Coral community changes in the Great Barrier Reef in response to major environmental changes over glacial-interglacial timescales

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Abstract

The Ribbon Reef 5 borehole offers a unique record of reef growth spanning the entire history of the northern Great Barrier Reef (GBR). Previous studies have reported the main stratigraphical, lithological and chronological patterns, as well as basic descriptions of the coralgal assemblages, but no detailed coral community analysis was undertaken. We present a quantitative analysis of the nature and distribution of Pleistocene coral communities and apply several statistical tools to define recurrent coral associations and compare the eight reef-building cycles recognized throughout the evolution of the GBR. The start of significant reef building occurs at 137 m based on a major change in coral community structure and the inception of the reef cycles (Cy1-8). This revision, along with available stratigraphical and chronological data, suggests that barrier reef initiation may have occurred prior to MIS 11, earlier than previous reports. The coral assemblages at 137 m reflect the transition from lower mesophotic (60-100 m) to upper mesophotic (30-60 m) settings, while the eight reef cycles above are characterized by three recurrent shallow-water reef-coral associations: \textit{Porites-Montipora}-faviids (Po-Mo-Fa), pocilloporids (Poc), and \textit{Acropora-Isopora} (Acro-Is). Typically,
these cycles begin with the Po-Mo-Fa association and end with the Acro-Iso association, reflecting shallowing and a catch-up growth mode. However, the first two cycles are characterized by a transitional phase dominated by the Poc association. The dominance of pocilloporids during the early stages of the GBR's history and the long-term shift to an Acropora-Isopora-dominated community may reflect an increase in competitive pressure of acroporids over pocilloporids. Our findings are consistent with the view that reef coral community structure is predictable over 100-kyr time scale. However, variations within reef cycles highlight the importance of environmental changes operating at millennial time scales. Further studies are needed to better refine the reef chronology and clarify the influence of environmental variables (i.e. sea surface temperature, turbidity) on reef coral community structure.

1. Introduction

Coral reef ecosystems are in decline worldwide (Bruno and Selig, 2007; Chin et al., 2011; De’ath et al., 2012; Jackson et al., 2014). The impact of local factors such as overfishing and pollution are compounded by the global influence of ocean warming and acidification on coral health and calcification potential (Hoegh-Guldberg, 2011). However, the decline of coral reef ecosystems is not uniform (Cinner et al., 2016) and future trends in reef community structure will depend on multiple factors, such as the intra- and interspecific adaptation potential of reef organisms, range shifts in coral species, and local anthropogenic factors like overfishing and coastal development (Pandolfi et al., 2011). Information on the responses of reef-corals exposed to environmental stressors such as elevated sea surface temperature (SST), reduced pH or high sedimentation rate can be obtained from in vivo experiments involving single coral colonies (e.g. Hoadley et al., 2015; Ganase et al., 2016) or, less commonly, a portion of a reef (Dove et al., 2013; Albright et al., 2016). Large-scale reef monitoring informs us on the current impact of global climate change and other factors as well as on the recent (few decades) history of coral reef ecosystems (e.g. Connell et al., 1997; Bak
et al., 2005; De’ath et al., 2012). These approaches are essential to our understanding of the susceptibility of reefs and reef communities to ongoing environmental perturbations. However, coral reef ecosystems are long-lived and crucial information about their long-term history and responses under various natural perturbations and environmental boundary conditions may be derived from the fossil record. Valuable information on the responses of coral communities to rapid environmental changes has been obtained from the study of Quaternary coral reef systems (Pandolfi and Greenstein, 2007; Camoin and Webster, 2015; Braithwaite, 2016). Of particular interest are the periods of rapid warming and sea level rise leading to interglacial highstands because these conditions may mimic those which coral reef ecosystems are experiencing today. Studies of fossil reefs provide important insights into the responses of coral reef ecosystems to sea level and climate changes (Woodroffe and Webster, 2014; Kiessling and Pandolfi, 2014). The Holocene and Last Interglacial records are the best documented and most extensively studied of Quaternary reef-building episodes, and improving our knowledge of older reef sequences stands as one of the major challenges of fossil reef studies (Camoin and Webster, 2015).

The Great Barrier Reef (GBR) is a passive margin and pre-Holocene reef limestones are not normally exposed at the surface (Hopley et al., 2007). Drilling is therefore necessary to study the history of reef growth and reef communities. Accumulation of reef limestones on the continental shelf occurred during interglacial periods when sea level was high enough to flood the shelf (Hopley et al., 2007; Davies, 2011). Reef growth there was consequently interrupted by sea level falls during glacial periods and became restricted to a narrow band along the shelf edge during sea level lowstands (Hopley et al., 2007; Davies, 2011). IODP Expedition 325 drilling into the submerged terraces and ridges off the modern GBR (Fig 1), combined with site survey data (Hinestrosa et al., 2016), uncovered multigenerational reef sequences developed during glacial sea level lowstands and subsequent deglacial sea level rises (Webster et al., 2011).

Few boreholes have penetrated the entire section of reef limestones deposited on the continental shelf during previous sea level highstands. The earliest, deep drilling operations were undertaken by the Great Barrier Reef Committee in 1926 at Michaelmas Cay (183 m) in the northern GBR and in 1937 at Heron Island (223 m) in the southern GBR. A petroleum exploration well was drilled at Wreck Island in 1958 (575 m) in the southern GBR (Davies, 2011). The thickness of the entire reef section in these boreholes is interpreted to be < 150 m but core recovery was poor. Two additional long, high quality boreholes were drilled in 1995, one at Ribbon Reef 5 (210 m) and the other at Boulder Reef (86 m), in the northern GBR (Alexander et al., 2001). Ribbon Reef 5 lies near the shelf edge facing the open ocean (outer-shelf reef) whereas Boulder Reef is close to the land and influenced by terrigenous
sedimentation (inner-shelf reef). These reefs lie, respectively, at opposite ends of the cross-
shelf gradient in wave energy and turbidity, and are characterized by distinct coral
communities (Done, 1982) (Fig. 1).

The relationship between the rate of vertical seafloor displacement (uplift vs.
subsidence) and eustatic sea level change controls the relative position of successive reef
sequences (Woodroffe and Webster, 2014). In relatively stable depositional settings such as
the GBR, the resulting geometry of multigenerational reef sequences is a vertical succession
of stacked reefs, each formed during a sea level highstand, bounded by low sea level erosion
surfaces (Davies et al., 1988, 1989). The erosion of the windward margin during sea level
lowstands may result in the retrogradation of successive highstand reef sequences (Davies et
al., 1988, 1989; Webster, 1999). The highstand stack model of reef development explains the
recession of shallow coralgal assemblages in the Ribbon Reef 5 cores (Webster and Davies,
2003). Similar successions of stacked Pleistocene reef units have been described in various
other locations, for example, at Eniwetok Atoll (Szabo et al., 1985), Mururoa Atoll (Camoin et
al., 2001), the Ryukyu Islands (Sagawa et al., 2001), New Caledonia (Cabioch et al., 2008),
the Florida Keys (Multer et al., 2002) and Belize (Gischler, 2007).

Previously, only two basic coral assemblages were described in the Ribbon Reef 5
borehole (Webster, 1999; Webster and Davies, 2003). One characterized by Isopora and
robust branching Acropora spp. (humilis gr. and robusta gr.), the other composed of massive
Porites and faviids associated with encrusting Porites and Montipora. Webster and Davies
(2003) interpreted these coral assemblages as representative of higher- and lower-energy
reef settings, respectively. The recurrence of apparently similar coral assemblages in the
Ribbon Reef borehole over at least 400 ka is consistent with detailed paleoecological studies
of uplifted Pleistocene reef terraces at Barbados (Jackson, 1992; Pandolfi and Jackson, 2006),
Huon Peninsula (Pandolfi, 1996, 1999), and, more recently, Egypt and Vanuatu (Mewis, 2016)
reporting the repetition of similar coral assemblages over multiple sea level highstands. These
observations suggest a remarkable persistence in coral community structure over geological
timescales of 10s to 100s kyr despite repeated sea level falls and major changes in SST
(Pandolfi, 1996; Pandolfi, 2002). The predictable nature of reef coral assemblages may result
from the high degree of ecological dependence of reef organisms due to their complex
interactions (e.g. competition, predation, and symbiosis), use of available resources, and
occupation (and re-occupation) of distinct habitats (Pandolfi, 1996; Bode et al., 2012).
However, variability in coral species composition and diversity over glacial-interglacial
timescales may arise from species migration related to elevated SST. Several studies have
presented evidence for latitudinal variations in coral species distribution related to elevated
SST occurring during the last interglacial (western Australia, Greenstein and Pandolfi, 2008;
at a global scale, Kiessling et al., 2012), the mid-Holocene (Florida, Precht and Aronson, 2004),
and in recent times (Japan, Yamano et al., 2011; Florida, Vargas-Angel et al., 2003; and
eastern Australia, Baird et al., 2012). Variability in reef-coral community structure also occurred
at a broader timescale during the Quaternary, with the abundance of Acropora increasing
markedly after the Pliocene to become the dominant reef-building coral worldwide during the
Middle Pleistocene (Renema et al., 2016). Fast growth rates and asexual reproduction via
fragmentation are attributes of the genus Acropora which make this coral particularly suitable
to track rapid Quaternary sea level changes (Renema et al., 2016). In addition, changes in
ocean surface circulation affecting larval dispersion and genetic connectivity of coral
populations during the Quaternary have been proposed as a key factor controlling the
distribution of reef-coral species (Veron, 1995).

The Ribbon Reef 5 borehole represents a rare archive of the long-term evolution of
coral assemblages in the GBR during successive sea level highstands since the inception of
reef growth in the Middle Pleistocene (for a recent review, see Davies, 2011). Until now the
published taxonomic information was largely qualitative and intended only to highlight basic
trends in taxonomic composition (Webster and Davies, 2003). A more quantitative analysis is
needed to assess the taxonomic similarity of successive coral assemblages and verify the
hypothesis that coral communities have highly predictable taxonomic compositions during
successive interglacial cycles. In this study we present a detailed analysis of the nature and
distribution of coral taxa in the Ribbon Reef 5 borehole based on a new and more
comprehensive taxonomic census. Several statistical approaches are used to identify
objectively the nature of recurrent coral assemblages with similar taxonomic compositions and
reconstruct the history of coral community changes at Ribbon Reef 5 since the inception of
the reef system. We discuss our new results within the context of previously published trends
in taxonomic composition and depositional units described in Webster and Davies (2003) and
the depositional units described in Braithwaite et al. (2004) and Braithwaite and Montaggioni
(2009). Finally, we discuss the implications of our results for understanding the response of
coral communities to individual glacio-eustatic cycles, from the colonization of bare substrate
during shelf inundation to reef demise caused by sea level fall, and coral assembly rules at
the scale of the whole history of the GBR during multiple glacio-eustatic cycles.

2. Material and methods

Ribbon Reef 5 is about 6.5 km long and 0.7–1 km wide (Fig. 1). It is one of many
ribbon reefs in the northern Great Barrier Reef that form a 700 km long ridge interrupted only
by narrow channels and forming an impressive shelf-edge barrier reef directly exposed to the
swells of the Pacific Ocean (Hopley et al., 2007).
The Ribbon Reef 5 borehole (15° 22.40' S, 145° 47.149' E) is 210 m long and the
recovery is 76% on average, although recoveries of 95% were common in the lower part of
the main reef section (Webster, 1999; Webster and Davies, 2003). The maximum length of a
core section recovered during one drill is 3 m. A total of 125 core sections (B1-B125) were
drilled with an average length of 1.68 m (Fig. 2A, B).

Three main sections have been recognized in previous publications (Fig. 2C): a basal
lower section composed of grainstones and packstones (210–158 m), a middle section rich in
rhodoliths (158–96 m), and an upper section composed of in situ reef framework (96–0 m)
(Alexander et al., 2001; boundaries revised by Webster and Davies, 2003). Webster and
Davies (2003) defined 6 reef units in the upper section (R1-R6) based on variations in coralgal
assemblages, the occurrence of soil horizons and stable isotope (O, C) data (Fig. 2D-F).
Two additional reef units (R7-R8) were identified within the middle section. Braithwaite et al.
(2004) divided the same borehole into 9 depositional units based on changes in lithology,
diagenetic features, and stable isotope data (Fig. 2G-J); evidence of emergence (erosional
surface, paleosoil) was reported between unit 6, 7, 8 and 9 in the upper section of the borehole.
The unit boundaries defined by Braithwaite et al. (2004) do not match those of Webster and
Davies (2003) except for the base of the uppermost Holocene unit at 16 m (R1 in Webster and
Davies, 2003; unit 9 in Braithwaite et al., 2004). The criteria used to define stratigraphic units
in each publication are detailed in Table 1. The diagenetic history of the borehole was
reconstructed by Braithwaite and Montaggioni (2009). Their study confirmed the correlation
between the nature and diversity of diagenetic features and the unit boundaries defined by
Braithwaite et al. (2004). Moreover, they found evidence for an additional erosional surface
within unit 6 (after Braithwaite et al. (2004)) and therefore defined two new units, i.e. 6a and
6b. Despite considerable age uncertainties, radiometric dating suggests that the main reef
section was probably accreted during the Middle Pleistocene <500 ka (MIS 13) and the lower
section could be as old as 700 ka (MIS 17) (Webster and Davies, 2003; Braithwaite et al.,
2004; Braithwaite and Montaggioni, 2009; Fig. 2K). Paleomagnetic data constrain the age of
the entire borehole to within the Brunhes chron (<780 ka, Braithwaite et al., 2004).

In the present study we reexamined the distribution, taxonomy and morphology of
reef corals (Scleractinia) in the borehole. A total of 1332 corals were recorded. Each was
categorized as either in situ (IS), probably in situ (IS?), not in situ (ISX), or context unknown
(ISN) (Webster et al., 2011). A combination of criteria was used to determine the context of fossil
corals: (1) the overall orientation of the corallum (orientation of surface projections, branches),
(2) the orientation of corallites, (3) the presence of thicker algal crusts on the upper surface of
the corallum, (4) the absence of evidence of transport (abraded or broken surfaces), (5) the
orientation of geopetal surfaces, and (6) the depositional setting (slumps, rubble) (Webster et al., 2011). Of all the corals examined, about 60% were tagged as ISX. The taxonomy of corals follows Veron (2000) except for *Isopora* which is treated as a genus (Wallace et al., 2007). Corals were identified at the species level whenever possible, but the identification was more often achieved at the genus level due to the obscuring of surface features by sediments or encrusters, or the lack of preservation. Species groups were defined for corals belonging to different species within the same genus that cannot be differentiated because they display close morphological affinities (e.g. *Favia* gr. *pallida* includes *F. pallida*, *F. speciosa*, and *F. matthaii*). For 17% of the corals examined, no taxonomic identification was possible; 84% of these unidentified corals are ISX corals. The following morphological traits were quantified: colony thickness, corallite width and branch width. Colonies attached to the substrate less than 5 cm in thickness are categorized as encrusting; the others are described as massive. Branch width is used to classify branching corals into the following three categories: fine-branching (BF, <1 cm), medium-branching (BM, 1-1.5 cm), and robust-branching (BR, >1.5 cm). Additionally the maximum thickness of coralline algal crusts was also measured.

In order to investigate the variations of coral taxonomic composition in the borehole and identify recurrent coral associations, we compared the taxonomic composition of the core sections using cluster analysis of the Bray-Curtis similarity (BC) coefficient calculated for each pair of core sections. The analysis was performed on presence-absence data and on abundance data for both the in situ (corals tagged IS and IS?) and non in situ (corals tagged ISX) fraction. The few corals for which the context was described as uncertain (ISN) were considered likely to be not in situ and were added into the list of non in situ corals (ISX). For the analysis involving abundance data, the BC coefficient was calculated using the square root of abundance values in order to mitigate the influence of taxa with high count numbers (Perry et al., 2008; Roche et al., 2011). The analysis performed on in situ corals involved the comparison of the distribution of 37 taxa across 75 core sections. For the analysis of ISX corals, the data matrix is composed of 21 taxa and 114 core sections. The lower number of taxa in the analysis of the ISX fraction results from the overall lower resolution of the taxonomic identification of allochtonous corals due to their poorer state of preservation. The results of these analyses enable us to identify any regularity in the sequence of corals observed in the borehole and highlight stratigraphic intervals displaying recurrent coral associations. 2-D MDS ordination of BC coefficients and analyses of similarities (ANOSIM test) are used to assess differences in taxonomic composition between these stratigraphic intervals. A similarity percentage analysis (SIMPER) is conducted to constrain the identity of taxa that are characteristic of the recurrent coral associations. Statistical analyses were performed using the computer software PRIMER v6 (Clarke and Gorley, 2006).
3. Results

The reexamination of the Ribbon Reef 5 borehole led to the identification of 58 species or species groups of scleractinian corals under 34 genera (Table 2, S1). Three additional genera of non-scleractinian corals have also been identified (Tubipora, Millepora and Sinularia?). The majority of in situ corals identified belong to Acropora, Isopora, Montipora, Porites, faviids and pocilloporids. There is a clear inflection point in the cumulative number of in situ corals identified in the borehole as a function of depth at around 120-125 m (Fig. 3). The thickness of in situ coral colonies and coralline algal crusts increases steadily in the lower half of the borehole, reaching a first maximum around 117 m and 132 m, respectively, and then shows large fluctuations (Fig. 4A,C). Upcore trends in colony thickness vary among coral genera. Faviids display a broadly decreasing trend in colony thickness at the scale of the borehole (Fig. 4A). The thickness of Porites and Montipora colonies is highly variable unlike that of Acropora and Isopora colonies (Fig. 4A). In addition, acroporids with robust-size branches become common above 130 m and increase in frequency toward the borehole top (Fig. 4B).

3.1. Analysis of in situ (IS, IS?) corals

3.1.1 Comparison of core sections

Cluster analysis of the BC coefficient calculated between each pair of core sections using presence-absence data produces 15 clusters (G1-G15) and two isolated core sections (54, 106) (Fig. 5A). These groups can be characterized by the systematic occurrence of one or a combination of the following taxa: Acropora, Isopora, encrusting and massive Porites, encrusting and massive Montipora, pocilloporids, and faviids (Fig. 5B). A large cluster defined by the association of encrusting Porites and Montipora (G12) can be further subdivided into 5 groups of core sections (a-e) and 1 isolated core section (41). Similar results are obtained using the same analysis based on abundance data (Figs S2 and S3).

There is a dramatic change in coral assemblage composition at around 137 m (Fig. 6A). Below that limit, the proportion of in situ corals is low and the coral assemblages are characterized by Galaxea (106), Goniastrea (G9), foliaceous pectiniids (most likely Echinophyllia, G2), encrusting Porites and/or Montipora (G11, G14, G7). Above that limit, the number of in situ corals increases sharply, and so does the diversity of coral assemblages. The sequence of coral assemblages above 137 m is complex and characterized by a high variability in composition at the scale of the core section. However, there is a cyclic pattern that is overprinted on this apparent complexity (Fig. 6B). This cycle is defined by repeated
intervals devoid of Acropora and characterized by encrusting and massive Porites, encrusting Montipora, and diverse faviids (mainly G12e). These intervals are systematically followed by intervals enriched in Acropora and/or Isopora (G5, G3, G12b, G12c and G12d). The transition is in places marked by the occurrence of a pocilloporid-rich interval (mainly G4). We therefore conclude that one complete cycle is defined by the following succession of coral associations: a Porites-Montipora-faviids association (Po-Mo-Fa), a pocilloporid association (Poc), and an Acropora-Isopora association (Acro-Iso) (Fig. 6A, B). We identify 8 cycles in total based on these recurrent shifts in composition (Cy1-Cy8) overlying the lower unit (Lw) (Fig. 6B). Two of these cycles (Cy8 and Cy7) are composed of all three coral associations. The Poc association is missing in 4 cycles (Cy6, Cy5, Cy4 and Cy1) and its presence at the base of Cy2 is uncertain due to the sparse occurrences of pocilloporids in this interval. The Po-Mo-Fa association is only absent in Cy3 (and perhaps Cy2), and is poorly developed in Cy8. Interestingly, the Po-Mo-Fa interval is thickest in Cy7 and becomes progressively thinner in subsequent cycles. Leptoseris occurs at the base of the Po-Mo-Fa interval in Cy7 and Cy6 and coexists with Pachyseris speciosa in Cy7. The Po-Mo-Fa interval in Cy6 also contains several colonies of Galaxea astreata. Massive Isopora occurs in the Po-Mo-Fa interval in Cy4 only. The Poc intervals in Cy7 and Cy6 are well developed and characterized mostly by Stylophora, in association with Seriatopora and an Echinopora-rich assemblage (G13) in Cy6. The Poc association at the base of Cy3 is also composed of Stylophora. The species composition of Acropora in the Acro-Iso association is variable from one cycle to another and includes the following major taxonomic groups: A. gr. humilis, A. gr robusta?, A. gr. formosa and various fine-branching morphological groups (corymbose, digitate, arborescent and platy). Isopora colonies display encrusting, massive or robust-branching growth forms. Acropora and Isopora may coexist or else may appear in sequence. In two cycles, Cy4 and Cy6, the shift from Isopora- to Acropora-dominated assemblages is particularly clear. The Acro-Iso association includes Porites and Montipora as well as diverse faviids in Cy6, Cy4 and Cy1.

In summary, comparison of the taxonomic compositions of core sections shows (1) high variability in taxonomic composition from one core to the next, (2) a regular pattern of taxonomic composition at the scale of several core sections characterized by the repetition of three main coral associations (Po-Mo-Fa, Poc and Acro-Iso), and (3) two main units at the scale of the whole borehole – a non-reefal unit with low density, mostly encrusting or foliaceous coral assemblages changing at around 137 m to a reefal unit with high-density, high-diversity coral assemblages displaying cyclicities in taxonomic composition.

3.1.2. Comparison of reef cycles (Cy1-Cy8) and the lower unit (Lw)

Cluster analysis of the BC coefficient calculated between each pair of cycles using
presence-absence data reveals two clusters: cluster 1 composed of cycles Cy8, Cy3 and Cy2, and cluster 2 composed of cycles Cy4, Cy5, Cy6 and Cy7 (Fig. 7A). The 2D MDS plot clearly shows the two groups of data points occupying distinct regions of space (Fig. 7B). The difference in taxonomic composition between clusters 1 and 2 is confirmed by the ANOSIM test which gives an R value of +0.80 (p=2.9%). The average BC similarities of the cycles in clusters 1 and 2 are 61.9% and 66.5%, respectively (Fig. 7C). The taxonomic diversity of the cycles in cluster 1 is lower than that of those in cluster 2. The SIMPER analysis shows that cluster 1 is characterized by robust-branching Acropora, encrusting and massive Porites, and Stylophora, whereas cluster 2 is defined by medium-branching Acropora, encrusting to massive Isopora, encrusting to massive Porites and Montipora, Stylophora, Favia, and pectiniids (mainly Echinophyllia) (Table 3A). Cy1 is more closely related to cluster 2 than cluster 1 and the lower unit of the borehole (Lw) is clearly distinct from the reef cycles based on presence-absence data.

Cluster analysis based on the square root of abundance data provides a slightly different result. The same cluster 2 is produced but Cy2 is grouped with Cy1 instead of with Cy3 and Cy8. Cycles Cy1 and Cy2 have in common the following taxa: fine-branching Acropora, encrusting to massive Porites and Montipora, and Favites. The lower unit (Lw) is grouped with Cy1 and Cy2 due to similarities in abundances of encrusting Montipora, and encrusting and massive Porites.

3.1.3. Comparison of coral associations (Po-Mo-Fa, Poc and Acro-Iso)

Cluster analysis and 2D MDS ordination of BC similarities were also used to compare the taxonomic compositions of the three coral associations (Po-Mo-Fa, Poc and Acro-Iso) among reef cycles and with the lower unit (Lw). The clustering reflects the separation between the three previously identified coral associations (Fig. 8A). Cluster 1 is composed of two of the four Poc intervals, and clusters 2 and 3 mostly include Po-Mo-Fa and Acro-Iso intervals, respectively. However, there is some overlap as the clustering is not entirely determined by the type of association to which each interval is assigned. The 2D MDS plot also shows that the three associations define three overlapping domains (Fig. 8B). The ANOSIM test suggests there is a significant difference in taxonomic composition between the three coral associations (R = +0.34). The SIMPER analysis highlights the corals that are the most representative of each association and the results are entirely consistent with the description presented above (Table 3B). Massive to encrusting Porites and encrusting Montipora are characteristic of both associations Po-Mo-Fa and Acro-Iso but the latter is distinguished primarily by the presence of diverse Acropora species. Stylophora is indicative of the Poc association. The average BC similarities of the intervals within each association are widely different, i.e. 50.3%, 37.7% and
23.2% for associations Acro-Iso, Po-Mo-Fa and Poc, respectively (Fig. 8C). This variability is illustrated by the spread of the data points associated with each domain in the 2D MDS plot. The association Acro-Iso displays the compositions that are the most consistent among different stratigraphic intervals. The composition of the lower unit (Lw) is most similar to that of the Po-Mo-Fa association of Cy6.

The separation between the three coral associations is less clear when the square root of abundance data is used for cluster analysis. This is mostly due to the influence of encrusting Porites and Montipora which can be equally abundant in intervals assigned to different coral associations so that these intervals are more closely related in the cluster diagram when abundance data are used.

3.2. Analysis of non-in situ (ISX) corals

The number and proportion of non-in situ corals is largest in the lower unit of the borehole below 137 m. The proportion of non-in situ corals that could be identified is lower than in the in situ fraction because non-in situ corals have commonly undergone some degree of physical alteration that tends to reduce the size of individual specimens and erase morphological details. The taxonomic composition of the non-in situ fraction is clearly dominated by Acropora and pocilloporids. Together these taxa represent 37-84% of the number of ISX corals identified in each cycle.

Cluster analysis of the BC coefficient calculated between each pair of core sections using presence-absence data for the ISX fraction leads to the segregation of 12 groups (Fig. 9). The occurrence of Acropora or pocilloporids together or separately clearly determines the clustering of most of the core sections. For example the large cluster G7 is defined primarily by the association of Acropora and pocilloporids whereas G11 is defined on the basis of the absence of all taxa but Acropora. Like the in situ corals, the composition of the lower detrital unit is distinct from that of the overlying reefal unit. The ISX coral fraction in the lower unit is characterized by pocilloporids, encrusting Porites and Montipora, and lesser agariciids (mostly Leptoseris) and pectiniids (mostly Echinophyllia) (Fig. 10). The main difference with the in situ fraction is the abundance of pocilloporids and agariciids. Interestingly, there is a difference in the generic composition of pocilloporids in the ISX fraction between the lower and upper unit: Seriatopora occurs more consistently in core sections of the lower unit whereas Stylophora and Pocillopora are generally dominant in the overlying reefal unit (with the notable exception of Cy7) (Fig. 10). There is also a significant increase in the frequency of occurrence and relative abundance of Acropora and pocilloporids in the reefal unit and most of the ISX coral assemblages defined by cluster analysis occurring in the main reefal unit are characterized by
a combination of pocilloporids and Acropora (Figs. 9, 10).

The cyclic pattern observed in the reefal unit above 137 m is not clearly reflected in the ISX fraction. However, there are variations in the ISX fraction that coincide with changes in the compositions of in situ corals. The transition between the Po-Mo-Fa and Poc associations in Cy8 and Cy7 coincides with an increase in the abundance of pocilloporids in the ISX fraction (Fig. 10). In addition, the Po-Mo-Fa intervals in Cy7 and Cy6 correlate with a marked increase in the abundance of non-in situ Porites and/or Montipora (Fig. 10).

4. Discussion

4.1. Long-term trends in coral community structure

Variations in the abundance, taxonomy and morphology of in situ corals in the Ribbon Reef 5 borehole indicate a general shallowing upward trend and a transition from a relatively deep, non-reefal setting to cycles of reef growth and demise, in agreement with previously published works (Alexander et al., 2001; Webster and Davies, 2003; Braithwaite et al., 2004; Braga and Aguirre, 2004). We identify the start of the major reef-building processes at 137 m based on: (1) a significant change in coral community structure and, (2) the inception of a cyclic pattern in coral succession which characterizes the upper part of the borehole. This boundary corresponds with the base of the first reef unit (i.e. R8) originally described in Webster and Davies (2003).

The in situ coral assemblage below 162 m is dominated by thin laminar Porites, Montipora and Echinophyllia, also occurring in the non in situ fraction with Leptoseris. The taxonomy and morphology of these corals and their association with Melobesioid algae (Braga and Aguirre, 2004) suggest a depositional setting deeper than 60 m (Abbey et al., 2013). Fine branching Seriatopora is common among coral clasts and could be derived from the upper mesophotic zone (30-60 m). Seriatopora is currently found down to 55 m in the GBR (Bridge et al., 2012) and forms dense populations in the upper mesophotic zone in the Ryukyu Islands (Sinniger et al., 2013; Sinniger, 2016). The transition at 162 m to recurrent Lithophylloid-rich intervals coincides with a marked increase in coral colony thickness (Fig. 4). Abbey et al. (2013) reported a similar shift in coral thickness at 60 m in the GBR with modern and postglacial mesophotic corals primarily thin platy to encrusting (less than 2 cm in thickness) below 60 m and more massive above 60 m. In addition, faviids, particularly Echinopora, became more common in the ISX fraction above 162 m in the Ribbon Reef 5 borehole. Faviids, in particular Echinopora, were reported in the mesophotic zone from depths <60 m by Abbey et al. (2013). In conclusion, the coralgal assemblages in the lower section of the Ribbon Reef...
5 borehole are similar to the mesophotic coralgal communities of the modern GBR and the evolution in taxonomic and morphological composition indicates the transition from a lower mesophotic (60-100 m) to an upper mesophotic (30-60 m) coralgal assemblage.

Above 137 m the thicknesses of corals and algae and the numbers and diversity of corals increase sharply. The 137 m boundary also marks a sharp increase in the abundance of branching *Isopora* and *Acropora* species (Figs. 4, 11), two major components of modern shallow exposed reef crest communities of outer shelf reefs in the GBR (Done, 1982). The evolution of coralgal assemblages in the Ribbon Reef 5 borehole clearly indicates a general shallowing trend initiated in the lower section (Webster and Davies, 2003; Braga and Aguirre, 2004). The Ribbon Reef 5 record suggests that *Isopora* and *Acropora* were important contributors to the reef-building process from the beginning of the reef growth history since the Acro-Isso association is present in the initial cycle (Cy8) and was reestablished during each subsequent cycle. This observation is in line with a recent compilation showing that *Acropora* became a dominant reef builder during the Middle Pleistocene, and this success has been attributed to the ability of *Acropora* to cope with rapid sea level rise (Renema et al., 2016). In the modern GBR *Isopora* is closely associated with *Acropora* in wave-exposed habitats (Done, 1982) and our record shows that this was also the case during the past 3-5 interglacial highstands (Webster, 1999; Braithwaite and Montaggioni, 2009), indicating that these two taxa have played a key role in not only the initiation but also the long-term maintenance of the barrier reef ecosystem during successive rapid post-glacial sea level rises.

4.2. Barrier reef initiation

Drilling into submerged fossil reefs along the shelf edge of the modern GBR has demonstrated that lowstand and early deglacial reef communities may have been important sources of coral propagules to support the early colonization of the newly inundated shelf (Webster et al., 2011). In the absence of a precursor lowstand reef ecosystem coral propagules may have been initially supplied by nearby non-reefal shallow communities. The morphology and taxonomy of the ISX corals in the lower section of the Ribbon Reef 5 borehole, mostly laminar *Porites*, *Montipora*, agariciids and fine-branching *Seriatopora*, suggests that the majority of coral clasts were derived from nearby deep mesophotic communities and no clear signature of shallow water coral reef communities is recognized. Another possibility involves a more distant source of propagules, either from locations farther north, i.e. the Torres Shelf or the Gulf of Papua, where reefs may have already been established (Davies et al., 1991), or from the Queensland Plateau (McKenzie et al., 1993). The latter seems more likely given the present-day configuration of ocean currents with the westward-flowing South Equatorial Current dividing around Cairns into the northward-flowing North Queensland...
Current and the southward-flowing East Australian Current (Choukroun et al., 2010). However, simulations of larval dispersal trajectories show that the connectivity between Papua New Guinea and the GBR may be enhanced during La Niña events (Treml et al., 2008).

The timing of barrier reef initiation is still poorly constrained. The warm SST’s and high-amplitude sea level during the MIS 11 interglacial have been proposed as triggers for the initiation of extensive barrier reef growth worldwide, including the GBR (Droxler et al., 2003; Montaggioni et al., 2011; Droxler and Jory, 2013). This view has been challenged by sedimentological studies of distal boreholes from the upper slope of the Marion Plateau placing the onset of the southern central GBR earlier, during MIS 15 (Dubois et al., 2008) or MIS 17 (Obrochta, MS 2004). Given that alkenone SST reconstructions in the region indicate MIS 11 was not particularly warm (Lawrence and Herbert, 2005), the claim that barrier reef initiation on the Eastern Australian Shelf occurred at MIS 11 needs to be reassessed. A similar pre-MIS 11 age (MIS 15 or MIS 13) has been suggested for reef initiation on the Western Australian Shelf and linked to the strengthening of the Leeuwin Current as well as increased aridity and alkalinity (Gallagher et al., 2014). Higher-amplitude sea level oscillations after the Mid-Pleistocene Transition (Elderfield et al., 2012) have also been proposed as a possible trigger for extensive barrier reef growth on the Eastern Australian Shelf through prolonged shelf flooding (Dubois et al., 2008) and the creation of a cyclone corridor reducing terrigenous sediment input on the outer shelf (Larcombe and Carter, 2004). Our analysis of the coral succession in the Ribbon Reef 5 borehole, combined with previously published data on coralline algae (Braga and Aguirre, 2004) and the currently available age data, suggest the emergence of a cyclic pattern of reef growth and demise took place prior to MIS 11. Based on the chronology of the Ribbon Reef 5 borehole presented in Montaggioni et al. (2011), reef initiation would therefore have occurred during MIS 15, in agreement with Dubois et al. (2008).

4.3. Environmental interpretation of the coral associations

The Ribbon Reef 5 borehole above 137 m is characterized by a cyclic pattern in the coral community structure. Each cycle is composed of up to three coral associations (Po-Mo-Fa, Poc and Acro-Iso). The Po-Mo-Fa association, dominated by encrusting to massive Porites and encrusting Montipora associated with faviids and agariciids, indicates a relatively deep, mid to lower reef slope habitat or a turbid environment (Done, 1982; Veron, 2000). Porites and Montipora are typical of highly turbid carbonate environments (Sanders and Baron-Szabo, 2005). The occurrence of Lithophylloid and Melobesioid algae in Cy7, with this coral association may indicate more temperate climatic conditions (Braga and Aguirre, 2004). The pioneer Po-Mo-Fa association is replaced by the Poc association in Cy8 and Cy7 which consists primarily of Stylophora pistillata, associated with Seriatopora hystrix and faviids.
(mostly branching *Echinopora*) only in Cy7. *Stylophora pistillata* and *Seriatopora hystrix* have a broad range of distribution, from shallow to deep (>30 m) reef habitats with *Stylophora pistillata* locally dominant on exposed reef fronts and *Seriatopora hystrix* typical of reef flats (Done, 1982; Veron, 2000; Bridge et al., 2012; Abbey et al., 2013). Dense communities of *Seriatopora hystrix* have been reported from the upper mesophotic zone in the Ryukyu Islands (Sinniger et al., 2013; Sinniger, 2016). The association of *Echinopora* (probably *E. mammiformis*) and *Seriatopora hystrix* in Cy7 indicates a low-energy upper reef slope or lagoonal setting (Done, 1982; Veron, 2000). The lithology in this interval is best described as a floatstone with bioclasts heavily encrusted by Lithophylloid algae (*Rhodolith unit 1* of Webster and Davies, 2003), in concordance with a hydrodynamic regime characterized with low-wave exposure. The Acro-Iso association, composed of *Isopora* and medium-size to robust branching *Acropora* gr. *humilis* and *Acropora* gr. *robusta*, indicates a shallow exposed (<10 m) reef setting in the GBR (Done, 1982) and other Indo-Pacific reefs (Cabloch et al., 1999; Hongo and Kayanne, 2010; Hongo, 2012). In contrast, the assemblage characterized by arborescent *Acropora* gr. *formosa* between 90-95 m in Cy7 is typically found in the modern GBR in lower-energy habitats on reef slopes or in lagoons (Done, 1982; Oliver et al., 1983; Wallace, 1999). Notable shifts in taxonomic composition occur within the Acro-Iso association and consist of transitions between *Isopora*-dominated and *Acropora*-dominated intervals. In Cy7, the transition from arborescent *Acropora* gr. *formosa* to *Isopora* was discussed above and interpreted as a shallowing-upward trend. In Cy6 and Cy4, the transition from *Isopora*-dominated to *Acropora*-dominated intervals does not seem to reflect any major change in palewater depth as both assemblages are associated with shallow Mastophoroid algae. Interestingly, the shift in these two cycles coincides with unit boundaries defined in Braithwaite et al. (2004). Transitions between *Acropora*-dominated and *Isopora* dominated intervals are observed in Holocene core sections from the southern GBR (Dechnik et al., 2015). In particular, the replacement of an *Acropora* assemblage by an *Isopora* assemblage on the windward margin of the Fitzroy reef was interpreted as reflecting a minor shallowing within the 0-10 m depth range. There is however no clear evidence, based on associated species and algal crust thicknesses, that the two assemblages in the Ribbon Reef 5 borehole occupied distinct reef zones.

4.4 Interpretation of reef cycles

The repeating cycles observed in the Ribbon Reef 5 borehole begins with the Po-Mo-Fa association and terminates with the Acro-Iso association with or without a transitional phase characterized by the Poc association. The repeated cycles of coral succession
observed in Ribbon Reef 5 are broadly similar to Holocene sequences described in the GBR, characterized by a pioneer assemblage of massive *Porites* and faviids replaced by a high-energy *Acropora-Isopora* assemblage (Montaggioni, 2005; Dechnik et al., 2015). This type of coral succession is common in the Holocene and interpreted as a shallowing-upward sequence reflecting a catch-up mode of reef growth (Montaggioni and Braithwaite, 2009). In a similar fashion, the Po-Mo-Fa association in the successive reef-building episodes observed at Ribbon Reef 5 likely represents the first stage of colonization of the shelf after inundation during each post-glacial sea level rise, perhaps also influenced by lower SSTs based on the occurrence of Lithophylloid and Melobesioid algae (Braga and Aguirre, 2004). The first of these pioneer corals in the Ribbon Reef 5 are colonies of *Goniastrea* (probably *G. edwardsi*) at the base of Cy8. Several species of *Goniastrea*, including *G. edwardsi*, are stress-tolerant, particularly to sedimentation and turbidity (Perry and Smithers, 2009; Darling et al., 2012), and therefore may be particularly tolerant to sediments resuspended during shelf inundation. Subsequent Po-Mo-Fa intervals are stratigraphically thicker and more diverse, characteristics which may reflect the increase in diversity of the regional species pool and/or higher amplitudes of sea level rise. Greater accommodation space created by higher-amplitude sea level rise could have led to thicker vertical accumulations of the initial Po-Mo-Fa assemblage but this remains to be explored.

The Poc association precedes the Acro-Iso association in three reef cycles, i.e. Cy8, Cy7 and Cy3. In Cy8, a *Stylophora*-Mastophoroid assemblage is overlain by an *Acropora* gr. *humilis*-Mastophoroid assemblage. Both indicate a shallow exposed (<10 m) reef setting. A similar interpretation can be proposed for the coral succession in Cy3. In Cy7, a *Stylophora*-Seriatopora and Lithophylloid assemblage is replaced by an *Acropora* gr. *formosa* and Lithophylloid assemblage, which is in turn replaced by an *Isopora* and Mastophoroid assemblage. The coralgal succession in Cy7 suggests a general shallowing-upward sequence. The transition to Mastophoroid algae could also reflect higher SSTs (Braga and Aguirre, 2004). However, it is not clear whether the transition between the first two assemblages results from decreasing paleowater depths as their distribution range overlaps. In conclusion, the transition from the Poc association to the Acro-Iso association in Cy8, Cy7 and Cy3 does not necessarily reflect any major change in depositional setting or environmental conditions and may result from variations in community structure within the same habitat caused by lateral reef accretion (Dechnik et al., 2016; Webb et al., 2016; Webster and Davies, 2003). However, this hypothesis does not explain the dominance of the Poc association in the first two reef cycles and the subsequent long-term shift to acroporid-dominated branching coral assemblages. An alternative explanation is that this transition reflects an ecological succession driven by intrinsic ecological factors. Two reasons may explain the success of *Stylophora* and *Seriatopora* during the early phase of the GBR evolution. First, the pool of *Acropora* and
Isopora colonies may have been less extensive during the early phase of the GBR history. The newly formed barrier reef may not have been as extensive as it is today due to the absence of an antecedent barrier reef to support further reef growth (Larcombe and Carter, 2004). The presence of well-developed Rhodolith facies (Rd1 and Rd2; Webster and Davies, 2003) in Cy7 supports this interpretation. Furthermore, the less abundant and patchier populations of fast-growing acroporids may have given an opportunity to pocilloporids to colonize the substrate first. This hypothesis is supported by the general upward increase in Acropora abundance at Ribbon Reef 5 (Fig. 11). Both Stylophora pistillata and Seriatopora hystrix are fast-growing corals (Pratchett et al., 2015), release fertilized larvae (Hugues et al., 1999), and have a broad depth distribution range in the GBR (Done, 1982, Bridge et al., 2012). They are successful early colonizers of denuded substrates after disturbance (Loya, 1976; Fan and Dai, 1996) and have been described as “weedy” species (Darling et al., 2012). Stylophora pistillata and Seriatopora hystrix are therefore ideal candidates to rapidly colonize available substrates during rapid environmental and sea level changes, in exposed and protected settings, respectively. The second reason is that environmental conditions early in the GBR history may have favored opportunistic species like S. pistillata and S. hystrix. The lack of a fully developed barrier reef system may have exposed the outer shelf reefs to more storm-induced disturbances and terrigenous influence (Larcombe and Carter, 2004), favoring opportunistic species like S. pistillata and S. hystrix. This would also explain the paucity of reef framework below 85 m despite the inception of the reef cycles much earlier (Webster et al., 2003; Braithwaite et al., 2004).

4.5. Comparison of reef cycles

The remarkable cycles of coral community structure observed in the Ribbon Reef 5 borehole and the repetition of similar types of coral associations in successive generations of reefs is consistent with records of high persistence in coral community structure during successive highstands reported elsewhere (Jackson, 1992; Pandolfi, 1996; Pandolfi and Jackson, 2006). Our analysis shows high similarity in taxonomic compositions between successive cycles, particularly between Cy4, Cy5, Cy6 and Cy7 that are also the cycles with the highest taxonomic diversity. However, the Ribbon Reef 5 record also shows that the competition between pocilloporids and acroporids may have caused variations in the relative abundance of these taxa during the history of the GBR. In addition, some of the cycles identified, specifically Cy4, Cy5 and Cy6, may represent more than one highstand episode based on the previous interpretation of the reef units in the same borehole (Webster, 1999). Braithwaite and Montaggioni (2009) also identified two subaerial erosion surfaces at 36 m and 57 m, respectively. We do not see any persistent change in reef setting associated with these events. However, it is possible that the initial coral association after the reflooding of the shelf
was an Acro-Iso association indicating a shallow exposed reef setting similar to that of the Acro-Iso association terminating the preceding cycle.

The similarities among intervals characterized by the same type of coral association (Po-Mo-Fa, Poc or Acro-Iso) are variable. Intervals displaying the highest similarities are characterized by the Acro-Iso association. Except for the interval in Cy7, the Acro-Iso association probably represents an aggrading phase of reef growth in a shallow exposed environment under relatively stable hydrodynamic conditions that may have promoted higher similarities in taxonomic composition. Conversely, the Po-Mo-Fa association represents the initial phase of reef development during sea level rise and initial conditions on the submerged shelf may have been more unpredictable (Dechnik et al., 2015). Furthermore the composition of the initial coral association depends on the pool of coral species available to recolonize the shelf that is, in turn, controlled by environmental conditions during the preceding lowstand and subsequent sea level rise. The higher variability in taxonomic composition among the Poc intervals may reflect the contrasting paleoenvironmental interpretations assigned to the Poc interval in Cy7 (low-energy) and those of Cy8 and Cy3 (high-energy).

Trends in colony thickness across reef cycles also vary from one taxon to another. Some trends underline similarities in community structure between intervals from different reef cycles. For example, in most cycles thicker *Porites* colonies are systematically associated with the first phase of reef growth, i.e. the Po-Mo-Fa intervals (Fig. 4A). Massive *Porites* associated with faviids typically occurs in a semi-exposed or sheltered environment in Indo-Pacific reefs consistent with our interpretation of the Po-Mo-Fa association (Montaggioni, 2005). In addition, peaks in *Montipora* colony thickness coincide with Acro-Iso intervals (Fig 4A). Massive *Montipora* is a major component of some shallow (<10 m) reef facies and agrees well with our interpretation of the Acro-Iso association (Camoin et al., 2012). Conversely, the colony thickness of faviids does not seem to be determined by the coral association, but rather shows a long-term decline across multiple reef cycles (Fig. 4A). This is correlated with a notable increase in the frequency of acroporids with robust branches toward the top of the borehole (Fig. 4B). One possible explanation for this would be an incremental increase in wave exposure due to the progressive retrogradation of reef sequences over multiple sea level highstands (Davies et al., 1988, 1989; Webster, 1999). In addition, the fast-growing acroporids may have had a long-term competitive advantage over slow-growing faviids (Renema et al., 2016).

Based on our analysis of the nature and distribution of coral taxa in the Ribbon Reef 5 borehole, we have identified patterns of coral community changes at varied time scales (Fig. 12). Superimposed on the long-term cycles of reef initiation and demise are variations in
community structure within each cycle, represented by successive stratigraphic intervals with
distinct coral associations as well as short-term variations in community structure within these
intervals. Coral succession in each cycle is clearly influenced by glacial-interglacial sea level
changes that ultimately control accommodation space and reef growth. In addition, millennial-
scale environmental changes, such as variations in SST and turbidity, associated with
deglacial conditions and shelf inundation are likely to influence coral community structure.
However, the importance of these factors is still poorly constrained. A key objective of future
studies will therefore be to quantify these environmental variables and analyze their
relationship with the observed patterns of coral community changes. Promising techniques
include laser abrasion ICP-MS U/Th measurements to improve reef chronologies and novel
geochemical proxies (REE, lithium isotopes) to reconstruct terrigenous sediment influx.

5. Conclusions

Our detailed study of the taxonomy and distribution of coral taxa in the Ribbon Reef 5
borehole, combined with previously published records, leads to the following conclusions:

1. The pattern of repeated reef growth and demise starts at 137 m. Available
stratigraphical and chronological data suggest that barrier reef initiation may have
occurred prior to MIS 11. The non-reefal section, below 137 m, shows a transition from
a lower to an upper mesophotic coral assemblage, replaced in turn by the initial coral
association of the first reef cycle at 137 m, indicating a shallowing-upward trend.

2. Three coral associations are identified in the reefal section: (1) encrusting to massive
Porites, encrusting Montipora and faviids (Po-Mo-Fa) – mid to lower reef slope habitat
or turbid environment, (2) pocilloporids (Poc) – shallow exposed reef fronts (Stylophora
pistillata) and protected settings (Seriatopora hystrix), and (3) massive or branching
Isopora and medium to robust-branching Acropora (Acro-Is) – shallow exposed (<10
m) reef settings (Isopora-Acropora gr. humilis-Acropora gr. robusta) and lower-energy
reef-slope or lagoonal settings (Acropora gr. formosa).

3. Eight reef cycles are identified. Each typically starts with the Po-Mo-Fa association
(pioneer) and ends with the Acro-Iso association. We interpret this as a shallowing-
upward sequence following shelf inundation during each successive post-glacial sea
level rise and highstand. Poor water quality due to sediment resuspension and/or lower
SST’s may also have influenced the pioneer association.

4. The Poc association is prominent in the first two reef cycles (Cy8, Cy7) and represents
a transitional phase between the Po-Mo-Fa and Acro-Iso associations. The singular
predominance of pocilloporids during the early stages (Cy8, Cy7) of reef history and
the long-term shift to an Acropora-Isopora-dominated shallow reef community may be
attributed to an increase in competitive pressure of acroporids over pocilloporids within
the same reef habitat.

5. The recurrence of broadly similar coral associations throughout multiple interglacial highstands is consistent with the view that reef coral community structure is predictable over 100-kyr time scales. However, variations within reef units indicate that other important processes are also operating on millennial scales, particularly during initial stages of shelf reflooding, causing differences in water clarity, SST, or the pool of coral species available to reseed the newly inundated substrate.

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Figure and Table captions

Figure 1: (A) Map showing the location of Ribbon Reef 5 and Boulder Reef in the northern Great Barrier Reef and (B) detailed bathymetric map of Ribbon Reef 5 based on Laser Airborne Depth Sounder (LADS) (0-40 m) and multibeam echo sounder (40-250 m) data (Beaman et al., 2008). The yellow and white sticks show the approximate location of the deep Ribbon Reef 5 bore hole and the shorter (<20 m) Holocene cores (Davies and Montaggioni, 1985). (C) Schematic profile of the continental shelf showing the broad geologic setting of the onshore boreholes Ribbon Reef 5 and Boulder Reef and the offshore IODP 325 boreholes (Webster et al., 2011).

Figure 2: (A) Representation of the core sections (1-125) of the Ribbon Reef 5 borehole with (B) core recovery. The basic subdivisions of the borehole defined in previous publications are presented in the other columns. (C) The three main sections of the borehole with boundaries from Webster and Davies (2003). (D-F) Depositional reef units (R1-R8) and corresponding variations in lithology and coralgal assemblages as described in Webster and Davies (2003). (G) Depositional units (U1-U9) and lithological variations (H), reported in Braithwaite et al.
(2004) (with U6 divided into U6a and U6b in Braithwaite and Montaggioni, 2009), δ¹⁸O and δ¹³C profiles (I, J) and age data (K) published in Braithwaite et al. (2004).

**Figure 3:** Cumulative numbers of corals as a function of depth (time). Note that the cumulative number of non in situ corals (ISX) is an underestimation.

**Figure 4:** Bar charts showing the variations in some key morphological characteristics of corals and coralline algae with depth: (A) thickness of coral colonies, (B) branch width of *Acropora* and *Isopora* and (C) thickness of coralline algal crusts.

**Figure 5:** (A) Group-averaged hierarchical clustering of the BC coefficient calculated between core sections based on taxonomic presence-absence data for in situ corals; (B) two-way table showing the taxa indicative of each cluster (coral assemblage).

**Figure 6:** (A) Column showing the succession of in situ (IS, IS?) coral assemblages defined by cluster analysis (using the same colour code as in Figure 5) and distribution of major taxonomic groups in the borehole; (B) succession of coral associations (Po-Mo-Fa, Poc and Acro-Iso) and reef cycles (Cy1-Cy8) defined on the basis of the sequence of coral taxa presented in this study; (C) comparison of the depositional units of Webster and Davies (2003) and of Braithwaite et al. (2004) (D) (modified by Braithwaite and Montaggioni, 2009).

**Figure 7:** (A) Group-averaged hierarchical clustering of the Bray-Curtis similarity coefficient calculated between each reef cycles (Cy1-Cy8) and the lower unit (Lw); (B) the same analysis but represented as a 2D MDS plot of the BC coefficient with the two clusters identified in (A) circled in black; (C) the average similarity between reef cycles in each cluster and the results of the ANOSIM test.

**Figure 8:** (A) Group-averaged hierarchical clustering of the Bray-Curtis similarity coefficient calculated between borehole intervals assigned to one of the three coral associations (Po-Mo-Fa, Poc and Acro-Iso) and the lower unit (Lw); (B) the same analysis but represented as a 2D MDS plot of the BC coefficient with colours identifying each interval as belonging to the association Po-Mo-Fa (black), Poc (orange), Acro-Iso (blue) and the lower unit (purple); (C) the average similarity within each group of intervals assigned to a coral association and the results of the ANOSIM test.

**Figure 9:** (A) Group-averaged hierarchical clustering of the BC coefficient calculated between core sections based on taxonomic presence-absence data for non-in situ (ISX) corals; (B) two-way table showing the taxa indicative of each cluster (coral assemblage).
Figure 10: Columns showing (A) the succession of non in situ (ISX) coral assemblages defined by cluster analysis (using the same colour code as in Figure 8), (B) the distribution of coral associations described in this paper and (C) the succession of reef cycles against stacked area charts showing the variations in the number of non-in situ corals identified in each core section for various major coral taxa.

Figure 11: Bar chart of the number of Acropora recorded in each core section for in situ (IS) and non in situ (ISX) specimens. The asterisks indicate core sections in which the number of non-in situ Acropora was likely underestimated. (A) Above the bar chart are displayed the available chronologic data for the Ribbon Reef 5 borehole, (B) the reef cycles and coral associations defined in this paper, (C) the depositional units published in Braithwaite and Montaggioni (2009), and (D) those defined by Webster and Davies (2003).


Table 1: Comparison of criteria used to define depositional unit boundaries.

Table 2: List of coral taxa identified in the Ribbon Reef 5 borehole.

Table 3: Results of the similarity percentage analysis (SIMPER).

Supplementary figure S1: Distribution of in situ (IS, IS?) and non in situ (ISX) coral taxa in the Ribbon Reef 5 borehole identified in this study. Each coral is represented by a horizontal bar (solid fill: IS, IS? no fill: ISX). Corals displayed in the column Po/Mo are those for which the distinction between Porites and Montipora could not be made and include mainly thin encrusting colonies. Bar charts showing the variations in the thickness of in situ corals and algal crusts in the borehole are also shown.
Supplementary figure S2: (A) Group-averaged hierarchical clustering of the BC coefficient calculated between core sections based on the square root of abundance data for in situ corals; (B) two-way table showing the taxa indicative of each cluster (coral assemblage).

Supplementary figure S3: Columns showing the succession of in situ (IS, IS?) coral assemblages defined by cluster analyses: (A) analysis of presence-absence data and (B) analysis of the square root of abundance data.
Figure 1

A. Australia

B. Boulder Reef

C. Onshore
- Boulder Reef
- Ribbon Reef 5

Offshore
- IODP 325

Inner shelf
- Turbidity: High
- Wave exposure: Low

Outer shelf
- Turbidity: Low
- Wave exposure: High

86 m — Borehole length — 210 m
Figure 2
Figure 3
Figure 4
Figure 6
**Figure 7**

### 2D Stress: 0.06

**Within-group similarity**

- **Cluster 1:** 61.91%
- **Cluster 2:** 66.49%

### ANOSIM

- **Global test**
  - $R = +0.84$
  - $p = 0.2\%$

- **Pairwise test**
  - Cluster 1 vs Cluster 2
  - $R = +0.80$
  - $p = 2.9\%$
C. Within-group similarity

Po-Mo-Fa: 37.65  
Poc: 23.20  
Acro-Iso: 50.30  

ANOSIM test

- Global test $R = +0.34$  
  $p = 0.3\%$

- Pairwise tests
  - vs vs $R = +0.31$  
    $p = 1.0\%$
  - vs vs $R = +0.49$  
    $p = 0.8\%$
  - vs vs $R = +0.49$  
    $p = 1.9\%$

Figure 8
Figure 9
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Asterisks indicate core sections in which the number of non-in situ corals was likely underestimated.
Figure 11
Table 1. Comparison of criteria used to define depositional unit boundaries.

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<th>Surface</th>
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| Criteria used in Webster (1999) and Webster and Davies (2003). |
| Criteria used in Braithwaite et al. (2004) and Braithwaite and Montaggioni (2009). |
| Subdivision of U6 into U6a and U6b proposed in Braithwaite and Montaggioni (2009). |
Table 2. List of coral taxa identified in the Ribbon Reef 5 borehole.

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<th>SCLERACTINIAN CORALS</th>
<th>NON-SCLERACTINIAN CORALS</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1. Acroporidae</strong></td>
<td></td>
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<tr>
<td>1. A. sp. 1 (BRF ARB)</td>
<td></td>
</tr>
<tr>
<td>2. A. sp. 2 (BRF COR)</td>
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<tr>
<td>3. A. sp. 3 (BRF DIG)</td>
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<tr>
<td>4. A. sp. 4 (BRF TUB)</td>
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</tr>
<tr>
<td>5. A. sp. 5 (BRM ARB)</td>
<td></td>
</tr>
<tr>
<td>6. A. gr. hyacinthus (PLATY)</td>
<td></td>
</tr>
<tr>
<td>7. A. gr. formosa (STAG)</td>
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</tr>
<tr>
<td>8. A. gr. humilis (DIG, COR)</td>
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<tr>
<td>9. A. gr. robusta?</td>
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<td>2. Isopora</td>
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</tr>
<tr>
<td>10. I. sp. 1 (BR)</td>
<td></td>
</tr>
<tr>
<td>11. I. sp. 2 (EN-M)</td>
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<tr>
<td>3. Astreapora</td>
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<tr>
<td>12. A. sp.</td>
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<td>4. Montipora</td>
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<tr>
<td>13. M. sp. 1 (EN)</td>
<td></td>
</tr>
<tr>
<td>14. M. sp. 2 (M)</td>
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<tr>
<td><strong>2. Poritidae</strong></td>
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<td>5. Portites</td>
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<td>15. P. sp. 1 (BR)</td>
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<tr>
<td>16. P. sp. 2 (KN)</td>
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<tr>
<td>17. P. sp. 3 (EN)</td>
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<tr>
<td>18. P. sp. 4 (M)</td>
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<td>6. Goniopora</td>
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<tr>
<td>19. G. sp. ISX</td>
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<td>7. Alveopora</td>
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</tr>
<tr>
<td>20. A. sp. ISX</td>
<td></td>
</tr>
<tr>
<td>3. Astrocoeniidae?</td>
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<tr>
<td>8. Stylocoeniella?</td>
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<tr>
<td>21. S. sp.</td>
<td></td>
</tr>
<tr>
<td>4. Pocilloporidae</td>
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<tr>
<td>9. Seriatopora</td>
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<tr>
<td>22. S. hystrix</td>
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<tr>
<td>10. Stylophora</td>
<td>6. Mussidae</td>
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<tr>
<td>23. S. pistillata</td>
<td>23. Symphyllia</td>
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<tr>
<td>11. Pocillopora</td>
<td>44. S. sp.</td>
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<tr>
<td>24. P. verrucosa</td>
<td>15. Tubiporidae</td>
</tr>
<tr>
<td>12. Favidae</td>
<td>27. Euphylliidae?</td>
</tr>
<tr>
<td>25. C. furcata ISX</td>
<td>24. Euphylla?</td>
</tr>
<tr>
<td>13. Favia</td>
<td>45. E. sp.?</td>
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<tr>
<td>27. F. stelligera</td>
<td>46. G. astreata</td>
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<tr>
<td>28. F. laxa</td>
<td>47. G. fascicularis ISX</td>
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<td>29. F. gr. pallida</td>
<td>9. Siderastraeidae</td>
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<tr>
<td>30. F. pentagona ISX</td>
<td>48. C. gr. columnna</td>
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<td>31. F. gr. abditia</td>
<td>10. Agarciidae</td>
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<tr>
<td>15. Goniastrea</td>
<td>27. Pavona</td>
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<tr>
<td>32. G. retiformis</td>
<td>49. P. clavus ISX</td>
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<tr>
<td>33. G. Edwardsii</td>
<td>28. Leptoseris</td>
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<tr>
<td>16. Platygryra</td>
<td>50. L. foliosa ISX</td>
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<tr>
<td>34. P. pini</td>
<td>51. L. gardineri ISX</td>
</tr>
<tr>
<td>35. P. gr. sinensis</td>
<td>29. Pachyseris</td>
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<tr>
<td>17. Leptoria</td>
<td>52. P. rugosa</td>
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<tr>
<td>36. L. phrygia</td>
<td>53. P. speciosa</td>
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<tr>
<td>18. Oulophyllia</td>
<td>30. Fungia</td>
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<tr>
<td>37. O. sp.</td>
<td>54. F. sp.</td>
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<tr>
<td>19. Montastrea</td>
<td>31. Cycloseris</td>
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<tr>
<td>38. M. cura</td>
<td>55. C. sp.</td>
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<tr>
<td>20. Leptastrea</td>
<td>12. Pectiniidae</td>
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<td>39. L. pruinosa</td>
<td>32. Echinophyllia</td>
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<tr>
<td>21. Echinopora</td>
<td>56. E. echnina ISX</td>
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<td>40. E. lamellosa</td>
<td>13. Merulinidae</td>
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<td>41. E. manmiformis</td>
<td>33. Hydnaphora</td>
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<tr>
<td>42. E. gemmacea ISX</td>
<td>57. H. sp.</td>
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<tr>
<td>22. Cyphastrea</td>
<td>14. Dendrophylliidae</td>
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<tr>
<td>43. C. serailia</td>
<td>34. Turbinaria</td>
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<tr>
<td>44. S. sp.</td>
<td>58. T. sp.</td>
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ISX The superscript ISX indicates taxa recorded only in the non-in situ fraction.
### Table 3
Results of the similarity percentage analysis (SIMPER).

**A. Comparison of reef cycles**

<table>
<thead>
<tr>
<th>Cluster 1</th>
<th>Av.Abund</th>
<th>Av.Sim</th>
<th>Sim/SD</th>
<th>Contrib%</th>
<th>Cum.%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acropora BR</td>
<td>1.00</td>
<td>11.60</td>
<td>11.63</td>
<td>18.73</td>
<td>18.73</td>
</tr>
<tr>
<td>Porites EN</td>
<td>1.00</td>
<td>11.60</td>
<td>11.63</td>
<td>18.73</td>
<td>37.47</td>
</tr>
<tr>
<td>Porites M</td>
<td>1.00</td>
<td>11.60</td>
<td>11.63</td>
<td>18.73</td>
<td>34.39</td>
</tr>
<tr>
<td>Stylophora</td>
<td>1.00</td>
<td>11.60</td>
<td>11.63</td>
<td>18.73</td>
<td>74.93</td>
</tr>
<tr>
<td>Acropora BM</td>
<td>0.67</td>
<td>4.17</td>
<td>0.58</td>
<td>6.73</td>
<td>81.66</td>
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<table>
<thead>
<tr>
<th>Cluster 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acropora BM</td>
</tr>
<tr>
<td>Isopora M</td>
</tr>
<tr>
<td>Montipora EN</td>
</tr>
<tr>
<td>Montipora M</td>
</tr>
<tr>
<td>Porites EN</td>
</tr>
<tr>
<td>Porites M</td>
</tr>
<tr>
<td>Po/Mo</td>
</tr>
<tr>
<td>Stylophora</td>
</tr>
<tr>
<td>Favia</td>
</tr>
<tr>
<td>Pectiniidae</td>
</tr>
<tr>
<td>Acropora BF</td>
</tr>
<tr>
<td>Pocillopora</td>
</tr>
<tr>
<td>Leptoria</td>
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</tbody>
</table>

**B. Comparison of coral associations**

<table>
<thead>
<tr>
<th>Po-Mo-Fa assoc.</th>
<th>Av.Abund</th>
<th>Av.Sim</th>
<th>Sim/SD</th>
<th>Contrib%</th>
<th>Cum.%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Po/Mo</td>
<td>1.00</td>
<td>12.95</td>
<td>3.19</td>
<td>34.39</td>
<td>34.39</td>
</tr>
<tr>
<td>Montipora EN</td>
<td>0.83</td>
<td>7.05</td>
<td>1.34</td>
<td>18.71</td>
<td>53.10</td>
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<tr>
<td>Porites M</td>
<td>0.83</td>
<td>7.05</td>
<td>1.34</td>
<td>18.71</td>
<td>71.82</td>
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<tr>
<td>Porites EN</td>
<td>0.67</td>
<td>4.05</td>
<td>0.78</td>
<td>10.75</td>
<td>82.57</td>
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</table>

<table>
<thead>
<tr>
<th>Poc assoc.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stylophora</td>
</tr>
<tr>
<td>Acropora BM</td>
</tr>
<tr>
<td>Montipora M</td>
</tr>
<tr>
<td>Acro-Iso assoc.</td>
</tr>
<tr>
<td>Stylophora</td>
</tr>
<tr>
<td>Acropora BM</td>
</tr>
<tr>
<td>Montipora M</td>
</tr>
</tbody>
</table>

- **a**: Results of the similarity percentage analysis for the two clusters identified in figure 6.
- **b**: Results of the similarity percentage analysis for the three coral associations (Po-Mo-Fa, Poc and Acro-Iso).
- **c**: Frequency of occurrence (1.00 meaning the coral occurs in 100% of the samples).
- **d**: Ratio of the contribution of a taxon to the average similarity of a group (SIM) to the standard deviation of their contribution (SD). Taxa with the highest Sim/SD are present most consistently among the samples of a group.
- **e**: The listed corals are those which account for 80-85% of the within-group similarity.
Supplementary figure S1