

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

Humblet, M.<sup>1</sup>, Potts, D.C.<sup>2</sup>, Webster, J.M.<sup>3</sup>, Braga, J.C.<sup>4</sup>, Iryu, Y.<sup>5</sup>, Yokoyama, Y.<sup>6</sup>, Bourillot, R.<sup>7</sup>, Séard, C.<sup>8,13</sup>, Droxler, A.<sup>9</sup>, Fujita, K.<sup>10</sup>, Gischler, E.<sup>11</sup>, and Kan, H.<sup>12</sup>

<sup>1</sup> Department of Earth and Planetary Sciences, Nagoya University, Nagoya 464-8601, Japan

<sup>2</sup> Department of Ecology & Evolutionary Biology, University of California, Santa Cruz, California 95064, USA

<sup>3</sup> Geocoastal Research Group, School of Geosciences, The University of Sydney, NSW 2006, Australia

<sup>4</sup> Departamento de Estratigrafía y Paleontología, Universidad de Granada, 18002 Granada, Spain

<sup>5</sup> Institute of Geology and Paleontology, Graduate School of Science, Tohoku University, Aobayama, Sendai 980-8578, Japan

<sup>6</sup> Atmosphere and Ocean Research Institute, and Department of Earth and Planetary Sciences, University of Tokyo, 5-1-5, Japan

<sup>7</sup> EA 4592 G&E, Ensegid, Bordeaux INP, Université Bordeaux Montaigne 1, allée F. Daguin, 33 607 Pessac Cedex, France

<sup>8</sup> Centre Européen de Recherches et d'Enseignement en Géosciences (Cerege), UMR-CNRS 7330, Aix-Marseille Université, 13545 Aix-en-Provence cedex 4, France

<sup>9</sup> Department of Earth Science, Rice University, 6100 Main Street, Houston, TX, 77005, USA

<sup>10</sup> Department of Physics and Earth Sciences, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 903-0213, Japan

<sup>11</sup> Institut für Geowissenschaften, J.W. Goethe-Universität, 60438 Frankfurt am Main, Germany

<sup>12</sup> Graduate School of Integrated Sciences for Global Society Kyushu University, 744 Motooka, Nishi-ku, Fukuoka 819-0395, Japan

<sup>13</sup> Present address : Le Grand Narbonne, 12 Boulevard Frédéric Mistral, 11100 Narbonne, France

## 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.

67

68

## 69 **1. Introduction**

70

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  $0.34 \text{ mm yr}^{-1}$ ): 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  $\sim 0.25$   
104  $\text{mm yr}^{-1}$ , 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).

130

131

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  $\geq 30$  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.

157

158

## 159 **2. Methods**

160

161

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

163

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).

196  
197  
198  
199

## 200 **2.2. Core description**

201  
202

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 ( $\geq 30$  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.

215  
216

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**

264

265

#### 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. *kotschyannum* 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.

320

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  $\leq 1$  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<sup>-1</sup> until 22.9 ka, falling to 0.1 mm  
449 yr<sup>-1</sup> 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<sup>-1</sup> (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 coralg-al-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<sup>-1</sup> (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 coralg-al-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 coralg-al  
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<sup>-1</sup> (Table S2). In contrast, the top 2 m of the core grew at a slower  
503 rate of 4.1 mm yr<sup>-1</sup> 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<sup>-1</sup> until 24 ka, falling to 0.6  
553 mm yr<sup>-1</sup> 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 coralg 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<sup>-1</sup> before slowing to 1.8 mm yr<sup>-1</sup> 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 coralg  
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 coralg



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<sup>-1</sup> with a brief peak at 7.3 mm yr<sup>-1</sup> 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<sup>-1</sup> (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<sup>-1</sup> (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 ( $\geq 30$  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; Hinestrosa 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<sup>-1</sup> in Hydrographers Passage and 0.5 mm yr<sup>-1</sup> 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<sup>-1</sup> in M0054B,  
781 which is less than in hole M0053A (ca. 3.8 mm yr<sup>-1</sup>) and about half the rate (4–4.3 mm  
782 yr<sup>-1</sup>) 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<sup>-1</sup>, 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<sup>-1</sup>) than in NOG-01B (up to 7.3 mm yr<sup>-1</sup>) 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 ( $\geq 30$  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<sup>-1</sup> at HYD-01A and 0.9–7.9 mm yr<sup>-1</sup> 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

### 1119 **Acknowledgements**

1120

1121 We thank IODP for the drilling operations and members of the Bremen Core Repository  
1122 for their assistance during the onshore science party, and we thank Dr. Terry Done for  
1123 sharing his knowledge on coral species distribution in the Great Barrier Reef. We are  
1124 also grateful to two anonymous reviewers for their constructive comments. Financial  
1125 support for this research was provided by the Australian Research Council (grant  
1126 DP1094001) and ANZIC (IODP) to J.M.W.

1127

1128

### 1129 **References**

1130 Abbey, E., Webster, J.M., 2011. Submerged reefs. In: Hopley, D. (Ed.), *Encyclopedia of*  
1131 *modern coral reefs: structure, form and process*. Encyclopedia of Earth Science  
1132 Series, Springer, 1058–1061.

1133 Abbey, E., Webster, J.M., Braga, J.C., Sugihara, K., Wallace, C.C., Iryu, Y., Potts, D.,  
1134 Done, T., Camoin, G., Seard, C., 2011a. Variation in deglacial coralline assemblages  
1135 and their paleoenvironmental significance: IODP Expedition 310, “Tahiti Sea Level”.  
1136 *Global and Planetary Change* 76, 1–15.

1137 Abbey, E., Webster, J.M., Beaman, R.J., 2011b. Geomorphology of submerged reefs  
1138 on the shelf edge of the Great Barrier Reef: The influence of oscillating Pleistocene  
1139 sea levels. *Marine Geology* 288, 61–78.

1140 Abbey, E., Webster, J.M., Braga, J.C., Jacobsen, G., Thorogood, G., Thomas, A.,  
1141 Camoin G., Reimer, P., 2013. Deglacial mesophotic reef demise on the Great Barrier  
1142 Reef. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 392, 473–494.

1143 Abdul, N. A., Mortlock, R.A., Wright, J.D., Fairbanks, R.G., 2016. Younger Dryas sea-  
1144 Level and meltwater pulse 1B recorded in Barbados reef-crest coral *Acropora*  
1145 *palmata*. *Paleoceanography* 31, 330–344.

1146 Adey, W.H., Townsend, R.A., Boykins, W.T., 1982. The crustose coralline algae  
1147 (Rhodophyta: Corallinaceae) of the Hawaiian Islands. *Smithsonian Contributions to*  
1148 *Marine Sciences* 15, 1–74.

1149 Asami, R., Felis, T., Deschamps, P., Hanawa, K., Iryu, Y., Bard, E., Durand, N.,  
1150 Murayama, M., 2009. Evidence for tropical South Pacific climate change during the  
1151 Younger Dryas and the Bølling-Allerød from geochemical records of fossil Tahiti  
1152 corals. *Earth and Planetary Science Letters* 288, 96–107.



- 1153 Athanasiadis, A., Ballantine, D.L., 2014. The genera *Melyvonnea* gen. nov. and  
1154 *Mesophyllum* s.s. (Melobesioideae, Corallinales, Rhodophyta) particularly from the  
1155 central Atlantic Ocean. *Nordic Journal of Botany* 32, 385-436.
- 1156 Bard, E., Hamelin, B., Delanghe-Sabatier, D., 2010. Deglacial meltwater pulse 1B and  
1157 Younger Dryas sea levels revisited with boreholes at Tahiti. *Science* 327, 1235–1237.
- 1158 Beaman, R.J., Webster, J.M., Wust, R.A.J., 2008. New evidence for drowned shelf  
1159 edge reefs in the Great Barrier Reef, Australia. *Marine Geology* 247, 17–34.
- 1160 Bittner, L., Payri, C.E., Maneveldt, G., Couloux, A., De Reviere, B., Le Gall, L., 2011.  
1161 Evolutionary history of the Corallinales (Coralinophycidae, Rhodophyta) inferred from  
1162 nuclear, plastidial and mitochondrial genomes. *Molecular Phylogenetics and Evolution*  
1163 61, 697–713.
- 1164 Blanchon, P., Blakeway, D., 2003. Are catch-up reefs artefact of coring? *Sedimentology*  
1165 50, 1271–1282.
- 1166 Blanchon, P., Granados-Corea, M., Abbey, E., Braga, J.C., Braithwaite, C., Kennedy,  
1167 D.M., Spencer, T., Webster, J.M., Woodroffe, C.D., 2014. Postglacial fringing-reef to  
1168 barrier-reef conversion on Tahiti links Darwin’s reef types. *Scientific Reports* 4, 4997,  
1169 DOI: 10.1038/srep04997
- 1170 Bongaerts, P., Ridgway, T., Sampayo, E.M., Hoegh-Guldberg, O., 2010. Assessing the  
1171 “deep reef refugia” hypothesis: focus on Caribbean reefs. *Coral Reefs* 29, 309–327.
- 1172 Braga, J.C., Aguirre, J., 2004. Coralline algae indicate Pleistocene evolution from deep,  
1173 open platform to outer barrier reef environments in the northern Great Barrier Reef  
1174 margin. *Coral Reefs* 3 (4), 547–558.
- 1175 Braga, J.C., Puga-Bernabéu, Á., Heindel, K., Patterson, M.A., Birgel, D., Peckmann, J.,  
1176 Sánchez-Almazo, I.M., Webster, J.M., Yokoyama, Y., Riding, R., Microbialites in Last  
1177 Glacial Maximum and deglacial reefs of the Great Barrier Reef (IODP Expedition 325,  
1178 NE Australia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 514, 1–17.
- 1179 Braithwaite, C. J. R., 2016. Coral-reef records of Quaternary changes in climate and sea-  
1180 level. *Earth-Science Reviews* 156, 137–154.
- 1181 Bridge, T., Done, T., Beaman, R., Friedman, A., Williams, S., Pizarro, O., Webster, J.,  
1182 2011a. Topography, substratum and benthic macrofaunal relationships on a tropical  
1183 mesophotic shelf margin, central Great Barrier Reef, Australia. *Coral Reefs*, 30 (1),  
1184 143–153.
- 1185 Bridge, T., Done, T., Friedman, A., Beaman, R., Williams, S., Pizarro, O., Webster, J.,  
1186 2011b. Variability in mesophotic coral reef communities along the Great Barrier Reef,  
1187 Australia. *Marine Ecology - Progress Series*, 428, 63–75.
- 1188 Bridge, T. C. L., Fabricius, K. E., Bongaerts, P., Wallace, C. C., Muir, P. R., Done, T. J.,

- 1189 Webster, J. M., 2012. Diversity of Scleractinia and Octocorallia in the mesophotic  
1190 zone of the Great Barrier Reef, Australia. *Coral Reefs* 31 (1), 179–189.
- 1191 Browne, N.K., Smithers, S.G., Perry, C.T., 2012. Coral reefs of the turbid inner-shelf of  
1192 the Great Barrier Reef, Australia: an environmental and geomorphic perspective on  
1193 their occurrence, composition and growth. *Earth Science Reviews* 115, 1–20.
- 1194 Budd, A. F., Fukami, H., Smith, N. D., Knowlton, N., 2012, Taxonomic classification of  
1195 the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia): *Zoological Journal*  
1196 of the Linnean Society, v. 166, no. 3, p. 465-529.
- 1197 Cabioch, G., Taylor, F.W., Récy, J., Edwards, L., Gray, S.C., Faure, G., Burr, G.S.,  
1198 Corrège, T., 1998. Environmental and tectonic influence on growth and internal  
1199 structure of a fringing reef at Tasmaloum (SW Espiritu Santo, New Hebrides island  
1200 arc, SW Pacific. In: Camoin, G., Davies, P.J. (Eds), *Special Publications -*  
1201 *International Association of Sedimentologists* 25, 261–277.
- 1202 Cabioch, G., Montaggioni, L.F., Faure, G., Ribaud-Laurenti, A., 1999. Reef coralgal  
1203 assemblages as recorders of paleobathymetry and sea-level changes in the Indo-  
1204 Pacific province. *Quaternary Science Reviews* 18 (14), 1681–1695.
- 1205 Cabioch, G., Banks-Cutler, K.A., Beck, W.J., Burr, G.S., Corrège, T., Edwards, R.L.,  
1206 Taylor, F.W., 2003. Continuous reef growth during the last 23 cal kyr BP in a  
1207 tectonically active zone (Vanuatu, South West Pacific). *Quaternary Science Reviews*  
1208 22, 1771–1786.
- 1209 Cabioch, G., Montaggioni, L., Frank, N., Sear, C., Sallé, E., Payri, C., Pelletier, B.,  
1210 Paterné, M., 2008. Successive reef depositional events along the Marquesas  
1211 foreslopes (French Polynesia) since 26 ka. *Marine Geology* 254, 18–34.
- 1212 Camoin, G.F., Ebrén, Ph, Eisenhauer, A., Bard, E., Faure G., 2001. A 300,000-yr coral  
1213 reef record of sea-level changes, Mururoa atoll (Tuamotu archipelago, French  
1214 Polynesia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 175, 325–341.
- 1215 Camoin, G.F., Sear, C., Deschamps, P., Webster, J.M., Abbey, E., Braga, J.C., Iryu, Y.,  
1216 Durand, N., Bard, E., Hamelin, B., Yokoyama, Y., Thomas, A.L., Henderson, G.M.,  
1217 Dussouillez, P., 2012. Reef response to sea-level and environmental changes during  
1218 the last glaciation: Integrated Ocean Drilling Program Expedition 310, Tahiti Sea  
1219 Level. *Geology* 40 (7), 643–646.
- 1220 Camoin, G., Webster, J. M., 2015. Coral reefs and sea-level change. In: Stein, R.,  
1221 Blackman, D., Inagaki, F, Christian-Larsen, H (Eds.), *Earth and life processes*  
1222 *discovered from seafloor environment – a decade of science achieved by the*  
1223 *Integrated Ocean Drilling Program (IODP)*, Amsterdam/New York, Elsevier.
- 1224 Caragnano, A., Foetisch, A., Maneveldt, G.W., Millet, L., Liu, L.-C., Lin, S.-M., Rodondi,

- 1225 G., Payri, C.E., 2018. Revision of Corallinaceae (Corallinales, Rhodophyta):  
1226 recognizing *Dawsoniolithon* gen. nov., *Parvicellularium* gen. nov. and  
1227 Chamberlainoideae subfam. nov. containing *Chamberlainium* gen. nov. and  
1228 *Pneophyllum*. *Journal of Phycology*, DOI: 10.1111/jpy.12644.
- 1229 Carter, R.M., Johnson, D.P., 1986. Sea-level controls on the post-glacial development  
1230 of the Great Barrier Reef, Queensland. *Marine Geology* 71, 137–164.
- 1231 Chappell, J., Polach, H., 1991. Post-glacial sea-level rise from a coral record at Huon  
1232 Peninsula, Papua New Guinea. *Nature* 349 (6305), 147–149.
- 1233 Cutler, K.B., Gray, S.C., Burr, G.S., Edwards, R.L., Taylor, F.W., Cabioch, G., Beck,  
1234 J.W., Cheng, H., Moore, J., 2004. Radiocarbon calibration and comparison to 50 kyr  
1235 BP with paired  $^{14}\text{C}$  and  $^{130}\text{Th}$  dating of corals from Vanuatu and Papua New Guinea.  
1236 *Radiocarbon* 46, 1127–1160.
- 1237 Davies, P.T., Marshall, J.F., Hopley, D., 1985. Relationships between reef growth and  
1238 sea level in the Great Barrier Reef. *Proceedings of the fifth International Coral Reef*  
1239 *Congress, Tahiti, volume 5*, 95–103.
- 1240 Davies, P.T., McKenzie, J.A., 1993. Controls on the Pliocene-Pleistocene evolution of  
1241 the northeastern Australian continental margin. In: McKenzie, J.A., Davies, P.J.,  
1242 Palmer-Julson, A. (Eds), *Proceedings of the Ocean Drilling Program, Scientific*  
1243 *Results* 133, 755–762.
- 1244 Dechnik, B., Webster, J.M., Davies, P.J., Braga, J.C., Reimer, P.J., 2015. Holocene  
1245 “turn-on” and evolution of the Southern Great Barrier Reef: Revisiting reef cores from  
1246 the Capricorn Bunker Group. *Marine Geology* 363, 174–190.
- 1247 Dechnik, B., Webster, J.M., Webb, G.E., Nothdurft, L., Dutton, A., Braga, J.C., Zhao, J.,  
1248 Duce, S., Sadler, J., 2017. The evolution of the Great Barrier Reef during the Last  
1249 Interglacial Period. *Global and Planetary Change* 149, 53–71.
- 1250 Deschamps, P., Durand, N., Bard, E., Hamelin, B., Camoin, G., Thomas, A.L.,  
1251 Henderson, G.M., Okuno, J., Yokoyama, Y., 2012. Ice-sheet collapse and sea-level  
1252 rise at the Bølling warming 14,600 years ago. *Nature* 483, 559–564.
- 1253 Done, T.J., 1982. Patterns in the distribution of coral communities across the central  
1254 Great Barrier Reef. *Coral Reefs* 1, 95–107.
- 1255 Done, T. J., 1983. Coral zonation: Its nature and significance. In: Barnes, D.J. (Ed.),  
1256 *Perspectives on coral reefs*. The Australian Institute of Marine Science, 107-147
- 1257 Drew, E.A., 1983. *Halimeda* biomass, growth rates and sediment generation on reefs in  
1258 the central Great Barrier Reef Province. *Coral Reefs* 2, 101–110.
- 1259 Dullo, W.C., Camoin, G.F., Blomeier, D., Colonna, M., Eisenhauer, A., Faure, G.,  
1260 Casanova, J., Thomassin, B.A., 1998. Morphology and sediments of the fore-slopes

- 1261 of Mayotte, Comoro Islands: direct observations from a submersible. In: Camoin,  
1262 G.F., Davies, P.J. (Eds), Reefs and carbonate platforms in the Pacific and Indian  
1263 Oceans, Special Publications of the International Association of Sedimentologists 25,  
1264 219–236.
- 1265 Fairbanks, R.G., 1989. A 17,000 year glacio-eustatic sea level record: influence of  
1266 glacial melting rates on the Younger Dryas event and deep-ocean circulation. *Nature*  
1267 342, 637–642.
- 1268 Felis, T., Merkel, U., Asami, R., Deschamps, P., Hathorne, E. C., Kölling, M., Bard, E.,  
1269 Cabioch, G., Durand, N., Prange, M., Schulz, M., Cahyarini, S.Y., Pfeiffer, M., 2012.  
1270 Pronounced interannual variability in tropical South Pacific temperatures during  
1271 Heinrich Stadial 1. *Nature Communications* 3:965, DOI: 10.1038/ncomms1973.
- 1272 Felis, T., McGregor, H.V., Linsley, B.K., Tudhope, A.W., Gagan, M.K., Suzuki, A., Inoue,  
1273 M., Thomas, A.L., Esat, T.M., Thompson, W.G., Tiwari, M., Potts, D.C., Mudelsee, M.,  
1274 Yokoyama, Y., Webster, J.M., 2014. Intensification of the meridional temperature  
1275 gradient in the Great Barrier Reef following the Last Glacial Maximum. *Nature*  
1276 *Communications* 5:4102, DOI: 10.1038/ncomms5102.
- 1277
- 1278 Gabrielson, P.W., Hughey, J.R., Díaz-Pulido, G., 2018. Genomics reveals abundant  
1279 speciation in the coral reef building alga *Porolithon onkodes* (Corallinales,  
1280 Rhodophyta). *J. Phycol.* 54, 429–434.
- 1281 Gischler, E., Thomas, A.L., Droxler, A.W., Webster, J.M., Yokoyama, Y., Schöne, B.R.,  
1282 2013. Microfacies and diagenesis of older Pleistocene (pre-last glacial maximum) reef  
1283 deposits, Great Barrier Reef, Australia (IODP Expedition 325): A quantitative  
1284 approach. *Sedimentology* 60, 1432–1466.
- 1285 Gischler, E., Hudson, J.H., Humblet, M., Braga, J.C., Eisenhauer, A., Isaack, A.,  
1286 Anselmetti, F.S., Camoin, G.F., 2016. Late Quaternary barrier and fringing reef  
1287 development of Bora Bora (Society Islands, south Pacific): First subsurface data from  
1288 the Darwin-type barrier-reef system. *Sedimentology* 63, 1522–1549.
- 1289 Greenstein, B.J., Pandolfi, J.M., 2008. Escaping the heat: range shifts of reef coral taxa  
1290 in coastal Western Australia. *Global Change Biology* 14, 1–16.
- 1291 Hallock, P., Schlager, W., 1986. Nutrient excess and the demise of coral reefs and  
1292 carbonate platforms. *Palaios* 1, 389–398.
- 1293 Harper, B.B., Puga-Bernabeau, A., Droxler, A.W., Webster, J.M., Gischler, E., Tiwari,  
1294 Lado-Insua, T., Thomas, A.L., Morgan, S., Jovane, L., Röhl, U., 2015. Mixed  
1295 carbonate-siliciclastic sedimentation along the Great Barrier Reef upper slope: a  
1296 challenge of the reciprocal sedimentation model. *Journal of Sedimentary Research*

- 1297 85, 1019-1036.
- 1298 Harris, P.T., Davies, P.J., 1989. Submerged reefs and terraces on the shelf edge of the  
1299 Great Barrier Reef, Australia: morphology, occurrence and implications for reef  
1300 evolution. *Coral Reefs* 8, 87–98.
- 1301 Hinestrosa, G., Webster, J.M., Beaman, R., Anderson, L.M., 2014. Seismic stratigraphy  
1302 and development of the shelf-edge reefs of the Great Barrier Reef, Australia. *Marine*  
1303 *Geology* 353, 1–20.
- 1304 Hinestrosa, G., Webster, J.M., Beaman, R., 2016. Postglacial sediment deposition  
1305 along a mixed carbonate-siliciclastic margin: new constraints from the drowned shelf-  
1306 edge reefs of the Great Barrier Reef, Australia. *Palaeogeography, Palaeoclimatology,*  
1307 *Palaeoecology* 446, 168–185.
- 1308 Hinestrosa, G., Webster, J.M., Beaman, R., 2019. Spatio-temporal patterns in the  
1309 postglacial flooding of the Great Barrier Reef shelf, Australia. *Continental Shelf*  
1310 *Research*. DOI: 10.1016/j.csr.2018.12.001.
- 1311 Hopley, D., 1982. *The Geomorphology of the Great Barrier Reef: Quaternary*  
1312 *Development of Coral Reefs*. John Wiley and Sons Ltd., New York.
- 1313 Hopley, D., Smithers, S.G., Parnell, K.E., 2007. *The geomorphology of the Great*  
1314 *Barrier Reef: development, diversity and change*. Cambridge University Press, USA.
- 1315 Huang, D., Benzoni, F., Fukami, H., Knowlton, N., Smith, N. D., Budd, A. F., 2014,  
1316 Taxonomic classification of the reef coral families Merulinidae, Montastraeidae, and  
1317 Diploastraeidae (Cnidaria: Anthozoa: Scleractinia): *Zoological Journal of the Linnean*  
1318 *Society*, v. 171, no. 2, p. 277–355.
- 1319 Huang, D., Arrigoni, R., Benzoni, F., Fukami, H., Knowlton, N., Smith, N. D., Stolarski,  
1320 J., Chou, L. M., Budd, A. F., 2016. Taxonomic classification of the reef coral family  
1321 Lobophylliidae (Cnidaria: Anthozoa: Scleractinia): *Zoological Journal of the Linnean*  
1322 *Society*, v. 178, no. 3, p. 436–481.
- 1323 Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M.,  
1324 Baird, A.H., Baum, J.K., Berumen, M.L., Bridge, T.C., Claar, D.C., Eakin, M.C.,  
1325 Gilmour, J.P., Graham, N.A.J., Harrison, H., Hobbs, J.P.A., Hoey, A.S., Hoogenboom,  
1326 M., Lowe, R.J., McCulloch, M.T., Pandolfi, J.M., Pratchett, M., Schoepf, V., Torda,  
1327 Gergely, Wilson, S.K., 2018. Spatial and temporal patterns of mass bleaching of  
1328 corals in the Anthropocene. *Science* 359, 80–83.
- 1329 Humblet, M., Webster, J.M., 2017. Coral community changes in the Great Barrier Reef  
1330 in response to major environmental changes over glacial-interglacial timescales.  
1331 *Palaeogeography, Palaeoclimatology, Palaeoecology* 472, 216–235.
- 1332 Iryu, Y., Nakamori, T., Matsuda, S., Abe, O., 1995. Distribution of marine organisms and

- 1333 its geological significance in the modern reef complex of the Ryukyu Islands.  
1334 *Sedimentary Geology* 99, 243–258.
- 1335 Iryu, Y., Takahashi, Y., Fujita, K., Camoin, G., Cabioch, G., Matsuda, H., Sato, T.,  
1336 Sugihara, K., Webster, J. M., Westphal, H., 2010. Sea level history recorded in the  
1337 Pleistocene carbonate sequence in IODP Hole 310-M0005D, off Tahiti. *Island Arc* 19,  
1338 690–706.
- 1339 Keats, D.W., 1995. *Lithophyllum cuneatum* sp. nov. (Corallinaceae, Rhodophyta), a new  
1340 species of non-geniculate coralline alga semi-endophytic in *Hydrolithon onkodes* and  
1341 *Neogoniolithon* sp. from Fiji, South Pacific. *Phycological Research* 43, 151–160.
- 1342 Keats, D.W., 1997. *Lithophyllum insipidum* Adey, Townsend et Boykins and *L. flavescens*  
1343 sp. nov.: two flat lithophylloid coralline algae (Corallinales, Rhodophyta) abundant in  
1344 shallow reef environments in Fiji. *Phycologia* 36, 351–365.
- 1345 Keats, D.W., Steneck, R.S., Townsend, R.A., Borowitzka, M.A., 1996. *Lithothamnion*  
1346 *prolifer* Foslie: a common non-geniculate coralline alga (Rhodophyta: Corallinaceae)  
1347 from tropical and subtropical Indo-Pacific. *Botanica Marina* 39, 187–200.
- 1348 Keats, D. W., Chamberlain, Y. M., Baba, M., 1997. *Pneophyllum conicum* (Dawson) comb.  
1349 nov. (Rhodophyta, Corallinaceae), a widespread Indo-Pacific non-geniculate coralline  
1350 alga that overgrows and kills coral. *Botanica Marina* 40, 263–279.
- 1351 Knowlton, N. 2001. The future of coral reefs. *Proceedings of the National Academy of*  
1352 *Sciences of the United State of America* 98, 5419–5425.
- 1353 Kojis, B.L., Quinn, N.J., 1984. Seasonal and depth variation in fecundity of *Acropora*  
1354 *palifera* at two reefs in Papua New Guinea. *Coral Reefs* 3, 165–172.
- 1355 Lighty, R.G., Macintyre, I.G., Stuckenrath, R., 1978. Submerged early Holocene barrier  
1356 reef south-east Florida shelf. *Nature* 275, 59–60.
- 1357 Littler, D.S., Littler, M.M., 2003. *South Pacific Reef Plants: A Diver's Guide to the Plant*  
1358 *Life of South Pacific Coral Reefs*. Offshore Graphics Inc., Washington DC.
- 1359 Maneveldt, G.W., Keats, D.W., 2014. Taxonomic review based on new data of the reef-  
1360 building alga *Porolithon onkodes* (Corallinaceae, Corallinales, Rhodophyta) along  
1361 with other taxa found to be conspecific. *Phytotaxa* 190, 216–249.
- 1362 Marshall, J.F., Macintyre, I.G., 1988. *Halimeda* bioherms of the northern Great Barrier  
1363 Reef. *Coral Reefs* 6, 139–148.
- 1364 McClanahan, T.R., Obura, D., 1996. Sedimentation effects on shallow coral  
1365 communities in Kenya. *Journal of Experimental Marine Biology and Ecology* 209,  
1366 103–122.
- 1367 Macintyre, I.G., Rützler, K., Norris, J.N., Smith, K.P., Cairns, S.D., Bucher, K.E.,  
1368 Steneck, R.S., 1991. An early Holocene reef in the western Atlantic: submersible

- 1369 investigations of a deep relict reef off the west coast of Barbados, West Indies. *Coral*  
1370 *Reefs* 10, 167–174.
- 1371 Montaggioni, L.F., 2005. History of Indo-Pacific coral reef systems since the last  
1372 glaciation: development patterns and controlling factors. *Earth-Science Reviews* 71,  
1373 1–75.
- 1374 Montaggioni, L.F., Braithwaite, C.J.R., 2009. Quaternary coral reef systems: history,  
1375 development processes and controlling factors. *Development in Marine Geology* 5, 1–  
1376 532.
- 1377 Muir, P., Wallace, C., Bridge, T.C.L., Bongaerts, P., 2015. Diverse staghorn coral fauna  
1378 on the mesophotic reefs of north-east Australia. *PLoS ONE* 10(2): e0117933. DOI:  
1379 10.1371/journal.pone.0117933
- 1380 Nelson, W. A., Sutherland, J. E., Farr, T. J., Hart, D. R., Neill, K. T., Kim, H. J., Yoon, H.  
1381 S., 2015. Multi-gene phylogenetic analyses of New Zealand coralline algae:  
1382 *Corallinapetra novaezelandiae* gen. et sp. nov. and recognition of the Hapalidiales ord.  
1383 nov. *Journal of Phycology* 51, 454–468.
- 1384 Neumann, A.C., Macintyre, I.G., 1985. Reef response to sea-level rise: keep-up, catch-  
1385 up or give-up. *Proceedings of the fifth International Coral Reef Congress, Tahiti,*  
1386 *volume 5*, 105–110.
- 1387 Pandolfi, J.M., 2011. The paleoecology of coral reefs. In: Dubinsky, Z., Stambler, N.  
1388 (Eds), *Coral Reefs: An Ecosystem in Transition*, Springer, 13–24.
- 1389 Payri, C., N'Yeurt, A.d.R., Orempuller, J., 2000. *Algae of French Polynesia. Au Vent des*  
1390 *Iles, Tahiti.*
- 1391 Peña, V., Le Gall, L., Rösler, A., Payri, C.E., Braga, J.C., 2018. *Adeylithon bosencei*  
1392 *gen. et sp. nov. (Corallinales, Rhodophyta): a new reef-building genus with*  
1393 *anatomical affinities with the fossil Aethesolithon.* *J. Phycol.*, DOI: 10.1111/jpy.12799
- 1394 Perry, C.T., Smithers, S.G., Johnson, K.G., 2009. Long-term coral community records  
1395 from Luggar Shoal on the terrigenous inner-shelf of the central Great Barrier Reef,  
1396 Australia. *Coral Reefs*, 28, pp. 941–948.
- 1397 Perry, C.T., Alvarez-Filip, L., Graham, N.A.J., Mumby, P.J., Wilson, S.K., Kench, P.S.,  
1398 Manzello, D.P., Morgan, K.M., Slangen, A.B.A., Thompson, D.P., Januchowski-  
1399 Hartley, F., Smithers, S.G., Steneck, R.S., Carlton, R., Edinger, E.N., Enochs, I.C.,  
1400 Estrada-Saldivar, N., Haywood, M.D.E., Kolodziej, G., Murphy, G.N., Perez-  
1401 Cervantes, E., Suchley, A., Valentino, L., Boenish, R., Wilson, M., Macdonald, C.,  
1402 2018. Loss of coral reef growth capacity to track future increases in sea level. *Nature*  
1403 558, 398–400.
- 1404 Potts, D.C., Done, T.J., Isdale, P.J., Fisk, D.A., 1985. Dominance of a coral community

- 1405 by the genus *Porites* (Scleractinia). *Marine Ecology Progress Series* 23, 79–84.
- 1406 Rao, V.P., Montaggioni, L., Vora, K.H., Almeida, F., Rao, K.M., Rajagopalan, G., 2003.
- 1407 Significance of relic carbonate deposits along the central and southwestern margin of
- 1408 India for late Quaternary environmental and sea-level changes. *Sedimentary Geology*
- 1409 159, 95–111.
- 1410 Reeves, J.M., Bostock, H.C., Ayliffe, L.K., T. Barrows, T.T., De Deckker, P., Devriendt,
- 1411 L.S., Dunbar, G.B., Drysdale, R.N., Fitzsimmons, K.E., Gagan, M.K., Griffiths, M.L.,
- 1412 Haberle, S.G., Jansen, J.D., Krause, C., Lewis, S., McGregor, H.V., Mooney, S.D.,
- 1413 Moss, P., Nanson, G.C., Purcell, A., van der Kaars, S., 2013. Paleoenvironmental
- 1414 changes in tropical Australasia over the last 30,000 years: a synthesis by the OZ-
- 1415 INTIMATE group. *Quaternary Science Reviews* 74, 97–114.
- 1416 Ringeltaube P, Harvey A (2000) Non-geniculate coralline algae (Corallinales,
- 1417 Rhodophyta) on Heron Reef, Great Barrier Reef (Australia). *Botanica Marina* 43,
- 1418 431–454.
- 1419 Rösler, A., Perfectti, F., Peña, V., Braga, J.C., 2016. Phylogenetic relationships of
- 1420 Corallinaceae (Corallinales, Rhodophyta): taxonomic implications for reef-building
- 1421 corallines. *Journal of Phycology*, DOI: 10.1111/jpy.12404.
- 1422 Rovere, A., Khanna, P., Bianchi, C.N., Droxler, A.W., Morri, C., Naar, D.F., 2018.
- 1423 Submerged reef terraces in the Maldivian Archipelago (Indian Ocean). *Geomorphology*
- 1424 317, 218–232.
- 1425 Salles, T., Pall, J., Webster, J.M., Dechnik, B., 2018. Exploring coral reef responses to
- 1426 millennial-scale climatic forcings: insight from the 1-D numerical tool pyReef-Core v1.0.
- 1427 *Geoscientific Model Development* 11, 2093–2110.
- 1428 Sanders, D., Baron-Szabo, R.C., 2005. Scleractinian assemblages under sediment
- 1429 input: their characteristics and relation to the nutrient input concept. *Palaeogeography,*
- 1430 *Palaeoclimatology, Palaeoecology* 216, 139–181.
- 1431 Sasaki, K., Omura, A., Miwa, T., Tsuji, Y., Matsuda, H., Nakamori, T., Iryu, Y., Yamada,
- 1432 T., Sato, Y., Nakagawa, H., 2006.  $^{230}\text{Th}/^{234}\text{U}$  and  $^{14}\text{C}$  dating of lowstand coral reef
- 1433 beneath the insular shelf off Irabu Island, Ryukyus, southwestern Japan. *Island Arc*
- 1434 15, 455–467.
- 1435 Sinniger, F., Morita, M., Harii, S., 2013. “Locally extinct” coral species *Seriatopora*
- 1436 *hystrix* found at upper mesophotic depths in Okinawa. *Coral Reefs* 32, 153.
- 1437 Tager, D., Webster, J.M., Potts, D.C., Renema, W., Braga, J.C., Pandolfi, J.M., 2010.
- 1438 Community dynamics of Pleistocene coral reefs during alternative climatic regimes.
- 1439 *Ecology* 91, 191–200.
- 1440 Taylor, F.W., Mann, P., Bevis, M.G., Edwards, R.L., Cheng, H., Cutler, K.B., Gray, S.C.,



- 1441 Burr, G.S., Beck, J.W., Phillips D.A., Cabioch, G., Récy, J., 2005. Rapid forearc uplift  
1442 and subsidence caused by impinging bathymetric features: examples from the New  
1443 Hebrides and Solomon arcs. *Tectonics* 24, TC6005, DOI: 10.1029/2004TC001650.
- 1444 Van der Merwe, E., Maneveldt, G.W., 2016. A modern account of the South African  
1445 non-geniculate Lithophylloideae (Corallinales, Corallinophycidae, Rhodophyta). *South  
1446 African Journal of Botany* 103, 247–267.
- 1447 Verheij, E., 1994. Nongeniculate Corallinaceae (Corallinales, Rhodophyta) from the  
1448 Spermonde Archipelago, SW Sulawesi, Indonesia. *Blumea* 39, 95–138.
- 1449 Veron, J.E.N., Pichon, M., 1976. Scleractinia of eastern Australia Part 1. Families  
1450 Thamnasteriidae, Astrocoeniidae, and Pocilloporidae. *Australian Institute of Marine  
1451 Science Monograph Series* 1, 1–84.
- 1452 Veron, J.E.N., Pichon, M., Wijsman-Best, M., 1977. Scleractinia of eastern Australia  
1453 Part 2. Families Faviidae and Trachyphylliidae. *Australian Institute of Marine Science  
1454 Monograph Series* 3, 1–233.
- 1455 Veron, J.E.N., Pichon, M., 1979. Scleractinia of eastern Australia Part 3. Families  
1456 Agariciidae, Siderastreidae, Fungiidae, Oculinidae, Merulinidae, Mussidae,  
1457 Pectiniidae, Caryophylliidae, and Dendrophylliidae. *Australian Institute of Marine  
1458 Science Monograph Series* 4, 1–457.
- 1459 Veron, J.E.N., Pichon, M., 1982. Scleractinia of eastern Australia Part 4. Family  
1460 Poritidae. *Australian Institute of Marine Science Monograph Series* 5, 1–168.
- 1461 Veron, J.E.N., Wallace, C.C., 1984. Scleractinia of Eastern Australia Part 5., Family  
1462 Acroporidae. *Australian Institute of Marine Science Monograph Series* 6, 1–485.
- 1463 Veron, J.E.N., 1986. *Corals of Australia and the Indo-Pacific*. Angus & Robertson, North  
1464 Ryde, N.S.W.
- 1465 Veron, J.E.N., 2000. *Corals of the World*, 3 vols, Australian Institute of Marine Science,  
1466 Townsville
- 1467 Veron, J.E.N., 2008. *A reef in time: the Great Barrier Reef from beginning to end*.  
1468 Harvard University Press, 304 pages.
- 1469 Vora, K.H., Wagle, B.G., Veerayya, M., Almeida, F., Karisiddaiah, S.M., 1996. A 1300  
1470 km long late Pleistocene-Holocene shelf barrier reef system along the western  
1471 continental shelf of India: occurrence and significance. *Marine Geology* 134, 145–  
1472 162.
- 1473 Wallace, C.C., Lovell, E.R., 1977. Topography and coral distribution of bushy and  
1474 Redbill Islands and surrounding reef, Great Barrier Reef, Queensland. *Atoll Research  
1475 Bulletin*, 194, pp. 1–22.
- 1476 Wallace, C.C., Chen, C.A., Fukami, H., Muir, P.R., 2007. Recognition of separate

- 1477 genera within *Acropora* based on new morphological, reproductive and genetic  
1478 evidence from *Acropora togianensis*, and elevation of the subgenus *Isopora* Studer,  
1479 1878 to genus (Scleractinia: Astrocoeniidae; Acroporidae). *Coral Reefs*, 26, pp. 231–  
1480 239
- 1481 Webster, J.M., Davies, P.J., 2003. Coral variation in two deep drill cores: significance  
1482 for the Pleistocene development of the Great Barrier Reef. *Sedimentary Geology*, 159  
1483 (1–2), pp. 61–80
- 1484 Webster, J.M., Clague, D.A., Riker-Coleman, K., Gallup, C., Braga, J.C., Potts, D.C.,  
1485 Moore, J.G., Winterer, E.L., Paull, C.K., 2004a. Drowning of the -150 m reef off  
1486 Hawaii: a casualty of global meltwater pulse 1A. *Geology* 32, 249–252.
- 1487 Webster, J.M., Wallace, L., Silver, E., Applegate, B., Potts, D., Braga, J.C., Riker-  
1488 Coleman, K., Gallup, C., 2004b. Drowned carbonate platforms in the Huon Gulf,  
1489 Papua New Guinea. *Geochemistry Geophysics Geosystems* 5 (11), 1–31,  
1490 DOI: 10.1029/2004GC000726.
- 1491 Webster, J.M., Davies, P., Beaman, R., Williams, S., Byrne, M., 2008. Evolution of  
1492 drowned shelf edge reefs in the GBR; implications for understanding abrupt climate  
1493 change, coral reef response and modern deep water benthic habitats. *Marine*  
1494 *National Facility RV Southern Surveyor 2007 Program: Voyage Summary SS07/*  
1495 *2007: Victoria, Australia (CSIRO)*.
- 1496 Webster, J.M., Yokoyama, Y., Cotterill, C., the Expedition 310 Scientists, 2011.  
1497 *Proceedings of the IODP*, 325, Integrated Ocean Drilling Program Management  
1498 International, Inc, Tokyo.
- 1499 Webster, J.M., Braga, J.C., Humblet, M., Potts, D.C., Iryu, Y., Yokoyama, Y., Fujita, K.,  
1500 Bourillot, R., Esat, T.M., Fallon, S., Thompson, W.G., Thomas, A.L., Kan, H.,  
1501 McGregor, H.V., and Hineostroza, G., Obrochta, S.P., Loughheed, B.C., 2018.  
1502 Response of the Great Barrier Reef to sea level and environmental changes over the  
1503 past 30 ka. *Nature Geoscience* 11, 426–432.
- 1504 Woodroffe, C. D., Webster, J. M., 2014, Coral reefs and sea-level change: *Marine*  
1505 *Geology*, v. 352, p. 248–267.
- 1506 Yagioka, N., Nakada, C., Fujita, K., Kan, H., Yokoyama, Y., Webster, J.M., 2019.  
1507 Depositional environments beneath the shelf edge slopes of the Great Barrier Reef,  
1508 inferred from foraminiferal assemblages: IODP Expedition 325. *Palaeogeography,*  
1509 *Palaeoclimatology, Palaeoecology* 514, 386–397.
- 1510 Yamano, H., Sugihara, K., Watanabe, T., Shimamura, M., Hyeong, K., 2012. Coral  
1511 reefs at 34°N, Japan: Exploring the end of environmental gradients. *Geology*, 40 (9),  
1512 835–838.

- 1513 Yokoyama, Y., Lambeck, K., De Deckker, P., Johnston, P., Fifield, L.K., 2000. Timing of  
1514 the Last Glacial Maximum from observed sea-level minima. *Nature* 406, 713–716.
- 1515 Yokoyama, Y., Purcell, A., Lambeck, K., Johnston, P., 2001a. Shore-line reconstruction  
1516 around Australia during the Last Glacial Maximum and Late Glacial Stage.  
1517 *Quaternary International* 83/85, 9–18.
- 1518 Yokoyama, Y., Esat, T.M., Lambeck, K., 2001b. Last glacial sea-level change deduced  
1519 from uplifted coral terraces of Huon Peninsula, Papua New Guinea. *Quaternary*  
1520 *International* 83/85, 275–283.
- 1521 Yokoyama, Y., 2011. Last glacial lowstand and shelf exposure. In: Hopley, D. (Ed.),  
1522 *Encyclopedia of modern coral reefs: structure, form and process*. Encyclopedia of  
1523 Earth Science Series, Springer, 620–621.
- 1524 Yokoyama, Y., Esat, T.M., Thompson, W.G., Thomas, A.L., Webster, J.M., Miyairi, Y.,  
1525 Sawada, C., Aze, T., Matsuzaki, H., Okuno, J., Fallon, S., Braga, J.C., Humblet, M.,  
1526 Iryu, Y., Potts, D.C., Fujita, K., Suzuki, A., Kan, H., 2018. Rapid glaciation and a two-  
1527 step sea level plunge into the Last Glacial Maximum. *Nature* 559, 603–607.

1528

1529

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 coralgal assemblages, vermetid gastropods, algal crust  
1561 thickness, and percentage of coralgal framework in cores recovered from transect  
1562 HYD-01C.

1563

1564 **Fig. 5.** Coralgal-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 coralgal assemblages, vermetid gastropods, algal crust  
1582 thickness, and percentage of coralgal 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).

# Figure 1

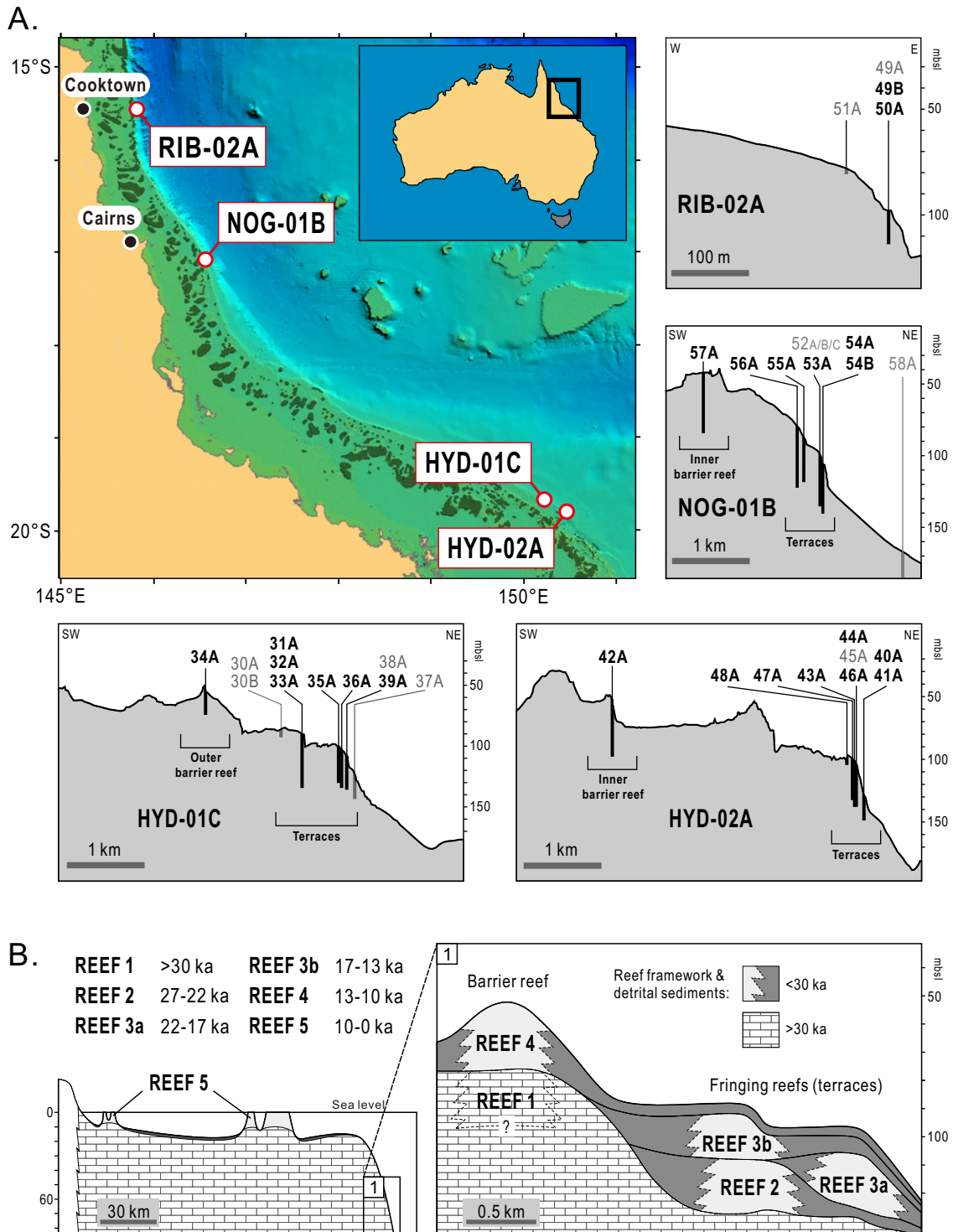


Figure 2

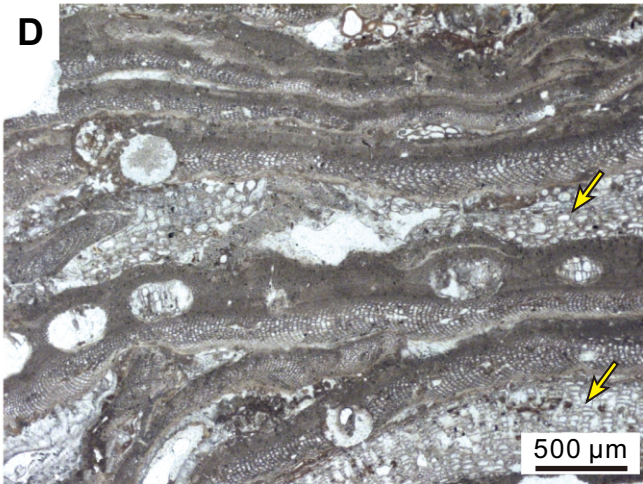
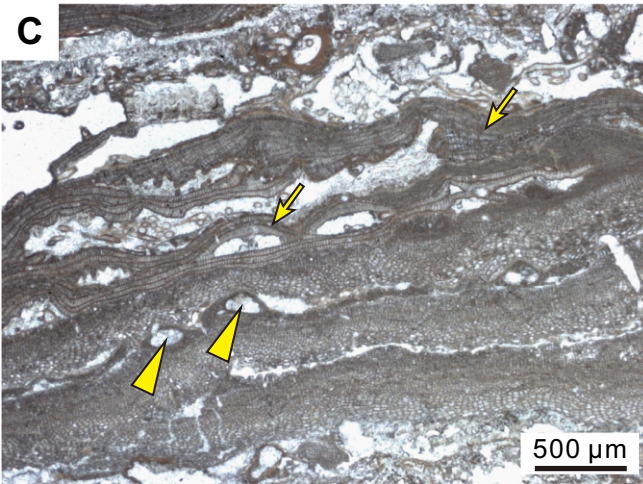
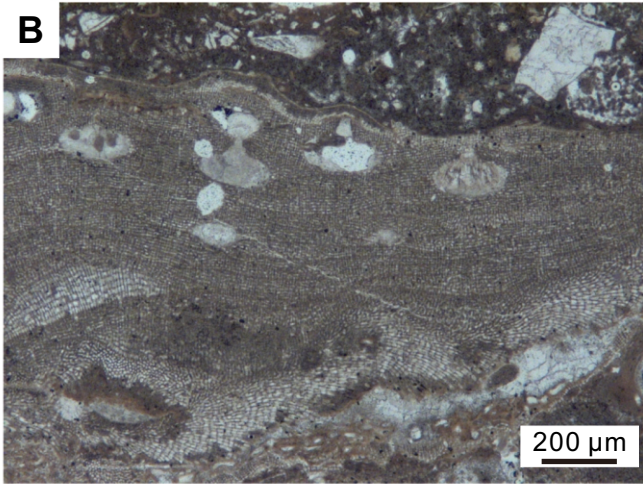
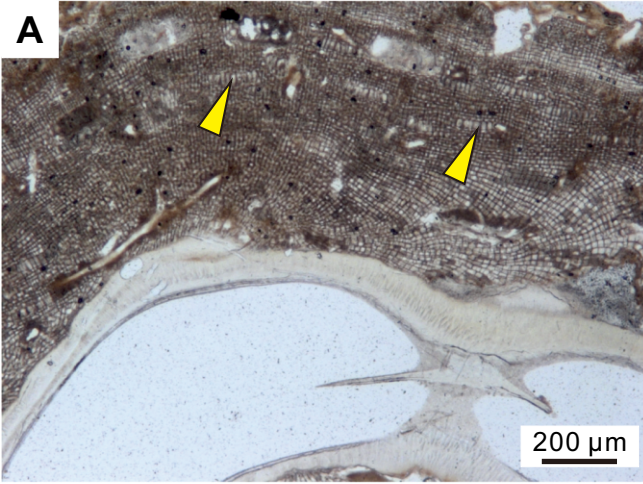
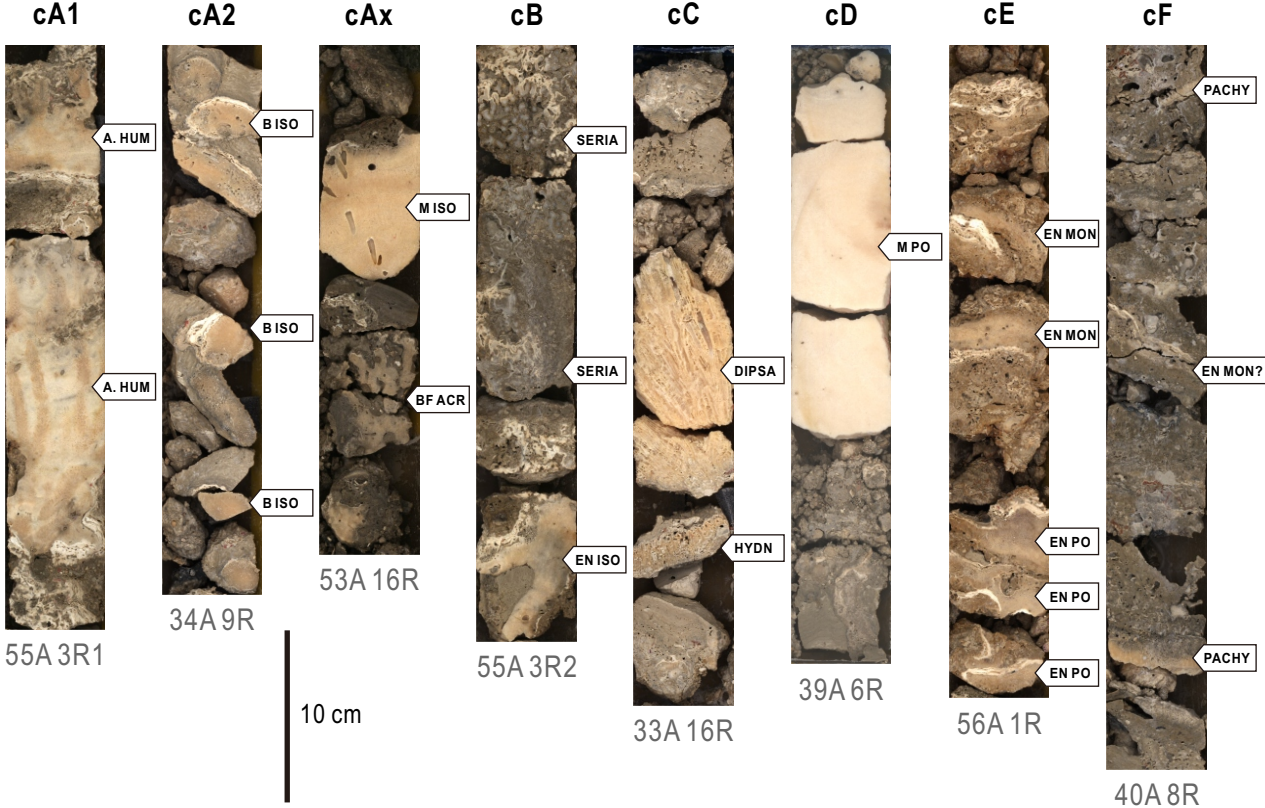
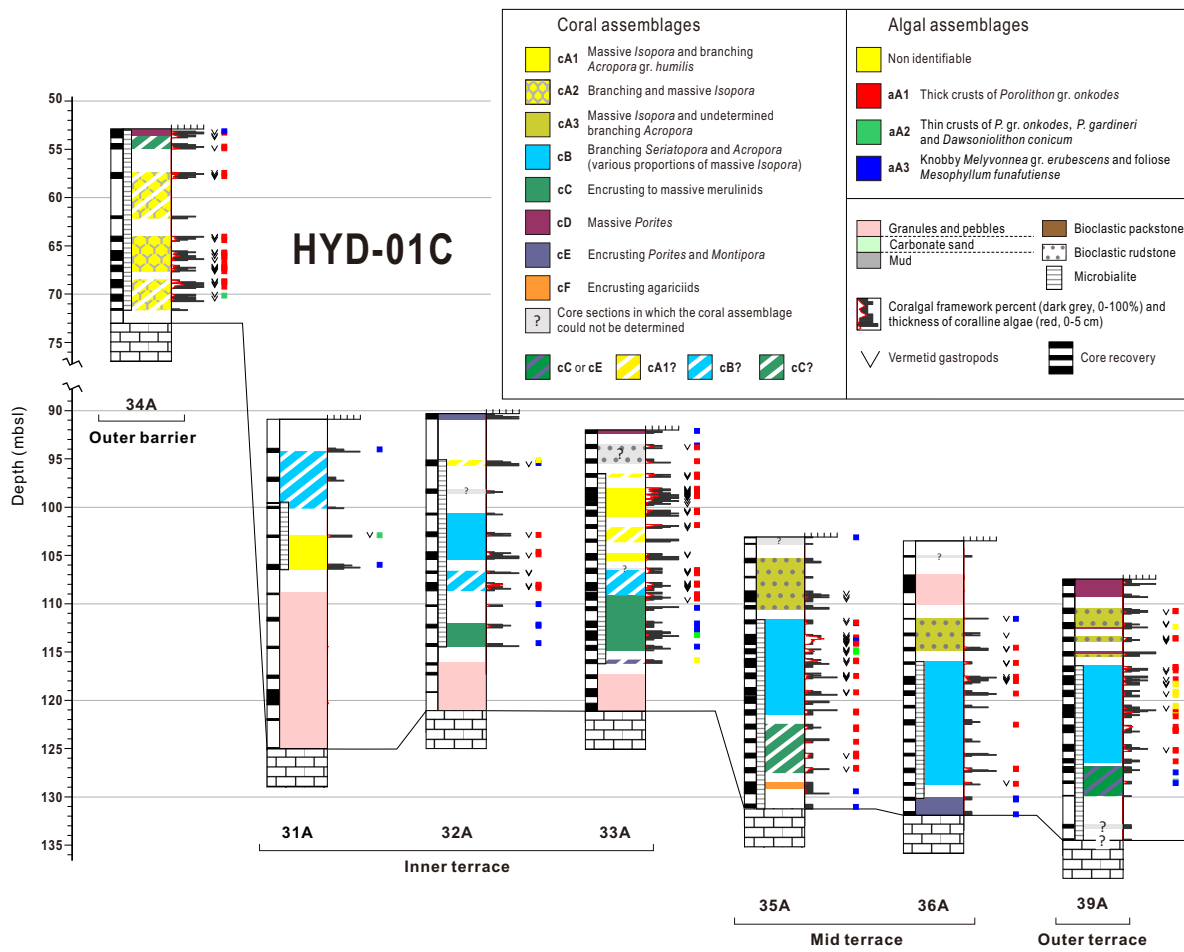




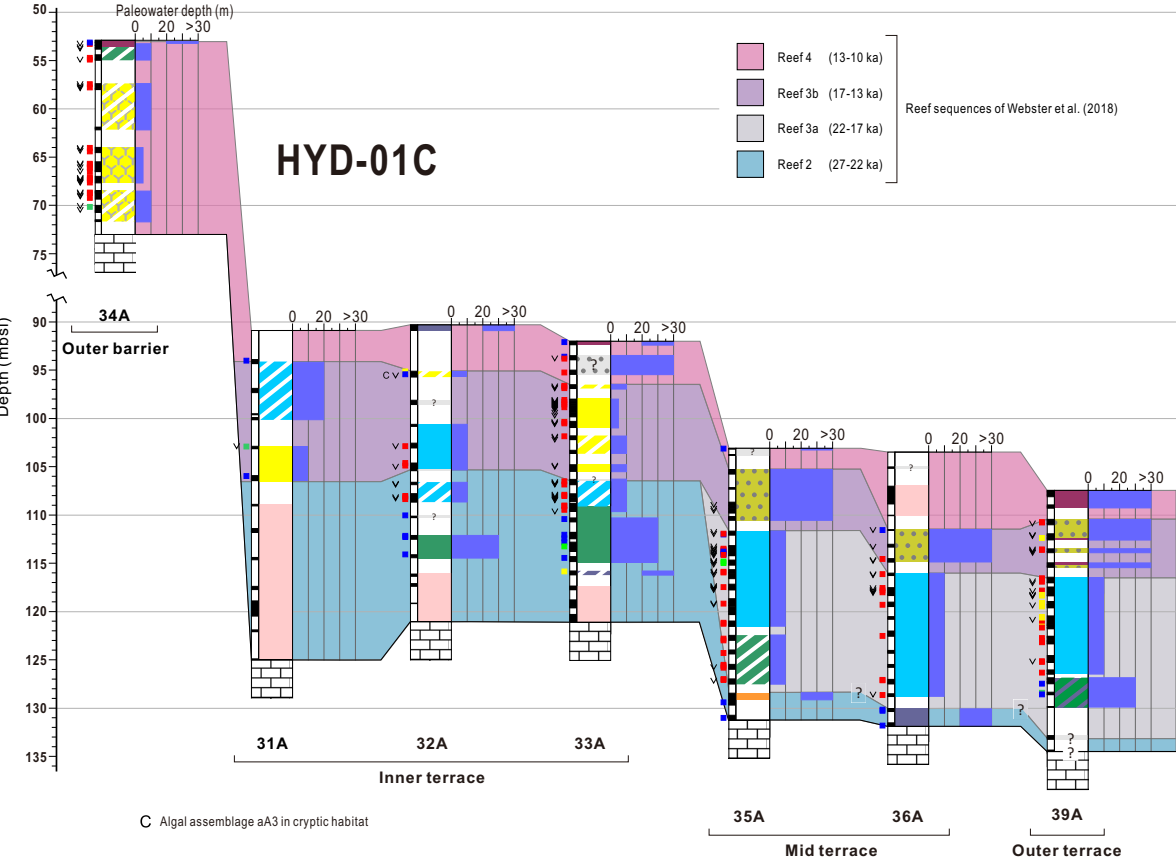
Figure 3



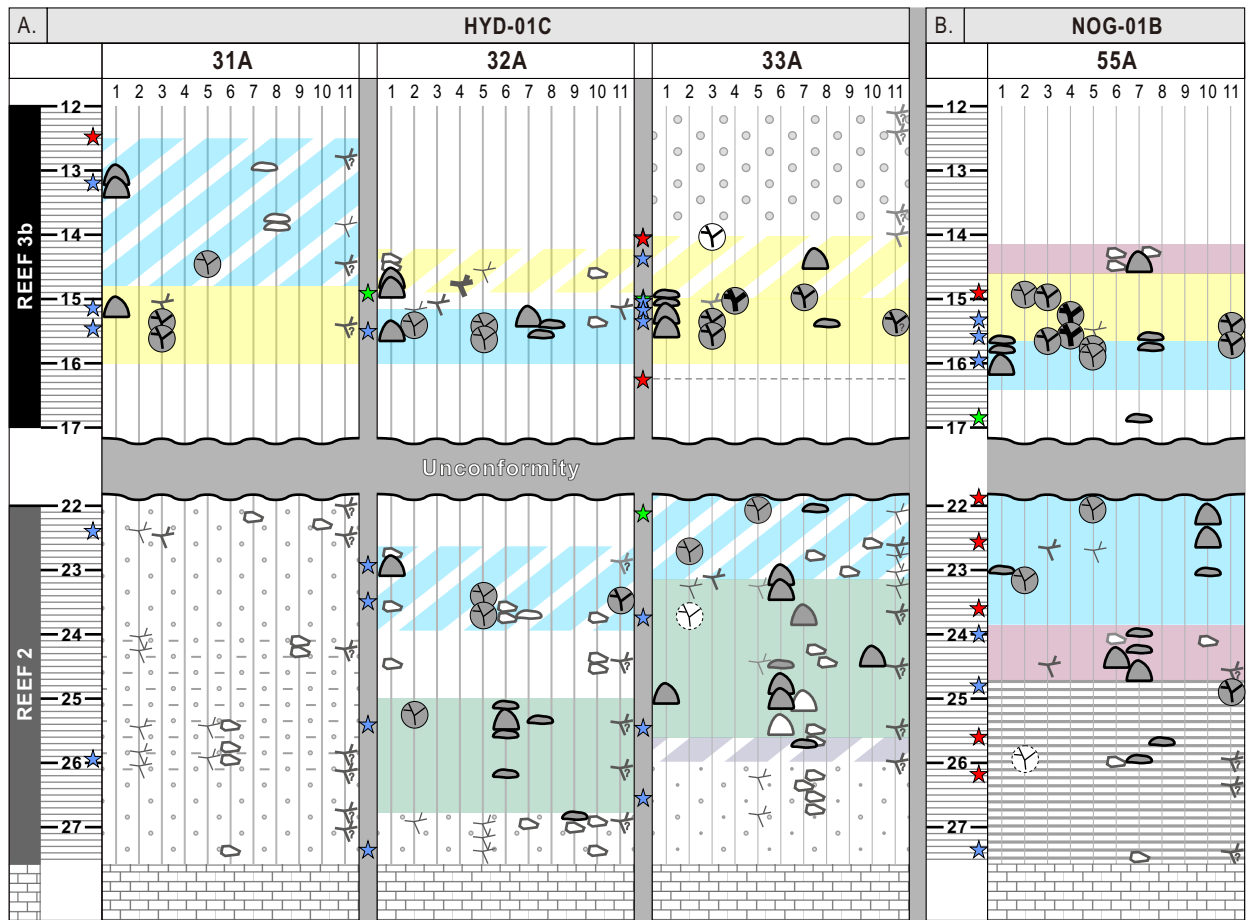
# Figure 4



# 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          |           |             |     |

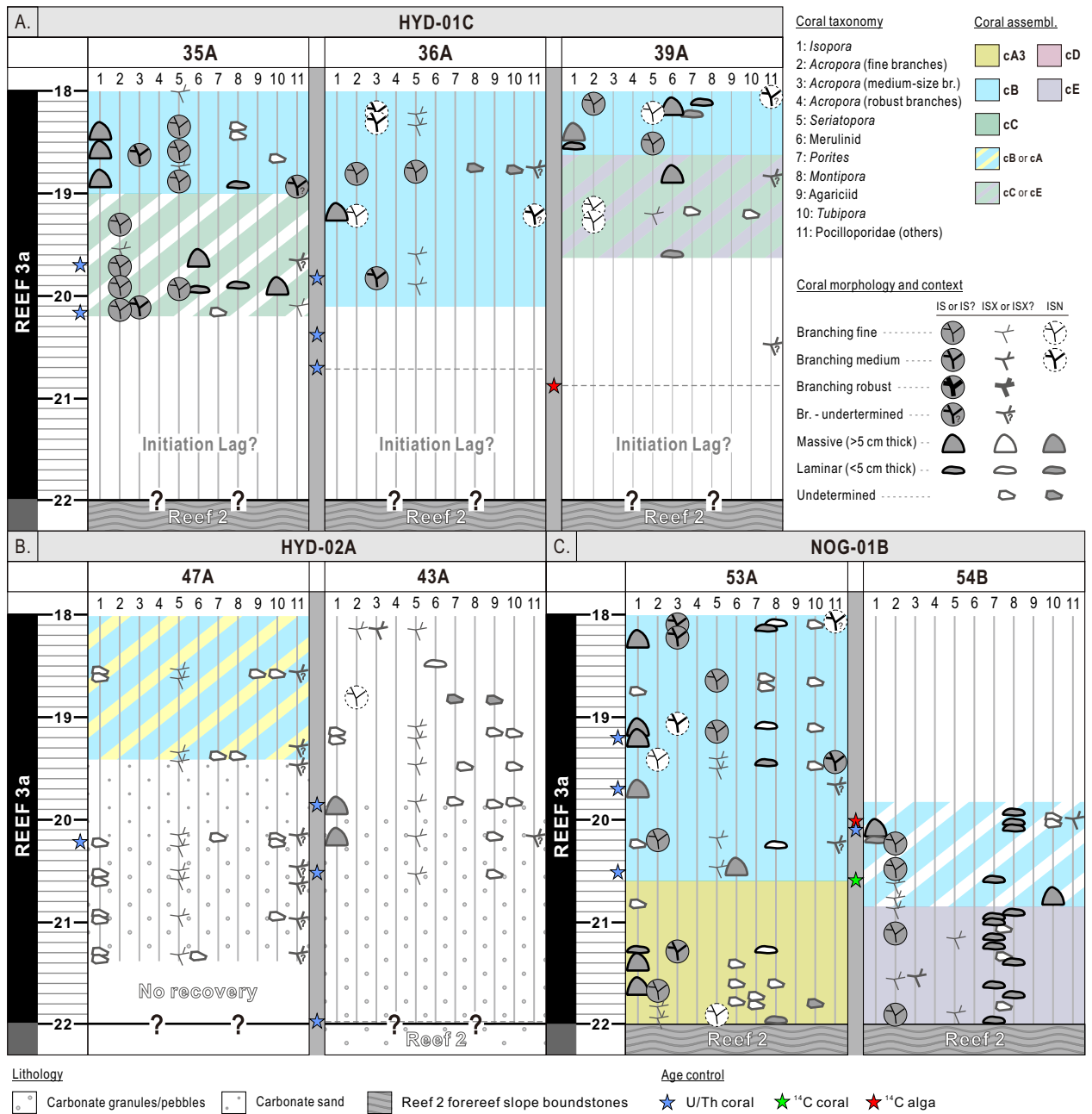
**Lithology**

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

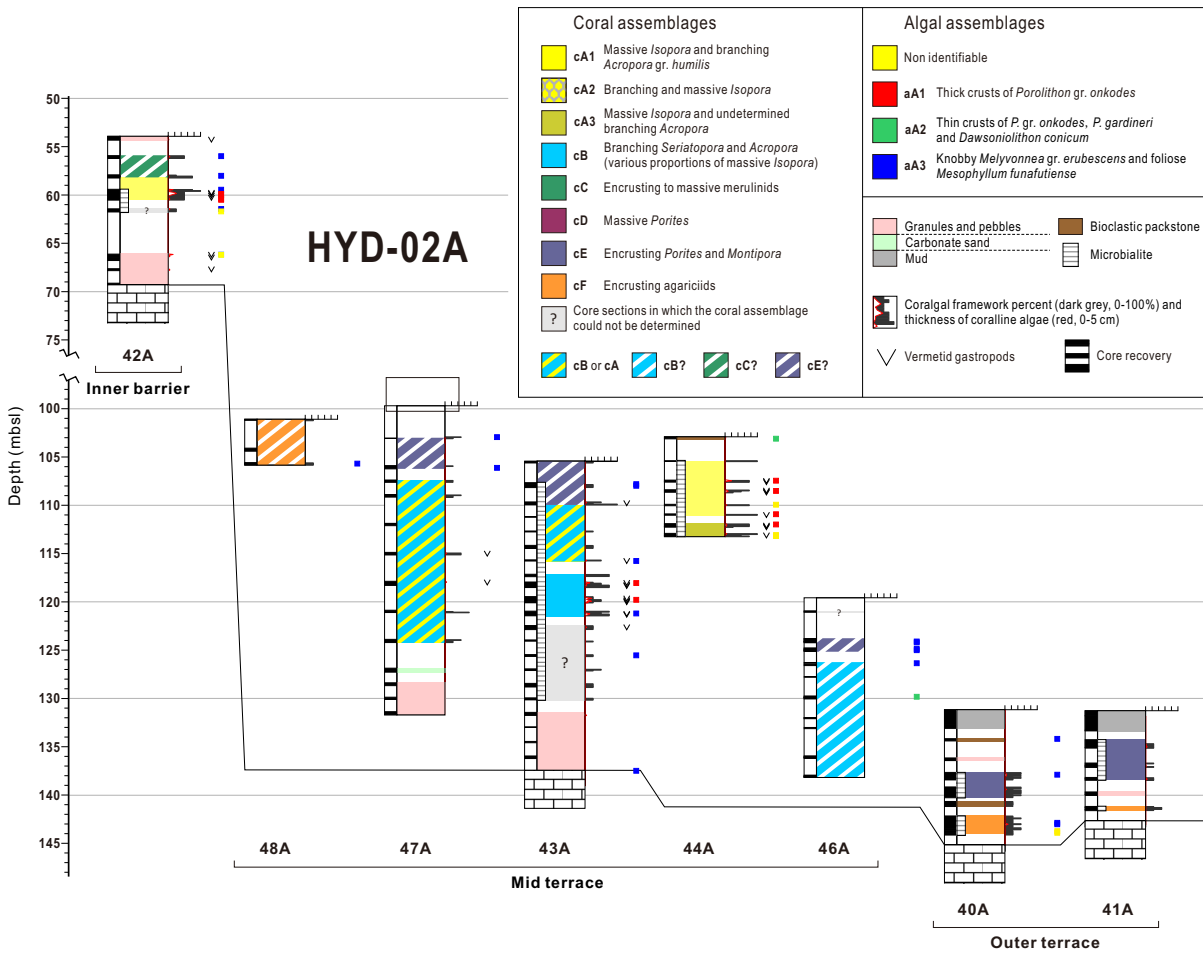
**Coral assemblages**

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

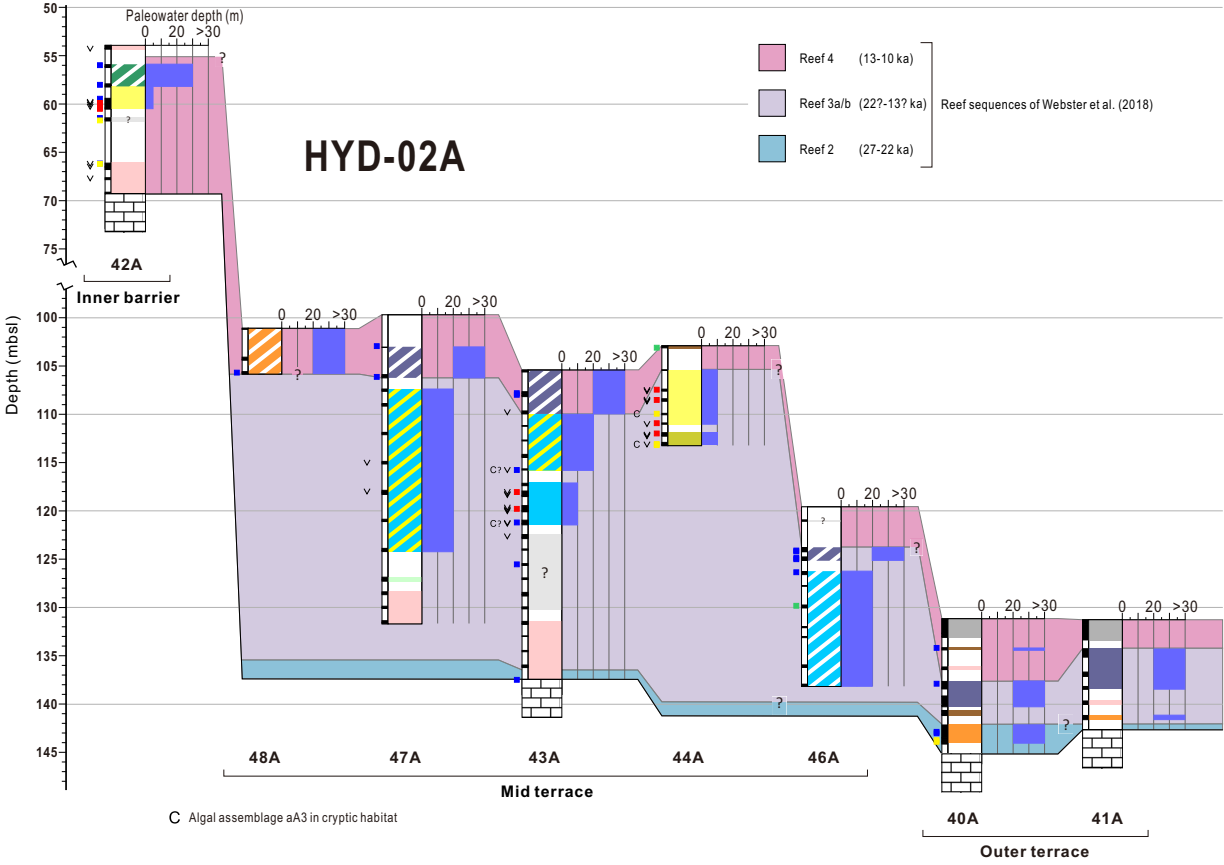
# Figure 7



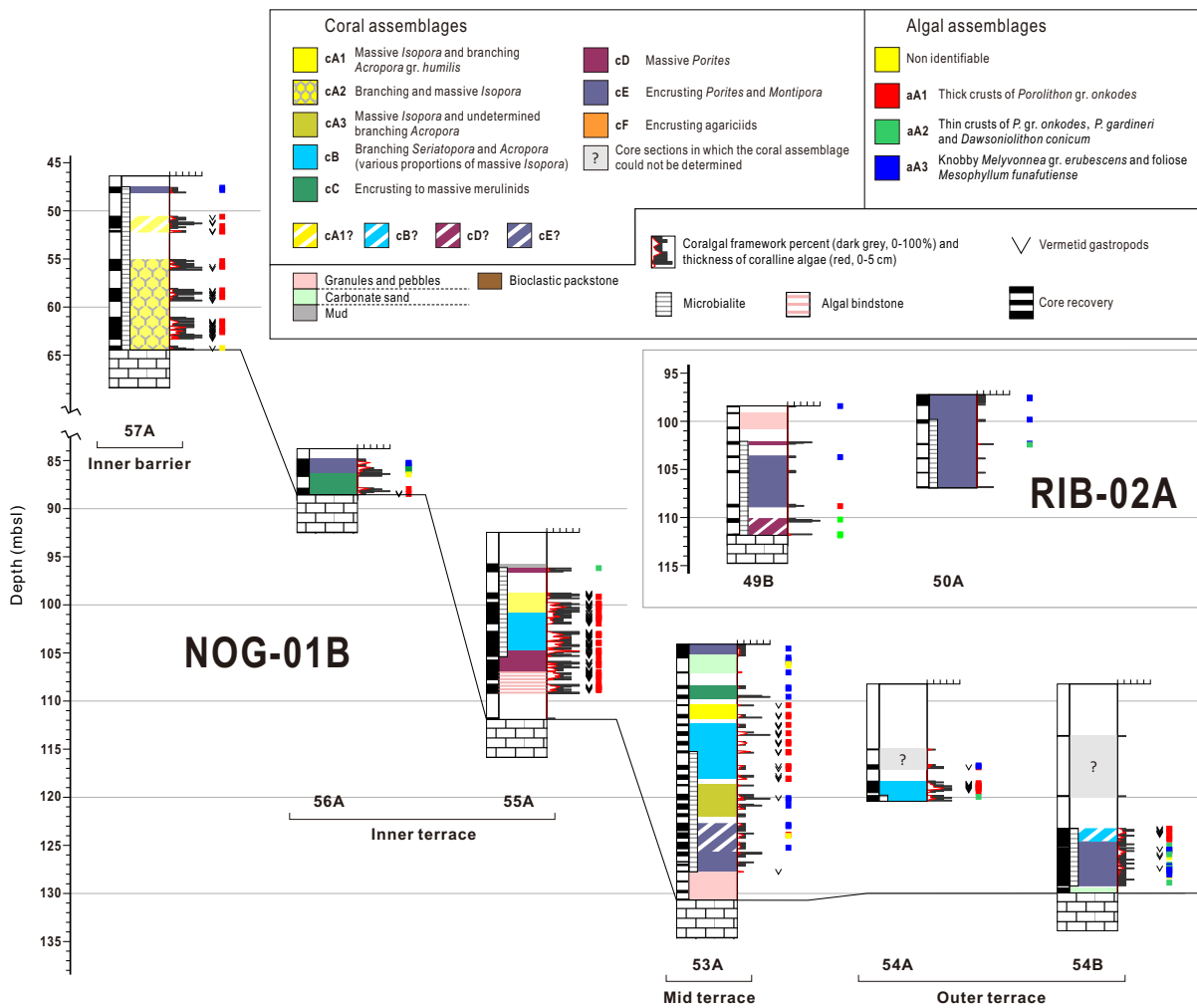
# Figure 8



# Figure 9

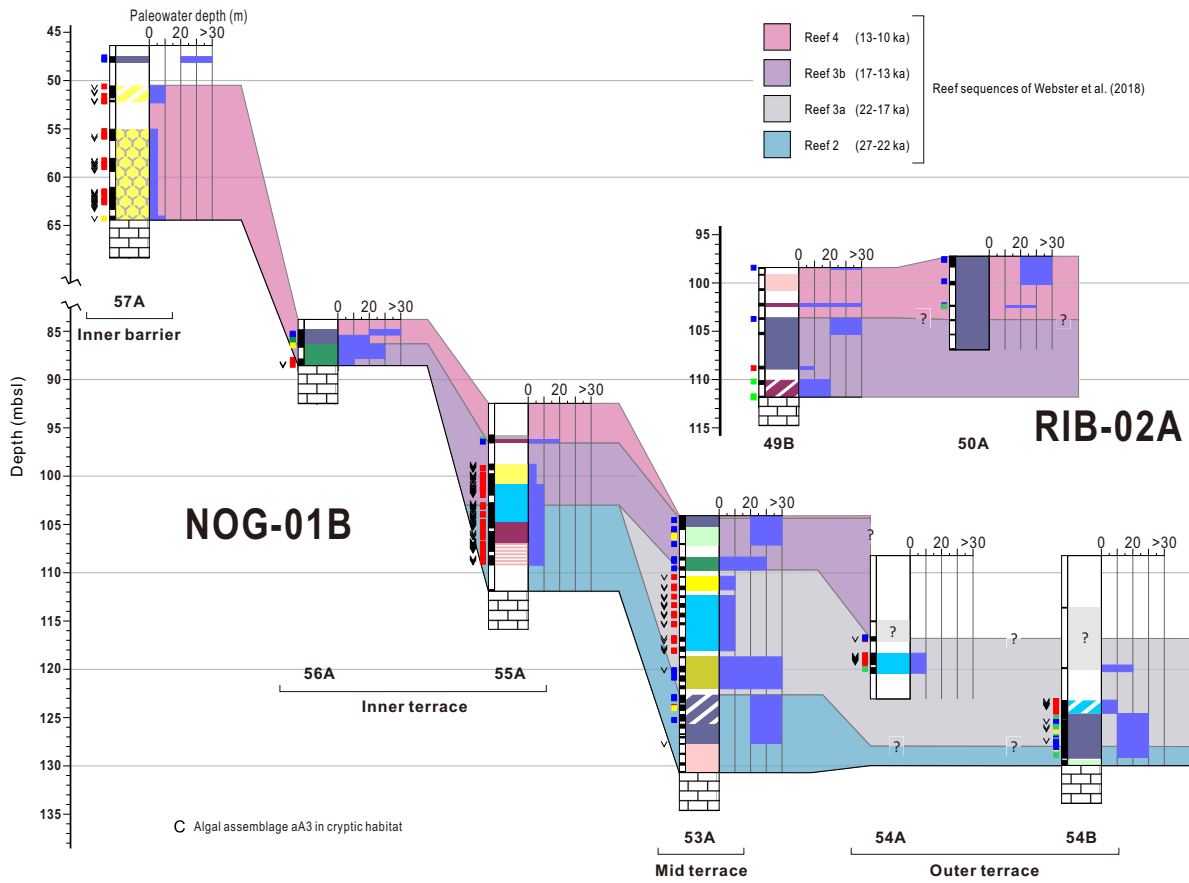


# Figure 10





# Figure 11



# Figure 12

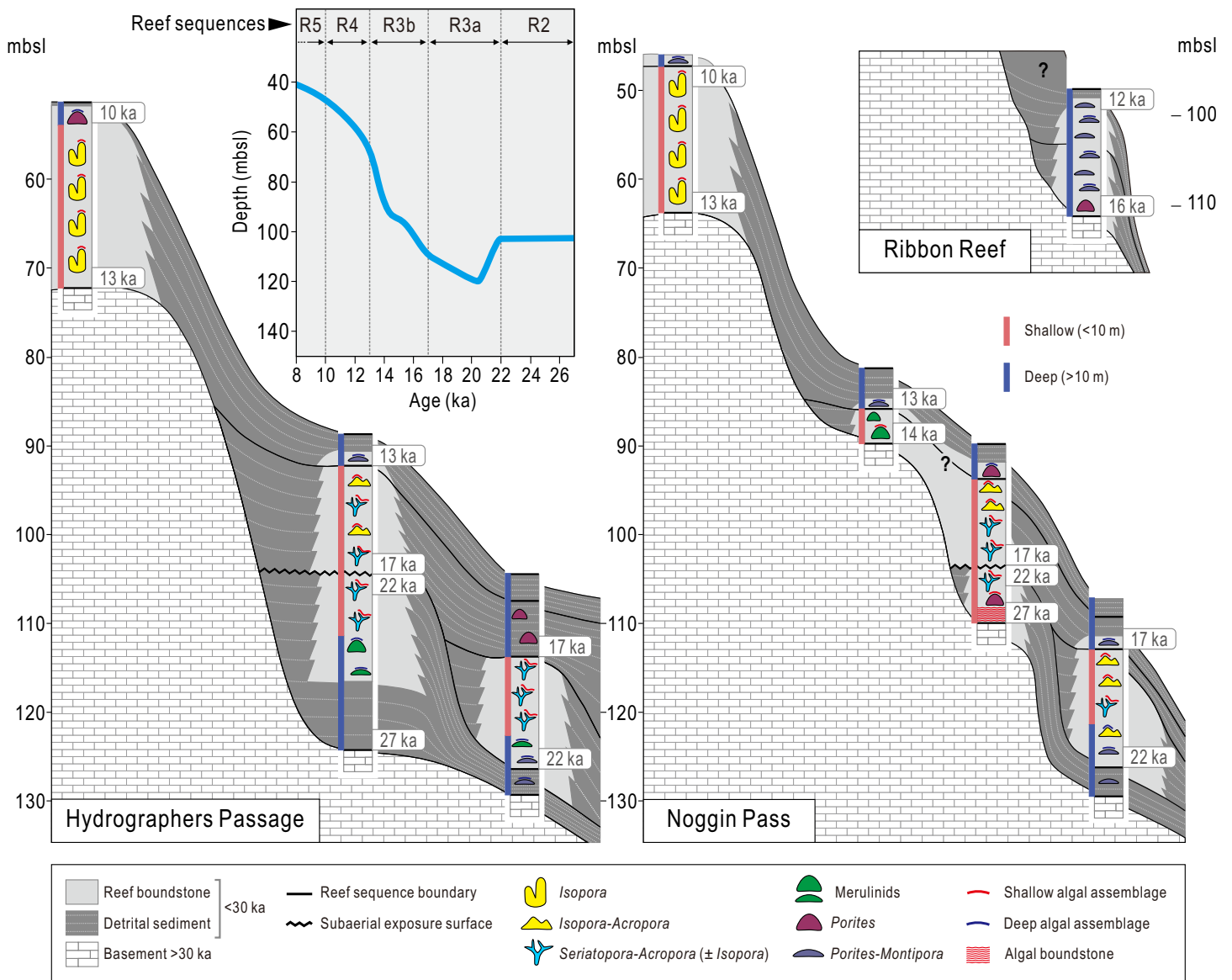


Table 1

## CORALLINE ALGAE

Order CORALLINALES		Order HAPALIDIALES
Family CORALLINACEAE		Family HAPALIDIACEAE
Subf. NEOGONIOLITHOIDEAE	Subf. LITHOPHYLLOIDEAE	Subf. MELOBESIOIDEAE
1. <i>Neogoniolithon</i> gr. <i>fosliei</i>	12. <i>Lithophyllum</i> <i>acrocampatum</i>	21. <i>Lithothamnion</i> <i>muelleri</i>
<i>Neogoniolithon</i> sp.	13. <i>Lithophyllum</i> <i>cuneatum</i>	22. <i>Lithothamnion</i> <i>prolifer</i>
2. <i>Spongites</i> <i>sulawesiensis</i>	14. <i>Lithophyllum</i> <i>insipidum</i>	23. <i>Lithothamnion</i> sp. 1 (34A-11-1)
3. <i>Spongites</i> sp.	15. <i>Lithophyllum</i> gr. <i>kotschyannum</i>	<i>Lithothamnion</i> sp. 2
Subf. HYDROLITHOIDEAE	16. <i>Lithophyllum</i> gr. <i>prototypum</i>	24. <i>Melyvonnea</i> gr. <i>erubescens</i>
4. <i>Adeylithon</i> <i>bosencei</i>	17. <i>Lithophyllum</i> gr. <i>pustulatum</i>	25. <i>Mesophyllum</i> <i>funafutiense</i>
5. <i>Hydrolithon</i> <i>boergesenii</i>	<i>Lithophyllum</i> sp.	26. <i>Mesophyllum</i> sp. 1 (55A- 5-CC)
(= <i>H. reinboldii</i> )	18. <i>Paulsilvella</i> sp.	<i>Mesophyllum</i> sp. 2
Subf. METAGONIOLITHOIDEAE	Subf. UNCERTAIN	Order SPOROLITHALES
6. <i>Harveylithon</i> gr. <i>munitum</i>	19. " <i>Hydrolithon</i> " <i>breviclavium</i>	Family SPOROLITHACEAE
7. <i>Harveylithon</i> <i>rupestre</i>	20. <i>Lithoporella</i> sp.	27. <i>Sporolithon</i> <i>ptychoides</i>
8. " <i>Hydrolithon</i> " <i>murakoshii</i>		28. <i>Sporolithon</i> sp.
9. <i>Dawsoniolithon</i> <i>conicum</i>		
10. <i>Porolithon</i> <i>gardineri</i>		
11. <i>Porolithon</i> gr. <i>onkodes</i>		

## SCLERACTINIAN CORALS

Family ACROPORIDAE		Family MERULINIDAE	
1. <i>Acropora</i> gr. FBR COR	27. <i>Astrea</i> <i>curta</i>	53. <i>Porites</i> gr. BR	
2. <i>Acropora</i> gr. <i>humilis</i>	28. <i>Caulastrea</i> sp.?	54. <i>Porites</i> gr. EN/PL	
3. <i>Acropora</i> gr. <i>hyacinthus</i>	29. <i>Cyphastrea</i> gr. <i>serailia</i>	55. <i>Porites</i> gr. M	
4. <i>Acropora</i> gr. <i>robusta</i>	30. <i>Cyphastrea</i> <i>microphthalma</i>	Family SIDERASTREIDAE	
5. <i>Acropora</i> <i>monticulosa</i>	31. <i>Dispastraea</i> gr. <i>laxa</i> ?	56. <i>Coscinaraea</i> <i>columna</i>	
6. <i>Astreopora</i> sp.	32. <i>Dispastraea</i> gr. <i>pallida</i>	57. <i>Psammocora</i> sp.?	
7. <i>Isopora</i> gr. BR	33. <i>Echinopora</i> <i>lamellosa</i>	INCERTAE SEDIS	
8. <i>Isopora</i> gr. M	34. <i>Echinopora</i> <i>mammiformis</i> ?	58. <i>Leptastrea</i> <i>pruinosa</i>	
9. <i>Montipora</i> gr. BR?	35. <i>Favites</i> <i>flexuosa</i> ?		
10. <i>Montipora</i> gr. EN/PL	36. <i>Favites</i> gr. <i>abdita</i>	NON-SCLERACTINIAN CORALS	
11. <i>Montipora</i> gr. M	37. <i>Favites</i> <i>pentagona</i>	Family HELIOPORIDAE?	
Family AGARICIIDAE	38. <i>Favites</i> <i>valenciennesi</i>	<i>Helipora</i> <i>coerulea</i> ?	
12. <i>Leptoseris</i> <i>explanata</i> ?	39. <i>Goniastrea</i> <i>pectinata</i> ?		
13. <i>Leptoseris</i> <i>foliosa</i>	40. <i>Goniastrea</i> <i>stelligera</i> ?	Family TUBIPORIDAE	
14. <i>Leptoseris</i> gr. <i>scabra</i>	41. <i>Hydnophora</i> <i>exesa</i>	<i>Tubipora</i> <i>musica</i>	
15. <i>Leptoseris</i> gr. <i>yabei</i>	42. <i>Leptoria</i> <i>phrygia</i>		
16. <i>Leptoseris</i> <i>papyracea</i>	43. <i>Platygyra</i> gr. <i>daedalea</i>	Family MILLEPORIDAE	
17. <i>Pachyseris</i> <i>speciosa</i>	44. <i>Platygyra</i> <i>pini</i> ?	<i>Millepora</i> sp.	
18. <i>Pavona</i> <i>clavus</i>	Family OCULINIDAE		
19. <i>Pavona</i> <i>maldivensis</i>	45. <i>Galaxea</i> <i>fascicularis</i>	Family ALCYONIDAE (soft corals)	
Family FUNGIIDAE	Family POCILLOPORIDAE	Spiculite ( <i>Sinularia</i> sp.?)	
20. <i>Cycloseris</i> sp.?	46. <i>Pocillopora</i> <i>damicornis</i>		
21. <i>Fungia</i> sp.	47. <i>Seriatopora</i> <i>hystrix</i>		
Family DENDROPHYLLIIDAE	48. <i>Stylophora</i> <i>pistillata</i>		
22. <i>Turbinaria</i> <i>frondens</i>	Family PECTINIIDAE		
23. <i>Turbinaria</i> <i>mesenterina</i> ?	49. <i>Echinophyllia</i> sp.?		
24. <i>Turbinaria</i> <i>peltata</i>	50. <i>Mycedium</i> <i>elephantotus</i>		
25. <i>Turbinaria</i> <i>reniformis</i>	Family PORITIDAE		
Family LOBOPHYLLIIDAE	51. <i>Alveopora</i> <i>verrilliana</i>		
26. <i>Lobophyllia</i> <i>corymbosa</i>	52. <i>Goniopora</i> gr. M		

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 S2

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