

Late glacial to deglacial variation of coralgal assemblages in the Great Barrier Reef, Australia

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Abstract

Integrated Ocean Drilling Program (IODP) Expedition 325 cored submerged reefs along the shelf edge of the Great Barrier Reef (GBR) to study sea-level and environmental changes and their impacts on reef communities and reef growth since the Last Glacial Maximum (LGM). Previous work defined five reef sequences (Reef 1-

37 5) that span the last 30,000 years. Here we examined the variation in coralgal
38 assemblages and their paleoenvironmental settings in late glacial to deglacial
39 sequences from 23 holes cored seaward of the modern GBR in water depths from 46
40 to 131 m along four transects at three localities: Hydrographers Passage (HYD-01C
41 and HYD-02A), Noggin Pass (NOG-01B), and Ribbon Reef (RIB-02A). We identified
42 three coralline algal assemblages and eight coral assemblages indicating a broad
43 range of reef settings from the shallow reef crest (0–5 m) to the deep forereef slope
44 (>20 m). We document in detail for the first time the distribution and composition of reef
45 communities that grew in the GBR during the LGM from 22,000–19,000 years ago.
46 They included coral taxa that are major reef builders today: *Isopora*, *Acropora* gr.
47 *humilis*, *Dipsastraea* gr. *pallida*, *Porites*, and *Montipora*. Prior to the fall in sea level to
48 the maximum extent of the LGM, late glacial reef communities developed more
49 proximally (landward) to the modern GBR along the shelf edge. Their distribution and
50 composition reflect influences of the older Pleistocene basement depth and possible
51 terrigenous sediment inputs. Post-LGM deglacial reef growth was vigorous in proximal
52 sites and characterized by the accretion of a very shallow high-energy coralgal
53 assemblage composed of medium to robustly branching *Acropora*, including *A.* gr.
54 *humilis*, and thick algal crusts of *Porolithon* gr. *onkodes* associated with vermetid
55 gastropods. More distally, reef growth was variably impacted by terrigenous input
56 following deglacial reflooding of antecedent reef terraces. The coralgal succession and
57 sedimentary facies in Noggin Pass indicate that an early drowning trend was linked to
58 increased turbidity that was likely controlled by shelf morphology (narrow shelf, steep
59 slope) and/or proximity to a paleo-river mouth. The deglacial succession in Ribbon
60 Reef lacks typical shallow-water indicators, which may reflect influences of the
61 particularly steep slope of the northern GBR shelf edge on reef zonation. A major sea-
62 level jump at the onset of the Younger Dryas displaced reef habitats further upslope,
63 forming a barrier reef system mainly composed of robustly branching acroporids
64 distinct from the more distal sites. Our results highlight the importance of sedimentation
65 and shelf morphology in addition to relative sea-level changes in controlling variations
66 in reef community over centennial to millennial timescales.

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69 **1. Introduction**

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71

72 Coral reefs worldwide are threatened by ocean warming that triggers mass coral

73 bleaching events, and there are concerns about the ability of coral reefs to recover
74 from mortality events which have recently become more intense and more frequent
75 (Hughes et al., 2018). Global warming also drives sea level rise, which poses another
76 threat to coral reefs already compromised by other factors, such as global warming,
77 pollution, and terrigenous sedimentation (Perry et al., 2018). To understand the
78 potential long-term impacts of these threats, the fossil record can be used to determine
79 how coral reefs and reef communities have responded to rapid environmental changes
80 (Pandolfi, 2011), constrain the conditions of reef initiation and demise, and inform
81 predictive models of reef development and biotic changes (Salles et al., 2018).

82
83 Offshore drilling of submerged reefs gives rare opportunities to study responses of
84 reefs and reef communities to glacial conditions and rapid post-glacial sea-level rise. In
85 addition, accurate sea-level reconstructions can be based on combining data from
86 paleowater depth indicators (e.g. corals, coralline algae, and vermetid gastropods) and
87 radioisotope dating (Chappell and Polach, 1991; Deschamps et al., 2012). Tectonically
88 stable locations far from the poles, such as the GBR and Tahiti, are of particular
89 interest because effects of post-glacial isostatic rebound are minimal (Yokoyama et al.,
90 2001a). Individual coral colonies are commonly used for paleoclimate reconstructions
91 based on geochemical proxies (Asami et al., 2009; Felis et al., 2012), and submerged
92 reefs are good candidates for geochemical studies because they are less likely to be
93 affected by prolonged subaerial exposure and meteoric diagenesis (Abbey and
94 Webster, 2011).

95
96 Submerged reefs exist in the Atlantic (e.g. Lighty et al., 1978; Macintyre et al., 1991),
97 Pacific (e.g. Cabioch et al., 2008; Webster et al., 2004a, 2004b), and Indian Oceans
98 (e.g. Dullo et al., 1998; Vora et al., 1996). The first cores drilled in submerged reefs
99 were from Barbados (Fairbanks, 1989), and their study suggested two brief episodes of
100 very rapid post-glacial sea-level rise punctuated a more gradual deglaciation curve
101 (postulating a constant uplift rate of 0.34 mm yr^{-1}): meltwater pulse MWP-1A at 14.2–
102 13.8 ka and MWP-1B at 11.5–11.1 ka (Deschamps et al., 2012; Abdul et al., 2016). In
103 contrast, studies of onshore and offshore cores from Tahiti, subsiding at a rate of ~ 0.25
104 mm yr^{-1} , found no evidence for MWP-1B (Bard et al., 2010), but confirmed the
105 existence of MWP-1A (Camoin et al., 2012; Deschamps et al., 2012). Despite the
106 abrupt MWP-1A sea-level rise, reef framework grew without interruption at Tahiti, but
107 there was a shift to fast-growing corals and retrogradation of shallow reef-edge coralgal
108 assemblages (Abbey et al., 2011a; Blanchon et al., 2014; Camoin et al., 2012). There

109 are very limited data on sea-level and reef growth histories during the late glacial to
110 early deglacial period (30–15 ka) before MWP-1A. Corals of Last Glacial Maximum
111 (LGM) age, including shallow-water *Acropora* species, have been recovered in the
112 Pacific Ocean by dredging submerged reefs and drilling on uplifted terraces (reviewed
113 by Braithwaite, 2016; Camoin and Webster, 2015; Montaggioni, 2005; Woodroffe and
114 Webster, 2014). The new IODP Expedition 325 record of sea level and reef growth in
115 the GBR region over the past 30 ka offers a unique window on reef community
116 changes during the LGM and last deglacial period (Yokoyama et al., 2018; Webster et
117 al., 2018).

118

119 In eastern Australia, the first evidence of glacial to early deglacial reef growth came
120 from 2D topographic surveys (echo sounder, seismic data) of the seafloor that revealed
121 the extensive distribution of probable submerged reef structures along the shelf edge of
122 the modern GBR (Carter and Johnson, 1986; Harris and Davies, 1989; Hopley, 1982).
123 More recently, high-resolution 3D bathymetric surveys of these features identified them
124 as relict barrier reefs and high-relief patch reefs between 40–70 m water depth, or as
125 fringing reefs and low-relief patch reefs between 80–100 m (Abbey et al., 2011b;
126 Beaman et al., 2008; Webster et al., 2008). Dredged samples from the tops of some of
127 these submerged reefs have provided new insights into the responses of mesophotic
128 coralgal communities to deglacial sea-level rise and associated environmental changes
129 (Abbey et al., 2013).

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132 IODP Expedition 325 (Exp. 325) in 2010 targeted submerged reefs along the shelf
133 edge of the modern GBR, with the goal of constraining the history of sea level and reef
134 growth since the LGM (Webster et al., 2011). The overall chronology of reef growth and
135 reef architecture derived from IODP Exp. 325 data are described by Webster et al.
136 (2018) and Yokoyama et al. (2018), and supported by seismic imaging of the GBR shelf
137 edge (Hinestrosa et al., 2014). Five main reef sequences can be distinguished over the
138 past 30 ka: (1) an early glacial reef sequence between 27 and 22 ka (Marine Isotope
139 Stage 2; MIS2) confined mainly to the inner reef terrace (Reef 2); (2) an LGM-early
140 deglacial reef sequence between 22 and 17 ka confined to the mid and outer terraces
141 (Reef 3a); (3) a deglacial reef sequence between 17 and 13 ka extending landward
142 following reflooding of the inner terrace (Reef 3b); (4) a late deglacial reef sequence
143 between 13 and 10 ka localized further upslope and developing into a proto-barrier reef
144 (Reef 4); and (5) the modern GBR reef sequence on the shelf from 10 ka to the

145 present. The older Pleistocene basement consisting of reef deposits ≥ 30 ka is defined
146 as Reef1. While a basic description of the coral and algal composition of the reef
147 boundstones is reported in Webster et al. (2018), we now provide the most complete
148 analysis of the Exp. 325 cores, including two transects RIB-02A and HYD-02A not
149 previously described. We present comprehensive, detailed descriptions of the coralgal
150 assemblages in each sequence, discuss their paleoenvironmental significance, and
151 use published age data to constrain the timing of changes in reef biotic composition.
152 We examine the responses of the GBR ecosystem to late glacial to deglacial sea-level
153 changes, based on spatial and temporal variation in coralgal assemblages. More
154 specifically, we offer the first glimpse into the taxonomic composition of the GBR during
155 the last glacial period and analyze the impact of deglacial flooding of the shelf on
156 coralgal communities.

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159 **2. Methods**

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162 **2.1. Geologic setting and drilling operations**

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164 The modern GBR lies on the continental shelf of northeastern Australia and extends
165 from 24° 30' S to 9° 30' S (Hopley et al., 2007). The geomorphology of the Eastern
166 Australian Shelf is characterized by a southward increase in shelf width (from ca. 50
167 km to >100 km) and a decrease in the angle of the slope at the shelf break: >30° at
168 Ribbon Reef, 15°–20° at Noggin Pass, and ca. 2° at Hydrographers Passage (Abbey et
169 al., 2011b; Hineostrova et al., 2016). Reef initiation took place during the Middle
170 Pleistocene, and successive highstand reef units formed on the shelf during interglacial
171 periods (Humblet and Webster, 2017). During glacial sea-level lowstands, the area of
172 potential reef accretion was restricted to a narrow band along the shelf edge (Hopley et
173 al., 2007). Bathymetric and seismic surveys have provided robust evidence for the
174 existence of submerged fossil reefs offshore of the modern GBR (e.g., Beaman et al.,
175 2008; Hineostrova et al., 2014). The reef structures targeted in this study consist of a
176 double – inner and outer – barrier reef rising from depths of 50 to 70 mbsl and three
177 reef terraces (formed by drowned fringing reefs) below 70 mbsl classified into inner,
178 mid, and outer terraces based on bathymetry (Abbey et al., 2011b; Beaman et al.,
179 2008; Hineostrova et al., 2014).

180

181 A total of 33 holes (M0030A–M0057A) were cored into distinct submerged reef
182 structures in water depths from 46.4 to 131.2 mbsl (meters below sea level, corrected
183 to the Lowest Astronomical Tide, LAT) and one (M0058A) on the forereef slope at
184 170.3 mbsl along the shelf edge of the GBR during IODP Exp. 325 (Webster et al.,
185 2011; Harper et al., 2015). Holes were arranged along four transects from landward
186 (proximal) to seaward (distal) in three geographic areas, from north to south: Ribbon
187 Reef (RIB-02A) at 15.5° S (offshore Cooktown and adjacent to Ribbon Reef 3), Noggin
188 Pass (NOG-01B) at 17.1° S (offshore Cairns), and Hydrographers Passage (HYD-01C
189 and HYD-02A) at 19.7°–19.8° S (offshore Mackay) (Fig. 1). Downhole gamma-ray
190 measurements were carried out on four holes and used as a proxy for fine-grained
191 terrigenous sediment flux (Webster et al., 2011). The depth of sedimentary and
192 biological constituents in IODP Exp. 325 cores reported in this paper does not account
193 for the uncertainty related to core recovery (for a detailed discussion on the issues of
194 core recoveries and depth uncertainties, see supplementary information in Webster et
195 al., 2018).

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200 **2.2. Core description**

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203 Cores were split lengthwise into an archive half and a working half. The former was
204 described visually after taking high-resolution digital images and performing
205 petrophysical measurements (as described by Webster et al., 2011). The present study
206 focuses on the late glacial MIS2 to last deglacial reef sequence. The older Pleistocene
207 basement (≥ 30 ka) was reached in 14 holes and consists mostly of reefal deposits
208 below the barrier reef and inner terrace, and grey packstone and grainstone containing
209 *Halimeda* segments and larger benthic foraminifers below the deeper terraces
210 (Gischler et al., 2013; Yagioka et al., 2019). Diagenetic alteration of the older
211 Pleistocene basement in holes from the barrier reef and inner terrace indicates
212 subaerial exposure prior to postglacial sea-level rise (Gischler et al., 2013; Webster et
213 al., 2011, 2018). The MIS2 to last deglacial reef sequence penetrated by coring varies
214 greatly in thickness, ranging from ca. 4.76 m in hole M0056A to 34.16 m in M0031A.

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217 Visual examination included descriptions of core disturbances (e.g. fracturing,
218 downhole contamination), lithologies, sedimentary and diagenetic features,
219 microbialites, and fossils (e.g., corals, coralline algae, mollusks). Corals were identified
220 to the lowest taxonomic level possible. Species groups were established when several
221 species of the same genus and with similar growth forms could not be distinguished.
222 The taxonomic classification follows Veron (2000) with more recent modifications by
223 Budd et al. (2012), Huang et al. (2014, 2016), and Wallace et al. (2007). Coral growth
224 forms and context (i.e. autochthonous vs. allochthonous) were characterized using
225 criteria detailed in Webster et al. (2011, 2018). A coral colony is described as
226 encrusting if its thickness is <5 cm and massive if >5 cm. The term “platy” refers to
227 colonies less than 5 cm thick with free margins, and the term “laminar” encompasses
228 both the encrusting and platy morphologies. Coral branches are referred to as fine,
229 medium, or robust, based on average diameters of <1 cm, 1–1.5 cm, or >1.5 cm,
230 respectively. Information on the across-shelf and depth distribution of scleractinian
231 corals in the GBR is summarized in Done (1982), Veron (1986, 2000), Veron and
232 Pichon (1976, 1979, 1982), Veron and Wallace (1984), and Veron et al. (1977).
233 Identification of coralline algae was based on examination of 385 thin sections, using
234 the same diagnostic criteria to delimit species and species groups that were applied to
235 living coralline algae in the Indo-Pacific areas (Verheij, 1994; Keats, 1995, 1997; Keats
236 et al., 1996, Athanasiadis and Ballantine, 2014; Maneveldt and Keats, 2014; Van der
237 Merwe and Maneveldt, 2016; Rösler et al., 2016; Caragnano et al., 2018, Peña et al.,
238 2018; Gabrielson et al., 2018). We followed the taxonomic schemes recently proposed
239 for coralline algae by Nelson et al. (2015), and by Rösler et al. (2016) for the family
240 Corallinaceae, order Corallinales, and the generic classification scheme proposed by
241 Rösler et al. (2016) and Caragnano et al. (2018) for this family. We created species
242 groups for species that share common characters observable in fossil corallines but
243 which are separated by features that are not preserved in fossil specimens. The
244 paleodepths inferred from coralline algal assemblages were derived from the published
245 distributions of living members of the identified taxa (Adey et al., 1982; Cabioch et al.
246 1999; Littler and Littler, 2003; Payri et al., 2000; Dechnik et al., 2017). Basic information
247 about coralgal assemblages and the distribution of vermetid gastropods has been
248 reported for transects HYD-01C and NOG-01B in Webster et al. (2018). These data are
249 now integrated with the other transects and with new detailed information on the
250 percent volume of coralgal framework, thickness of coralline algal crusts, and the
251 presence/absence of vermetid gastropods at 10 m intervals in all Exp. 325 cores. Our
252 new paleowater depth reconstruction is based on integration of all coral, coralline

253 algae, and vermetid gastropod information, all of which have been widely used as
254 depth indicators in reconstructions of Quaternary sea-level changes (Abbey et al.,
255 2011a; Braga and Aguirre, 2004; Cabioch et al., 1999; Dechnik et al., 2017; Iryu et al.,
256 2010; Webster and Davies, 2003). Occurrences of algal and coral taxa identified in the
257 reef sequences are presented in Table S1. The rates of vertical reef accretion
258 presented in this paper are those reported in Webster et al. (2018) based on the linear
259 visual fit analysis of the *in situ* corals and coralline algae age vs. depth plots for
260 transects HYD-01C and NOG-01B (Table S2).

261

262

263 **3. Results**

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266 **3.1. Coralline algal assemblages and paleoenvironmental interpretations**

267

268 In the MIS2 to last deglacial reef sequence in the GBR, coralline algae occur mainly as
269 crusts that build boundstones by growing over and between corals and other
270 encrusting organisms, such as vermetids, bryozoans, serpulid worms and foraminifers.
271 Corallines also appear as fragments within the internal sediment and, very rarely, form
272 small nodules around bioclastic nuclei. Twenty eight species or species groups
273 belonging to 15 genera were recognized in this study, although the generic attribution
274 of two species included in *Hydrolithon* (*H. murakoshii* and *H. breviclavium*) needs
275 revision (Table 1). Except for *Lithoporella*, species that only form thin encrusting thalli
276 (<100 µm thick) have not been identified since preservation of their diagnostic
277 anatomical features is uncommon. In the best preserved transects, HYD-01C and
278 NOG-01B, there were totals of 19 species and species groups in both the early glacial
279 (Reef 2) and late deglacial (Reef 4) coralline algal assemblages; totals were slightly
280 higher in the LGM (Reef 3a) and early deglacial assemblages (Reef 3b) with 25 and 22
281 species and species groups, respectively, due to a few rare species not recorded in the
282 other assemblages (Table 1). All identified genera and species were reported in
283 present-day Pacific reefs, some of them under different names from those currently
284 accepted (Verheij, 1994; Adey et al., 1982; Cabioch et al., 1999; Payri et al., 2000;
285 Ringeltaube and Harvey, 2000; Littler and Littler, 2003; Rösler et al., 2016; Dechnik et
286 al., 2017; Caragnano et al., 2018; Peña et al., 2018). Because some extant species or
287 species groups only live in relatively narrow depth ranges, their present-day
288 distributions can be used to infer the paleodepth of boundstone formation. Three

289 different coralline algal assemblages are recognized with characteristic paleodepth
290 ranges (Table 2 and Fig. 2).

291

292 **Assemblage aA1** indicates paleodepths of less than 10 m and is characterized by
293 thick crusts of *Porolithon* gr. *onkodes*. At One Tree Reef (near the southern end of the
294 GBR at 23° S), thick crusts of *P.* gr. *onkodes* are abundant and often the dominant
295 coralline algae encrusting coral colonies in the shallowest settings (less than 10 m),
296 and thin crusts of this species occur down to 20 m (Dechnik et al., 2017). *P.* gr.
297 *onkodes* is similarly abundant in the shallowest coralline algal assemblages of many
298 other Pacific reefs (Adey et al., 1982; Verheij, 1994; Iryu et al., 1995; Cabioch et al.,
299 1999; Payri et al., 2000; Littler and Littler, 2003). Common accessory components of
300 aA1 include *Porolithon gardineri*, *Lithophyllum* gr. *kotschyianum* and *Neogoniolithon* gr.
301 *fosliei*. Others species, more common in assemblage 2 (see below), can also be
302 accessories in aA1.

303

304 **Assemblage aA2** is characterized by several species. Key components are *P.*
305 *gardineri* with occasional thin crusts of *P.* gr. *onkodes*, while additional components
306 include *Harveyolithon* gr. *munitum*, *Hydrolithon boergesenii* (= *H. reinboldii*),
307 *Neogoniolithon* gr. *fosliei*, *Dawsoniolithon conicum* (= *Pneophyllum conicum* in Keats et
308 al., 1997 and *Porolithon conicum* in Bittner et al., 2011) and *Lithophyllum* gr.
309 *prototypum* (reported as *Titanoderma tessellatum* by Cabioch et al., 1999). *P. gardineri*
310 can extend down to 20 m depth (Littler and Littler, 2003), which is also the maximum
311 depth for *P.* gr. *onkodes* (Cabioch et al., 1999, Payri et al., 2000). Other species in the
312 assemblage can be found in deeper settings.

313

314 **Assemblage aA3** is defined primarily by the absence of shallower coralline species
315 characteristic of assemblages aA1 and aA2, and indicates paleoenvironments below
316 20 m. Key components are knobby *Melyvonnea* gr. *erubescens*, and foliose
317 *Mesophyllum*, mainly *M. funafutiense*, while accessory species include *Lithothamnion*
318 *prolifer*, *Lithophyllum* gr. *prototypum*, thinly encrusting *Lithoporella*, and laminar
319 *Lithothamnion* sp. crusts.

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321

322 **3.2. Coralgal assemblages and paleoenvironmental interpretations**

323

324

325 A total of 58 species or species groups of zooxanthellate scleractinian corals were
326 identified from 35 genera in 11 families (Table 1). After combining data from the two
327 best preserved transects, HYD-01A and NOG-01B, the total numbers of species or
328 species groups identified on each reef were: early glacial (Reef 2), 30 species; LGM
329 (Reef 3a), 27 species; early deglacial (Reef 3b), 27 species; and late deglacial (Reef
330 4), 25 species. The dominant corals in transects NOG-01B, HYD0-1C, and HYD-02A
331 are massive *Isopora*, branching *Acropora* and *Seriatopora*, encrusting to massive
332 merulinids, *Porites* and *Montipora*, and encrusting agariciids. The octocorallian
333 *Tubipora musica* is also common in these transects. Robustly branching *Isopora* is
334 common in the barrier reefs in transects HYD-01C (M0034A) and NOG-01B (M0057A).
335 In contrast, the taxonomic composition of coral assemblages at RIB-02A differs from
336 that of the three other transects as it lacks massive *Isopora*, is dominated by encrusting
337 *Porites* and *Montipora*, and contains only a few branching *Acropora*.

338

339 Eight coral assemblages were defined based on the taxonomic and morphological
340 compositions of dominant and associated coral taxa. Their paleoenvironments are
341 interpreted based on the distributions of their modern analogues in the GBR, the
342 morphology and taxonomic composition of co-occurring coralline algae, and the
343 presence or absence of vermetid gastropods (Table 2 and Fig. 3).

344

345 **Assemblage cA1** is dominated by massive *Isopora* and branching corymbose to
346 digitate *Acropora* gr. *humilis* associated occasionally with *A. monticulosa* and
347 encrusting *Porites*. These corals coexist with thick crusts of *P. gr. onkodes* (aA1) and
348 vermetid gastropods. On modern reefs, this coral community lives in upper forereef
349 slope and reef crest environments between 0 and 10 m water depth, but is most
350 common between 0 and 5 m (Cabioch et al., 1999; Done, 1982,1983; Veron, 1986).
351 The occurrence of thick crusts of *P. gr. onkodes* (aA1) and vermetid gastropods is also
352 suggestive of a depth range of 5 m or less. In Indo-Pacific reefs, thick coralline algal
353 crusts and abundant vermetid gastropods are characteristic of the shallowest (<5–6 m)
354 high-energy reef setting (Cabioch et al., 1999). Vermetid gastropods are considered a
355 robust sea-level indicator in Indo-Pacific and Caribbean reefs (Montaggioni and
356 Braithwaite, 2009), and their association with thick coralline crusts is a common feature
357 of Holocene high-energy reef facies (Dechnik et al., 2015; Gischler et al., 2016)

358

359 **Assemblage cA2** is characterized by robustly branching and massive *Isopora*.
360 Accessory constituents are *Acropora* gr. *humilis*, and *A. gr. robusta*. These robustly

361 branching acroporids are all characteristic of shallow-water, high-energy reef settings,
362 probably less than 5 m deep, and certainly no deeper than 10 m (Montaggioni, 2005).
363 We restrict the paleowater depth of cA2 to 0–5 m when it is associated with thick algal
364 crusts of *P. gr. onkodes* and vermetid gastropods.

365

366 **Assemblage cA3** is characterized by massive *Isopora* and branching *Acropora*
367 species. Accessory corals are encrusting *Porites*. The depth limit of this assemblage is
368 determined by the range of *Isopora*, usually between 0 and 20 m (Done, 1982), but
369 occasionally extends to 40 m (Muir et al., 2015). We restrict the paleowater depth to <
370 10 m, when corals are associated with thick crusts of *P. gr. onkodes* and vermetid
371 gastropods.

372

373 **Assemblage cB** is dominated by branching *Seriatopora* and a diverse array of
374 *Acropora* species with branch diameters ≤ 1 cm. Associated corals include variable
375 proportions of massive *Isopora*, branching *Stylophora*, encrusting *Porites* and
376 *Montipora*, massive *Tubipora*, and to a lesser extent, encrusting to massive merulinids.
377 *Seriatopora* is common in sheltered environments on the shallow leeward side of reef
378 islands, and in deeper settings on the windward forereef slope (Done, 1982). The
379 association of *Seriatopora* with *Acropora* is common in a broad range of protected
380 environments down to the mesophotic zone, below 30 m (Bridge et al., 2012). The
381 presence of *Isopora* restricts the depth range to 0–20 m, and thick crusts of *P. gr.*
382 *onkodes* and vermetid gastropods further constrain depths to 0–10 m

383

384 **Assemblage cC** is dominated by encrusting to massive merulinids, mainly *Dipsastraea*
385 and less commonly *Cyphastrea* and *Platygyra*. Associated corals are finely branching
386 *Acropora*, encrusting *Porites* and *Montipora*, and *Hydnophora*. Merulinids can be
387 dominant in very shallow reef settings in the GBR, such as shallow reef flat to back reef
388 area in less than 6 m depth (Done, 1982). Merulinids are associated with a coral
389 community dominated by tabular *Acropora* on the forereef slope of Indo-Pacific reefs
390 from 6 to 15 m (Cabiocch et al., 1999), and *Dipsastraea* species are often common
391 down to at least 25 m on forereef slopes of the GBR (Done, 1982) and also in shallow,
392 turbid environments (Veron, 1986). *Cyphastrea* and *Hydnophora* are sediment-tolerant
393 genera, often associated with *Dipsastraea* and other corals, such as *Goniopora* and
394 *Turbinaria*, in turbid, low energy, inner-shelf reefs of eastern Australia (Perry et al.,
395 2009). Assemblage cC may represent a depth range of 0–30 m, but less in shallow
396 turbid environments. The depth range is restricted to 0–10 m when associated with

397 thick crusts of *P. gr. onkodes* and vermetid gastropods.

398

399 **Assemblage cD** is characterized by massive *Porites* (5–20 cm thick) associated
400 mainly with encrusting *Montipora* and encrusting merulinids. The label cD is also used
401 to refer to single massive *Porites* colonies growing immediately above the postglacial
402 reef sequence in several holes (M0033A, M0034A, M0039A, and M0055A). *Porites* has
403 a wide environmental range (Veron and Pichon, 1982) but massive *Porites* may
404 dominate shallow semi-exposed to sheltered habitats (Done, 1982), also in turbid
405 inshore environments (Potts et al., 1985). *Porites* with flattened growth forms occur
406 with *Montipora* and *Pachyseris speciosa* on steep slopes below 10 m in Coral Sea
407 reefs (Done, 1982), and down to 60 m in the GBR (Bridge et al., 2012). Assemblage cD
408 indicates a wide depth range between 0 and 60 m, and other criteria, such as the
409 composition and thickness of algal crusts and the presence or absence of vermetid
410 gastropods, are used to constrain the depth range of this assemblage.

411

412 **Assemblage cE** is dominated by encrusting *Montipora* and *Porites* associated with
413 encrusting merulinids (mainly *Cyphastrea*) and small finely branching *Acropora*
414 colonies. This assemblage is commonly associated with thin crusts of aA3, devoid of
415 vermetid gastropods. A similar assemblage has been recorded in the GBR mesophotic
416 zone below 40 m (Abbey et al., 2013; Bridge et al., 2012). Assemblage cE combined
417 with aA3 indicates a forereef slope habitat deeper than 20 m to at least 100 m.
418 However, this assemblage may extend into shallower waters on steep slopes, or in
419 higher turbidity (Done, 1982, Browne et al., 2012).

420

421 **Assemblage cF** is dominated by agariciids (e.g. *Leptoseris gr. yabei*, *Pachyseris*
422 *speciosa*) associated with encrusting *Montipora* and *Porites*. *Leptoseris* and *Pachyseris*
423 *speciosa* are important constituents of mesophotic coral communities of the GBR
424 (Abbey et al., 2013; Bridge et al., 2012). Like assemblage cE, the depth distribution of
425 assemblage cF is constrained to >20 m when associated with thin crusts of aA3 devoid
426 of vermetids. Both mesophotic assemblages, cE and cF, have a greater diversity of
427 coral species above 60 m than from 60 m to 102 m (Bridge et al., 2011a, b; Abbey et
428 al., 2013).

429

430

431 **3.3. Spatial and temporal variations in coralgal assemblages**

432

433 **3.3.1. Hydrographers Passage (transects HYD-01C and HYD-02A)**

434

435 **3.3.1.1. Northern transect (HYD-01C)**

436

437 Late glacial MIS2 reef growth (27–22 ka, Reef 2) initiated on the inner terrace in holes
438 M0031A–33A (Webster et al., 2018) on a basement substrate overlain by
439 unconsolidated granule- to pebble-sized bioclasts of corals, *Halimeda*, mollusks,
440 echinoids, and larger foraminifers (Figs. 4 and 5). The unconsolidated sediment is
441 overlain in M0032A and M0033A (at ca. 116.2–114.4 mbsl) by a coralgal-microbialite
442 boundstone composed mainly of encrusting to massive merulinids (e.g. *Dipsastraea*,
443 *Cyphastrea*), encrusting *Hydnophora*, and finely branching *Acropora* (cC) associated
444 with thin crusts of aA3. Coralline algae shift to thicker crusts of *P. gr. onkodes*
445 containing vermetid gastropods at ca. 109.2 mbsl, which coincides with the coral
446 community changing from cC to an assemblage composed of massive *Isopora* and a
447 few (possibly *in situ*) branching *Seriatopora* (cB?) (Figs. 4 and 6A). The average
448 accretion rate on the inner terrace is ca. 1.9–3.4 mm yr⁻¹ until 22.9 ka, falling to 0.1 mm
449 yr⁻¹ between 22.9 and 22.1 ka (Table S2), with little accretion on the mid and outer
450 terraces between 27 and 22 ka. In M0035A, the basement substrate is covered with
451 microbialite boundstone containing few thin laminar agariciids (cF), while in M0036A it
452 is covered by a coralgal boundstone composed of encrusting corals, such as *Montipora*
453 and *Cyphastrea* (cE), thinly encrusted with aA3. On the inner terrace, a major hiatus in
454 reef growth at ca. 106.5–105.3 mbsl was caused by the rapid sea-level fall leading to
455 the LGM, and marks the termination of Reef 2 (Webster et al., 2018).

456

457 The abrupt LGM sea-level fall displaced shallow reef facies seaward at an average rate
458 of 1.5 m/year (Webster et al., 2018; Yokoyama et al., 2018). Consequently, LGM to
459 early deglacial reef growth (22–17 ka, Reef 3a) is confined to the mid and outer
460 terraces. LGM coralgal-microbialite boundstone began to accumulate at ca. 127.5 mbsl
461 in M0035A, ca. 128.8 mbsl in M0036A, and ca. 130.0 mbsl in M0039A. LGM corals
462 (22–19 ka) are diverse, and include *Acropora* (e.g. finely branching species and *A. gr.*
463 *humilis*), encrusting to massive merulinids (e.g. *Dipsastraea gr. pallida*, *Cyphastrea*),
464 branching *Seriatopora*, encrusting *Porites* and *Montipora*, massive *Tubipora* and
465 *Isopora* (i.e. cC? in M0035A, cB in M0036A, and cE/cC? in M0039A) (Figs. 4, 5 and
466 7A). The associated algal assemblages are composed of crusts of aA1 reaching 1 cm
467 thick with vermetid gastropods in M0035A and M0036A and thinner crusts of aA3 with
468 no vermetid gastropods in M0039A. A notable change in the coral assemblage in

469 M0035A, at ca. 121.5 mbsl, marks the initiation of a ca. 10 m thick interval dominated
470 by massive *Isopora* and branching *Seriatopora* associated with encrusting *Montipora*
471 and few *Acropora* gr. *humilis* (*Isopora*-rich cB). The thickness of algal crusts and the
472 frequency of vermetid gastropods increase upward. There is a similar trend in M0036A.
473 The corresponding stratigraphic interval in M0039A is composed of finely branching
474 *Acropora*, *Seriatopora* and encrusting *Porites* and/or *Montipora* (*Acropora*-rich cB) from
475 126.5 to 116.5 mbsl. The frequency of vermetid gastropods increases upward, as in the
476 two other holes, but the vertical trend in coralline algae is more complex. The algal
477 assemblage is composed of thin and thick crusts of aA1, except between 120.8 and
478 118.4 mbsl, where algal crusts are thinner and consist of aA3 and the coral
479 assemblage is characterized by branching *Echinopora*. The average accretion rate of
480 Reef 3a on the mid and outer terraces at HYD-01C is ca. 4–4.3 mm yr⁻¹ (Table S2).

481

482 Postglacial reef growth resumed on the inner terrace (17–13 ka; Reef 3b; Webster et
483 al., 2018) at ca. 106.5–105.3 mbsl with deposition of a coralgal-microbialite boundstone
484 containing encrusting and massive *Isopora* commonly associated with aA1 (up to 2 cm
485 thick in M0033A) and vermetid gastropods (Figs. 4 and 5). *Isopora* occurs with
486 *Acropora* gr. *humilis* (cA1) in M0031A, with *A. gr. humilis* and *A. monticulosa* (cA1) in
487 M0033A, and with *Stylophora* and *Seriatopora* (cB) in M0032A. These shallow reef
488 facies have high average accretion rates of up to 39.4 mm yr⁻¹ (Table S2). On the mid
489 and outer terraces, the facies is mostly bioclastic and comprised of *Isopora* and
490 *Acropora* fragments (cA3, see bioclastic rudstone in Fig. 4). Massive colonies of
491 *Porites*, probably *in situ*, are present in M0039A.

492

493 Subsequent reef growth (13–10 ka, Reef 4) took place further upslope where a ca. 19
494 m thick coralgal-microbialite boundstone was recovered from M0034A on the outer
495 barrier reef (Webster et al., 2018). On the inner and outer terraces, the tops of
496 M0032A, M0033A and M0039A correlate with Reef 4, and are occupied by massive
497 *Porites* (cD) or encrusting *Montipora* (cE). *Porites* is associated with thin crusts of aA3
498 in M0033A (Figs. 4 and 5). In M0034A on the outer barrier reef, the coralgal
499 assemblage between 71.7 and 57.3 mbsl consists mainly of massive and robustly
500 branching *Isopora* associated with *Acropora* (e.g. *A. gr. humilis*, *A. gr. hyacinthus*)
501 (cA2) and 1 cm thick crusts of aA1 with vermetid gastropods. The average accretion
502 rate is 4.5–11.4 mm yr⁻¹ (Table S2). In contrast, the top 2 m of the core grew at a slower
503 rate of 4.1 mm yr⁻¹ or less, and consists of an assemblage of encrusting to massive
504 merulinids (e.g. *Platygyra*), branching *Stylophora*, and encrusting *Montipora* (cC?),

505 overlain by a ca. 30 cm thick *Porites* colony (cD) on top of the postglacial sequence;
506 this marks the end of reef growth in M0034A.

507

508 **3.3.1.2. Southern transect (HYD-02A)**

509

510 Reef boundstone of MIS2 age (Reef 2; 27–22? ka), composed mainly of microbialite,
511 was recovered only from hole M0040A on the outer terrace between ca. 144 and 142.1
512 mbsl. Corals in this interval are primarily laminar *Pachyseris speciosa* (cF) associated
513 with algal assemblage aA3 (Figs. 8 and 9). Most material recovered from the mid reef
514 terraces is a coralgall and coralgall-microbialite boundstone containing mainly *Isopora*,
515 branching *Acropora*, and branching *Seriatopora* (cA and cB) that accumulated between
516 22 and 15? ka (Reef 3a/b) (Figs. 7B and 8). In contrast, material recovered from
517 M0040A and M0041A on the outer terrace is composed of a microbialite boundstone
518 formed mostly between 27 and 14 ka (Webster et al., 2018) in which agariciids (cF) are
519 replaced by encrusting *Porites* and *Montipora* (cE) at ca. 140.3 mbsl in M0040A and
520 138.5 mbsl in M0041A. The algal assemblages also vary along the transect with aA1
521 characteristic of proximal holes (M0042A, M0043A, and M0044A), and aA3 more
522 common in distal holes (M0046A and M0040A). A 2 m thick layer of unconsolidated
523 sediment, mostly mud, covers the postglacial reef sequence in M0040A and M0041A.
524 The tops of the mid-terrace holes consist of a coralgall boundstone with common
525 encrusting *Porites* (cE?) thinly encrusted by aA3, except in M0044A which is capped by
526 a bioclastic packstone. Following reef growth termination on the mid and outer
527 terraces, a new phase of reef growth began further upslope in M0042A (Reef 4). The
528 postglacial reef sequence in M0042A begins at 69.3 mbsl with unconsolidated
529 bioclastic sediment containing pebble-sized coral fragments (e.g. *Porites* and
530 *Montipora*); a coralgall microbialite boundstone begins at 60.5 mbsl. The coral fauna
531 around 59.3 mbsl includes robustly branching *Acropora monticulosa* (cA1) associated
532 with thin and thick crusts of aA1 and vermetid gastropods. The previous coralgall
533 assemblage is replaced at 58.1 mbsl by an association of encrusting to massive
534 merulinids and branching *Acropora* (cC?) thinly encrusted by aA3 before the reef finally
535 drowned.

536

537 **3.3.2. Noggin Pass (transect NOG-01B)**

538

539 The initial late glacial MIS2 reef growth (Reef 2) is recorded in M0055A and M0053A on
540 the inner and mid terrace, respectively, and in M0054B on the outer terrace (Webster et

541 al., 2018). The reef boundstone above the basement between 112 and 107 mbsl in
542 M0055A is an algal bindstone composed primarily of thick, heavily bored, coralline algal
543 crusts (aA1) associated with vermetid gastropods. Some corals are diagenetically
544 altered, and include massive *Goniopora*, branching *Acropora*, and *Stylophora?* (Figs.
545 6B, 10 and 11). A coral community dominated by massive *Porites* associated with
546 encrusting to massive merulinids (e.g. *Goniastrea?*) (cD) occupies the overlying 2 m
547 interval (at 105.3 mbsl) in which microbialite becomes part of the reef framework.
548 Subsequently, the coral fauna changes into a diverse assemblage of *Lobophyllia*
549 *corymbosa*, encrusting *Isopora*, massive *Tubipora*, and branching *Seriatopora* and
550 *Acropora* (cB). In contrast with the variable coral fauna, the algal assemblage (up to 5
551 cm thick crusts of *P. gr. onkodes*) and the abundance of vermetid gastropods remain
552 unchanged. Reef 2 grew at average rates of 0.5–3.5 mm yr⁻¹ until 24 ka, falling to 0.6
553 mm yr⁻¹ between 24 and 21.8 ka (Table S2). Late glacial reef growth in M0053A is
554 characterized by a microbialite boundstone between 127.8 and 122.7 mbsl composed
555 of encrusting *Porites* and *Montipora*, encrusting to massive merulinids (e.g.
556 *Cyphastrea*, *Favites* gr. *abdita*), and finely branching *Acropora* (cE) associated with
557 less than 1 cm thick algal crusts (mostly aA3). Reef 2 in M0054B has a similar
558 association of encrusting *Porites* and *Montipora*, finely branching *Acropora* (cE), and
559 thin algal crusts (mainly aA2 and aA3). The top of Reef 2 in M0054B may extend to
560 126.5 mbsl, based on the available age data. A major hiatus in reef growth at ca. 103
561 mbsl in M0055A marks the termination of Reef 2 (Webster et al., 2018).

562

563 LGM to early deglacial reef growth (Reef 3a) is limited to the mid and outer terraces
564 (M0053A, M0054A/B). The LGM reef initiated at ca. 122 mbsl in M0053A and at ca.
565 126.5 mbsl in M0054B. Microbialite dominates the LGM reef framework in M0054B, but
566 is less abundant in M0053A. The LGM coralgal community (22–19 ka) in M0053A is
567 diverse and composed of massive *Isopora*, branching *Acropora*, massive *Tubipora*, and
568 encrusting *Montipora* (cA3) associated with up to 1 cm thick crusts of aA3. In this hole,
569 Reef 3a grew at an average rate of 3.8 mm yr⁻¹ before slowing to 1.8 mm yr⁻¹ at around
570 19 ka (Table S2). In contrast, the LGM reef in M0054B is composed primarily of
571 encrusting *Porites* and *Montipora* associated with finely branching *Acropora* (cE) and
572 algal crusts composed mainly of aA2 and aA3 and generally less than 1 cm thick (Figs.
573 7C and 10). During the early phase of deglacial reef growth in M0054A/B, the coralgal
574 assemblage changes at 124.55 mbsl with the appearance of branching *Seriatopora*,
575 encrusting to massive *Isopora*, branching *Acropora* (cB), and the development of
576 thicker algal crusts of *P. gr. onkodes* with vermetid gastropods. A similar coralgal

577 assemblage accumulated over 5.8 m in M0053A and is overlain at 111.8 mbsl by
578 massive *Isopora* and *Acropora* gr. *humilis* (cA1). Thin algal crusts of aA3, devoid of
579 vermetid gastropods and associated with massive *Platygyra?* and *Hydnophora* (cC),
580 replace the previous algal assemblage at ca. 109.7 mbsl.

581

582 Reef growth resumed on the inner terrace (Reef 3b) at ca. 103 mbsl in M0055A. On the
583 mid terrace, the Reef 3b interval occupies the top 3 m of M0053A, and consists of
584 carbonate sand overlain by encrusting *Porites* and/or *Montipora* (cE) in association with
585 aA3. In M0055A, the initial coralgal assemblage is composed of massive *Isopora*,
586 branching *Seriatopora*, massive *Tubipora*, and branching *Stylophora* (*Isopora*-rich cB)
587 associated with thick crusts of *P.* gr. *onkodes* and vermetid gastropods (Figs. 6B and
588 10). This coral assemblage accumulated over 2.2 m and is overlain at 100.8 mbsl by a
589 2 m thick interval containing various medium to robustly branching *Acropora* species,
590 including *Acropora* gr. *humilis* and possibly *A. monticulosa* (cA1). More proximally, on
591 the inner terrace, Reef 3b in M0056A overlies the older Pleistocene basement at 88.5
592 mbsl and is composed of massive merulinids (e.g., massive *Cyphastrea*) (cC). The
593 postglacial corals of Reef 3b in M0056A are associated with thin and thick crusts of
594 aA1 with no vermetid gastropods except at the base of the sequence. Reef 3b at NOG-
595 01B grew at average rates of 0.1–3.9 mm yr⁻¹ with a brief peak at 7.3 mm yr⁻¹ in
596 M0055A (Table S2).

597

598 The next reef sequence (Reef 4) is recorded on the inner barrier reef in M0057A and
599 more distally on the tops of M0053A, M0055A, and M0056A (Figs. 10 and 11). Hole
600 M0053A is capped by a thin veneer of Reef 4 material containing encrusting or platy
601 *Porites* and *Montipora* (cE). The top of M0055A is occupied by a massive *Porites*
602 colony (cD) with thin crusts of aA2, while encrusting *Porites* and *Montipora* (cE) form
603 the top 1.5 m of M0056A. In M0057A, the older Pleistocene basement is overlain by a
604 13.8 m thick coralgal boundstone composed mostly of massive and robustly branching
605 *Isopora* and *Acropora* gr. *robusta* (cA2) associated with thick crusts of aA1 and
606 vermetid gastropods (Fig. 6A). Reef 4 accumulated at an average rate of 4.5–7.9 mm
607 yr⁻¹ (Table S2). The top of the postglacial reef sequence in M0057A (Reef 5) consists of
608 encrusting *Porites* and/or *Montipora* (cE) associated with thin crusts of aA3 and is
609 marked by a lower accretion rate of 0.1–1.3 mm yr⁻¹ (Table S2).

610

611 **3.3.3. Ribbon Reef (transect RIB-02A)**

612

613 A preliminary chronology based on a limited number of radiometric ages suggests that
614 coring may have penetrated the older Pleistocene (≥ 30 ka) in M0049B. Postglacial
615 coralgal-microbialite boundstone (16–12 ka) was recovered down to 111.8 mbsl in
616 M0049B and 106.9 mbsl in M0050A (Figs. 10 and 11). Below ca. 111.8 mbsl in M0049B
617 the older Pleistocene reef boundstone has evidence of episodic subaerial exposure,
618 such as dissolution cavities and red staining (Webster et al., 2011). Microbialite is
619 volumetrically more abundant than corals and coralline algae. Corals are mainly
620 encrusting *Porites* and *Montipora* (cE). Above 111.8 mbsl, the proportions of corals,
621 coralline algae, and microbialite vary. The base of the post-glacial section in M0049B is
622 characterized by massive *Porites* and *Astreopora* (cD?). From 108.9 to 103.6 mbsl,
623 encrusting *Porites* and *Montipora* are common and associated with agariciids and, to a
624 lesser extent, merulinids (cE). A similar assemblage was recovered in M0050A. In
625 M0049B, a massive *Porites* colony (cD) is present at 102.2 mbsl, and algal crusts are
626 thin and composed mainly of aA2 and aA3, except for aA1 at ca. 108.8 mbsl. The
627 postglacial reef boundstone recovered from transect RIB-02A lacks *in situ* *Isopora*,
628 *Acropora*, and *Seriatopora*, in striking contrast to the other sites where these corals are
629 common.

630

631 **3.4. Integration of coralline and coral interpretations**

632

633 There is usually good agreement between alga- and coral-based paleoenvironmental
634 interpretations. The shallowest reef facies (0–5 m) is typically composed of an
635 association of *Acropora* gr. *humilis* (cA1) and/or other acroporids with robust branches
636 (cA2), thick crusts of *P.* gr. *onkodes* (aA1), and abundant vermetid gastropods (Table
637 2). Coral assemblages on the shallow to mid-depth forereef slope (0–20 m) are
638 composed of various proportions of massive *Isopora*, branching *Acropora* and
639 *Seriatopora* (cA3, cB), and they are associated with aA1 or aA2 crusts of variable
640 thickness. The deep (>20 m) forereef coral assemblages dominated by encrusting
641 *Porites* and *Montipora* (cE) and agariciids (cF) are typically associated with thin crusts
642 of aA3. The paleowater depths of coral assemblages with broader depth ranges (cC,
643 cD) can be further constrained using the composition and morphology of associated
644 coralline algal crusts and the presence or absence of vermetid gastropods. Since the
645 distribution of coralline algae is controlled by irradiance, the typically deeper algal
646 assemblage aA3 may occur in less than 20 m depth in cryptic habitat like crevices,
647 undersides of coral colonies, shaded spaces between adjacent coral colonies, or under
648 turbid conditions (Abbey et al., 2011a). In such cases, more reliable paleowater depths

649 are provided by shallow-water coralgal components in the same core (Abbey et al.,
650 2011a).

651

652

653 **4. Discussion**

654

655 **4.1. Coralgal assemblages during the late glacial (MIS2) reef (Reef 2; 27–22 ka)**

656

657 4.1.1. The inner terrace prior to the 22–17 ka hiatus

658

659 In transect HYD-01C, the late glacial (MIS2) Reef 2 is composed of coralgal
660 microbialite boundstone resting on unconsolidated sediments of granule-, pebble-, and
661 sand-sized bioclasts. Inception of Reef 2 was likely influenced by increased terrigenous
662 inputs, based on the downhole gamma-ray profile of M0031A (Fig. S1 in Webster et al.,
663 2018; Fig. 4 in Hinestrosa et al., 2019). The initial coral assemblages in M0032A and
664 M0033A are dominated by various encrusting merulinids (e.g. *Dipsastraea*,
665 *Cyphastrea*) and *Hydnophora* associated with thin crusts of aA3 (Figs. 4 and 6A).
666 *Hydnophora* is relatively tolerant of sedimentation (McClanahan and Obura, 1997).
667 *Dipsastraea* and *Cyphastrea* are constituents of nearshore communities influenced by
668 terrigenous sedimentation in the GBR (Perry et al., 2009) and they also occur, with
669 *Hydnophora*, on turbid high-latitude reefs in Japan (Yamano et al., 2012). Therefore it is
670 likely that both depth and sedimentation have influenced the timing and composition of
671 the initial coral assemblage on the inner terrace of HYD-01C. Fewer corals, probably
672 allochthonous, were recovered from M0031A, where deposits consisting mainly of
673 unconsolidated sediments, including a thick layer of *Halimeda*-rich, pebble-sized
674 bioclasts, are coeval with high terrigenous input (indicated by the gamma-ray signal).
675 The late glacial production of *Halimeda* segments resembles modern mid- and outer-
676 shelf reef environments of the GBR where *Halimeda* is particularly common (Drew,
677 1983) and may be linked to high nutrient levels (Marshall and Davies, 1988). High
678 nutrient inputs also may have favored *Halimeda* growth in some areas of the inner
679 terrace at Hydrographers Passage (Abbey et al., 2013).

680

681 The initial late glacial (Reef 2) coralgal community in Noggin Pass (M0055A) consists
682 of very few corals in an algal bindstone composed of thick, heavily bored crusts of *P. gr.*
683 *onkodes* and vermetid gastropods (Figs. 6B and 10). This association is typical of
684 shallow exposed reef crests (Blanchon, 2011; Blanchon et al., 2014) and suggests a

685 shallower reef setting than the coeval reef facies on the inner terrace of transect HYD-
686 01C. These differences in reef community composition probably reflect the shallower
687 depth of the older Pleistocene basement at Noggin Pass (Fig. 11, Webster et al., 2018)
688 where the algal bindstone is overlain by a *Porites*-dominated assemblage (cD, Fig. 6B
689 and 10). Some massive *Porites* species are sediment-tolerant corals common in
690 nearshore communities of the modern GBR (Browne et al., 2012), and may indicate the
691 influence of sedimentation, as the merulinids do in transect HYD-01C. Massive *Porites*
692 colonies are also common near the base of the outer cores of Tahiti Exp. 310, and
693 were interpreted as indicative of inimical conditions at the beginning of reef growth
694 (Abbey et al., 2011a). The development of coralg communities in Reef 2 on the inner
695 terrace of transect HYD-01C involves a shift from assemblage cC to assemblage cB?
696 (with the latter associated with aA1 and vermetid gastropods) that reflects a shallowing
697 trend interpreted as a catch-up mode of reef growth (Webster et al., 2018; Fig. 5). A
698 similar shift to assemblage cB in M0055A at Noggin Pass was not associated with
699 changes in abundance of encrusting algae and vermetids, and this indicates a
700 continuously shallow reef setting and a keep-up mode of reef growth (Webster et al.,
701 2018; Fig. 11). In addition, a decrease in terrigenous input, indicated by the downhole
702 gamma-ray profile of M0031A (Webster et al., 2018; Hinestroza et al., 2019), may have
703 promoted colonization by species less tolerant of sediments, such as *Isopora* and
704 *Tubipora* (Fabricius and Alderslade, 2001; Kojis and Quinn, 1984). The different modes
705 of reef growth on the inner terraces of HYD-01C and NOG-01B are probably related to
706 their different reef initiation depths, which also may have determined accretion rates of
707 3.4 mm yr⁻¹ in Hydrographers Passage and 0.5 mm yr⁻¹ in Noggin Pass (Table S2). The
708 inner terrace was exposed and Reef 2 terminated at ca. 22 ka, when sea-level dropped
709 to its peak LGM position (Webster et al., 2018). Reef growth re-initiated on the inner
710 terrace at ca. 17 ka (Reef 3b) during the postglacial sea-level rise.

711

712 4.1.2. The mid and outer terraces

713

714 Unlike the coralg assemblages of the inner terrace, compositions of those on the mid
715 and outer terraces have limited variation within and among sites. These assemblages
716 are either cE (M0036A, M0053A) or cF (M0035A, M0040A), and most algal crusts are
717 composed of aA3, both of which indicate deeper environments, consistent with their
718 deeper, more distal positions along the transects (Figs 5, 9 and 11).

719

720 4.2. Coralg assemblages during the LGM and early deglacial (Reef 3a; 22–17

721 **ka)**

722

723 **4.2.1. The LGM reef (Reef 3a; 22–19 ka)**

724

725 The peak of the Last Glacial Maximum (LGM) when ice sheets reached their maximum
726 extent and sea level was lowest ~118 m occurred at 20.5 ka (Yokoyama et al., 2018).

727 In the GBR region, despite the extreme conditions of the LGM, sea surface
728 temperatures (SSTs) inferred from a multiproxy study of marine sediment cores were
729 only 1 to 2.5°C cooler than today (Reeves et al., 2013). This contrasts with a recent
730 SST reconstruction suggesting 4–5°C cooling, based on Sr/Ca records of LGM corals
731 collected during IODP Exp. 325 (Felis et al., 2014). Based on similar estimates of no
732 more than 5°C cooling, Veron (2008) surmised that LGM SSTs had little impact on the
733 survival of reef corals in eastern Australia. A much greater disturbance for coral reefs
734 was the drastic landscape modification driven by sea-level fall that exposed most of the
735 continental shelf and restricted reef growth to a narrow band below the current shelf
736 break (Hinestroza et al., 2014, Hopley et al., 2007; Veron, 2008; Webster et al., 2018).
737 The decreasing angle of slope at the shelf break determined the extent of available
738 substrate and also influenced the effects of deglacial sea-level rise on subsequent reef
739 growth and distribution (Abbey et al., 2011b). Coral reefs must maintain higher growth
740 rates to track sea-level rise on steeper slopes where less space is available for
741 landward migration by establishing new reefs in shallower water (Neumann and
742 Macintyre, 1985). Davies et al. (1985) and Davies and McKenzie (1993) suggested that
743 the slope steepness and the unconsolidated, possibly muddy nature of the pre-LGM
744 substrate probably led to development of specialized reef communities very different
745 from those of the modern GBR. They concluded that an external refuge, such as the
746 Queensland Plateau in the middle of the Coral Sea, was necessary as a source of
747 coral larvae for recolonizing the shelf during the postglacial sea-level rise. In contrast,
748 Veron (2008) hypothesized that most corals were able to withstand LGM conditions,
749 and continued to recruit on the slope, with or without building reefs. While LGM reefs
750 have been reported from several locations throughout the tropics (Montaggioni, 2005),
751 previous evidence of LGM reef growth in the GBR region was restricted to the
752 identification of probable submerged reef structures along the shelf edge (Abbey et al.,
753 2011b; Beaman et al., 2008; Harris and Davies, 1989).

754

755 Data from IODP Exp. 325 now provide the first direct evidence that an LGM reef
756 system existed along the shelf edge of the GBR (Webster et al., 2011, 2018). LGM reef

757 material was recovered from eight holes on the mid and outer terraces: two at Noggin
758 Pass (M0053A, M0054B) and six at Hydrographers Passage (M0035A, M0036A,
759 M0039A, M0047A, M0043A, and M0040A) (Fig. 7). The LGM correlates with the base
760 of Reef 3a (22–17 ka) in the chronological reef growth scheme delineated in Webster
761 et al. (2018). The LGM reef (22–19 ka) varies in thickness from 3.5 m (M0036A) to 8 m
762 (M0053A) and the LGM lithologies comprise coralg-al-microbialite and microbialite
763 boundstone, bioclastic packstone, and unconsolidated carbonate granules, pebbles
764 and sand. Timing of the initiation of LGM reef growth varies spatially. Early LGM reef
765 framework material was recovered in Noggin Pass where a microbialite boundstone
766 (cA3) contains an *Isopora* colony at ca. 121 mbsl in M0053A dated to 21 ka (Fig. 7B).
767 In holes M0036A and M0039A in Hydrographers Passage, reef initiation was delayed
768 and fewer corals of LGM age were recovered. The oldest pioneer corals include a 21.8
769 ka *Cyphastrea* and several *Acropora* colonies with ages of 20.2–20.3 ka in M0035 (Fig.
770 7A). In M0039A the first coralg-al community (cE/C?/aA3) indicates that reef growth
771 began later (19.1 ka), and probably in a relatively deeper setting (Fig. 7A). The gamma-
772 ray profile of M0036A contains no evidence that the initiation lag in HYD-01C is related
773 to increased terrigenous input during the LGM. Instead, it is likely that the steeper
774 latitudinal SST gradient during the LGM, with substantially lower SSTs in the southern
775 GBR may have retarded development of reef communities at HYD-01A (Felis et al.,
776 2014). Conversely, at Noggin Pass, the gamma-ray of M0054B, on the outer terrace of
777 NOG-01B, indicates a pulse of terrigenous sediments at ca. 20 ka (Webster et al.,
778 2018; Hinestrosa et al., 2019). This conclusion is supported by the siliciclastic content
779 of microbialites in M0054B being higher than in any other hole studied (Webster et al.,
780 2018; Braga et al., 2019), and by the LGM reef growing at 1.8 mm yr⁻¹ in M0054B,
781 which is less than in hole M0053A (ca. 3.8 mm yr⁻¹) and about half the rate (4–4.3 mm
782 yr⁻¹) in HYD-01C holes (Table S2). A marked coralg-al shift from cA3/aA3 to cB/aA1 and
783 cE/aA3 to cB/aA1 around 20.5 ka in M0053A and M0054B, respectively, indicates
784 upward shallowing (Figs. 7C and 11). This community change is also synchronous with
785 a shift in the gamma-ray signal in M0054B that might indicate a slight decrease in
786 terrigenous input (Webster et al., 2018; Hinestrosa et al., 2019). While less terrigenous
787 sediment might increase recruitment of more vulnerable taxa (e.g., *Isopora* and
788 *Tubipora*) (Fabricius and Alderslade, 2001; Kojis and Quinn, 1984; Fig. 7C), the
789 siliciclastic content in microbialites did not decline in this hole (Webster et al., 2018;
790 Braga et al., 2019), and another explanation for the gamma-ray change must be
791 invoked.
792

793 In conclusion, our data show that oceanographic conditions and modifications of
794 coastal physiography associated with the LGM did not preclude survival of the key reef-
795 building corals prevailing on today's GBR, including *Isopora* (M0053A), *Acropora* gr.
796 *humilis* (M0035A, M0036A), *Dipsastraea* gr. *pallida* (M0035A), and *Porites* and
797 *Montipora* (M0054B) (Fig. 7). At least in areas like Noggin Pass, LGM conditions were
798 suitable for early colonization by a diverse coral fauna and for fast relocation of coralgal
799 communities across the shelf edge as sea level fell rapidly. We propose that these
800 areas were refuges that became important local sources of coral larvae for recolonizing
801 new substrates during the postglacial sea-level rise (Webster et al., 2018), and may
802 have ensured the resilience of the GBR over multiple glacial-interglacial cycles
803 (Humblet & Webster, 2017).

804

805 **4.2.2. Early deglacial coralgal assemblages (Reef 3a; 19–17 ka)**

806

807 The earliest deglacial development of reef communities on the mid and outer terraces
808 of HYD-01C is characterized by the predominance of coral assemblage cB and thin to
809 thick algal crusts (aA1) associated with vermetid gastropods (Fig. 5). The proportion of
810 finely branching *Acropora* and, to a lesser extent, merulinids increases seaward (e.g.
811 *Acropora*-rich cB in M0039A); the trend is opposite for massive *Isopora* and branching
812 *Seriatopora* (e.g. *Isopora*-rich cB in M0035A). A similar shallow coralgal assemblage
813 developed in hole M0043A on transect HYD-02A (Fig. 9). In contrast, the early
814 deglacial coralgal assemblage in M0040A and M0041A in the same transect is
815 dominated by encrusting *Porites* and *Montipora* (cE) associated with aA3, reflecting
816 their deeper, more distal locations relative to other sites in Hydrographers Passage
817 (Fig. 9). Shallow coralgal assemblages are also recorded on the mid and outer terraces
818 in Noggin Pass (cA1/aA1 in M0053A and cB/aA1 in M0054A, Fig. 11). Deglacial
819 sections continuously recording a shallow coralgal assemblage have been reported
820 elsewhere and reflect a keep-up mode of reef growth (Montaggioni and Braithwaite,
821 2009). In several holes along transects HYD-01C and NOG-01B, upward increases in
822 algal crust thickness (M0035A, M0054A/B) and in abundances of vermetid gastropods
823 (M0035A, M0036A, and M0039A) (Figs. 4 and 10) suggest some shallowing (Cabiocch
824 et al., 1999).

825

826 In contrast with the continuous shallow reef sequence recorded in other sites, hole
827 M0039A has a brief interval at around 120 mbsl dominated by the aA3 algal
828 assemblage. This algal interval, however, is not correlated with a change in the coral

829 assemblage (cB) and may be due to sampling algae growing in cryptic habitats (Fig. 5).

830

831 **4.3. Deglacial corallgal assemblages after the inner terrace reflooding (Reef 3b;**

832 **17–13 ka)**

833

834 **4.3.1. Recolonization of the inner terrace after the 22–17 ka hiatus**

835

836 The unconformable contact between the late glacial Reef 2 and deglacial Reef 3b was
837 penetrated on the inner terrace of transect HYD-01C at ca. 106.5–105.3 mbsl

838 (M0031A, M0032A, and M0033A) and transect NOG-01B at ca. 103 mbsl (M0055A).

839 The composition of Reef 3b above the hiatus is consistent among all sites. The initial
840 coral community is dominated by massive *Isopora*, and branching *Acropora* gr. *humilis*,
841 *Stylophora* and *Seriatopora* (cA1 and cB), in association with aA1 crusts and vermetid
842 gastropods (Fig. 6). Similarities in reef community composition before and after the

843 hiatus, such as the reoccurrence of massive *Isopora* and branching *Seriatopora*, aA1
844 algal crusts, and vermetid gastropods (Fig. 6, see also section 4.2.1.), point to broadly

845 similar shallow-water reef settings before and after the hiatus. There are also some
846 conspicuous differences, including disappearance of *Tubipora* in M0055A and

847 increased abundance of fast-growing corals (e.g. *Isopora*, *Acropora* gr. *humilis* and
848 *Seriatopora*) above the hiatus (Fig. 6). These changes also coincide with a sharp

849 increase in the vertical accretion rate, from 0.1–1.9 to 1.1–7.4 mm yr⁻¹, on the inner
850 terrace of HYD-01C (Table S2). The contexts in which reef communities developed

851 before and after the hiatus also differ: the late glacial sea-level lowstand prior to the
852 LGM sea-level fall led to terrace emersion and reef turn-off at 22 ka, while the

853 subsequent deglacial sea-level rise led to terrace inundation and reef turn-on at 17 ka
854 (Webster et al., 2018). This reflooding of the inner terrace correlates with an increase in

855 the gamma-ray signal in M0031A and M0036A, and is consistent with a large input of
856 fine terrigenous sediments eroded during terrace inundation (Webster et al., 2018;

857 Hinestrosa et al., 2019), although this input is not reflected in the siliciclastic content of
858 microbialites in M0039A, the furthest offshore hole of HYD-01C (Braga et al., 2019).

859 Reef 3b began growth slightly earlier on the inner terrace at Noggin Pass (M0055A,
860 Fig. 6), even though the substrate at that location is shallower (103 mbsl) than at HYD-

861 01C (106.5–105.3 mbsl). Delayed reef initiation may be related to inundation of a

862 broader coastal area and resuspension of a greater sediment load at HYD-01C (Abbey
863 et al., 2011b; Hinestrosa et al., 2014, 2019). At Noggin Pass, reflooding of the inner

864 terrace coincided with incipient reef drowning on the mid and outer terraces (see

865 section 4.3.2), but resuspension did not have a lasting impact on reef growth on the
866 inner terrace. Conditions favoring vigorous reef growth, including increased
867 accommodation space and higher SSTs, then promoted colonization by fast-growing
868 corals and enabled Reef 3b to keep up with sea-level rise (Felis et al., 2014). The thick
869 crusts of *P. gr. onkodes*, abundant vermetid gastropods, and medium to robust
870 branching *Acropora* (cA1) in M0033A of HYD-01C and M0055A of NOG-01B indicate
871 very shallow reef settings exposed to strong wave action (Figs. 5, 6, and 11). On the
872 inner terrace of HYD-01C, where reef initiation was delayed, accretion rates much
873 higher (up to 39.4 mm yr⁻¹) than in NOG-01B (up to 7.3 mm yr⁻¹) enabled the
874 Hydrographers reef to quickly catch up with sea-level rise (Table S2).

875
876 Reef growth at the most proximal site of the inner terrace of NOG-01 (M0056A) was
877 delayed by the higher elevation of the older Pleistocene basement. Consequently, only
878 3.7 m of coralgall boundstone accumulated at this site prior to the Younger Dryas sea-
879 level jump (Webster et al., 2018). The coral assemblage is associated with thick crusts
880 of *P. gr. onkodes*, suggesting a very shallow-water environment, but it lacks coral taxa
881 typical of high-energy shallow water, such as *Isopora* and *A. gr. humilis*. Instead, the
882 dominant corals are massive merulinids (e.g., *Cyphastrea* and *Platygyra*). *Cyphastrea*
883 is a locally important component of turbid nearshore communities in the GBR (Perry et
884 al., 2009), and its presence at the base of Reef 3b in M0056A may indicate that
885 conditions on the high-angle slope during the late glacial sea-level rise were
886 unfavorable.

887

888 **4.3.2. Recolonization of mid and outer terraces**

889

890 Coralgall communities at different locations on the mid and outer terraces responded in
891 various ways to reflooding of the inner terrace (Figs. 5, 9 and 11). In HYD-02A and
892 NOG-01B, reflooding coincides with reef drowning in distal holes (Figs. 9 and 11).
893 Holes M0040A and M0041A, on the outer terrace of HYD-02A, lie well below the shelf
894 break at depths of 100–110 mbsl at Noggin Pass and Hydrographers Passage (Abbey
895 et al., 2011b). Coralgall successions are consistent with a deep forereef setting at the
896 LGM that persisted throughout the deglacial sequence (22–14 ka); their location on the
897 shelf margin may have been too deep for reef-building organisms to keep up with rapid
898 sea-level rise. While M0054A and B on NOG-01B also occupy a relatively deep
899 position, a community shift from cE/aA2 and aA3 to cB/aA1 and vermetids at 124.55 mbsl
900 suggests that these coralgall communities were able to catch up, and then keep up with

901 early deglacial sea-level rise before drowning around 17–16 ka. Despite being a
902 relatively shallow site, M0053A also records a drowning trend (shift from cA1/aA1 to
903 cC/aA3) around 17–16 ka at ca. 110 mbsl. In contrast, the mid and outer terraces in
904 HYD-01C (M0035A, M0036A and M0039A) are characterized by bioclastic slope
905 deposits with some, possibly *in situ*, *Porites* colonies in M0039A. Reflooding of the
906 inner terrace increased sediment input, probably at all sites (Webster et al., 2018). In
907 the Reef 3b section in M0053A of NOG-01B, silt- to fine sand-sized calcareous grains
908 fill constructional voids and the core top is enriched in mud; this section has coarser
909 sediments on the mid and outer terraces of HYD-01C (Webster et al., 2011). These
910 observations suggest conditions were more turbid on the mid terrace in NOG-01B
911 during the late deglacial sea-level rise, and this is a possible cause of reef demise
912 (Hallock and Schlager, 1986; Sanders and Baron-Szabo, 2005). Lower turbidity in
913 HYD-01C may be due to the greater distance from the coastline, the gentler slope of
914 the continental shelf, and the presence of back-reef depressions that would have
915 limited transport of resuspended sediments to offshore sites (Abbey et al., 2011b;
916 Hinestrosa et al., 2014). In addition, NOG-01B is 9 km north of a relict fluvial system
917 that may have supplied siliciclastics to the Noggin Pass area (Abbey et al., 2011b).
918 There are no large fluvial systems near HYD-01C (Hinestrosa et al., 2016). Late
919 deglacial reef growth in M0039A, on the outer terrace of HYD-01C, is characterized by
920 the occurrence of massive, up to 22 cm thick *Porites* colonies (Fig. 5) which, when
921 compared with the timing of shallow reef accretion in more proximal holes, probably
922 reflects a deeper, more protected reef setting.

923

924 **4.3.3. The Ribbon Reef transect**

925

926 The late deglacial reef sequence in the Ribbon Reef transect (M0049B and M0050A)
927 lacks the typical high-energy shallow-water coralgall communities of *Isopora* and
928 *Acropora* gr. *humilis* associated with aA1 crusts. Instead it is characterized by
929 encrusting to massive *Porites* and encrusting *Montipora* (cD and cE, Fig. 11) that were
930 themselves encrusted by aA2 and aA3. The Ribbon Reef terraces are narrow and
931 adjacent to a very steep shelf break slope (Abbey et al., 2011b) that may have
932 influenced reef zonation in RIB-02A. On steeper slopes or more turbid inner-shelf reefs,
933 the distribution of coral assemblages adapted to lower irradiance may extend into
934 shallower parts of the reef slope (Done, 1982), displacing the shallow reef communities
935 observed in other localities. Consequently, these communities may have occupied
936 shallower paleowater depths than the interpreted intervals in Fig. 11. Further, the

937 deglacial reef deposits directly overlying the older Pleistocene basement (≥ 30 ka) at
938 112.4 mbsl in M0049B suggests there was a hiatus in reef growth during MIS2 at this
939 location - the steep slope of the shelf edge at Ribbon Reef may not have been suitable
940 for re-establishment of reef-building communities after a sea-level fall.

941

942 **4.4. Late deglacial coralgal assemblages (Reef 4; 13–10 ka)**

943

944 Following the sea-level jump preceding the Younger Dryas at ca. 13.4 ka (Webster et
945 al., 2018), reef growth reinitiated further upslope and formed a barrier reef system
946 rising from depths that are now 50-70 mbsl (Abbey et al., 2011b; Hinestrosa et al.,
947 2016; Webster et al., 2018). However, due to rapid retrogradation/backstepping we are
948 unable to see the fringing to barrier transition directly in the cores. The proto-barrier
949 consists of approximately 15 m of reef framework dominated by robustly branching
950 acroporids (cA2) with thick crusts of *P. gr. onkodes* and vermetids (aA1) accumulated
951 over the older Pleistocene basement in M0034A of HYD-01C and M0057A of NOG-01B
952 (Figs. 5 and 11). A similar facies is recognized in M0042A of HYD-2A, although limited
953 recovery means the prevalence of cA2 cannot be confirmed in this hole. This facies is
954 typical of shallow, high-energy reef settings (Montaggioni, 2005), and the continued
955 accumulation of a single shallow-water assemblage in these holes indicates a keep-up
956 mode of reef growth (Montaggioni and Braithwaite, 2009). Reef 4 grew at average
957 rates of 0.1–11.4 mm yr⁻¹ at HYD-01A and 0.9–7.9 mm yr⁻¹ at NOG-01B (Table S2).
958 The taxonomic composition and abundance of robustly branching acroporids in
959 M0034A of HYD-01C, M0057A of NOG-01B, and probably M0042A of HYD-02A, have
960 no equivalents in other holes, but their tops show a common deepening trend prior to
961 final reef drowning. This deepening is seen in the occurrence of aA3 associated with
962 encrusting *Porites* and *Montipora* in M0057A (cE), massive *Porites* in M0034A (cD),
963 and fragments of merulinids in M0042A (cC?). Reconstructions of slope sedimentation
964 rates and shelf flooding history (Webster et al., 2018) suggest that drowning of Reef 4
965 probably resulted from the combined effects of a rapid sea-level rise and a massive
966 input of terrigenous sediments associated with flooding of the continental shelf.

967

968

969 **4.5. Responses of reef corals to glacial and deglacial conditions**

970

971 The IODP 325 record of last glacial to deglacial reef growth is the most extensive
972 obtained from a stable margin in the Indo-Pacific region (Fig. 12). Another long record,

973 obtained by onshore drilling 2000 km east of the GBR at Tasmaloum on Espiritu Santo
974 Island, Vanuatu, shows reef turn on at 24 ka, but the history of reef growth was
975 influenced by multiple uplift events (Cabiocch et al., 1998). The Tasmaloum record, and
976 a nearby record from a more sheltered site at Urelapa, both contain a succession of
977 shallow-water facies dominated by *Acropora* spp., with intervals rich in *A. gr. robusta* at
978 the more exposed Tasmaloum site. LGM reef material has been recovered from other
979 Indo-Pacific localities using various sampling techniques: onshore drilling on Mururoa
980 (French Polynesia; Camoin et al., 2001), Rendova (Taylor et al., 2005) and the Huon
981 Peninsula (Papua New Guinea; Cutler et al., 2004); sampling from a submersible off
982 Mayotte (Comoro Islands; Dullo et al., 1998); and offshore drilling near Irabu-jima,
983 Ryukyu Islands (Japan; Sasaki et al., 2006). In addition, bathymetric surveys suggest
984 possible LGM/early deglacial reef growth exists at several other localities: Hawaii
985 (Webster et al., 2004a); Huon Gulf (Papua New Guinea; Webster et al., 2004b);
986 western India (Rao et al., 2003); and the Maldives (Rovere et al., 2018). These
987 observations all point to the resilience of coral reef ecosystems in various tectonic
988 settings during the last glaciation, and to their ability to track sea-level changes.

989
990 Despite this apparent resilience, the potential to rebuild a reef is influenced by the
991 antecedent topography, as shown in Mayotte and Mururoa where the steepness of the
992 slope prevented thick accumulations during the last glacial to early deglacial period
993 (Camoin et al., 2001; Dullo et al., 1998). The IODP 325 record highlights the
994 importance of antecedent topography in controlling the depths at which reef-builders
995 colonize substrates and, therefore, the nature of the initial reef communities (Fig. 12).
996 Our data also strongly suggest that shelf morphology and the presence or absence of
997 nearby rivers influenced glacial-deglacial coralgall successions by controlling
998 sedimentation regimes along the shelf (Hinestrosa et al., 2016, 2019), and perhaps
999 even preventing MIS2 reef growth locally (e.g. at Ribbon Reef). Although lower SSTs
1000 during the LGM clearly did not inhibit all reef growth, a steeper SST latitudinal gradient
1001 in the central GBR region may have delayed reef initiation at Hydrographers Passage
1002 (Felis et al., 2014), and SST impacts may have been even more pronounced at
1003 localities south of Hydrographers Passage. Variation in SST during glacial-interglacial
1004 cycles is linked to changes in the geographic distribution of coral species. For example,
1005 warmer SSTs at high latitudes during the last interglacial, expanded the latitudinal
1006 range of tropical coral species in Western Australia (Greenstein and Pandolfi, 2008).
1007 Since the IODP 325 holes are all well within the tropics, they are unlikely to record
1008 possible expansion or contraction of the range of individual coral species.

1009

1010

1011 Little is known about the composition of reef communities during glacial sea-level
1012 lowstands. Tager et al. (2010) analyzed multiple generations of submerged reef crest
1013 communities in the Huon Gulf (PNG) that formed during successive glaciations and
1014 compared those to the uplifted Huon Peninsula highstand reef terraces. Their results
1015 show gradual shifts in species composition of coral assemblages from one glacial
1016 period to the next, and differences between lowstand and highstand communities,
1017 apparently related to changing environmental conditions during the progressive closure
1018 of the Huon Gulf (Tager et al., 2010). In the IODP 325 record, temporal variations in
1019 coralgal assemblages are most easily explained by the influence of changing
1020 hydrodynamic conditions controlled by the interplay of reef growth and sea-level
1021 change. One notable trend is the peak in abundance of *Seriatopora* (cB) in shallow
1022 water facies between 16 and 19 ka; *Isopora* and medium to robustly branching
1023 *Acropora* (cA1/2) dominate shallow-water assemblages after 16 ka (Fig. 12). Since
1024 *Seriatopora* is more common in protected environments in the modern GBR (Done,
1025 1982), increases in the abundance of this genus during the last deglaciation may
1026 indicate that reef growth was lagging behind sea-level rise, so that reef tops remained
1027 below the high energy surf zone. The shift from cB (lower exposure to waves) to aA1
1028 (higher exposure to waves) in M0053A (Reef 3a) and M0055A (base of Reef 3b)
1029 probably reflects a slight shallowing trend during a catch-up mode of reef growth.
1030 Another possibility is that the observed vertical succession was not caused by shift in
1031 coral community structure, but rather by lateral migration of a shallow, exposed reef
1032 front retrograding as it kept up with sea-level rise (i.e., in keeping with Walther's Law;
1033 Webster and Davies, 2003; Blanchon and Blakeway, 2003).

1034

1035 The roles of intrinsic ecological factors, such as larval dispersal ability and substrate
1036 preferences, may also have influenced coral community structure during glacial and
1037 early deglacial periods (Tager et al., 2010). The IODP 325 record shows that responses
1038 of coral communities to sea-level rise along the shelf varied over a latitudinal gradient.
1039 Glacial to early deglacial reefs grew adjacent to the shelf edge and probably were more
1040 directly affected by terrigenous input from nearby rivers, a configuration that may have
1041 created a more discontinuous reef tract that may have limited the potential of larval
1042 dispersal from one reef to another. In this context, coral species with brooded larvae
1043 able to settle immediately after release including *Seriatopora* and *Stylophora* may have
1044 been able to rebuild populations more quickly after the LGM sea-level drop than

1045 species that broadcast gametes and larvae into the plankton (Knowlton, 2001).
1046 Because corals like *Seriatopora* live in a wide depth range extending to the mesophotic
1047 zone (Sinniger et al., 2012), they may potentially survive at depth when shallow
1048 populations are subaerially exposed. This may have contributed to the success of
1049 *Seriatopora* after the LGM disturbance (Humblet & Webster, 2017). This reasoning
1050 invokes the concept of deep reef refugia proposed by several previous authors (see
1051 Bongaerts et al., 2010 for a review).

1052
1053 Finally, the IODP 325 record highlights the interdependence of reef morphology and
1054 coral community structure. The barrier reef (Reef 4) framework consists mostly of
1055 robustly branching acroporids, unlike the composition of shallow facies during earlier
1056 reef-building episodes (Reef 2, 3a, and 3b) (Fig. 12). Blanchon et al. (2014) inferred a
1057 comparable, possible fringing to barrier reef transition in Tahiti, where the barrier reef
1058 formed on the edge of an older Pleistocene reef platform concurrently with creation of a
1059 lagoon that, by acting as a sediment trap, promoted fast-growing coral species on the
1060 exposed reef front. A similar scenario may explain the formation of Reef 4 along the
1061 shelf edge of the modern GBR. However, unlike the Tahiti reef, development of Reef 4
1062 terminated at ca. 10 ka, which has been linked to increased sedimentation and decline
1063 in water quality as most of the shelf became flooded by 10 ka (Webster et al., 2018).

1064

1065 **5. Conclusions**

1066

1067 Our study of cores extracted from submerged reefs along the shelf edge of the Great
1068 Barrier Reef enabled us to examine the evolution of reef communities since the late
1069 glacial period over a broad latitudinal range at three localities with different shelf
1070 morphologies. The following conclusions can be drawn from our investigations:

1071

1072 1. We identified three algal assemblages and eight coral assemblages. The taxonomy
1073 and morphology of corals and algal crusts, and the presence or absence of vermetid
1074 gastropods, were used to constrain paleoenvironments. Based on analogies with
1075 modern reefs, we distinguish three basic reef slope environments: reef crest to shallow
1076 upper reef slope (0–5 m or 0–10 m), shallow to medium-depth reef slope (0–20 m), and
1077 deep forereef slope (>20 m).

1078

1079 2. Reef communities relocated across the shelf edge in response to sea-level changes.
1080 During the Last Glacial Maximum the shelf edge provided a refuge for a diverse coral

1081 fauna that included the key reef builders of modern GBR reefs, i.e. *Isopora*, *Acropora*
1082 *gr. humilis*, *Dipsastraea gr. pallida*, *Porites*, and *Montipora*. These corals may have
1083 been an important source of coral larvae that reseeded the reef during the postglacial
1084 sea-level rise. The timing of reef turn-on at lower elevations following the LGM sea
1085 level fall varied geographically.

1086

1087 3. The depth of the pre-MIS2 basement and possibly terrigenous input influenced the
1088 composition of the late glacial MIS2 reef communities and the mode of reef growth. On
1089 the inner terrace, late glacial reef growth was terminated at ca. 22 ka when sea-level
1090 dropped to its LGM position and reef growth became restricted to the mid and outer
1091 terraces until sea level reinvaded the inner terrace at ca. 17 ka. Deglacial sea-level rise
1092 promoted recolonization of the inner terrace by fast-growing corals, such as *Isopora*,
1093 *Acropora gr. humilis*, and *Seriatopora*, despite sediment resuspension.

1094

1095 4. Shelf morphology greatly influenced the survival of coralgal communities in distal
1096 sites following the reflooding of the inner terrace at 17 ka. In Hydrographers Passage
1097 where the shelf is widest and the shelf break is gently sloping, reef growth was delayed
1098 on the inner terrace, while bioclastic slope deposits and local *in situ* coral growth
1099 occurred on the mid and outer terraces. In Noggin Pass, where the shelf is narrow and
1100 the shelf break is steep, reef growth initiated early on the inner terrace but ceased
1101 prematurely on the mid and outer terraces due to increased turbidity. Terrigenous
1102 sediments may have been supplied by a nearby fluvial system revealed by bathymetric
1103 and seismic data.

1104

1105 5. Following the sea-level jump preceding the Younger Dryas, reef habitats migrated
1106 further upslope, forming a barrier reef system composed of a robustly branching
1107 acroporid assemblage not seen in more distal terrace holes.

1108 Retrogradation/backstepping prevented the formation of direct superposition of
1109 fringing-to-barrier reef transitions in cores.

1110

1111 6. The dominance of *Porites* and *Montipora* in the late deglacial sequence at Ribbon
1112 Reef may be caused by a shallowing of the deep forereef coral fauna related to the
1113 steepness of the shelf break at this locality.

1114

1115 7. Reef drowning signatures are consistent across all sites, and are composed of
1116 encrusting to massive *Porites* and/or encrusting *Montipora* with thin encrustations of a

1117 deep forereef, coralline algal assemblage covering the deglacial sequence.

1118

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1120

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1127

1128

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1530

1531 **Figure captions**

1532

1533 **Fig. 1.** A. Locations and bathymetric profiles of transects and all IODP Exp. 325 holes.
1534 Holes not included in this study are shaded grey. The map is from Camoin and Webster
1535 (2015) and has been modified to show the modern GBR (in shaded grey). B.
1536 Schematic section of the continental shelf of eastern Australia showing the location of
1537 the modern GBR (Reef 5), and stratigraphic distribution of fossil submerged reef
1538 sequences (Reef 1-4) occurring along the shelf edge (inset 1) and described in
1539 Webster et al. (2018).

1540

1541 **Fig. 2.** Examples (thin sections) of coralline algal assemblages identified in this study.
1542 A. Thick thallus of *Porolithon* gr. *onkodes*, the key component of assemblage aA1,
1543 growing on a vermetid shell (lower part). Note trichocyte (hair cell) fields (arrowheads)
1544 typical of this species. B. Thallus of *Harveyolithon* gr. *munitum*, common in assemblage
1545 aA2, and accessory in aA1. C. Foliose branches (thalli) of *Dawsoniolithon conicum*
1546 (lower part), a common component of assemblage aA2 and accessory in aA1. Note
1547 preserved conceptacles (arrowheads) that are usually shed after spore release. Arrows
1548 indicate encrusting thalli of *Lithophyllum*. D. Foliose branches or thalli of *Mesophyllum*

1549 *funafutiense*, characteristic of assemblage aA3, intergrown with encrusting foraminifers
1550 (arrows).

1551

1552 **Fig. 3.** Examples (core sections) of the eight coral assemblages identified in this study.
1553 Upper labels name assemblages and lower labels identify hole and core. The
1554 taxonomic names of fossil corals are indicated next to each core section. A HUM
1555 *Acropora* gr. *humilis*, B ISO branching *Isopora*, BF ACRO finely branching *Acropora*,
1556 DIPS *Dipsastraea*, EN ISO encrusting *Isopora*, M ISO massive *Isopora*, EN MON
1557 encrusting *Montipora*, EN PO encrusting *Porites*, HYDN *Hydnophora*, M PO massive
1558 *Porites*, PACHY *Pachyseris speciosa*, SERIA *Seriatopora*.

1559

1560 **Fig. 4.** Distribution of corallgal assemblages, vermetid gastropods, algal crust
1561 thickness, and percentage of corallgal framework in cores recovered from transect
1562 HYD-01C.

1563

1564 **Fig. 5.** Corallgal-based interpretations of paleowater depths of reef sequences in cores
1565 from transect HYD-01C.

1566

1567 **Fig. 6.** Temporal distribution of coral taxa in the late glacial (MIS2) reef sequence (Reef
1568 2), and the deglacial reef sequence after reflooding of the inner terrace (Reef 3b) in
1569 transects HYD-01C and NOG-01B. The context of each coral is categorized as IS (*in*
1570 *situ*) or IS? (probably *in situ*), ISN (context unknown), or ISX (not *in situ*) or ISX?
1571 (probably not *in situ*). Colored intervals indicate the distributions of the coral
1572 assemblages illustrated in Figs. 3–5. Time is indicated in thousands of years (ka). Stars
1573 indicate age controls.

1574

1575 **Fig. 7.** Temporal distribution of the coral taxa in the LGM reef sequence (Reef 3a) in
1576 transects HYD-01C, HYD-02A, and NOG-01B. The context of each coral is categorized
1577 as IS (*in situ*) or IS? (probably *in situ*), ISN (context unknown), or ISX (not *in situ*) or
1578 ISX? (probably not *in situ*). Colored intervals indicate the distribution of coral
1579 assemblages illustrated in Figs. 3–5. Time is indicated in thousands of years (ka).

1580

1581 **Fig. 8.** Distribution of corallgal assemblages, vermetid gastropods, algal crust
1582 thickness, and percentage of corallgal framework in cores recovered from transect
1583 HYD-02A.

1584

1585 **Fig. 9.** Coralgal-based interpretations of paleowater depths of reef sequences in cores
1586 from transect HYD-02A.

1587

1588 **Fig. 10.** Distribution of coralgal assemblages, vermetid gastropods, algal crust
1589 thickness, and percentage of coralgal framework in cores recovered from transects
1590 NOG-01B and RIB-02A.

1591

1592

1593

1594

1595 **Fig. 11.** Coralgal-based Interpretations of paleowater depths in cores from transects
1596 NOG-01B and RIB-02A. Due to the steepness of the shelf break slope, interpreted
1597 paleowater depths in cores of transect RIB-02A may be overestimated.

1598

1599 **Fig. 12.** Schematic representation of the trends in coralgal assemblages in IODP Exp.
1600 325 holes in the three geographic areas studied (Hydrographers Passage, Noggin
1601 Pass, and Ribbon Reef), their chronostratigraphic relationships, and variations in
1602 paleo-water depth. Ages of reef sequence boundaries are indicated in grey next to the
1603 logs. The blue curve is the combined relative sea level curve based on IODP Exp. 325
1604 core material from HYD-01A and NOG-01B (derived from Fig. 3 in Yokoyama et al.,
1605 2018).

1606

1607

1608 **Table captions**

1609

1610 **Table 1.** Coralline algae and corals identified in post-MIS3 core sections of IODP Exp.
1611 325. See Webster et al. (2018) and the text of the present paper for definitions of reef
1612 sequences: R2 Reef 2, R3a Reef 3a, R3b Reef 3b, R4 Reef 4. BR branching, COR
1613 corymbose, EN encrusting, FBR fine branching, M massive, PL platy.

1614

1615 **Table 2.** Algal and coral assemblages and their paleoenvironmental interpretations.
1616 The paleowater depths of coral assemblages are divided into two columns. Paleowater
1617 depths listed in the first column (left) are based solely on the association of coral
1618 species; those listed in the second columns (right) are further constrained by the
1619 occurrence of thick crusts of *Porolithon gr. onkodes* and vermetid gastropods.

1620

1621

1622 **Supplementary material**

1623

1624 **Table S1.** Occurrences of algal and coral taxa identified in the reef sequences 2 (R2, 27-
1625 22 ka), 3a (R3a, 22-17 ka), 3b (R3b, 17-13 ka), and 4 (R4, 13-10 ka). Grey cells
1626 correspond to one occurrence or more. Question marks indicate uncertainty in the
1627 taxonomic identification or the age. If a taxon occurs only in one core section, the name
1628 of the core section is indicated next to column R4. BR branching, COR corymbose, EN
1629 encrusting, FBR fine branching, M massive, PL platy.

1630

1631 **Table S2.** Vertical reef accretion rates calculated at HYD-01A and NOG-01B (derived
1632 from Table S2 of Webster et al., 2018). The rates were calculated between successive
1633 inflection points identified on the maximum relative sea level curves constructed for HYD-
1634 01A and NOF-01B (visual fit method). For details about the method, see Webster et al.
1635 (2018).

Table 1

CORALLINE ALGAE

Order CORALLINALES

Family CORALLINACEAE

Subf. NEOGONIOLITHOIDEAE

1. *Neogoniolithon* gr. *fosliei*
- Neogoniolithon* sp.
2. *Spongites* *sulawesiensis*
3. *Spongites* sp.

Subf. HYDROLITHOIDEAE

4. *Adeylithon* *bosencei*
5. *Hydrolithon* *boergesenii*
(= *H. reinboldii*)

Subf. METAGONIOLITHOIDEAE

6. *Harveylithon* gr. *munitum*
7. *Harveylithon* *rupestre*
8. "*Hydrolithon*" *murakoshii*
9. *Dawsoniolithon* *conicum*
10. *Porolithon* *gardineri*
11. *Porolithon* gr. *onkodes*

Subf. LITHOPHYLLOIDEAE

12. *Lithophyllum* *acrocampium*
13. *Lithophyllum* *cuneatum*
14. *Lithophyllum* *insipidum*
15. *Lithophyllum* gr. *kotschyannum*
16. *Lithophyllum* gr. *prototypum*
17. *Lithophyllum* gr. *pustulatum*
18. *Paulsilvella* sp.

Subf. UNCERTAIN

19. "*Hydrolithon*" *breviclavium*
20. *Lithoporella* sp.

Order HAPALIDIALES

Family HAPALIDIACEAE

Subf. MELOBESIOIDEAE

21. *Lithothamnion* *muelleri*
22. *Lithothamnion* *prolifer*
23. *Lithothamnion* sp. 1 (34A-11-1)
Lithothamnion sp. 2
24. *Melyvonnea* gr. *erubescens*
25. *Mesophyllum* *funafutiense*
26. *Mesophyllum* sp. 1 (55A- 5-CC)
Mesophyllum sp. 2

Order SPOROLITHALES

Family SPOROLITHACEAE

27. *Sporolithon* *ptychoides*
28. *Sporolithon* sp.

SCLERACTINIAN CORALS

Family ACROPORIDAE

1. *Acropora* gr. FBR COR
2. *Acropora* gr. *humilis*
3. *Acropora* gr. *hyacinthus*
4. *Acropora* gr. *robusta*
5. *Acropora* *monticulosa*
6. *Astreopora* sp.
7. *Isopora* gr. BR
8. *Isopora* gr. M
9. *Montipora* gr. BR?
10. *Montipora* gr. EN/PL
11. *Montipora* gr. M

Family AGARICIIDAE

12. *Leptoseris* *explanata* ?
13. *Leptoseris* *foliosa*
14. *Leptoseris* gr. *scabra*
15. *Leptoseris* gr. *yabei*
16. *Leptoseris* *papyracea*
17. *Pachyseris* *speciosa*
18. *Pavona* *clavus*
19. *Pavona* *maldivensis*

Family FUNGIIDAE

20. *Cycloseris* sp.?
21. *Fungia* sp.

Family DENDROPHYLLIIDAE

22. *Turbinaria* *frondens*
23. *Turbinaria* *mesenterina* ?
24. *Turbinaria* *peltata*
25. *Turbinaria* *reniformis*

Family LOBOPHYLLIIDAE

26. *Lobophyllia* *corymbosa*

Family MERULINIDAE

27. *Astrea* *curta*
28. *Caulastrea* sp.?
29. *Cyphastrea* gr. *serailia*
30. *Cyphastrea* *microphthalma*
31. *Dispastraea* gr. *laxa* ?
32. *Dispastraea* gr. *pallida*
33. *Echinopora* *lamellosa*
34. *Echinopora* *mammiformis* ?
35. *Favites* *flexuosa* ?
36. *Favites* gr. *abdita*
37. *Favites* *pentagona*
38. *Favites* *valenciennesi*
39. *Goniastrea* *pectinata* ?
40. *Goniastrea* *stelligera* ?
41. *Hydnophora* *exesa*
42. *Leptoria* *phrygia*
43. *Platygyra* gr. *daedalea*
44. *Platygyra* *pini* ?

Family OCULINIDAE

45. *Galaxea* *fascicularis*

Family POCILLOPORIDAE

46. *Pocillopora* *damicornis*
47. *Seriatopora* *hystrix*
48. *Stylophora* *pistillata*

Family PECTINIIDAE

49. *Echinophyllia* sp.?
50. *Mycedium* *elephantotus*

Family PORITIDAE

51. *Alveopora* *verrilliana*
52. *Goniopora* gr. M

53. *Porites* gr. BR

54. *Porites* gr. EN/PL

55. *Porites* gr. M

Family SIDERASTREIDAE

56. *Coscinaraea* *columna*

57. *Psammocora* sp.?

INCERTAE SEDIS

58. *Leptastrea* *pruinosa*

NON-SCLERACTINIAN CORALS

Family HELIOPORIDAE?

- Heliopora* *coerulea* ?

Family TUBIPORIDAE

- Tubipora* *musica*

Family MILLEPORIDAE

- Millepora* sp.

Family ALCYONIDAE (soft corals)

- Spiculite (*Sinularia* sp.?)

Table 2

ALGAL ASSEMBLAGE	Key components	Accessory components	Paleowater depth	
Assemblage aA1	Thick crusts of <i>Porolithon</i> gr. <i>onkodes</i>	<i>Porolithon gardineri</i> , <i>Lithophyllum</i> gr. <i>kotschy anum</i> , and <i>Neogoniolithon</i> gr. <i>fosliei</i>	0–10 m	
Assemblage aA2	Thin crusts of <i>Porolithon</i> gr. <i>onkodes</i> , <i>Porolithon gardineri</i> and <i>Harveyolithon</i> gr. <i>munitum</i>	<i>Hydrolithon boergesenii</i> , <i>Neogoniolithon</i> gr. <i>fosliei</i> and <i>Dawsoniolithon conicum</i> , <i>Lithophyllum</i> gr. <i>prototypum</i>	0–20 m	
Assemblage aA3	Knobby <i>Melyvonnea</i> gr. <i>erubescens</i> and foliose <i>Mesophyllum funafutiense</i> , lack of key components of aA1 and aA2	<i>Lithothamnion prolifer</i> , <i>L.</i> gr. <i>prototypum</i> , thin encrusting <i>Lithoporella</i> sp. and laminar <i>Lithothamnion</i>	>20 m	
CORAL ASSEMBLAGE	Key components	Accessory components	Paleowater depth	
Assemblage cA1	Encrusting to massive <i>Isopora</i> and medium branching <i>Acropora</i> gr. <i>humilis</i>	Medium to robust branching <i>Acropora</i> , encrusting <i>Porites</i>	0–10 m	0–5 m *
Assemblage cA2	Branching and massive <i>Isopora</i>	Medium branching <i>Acropora</i> gr. <i>humilis</i> and robust branching <i>Acropora</i> gr. <i>robusta</i>	0–10 m	0–5 m
Assemblage cA3	Encrusting to massive <i>Isopora</i> and branching <i>Acropora</i>	Encrusting <i>Porites</i> and <i>Montipora</i>	0–20 m	0–10 m
Assemblage cB	Branching <i>Seriatopora</i> and <i>Acropora</i>	Encrusting to massive <i>Isopora</i> and merulinids, branching <i>Stylophora</i> sp., massive <i>Tubipora</i> , encrusting <i>Porites</i> and <i>Montipora</i>	0–20 m	0–10 m
Assemblage cC	Encrusting to massive merulinids (e.g. <i>Dipsastrea</i> gr. <i>pallida</i> , <i>Hydnophora</i> sp.**)	Encrusting <i>Porites</i> and <i>Montipora</i> , branching (fine br.) <i>Acropora</i>	0–30 m	0–10 m
Assemblage cD	Massive <i>Porites</i>	Encrusting <i>Montipora</i> and merulinids (e.g. <i>Platygyra</i>)	0–60 m	0–10 m
Assemblage cE	Encrusting <i>Porites</i> and <i>Montipora</i>	Fine branching <i>Acropora</i> and encrusting <i>Cyphastrea</i>	>20 m	
Assemblage cF	Encrusting agariciids (e.g. <i>Leptoseris</i> gr. <i>yabei</i> , <i>Pachyseris speciosa</i>)	Encrusting <i>Porites</i> and <i>Montipora</i>	>20 m	

* When associated with thick crusts of *Porolithon* gr. *onkodes* and vermetid gastropods

** Only relatively common in Reef 2 at location HYD-01C

Table S1

CORALLINE ALGAE				CORALLINE ALGAE					
	R2	R3a	R3b	R4		R2	R3a	R3b	R4
Order CORALLINALES					Order HAPALIDIALES				
Family CORALLINACEAE					Family HAPALIDIACEAE				
Subf. NEOGONIOLITHOIDEAE					Subf. MELOBESIOIDEAE				
<i>Neogoniolithon</i> gr. <i>fosliei</i> -----	■	■	■	■	<i>Lithothamnion</i> <i>muelleri</i> -----	■	■	■	■
<i>Neogoniolithon</i> sp. -----	■	■	■	■	<i>Lithothamnion</i> <i>prolifer</i> -----	■	■	■	■
<i>Spongites</i> <i>sulawesiensis</i> -----	■	■	■	■	<i>Lithothamnion</i> sp. -----	■	■	■	■
<i>Spongites</i> sp. -----	■	■	■	■	<i>Lithothamnion</i> sp. -----	■	■	■	■
Subf. HYDROLITHOIDEAE					<i>Melyonnea</i> gr. <i>erubescens</i> ----				34A-11-1
<i>Adeylithon</i> <i>bosencei</i> -----	■	■	■	■	<i>Mesophyllum</i> <i>funafutiense</i> -----	■	■	■	■
<i>Hydrolithon</i> <i>boergesenii</i> -----	■	■	■	■	<i>Mesophyllum</i> sp. -----	■	■	■	■
(= <i>H. reinboldii</i>)					<i>Mesophyllum</i> sp. -----	■	■	■	■
Subf. METAGONIOLITHOIDEAE					Order SPROLITHALES				
<i>Porolithon</i> <i>gardineri</i> -----	■	■	■	■	Family SPOROLITHACEAE				
<i>Porolithon</i> gr. <i>onkodes</i> -----	■	■	■	■	<i>Sporolithon</i> <i>pychoides</i> -----	■	■	■	■
<i>Harveyolithon</i> gr. <i>munitum</i> -----	■	■	■	■	<i>Sporolithon</i> sp. -----	■	■	■	■
<i>Harveyolithon</i> <i>rupestre</i> -----	■	■	■	■					
" <i>Hydrolithon</i> " <i>murakoshii</i> -----	■	■	■	■					
<i>Dawsonolithon</i> <i>conicum</i> -----	■	■	■	■					
Subf. LITHOPHYLLOIDEAE									
<i>Lithophyllum</i> <i>acrocampatum</i> -----	■	■	■	■					
<i>Lithophyllum</i> <i>cuneatum</i> -----	■	■	■	■					
<i>Lithophyllum</i> <i>insipidum</i> -----	■	■	■	■					
<i>Lithophyllum</i> gr. <i>kotschyanum</i> ----	■	■	■	■					
<i>Lithophyllum</i> gr. <i>prototypum</i> ----	■	■	■	■					
<i>Lithophyllum</i> gr. <i>pustulatum</i> ----	■	■	■	■					
<i>Lithophyllum</i> sp. -----	■	■	■	■					
<i>Paulsilvella</i> sp. -----	■	■	■	■					
Subf. UNCERTAIN									
" <i>Hydrolithon</i> " <i>breviclavium</i> ----	■	■	■	■					
<i>Lithoporella</i> sp. -----	■	■	■	■					
SCLERACTINIAN CORALS					SCLERACTINIAN CORALS				
	R2	R3a	R3b	R4		R2	R3a	R3b	R4
Family ACROPORIDAE					Family ACROPORIDAE				
<i>Acropora</i> gr. FBR COR -----	■	■	■	■	<i>Favites</i> <i>flexuosa</i> ? -----	■	■	■	■
<i>Acropora</i> gr. <i>humilis</i> -----	■	■	■	■	<i>Favites</i> gr. <i>abdit</i> -----	■	■	■	■
<i>Acropora</i> gr. <i>hyacinthus</i> -----	■	■	■	■	<i>Favites</i> <i>pentagona</i> -----	■	■	■	■
<i>Acropora</i> gr. <i>robusta</i> -----	■	■	■	■	<i>Favites</i> <i>valenciennesi</i> -----	■	■	■	■
<i>Acropora</i> <i>monticulosa</i> -----	■	■	■	■	<i>Goniastrea</i> <i>pectinata</i> ? -----	■	■	■	■
<i>Astreopora</i> sp. -----	■	■	■	■	<i>Goniastrea</i> <i>stelligera</i> ? -----	■	■	■	■
<i>Isopora</i> gr. BR -----	■	■	■	■	<i>Hydnophora</i> -----	■	■	■	■
<i>Isopora</i> gr. EN/M -----	■	■	■	■	<i>Hydnophora</i> <i>exesa</i> -----	■	■	■	■
<i>Montipora</i> gr. BR? -----	■	■	■	■	<i>Leptoria</i> <i>phrygia</i> -----	■	■	■	■
<i>Montipora</i> gr. EN/PL -----	■	■	■	■	<i>Platygyra</i> -----	■	■	■	■
<i>Montipora</i> gr. M -----	■	■	■	■	<i>Platygyra</i> gr. <i>daedalea</i> -----	■	■	■	■
Family AGARICIIDAE					<i>Platygyra</i> <i>pini</i> ? -----				53A-1-1
<i>Leptoseris</i> -----	■	■	■	■	Family OCULINIDAE				
<i>Leptoseris</i> <i>explanata</i> ? -----	■	■	■	■	<i>Galaxea</i> <i>fascicularis</i> -----	■	■	■	■
<i>Leptoseris</i> <i>foliosa</i> -----	■	■	■	■	Family POCILLOPORIDAE				
<i>Leptoseris</i> gr. <i>scabra</i> -----	■	■	■	■	<i>Pocillopora</i> -----	■	■	■	■
<i>Leptoseris</i> gr. <i>yabei</i> ? -----	■	■	■	■	<i>Pocillopora</i> <i>damicornis</i> -----	■	■	■	■
<i>Leptoseris</i> <i>papyracea</i> -----	■	■	■	■	<i>Seriatopora</i> -----	■	■	■	■
<i>Pachyseris</i> <i>speciosa</i> -----	■	■	■	■	<i>Sylophora</i> <i>pistillata</i> -----	■	■	■	■
<i>Pavona</i> -----	■	■	■	■	Family PECTINIIDAE				
<i>Pavona</i> <i>clavus</i> -----	■	■	■	■	<i>Echinophyllia</i> sp.? -----	■	■	■	■
<i>Pavona</i> <i>maldivensis</i> -----	■	■	■	■	<i>Mycedium</i> <i>elephantotus</i> -----	■	■	■	■
Family FUNGIIDAE					Family PORITIDAE				
<i>Cycloseris</i> sp.? -----	■	■	■	■	<i>Alveopora</i> -----	■	■	■	■
<i>Fungia</i> sp. -----	■	■	■	■	<i>Alveopora</i> <i>verilliana</i> -----	■	■	■	■
Family DENDROPHYLLIIDAE					<i>Goniopora</i> gr. M -----				53A-7-1
<i>Turbinaria</i> -----	■	■	■	■	<i>Porites</i> gr. BR -----	■	■	■	■
<i>Turbinaria</i> <i>frondens</i> ? -----	■	■	■	■	<i>Porites</i> gr. EN/PL -----	■	■	■	■
<i>Turbinaria</i> <i>mesenterina</i> ? -----	■	■	■	■	<i>Porites</i> gr. M -----	■	■	■	■
<i>Turbinaria</i> <i>peltata</i> -----	■	■	■	■	Family SIDERASTREIDAE				
<i>Turbinaria</i> <i>reniformis</i> -----	■	■	■	■	<i>Coscinaraea</i> -----	■	■	■	■
Family LOBOPHYLLIIDAE					<i>Coscinaraea</i> <i>columna</i> -----				41A-2-1
<i>Lobophyllia</i> <i>corymbosa</i> -----	■	■	■	■	<i>Psammocora</i> sp.? -----	■	■	■	■
Family MERULINIDAE					INCERTAE SEDIS				
<i>Astrea</i> <i>curta</i> -----	■	■	■	■	<i>Leptastrea</i> <i>pruinosa</i> -----	■	■	■	■
<i>Caulastrea</i> sp.? -----	■	■	■	■					
<i>Cyphastrea</i> -----	■	■	■	■					
<i>Cyphastrea</i> gr. <i>serailia</i> -----	■	■	■	■					
<i>Cyphastrea</i> <i>microphthalma</i> -----	■	■	■	■					
<i>Dipsastraea</i> -----	■	■	■	■					
<i>Dispastraea</i> gr. <i>laxa</i> ? -----	■	■	■	■					
<i>Dispastraea</i> gr. <i>pallida</i> -----	■	■	■	■					
<i>Echinopora</i> -----	■	■	■	■					
<i>Echinopora</i> <i>lamellosa</i> -----	■	■	■	■					
<i>Echinopora</i> <i>mammiformis</i> ? -----	■	■	■	■					
NON-SCLERACTINIAN CORALS					NON-SCLERACTINIAN CORALS				
	R2	R3a	R3b	R4		R2	R3a	R3b	R4
Family HELIOPORIDAE?					Family HELIOPORIDAE?				
<i>Heliopora</i> <i>coerulea</i> ? -----	■	■	■	■	Family TUBIPORIDAE				
Family TUBIPORIDAE					<i>Tubipora</i> <i>musica</i> -----				
<i>Tubipora</i> <i>musica</i> -----	■	■	■	■	Family MILLEPORIDAE				
Family MILLEPORIDAE					<i>Millepora</i> sp. -----				
<i>Millepora</i> sp. -----	■	■	■	■	Family ALCYONIDAE (soft corals)				
Family ALCYONIDAE (soft corals)					<i>Spiculite</i> (<i>Simularia</i> sp.?) -----				
<i>Spiculite</i> (<i>Simularia</i> sp.?) -----	■	■	■	■					

Table S2

Site	Reef	Growth segment	Sample number (n)	Median age range (ka)		Average vertical accretion rate (mm yr ⁻¹)
				Min	Max	
HYD-01C						
Inner terrace						
31-33A	R2	S1	14	25.4	23.5	3.4
31-33A	R2	S2	8	23.5	22.9	1.9
31-33A	R2	S3	4	22.9	22.1	0.1
31-33A	R3b	S4	6	16.2	15.5	1.1
31-33A	R3b	S5	8	15.5	15.2	7.4
31-33A	R3b	S6	6	15.2	15.0	39.4
31-33A	R3b	S7	14	15.0	14.0	0.4
31-33A	R3b (meso)	S8	4	14.0	13.2	2.9
31-33A	R3b, R4 (meso)	S9	6	13.2	10.6	1
Mid terraces						
35-36A	R3a, R2 (meso)	S1	3	29.6	20.7	0.4
35-36A	R3a	S2	45	20.7	17.1	4.3
Outer terraces						
39A	R3a,b	S1	21	20.9	15.2	4
39A	R3b	S2	2	15.2	13.8	2.4
39A	R3b, R4 (meso)	S3	2	13.8	12.7	0.1
Outer Barrier						
34A	R4	S1	10	13.1	12.3	4.5
34A	R4	S2	14	12.3	11.3	11.4
34A	R4	S3	6	11.3	10.3	4.1
34A	R4	S4	5	10.3	9.6	0.1
NOG-01B						
Inner terrace						
55A	R2	S1	10	27.6	24.8	0.5
55A	R2	S2	8	24.8	24.0	3.5
55A	R2	S3	11	24.0	21.8	0.6
55A	R3b	S4	12	16.9	15.9	0.1
55A	R3b	S5	10	15.9	15.6	7.3
55A	R3b (meso)	S6	10	15.6	13.9	2.3
56A	R3b	S1	7	14.5	13.7	0.5
56A	R3b	S2	3	13.7	13.4	3.9
56A	R4 (meso)	S3	10	13.4	12.3	0.9
Mid terraces						
53A	R3a	S1	22	22.4	19.2	3.8
53A	R3a,b	S2	10	19.2	14.6	1.8
53A	R3b (meso)	S3	3	14.6	13.4	0.7
Outer Barrier						
54A,B	R3a	S1	30	23.0	16.6	1.8
54A,B	R3b (meso)	S2	2	16.6	16.0	0.2
Inner Barrier						
57A	R4	S1	14	13.0	12.3	7.9
57A	R4	S2	26	12.3	10.4	4.5
57A	R5 (meso)	S3	6	10.4	8.2	1.3
57A	R5 (meso)	S4	3	8.2	7.8	0.1

Figure 1

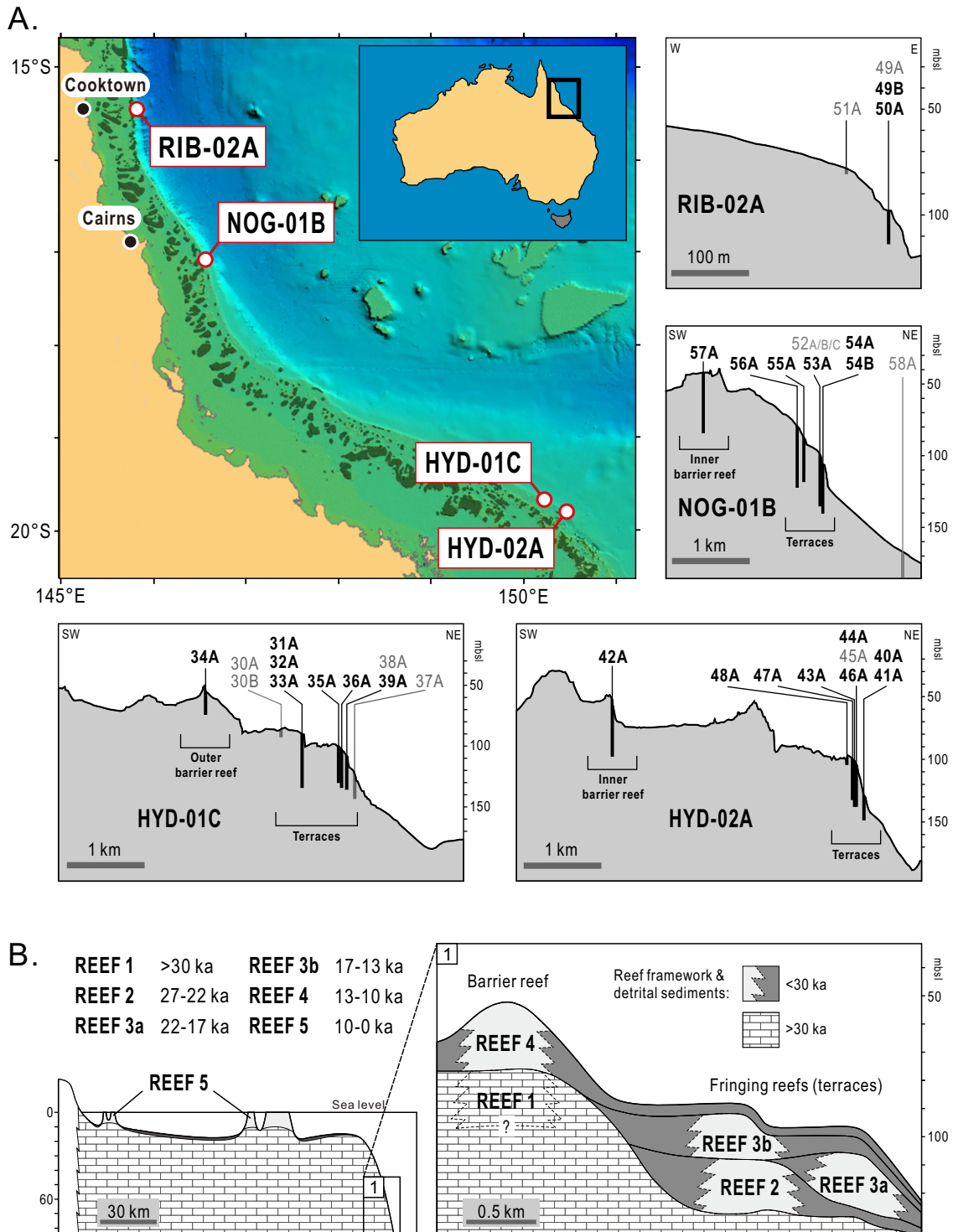


Figure 2

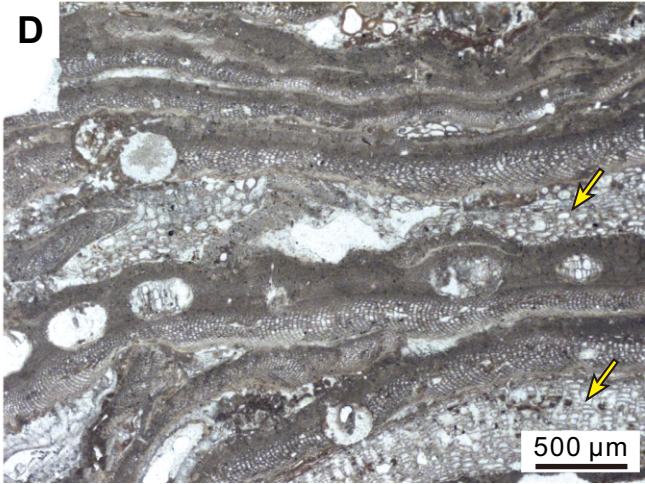
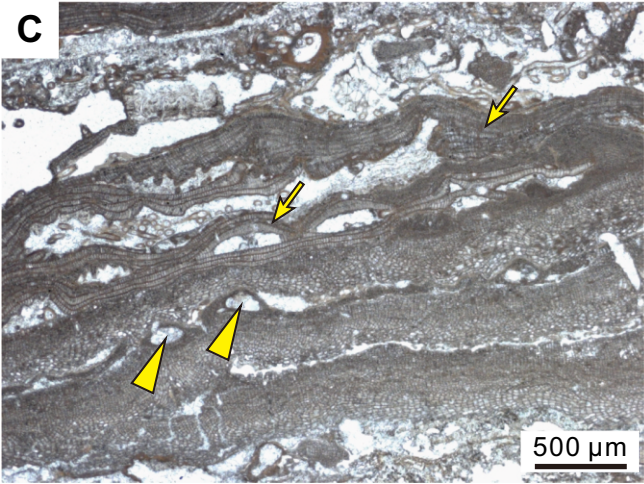
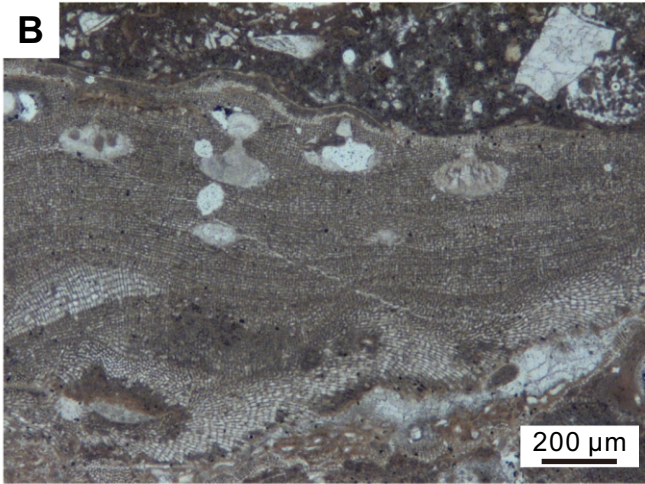
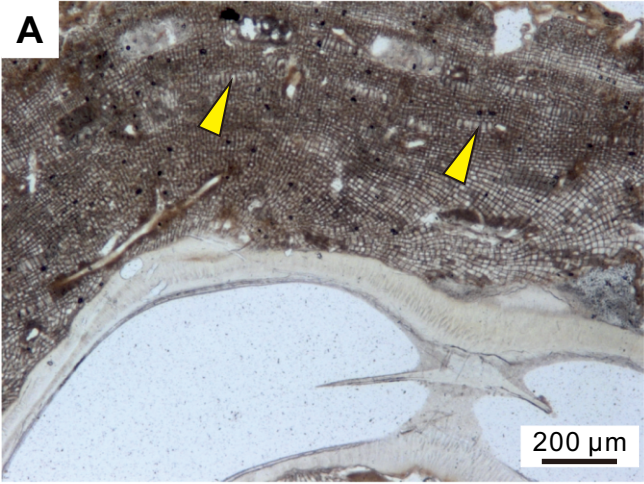


Figure 3

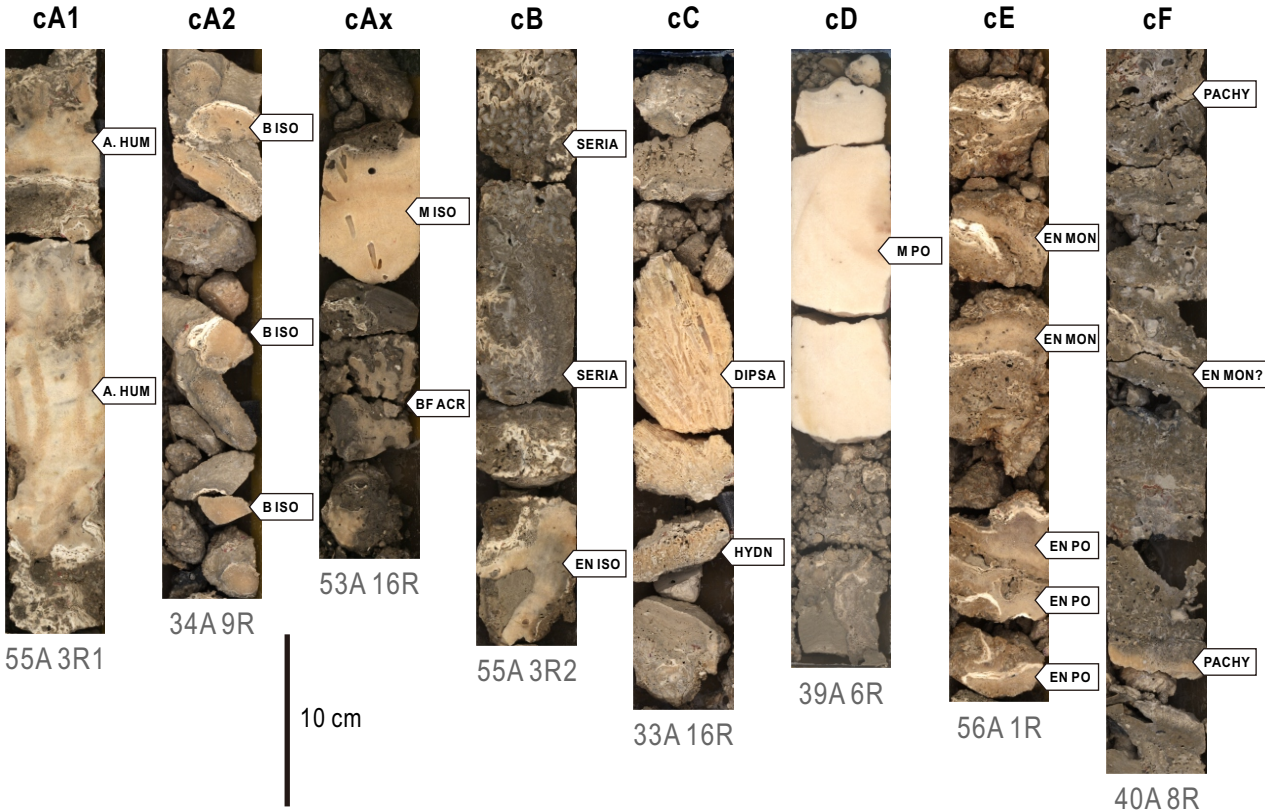


Figure 4

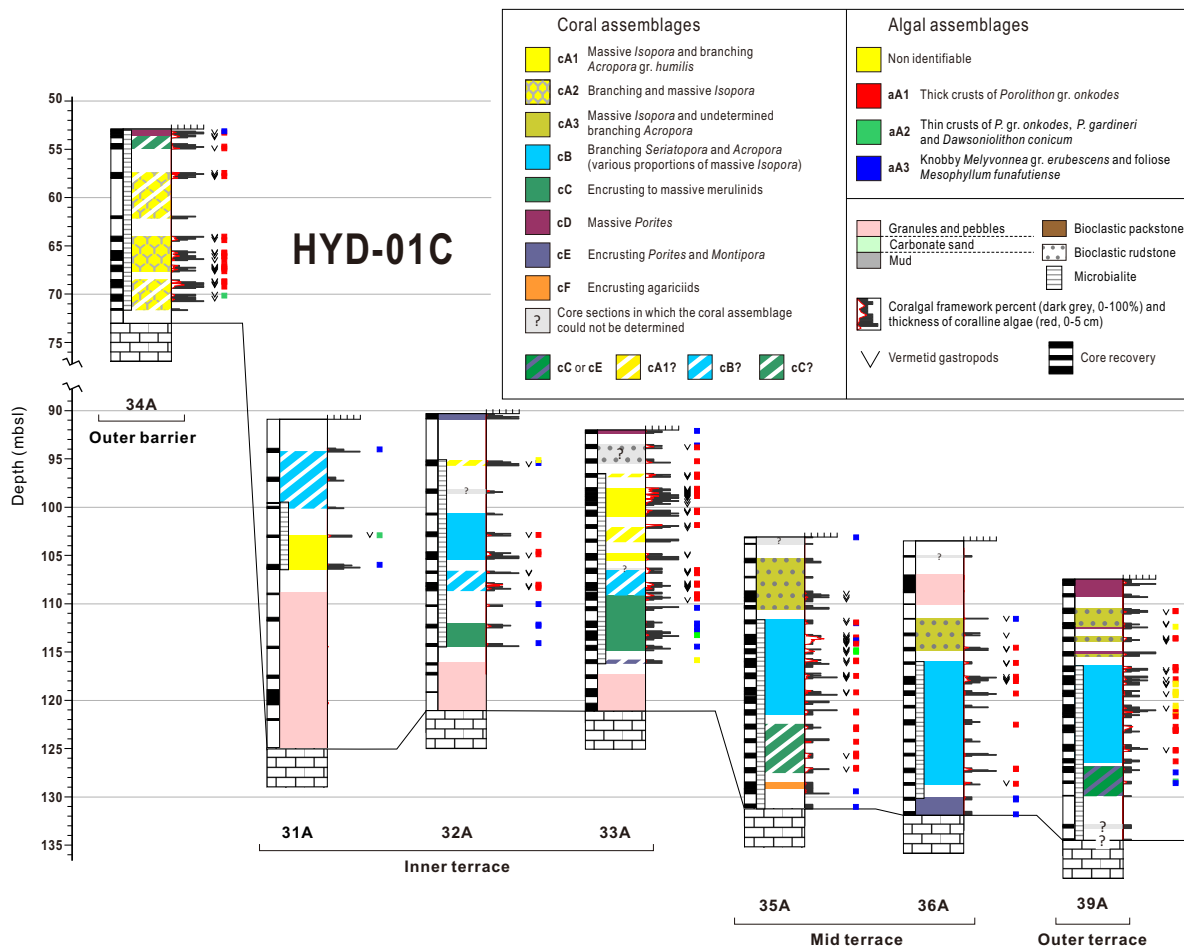


Figure 5

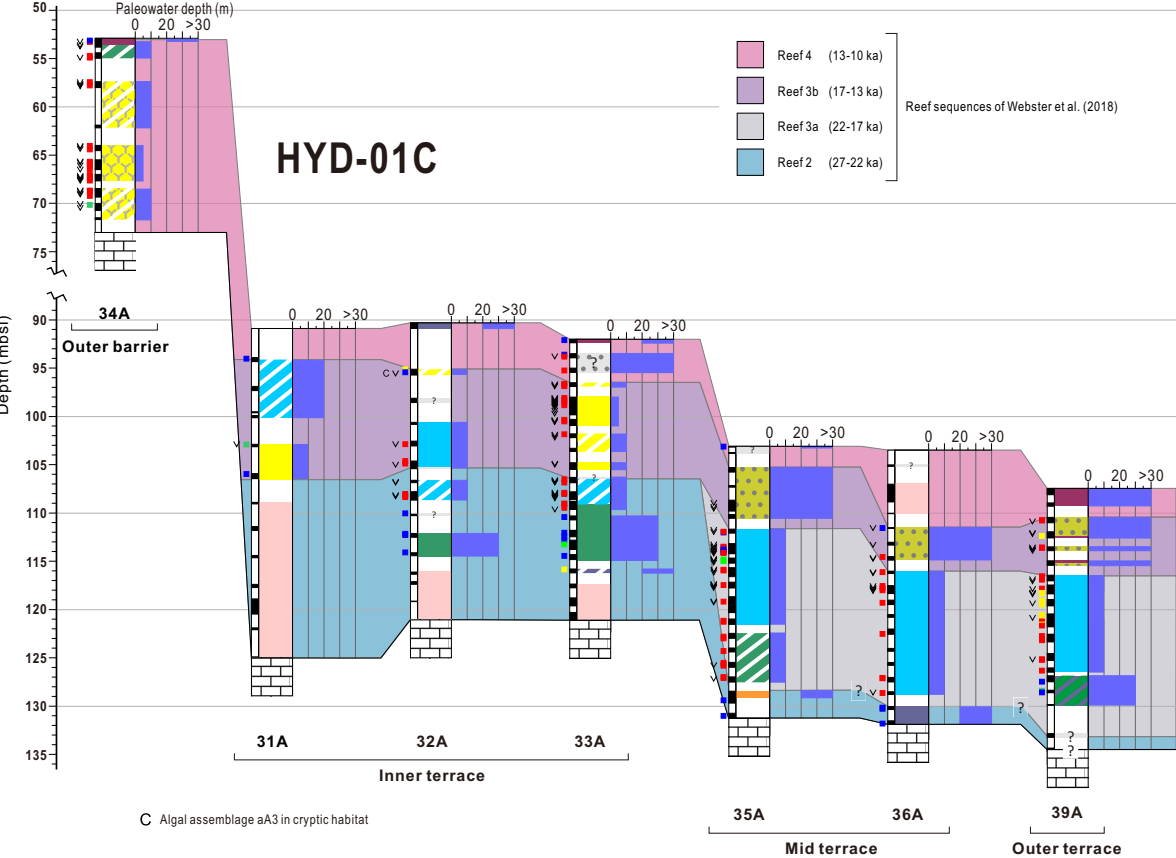
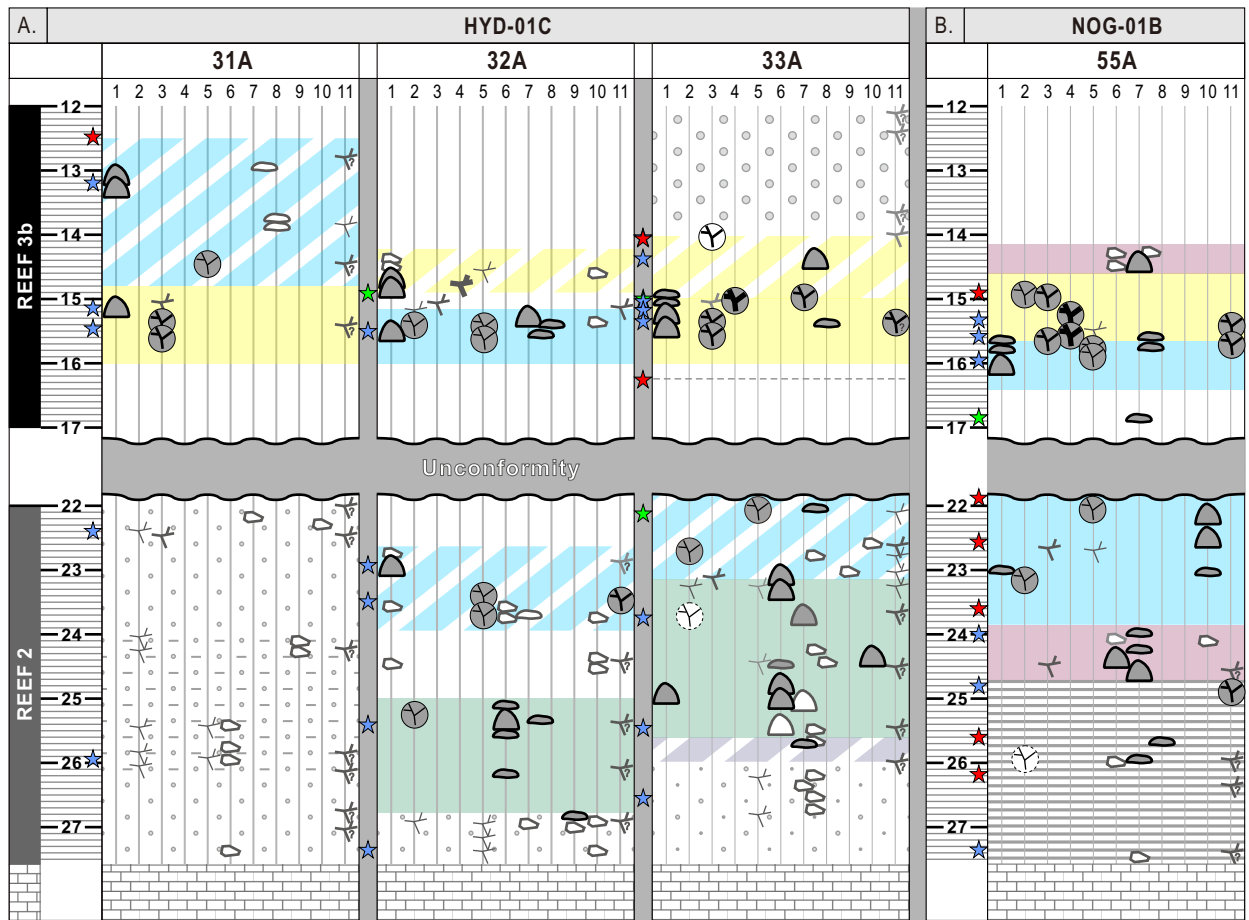


Figure 6



Coral taxonomy

- 1: *Isopora*
- 2: *Acropora* (fine branches)
- 3: *Acropora* (medium-size branches)
- 4: *Acropora* (robust branches)
- 5: *Seriatopora*
- 6: Merulinid
- 7: *Porites*
- 8: *Montipora*
- 9: Agariciid
- 10: *Tubipora*
- 11: Pocilloporidae (others)

Coral morphology and context

- | | IS or IS? | ISX or ISX? | ISN |
|-----------------------|-----------|-------------|-----|
| Branching fine | | | |
| Branching medium | | | |
| Branching robust | | | |
| Br. - undertermined | | | |
| Massive (>5 cm thick) | | | |
| Laminar (<5 cm thick) | | | |
| Undetermined | | | |

Lithology

- Rudstone
- Carbonate granules/pebbles
- Carbonate granules/pebbles/sand
- Halimeda*-rich carbonate pebbles
- Carbonate sand
- Algal bindstone
- Pre-MIS2 basement

Coral assemblages

- | | | |
|-----|----|----|
| cA1 | cC | cE |
| cB | cD | |
- Age control**
- U/Th coral
 - ¹⁴C coral
 - ¹⁴C alga

Figure 7

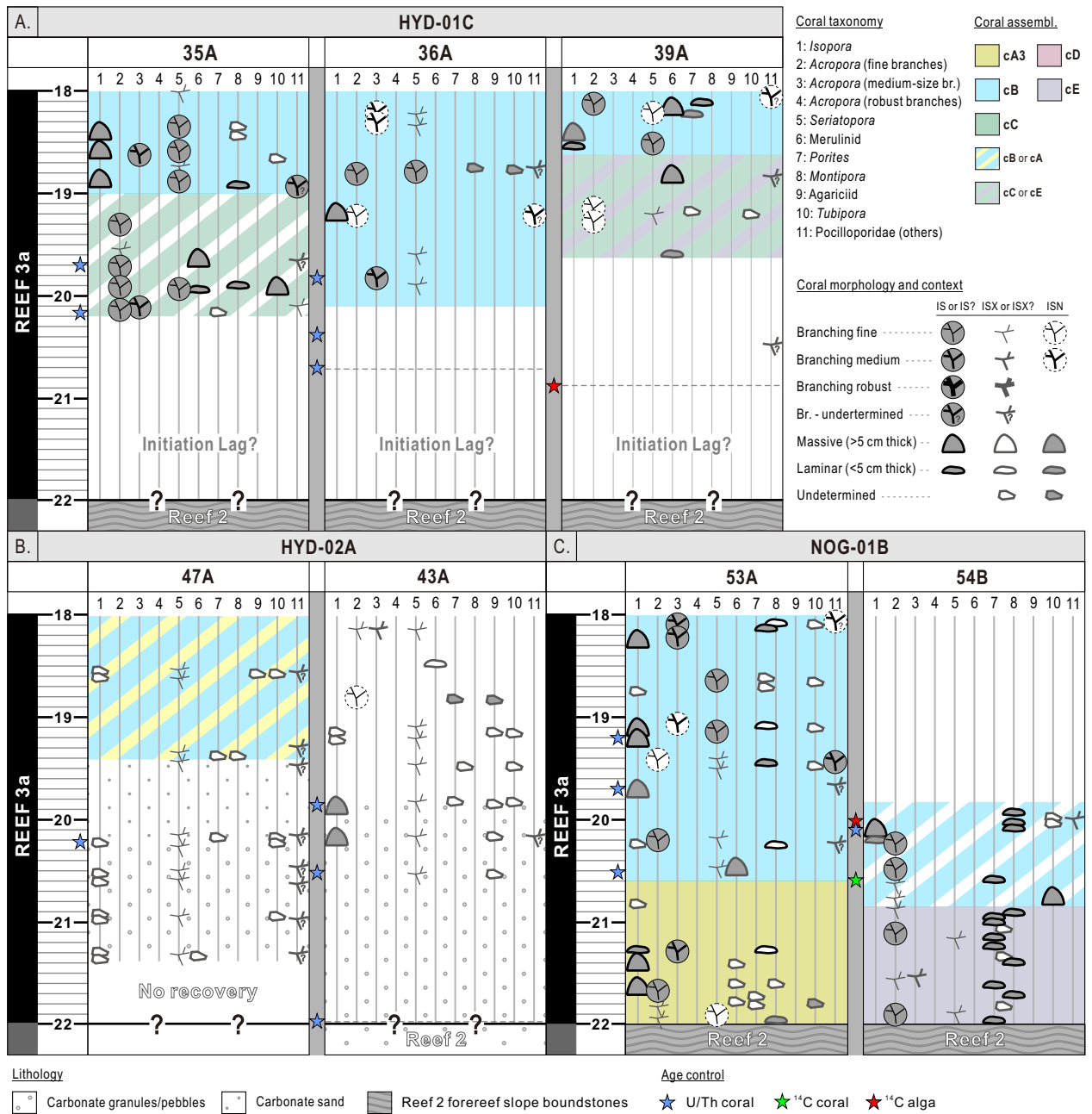


Figure 8

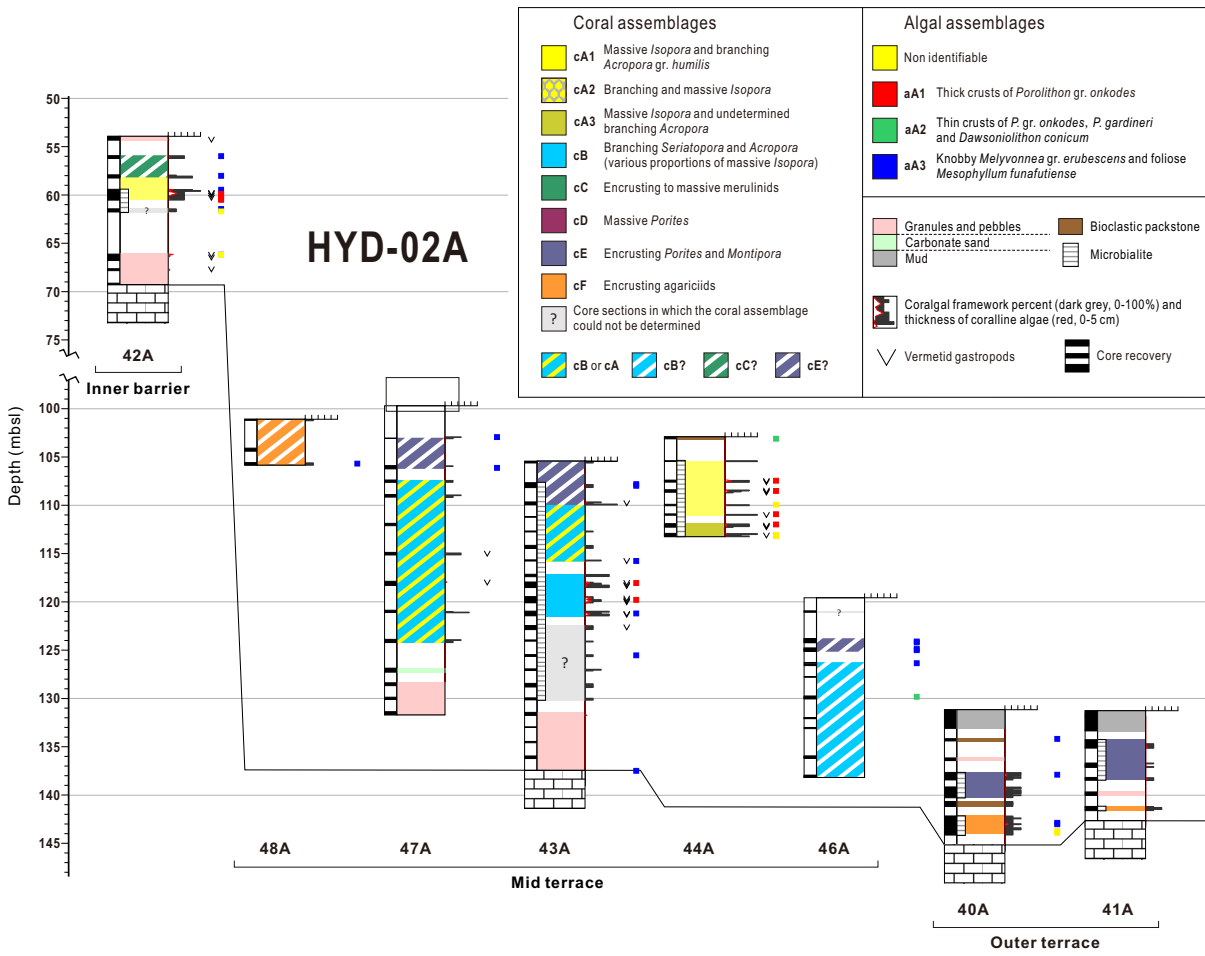


Figure 9

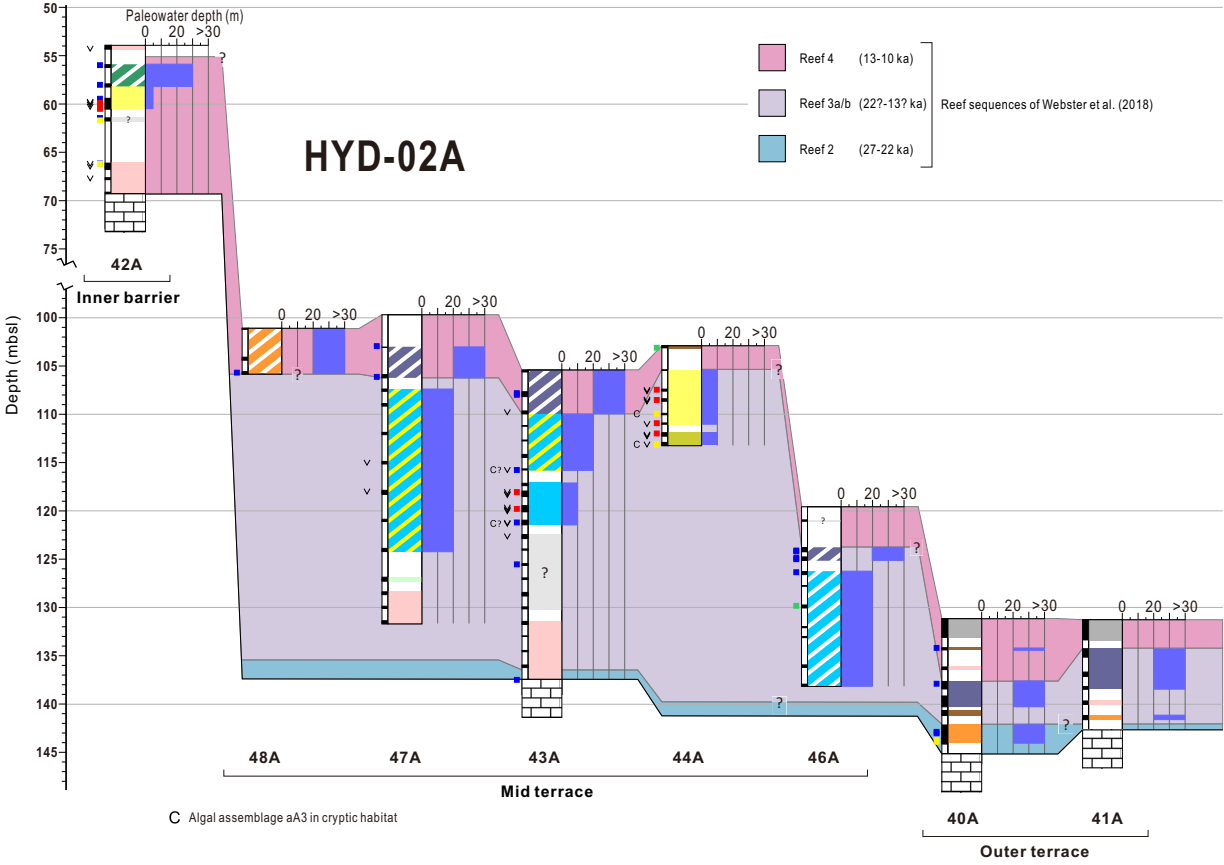


Figure 10

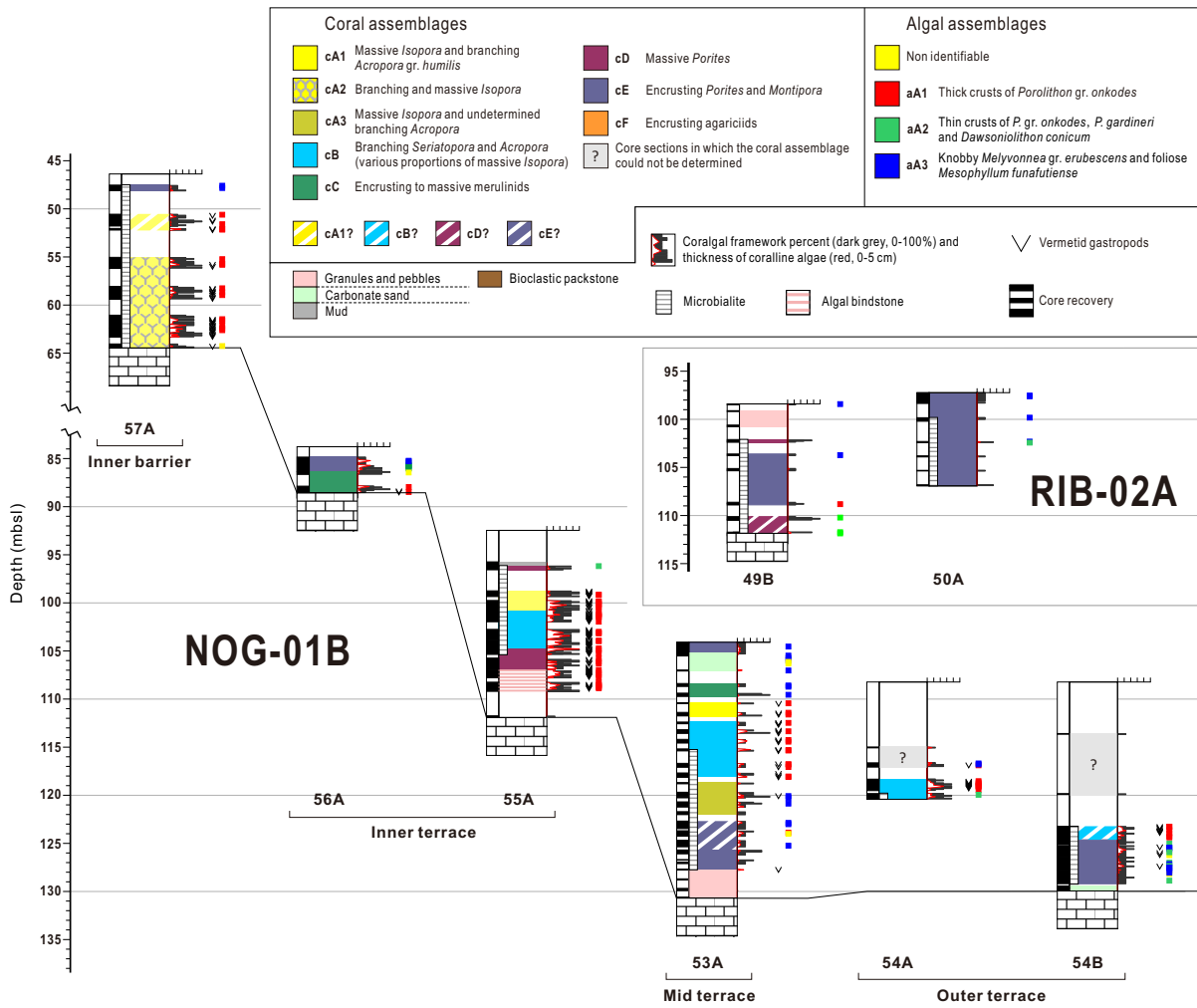


Figure 11

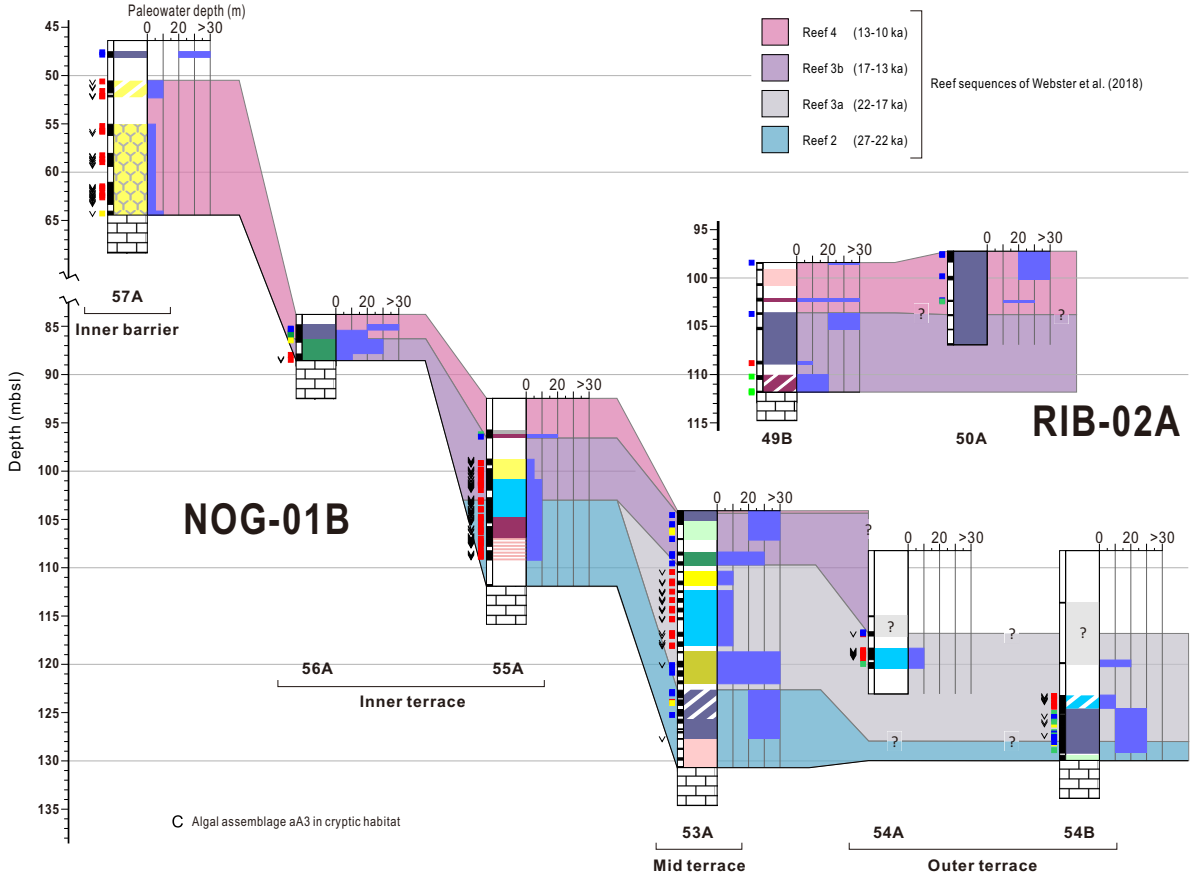


Figure 12

