanata (120)	*Planostegina operculinoides* (126)	*Parasorites* sp. (54)

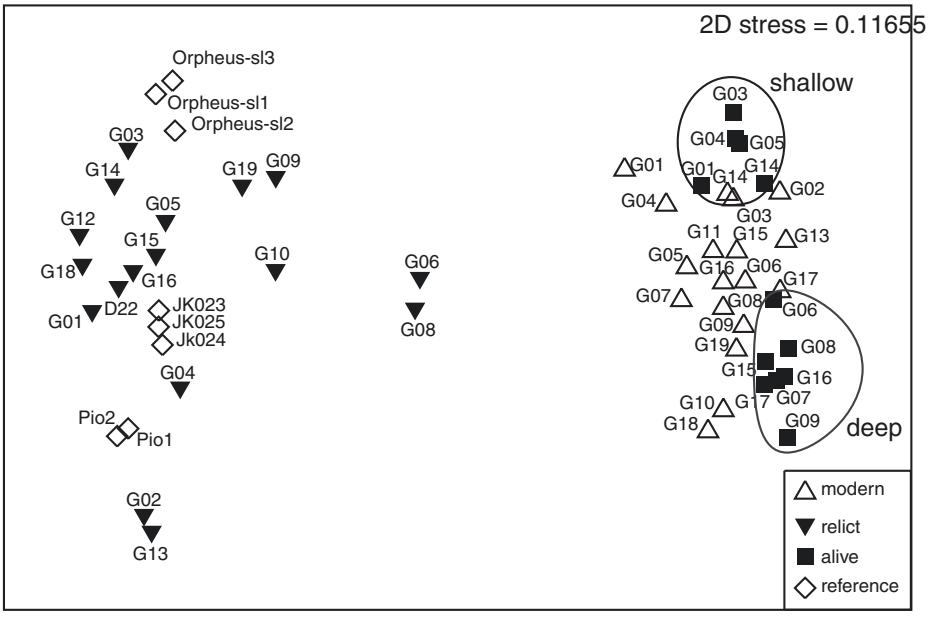


Fig. 4. NMDS ordination all samples containing more than 40 larger benthic foraminifera. The horizontal axis accounts for 68% of the variation in the data while the vertical axis accounts for 19%.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.marmicro.2013.03.002.

References

Abbey, E., Webster, J.M., Beaman, R.J., 2011. Geomorphology of submerged reefs on the shelf edge of the Great Barrier Reef: the influence of oscillating Pleistocene sea-levels. Marine Geology 288, 61–78.

Beaman, R.J., Bridge, T., Done, T., Webster, J.M., Williams, S., Pizarro, O., 2012. Habitats and benthos at Hydrographers Passage, Great Barrier Reef, Australia. In: Harris, P.T., Baker, E.K. (Eds.), Seafloor Geomorphology as Benthic Habitat: GeoHab Atlas of Seafloor Geomorphic Features and Benthic Habitats. Elsevier, Amsterdam, Netherlands, pp. 425–434.

Briguglio, A., Hohenegger, J., 2011. How to react to shallow water hydrodynamics: the larger benthic foraminifera solution. Marine Micropaleontology 81, 63–76.

Clarke, K.R., 1993. Non-parametric multivariate analysis of changes in community structure. Australian Journal of Ecology 18, 117–143.

Clarke, K.R., Somerfield, P.J., Gorley, R.N., 2008. Testing of null hypotheses in exploratory community analysis: similarity profiles and biota–environment linkage. Journal of Experimental Marine Biology and Ecology 366, 56–69.

Hallock, P., 1981. Production of carbonate sediments by selected large benthic foraminifera on two Pacific coral reefs. Journal of Sedimentary Petrology 51, 467–474.

Hallock, P., 1984. Distribution of selected species of living algal symbiont-bearing Foraminifera on two Pacific coral reefs. Journal of Foraminiferal Research 14, 250–261.

Hallock, P., Lidz, B.H., Cockey-Burkhard, E.M., Donnelly, K.B., 2003. Foraminifera as bioindicators in coral reef assessment and monitoring: the FORAM index. Environmental Monitoring and Assessment 81, 221–238.

Hohenegger, J., Yordanova, E., 2001. Displacement of larger foraminifera at the western slope of Motobu peninsula (Okinawa, Japan). Palaios 16, 53–72.

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

Hohenegger, J., Yordanova, E., Hatta, A., 2000. Remarks on West Pacific Nummulitidae (Foraminifera). Journal of Foraminiferal Research 30, 3–28.

Hottinger, L., 1977. Distribution of larger Peneroplidae, *Borelis* and Nummulitidae in the Gulf of Elat, Red Sea. Utrecht Micropaleontological Bulletins 15, 35–109.

James, N.P., Collins, L.B., Bone, Y., Hallock, P., 1999. Rottnest shelf to Ningaloo reef: cool-water to warm-water carbonate transition on the continental shelf of Western Australia. Journal of Sedimentary Research 69, 1297–1321.

Jorry, S.J., Hasler, C.A., Davaud, E., 2006. Hydrodynamic behaviour of *Nummulites*: implication for depositional models. Facies 52, 221–235.

Kidwell, S.M., 1991. The stratigraphy of shell concentrations. In: Allison, P.A., Briggs, D.E.G. (Eds.), Taphonomy: Releasing the Data Locked in the Fossil Record. Topics in Geobiology. Plenum press, pp. 211–290.

Kidwell, S.M., Flessa, K.W., 1996. The quality of the fossil record: populations, species and communities. Annual Review of Earth and Planetary Sciences 24, 433–464.

Li, Q., McGowran, B., James, N.P., Bone, Y., 1996. Foraminiferal biofacies on the mid-latitude Lincoln Shelf, South Australia: oceanographic and sedimentological implications. Marine Geology 129, 285–312.

Lobegeier, M.K., 2002. Benthic foraminifera of the family Calcarinidae from Green Island Reef, Great Barrier Reef Province. Journal of Foraminiferal Research 32, 201–216.

Martin, R.E., 1999. Taphonomy, a process approach. Cambridge Paleontology series 4. Cambridge University Press, Cambridge pp 508.

Murray, J.W., 1991. Ecology and paleoecology of benthic foraminifera. Longman Science and Technology, Essex. p 397.

Renema, W., 2002. Larger benthic foraminifera as environmental indicators. Scripta Geologica 124, 1–260.

Renema, 2006a. Large benthic foraminifera from the deep photic zone of a mixed siliciclastic-carbonate shelf off East Kalimantan, Indonesia. Marine Micropaleontology 58, 73–82.

Renema, W., 2006b. Habtat variables determining the occurrence of larger benthic foraminifera in the Berau area (East Kalimantan, Indonesia). Coral Reefs 25, 351–359.

Renema, 2010. Is increased calcarinid (foraminifera) abundance indicating a larger role for macro-algae in Indonesian Plio-Pleistocene coral reefs? Coral Reefs 29, 165–173.

Renema, W., Troelstra, S.R., 2001. Larger foraminifera distribution on a mesotrophic carbonate shelf in SW Sulawesi (Indonesia). Palaeogeography, Palaeoclimatology, Palaeoecology 175, 125–147.

Tudhope, A.W., Scoffin, T.P., 1988. The relative importance of benthic foraminiferans in the production of sediments on the central Queensland shelf. Proceedings of the Sixth International Coral Reef Symposium Australia, 2, pp. 583–588.

Uthicke, S., Patel, F.M., Ditchburn, R.G., 2012a. Elevated land runoff after European settlement perturbs persistent foraminiferal assemblages on the Great Barrier Reef. Ecology 93, 111–121.

Uthicke, S., Vogel, N., Doyle, J., Schmidt, C., Humphrey, C., 2012b. Interactive effects of climate change and eutrophication on the dinoflagellate-bearing benthic foraminifer *Marginopora vertebralis*. Coral Reefs 31, 401–414.

Webster, J.M., Yokoyama, Y., Cotterill, C., Expedition 325 Scientists, 2011. Proceedings of the Integrated Ocean Drilling Program, 325. http://dx.doi.org/10.2204/iodp.proc.325.2011.

Webster, J.M., Beaman, R.J., Puga-Bernabi, A., Ludman, D., Renema, W., Wust, R.A.J., George, N.P.J., Reimer, P.J., Jacobsen, G.E., Moss, P., 2012. Late Pleistocene history of turbidite sedimentation in a submarine canyon. Palaeogeography, Palaeoclimatology, Palaeoecology 331–332, 75–89.

Wilson, M.E.J., 2012. Equatorial carbonates: an earth systems approach. Sedimentology 59, 1–31.

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

Yokoyama, Y., Webster, J.M., Cotterill, C., Braga, J.C., Jovane, L., Mills, H., Morgan, S., Suzuki, A., Expedition 325 Scientists, 2011. IODP Expedition 325: Great Barrier Reefs reveals past sea-level, climate and environmental changes during the end of the last Ice age. Scientific Drilling 12, 32–45. http://dx.doi.org/10.2204/iodp.sd.12.04.2011.