

Report (Coral Reefs)

Coral community structure in life and death assemblages from the Swain Reefs, Great Barrier Reef, Australia

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Abstract

The recent degradation of coral reef ecosystems has led to concern about their ability to overcome future stress events. I compared the ecological structure of coral life and radiometrically aged death assemblages to quantify coral reef degradation from inner and outer reefs of the Great Barrier Reef (GBR). Life assemblages from the Swain Group of the GBR were censused using photos of 0.5 m quadrants taken every 2 m along 50 m transects at each of 6 reef sites. Death assemblages were censused by collecting loose coral rubble from the same sites (there were 2 sites at each reef). Life and death assemblages were significantly different, with the difference driven primarily by Round Top Island and Derwent Island. Abundance of Acroporidae growth forms from the inner shelf was also significantly different from those of outer reef.

Age structure of the coral death assemblages was consistent over different sites at the same reef, suggesting that it should be possible to relate major community structure changes over time to environmental events of known age.

A complementary study of living massive coral colonies was undertaken to investigate whether or not coral bleaching left any 'signature' within the coral colony skeletal structure. Preliminary results found no detectable signature.

Introduction

During the past two decades, there has been increasing concern over the worldwide degradation of coral reef ecosystems (Hughes et al. 2003), with significant increases in anthropogenic impacts such as climate change (Hoegh-Guldberg 1999), increased nutrient loading (McCulloch et al. 2003), and over-fishing (Jackson et al. 2001). Recent reports suggest that the original “pristine” perception many people have of reef ecosystems from the 1970’s was not actually pristine but already severely degraded by multiple anthropogenic impacts, resulting in the “shifting base-line syndrome” (Pauly 1995; Jackson 1997; Greenstein et al. 1998). In order to create effective management strategies we must first establish what pristine reefs looked like, prior to the effects of anthropogenic impacts becoming apparent (Pandolfi 2002; Pandolfi et al. 2003)

Many modern, inner-shore reef communities on the southern Great Barrier Reef (GBR) are dominated by intact dead branching coral (*Acropora* spp.) overgrown with macroalgae (Done 1992; van Woesik and Done 1997). Little is known about the original community structure of these reefs, how the ecology of these communities has changed over time, or the potential causes of degradation. The main goal of this study is to determine the degree to which coral community structure has changed over time and what effects might have caused that change. I also used newly developed high precision dating methods to age the past coral death assemblages in an attempt to identify specific events that might be correlated with the changes in community structure. An excellent example of one of these sites is at Keswick Island off the coast of Mackay in the Swain reef group of the GBR, Australia. It was for this reason that Keswick Island along with 5 other reefs in the area were chosen as sites for this study.

Community structure over time

The calcium carbonate skeleton of reef building corals is one of their most defining characteristics. It is secreted while the organism is living and used in taxonomic classification usually down to species and growth form. When a coral dies, the skeleton becomes part of the death assemblage whether its designation remains intact or breaks off into coral rubble (Pandolfi and Greenstein 1997a). Death assemblages and fossil coral records are important because they preserve coral community characteristics during earlier periods of the reefs history.

A great deal of work has been done to establish the capacity for the fossil coral record and coral death assemblages to provide an ideal “database” of information for understanding ecological change through time (Pandolfi and Minchin 1995; Pandolfi and Greenstein 1997a,1997c; Greenstein et al. 1998; Edinger et al. 2001). Previous studies on the topic have been based on fossil assemblages from raised reef terraces for example the Pleistocene reef on the Huon Peninsula in Papua New Guinea (Pandolfi 1996). Death assemblages have primarily been used to understand more recent changes in the life assemblages.

Death assemblages were used for this study because they were easily accessible and there was no fossil record within the vicinity of the study sites. One particularly important question is whether a death assemblage is an accurate representation of the life assemblage from which it was derived. Death assemblages have been shown to provide a useful tool for palaeoecology but certain taxa may become over or under

represented and time-averaging means that individual cohorts cannot be traced. For example, branching growth forms are normally over represented in coral death assemblages because they have much higher growth rates and tend to fragment at higher frequencies than other corals (Highsmith 1982). Slower-growing massive coral skeletons are better designed to withstand mechanical stress than branched colonies (Chamberlain 1978). Special consideration must be given to results finding higher abundance of branching corals in the death assemblage because they might not be ecologically significant due to overrepresentation (Pandolfi and Greenstein 1997a,1997c). This study also investigates the benefits of comparing 2 dependant measurements of the death assemblage being the number of colonies per taxa collected from each site and the weight of those colonies per taxa.

The effects of time averaging must also be carefully considered when interpreting death assemblage results. However, these effects are often beneficial to providing a long term record of community structure of coral reefs, by averaging short term disturbances (Edinger et al. 2001). The addition of precisely dated coral colonies from the death assemblage will assist with identifying the time span from which the death assemblage covers. This problem is more prone to fossil sequences that cover larger spans of time.

Recent advances in high precision Uranium-series dating allows dating of *in situ* dead coral and loose coral rubble (also known as a “death assemblage” (Pandolfi and Minchin 1995) at approximately 1-3 years standard error (Collins et al. 2006). This results in high resolution dating of death assemblages, allowing temporal grouping of significant mortality events dating back to the time of European settlement of

Queensland and beyond. Although a definitive answer is beyond the scope of this study; I hypothesize that death assemblage age structure of inshore coral communities from the GBR can be linked to major human developmental events and recent mass mortality events related to global warming. If the cause of these mortality events can be determined, management can be concentrated towards mitigating those sources and preserving extant coral communities.

Since initial European settlement in the Mackay region there has been large-scale modification of the Pioneer river catchment area (1570 sq km) occurring from grazing, agriculture, mining and other activities. Sugar cane farming is the largest component of agriculture in the area; it was introduced in 1865 and became quite successful by 1874 with over 2000 ha under cultivation and 16 sugar mills in operation. Cattle farming and mining also became common in the late 1880's (Gourley and Hacker 1986). Modification of the river catchment area aided excess nutrients from fertilizers to drift downstream, especially during flooding events, and eventually reached coral reef communities off shore (Brodie 2004; QLDGov 2005). One of the sites for this study, Round Top Island, is located only 5 km away from the mouth of the Pioneer River. It can be difficult to associate increased levels of terrestrial runoff and nutrient loads with reductions in coral cover because of the complex transition and other possible causes of a shift from coral to algal dominated communities (Done 1992).

McCulloch *et al.* (2003) described a new method based on geochemical tracers in corals that can provide information of actual sediment and nutrient fluxes that are being delivered to corals. Recent unpublished work has suggested that the Mackay

region corals have been under particularly heavy sediment and nutrient fluxes associated with anthropogenic impacts. Coral geo-chemical records are normally obtained from massive *Porites* spp. cores that contain a vast suite of information regarding changes in the environment, however as of today any association between the actual health of the corals and isotopic composition recorded in their skeleton are unknown.

Coral bleaching events

Coral reefs have also been subject to massive bleaching events, which may indirectly be related to anthropogenic impacts (Hoegh-Guldberg 1999). Coral bleaching is the expulsion of symbiotic dinoflagellate algae (zooxanthallae) that normally live within the live coral's tissue (Coles and Brown 2004). Bleaching episodes cause large disturbances in coral reefs and the effects of bleaching include reduced coral growth and reproduction, and increased coral mortality (Marshall and Baird 2000). Bleaching events are normally associated with increased sea surface temperature and within the last 2 decades have been occurring with unprecedented frequency (Gleeson and Strong 1995) leading to much concern about the resilience of coral reef ecosystems and their ability to recover from such devastating events (Hoegh-Guldberg 1999; Hughes et al. 2003; Obura 2005). This, along with anthropogenic effects, has led to the investigation of long-term effects of climate change on coral reefs through preserved community structure in the fossil record and death assemblages. Recently, the possibility of recorded bleaching events in coral skeleton has been considered, with the anticipation of applying it to the fossil record. The identification of a bleaching signal will be essential for detection of past coral bleaching events under

undisturbed, natural conditions. A secondary aim of this study was to investigate the possibility of certain trace metals being associated with bleaching events.

One of the largest mass bleaching events occurred in Fiji in the year 2000 where 64% of colonies had bleached at sites covering most of Fiji except at Vanua Levu. The sites were revisited 4 months later and 10-40% of the colonies had died. Muaivuso in Viti Levu was one of the most adversely affected areas, possibly because the reef flat is shallower than most of the surrounding reefs (Wilkinson 2002). The identification of a robust bleaching signature recorded in coral skeleton is essential for the eventual application to fossil assemblages.

A study by Burr (2005) used inductively-coupled plasma atomic emission spectrometry (ICPAES) on 29 bleached and 29 non-bleached coral skeleton samples of *Porites divaricata* from Punta Cana in the Dominican Republic. Burr found higher trace metal/Ca ratios for Ag, As, Cd and Co in skeletal material from the bleached samples. Ag was undetectable in the non-bleached samples and mean content of the other elements were 50%, 54% and 85% higher respectively in the bleached samples. This suggests that in *P. divaricata* the uptake and deposition of elements into the skeleton were affected by bleaching (Burr 2005). Though these samples were from modern corals, it is possible that bleaching causes a permanent incorporation of trace levels of Ag, As, Cd and Co into the coral skeleton. These trace metal levels, especially Ag and Co, may provide a suitable signature for recognition of coral bleaching throughout the fossil record. *Diploastrea heliopora* cores were collected from Muaivuso, Fiji for testing because it was known that those particular corals had bleached during the mass bleaching event in 2000 and had survived to collection.

This study will be investigating the levels of Ag, As, Cd and Co present in coral skeleton that was most likely laid down during a massive bleaching event in the year 2000.

Massive corals are normally used for long-term geochemical records; for example palaeoclimate reconstruction. This is because they are resistant to mechanical breakage and erosion, and can form colonies 5-10 m high, which can be several centuries old depending on the growth rate of the coral, and also grow in a standard form which make collection and processing simpler (Corrége 2006). Although *Porites* is the most common coral used for paleoclimatic studies recently *Diploastrea heliopora* has been found useful under certain circumstances (Bagnato et al. 2001) to be equally suitable and was the species used for this study. *D. heliopora* is the only representative of its genus, and grows 3-5 mm per year (in vertical skeleton accretion), which is less than half the growth of corals from the genus *Porites*. One of the reasons the growth rate of *D. heliopora* is slower than *Porities* is because its polyps are usually more than 5 times larger. However this also means that *D. heliopora* colonies, which are the same size as a *Porites* colonies, can potentially contain twice as much geochemical record (Bagnato et al. 2001). *D. heliopora* is also less affected by grazing and boring organisms which create growth discontinuities in the data and should be avoided at all costs (Corrége 2006). Sr/Ca ratios in *D. heliopora* have also been shown to follow the same trend as *Porites* Sr/Ca ratio's, within error (Corrége et al. 2004). Though *D. heliopora* seems it would be an excellent candidate for long-term geo-chemical records there are some fundamental differences between it and *Porites*. This becomes problematic when transferring techniques for lab and fieldwork that have been developed with *Porites*.

Methods

Coral bleaching events

Study Site- The study site was located at Muaivuso Bay, Viti Levu, Fiji, approximately 13 km from the capital city of Suva (S18°08'53.7, E178°21'40.5). The bay is part of a Locally Managed Marine Area by the Yavusu district villagers. The total district population is approximately 600 people (Cakacaka et al. 2005).

4 *D. heliopora* cores were collected (each from a different colony) during a 2 week trip in April/May 2006 in collaboration with Dr. Ed Lovell and Dr. Leon Zann at the University of the South Pacific. The cores were collected using a pneumatic drilling rig fitted with a 2200RPM Shinzano hand drill fitted to a 55 mm diameter bore and a 50 cm long-diamond tipped coring barrel. A specially designed level was also used to drill straight down from the top of the colony. The drilling setup was custom-built at the ANU Research School of Earth Sciences workshop.

The slow growth rate of *D. heliopora* did not have the advantageous effects that were hoped for and described by (Bagnato et al. 2001), those good attributes may be true, however area of no benefit if you are unable to sample the coral efficiently. While the cores were being collected in the field drilling took twice as long as it would normally take to get the same length of *Porites*. Also, in the lab, the skeleton could not be cut with a scalpel, as is normally done with *Porites* because it would break off at irregular lengths (due to its large, intricate polyp structure), which is why the hand Dremel

was used. The slow growth rate also results in smaller annual bands that can be difficult to distinguish from the x-rays.

Once the cores were collected, an approximately 0.7 cm thick slice was cut and X-rayed at 50 kV, 100mA for 80 milliseconds to examine the annual growth bands. The 2000-year band was located and identified on the slice itself by counting down the growth bands from the top of the core. Then a 1x2 mm section was cut from the side of the core. The section was labeled with 1 mm marked tracing paper. Approximately 50 mg sections of powdered skeleton were ground off using a diamond tipped Dremel handrill, achieving 4 samples per mm of skeleton. This resulted in 1-2 month resolution for this sample. The powdered samples were dissolved in acid and diluted for ICPAES analysis (Kamber 2001). Two isotopes of Ag (Ag^{107} , Ag^{109}), Co^{59} and As^{75} Cd^{111} were analyzed. The ideal sampling method for this process uses a modified computer automated Micromill machine (Charlier et al. 2006), however due to time restrictions the method was not able to be used.

Community structure over time

Study Sites Data was collected from 6 reefs (Fig. 1) located in the Mackay/Capricorn group, one of the southern most parts of the Great Barrier Reef (GBR), sometimes referred to as the Swain Reefs. The sites ranged from inner shore to the inside shelf of the outer reef, henceforth referred to as the outer reef (Table 1). Sites from Derwent Island, Big Kindemar and Little Kindemar range from mid-shelf reef to the inner shelf of the outer reef, in order to balance the sites for analysis they were all considered outer shore reefs. Sites were also classified as sheltered or exposed according to

whether they were leeward or windward; sites that were on the windward side of the island but sheltered by another island were considered sheltered (pers obs) (Table 1).

Sampling- All field data and samples were collected by surface-supported SCUBA in water depths ranging from 2-7 m. In both the life and death assemblages, coral colonies were identified as follows: *Montipora*, Acroporidae, Pocilloporidae, Faviidae and Poritidae. All other corals were referred to as “other”. For this study *Montipora* was kept in a separate group and not included in the Acroporidae because a majority of them were encrusting species that would bias the growth form information gathered for the Acroporidae group. Growth forms were identified for colonies from the Acroporidae according to Wallace (1999) and included cuneiform, digitate, arborescent, caespitose and tabular (including plate and table coral).

Life assemblages were described by taking photographs of 50 cm² quadrats every 2 m along a 50m transect. There were 2-3 sites at each reef and 1 transect at each site. Photographs were all taken by the same person while swimming directly above the transect tape at approximately the same distance above the tape. Photos were later analyzed using Coral Point Count with Excel extensions v3.3 software that generated 30 random points on each quadrat. This method is well established and described as an excellent tool for estimating the community structure of benthos (Kohler, and Gill 2006). Only points that fell on live hard coral and could be identified were included.

Normally a death assemblage includes all dead coral in the area, included corals still incorporated into the reef, however for this study the death assemblage was considered to be composed of loose coral rubble only. Colony collection methods

were adapted from Greenstein & Pandolfi (1997). There were 6 samples collected along the same 50 m transect laid out for the life assemblages. Each sample was collected at a point along the transect where coral rubble was present. Rubble was collected in 5 mm mesh bags and excavated from the same point, approximately 10 cm in depth first, then within 2 m, until approximately a liter volume had been collected. The coral rubble was then soaked overnight in 10% bleach, rinsed, sun dried and then transported to the lab. Once in the lab the samples were dried in a 60° C oven overnight. Only colonies >5 mm in size and with sufficient skeletal structure for taxonomic identification were weighed, counted and included in the study.

Coral colonies were also radiometrically dated to determine the age structure of the death assemblages. The U-series dating method used is complex, time –consuming and expensive. Thus it was only possible to date 10 coral colonies. They were all selected from the Keswick Island death assemblages to provide a more thorough understanding of death assemblage age structure within a site. All of the colonies selected were from the Acroporidae group to avoid any taxonomic variation. All the Acroporidae colonies from the Keswick Island death assemblage were cut in half to observe the internal preservation, then the 5 best preserved from each site were dated. Material for dating was always selected from the very center of the colony and within 2 cm of the branch tip if the colony was a branching growth type.

There were a total of 12 death assemblages, 2 from each reef, and a total of 12 life assemblages, 2 each from Keswick Island, Little Kindemar and Big Kindemar and 3 each from Derwent Island and Scawfell Island. No life assemblage data were collected at Round Top Island due to weather conditions. The community structure of

the death assemblage from Round Top Island is included in all analysis unless otherwise noted.

U-series dating methods-U-series dating is based on the ratio of uranium and thorium isotopes present in the coral skeleton. When corals are alive they secrete a calcium carbonate skeleton and incorporate uranium atoms from the water column, while initially excluding thorium atoms at the same time. Uranium decays into ^{230}Th at a known rate, so determining the ration of ^{238}U to ^{230}Th yields a precise date. The isotopic composition of ^{238}U and ^{230}Th was measured by thermal ionization mass spectrometer (TIMS). The method of U-series dating was first developed and tested by Edwards et al. (1987). Then Stirling et al. (1995) refined the method for corals. The method was modified again for high precision dating of modern corals and can now produce a <4 year typical standard error. This high precision dating method is the method used for this study (Weisler et al. 2005). Dates were acquired from the Centre for Microscopy and Microanalysis in the Faculty of Eng, Phys Sci and Arch at the University of Queensland.

Data analysis-Using the statistical analysis software, PRIMER v5.2.9. The abundance data was square root transformed to reduce the influence of occasional large values of some taxonomic groups (Field et al. (1982). Then the data was standardized by site to equalize the contribution of each site because the methods resulted in different units from the life and death assemblages. Standardization allowed for each site to contribute to the results equally. Comparisons of community composition were then made by computing the Bray-Curtis dissimilarity coefficient between every possible combination of sites, resulting in a dissimilarity matrix (Bray and Curtis 1957).

Dissimilarity values range from 0-1, a value of 0 means that the 2 sites have identical taxonomic group abundances and a value of 1 means that the 2 sites share no taxonomic group abundances in common.

Analysis of similarities (ANOSIM; Clarke 1993) was then performed to test for taxonomic variation between reef sites and between life vs. death assemblages. ANOSIM has been used for similar work on coral reefs (Pandolfi and Minchin 1995; Pandolfi and Greenstein 1997b; Edinger et al. 2001). The ANOSIM uses the rank values from the Bray-Curtis dissimilarity matrix and computes a statistic that describes the observed differences among replicates between sites, contrasted with differences among replicates within sites. The ANOSIM test results in a percent significance or P-value. A value <0.05 or 5% is considered significant. All the ANOSIM tests performed were one-way with one of the following main effects; Life vs Death assemblages; the Exposed vs Sheltered reef sites; and Inner shelf vs Outer shelf sites.

To visualize the data, a non-metric multidimensional scaling (nMDS) ordination was created from the Bray-Curtis dissimilarity matrices. The nMDS ordination provides a 2 dimensional plot that helps in visualizing the degree of separation of data groupings. Abundance data for the death assemblages was calculated separately based on both the weight and the number of colonies of each taxonomic group. In one analysis, all taxa were analyzed together, and in another, just the growth forms of the Acroporidae were analyzed. When the Acroporidae was included with all other taxa the growth forms were pooled together. Results of averaged data include $\pm 1SE$ except for the dating results that are $\pm 2SE$, which is the standard used for U-series dating results.

The data for the fertilizer use and cane harvesting was compiled from J. Brodie (2004). For comparisons between the death assemblage age structure and fertilizer and cane harvesting use the of colonies dated before 1915 were pooled together because there was no cane harvesting or fertilizer use before that time.

Results

Coral bleaching events

On average annual growth was 3 ± 2 mm year⁻¹ for each of the 4 cores. There were also some interesting dark and green banding on the cores. One of the cores was especially affected (Fig 4). Only one core was analyzed for trace elements. The ICPAES analysis found no trace amounts of Ag¹⁰⁷ in any *D. heliopora* coral skeleton samples, including the samples taken from the 2000 annual band. The other elements analyzed had interference and were unusable. Interference occurs when there are other molecules present that are the same molecular weight as the isotope being measured. The result of interference is unfeasibly high values of the trace elements being analyzed. The trace levels of Ag¹⁰⁷ never reached above 100 counts per second and blanks were normally 40-60 counts. Blank counts are used to test error by measuring the amount of Ag¹⁰⁷ in a blank sample with no Ag. A test of 1 ppb silver solution yielded 24000 counts per second.

Community structure over time

The life and death assemblages were both strongly dominated by Acroporidae ranging from 29-53% composition at an individual site (Fig 2a). The next highest abundance was 26% for Faviidae in the Scawfell Island life assemblage (Fig. 2d). The taxonomic proportions for the death assemblage are from 2 different data sets that were obtained from the same samples. There was no obvious difference between the 2 death assemblage data sets. Arborescent Acroporidae represented from 0-67% of the Acroporidae growth forms (Fig 3a). The other growth forms were also more variable between sites in the death assemblage ranging from 0-57% and 0-50% in the life assemblage (Fig. 3a-e).

The ANOSIM tests were performed 4 times to compare the differences between using all taxa or just the Acroporidae growth forms, and using the 2 different death assemblage data sets (Table 2). They showed that there was a significant difference between the death and life assemblages with all the taxa combined, and within the Acroporidae growth forms. The test for all taxa with the abundance death assemblage data set was more significant than with the test with the weight by taxon data set.

The influence of wave energy was tested in 2 ways: sheltered or exposed sites were compared and inner or outer shelf locations were compared. The only significant test for the influence of wave energy was from the Outer vs Inner shelf effect with the Acroporidae growth form and death assemblage by weight per taxa (Table 2).

Differences in coral taxonomic composition between the life and death are illustrated in the nMDS where some separation is visible (Figure 5a). The same analysis with the second death assemblage data set revealed a much more noticeable separation

along the Dimension 1 axis (Fig 5b). The pairwise analysis of the same ANOSIM revealed significant values between the Derwent Island sites. When the test was run again without the Derwent Island sites the results were not significant, so they were the main drivers for the initial significance. The nMDS's in figure 5c-d both reveal a clear separation between assemblages. In figure 5d the death assemblage seems to be clustering more tightly and one of the life assemblage sites is clustering with them.

The oldest colony from the Keswick Island death assemblage was 214 ± 12 years old and the youngest was 17 ± 31 years old (Fig 6a). The death assemblage from each site had a very similar age structure (Fig 6b). In Queensland, cane harvesting and fertilizer use started from 1915-1930 and continued on a steep increasing slope (Figure 7). The same data from figure 6a was plotted along with the data in an attempt to observe age structure of the death assemblage. From the small amount of data collected it seems that the age of the death assemblage decreases as the use of fertilizers increase (Fig 7).

Discussion

Community structure over time

As expected the results confirm that there have been changes to the community structure of the Swain reefs over time. However, this study also investigated the possibility of using the weight of each taxa to help control for the over representation of branching corals. Past studies have generally used number of colonies per taxa to describe the death assemblage's community structure (Pandolfi and Greenstein

1997a). The main advantage of this method is that it results in “data points” that can be directly comparable to the life assemblage without having to standardize the data, which is statistically undesirable. However, even if great care is taken, each site can still end up with a highly variable amount of data points (usually due to branching corals) which results having to standardize the data anyway, for example this happened in Pandolfi and Greenstein (1997a). It seemed feasible that branching taxa were being over represented because they are more prone to breakage, which resulted in a higher abundance (Highsmith 1982).

If that were the case then measuring by weight should remove that bias. Figures 2 and 3 show little variation between the 2 death assemblage data sets. However the results of the nMDS's in figure 5 show some obvious differences. The death assemblage data from abundance shows a clearer separation from the life assemblage. It is likely that this is caused by an over representation of Acroporidae colonies in the death assemblage. The death assemblage determined by weight gives a more representative view of the difference between the life and death assemblages.

This trend has been observed in other systems as well. In the death assemblages of foraminifera, fragile tests (skeletons) were more susceptible to destruction than robust forms and therefore less common in areas of high water activity. This was found interfere with the palaeoecological interpretations (Martin, and Wright 1988). They still determined that apart from some mis-representation the death assemblage reflected living assemblages.

The Acroporidae taxon was also considered individually in figure 5c-d. It is interesting to compare the variability within the growth forms to the variability over the whole taxon, because there should be no over representation present in the Acroporidae group. The arborescent growth type was the most susceptible to breakage (Highsmith 1982) and also it had the highest abundance than any other growth type. I would expect that it would be the driving factor for the differences between figure 5c and 5d. In figure 5d one of the life assemblage sites is grouping with the death assemblages. This site was from Keswick Island and contained no living coral which made meaningful analysis of it extremely difficult. It is clear that there are differences between the 2 methods and in my opinion there should be greater ecological significance given to death assemblages measured by weight

I also tested for environmental effects that might have influenced the data regardless of time. When whole reefs including the life and death assemblage sites were compared to each other they resulted in a significant difference between sites. This was significant for the all taxa and Acroporidae growth forms, but only for the death assemblage calculated from weights per taxon. This is interesting because it suggests that although life community structure has changed from the death assemblage each reef has remained differentiated from each other over the period of the death assemblage age structure. Acropora growth forms from the inner shore were also statistically different from the outer shore. Unfortunately due to the sampling design, I was unable to make comparisons within or between growth types or taxon. This was because I did not have enough replicates and there was too much variation between sites. Van Woesik and Done (1992) noted that there is a strong current that runs through the center of the Swain Reefs. This among other effects might create isolated

environments between the inner and outer shore and between reefs (Done 1992; van Woosik, and Done 1997). The fact that they are significantly different especially between individual reefs might suggest that more consideration needs to be given to site environment. In the future I think studies should concentrate on acquiring more transects at less sites. A better analysis to do would be a two-way nested ANOSIM with sites nested within reefs.

Corals from death assemblages that were radiometrically age dated all came from the last 250 years with a negative relationship between number of corals and coral age. This might suggest that there was more branching acroporid coral present in the area to contribute to the death assemblage approximately 100-250 years ago than there is now. These dates, however, could also be explained by a number of reasons due to the incomplete sampling regime. The death assemblage is not a permanent assemblage and does become degraded over time. It is possible that older colonies are simply not present in the death assemblage because they have become completely degraded. The addition of death assemblage age structure from different sites in the future will add to the strength of this study.

The cost and time that it takes to date samples is limiting. It would be useful to develop a way to determine how many samples from a death assemblage need to be dated in order to accurately represent the age structure, because it is not possible to date every colony in a death assemblage. A majority of the death assemblage had been affected by epibionts like encrusting foraminifera, encrusting coralline algae and also endobionts like bio-eroding sponges. It might be interesting to determine an “estimate” age for the death assemblage colonies based on settling rates of epibionts.

The effect of epibionts on the degradation of coral, as well as the growth rates of most encrusting foraminifera have been investigated (Pandolfi and Greenstein 1997c; Adey and Vassar 1975).

Coral bleaching events

The X-rays of the *D. heliopora* cores showed well-defined stratigraphy of the annual carbonate density bands, which is important for accurately dating time series records. However, bands were less distinguishable in the most recent 10 years (the area of interest), which apparently is not uncommon in *Porites* but has not been noted in *D. heliopora* (Lough and Barnes 1997). There were also some unusual green and dark bands visible on the core (Fig 4). This has also been observed in *Porites*, but unreported in *D. heliopora* and is thought to have to do with an increased abundance of endolithic algae followed by an increase in skeletal density (Priess et al. 2000).

Previous work by Burr (2005) demonstrated that there might be elevated levels of Ag and Co during bleaching events in *Porites*. Our preliminary findings do not support the observation that increased proportions of Ag and Co is incorporated into the skeletal lattice of the *D. heliopora* skeleton so *D. heliopora* might not be a suitable species for establishing a geochemical bleaching signature. Various explanations could account for this result, including inter-species variation, or the fact that Fiji is a more pristine environment than the Dominican Republic, where Burr's samples were taken. Also, those elements might not be present in the water column for the coral to absorb and include in skeletal secretion. It is most likely that the sampling method used did not have a high enough resolution to isolate the bleaching event in *D.*

heliopora. Another possibility is that laboratory contamination might have lead to Burr's results, as a full scientific paper has never been published on the results of the abstract. Future research should focus on establishing a robust geochemical tracer of coral bleaching in the commonly used species *Porites*. The species is well described and less difficult to work with in the lab.

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References

- Adey WH, Vassar M (1975) Colonization, succession and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales). *Phycologia* 14:55-69
- Bagnato S, Linsley B, Wellington G, Howe S (2001) Developing the use of the massive coral genus *Diploastrea* for paleoclimate reconstruction. GSA Annual Meeting
- Bray J, Curtis J (1957) An ordination of the Upland Forest Communities of Southern Wisconsin. *Ecological Monographs* 27:326-349
- Brodie J (2004) Mackay Whitsunday Region: State of the waterways report. Australian Centre for Tropical Freshwater Research:161.
- Burr S (2005) Micromorphology and Trace Metal Content as Indicators of Bleaching in Skeletons of Modern and Holocene Corals. American Geophysical Union, Spring Meeting 2005
- Cakacaka A, Meo S, Degei M, Ratuniata R (2005) Site Report: Learning framework database Locally-Managed Marine Area Network
- Chamberlain J (1978) Mechanical properties of coral skeleton: compressive strength and its adaptive significance. *Paleobiology* 4:419-435
- Charlier BLA, Ginibre C, Morgan D, Nowell GM, Pearson DG, Davidson JP, Ottley CJ (2006) Methods for the microsampling and high-precision analysis of strontium and rubidium isotopes at single crystal scale for petrological and geochronological applications. *Chemical Geology* 232:114-133
- Coles S, Brown B (2004) Coral bleaching-capacity for acclimatization and adaptation. *Advances in Marine Biology* 46:183-223
- Collins L, Zhao J, Freeman H (2006) A high-precision record of mid-late Holocene sea-level events from emergent coral pavements in the Houtman Abrolhos Islands, southwest Australia. *Quaternary International* 145-146:78-85
- Corrége C (2006) Sea Surface temperature and salinity reconstruction from coral geochemical tracers. *Palaeogeography, Palaeoclimatology, Palaeoecology* 232:408-428
- Corrége C, Gagan M, Beck J, Burr G, Cabioch G, Cornec F (2004) Interdecadal variation in the extent of South Pacific tropical waters during the Younger Dryas event. *Nature* 428:927-929
- Done T (1992) Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247:121-132
- Edinger E, Pandolfi J, Kelly R (2001) Community structure of Quaternary coral reefs compared with Recent life and death assemblages. *Paleobiology* 27:669-694
- Edwards R, Chen J, Wasserburg G (1987) ^{238}U - ^{234}U - ^{230}Th - ^{232}Th systematics and the precise measurement of time over the past 500 000 years. *Earth and Planetary Science Letters* 81:175-192
- Field J, Clarke K, RM W (1982) A practical strategy for analysing multispecies distribution patterns. *Marine Ecology-Progress series* 8:37-52
- Gleeson M, Strong A (1995) Applying MCSST to coral reef bleaching. *Adv. Space Res.* 16:151-154
- Gourley M, Hacker J (1986) Pioneer River Estuary: Sedimentation Studies. University of Queensland Printery, St. Lucia
- Greenstein B, Curran H, Pandolfi J (1998) Shifting ecological baselines and the demise of *Acropora cervicornis* in the western North Atlantic and Caribbean Province: a Pleistocene perspective. *Coral Reefs* 17:249-261

- Highsmith R (1982) Reproduction by fragmentation in corals. *Marine Ecology-Progress series* 7:207-226
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* 50:839-866
- Hughes T, Baird A, Bellwood D, Card M, Connolly S, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson J, Kleypas J, Lough J, Marshall P, Nyström M, Palumbi S, Pandolfi J, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929-933
- Jackson J (1997) Reefs since Columbus. *Coral Reefs* 16:23-32
- Jackson J, Kirby M, Berger W, Bjorndal K, Botsford L, Bourque B, Bradbury R, Cooke R, Erlandson J, Estes J, Hughes T, Kidwell S, Lange C, Lenihan H, Pandolfi J, Peterson C, Steneck R, Tengner M, Warner R (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629-638
- Kamber B, GE Webb (2001) The geochemistry of late Archaean microbial carbonate: Implications for ocean chemistry and continental erosion history. *Geochimica et Cosmochimica Acta* 65:2509-2525
- Kohler K, Gill S (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers & Geoscience* 32:1259-1269
- Lough J, Barnes D (1997) Several centuries of variation in skeletal extension, density and calcification in massive *Porities* colonies from the Great Barrier Reef: A proxy for seawater temperature and a background of variability which to identify unnatural change. *Journal of Experimental Marine Biology and Ecology* 211:29-67
- Marshall P, Baird A (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* 19:155-163
- Martin R, Wright R (1988) Information loss in the transition from life to death assemblages of foraminifera in the back reef environment. *J. Paleontol.* 62:399-410
- McCulloch M, Fallon S, Wyndham T, Hendy E, Lough J, Barnes D (2003) Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. *Nature* 421:727-773
- Obura D (2005) Resilience and climate change: lessons from coral reefs and bleaching in the Western Indian Ocean. *Estuarine, Coastal and Shelf Science* 63:353-372
- Pandolfi J (2002) Coral community dynamics at multiple scales. *Coral Reefs* 21:13-23
- Pandolfi J, Bradbury R, Sala E, Hughes T, Bjorndal K, Cooke R, McArdle D, McClenachan L, Newman M, Paredes G, Warner R, Jackson J (2003) Global Trajectories of the Long-Term Decline of Coral Reef Ecosystems. *Science* 301:955-959
- Pandolfi J, Greenstein B (1997a) Preservation of community structure in death assemblages of deep-water Caribbean reef corals. *Limnol. Oceanogr.* 42:1505-1516
- Pandolfi J, Greenstein B (1997b) Preservation of community structure in modern reef coral life and death assemblages of the Florida Keys: implications for the quaternary fossil record of coral reefs. *Bulletin of Marine Science* 61:431-452
- Pandolfi J, Greenstein B (1997c) Taphonomic alteration of reef corals: effects of reef environment and coral growth form. I. The Great Barrier Reef. *Palaios* 12:27-42

- Pandolfi J, Minchin P (1995) A comparison of taxonomic composition and diversity between reef coral life and death assemblages in Madang Lagoon, Papua New Guinea. *Palaeogeography, Palaeoclimatology, Palaeoecology* 119:321-341
- Pauly D (1995) Anecdotes and the shifting baseline syndrome of fisheries. *Trands Ecol. Evol.* 10:430
- Priess K, Campion-Alsumard T, Golubic S, Gadel F, Thomassin B (2000) Fungi in corals: black bands and density-banding of *Porities lutea* and *P. lobata* skeleton. *Marine Biology* 136:19-27
- QLD Gov (2005) Mackay Coast Study. Queensland Government: Environmental Protection Agency Queensland Parks and Wildlife Service
- Stirling C, Esat T, McCulloch M, Lambeck K (1995) High-precision U-series dating of corals from Western Australia and implications for the timing and duration of the Last Interglacial. *Earth and Planetary Science Letters* 135:115-130
- van Woerik R, Done T (1997) Coral communities and reef growth in the southern Great Barrier Reef. *Coral Reefs* 16:103-115
- Wallace C (1999) Staghorn corals of the world: A revision of the coral genus *Acropora*. CSIRO Publishing
- Weisler M, Collerson K, Feng Y, Zhao J, Yu K (2005) Thorium-230 coral chronology of a late prehistoric Hawaiian chiefdom. *Journal of Archaeological Science* 33:273-282
- Wilkinson C (2002) Status of Coral Reefs of the World. Australian Institute of Marine Science 2002

Figure Legends

Figure 1. Map of study area from the Swain Group of the Great Barrier Reef, Australia, including indications of specific island or reef locations where samples were collected.

Figure 2. Sliced coral core from living *Diploastrea heliopora*. On the left is the unaltered core - note the green and dark banding. On the right is the same core that has been X-rayed to reveal annual density banding. The 2 white asterisks on either side of the core indicate the low density band from the year 2000.

Figure 3. Proportion of coral taxa from the life assemblage; the death assemblage by the number of colonies in each taxa; and the death assemblages by the weight of each taxa at each of 5 sites (Keswick Island, Scawfell Island, Derwent Island, Little Kidemar and Big Kindemar.) Proportions are given for a) Acroporidae, b) Pocilloporiidae, c) Poritidae, d) Faviidae and e) *Montipora*.

Figure 4. Proportion of Acroporidae growth forms from the life assemblage; the death assemblage by the number of colonies in each taxa; and the death assemblages by the weight of each taxa at each 5 sites (Keswick Island, Scawfell Island, Derwent Island, Little Kidemar and Big Kindemar.) Proportions are given for a) Arborescent, b) Caespitose, c) Cuneiform, d) Tabular and e) Digitate.

Figure 5. Non-metric multidimensional scaling (nMDS) ordination of all taxa from life and death assemblages. A-b) include data from all taxa, c-d) uses the Acroporidae growth forms. A) and c) use the death assemblage data that was calculated by the weight of each taxon. B) and d) use the death assemblage data that was generated from number of colonies per taxon. The minimum stress value was a) 0.17, b) 0.17, c) 0.12, d) 0.08.

Figure 6. U-series dating of 10 colonies from the Keswick Island death assemblage site A or B. A) each individual colony plotted against age. There were 5 colonies from site A and 5 from site B. Data is presented as age $\pm 2SE$. B) average age of the death assemblage from each site.

Figure 7. Mackay fertilizer used and cane harvested vs. age of death assemblage colonies over time. Colonies from before 1900 were included as a single group because there was no data before that time. The number of colonies in each group is indicated with a number above the point. The Mackay fertilizer and cane harvested data was compiled from (Brodie 2004).

Table 1. Site and individual transect descriptions. There was one 50 m transect done at each site and 2 sites at each Island (Is.) or reef; they are differentiated by an A or B at the end of the name.

Island (Is.)/Reef site	Is./Reef Distance from Mackay	Shelf	Exposure
Round Top Is. A	5 km	inner	exposed
Round Top Is. B	5 km	inner	exposed
Keswick Is. A	33 km	inner	sheltered
Keswick Is. B	33 km	inner	sheltered
Scawfell Is. A	50 km	inner	sheltered
Scawfell Is. B	50 km	inner	sheltered
Derwent Is. A	65 km	outer	sheltered
Derwent Is. B	65 km	outer	sheltered
Little Kindemar A	135 km	outer	sheltered
Little Kindemar B	135 km	outer	exposed
Big Kindemar A	135 km	outer	sheltered
Big Kindemar B	135 km	outer	sheltered

Table 2. Results of ANOSIM analysis for all taxa and Acroporidae growth types. The death assemblage was calculated using the weight of each taxa, as well as, the number of colonies from each taxon. ANOSIM analysis was performed with both methods.

	Main effect (number of variables)	death data by weight		by number of colonies	
		R-stat	P-value	R-stat	P-value
all taxa	Life vs Death pooled (2)	0.1116	0.045	0.33	0.01
	Reef vs Reef (6)	0.157	0.049	0.076	0.195
	Life Reefs vs Death Reefs (11)	0.212	0.058	0.337	0.007
Acroporidae growth types	Life vs Death (6)	0.38	0.001	0.401	.001
	Inner shelf vs Outer shelf (2)	0.207	0.0013	0.149	0.022
	Reef vs Reef (6)	0.257	0.008	0.114	1.0
	Life Reefs vs Death Reefs (11)	0.489	0.001	0.463	0.001

Figure 1

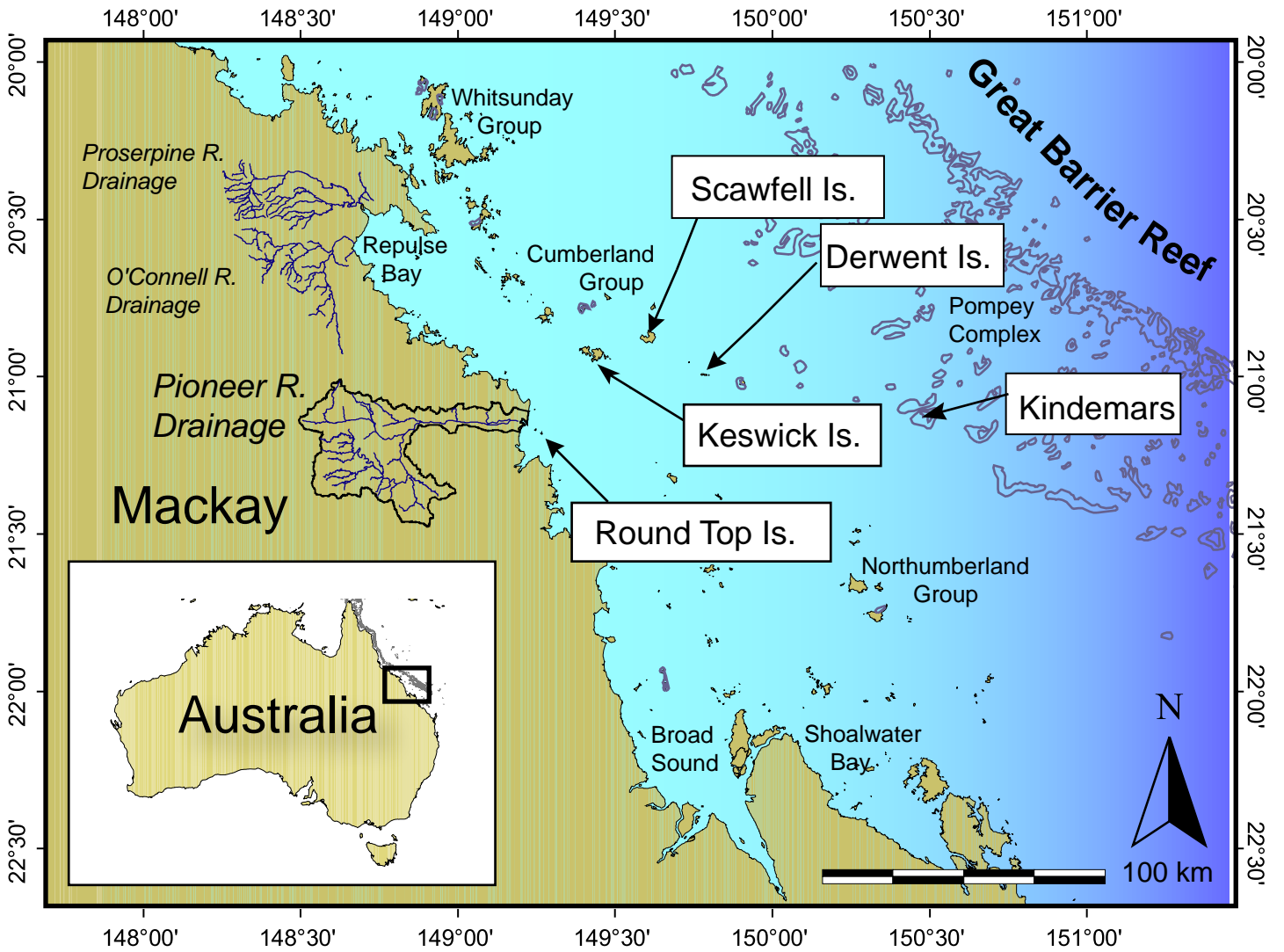
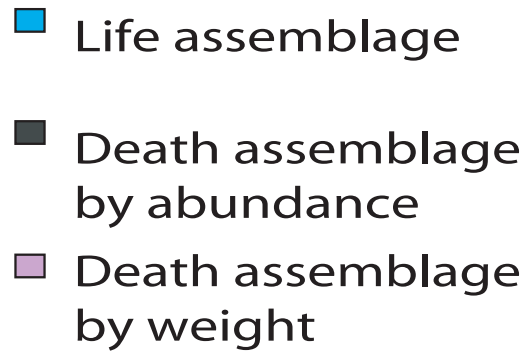
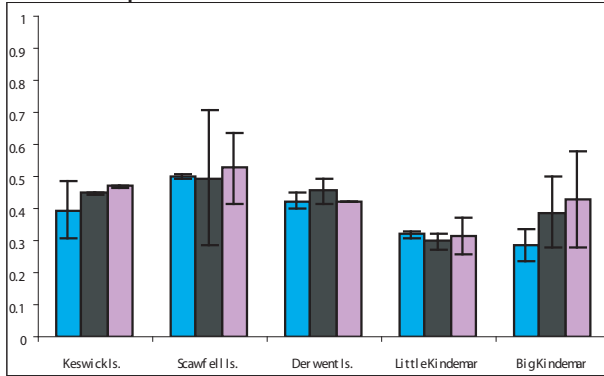
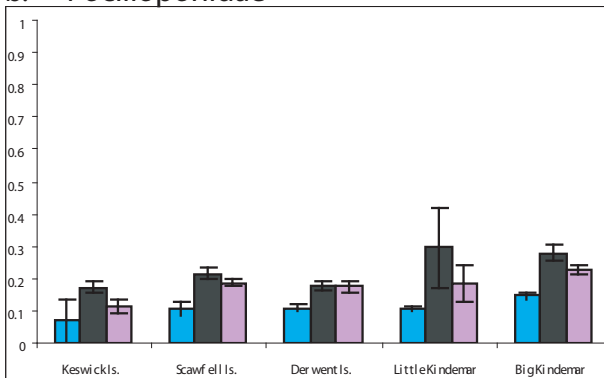


Figure 2

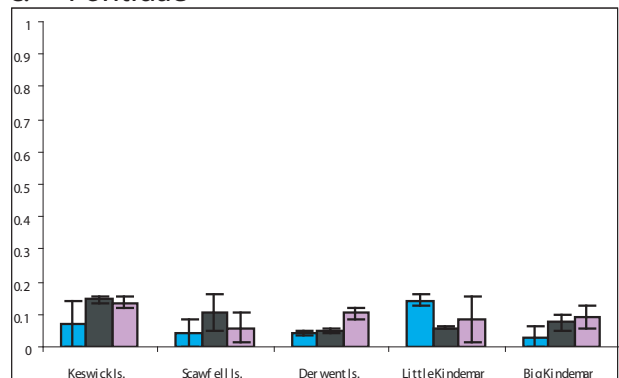
a. Acroporidae



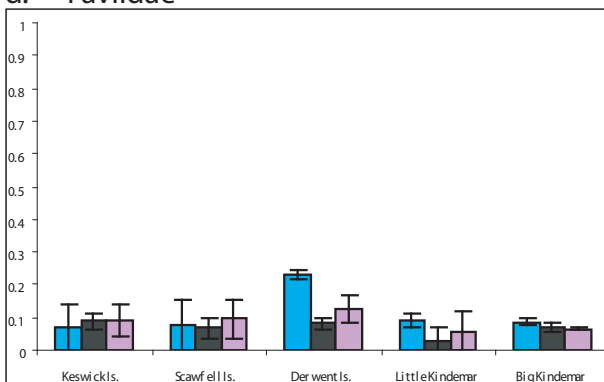
b. Pocilloporiidae



c. Poritidae



d. Faviidae



e. Montipora

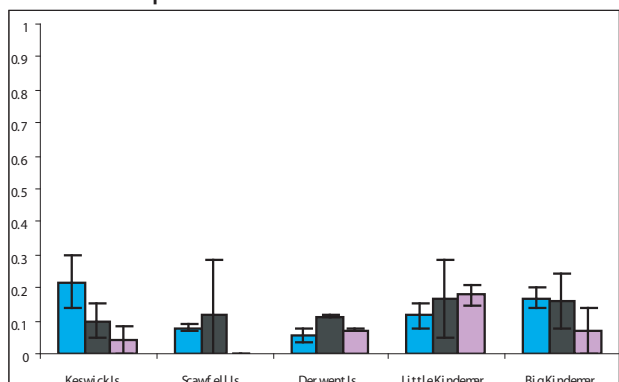


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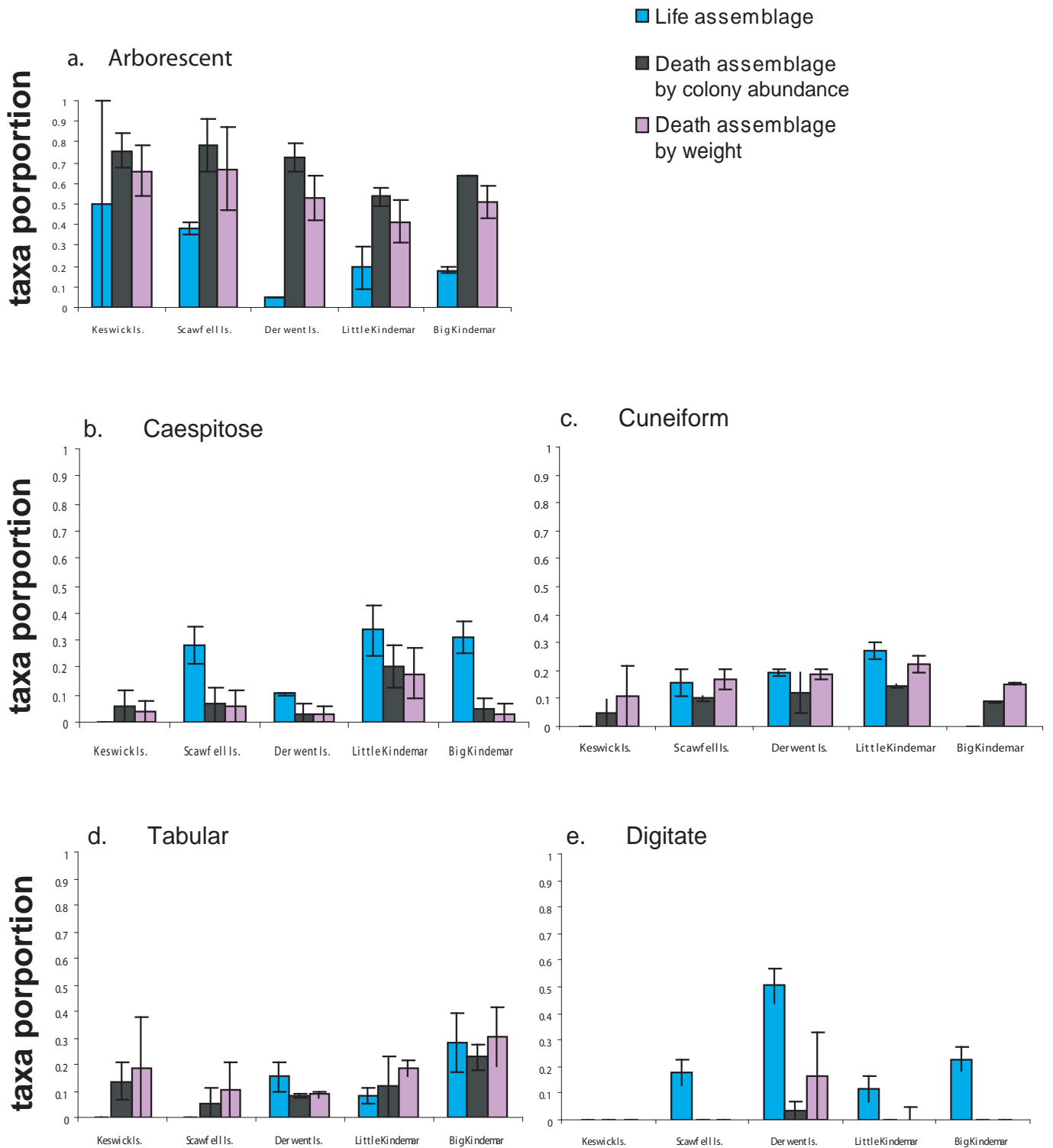


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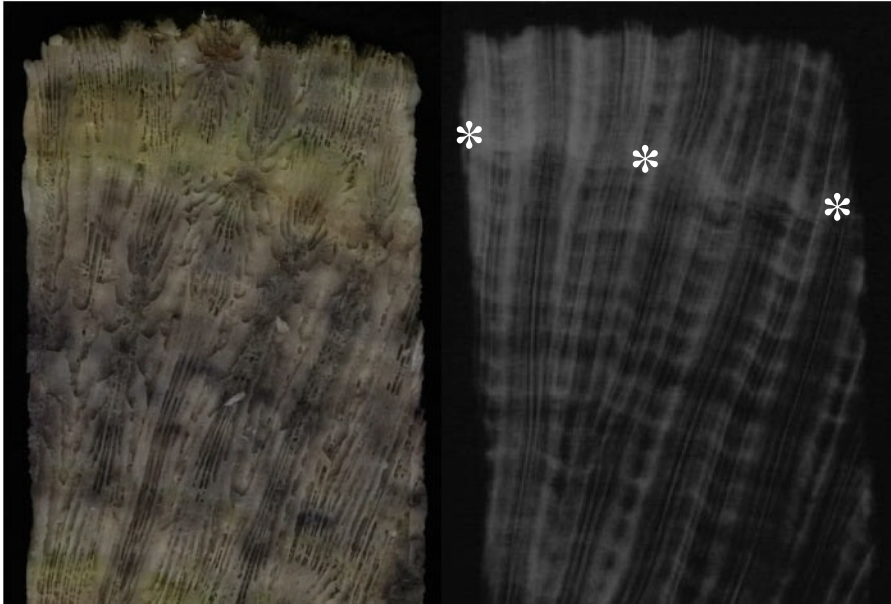


Figure 5

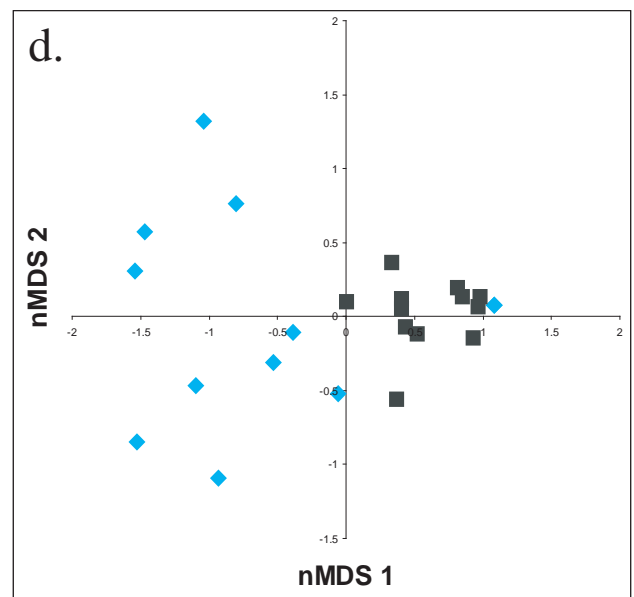
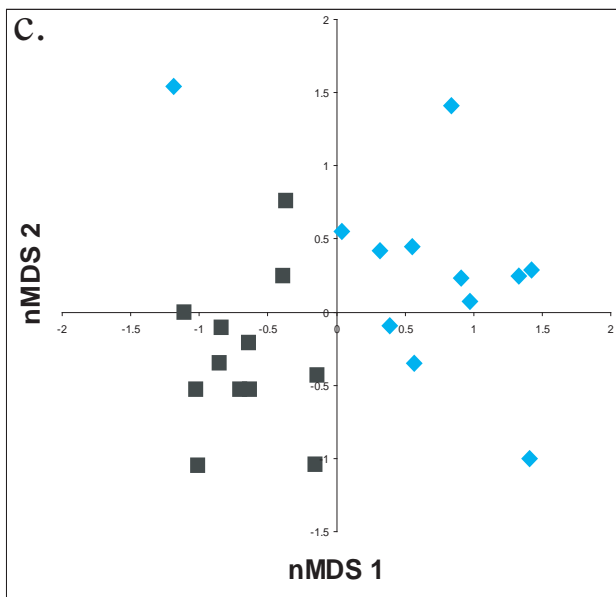
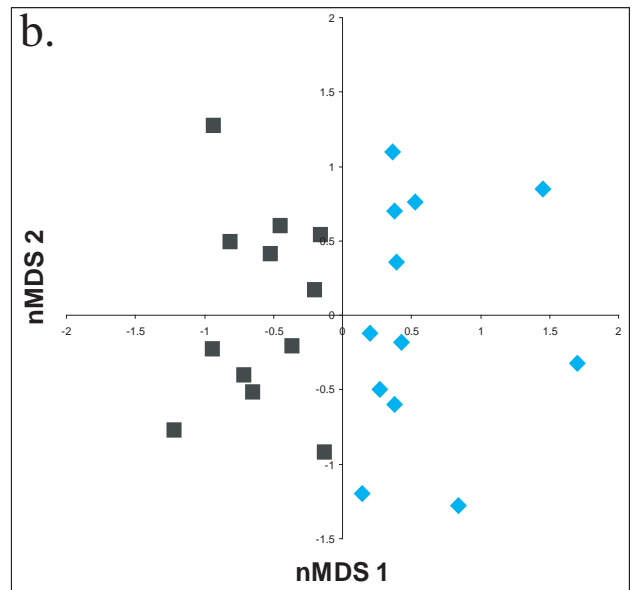
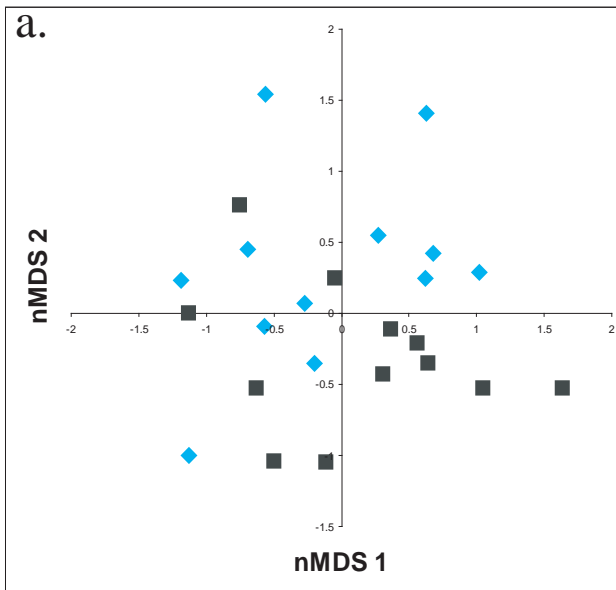
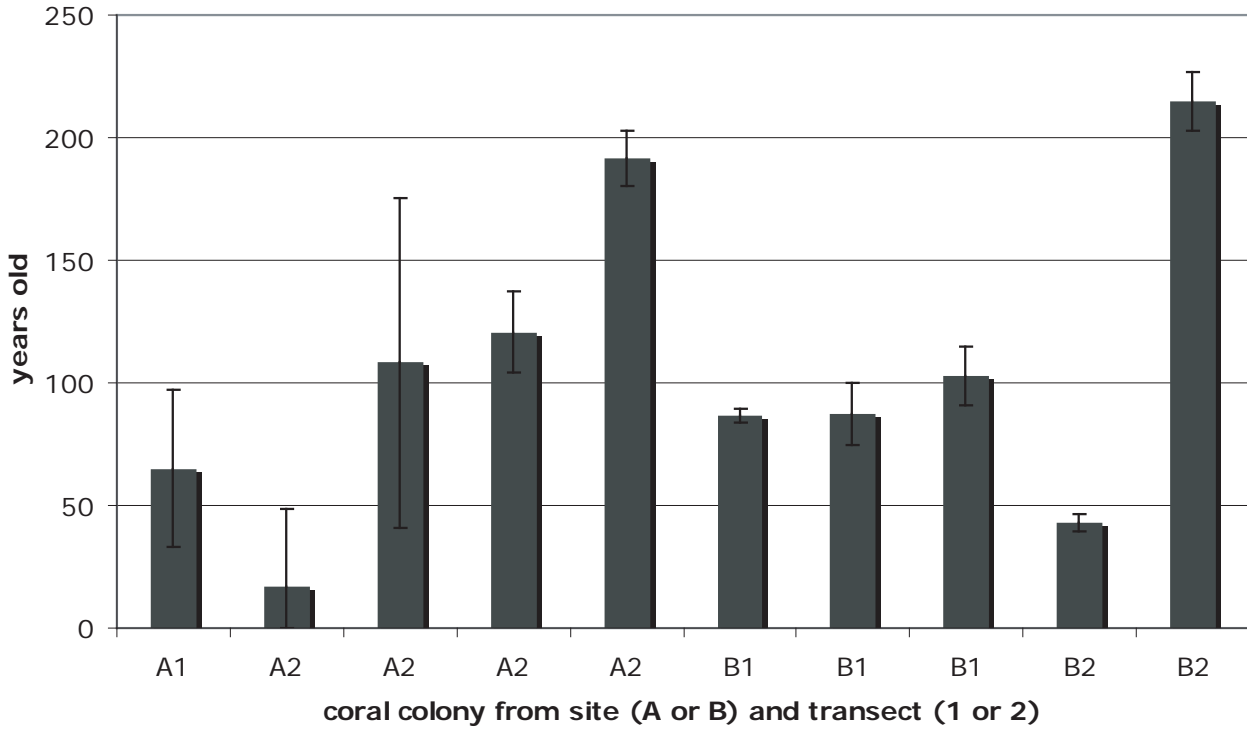


Figure 6

a.



b.

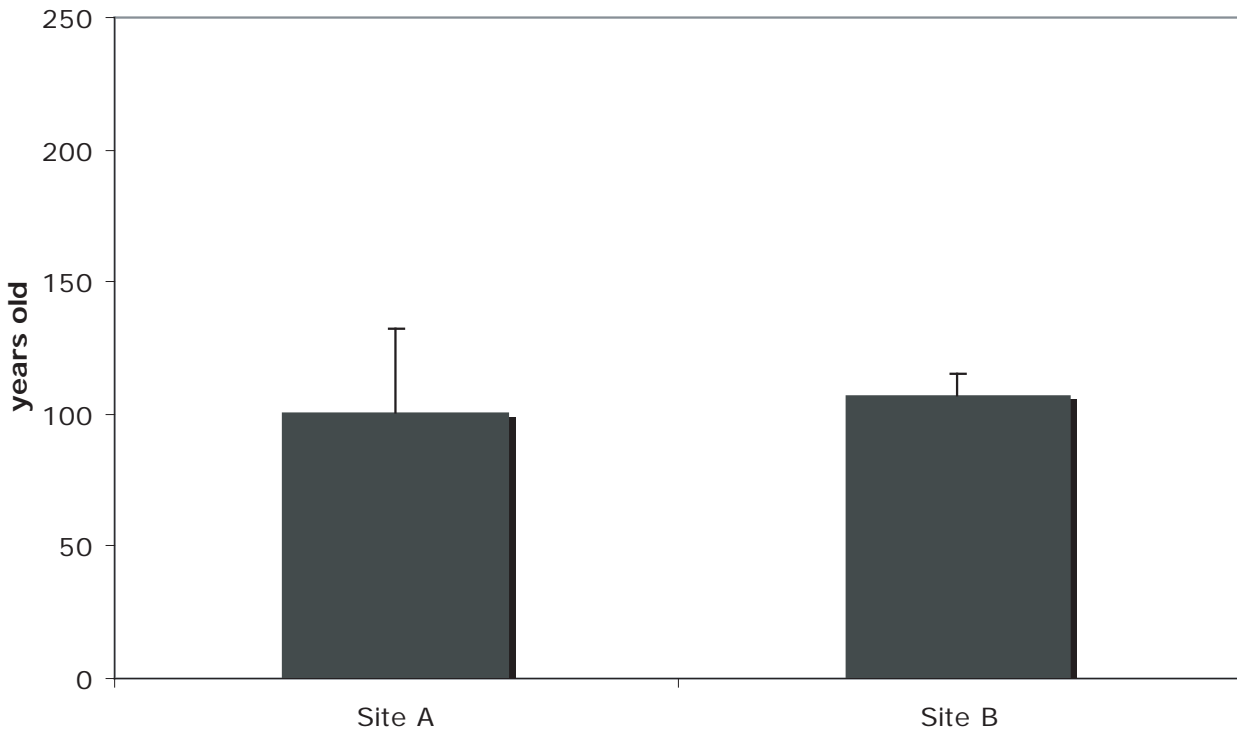


Figure 7

