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Dead shell assemblages faithfully record living molluscan assemblages at One Tree Reef

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ABSTRACT

Reef-associated sediments accumulate over time recording the history of biological communities. The agreement between live and dead assemblages has been extensively studied, because discrepancies between the two can reveal taphonomic bias, anthropogenic impact, and/or a decrease in temporal resolution of dead assemblages to centennial scales (i.e., time averaging). Given the potential of sedimentary assemblages to provide temporal perspectives on the history of modern communities, assessments of live-dead agreement in reef mollusk assemblage composition are necessary and timely for understanding rapid environmental change. One Tree Reef (OTR) (southern Great Barrier Reef, Australia) has had very little direct anthropogenic influence over the past four decades, making it a good system for focusing on taphonomic patterns. Live ($n = 1335$) and dead ($n = 6919$) molluscan assemblages were collected from three shallow (6 m) carbonate soft-sediment lagoons. Diversity and evenness metrics indicated no significant difference between the live and dead assemblages, and dead assemblage rank order abundance explains 82% of that of the live assemblage. Differences in composition were largely due to sample size, the low probability of sampling rare species and to a lesser degree differences in skeletal durability. Taphonomic factors were responsible for less than 20% of the differences in species composition between live and dead shell assemblages. The live molluscan assemblage sampled was similar to the live assemblage sampled 30 years ago. Given that time averaging is approximately 19 years in the OTR lagoon, we conclude that the composition of the living assemblage has remained largely unchanged for the last 30 years. These findings indicate that dead assemblages preserved in shallow, fully carbonate environments primarily reflect the composition of the original source communities, making them useful to identify recent changes in coral reef areas where anthropogenic impacts are present.

1. Introduction

Given the long history of human-mediated changes to tropical reef communities (Jackson, 1997; Jackson et al., 2001; Pandolfi et al., 2003), it is difficult to find a natural baseline against which to measure historical as well as future changes (Jackson et al., 2001; Kidwell, 2013). Ecological, historical, archaeological and paleoecological records have shown evidence of strong changes to coral reef ecosystem structure caused by even low levels of human influence (Jackson et al., 2001; Sandin et al., 2008; Roff et al., 2012). While data obtained by community ecologists provide quantitative information with more precision than archaeological or paleoecological records, they are restricted to the 20th century (Kosnik and Kowalewski, 2016). Therefore, in order to quantify and understand anthropogenic impacts on extant marine communities, community ecologists need to extract quantitative temporal information on community composition from dead and fossil assemblages (Dietl and Flessa, 2011; Kidwell and Tomašových, 2013; Dietl et al., 2015; Smith and Dietl, 2015; Kosnik and Kowalewski, 2016). Live assemblages (LAs) are typically sampled only once (or a few times), and are thus considered surrogates for the true source community from which the dead assemblages (DAs) derive (Tomašových and Kidwell, 2011). Changes in temporal and spatial scale affect the variability in live communities and the preservation of dead assemblages (Tomašových and Kidwell, 2010a, b). Therefore, comparing live and dead assemblages sampled at the same time requires accounting for biological, geological, physical and chemical processes. Firstly, biological processes such as recruitment pulses result in variable species composition (e.g. Powell et al., 1986) making LAs poor surrogates (Tomašových and Kidwell, 2011). Another biological phenomenon that can make LAs poor surrogates is lifespan bias (Van Valen, 1964; Kidwell and Rothfus, 2010). This bias occurs when there is an over representation of a species in a death assemblage because it is more productive, or its individuals have shorter life spans, relative to other species (Kidwell and Rothfus, 2010). This difference between the expected proportional abundance

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of a species in a death assemblage and its observed abundance in the live assemblage can thus explain some variations in relative species composition (Kidwell and Rothfus, 2010). Second, other biological factors that can result in variable preservation between species are certain morphological, mineralogical and shell-structural traits, or a combination of traits that may convey higher durability in the sediment (Glover and Kidwell, 1993; Lockwood and Work, 2006; Kosnik et al., 2009). When organisms die, biological processes such as bioturbation or bioerosion also affect preservation (Kiene and Hutchings, 1994; Roy et al., 1994; Lescinsky et al., 2002; Gordillo and Archuby, 2014). Physical factors such as sedimentation rate, wave energy, abrasion and fragmentation, chemical dissolution and cementation can also impact the formation of dead shell and fossil assemblages (Fürsich and Aberhan, 1990; Kidwell and Bosence, 1991; Pandolfi, 1992; Parsons-Hubbard et al., 1999; Powell et al., 2002, 2008, 2011). The nature of the sediment, whether it is carbonate or siliciclastic, also affects shell preservation (Best and Kidwell, 2000a, b). For example, studies in the Caribbean have found that bivalve shells are better preserved and show less damage in siliciclastic than in carbonate sediments (Best and Kidwell, 2000a, b). Thus, the preservation of live communities in dead shell assemblages will vary depending on species composition and biological processes, and the nature of the sediment and overall environment.

Carbonate sediments from One Tree Reef (southern Great Barrier Reef) have been recently found to be stratigraphically ordered, suggesting they are suitable to study temporal changes in biological communities (Kosnik et al., 2015). Sediment and molluscan shell obtained from a 1.2 m core indicate that the top meter of sediment preserves the last 600 years, while the taphonomically active zone (top 15 cm of sediment) preserves shells with a median age of ~10 years and 1σ time averaging of 19 years (Kosnik et al., 2015). While this stratigraphic record is ordered not all reef sediments are ordered (Kosnik et al., 2007, 2013), leading to disagreements over the use of reef-associated sediments to study long-term changes in communities. The fidelity of coral reef-associated death assemblages was an important point of contention following Walbran et al.'s (1989) historical analysis of *Acanthaster planci* outbreaks on the Great Barrier Reef (Fabricius and Fabricius, 1992; Keesing et al., 1992; Pandolfi, 1992). Doing a critical re-evaluation of the sedimentary record of population outbreaks of crown-of-thorns, Keesing et al. (1992) and Pandolfi (1992) point out that several assumptions in Walbran et al. (1989) overlook the importance of physical, biological and taphonomic processes that take place when sediments are accumulating. Keesing et al. (1992) and Pandolfi (1992) warrant that the lack of rigor in these assumptions may invalidate the patterns found by Walbran et al. (1989). This example illustrates the importance of adequately accounting for biological, physical and taphonomic biases. Given that directly comparing live and dead assemblages at a timescale appropriate to the time averaging in the death assemblage is not possible (live assemblages are typically sampled once or at a smaller timescale than the time averaging), the associated biases need to be quantified.

Mollusks are often used in paleobiological studies and they have been the subject of many studies comparing live and dead assemblages (e.g. Kidwell, 2001 and references therein; Zuschin and Oliver, 2003; Lockwood and Chastant, 2006; Zuschin and Stachowitsch, 2007; Tomašových and Kidwell, 2009; Albano and Sabelli, 2011; Feser and Miller, 2014; Korpanty and Kelley, 2014; Smith and Dietl, 2015). These invertebrates are an integral part of benthic reef ecosystems because they carry out important ecosystem functions such as nutrient cycling, particle filtering that contributes to water clarity, and energy transfer to benthic and larger pelagic predators in the trophic chain (Wilson, 1991; Snelgrove, 1999; Przeslawski et al., 2008). Given the relevance of these components of the soft sediment fauna, they can be indicative of future, broader implications for the overall functioning of reef ecosystems (Przeslawski et al., 2008).

An informative approach to look at and monitor temporal changes in molluscan faunas is to use mollusk dead shell assemblages (Kidwell, 2001, 2007, 2013). These assemblages can be defined as 'taxonomically identifiable empty shells that are collected from a standardized area or volume of seabed' (Kidwell, 2013). Extensive research by paleontologists in different marine environments has shown that the live-dead agreement between molluscan faunas has implications for conservation of marine and coastal environments (Kidwell, 2001, 2007, 2013; Kidwell and Tomašových, 2013; Dietl and Flessa, 2011; Dietl et al., 2015; Smith and Dietl, 2015). In particular, Kidwell (2007) found that DAs from areas with high anthropogenic impact (i.e. eutrophication) showed a higher disagreement with their live community relative to DAs from less impacted areas. Examples of similar live-dead studies for mollusks in reef communities are limited (e.g. Zuschin et al., 2000; Zuschin and Oliver, 2003; Zuschin and Stachowitsch, 2007; but see Greenstein and Pandolfi, 1997; Edinger et al., 2001 for corals) and there is none for the Great Barrier Reef.

Here, we quantify the agreement between live and dead assemblages in tropical reef sediments from One Tree Reef (OTR), southern Great Barrier Reef. OTR is a useful study system given that sediments are chronologically ordered and time averaging has been quantified (Kosnik et al., 2015). OTR is in a Scientific Research Zone within the Capricornia section of the Great Barrier Reef Marine Park. Located 100 km off the Queensland coast, it is relatively isolated and local anthropogenic impacts are limited to researchers at One Tree Island Research Station (established in 1974). In this context, the differences between the live and dead mollusk assemblages should be primarily driven by taphonomic rather than human factors if natural variation in molluscan communities is small. Otherwise, time averaging will also produce mismatch, even in the absence of any taphonomic bias. This live-dead study is the first of its kind for the Great Barrier Reef as well as for a relatively intact fully carbonate lagoon.

2. Materials and methods

2.1. Study area and sample processing

Sampling was carried out at One Tree Reef, southern Great Barrier Reef, Australia (23°20′ S, 152°06′ E, Fig. 1). The reef crest surrounds three soft sediment lagoons, of roughly 10–13 km^2 in area (Davies et al., 1976). Infauna were collected at three sites in each of the three lagoons. Sampling was carried out four times in 2012, totaling 36 samples. Some sites were re-sampled during subsequent sampling (see Table 1), but the same sediment was not recollected, so samples are considered to be independent. Sites with a low abundance of live mollusks were replaced by different ones during subsequent sampling trips (indicated by the different site numbers in Fig. 1). All sites ranged

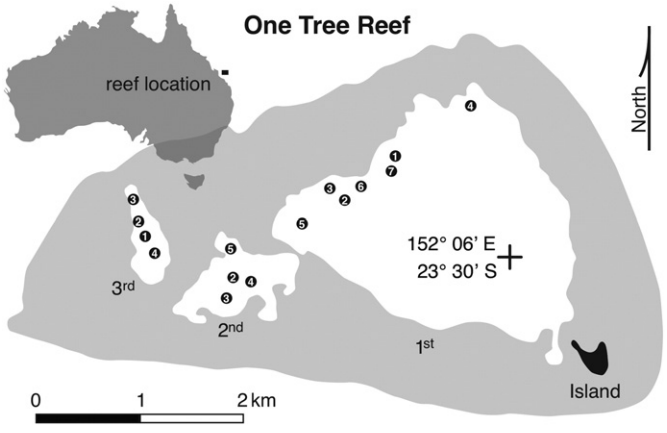

Fig. 1. Map of One Tree Reef, southern Great Barrier Reef. The reef area shaded gray is exposed during low tides, the three lagoons are in white, and One Tree Island in black. Site numbers inside each lagoon correspond to the samples listed in Table 1. Reef and lagoon outline were traced from Google Earth imagery.

Table 1
Details of samples used for analyses. Sample number, month of collection and replicates (processed quadrats) are indicated. Site names coincide with the ones in Fig. 1. The absolute abundance of live (L) and dead (D) individuals per site is presented, as well as species richness, Shannon diversity index and Pielous' evenness index.

Sample	Month	Site name	Geographic coordinates	Depth (m)	Quadrats processed	Abundance		Richness		Diversity		Evenness	
						L	D	L	D	L	D	L	D
1	Feb	3rd Lagoon 1	−23.50°, 152.05°	5.3	842,844,848	79	261	8	7	1.20	0.87	0.58	0.45
2	Feb	3rd Lagoon 2	−23.50°, 152.05°	5.9	850,852,854	35	390	6	20	1.36	1.35	0.76	0.45
3	Feb	3rd Lagoon 3	−23.50°, 152.05°	6	858,860	21	87	10	10	1.62	1.17	0.71	0.51
4	Feb	1st Lagoon 1	−23.49°, 152.07°	4.7	794,796,798,800	105	553	14	29	1.64	1.87	0.62	0.56
5	Feb	1st Lagoon 3	−23.49°, 152.07°	5.9	812,814,816	45	318	10	15	1.79	1.38	0.78	0.51
6	Feb	2nd Lagoon 2	−23.50°, 152.06°	4.9	826,828,830,832	67	285	18	22	2.26	2.06	0.78	0.67
7	Feb	2nd Lagoon 3	−23.50°, 152.06°	4.6	834,836,838,840	66	167	9	11	1.56	1.42	0.71	0.59
8	May	3rd Lagoon 2	−23.50°, 152.05°	5.9	948,952,954	43	847	7	22	1.67	1.38	0.86	0.45
9	May	1st Lagoon 1	−23.49°, 152.07°	4.7	916,918	82	293	7	22	0.78	2.14	0.40	0.69
10	May	2nd Lagoon 2	−23.50°, 152.06°	4.9	904	21	229	6	16	1.49	1.53	0.83	0.55
11	May	2nd Lagoon 3	−23.50°, 152.06°	4.6	932,934,936	82	329	12	8	1.77	0.97	0.71	0.47
12	Sep	3rd Lagoon 1	−23.50°, 152.05°	5.3	1002	29	35	5	5	1.26	1.57	0.79	0.98
13	Sep	1st Lagoon 5	−23.49°, 152.07°	4.5	956,962	37	185	9	9	1.21	1.70	0.55	0.77
14	Sep	1st Lagoon 6	−23.49°, 152.07°	5.3	968,970	47	127	8	11	0.91	1.22	0.44	0.51
15	Sep	1st Lagoon 7	−23.49°, 152.07°	4.3	974,976	95	100	6	11	0.70	1.49	0.39	0.62
16	Sep	2nd Lagoon 2	−23.50°, 152.06°	4.9	982,984	21	189	7	10	1.79	1.53	0.92	0.66
17	Sep	2nd Lagoon 3	−23.50°, 152.06°	4.6	1024,1026	36	219	6	9	1.23	1.32	0.69	0.60
18	Sep	2nd Lagoon 5	−23.50°, 152.06°	5	988,990	64	221	10	15	1.69	1.46	0.73	0.54
19	Nov	3rd Lagoon 1	−23.50°, 152.05°	5.3	1126,1130	63	487	10	22	1.51	1.52	0.66	0.49
20	Nov	1st Lagoon 5	−23.49°, 152.07°	4.5	1118,1120	39	128	2	8	0.38	1.47	0.55	0.71
21	Nov	3rd Lagoon 3	−23.50°, 152.05°	6	1142,1146	48	483	9	14	1.62	1.48	0.74	0.56
22	Nov	1st Lagoon 1	−23.49°, 152.07°	4.7	1100,1104	37	109	4	13	0.54	1.74	0.39	0.68
23	Nov	1st Lagoon 2	−23.49°, 152.07°	4.9	1108,1114	52	175	12	19	1.38	1.71	0.55	0.58
24	Nov	2nd Lagoon 2	−23.50°, 152.06°	4.9	1156,1162	39	220	10	8	1.54	1.33	0.67	0.64
25	Nov	2nd Lagoon 3	−23.50°, 152.06°	4.6	1148,1152	48	183	11	8	1.70	1.26	0.71	0.61
26	Nov	2nd Lagoon 5	−23.50°, 152.06°	5	1168,1170	34	299	7	18	1.15	1.40	0.59	0.48

between 4.3 to 6.1 m ponded depth. For each sample, divers used an 80 mm diameter air-lift and 1 mm mesh bags to collect the top 0.1 m of sediment of four 0.25 m^2 quadrats.

Some previous studies (e.g. Kidwell, 2001) used 2 mm sieves for mollusk live-dead comparisons, but we used the molluscan material retained by a 4 mm sieve because we observed juvenile recruitment pulses in the 2 mm sieve fractions and reduced confidence in our ability to consistently identify all living individuals in <4 mm sieve fractions. Transitory settlement events distract from our focus on the live-dead agreement between samples, and the comparability with the fossil record (Kidwell, 2001). In addition, sampling juveniles makes identification more difficult as sometimes they can be confounded with micromollusks. Because live faunal abundance is the limiting factor for live-dead comparisons, samples with fewer than 20 living individuals were not included in the analyses. The abundance of live mollusks was variable between samples, so we processed between one and four replicate quadrats to meet the minimum of 20-live-collected individuals per sample (replicate quadrats used per sample are indicated in Table 1). We ran initial analyses comparing abundance and diversity of mollusks between sampling months and sampling lagoons. Because we found no effects of seasonality or lagoon (see SOM), we pooled all the live-collected replicate quadrats for each sample, and did the same with the dead shells from the matching quadrats and samples. The total number of samples analyzed was 26 (Table 1).

2.2. Species identification

We used published literature (Lamprell and Whitehead, 1992; Lamprell and Healy, 1998), the Australian Museums' Malacology collections, and help from mollusk taxonomists to identify individual shells to the species level. Once species were identified, individuals from bivalve and gastropod species were counted. For bivalves, the minimum number of individuals was estimated as the number of articulated valves plus the total number of right valves. Because mollusks were very abundant in the samples, we did not include fragmented shells to increase numbers of individuals.

2.3. Abundance and diversity metrics

Species relative abundances per sample were calculated for live assemblages (LAs) and dead shell assemblages (DAs) to test for a live-dead agreement at site and regional scales (i.e. pooled bivalves and gastropods from all sites). High live-dead agreement is indicated by species plotting along a 1:1 line in a bivariate plot of live versus dead relative abundance (e.g. Kidwell, 2007; Tomašových and Kidwell, 2011, see Fig. 2). Dead relative abundance (dependent variable) was

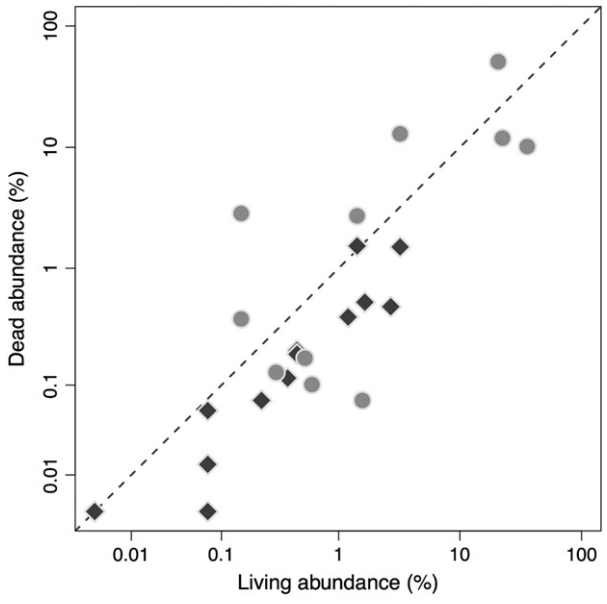

Fig. 2. Species relative abundance in dead shell assemblages (DAs) as a function of relative abundances in live assemblages (LAs). Dark gray circles represent bivalve species and light gray diamonds represent gastropod species. The dashed line indicates a 1:1 relationship between DAs and LAs relative abundance.

regressed on live relative abundance (independent variable) for a) the total relative abundance, b) the relative abundance of bivalves, and c) the relative abundance of gastropods. To test if the slopes of those regressions were significantly different from 1 we calculated the upper and lower confidence intervals. If a slope of 1 fell within the confidence intervals we assumed that differences were not significant. The residuals for the regression with the total relative abundances were inspected to identify potential outliers. Species were considered outliers if they had a very high abundance in the dead assemblage and were absent or had low abundances in the living assemblage.

Different diversity indices were used to determine live-dead agreement. We calculated Shannon's diversity index (Shannon and Weaver, 1963), Pielou's evenness index (Pielou, 1966), and Chao's Jaccard similarity index (Chao et al., 2005). Chao's Jaccard index includes the effect of species that are shared but unseen (either because they are rare or because the samples that are being compared have substantial differences in size such as these live-dead assemblages). By accounting for unseen species, this estimator is less biased than the classic Jaccard index that is only based on presence-absence data (Chao et al., 2005). Lastly, we used Spearman rank order correlation of species relative abundance as an indicator of similarity between LAs and DAs (e.g. Kidwell, 2001). Chao's Jaccard similarity index and Spearman's rank order correlation are typically plotted on bivariate plots to represent compositional and abundance similarity in the live and dead assemblages. In this plot, sites located in the upper right hand quadrant have the highest live-dead agreement and sites in the lower left hand quadrant have the lowest live-dead agreement (Kidwell, 2007). Samples with fewer than five live individuals or fewer than two species were excluded from these analyses (Zuschin and Ebner, 2015). Indices were calculated with the 'diversity' and 'chao.jaccard' functions, in the 'vegan' and 'fossil' packages in the statistical programming language R (Version 3.1.2; R Core Team, 2014).

Rarefaction analyses were carried out to further compare diversity in the live and dead assemblages. A rarefied value of richness was calculated for every site from the live and dead assemblages and compared with the observed value of richness in the same sites. By standardizing for a set sample size (the smallest for the live and dead respectively), rarefaction allowed for meaningful comparison between datasets (Gotelli and Colwell, 2001). Species rarefaction curves were also done at the site level for live and dead assemblages. Rarefied richness was calculated with the 'rarefy' function that uses the formulation by Hurlbert (1971). Rarefaction curves were done using the 'rarecurve' function; both functions used are in the 'vegan' package in the statistical programming language R (Version 3.1.2; R Core Team, 2014).

Species rank abundance plots are also good descriptors of communities (McGill et al., 2007). Several theories and models have been proposed to explain the different shape of rank abundance plots in communities (see McGill et al., 2007 for a review). Here we fit five of these models (Broken stick, Pre-emption, log-Normal, Zipf and Zipf-Mandelbrot) to the rank abundance orders of the live and dead assemblages to determine the best fit model for each dataset. The best model was chosen based on at least a two-point difference in Akaike Information Criterion (AIC). We carried out these analyses with the 'radfit' function in the 'vegan' package in the statistical programming language R (Version 3.1.2; R Core Team, 2014).

2.4. Live-dead agreement and spatial ordination

A non-metric multidimensional scaling (NMDS) plot was used to visually assess the similarity between live and dead assemblages in a multidimensional space. Each DA was resampled without replacement to the size of its corresponding LA. These absolute abundances were square-root transformed and Bray-Curtis dissimilarity was used. An overlap in the plotting of the live and dead assemblages is an indicator of compositional similarity. The rarefaction of the DAs was done using the 'rarefy' function in the 'vegan' package in the statistical programming language R, while the NMDS was done using the 'metaMDS' function also in the 'vegan' package in R (Version 3.1.2; R Core Team, 2014).

2.5. Live-dead agreement and temporal autocorrelation

Given that the median age of *Abranda* shells from the taphonomically active zone was less than 10 years (Kosnik et al., 2015), it is highly likely that LAs and DAs are temporally autocorrelated. Therefore, we complement univariate metrics with a method developed by Tomašových and Kidwell (2011) that accounts for temporal autocorrelation in live-dead assemblages. By accounting for temporal autocorrelation, this method allows for the deconstruction of live-dead variation into pre-mortem and post-mortem components. Examples of pre-mortem processes (inherent to live communities) are biological and sampling biases such as demographic stochasticity, migration rates, and sampling effects (Powell et al., 1986; Lande, 1993; Moore et al., 2007). Examples of post-mortem processes are differences in population turnover (recruitment) and preservation rates between species.

The approach developed by Tomašových and Kidwell (2011) is based on a modification of HMD (homogeneity of multivariate dispersions), a non-parametric method that looks for differences in the multivariate dispersions among groups (Anderson, 2006). The method assumes that the sampled LAs are equivalent to the source live communities (at larger spatial scales), and that the dispersion based on replicate LAs accounts for biological stochasticity. This dispersion delimits the bounds for the compositional variation that can be expected among DAs if there are no post-mortem effects. The total live-dead variation is thus the average distance among individual DAs and the centroid of LAs. The post-mortem variation not explained by variation among LAs is the average distance between LAs and their centroid (the pre-mortem variation) minus the average distance among DAs and the centroid of LAs. The average distance among DAs and the centroid of LAs measures over- or under-dispersion of DAs relative to the composition of LAs. Under-dispersion of DAs indicates a loss of variation compared with that of LAs. Over-dispersion of DAs indicates that DAs occupy portions of multivariate space outside those occupied by LAs (Tomašových and Kidwell, 2011). The significance of this over- and under-dispersions is evaluated by a p value that determines if DAs are significantly more or less dispersed relative to the centroid of LAs than are LAs.

We carried out these live-dead agreement analyses with different grouping possibilities for our samples to make sure over- and under-dispersion patterns were consistent at different spatial scales. For example, we conducted the analyses using 26 samples collected at small spatial scales but we also grouped the samples from each lagoon together (three larger samples) to validate our results at different spatial scales. All analyses were carried out using the 'vegan' and 'ade4' packages in the statistical programming language R (Version 3.1.2; R Core Team, 2014). The distance metric used was Horn-Morisita following Tomašových and Kidwell (2011); the R script used for these analyses was provided by Adam Tomašových.

3. Results

3.1. Abundance and diversity metrics

The 26 samples analyzed yielded LAs comprised of 1335 live-collected individuals representing 37 species, and DAs comprised of 6919 shells without live mollusks representing 55 species (Table 1). There was a combined richness of 68 species, of which 24 were found both in live and dead assemblages.

Univariate raw unstandardized diversity metrics were not significantly different between LAs and DAs (Table 1). Species richness was not significantly different (Kruskal-Wallis rank sum test, $\chi^2 = 13.57$, $p = 0.48$), neither were Shannon's or Pielou's diversity indices

(Kruskal-Wallis rank sum test, $\chi^2 = 25$, $p = 0.46$ for both tests). In addition, species relative abundances in live and dead assemblages showed a significant positive rank correlation (Spearman correlation, rho = 0.82, $p < 0.001$, Fig. 2). Linear models also indicated that abundances of species collected alive were significant predictors of the species relative abundance in dead assemblages for the total assemblage (adjusted $R^2 = 0.66$, $F = 50$, $p < 0.001$), bivalves (adjusted $R^2 = 0.45$, $F = 9.17$, $p = 0.01$), and gastropods (adjusted $R^2 = 0.87$, $F = 93.16$, $p < 0.001$). Confidence intervals also indicated that slopes were not significantly different from 1 for the total assemblage (lower CI = 0.82, upper CI = 1.49), bivalves (lower CI = 0.21, upper CI = 1.44), and gastropods (lower CI = 0.74, upper CI = 1.72). Chao's Jaccard index for median compositional similarity between live and dead shell assemblages was 0.89 for the total assemblage (n sites = 26), 0.92 for bivalves (n sites = 26), 0.53 for gastropods (n sites = 17). Moreover, a visual inspection of the bivariate plot with Chao's Jaccard similarity index and Spearman's rho shows that 92% of the sites fall in the upper right hand quadrant, indicating that live-dead agreement is high (Kidwell, 2007, Fig. 3, Table 2). Significance for Spearman rank correlations for total individuals, bivalves and gastropods per site are shown in Table 2.

Rarefaction analyses indicated that observed richness was lower than expected richness for both live and dead shell assemblages, and that it was generally lower for the latter (Fig. 4A, B).

3.2. Species composition of LAs and DAs

Two thirds of the species found alive were also present in DAs (Table 3). Of the missing taxa, 85% were singletons in the live community (yielding an expectation of approximately five individuals in the dead assemblage: 1335 live/6919 dead = 0.19), and the other 15% had fewer than five live individuals (yielding an expectation of fewer than 15 individuals in the dead assemblage). It is worth pointing out that some of the live singletons missing from the dead assemblage had particularly fragile shells (e.g. Pinnid indet.) or fragile shells and chemoautotrophic life habit (*Solemya* indet.). The other two non-singleton taxa missing from the DAs were a tellinid bivalve that could have been misidentified, and *Atys cylindricum* (Haminoeidae), a very thin-shelled bubble snail. Despite these particular cases, our results suggest that sampling probability of rare species is the main reason for these disagreements between live and dead assemblages (Table 3).

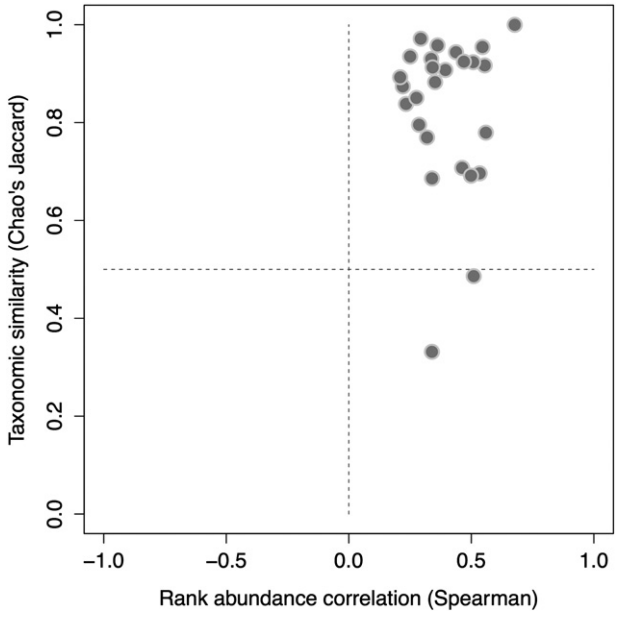

Fig. 3. Bivariate plot of taxonomic similarity (Chao's Jaccard) and rank-order correlation of relative abundances (Spearmans' rho) for bivalves and gastropods in the live and dead assemblages from One Tree Reef, southern Great Barrier Reef. Sites located in the upper right hand quadrant have the highest live-dead agreement and the two sites in the lower left hand quadrant have the lowest live-dead agreement (Sites 2 and 10, see Tables 1 and 2).

Table 2
Spearman rho for rank order correlations and Chao's Jaccard similarity index for total assemblages, bivalves and gastropods respectively. Values in bold indicate significant correlations.

Sample	Total assemblage		Bivalves		Gastropods	
	Spearman's rho	Chao's J	Spearman's rho	Chao's J	Spearman's rho	Chao's J
1	**0.437**	0.943	**0.525**	0.958	–	–
2	**0.339**	0.331	0.323	0.348	–	–
3	**0.394**	0.907	**0.347**	0.931	**0.427**	0.396
4	0.233	0.838	0.312	0.823	–	–
5	0.220	0.874	0.206	0.920	–	–
6	**0.362**	0.957	**0.501**	0.968	–	–
7	**0.545**	0.954	**0.418**	0.917	**0.782**	0.722
8	**0.250**	0.935	**0.349**	0.913	0.186	0.837
9	**0.339**	0.685	0.285	0.744	**0.366**	0.307
10	**0.509**	0.486	**0.364**	0.445	**0.611**	0.705
11	**0.336**	0.930	0.282	0.898	**0.355**	0.717
12	**0.554**	0.916	**0.404**	0.955	**0.421**	0.724
13	**0.275**	0.850	**0.453**	0.937	0.242	0.489
14	**0.286**	0.795	**0.415**	0.918	–	–
15	**0.534**	0.696	**0.765**	0.810	**0.373**	0.412
16	**0.319**	0.769	**0.476**	0.786	0.133	0.421
17	**0.507**	0.923	**0.552**	0.949	**0.343**	0.292
18	**0.293**	0.971	**0.528**	0.996	−0.097	0.000
19	**0.469**	0.924	**0.674**	0.976	–	–
20	**0.677**	0.999	**0.590**	0.996	–	–
21	**0.462**	0.707	**0.603**	0.708	**0.335**	0.664
22	**0.498**	0.691	**0.474**	0.431	**0.530**	0.450
23	**0.342**	0.912	**0.483**	0.911	0.257	0.613
24	**0.559**	0.779	**0.502**	0.528	**0.630**	0.856
25	**0.352**	0.882	**0.527**	0.919	0.291	0.529
26	0.209	0.892	0.271	0.865	–	–

Approximately 44% of the species from the dead assemblages were found alive. Of the dead species missing from live assemblages 32% were singletons meaning that even in the dead assemblage they each had a sampling probability of 1 in 6919, so we only expect to sample 0.19 of an individual from a live collected sample of 1335 individuals. An additional 48% had fewer than five individuals (an expectation of sampling approximately one live individual), and only 20% had an expectation of sampling as many as 10 live individuals (still expected to be fewer than 1% of the live fauna). All of the missing species are rare. Using the proportion of sum definition of rarity (abundances fewer than x% of the summed abundances of all species in the assemblage, Gaston, 1994), none of the species missing from the live community had a proportional abundance in the dead assemblage higher than 0.8%. This finding is not surprising given that very high numbers of rare taxa have also been found in DAs from other tropical molluscan communities (e.g. Bouchet et al., 2002; Zuschin and Graham Oliver, 2005).

Only two species present in both live and dead assemblages were found to be outliers in the regression models. These species had notably different live and dead relative abundances, and this was the case both for the pooled assemblage and for the assemblage from each individual lagoon. The first species, *Abranda jeanae* was more abundant than expected in the living community (Table 3), particularly in First Lagoon. We found three times more live individuals than expected based on their abundance in the death assemblage (136 predicted live based on dead vs. 478 found live). The second species, *Ctena bella* was more abundant in the dead assemblage than in the live community (Table 3), particularly in Second Lagoon. We found 5% of the expected number of live *Ctena bella* based on their abundance in the death assemblage (38 predicted live based on dead vs. 2 found live).

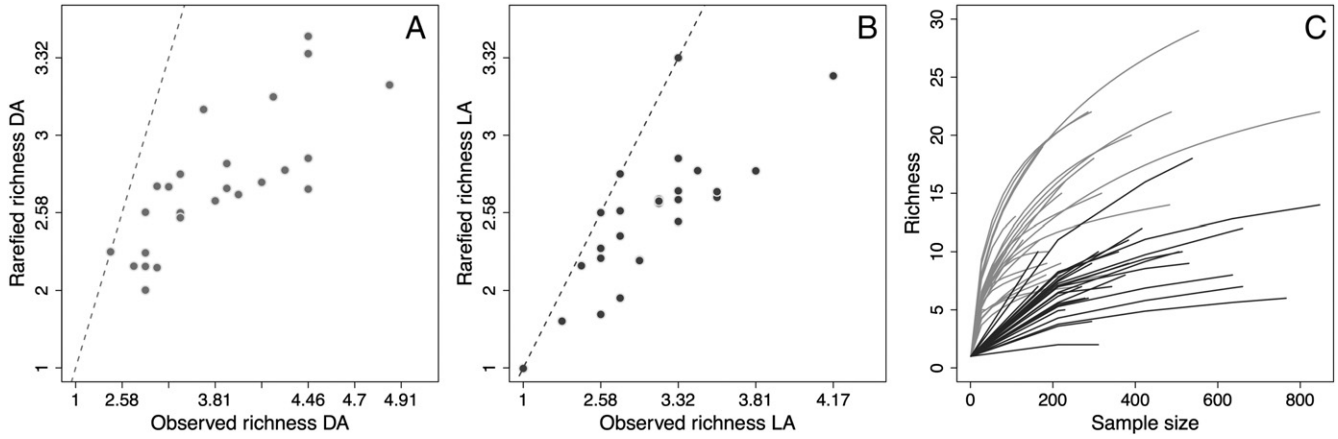

Fig. 4. Bivariate plots showing observed species richness and rarefied species richness for (A) dead assemblages, and (B) live assemblages. Species rarefaction curves (C) show the rarefaction curve for each site for dead assemblages (light gray) and live assemblages (dark gray).

3.3. Rank abundance distributions

Species rank abundance distributions for LAs and DAs were best explained by Zipf-Mandelbrot models, as indicated by AIC (Table 4A, B, Fig. 5A, B). The main difference between the three model parameters between LAs and DAs was observed for parameter 1, which represents the fitted abundance of the most abundant species (Wilson, 1991). This parameter had a higher value for LAs (compare the position of the three dominant species from Fig. 5A to those in Fig. 5B, Table 4A). The other two model parameters (2 and 3 in Table 4) can be interpreted as parameters β and γ in the original model (Wilson, 1991). β represents the potential niche diversity of the environment, and a positive β results in greater evenness among the most abundant species (Frontier, 1985 in Wilson, 1991). The parameter γ represent the average probability of the appearance of a species, with values close to 1 indicating greater evenness (Frontier, 1985 in Wilson, 1991). Differences in these parameters between the live community and the dead assemblage indicate that the dead assemblage has greater evenness because γ (parameter 3) is closer to 1 (1.47 dead vs. 3.96 live, Table 4A and B), and β (parameter 2) is less negative than for the live community (−2.66 dead vs. −3.46 live, Table 4A and B).

3.4. Live-dead agreement and spatial ordination

The NMDS plot shows that DAs and LAs overlap in a two-dimensional space (Fig. 6), indicating compositional similarity. The associated stress value for LAs NMDS was 0.14 while the one for DAs was 0.22.

3.5. Live-dead agreement and temporal correlation

Species composition in the 26 live and dead assemblages analyzed was not significantly different (Test of homogeneity of multivariate dispersions, $p = 0.43$). The homogeneity of dispersions test used takes into account the temporal autocorrelation between LAs and DAs instead of assuming (such as metrics used previously do) that they are independent. To compare species composition, the mean composition of the source LAs (or centroid in a multivariate space) is considered to be the same as the one of the LAs that gave rise to the dead assemblages (Tomašových and Kidwell, 2011). A non-significant p value indicated that the variation among DAs and the LAs centroid was not significantly different from variation among LAs and their centroid. Thus, neither pre-mortem nor post-mortem processes dominated.

The magnitude of total live-dead variation (mean distance between each DA and the LAs centroid) in the 26 assemblages was 0.38 (Fig. 7A). From this total, the magnitude of pre-mortem variation (mean distance between each LA to the LAs centroid) was 0.35 (Fig. 7B) and the magnitude of total post-mortem variation (Pre-mortem variation - Total variation) was 0.03 (Fig. 7C). So, while the variation among the LAs and DAs was not significantly different, variability in LAs contributes more to the total live-dead variation than the variability in the DAs. Analyses using data pooled at the lagoon level yielded no notable difference from those conducted at the sample level.

4. Discussion

The weak differences in diversity, species composition and in the shape of rank abundance distributions indicate that DAs in fully carbonate lagoons preserve LAs with high fidelity. The observed differences are attributable to sample sizes, sampling probability of rare species and the time-averaged nature of the DAs (even if over a short time period). Species present in both assemblages had very similar live and dead abundances, with the exception of two species that were identified as outliers in the residuals of the linear regression models. Similarly, analyses accounting for temporal autocorrelation indicated non-significant differences in species composition of live and dead assemblages. These findings in general are consistent with other contributions and meta-analysis from non-reef, sea-grass associated, and other soft sediment areas (Albano and Sabelli, 2011; Albano et al., 2016; Feser and Miller, 2014; Kidwell, 2001, 2013; Korpanty and Kelley, 2014; Zuschin and Ebner, 2015); and they also strengthen previously documented contrasts with rocky reefs and hard-bottom environments (Archuby et al., 2015; Zuschin et al., 2000; Zuschin and Oliver, 2003; Zuschin and Stachowitsch, 2007) that show lower live-dead agreement. Our study from a low-impacted, fully carbonate lagoon shows that these environments preserve with high fidelity the composition of soft sediment molluscan communities.

4.1. Compositional differences between live and dead assemblages

Species that were found both in LAs and DAs showed agreement in relative abundance with the exception of *Abranda jeanae* and *Ctena bella*. For these species, the differences in abundances between LAs and DAs are likely due to morphological traits that affect their preservation potential (e.g. Kosnik et al., 2009). One of these traits is thickness, as thicker shells need more force to break (Zuschin and Stanton, 2001). *Abranda jeanae* (overly represented in LAs relative to its dead abundance) has a median size of 122 mm and a median thickness of 0.17 mm ($n = 196$), suggesting a low preservation potential. On the contrary, *C. bella* (poorly represented in LAs relative to its dead abundance) has a median size of 38.43 mm and a median thickness of 0.48 mm ($n = 127$), suggesting a higher preservation potential. Despite being smaller, *C. bella* shells are much thicker possibly conferring

Table 3
Species composition, absolute and relative abundances in living and dead shell assemblages from One Tree Reef. Species also present in the Jones et al. (1990) dataset are indicated with an 'X'.

Gastropoda	Absolute abundance		Present in Jones et al. (1990)
	Dead	Live	
Acteonidae			
Pupa nitidula	106	19	X
Pupa sulcata	1	1	X
Architectonicidae			
Architectonicidae indet.	0	1	
Cerithiidae			
Rhinoclavis fasciata	0	1	X
Cerithium indet. 1	1	0	
Cerithium indet. 2	0	1	
Cerithiidae indet. 1	43	0	
Columbellidae			
Mitrella ligula	27	16	X
Costellariidae			
Costellariidae indet.	1	1	
Eucyclidae			
Herpetopoma atrata	3	0	
Herpetotoma aspersa	4	0	
Epitoniidae			
Epitonium philippinarum	0	1	
Fissurellidae			
Emarginula indet.	13	0	
Fissurellidae indet.	15	0	
Haliotidae			
Haliotis indet.	4	0	
Haminoeidae			
Atys cylindricum	0	3	X
Atys hyalina	104	43	
Atys naucum	6	3	
Liloa indet.	1	0	
Nassaridae			
Nassarius (*Zeuxis*) *bicallosus*	33	36	
Nassarius cf. *estilbus*	14	6	X
Naticidae			
Natica (*Naticarius*) *onca*	4	0	X
Notocochlis gualtieriana	36	22	X
Polinices mammilla	13	6	X
Tectonatica bougei	4	0	
Ranellidae			
Gyrineum lacunatum	3	0	
Strombidae			
Strombus gibberulus	1	1	X
Terebridae			
Terebridae indet.	1	0	
Turbinidae			
Astralium indet.	1	0	
Triviidae			
Trivia (*Trivirostra*) *oryza*	4	0	
Trochidae			
Ethalia guamensis	4	1	X
Stomatella indet.	1	0	
Trochidae indet.	1	0	
Turridae			
Lophiotoma acuta	8	5	X
Gastropoda indet. 1	3	0	
Gastropoda indet. 2	1	0	
Gastropoda indet. 3	2	0	

Bivalvia	Dead	Live	Present in Jones et al. (1990)
Arcidae			
Barbatia indet.	2	0	
Cardidae			
Fragum fragum	188	19	X
Fulvia indet.	0	1	X
Microfragum festivum	26	2	
Nemocardium indet.	3	0	
Galeommatidae			
Ambuscintilla praemium	9	4	
Marikellia indet.	4	0	
Lucinidae			
Cavatidens omissa	0	1	X
Ctena bella	197	2	

Table 3 (*continued*)

Bivalvia	Dead	Live	Present in Jones et al. (1990)
Wallucina fijiensis	10	0	
Mytilidae			
Brachidontes indet.	3	0	
Pinnidae			
Pinnid indet.	0	1	
Solemyidae			
Solemya indet.	0	1	X
Tellinidae			
Abranda jeanae	703	477	X
Cadella semen	0	1	X
Loxoglypta clathrata	825	299	X
Loxoglypta virgulata	7	8	X
Pinguitellina robusta	3515	276	X
Scissulina dispar	894	43	X
Tellina (*Quadrans*) *gargadia*	25	0	X
Tellina fijiensis	20	0	
Tellina indet. 1	0	1	
Tellina virgata	5	21	
Tellinidae indet. 1	0	3	
Veneridae			
Callista (*Striacallista*) *phasianella*	12	7	X
Dosinia amphidesmoides	1	0	X
Pitar (*Pitarina*) indet.	1	0	
Venerid indet. 1	1	0	
Venerid indet. 2	0	1	
Venerid indet. 3	3	0	
Bivalvia indet.	2	0	

greater durability relative to translucently thin *A. jeanae* shells; supporting the idea that morphological traits are important predictors of preservation potential in reef sediments (Kosnik et al., 2007; Kosnik et al., 2009).

Despite the potential biases associated with shell size and durability in DAs, we omitted small individuals (<4 mm) and shell fragments in the analyses. These omissions could affect fidelity between DAs and LAs. For example, DAs typically have higher richness than LAs but we did not find that in OTR shell assemblages. Perhaps if smaller individuals and shell fragments were included, DA richness would have been higher. Studies in tropical environments have found high mollusk diversity in small size fractions (Bouchet et al., 2002) therefore we cannot rule out the possibility that a part of the mollusk fauna went undetected. However, while processing samples we noticed that the large majority of individuals in the 2 mm size fraction were juveniles of species in the 4 mm size fraction rather than additional species. Moreover, Jones et al. (1990) used a 1 mm mesh size to study population dynamics of mollusk species at One Tree Reef. As indicated by their qualitative data (presented in Table 3), the species composition captured with a 1 mm sieve is not overly different from the species composition obtained with a 4 mm sieve. Therefore it is unlikely that sieve size significantly affected the fidelity between LAs and DAs. The other element we omitted from the individual counts were shell fragments. Fragments are an informative component of dead shell assemblages as they provide information about delicate specimens that are rarely preserved whole. Our samples are dominated by tellinid shells that are fragile and can be fragmented as a result of sampling procedures (airlift) and also by post-collection fragmentation (Flessa et al., 1992). The compacting of samples and its transportation from the collection place (OTR) to final destination (Sydney) usually took a few weeks and given the fragility of tellinid shells it is likely that some of them were broken. Despite this, thousands of fragile tellinid shells were sampled, transported and processed without suffering any breakage. Even if the omission of fragments can lead to missing fragile specimens (Zuschin et al., 2003) and lead to a reduction in the scale of time averaging captured, our sample sizes are very large and shells that were broken were also found whole, suggesting it is unlikely we missed a large percentage of the mollusk fauna by omitting fragments. In general, all the diversity and community level results indicate that LAs and DAs are remarkably similar making it unlikely that the addition of shell fragments or smaller individuals would significantly alter the results.

Other sources of disagreement between LAs and DAs are biological processes such as variations in recruitment pulses, lifespan bias and bioturbation by surrounding fauna. Recruitment pulses were partly accounted for – at least the pulses previous to the sampling months – because we avoided the juvenile size fraction. If the different species that contribute to the formation of a DA have different life spans, then species with short life spans are expected to be overrepresented in DAs. This expected overrepresentation is termed life span bias (Kidwell and Rothfus, 2010) and it can be calculated as the difference between the expected relative abundance of a species in a DA and its observed relative abundance in the LA. Of the species present in the samples, the two that differed in their live and dead abundances were *Abranda jeanae* and *Ctena bella*. Life span information is unfortunately not available for the species so we cannot calculate expected relative

Table 4
Model fit results from the 'radfit' function for the (A) live and (B) dead assemblages. The parameters for the five different fitted models are shown. Decreasing AIC values provide support to the Zipf-Mandelbrot model.

A) Live

Model	Parameter 1	Parameter 2	Parameter 3	AIC
Null	–	–	–	1728.99
Preemption	0.294	–	–	464.93
Lognormal	1.591	2.179	–	390.94
Zipf	0.474	−1.590	–	440.40
Zipf - Mandelbrot	99.861	−3.459	3.967	274.11

B) Dead

Model	Parameter 1	Parameter 2	Parameter 3	AIC
Null	–	–	–	13,900.67
Preemption	0.324	–	–	2698.36
Lognormal	1.676	2.762	–	791.54
Zipf	0.546	−1.800	–	949.63
Zipf - Mandelbrot	5.379	−2.664	1.467	672.65

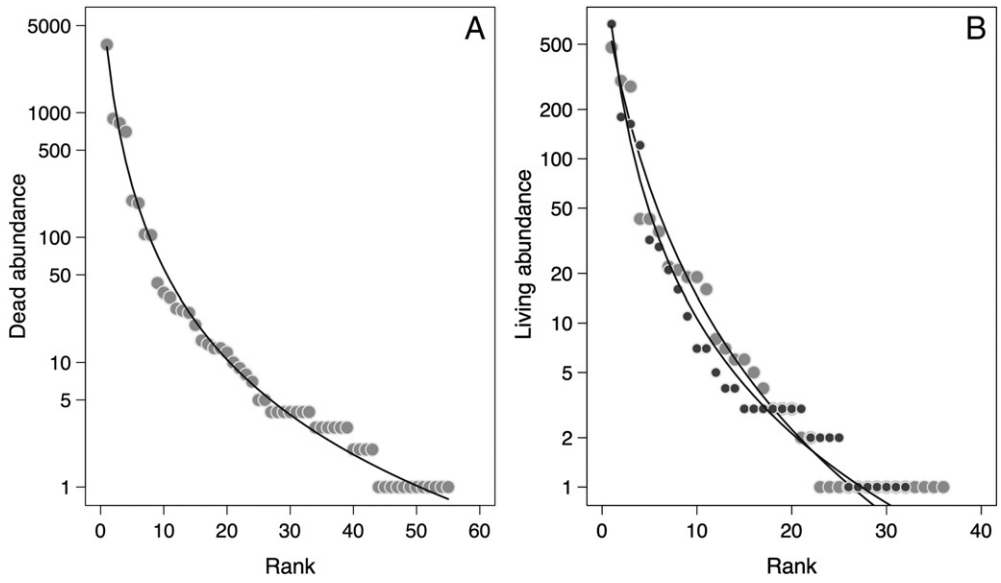

Fig. 5. Rank abundance distribution for (A) dead assemblages, and (B) live assemblages. Dead assemblages were resampled to total live assemblage abundance (1300) and the corresponding rank abundance distribution is plotted over (B) in smaller dark gray circles. Black lines indicated best fit abundance distribution model (Zipf-Mandelbrot, see Table 4 for model parameters).

abundance in DAs. However, a meta-analysis looking at the influence of life span affecting the preservation of bivalve relative abundances in DAs found that ecological and taphonomic factors are more important than life span/mortality in preserving abundance information (Kidwell and Rothfus, 2010). Thus, as discussed above, the morphological characteristics of these species that likely confer different preservation potential in DAs probably explain deviations from expected relative abundances more than life span bias. Lastly, a stratigraphically ordered sediment at OTR (Kosnik et al., 2015), together with our personal observations of the underwater environment indicate that bioturbation by callianassid shrimp is low (Kosnik et al., 2015). Differential preservation due to macrobioerosion is probably minimal because bioeroders such as clionid sponges were not observed in shells from the dead assemblage.

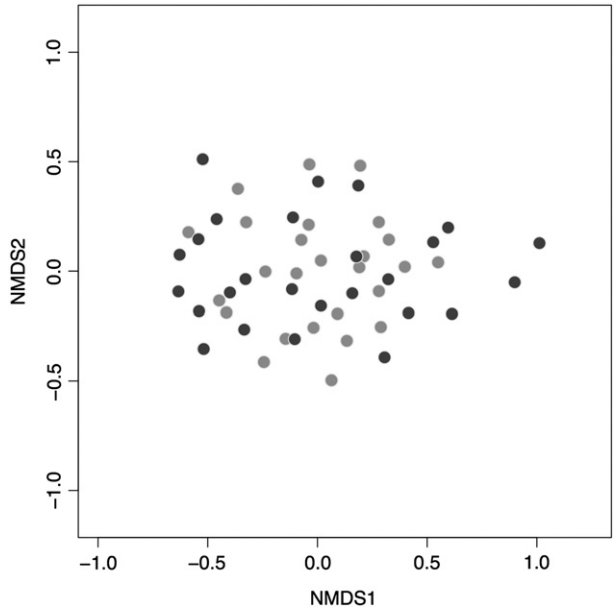

Fig. 6. Non-metric multidimensional scaling plots of dead assemblages (light gray) and live assemblages (dark gray), after resampling dead assemblages to the sample size of the respective live assemblage. Abundance data were square-root transformed and Bray-Curtis dissimilarity was used. The overlapping of sites in the plot indicates compositional similarity.

Other macrobioerosion traces that could affect preservation i.e. drill holes (Roy et al., 1994; but see Zuschin and Stanton, 2001; Kelley, 2008) are unlikely to have a major influence given that the percentage of shells with drill holes in our samples was small (mean assemblage predation frequency = 7%, Martinelli et al., 2015).

4.2. Sediment age and taphonomic inertia in One Tree Reef

The degree of temporal autocorrelation between DAs and LAs is dependent on time-averaging (Tomašových and Kidwell, 2011). With increasing newly dead individuals from LAs, the length of time averaging (either due to higher preservation rates or lower net sedimentation rates), in which younger cohorts will become proportionally less frequent will also affect the live-dead agreement (Olszewski, 1999, 2004; Tomašových et al., 2014) and the potential for rapid incorporation of changes in live communities into death assemblages will be smaller. However, changes in LAs, sometimes even seasonal variations, can get incorporated to DAs in less than a decade (Cummins et al., 1986; Feser and Miller, 2014). Therefore, good agreement between LAs and DAs does not necessarily mean that the environment has not changed, but rather that DAs are rapidly incorporating these changes (Feser and Miller, 2014). This phenomenon is particularly relevant to OTR sediments given the young age of shells in the taphonomically active zone (<10 years, Kosnik et al., 2015). We know however that the stratigraphic record of OTR is ordered (Kosnik et al., 2015), so even if changes are recorded fast by the first 20 cm of the sediment (shallowest sampling interval of Kosnik et al., 2015), the record below 20 cm can still be used for paleontological studies.

Examination of the species list from OTR mollusk fauna collected in 1985 (Jones et al., 1990) supports the conclusion that the sediments from the top 20 cm are not just rapidly absorbing changes. Sampling carried out by Jones et al. (1990) found the same dominant species as found in the DAs and LAs sampled in 2012. Most of the species found in the 1985 dataset were sampled in 2012, or are co-generic (see Table 3). Because there are no voucher specimens or abundance data available for the 1985 dataset (Doug Ferrell pers. comm.), critical analyses of taxonomic differences or changes in taxon abundance are not possible. The only major difference in composition is the presence of the gastropods *Atys hyalina* and *Nassarius* (*Zeuxis*) *bicallosus* in the 2012 samples, but not in the 1985 samples. Without being able to compare specimens we cannot be certain if these species were missing from

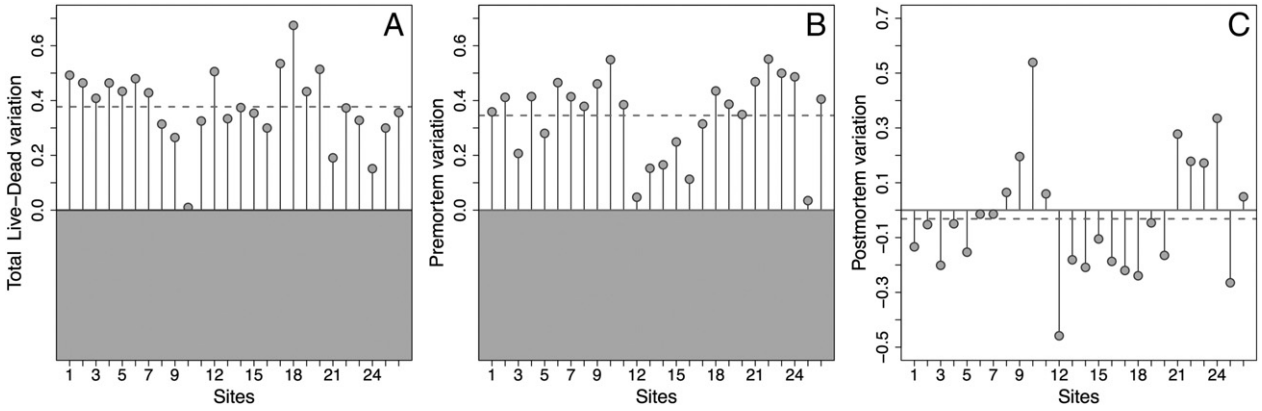

Fig. 7. Results from the homogeneity of multivariate dispersions test. (A) total live-dead variation for the 26 samples, (B) the contribution of pre-mortem processes to the total live-dead variation, (C) the contribution of post-mortem processes to the total live-dead variation. The dashed line in each panel represents the mean value for each variation among the 26 samples. Total live-dead variation and the pre-mortem variation can only have positive values, whereas the post-mortem variation can have negative values (pre-mortem variation minus total live-dead variation).

the previous qualitative samples or if the taxa were given different species names. Minor differences in taxonomic composition could be caused by several factors. First, it is possible that there are differences between identifications and taxonomies. For example, the differences between *Atys hyalina* and *Atys cylindricum* are very subtle and may explain discrepancies between Jones et al. (1990) and this work. Second, the two studies sampled different areas of the OTR lagoon. Their sampling was carried out in different areas of First Lagoon (see Jones et al., 1990, Fig. 1), whereas we focused on the northern edge of First Lagoon and sampled Second and Third Lagoons (see Fig. 1). Third, there are likely to be natural biannual or multi-annual changes in community composition and/or abundance related to seasonal pulses in recruitment. Fourth, there may have been slight, but genuine directional changes in minor constituents of the community that could explain the minor disagreements between datasets. Regardless, the overall agreement between the 2012 and 1985 datasets is particularly important given that the Jones et al. (1990) samples pre-date our DA (i.e. sediments from the same age they sampled are buried below the ones we sampled). A simple exercise is to take the data available about shell burial rates at OTR from Kosnik et al. (2015) and use it to estimate how deep the shells from 1985 would now be buried. This information can provide a conservative estimate of how long this community has been stable for. The mean shell burial rate in the top 15 cm is 5.6 mm/year (Kosnik et al., 2015). The Jones dataset was collected in 1985, that is 27 years before our samples were collected. Multiplying the burial rate by 27 indicates that those shells would now be 15 cm below the sediment they were living in during 1985. Of seventeen shells dated from the top 15 cm only 1 shell had an inferred age less than 27 yrs. (94% of shells from the taphonomically active zone were younger than 1985) (Kosnik et al., 2015). Thus, the DA investigated here firmly post-date the Jones et al. (1990) fieldwork. These shells also post-date the establishment of OTIRS in 1974 and local human impact at the reef became restricted to research activities.

4.3. Effects of substrates and spatial heterogeneity on live-dead fidelity

Paleontologists have a good understanding of how the nature of the environment (e.g., soft sediments vs. hard substrates), its heterogeneity (e.g., homogeneous sandy/muddy bottoms vs. patchy seagrass or rocky reefs), the degree of human impact (e.g., proximity to coasts and other sources of eutrophication), and the size of the shells studied (e.g., sieve mesh size) can affect the fidelity of dead shell assemblages relative to live ones (see reviews and meta-analysis by Kidwell, 2001, 2007, 2013, and numerous references therein). In this regard, one of the most important predictors of fidelity is the nature of the sediment (soft versus hard substrates). The extensive literature from sandy and muddy benthic environments consistently reports high live-dead fidelity such as that observed here. Meta-analysis of 85 molluscan datasets has shown that DAs from soft-sediment environments provide a reliable estimate of species abundances (Kidwell, 2001). There were however no fully carbonate soft-sediment assemblages included as part of that meta-analysis, and the few available studies carried out in reef environments are from hardgrounds (see Zuschin et al., 2000; Zuschin and Oliver, 2003; Zuschin and Stachowitsch, 2007). For example, the live-dead agreement in species abundances from rocky reefs in the Red Sea was as low as 6% and rarely above 50% (Zuschin et al., 2000). Hardgrounds from the Seychelles showed an overlap in species composition and rank order correlations between LAs and DAs, but this similarity was not found in coral-associated (instead of hardground-associated) molluscan assemblages (Zuschin and Oliver, 2003). The poor live-dead agreement found in reef hardgrounds was suggested to be due to dead specimens being overgrown by living organisms, which made dead shells hard to sample (Zuschin et al., 2000; Zuschin and Stachowitsch, 2007). Other benthic ecosystems with high environmental heterogeneity such as seagrass and coralligenous algae assemblages also have shown lower live-dead agreement than soft-sediment (e.g. Albano and Sabelli, 2011; Feser and Miller, 2014; Korpanty and Kelley, 2014). For example, a three-decade analysis of seagrass mollusks from St Croix (Virgin Is.) revealed that the composition of LAs and DAs varied significantly, mainly due to shifts in rank orders of the key species through time (Feser and Miller, 2014).

4.4. Using a live-dead approach to monitor reef ecosystems

Ecologists and conservation planners are increasingly aware of the importance of long-term temporal perspectives to understand changes to species, communities and ecosystems (e.g. Jackson et al., 2001; Kidwell, 2001; Dietl and Flessa, 2011; Dietl et al., 2015; Smith and Dietl, 2015). The mismatch between living communities and dead assemblages can be powerful metrics for environmental assessment (Kidwell, 2007; Dietl and Flessa, 2011; Dietl et al., 2015; Smith and Dietl, 2015), and as such they can also provide valuable information to assess reef health. Previous studies have suggested that the status of a reef should be determined by using taxa in addition to corals and fish, given that the presence and abundance of other invertebrates is strongly linked to the healthy functioning of reefs (Zuschin and Stachowitsch, 2007; Przeslawski et al., 2008). Therefore, the fact that mollusks have been one of the main taxonomic groups used in taphonomic studies (but see Pandolfi and Minchin, 1996; Greenstein and Pandolfi, 1997; Edinger et al., 2001) provides an added benefit. Here, we show that compositional data preserved in dead assemblages indicates that the OTR mollusk community has been stable for the last decade. Having

this temporal baseline can be useful for rapid assessments of coral reef diversity and health (Wells, 2000).

We present the first live-dead agreement study for soft sediment molluscan communities from a fully carbonate environment for the Great Barrier Reef, Australia. Results from species richness, evenness, relative abundance, rank order correlations, among other analyses, show that the live-dead agreement is high. Differences in composition and abundance seem to be driven by rare species. Some species-specific morphological traits could also be conferring greater preservation potential. Our results are further supported by compositional agreement with a 30-year-old mollusk dataset from OTR, indicating temporal stability in composition outside the window of time averaging. Thus, together with previous research at OTR, our data shows that soft sediments from low-impacted fully carbonate systems have a high potential for conservation paleobiology studies, which are much needed to yield baseline ecological information about coral reef health in changing oceans.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2016.06.002.

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