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Self-generated morphology in lagoon reefs

The shapes and forms of coral reefs are generally attributed to external controls such as substrate topography or hydrodynamic influences. Little is known about inherent reef morphology in the absence of external control. Here we use reef growth simulations, based on observations in the cellular reefs of Western Australia's Houtman Abrolhos Islands, to show that reef morphology is fundamentally determined by the mechanical behaviour of the reef-building organisms themselves—specifically their tendency to either remain in place or to collapse. A spectrum of realistic reef forms can be generated by varying a single parameter representing this characteristic. Reef-building organisms that tend to remain in place, such as massive and encrusting corals or coralline algae, produce nodular reefs, whereas those that tend to collapse, such as branching *Acropora*, produce cellular reefs. Inherent reef growth forms are best expressed in sheltered lagoons. The purest forms arise where a single type of reef builder prevails, as in the cellular reefs of the Abrolhos. In these cases reef morphology can be considered a phenotype of the predominant reef building organism.

1 **Self-generated morphology in lagoon reefs**
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Introduction

The three-dimensional form of a coral reef influences, and is influenced by, virtually all processes occurring within and around it (Roberts et al. 1975; Hopley, Smithers & Parnell 2007). Understanding the morphological development of reefs can therefore help provide a context for interpreting present-day reef processes and predicting their future.

Reef morphology is determined by different influences at different scales, from the inherent forms of reef-building organisms at the small scale to the configuration of continental shelves at the large scale. Over intermediate scales (metres to kilometres) reefs exhibit a great diversity of forms, reflecting the multitude of interacting processes affecting them. But within the diversity is a subset of globally recurring forms, indicating that there are some universal rules governing reef morphology (Hatcher 1997; Blanchon 2011; Purkis and Schlager 2014). Traditionally, these rules have been envisaged as external controls operating at or above the scale of the morphological features, for example substrate topography (MacNeill 1954, Purdy 1974; Choi & Ginsburg 1982) or the wave field (Munk & Sargent 1954; Roberts 1974). While these factors undoubtedly influence the morphology of many reefs, they raise an interesting question: what would reefs look like in the absence of such external influences? This question brings the focus down to the reef-building organisms themselves. Because these organisms cumulatively become the reef, there is significant potential for behaviour and events at their scale to be expressed in reef morphology at the intermediate scale. Such 'emergence' of self-organised patterns from small scale processes is ubiquitous in physical and biological systems (Nicolis and Prigogine 1977; Camazine et al. 2001). While it is recognised that coral reefs are likely to exhibit this trait (Mistr and Bercovici 2003; Rietkirk and van de Koppel 2008; Blanchon 2011; Schlager and Purkis 2014), it has not been demonstrated.

Lagoons are the most likely setting for inherent reef growth forms to arise, as they are generally flat-floored and sheltered. Several characteristic lagoon reef forms are repeated worldwide, ranging from simple mound-like patch reefs to complex cellular[1] reefs (Stoddart 1969; Hopley 1982; Blanchon 2011; Fig. 1). The development of patch reefs can be readily visualised in terms of expansion from a nucleus, and this mode of growth has been

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[1] Cellular reefs (terminology after Hoskin 1963) are also widely known as reticulate reefs, from the latin *reticulum*: a network or net-like structure. However reticulate is also applied to another characteristic lagoon reef form: anastomosing reefs. Therefore we consider cellular and anastomosing as subdivisions of reticulate. As in most natural classifications, boundaries are transitional.

43 demonstrated repeatedly, from various nuclei including topographic highs in underlying

44 limestones (Halley et al 1977; Mazzullo et al. 1992), sedimentary structures (Perry et al.

45 2012; Novak et al. 2013), or early-colonising corals (Jones 1977; Crame 1981). Cellular reef

46 morphology, in contrast, is not an intuitive growth form. Cellular reefs distinctly resemble

47 negative landforms, particularly karst terrains (terrestrial erosion landforms created in

48 limestone through dissolution by rainwater). Based on this resemblance, and the recognition

49 that the foundations of most reefs have been exposed to at least 100,000 years of weathering

50 during Interglacial periods, cellular reef morphology has long been interpreted as an

51 inheritance from underlying karst (Fairbridge 1948; Purdy 1974; Guilcher 1988; Searle 1994;

52 Macintyre, Precht & Aronson 2000; Purkis et al. 2010; Kan et al. 2014). However there has

53 always been an opposing view attributing cellular morphology to reef growth (Dakin 1919;

54 Rossfelder 1990; Collins et al. 1993; Wyrwoll et al. 2006; Barott et al. 2010; Blanchon 2011;

55 Schlager and Purkis 2014). The growth alternative is gradually gaining acceptance, having

56 been confirmed for the cellular reefs of Mataiva Atoll in French Polynesia (GIE Raro Moana

57 1985; Rossfelder 1990) and the Houtman Abrolhos Islands in Western Australia (Collins et al

58 1993; Collins, Zhu & Wyrwoll 1996; 1998; Wyrwoll 2006). Seismic surveys and coring at

59 Mataiva showed the Holocene reef to be 10-20 m thick and demonstrated that, although the

60 reef is underlain by a karst Tertiary limestone, the karst features are relatively small-scale and

61 were infilled before submergence, such that the present reef morphology is independent of

62 the substrate (Rossfelder 1990). Similarly, seismic and coring in the Abrolhos lagoons

63 recorded a Holocene reef thickness of 40 m over a flat Last Interglacial grainstone, again

64 demonstrating independence from the substrate (Collins et al. 1993; Collins, Zhu & Wyrwoll

65 1996; 1998).

66

67 While this work has removed all doubt that the cellular reefs of Mataiva and the Abrolhos

68 have grown into their present configuration, it has not provided a generally accepted growth

69 mechanism. Three alternative mechanisms have been proposed. The first, developed

70 independently by GIE Raro Moana (1985) at Mataiva and Barott et al. (2010) at Millenium

71 Atoll, is the colonisation of the lagoon floor by networks of massive corals, which are

72 subsequently colonised by other corals and grow upward to the surface. The second,

73 proposed by Wyrwoll et al. (2006) for the Abrolhos, is growth to sea level of isolated

74 branching *Acropora* pinnacle, reticulate and stellate (star-shaped) patch reefs, which

75 subsequently extend and coalesce to surround enclosed depressions. The third, proposed by

76 Blanchon (2011), is a self-limitation mechanism based on negative feedback between reef

growth and water circulation—reef growth reduces water circulation which reduces reef growth, such that the cellular depressions become self-reinforcing as the surrounding reefs grow.

The network mechanism (GIE Raro Moana 1985; Barott et al. 2010) has an inherent problem explaining how massive corals might colonise the lagoon floor in a network. While it can't be discounted it seems unlikely. Coalescence of pinnacle, reticulate and stellate patch reefs (Wyrwoll 2006) seems a better mechanism but doesn't explain why patch reefs composed of a uniform coral type developing on a uniform surface would develop non-uniform shapes. Blanchon's (2011) self-limiting concept is arguably a much better proposition as nothing is predefined; structure emerges from the interaction between reef builders and their environment. However it is a loosely defined concept with no details of the interaction and no specific mechanism initiating the cellular morphology.

Here we examine the process of cellular reef growth using computer simulation based on field observations in the Abrolhos cellular reefs. These reefs provide an ideal case study for cellular reef development due to their flat pre-Holocene substrate, known accretion history and very pure reef-building community—cores through the Abrolhos cellular reefs consist almost entirely of branching *Acropora*, with a few tabular *Acropora* appearing as the reefs approached sea level (Collins et al. 1993; Collins, Zhu & Wyrwoll 1996; 1998).

Survey methods

An apparent sequence of cellular reef development is evident in the Abrolhos lagoons, progressing from circular patch reefs to coalescing stellate reefs surrounding semi-enclosed depressions to a reef platform surrounding enclosed depressions (Wyrwoll et al. 2006; Fig. 1; Fig. 2). Under the assumption that these are sequential stages of reef development, surveys of the circular-stellate-enclosed sequence represent surveys through time. Space-for-time substitution (Darwin 1842; Davis 1899) may therefore be applied to describe the evolution of the Abrolhos cellular reefs and, potentially, to reveal their formative mechanism. We examined replicate sites of each stage in a 15 km^2 cellular reef complex known as 'the Maze' in the Easter Group of the Abrolhos (Fig. 2; 28°41'S, 113°49'E). We surveyed fifteen sites in detail and many more in brief visits, including some in the Pelsaert Group to the south and the Wallabi Group to the north. At each of the fifteen sites we established four transects oriented to the cardinal directions, running from the deepest to shallowest habitat. We

111 quantified substrate composition by point counting video records of each transect, and

112 constructed topographic profiles by recording tide-corrected depth every metre along each

113 transect. We used twenty five categories in point count analysis and condensed these into

114 seven categories for graphical representation: tabular *Acropora*, branching *Acropora*, other

115 scleractinia, soft coral, macroalgae, dead coral, and sediment/rubble.

116

Survey results

118 Underwater observations show that the different reef stages are all connected in a continuous

119 reef blanket with a distinctive 'egg carton' form. The relationship between the reef shapes

120 can be envisaged by imagining sequentially deeper horizontal slices through a solid egg

121 carton. The initial slices contact the peaks, producing circular reefs. Deeper slices reach the

122 ridges between adjacent peaks, producing stellate reefs. Subsequent slices produce a platform

123 surrounding enclosed depressions and eventually a solid platform. Below we describe the

124 sequence in the three idealised stages: circular, stellate and enclosed. However it should be

125 noted that the sequence is a continuum and that sites within each stage often have features of

126 earlier and/or later stages. Fig. 3 shows representative transect profiles from each stage and

127 Fig. 4 is a schematic block diagram incorporating the main features of the idealised reef

128 stages.

129

Circular reefs

131 Circular reefs occur around the margin of the Maze (e.g. sites K and M; Fig. 2). The reef at

132 these sites has a sinusoidal profile, curving up over dome-shaped reef tops then descending

133 into bowl-shaped depressions (Fig. 3). The wavelength and amplitude of the profile varies

134 within a range of approximately 40-100 m and 15-30 m respectively. Adjacent circular reef

135 tops are linked by saddle-shaped ridges, and the topography is covered by a blanket of

136 branching *Acropora*, primarily *A. formosa* and *A. abrolhosensis*. Tabular *A. spicifera* is

137 abundant at site M on the exposed northern margin of the Maze but absent from the more

138 sheltered site K to the south. Live *Acropora* cover is 60-100% on the reef tops and ridges at

139 both sites, decreasing to approximately 30% within the site M depressions and 0% within the

140 more enclosed and restricted site K depressions. Dead *Acropora* branches at depth are

141 occupied by macroalgae at both sites, predominantly *Sargassum* spp. at site M and

142 *Lobophora variegata* at site K. Beyond the outermost circular reefs, the reef surface slopes

143 down to a flat sandy seafloor at 35 m without breaking into isolated patches. Corals on the

144   outer slopes are predominantly tabular and branching *Acropora* to 25 m depth. Below 25 m

145   the community is more diverse, consisting predominantly of foliose agariciids and pectiniids.

146

147   Three islands of storm-deposited *Acropora* rubble line the eastern margin of the Maze

148   (Collins, Zhao & Freeman 2006), and a series of submerged east-west trending linear reef

149   banks occur on the northern margin of the Maze. Two banks can be seen in Fig. 2 and two

150   deeper banks lie beyond them. The bank crests are 2 to 15 m deep, sloping downward at

151   approximately 30° to U-shaped troughs at 20 to 30m. The outermost bank reaches the

152   seafloor at 35m. Coral cover and zonation on the banks is equivalent to that of the circular

153   reefs.

154

155   **Stellate reefs**

156   In the stellate stage the circular reef tops and shallow ridges reach sea level, producing a

157   discontinuous network of flat-topped, coralline algal-cemented and macroalgal-covered

158   stellate platforms (sites B, E, F, J, L, N). Water circulation within the intervening depressions

159   is further reduced and the water column is often stratified and stagnant. Live coral is

160   consequently restricted to shallow depths, often less than 15 m in the more enclosed

161   depressions. Shallow subtidal habitat remains dominated by live branching *Acropora* (Fig. 5)

162   and occasional foliose *Montipora*. Dead *Acropora* branches at depth are colonised by

163   *Nephthea* soft corals and *Lobophora variegata*, and fine sediment accumulates in the bases of

164   the depressions. A distinct shallow coral community begins to appear in the stellate stage,

165   consisting of diverse massive and encrusting corals, predominantly faviids, pectiniids,

166   *Montipora* and *Astreopora*. Several apparent developmental stages of this community are

167   present, initiating as a discontinuous cover of small colonies on dead *Acropora* branches (Fig.

168   6A) and culminating in vertical or overhanging walls descending from the surface to as deep

169   as ten metres, but typically between two and eight metres (Fig. 6B).

170

171   **Enclosed depressions**

172   In the enclosed stage (sites C, D, I, O) the previously-established patterns strengthen: most

173   depressions are rimmed by vertical walls, the water column is often stratified and turbid, live

174   coral cover declines rapidly with depth, and most depressions have a deep sediment fill. Late-

175   stage enclosed depressions (A, G, H) gradually fill with sediment to the level of the

176   surrounding reef flat. As they fill, the fringe of live *Acropora* beneath the vertical walls

177 migrates upward, eventually overgrowing the walls and encroaching over the depression

178 floors.

179

180 Based on the descriptions above, the Abrolhos cellular reefs appear to exhibit a

181 straightforward developmental sequence. However they provide little insight into the origin

182 of cellular morphology because the cellular form is already present at the circular reef stage.

183 Given the higher coral cover on the reef tops and ridges than the depressions, subsequent

184 growth will inevitably lead to enclosed depressions from the circular reef stage. Several

185 processes appear to be suppressing live coral cover at depth within the circular reef

186 depressions, including reduced water circulation and macroalgal colonisation. But without

187 being able to see further back into the Holocene it is impossible to determine whether any of

188 the current processes could have initiated the cellular morphology or whether they are

189 consequential.

190

191 **Model**

192 In the absence of conclusive indicators of cellular origin in the real reefs, we used a cellular

193 automaton to model their development (Blakeway 2000; see Data S1 for code). A cellular

194 automaton (Ulam 1962; von Neumann 1963) is an array of identically-programmed

195 interacting cells. This structure is well-suited to modeling reef development because each cell

196 in the array can be considered to represent a square metre of seafloor, and reefs can develop

197 on the seafloor as three-dimensional stacks of cubic 'corals'. Using this approach we first

198 describe a basic patch reef system in which growth is essentially random and unconstrained

199 but for sea level, and subsequently introduce a parameter representing branching *Acropora*.

200

201 Each run of the model is initialised by defining the dimensions of the array, the seafloor

202 depth, and the number of coral 'recruits'. We used a consistent configuration for most model

203 runs: an array of 160 x 160 cells (representing 160 x 160 m, or 2.56 hectares, of seafloor), a

204 uniform depth of 30 m, and 64 randomly-spaced coral recruits, occupying 0.25% of the array

205 (variations to this configuration are described later in supporting figures). We chose 30 m as

206 the default depth, rather than the 40 m of the Maze, because cellular reefs elsewhere appear to

207 be thinner than the Maze; those at Mataiva for example are only 10-20 m thick (Rossfelder

208 1990). The 160 x 160 m array is embedded within a larger array of 250 x 250 m, giving the

209 reefs a 45 metre margin for lateral growth.

210

211 Corals can grow upward and outward in increments of one metre per iteration, with vertical
212 growth halted at sea level. Each cell in the array is assigned two growth probabilities in each
213 iteration: a vertical probability representing the likelihood of the cell growing upward itself
214 and a neighbour probability representing the likelihood of the cell being overgrown by a
215 neighbouring coral (Fig. 7). The vertical probability of vacant seafloor cells is zero and the
216 vertical probability of coral-filled cells is random. The neighbour probability of each cell is
217 the product of a random number between zero and one and a 'neighbour value' that depends
218 on the state of the eight surrounding cells. Cells with no shallower neighbours are assigned a
219 neighbour value of zero; otherwise the cell's neighbour value rises incrementally for each
220 shallower neighbour. If a cell becomes surrounded by shallower neighbours it is guaranteed
221 to be overgrown. Otherwise growth is determined by comparing the cell's vertical and
222 neighbour probabilities against two random numbers between zero and one. If either or both
223 probabilities exceed their respective random numbers, the cell grows by one metre when the
224 array is updated prior to the next iteration.
225
226 Patch reefs created with the random model appear circular in plan view and steeply conical in
227 oblique view (Fig. 8A and B). They maintain their conical form as they enlarge, and become
228 flat-topped at sea level. In the multiple patch reef system, each individual patch develops
229 similarly, eventually coalescing and fusing with neighbouring patches (Fig. 8C and D). While
230 these reefs appear realistic they bear little resemblance to cellular reefs. In fact their shapes
231 are the inverse of cellular reefs; the model reefs appear nodular and subcircular in plan view
232 whereas cellular reefs are concave and stellate, surrounding subcircular depressions.
233 However, the random model is generic and does not intentionally represent any particular
234 coral type.
235
236 In considering modifications to represent branching *Acropora*, one aspect of the random reefs
237 is immediately apparent—coral spires projecting up to four metres above neighbouring cells
238 (Fig. 8B). Such projections cannot occur on real branching *Acropora* reefs because, due to
239 their 'brittle tree' morphology, colonies that grow to project more than a metre or two above
240 their surroundings will inevitably collapse (Maragos 1972; Bak 1976; Fig. 9). This is not
241 necessarily a disadvantage. Because broken fragments can survive and grow to form new
242 colonies, fragmentation is recognised as an inherent and significant mode of reproduction and
243 short range dispersal in branching *Acropora* (Gilmore and Hall 1976; Tunnicliffe 1981;
244 Bothwell 1982; Highsmith 1982). Collapse is represented in a branching coral model by

245 imposing a maximum height differential between neighbours (hereafter termed collapse limit)

246 of two metres, such that corals growing to project two metres above any neighbouring cell are

247 prevented from growing upward until the deeper cell grows. Although they cannot grow

248 upward, projecting corals contribute to the growth probability of neighbouring cells in two

249 ways: first, they 'support' neighbouring corals, ensuring they are unrestricted by the collapse

250 limit, and second they may 'collapse into' deeper neighbouring cells (i.e. they increase the

251 neighbour probability of those cells). Although this representation of collapse involves no

252 subtraction of height from the collapsing colony, it remains valid because it is equivalent to

253 the projecting colony growing a metre then collapsing back a metre during the iteration.

254

255 Reefs created with the branching coral model closely resemble the Abrolhos cellular reefs

256 (Fig. 10). The model reproduces the characteristic egg carton form of the real reefs and all its

257 corollaries including circular reefs, stellate reefs with radiating ridges, scalloped platform

258 margins, bowl-shaped depressions and the presence of multiple small depressions within

259 larger multi-lobed depressions. The 45° reef slopes of the model reefs are steeper than the

260 mean of the real *Acropora* slopes (37° ± SD 6°) but within their recorded range.

261

262 Fig. 11 shows sequential stages in the development of the branching coral reefs,

263 demonstrating the emergence of their egg carton form. The key process is the formation of

264 ridges between adjacent patch reefs. This process begins when the patch reefs meet,

265 whereupon the valleys between them grow rapidly upward to become saddle-shaped ridges

266 (Fig. 11C and D). The depressions surrounded by the reefs and ridges are initially irregular in

267 outline but are progressively smoothed to subcircular shapes as the surrounding reef grows.

268 Eventually the depressions become completely enclosed within the reef platform and infilled

269 by coral (Fig. 11E).

270

271 Progressively relaxing the collapse limit produces intermediate forms between the branching

272 and random models. A three metre collapse limit creates reefs with weakly developed

273 subcircular depressions (Fig. 12A and B) and a four metre collapse limit creates reefs with

274 very few depressions (Fig. 12C and D). Collapse limits of more than four metres produce

275 nodular reefs equivalent to those of the random model.

276

277 We examined the morphological effects of several variations to the model, including altering

278 depth (Fig. S1), altering colonisation density (Fig. S2), and incorporating sea level rise and

279 depth-dependent accretion (Fig. S3). With respect to the cellular morphology, the most

280 influential modification was reducing water depth. Reducing depth reduces reef thickness,

281 which constrains the morphological expression of the collapse limit such that the appearance

282 of the branching coral reefs transforms from cellular to nodular as depth decreases. In the

283 extreme case of reefs grown in only one or two metres water depth, where the collapse limit

284 has no effect, all variants of the model produce identical nodular reefs.

285

286 **Discussion**

287 **Model**

288 The resemblance in shape and form between the model branching coral reefs and the

289 Abrolhos cellular reefs suggests that the model adequately represents reality. This

290 interpretation is supported by the model's simplicity: it has only one rule—collapse if too

291 steep—which is intuitively reasonable and supported by field observations. Model reef

292 morphology is hyper-sensitive to that rule, running through a nodular to cellular spectrum as

293 permissible steepness is reduced and collapse becomes more frequent.

294

295 The nodular reefs produced by the random model appear straightforward and visually

296 'correct' as growth forms, because the individual patch reefs maintain their forms as they

297 grow and merge. This straightforward morphology is indicative of pure in-situ (in place)

298 growth. Cellular reefs are more complex because the patch reefs transform as they merge,

299 eventually becoming linked by a network of ridges. This transformation results from the high

300 frequency of collapse in the branching coral model. However, it is not simply the frequency

301 of collapse that produces ridges; more important is the distribution of collapse. Because the

302 valleys between merging patch reefs are low points in the reef structure, coral colonies in the

303 valleys are less likely to project above their neighbours than corals elsewhere. Consequently,

304 they are relatively unrestricted by the collapse limit and are therefore more likely to remain in

305 place as they grow, and less likely to collapse, than colonies elsewhere (Fig. 13). The

306 retention of in-situ colonies transforms the V-shaped valleys into U-shaped ridges that grow

307 to sea level, enclosing depressions (Fig. 11C and D). The subcircular shapes of the

308 depressions arise through the same non-uniform distribution of collapse. Colonies in the re-

309 entrant concavities of the early-stage depressions are supported by neighbours and therefore

310 tend to remain in place while those on projecting convexities tend to collapse. Over time this

311 creates smooth rounded shapes, the ultimate smooth shape being a circle.

312

Abrolhos cellular reefs

The foregoing descriptions of the model branching coral reefs provide two testable predictions regarding real cellular reefs. First, their slopes should have a consistent and relatively low gradient, representing the angle of repose (maximum slope stability angle) of branching *Acropora*. Second, the proportion of collapsed colonies should be lowest in the valleys and ridges and highest on reef slopes. Both predictions are supported in the Abrolhos, where *Acropora* slopes average 37° ± SD 6° (Fig. 4) and *Acropora* colonies in valleys and ridges are generally upright (Fig. 5) while those on reef slopes are often overturned (Fig. 9). We conclude that the Abrolhos cellular reefs have developed according to the model and that Fig. 11 closely describes their morphological progression.

One significant difference between the real and model reefs is the reduced accretion rate of the real reefs once they reach sea level. Model reefs first reach sea level in approximately 100 iterations and only require 60 more iterations to fill the platform, whereas the Maze reefs first reached present sea level in approximately 4000 years (Eisenhauer et al. 1993; Collins et al 1993) but still have not filled the platform 7000 years later. The reduced accretion of the real reefs probably results from two factors not represented in the model. The first is the reduction of *Acropora* cover and vitality at depth as water circulation is restricted by the enclosure of the depressions (Wyrwoll 2006). This is an example of self-limitation through negative feedback between reef growth and water circulation (Blanchon 2011). Self-limitation is therefore a significant influence on the Abrolhos cellular reefs, but operates primarily on their accretion rate not their morphology. The second factor is the colonisation of upper depression slopes by relatively slow-growing massive and encrusting corals. The steep walls created by these corals effectively exclude branching *Acropora*, because any branching *Acropora* that colonise the walls are likely to fall off once they grow too large to be supported by their basal attachment. By 'engineering' steep walls (*sensu* Jones et al. 1994), massive and encrusting corals monopolise—for thousands of years—prime shallow subtidal habitat that would otherwise be occupied by fast-growing branching *Acropora*. The combination of reduced water circulation at depth and steep walls in the shallows restricts live *Acropora* to a fraction of their previous distribution, significantly slowing the overall reef accretion rate. Model cellular reefs, in contrast, rapidly fill the platform because 'live' *Acropora* occupy all habitats including the depression slopes and floors.

346 Another significant difference between the real and model reefs is the series of linear reef

347 banks on the northern margin of the Maze. We interpret these as early to mid Holocene wave-

348 deposited structures, resulting either from extratropical storms, cyclones (Scheffers et al.

349 2012) or tsunami (Scheffers et al. 2008).

350

351 **Application to other reefs**

352 The morphology of cellular reefs elsewhere appears similar enough to the Abrolhos reefs to

353 suggest they have developed the same way, an inference supported by the abundance of

354 branching *Acropora* in documented examples (Alacran Reef: Hoskin 1963; Solomon Islands:

355 Morton 1974; Cocos-Keeling Atoll: Williams 1994; Pelican Keys: Aronson et al. 1998;

356 Elizabeth Reef: Woodroffe et al. 2004; Pohnpei: Turak and DeVantier 2005; Tun Sakaran:

357 Montagne et al. 2013; Palau-no reference yet; Nagura Bay: Kan et al. 2014). At least two of

358 these examples, the Solomon Islands (Morton 1974) and Nagura Bay (Kan et al. 2014),

359 exhibit vertical walls of massive and encrusting corals above the *Acropora* zone, suggesting

360 they have undergone the late-stage shallow coral community succession observed in the

361 Abrolhos.

362

363 We have separated Mataiva Atoll from the list above as *Porites* is abundant there and has

364 been considered responsible for the cellular morphology (GIE Raro Moana 1985; Delesalle

365 1985). However, branching *Acropora* are also abundant at Mataiva (Delesalle 1985;

366 Rossfelder 1990). We suggest that branching *Acropora* are the primary reef-builders at

367 Mataiva and *Porites* are colonisers of the *Acropora* reef, not framework builders. Another

368 possible exception to the rule of *Acropora* dominance is the 'Type-1' reticulate reef of the

369 Red Sea (Purkis et al. 2010) where *Porites* is also abundant (Bruckner 2011). However, we

370 would not classify all Type-1 Red Sea reefs as cellular because, although deep, the

371 depressions are not always circular, more often resembling the transitional depressions

372 produced by intermediate collapse limits (see Purkis et al.'s Fig. 2). Some Red Sea reefs are

373 distinctly cellular and we predict those to be *Acropora*-dominated (e.g. 27°57'N, 35°13'E).

374 Closer examination of these and other cellular reefs is required to determine whether the

375 predominance of branching *Acropora* is universal, and whether the slope gradients and the

376 distribution of collapsed colonies conform to the Abrolhos example.

377

378 We have not classified the previously-mentioned Millenium Atoll with the cellular reefs

379 listed above because the scale of the cellular morphology at Millenium and in many other

380   Pacific atoll lagoons is up to an order of magnitude larger than the Abrolhos. While the large-

381   scale cellular reefs also seem to consist predominantly of branching *Acropora* (Roy and

382   Smith 1971; Grovhoug and Henderson 1973; Valencia 1977; Barott et al. 2010), we do not

383   believe our model applies directly to them because it cannot produce cells of their dimensions

384   unless it is scaled up massively, to unrealistic depths of at least 100 m. We are currently

385   investigating the large-scale cellular morphology.

386

387   The intermediate to nodular shapes produced in the model are common in real reefs (e.g. Fig.

388   14). The simplest interpretation of these shapes is that they indicate coral types, or mixtures

389   of coral types, progressively less prone to collapse than branching corals. In this

390   interpretation, nodular shapes (i.e. circular in plan view) represent reef builders that rarely

391   collapse, such as massive and encrusting corals or coralline algae. However, the model

392   indicates that intermediate to nodular shapes are not necessarily diagnostic of coral type,

393   because even branching coral patch reefs appear nodular before they merge with adjacent

394   patch reefs, and after they merge in shallow water. This suggests that additional information

395   on water depth, reef slope gradients and reef thickness will be required to reliably infer

396   ecology from morphology in intermediate to nodular reefs. Such three-dimensional data is

397   becoming increasingly available through reef-oriented remote sensing (Goodman et al. 2013

398   and references therein). In two-dimensional aerial images, however, the only diagnostic

399   morphology is cellular—signifying relatively thick ($\geq$~10m) reefs constructed by collapse-

400   prone organisms.

401

402   The default collapse-prone reef builders on modern reefs are branching *Acropora*. While it

403   seems possible for other branching coral genera or other calcareous branching invertebrates

404   (e.g. *Millepora*) to create cellular reefs, observations worldwide (listed above) suggest it is

405   invariably *Acropora*: *A. cervicornis* in the Caribbean and multiple species in the Indo-Pacific.

406   This is probably because branching *Acropora* have the ultimate strategy for rapid pre-

407   emption of space in lagoon environments. *Acropora* branches not only grow quickly (up to 19

408   cm.yr^{-1} in the Maze; Blakeway 2000), they regularly develop new branches which themselves

409   branch and rebranch, giving them the potential for exponential expansion (Shinn 1976).

410   Constant growth and branching produces an open three-dimensional structure that allows

411   *Acropora* to rapidly fill lagoons. Our model indicates that, given adequate depth, cellular

412   reefs are the inevitable result. Cellular reefs are essentially a phenotype of the branching

413 *Acropora* genome(s), emerging from the innate behaviour of branching *Acropora* colonies

414 just as colony morphology emerges from the innate behaviour of polyps.

415

416 If the relationship between cellular reef morphology and branching *Acropora* holds, the

417 distinctive shapes of cellular reefs in remotely-sensed images can potentially be used to

418 identify and map branching *Acropora* habitat. This could be useful in reef health assessments,

419 as the sensitivity of branching *Acropora* to environmental conditions makes them something

420 of a canary in the coral reef coalmine (Loya et al. 2001; Roth and Dehyn 2013). However,

421 care should be taken in attributing cause and effect in apparently degraded *Acropora*-

422 dominated lagoons because natural self-limitation and community succession can drastically

423 reduce *Acropora* cover and vitality in the mid to late stages of reef development. Before

424 assessing anthropogenic impacts, careful work may be required not only to understand natural

425 intrinsic environmental and successional change but also to determine if and how the reef

426 community may have been modified by less predictable natural extrinsic influences (Aronson

427 et al. 1998).

428

429 **Conclusions**

430 Our research indicates that the fundamental control on reef morphology is the nature of the

431 reef building organisms. This control is best expressed in lagoons, where diminished

432 hydrodynamic and substrate influences allow reefs to grow into their inherent forms. The

433 purest growth forms arise where a single type of reef builder prevails, as in the cellular reefs

434 of the Abrolhos. In these cases reef morphology can be considered a phenotype of the

435 predominant reef building organism.

436

437 The extent to which reef building organisms either remain in place or collapse appears to

438 explain the nodular to cellular spectrum of lagoon reef morphology. Many more relationships

439 between reef ecology and morphology remain to be discovered. Most of the recurrent patterns

440 in reef morphology, including the large-scale cellular reefs and anastomosing reefs, are likely

441 to be partly or wholly ecological phenomena (Blanchon 2011; Schlager and Purkis 2014).

442 Investigation of these relationships is benefiting from the increasing availability and

443 resolution of remotely sensed imagery. However, the single most important research

444 technique remains careful underwater observation, preferably without any preconceptions

445 regarding process. Any consistent correlations between reef morphology and underwater

446 survey data, such as coral type, can be considered potential causal relationships warranting

447 closer examination.

448

449 In surveying modern reefs it should be recognised that a reef's current state may not represent

450 its formative Holocene (or earlier) state, particularly if the reef has reached sea level. While

451 seismic and coring can access the history stored within such reefs, both techniques are

452 logistically demanding and expensive. The complementary methods we employed in the

453 Abrolhos, space-for-time substitution and computer simulation, are relatively simple and

454 inexpensive but can provide a comprehensive reconstruction of a reef's history and a sound

455 basis for extrapolating its future development.

456
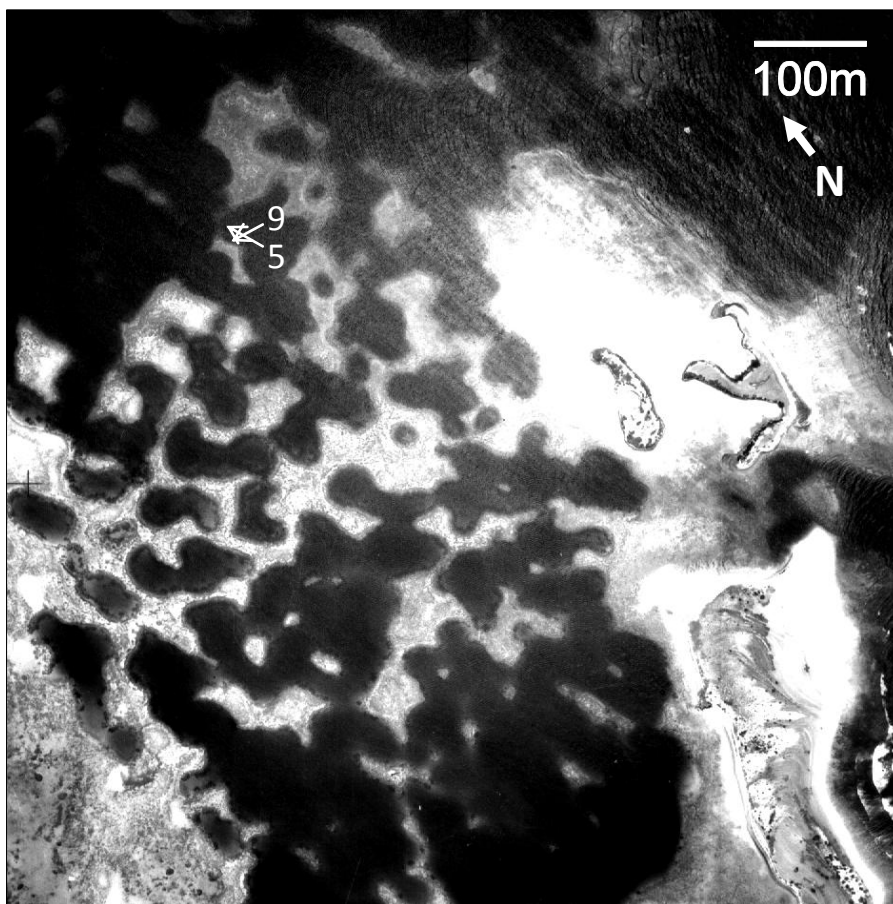
Figure 1. Cellular reefs in the northeastern lagoon of the Pelsaert Group, Houtman Abrolhos Islands, 28°54'S 114°E. Islands of storm-deposited coral rubble line the eastern platform margin. The numbers at top left refer to subsequent figures and the direction of the arrows corresponds to the direction from which the figures (photographs) were taken. (note the arrows clash in the pdf conversion – to be fixed, maybe better as an enlarged inset?).

Figure 2. Aerial photograph of the Maze showing the 15 survey sites labelled A to O.
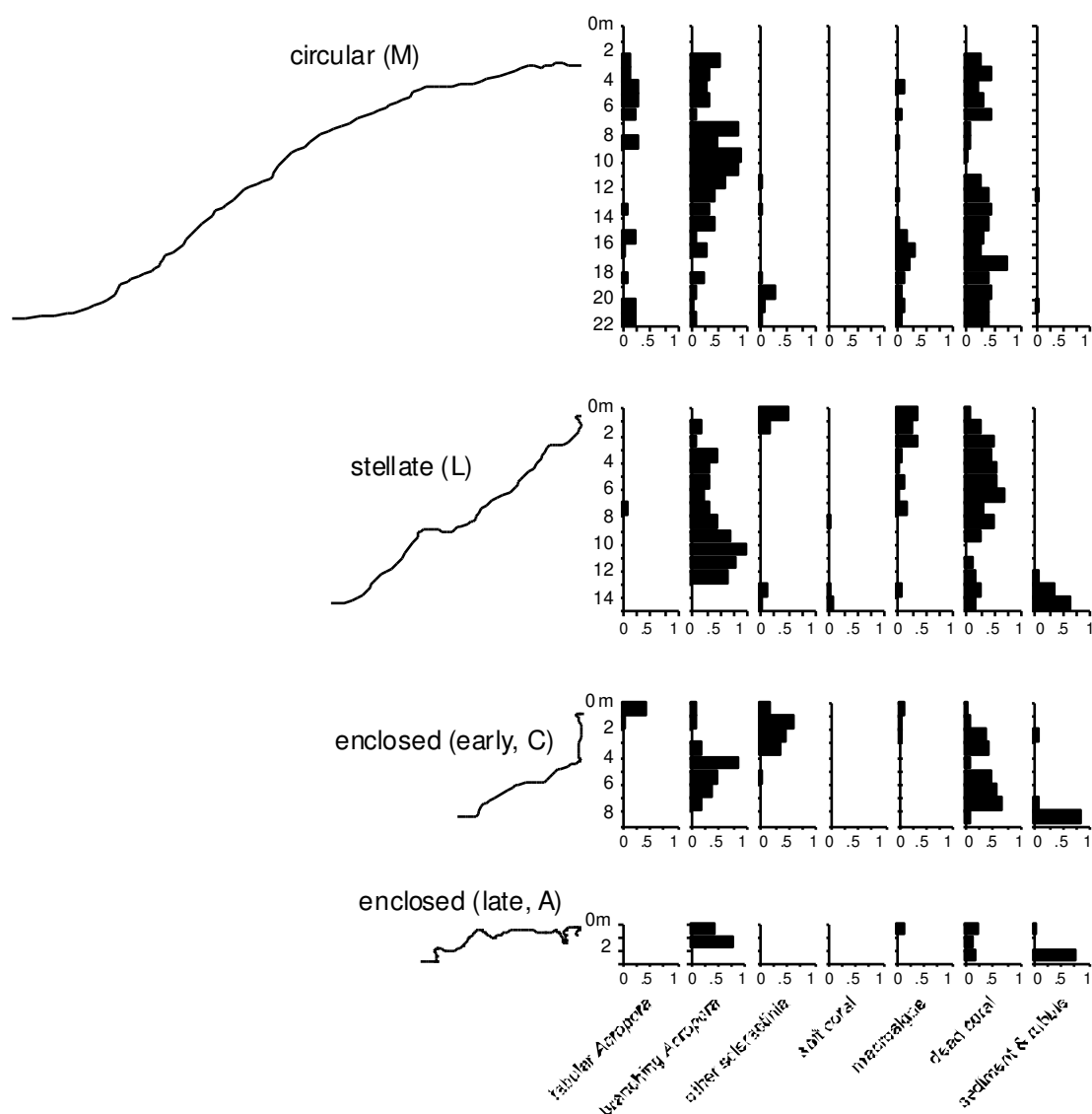
466
467 **Figure 3.** Representative transect profiles and substrate composition from sites of each stage.
468 The x-axis legend (text problem to be fixed) reads tabular *Acropora*, branching *Acropora*,
469 other scleractinia, soft coral, macroalgae, dead coral, sediment & rubble.
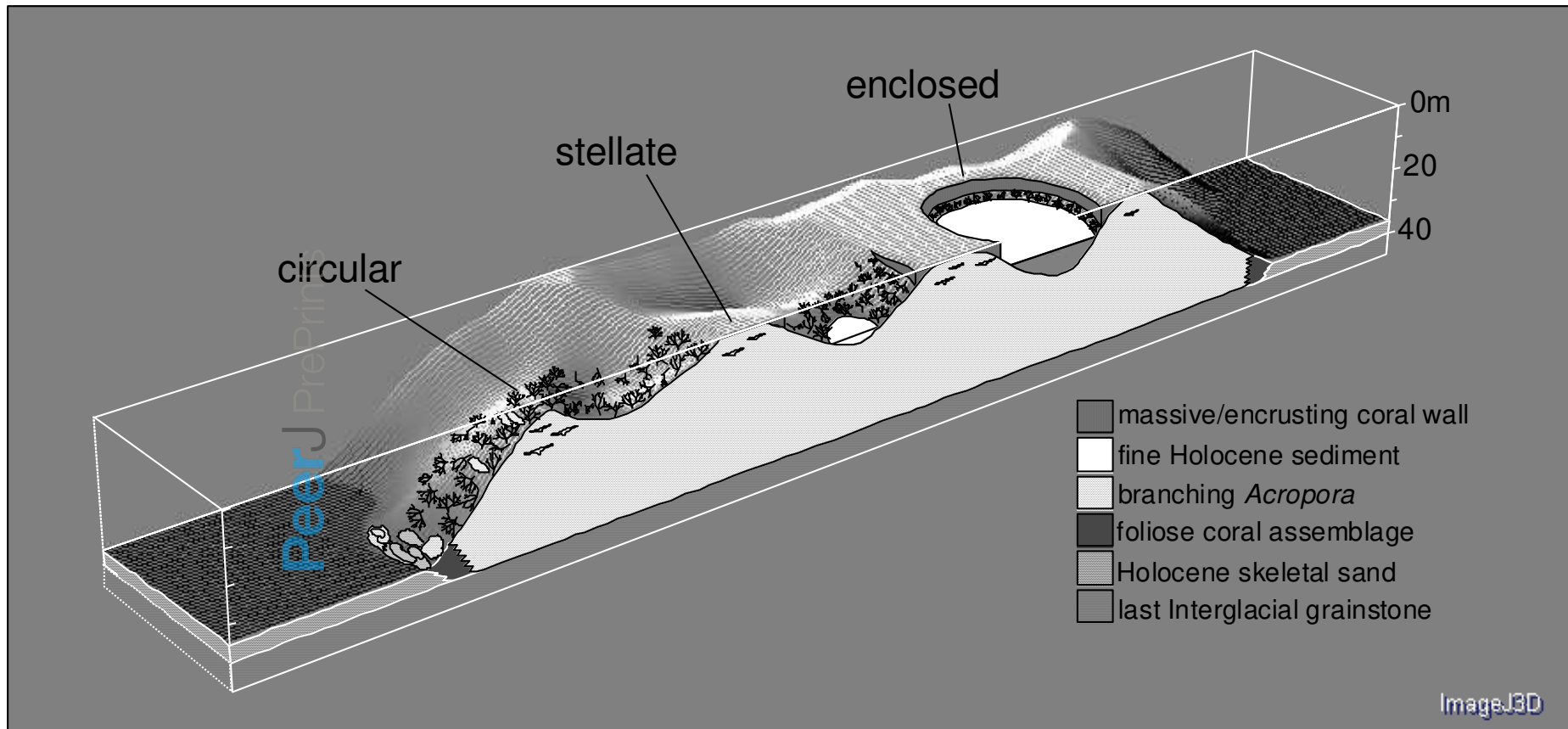
Figure 4. Block diagram illustrating the three idealised reef stages. The cross-section is hypothetical but consistent with survey observations and seismic/core data. (note this figure has come out poorly in pdf, the eps is better)

19

Figure 5. Dense branching *Acropora* on the ridge extending northeast from the stellate reef shown in Fig. 1.
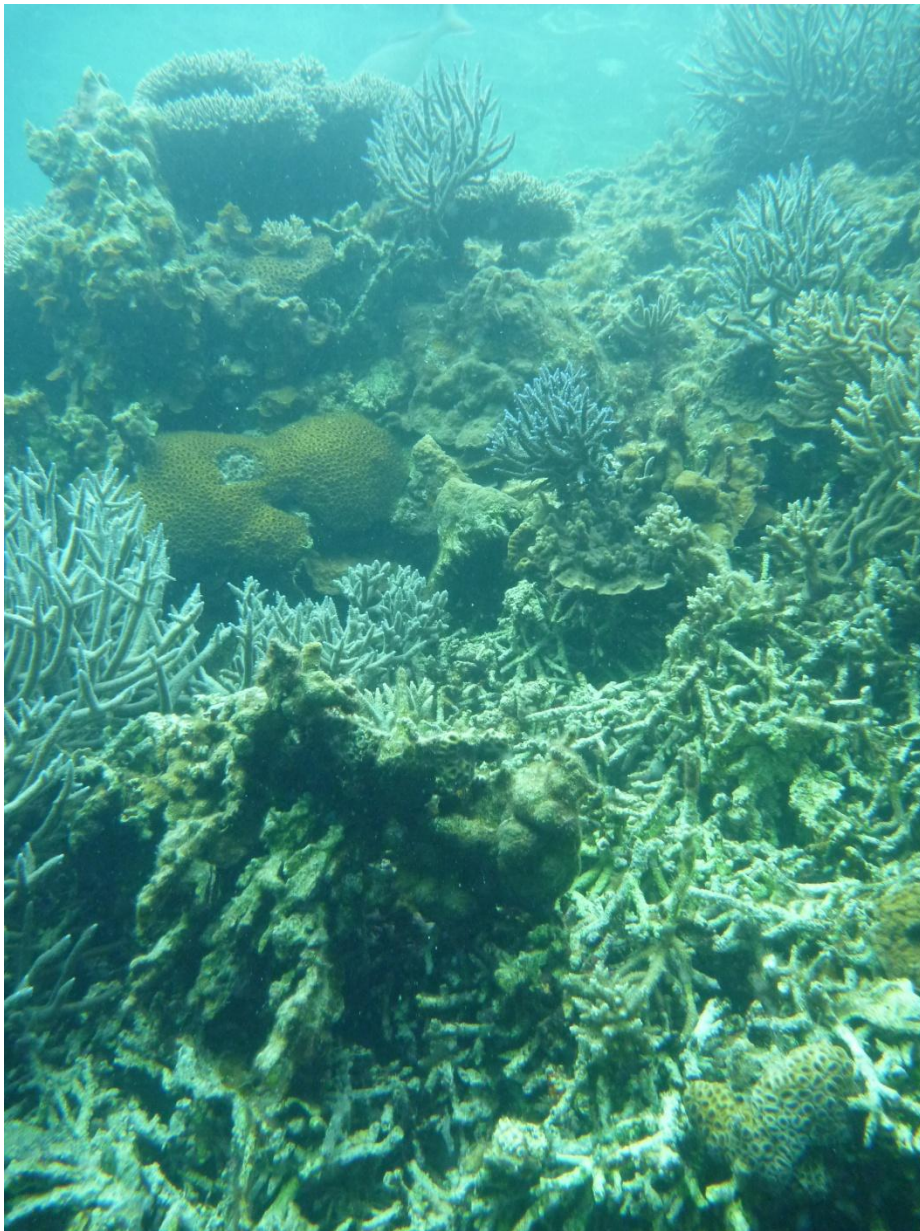
476
477 **Figure 6A.** Inferred early-stage of reef wall development, in which dead *Acropora* branches
478 are colonised by massive and encrusting corals.

479

Figure 6B. Inferred late-stage of reef wall development, in which massive and encrusting corals have grown to form a vertical wall.
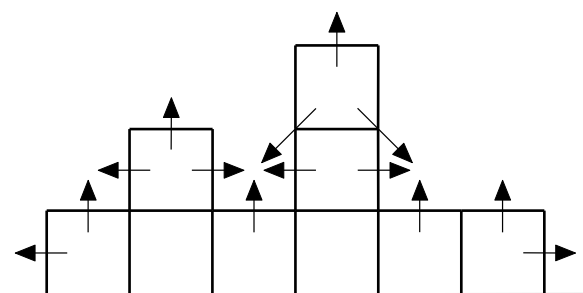
Figure 7. Cross-section through a hypothetical model reef. Upward-pointing arrows indicate vertical growth directions, horizontal and diagonal arrows indicate neighbour growth directions.

486

487
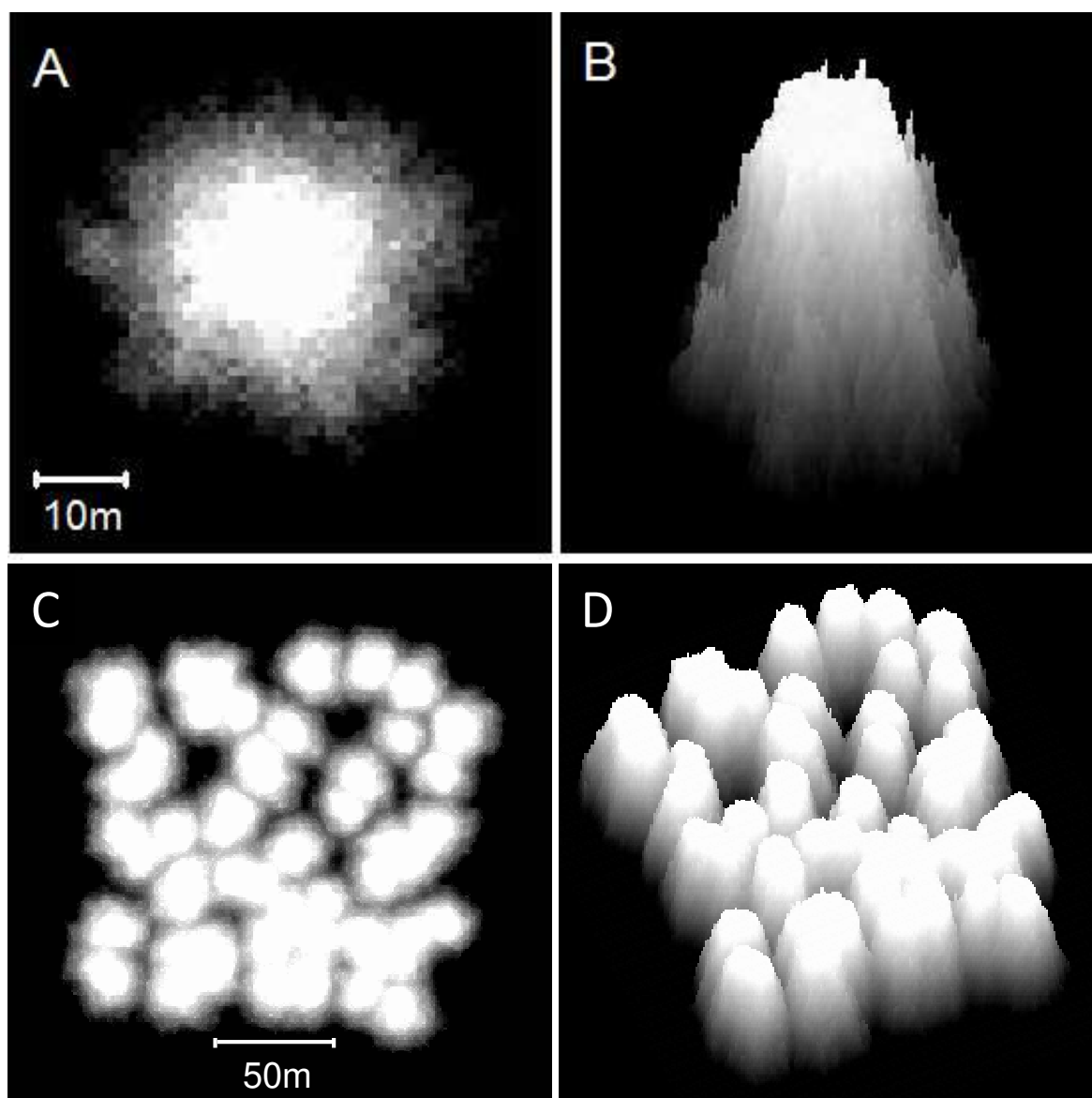
Figure 8. A) Two-dimensional plan view of a simulated patch reef after 80 iterations of
growth from a single seed coral using the random model. Shading corresponds to
depth—the reef top at sea level is white and the surrounding seafloor at 30m depth is
black. This patch reef reached sea level in approximately 45 iterations, and by 80
iterations has developed a 15m wide reef flat. **B)** Three-dimensional oblique view of the
patch reef in A. **C)** Two-dimensional plan view of multiple patch reefs after 80 iterations
of growth from 64 seed corals, occupying 0.25% of the 160 x 160m seed array. Only the
uppermost 10m of the reefs is shown, simulating an aerial view with 10m water
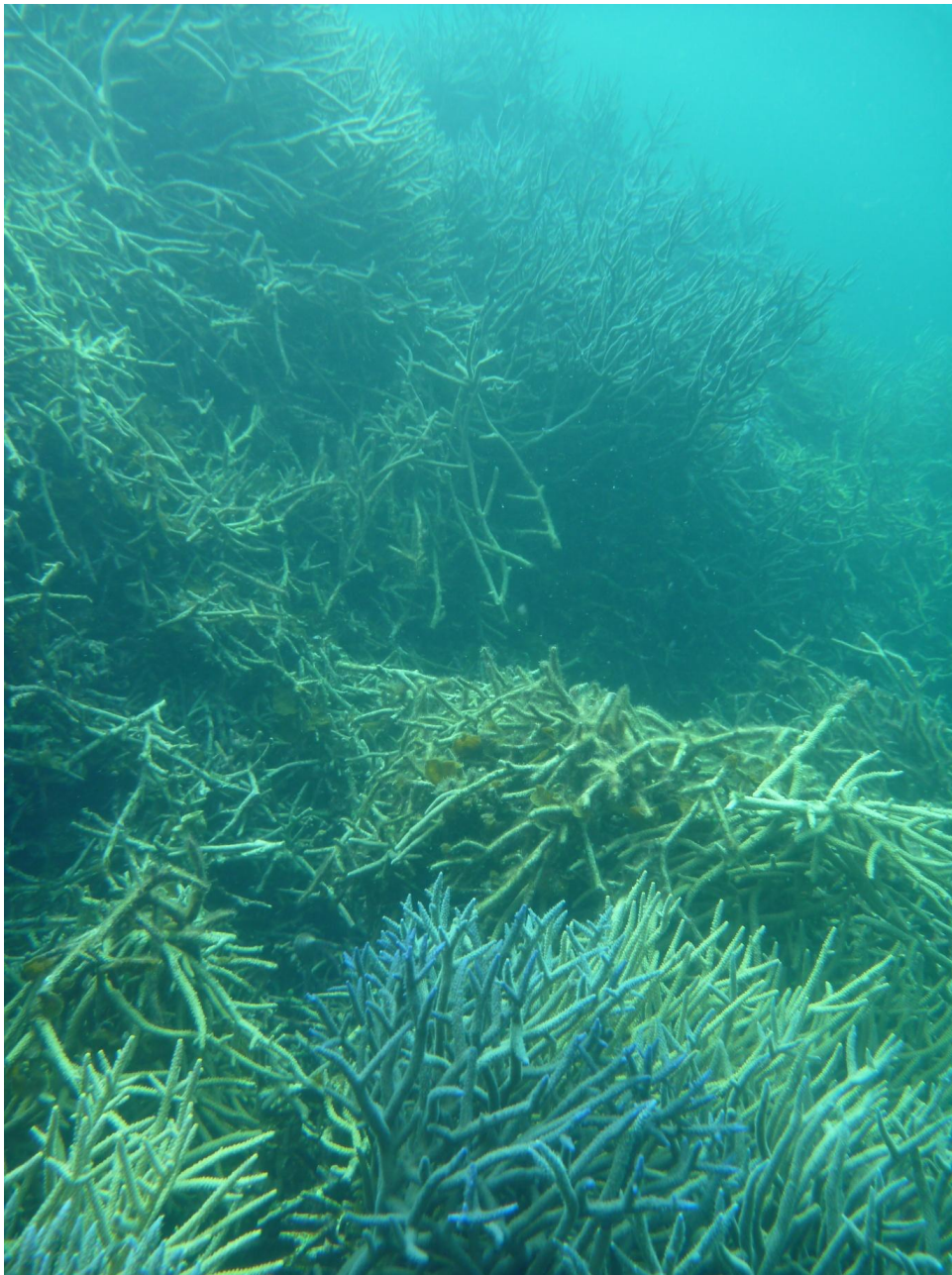visibility**. D)** Three-dimensional oblique view of the reefs in C.

497

Figure 9. Collapsed branching *Acropora* colonies on the slope of the stellate reef shown in
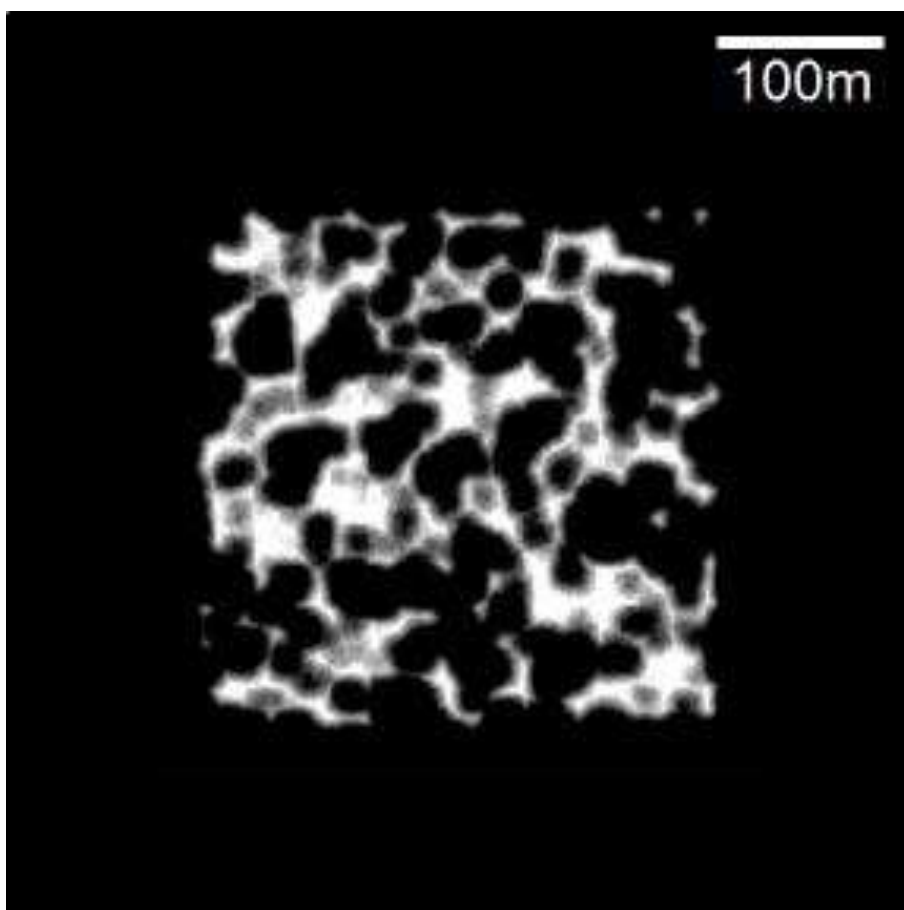
499   Fig. 1.

Figure 10. Plan view of a branching coral model reef after 100 growth iterations. Only the uppermost 10m of the reef is shown, simulating an aerial view with 10m water visibility. This reef developed from 225 randomly spaced seed corals, occupying 0.25% of a 300 x 300m seed array.
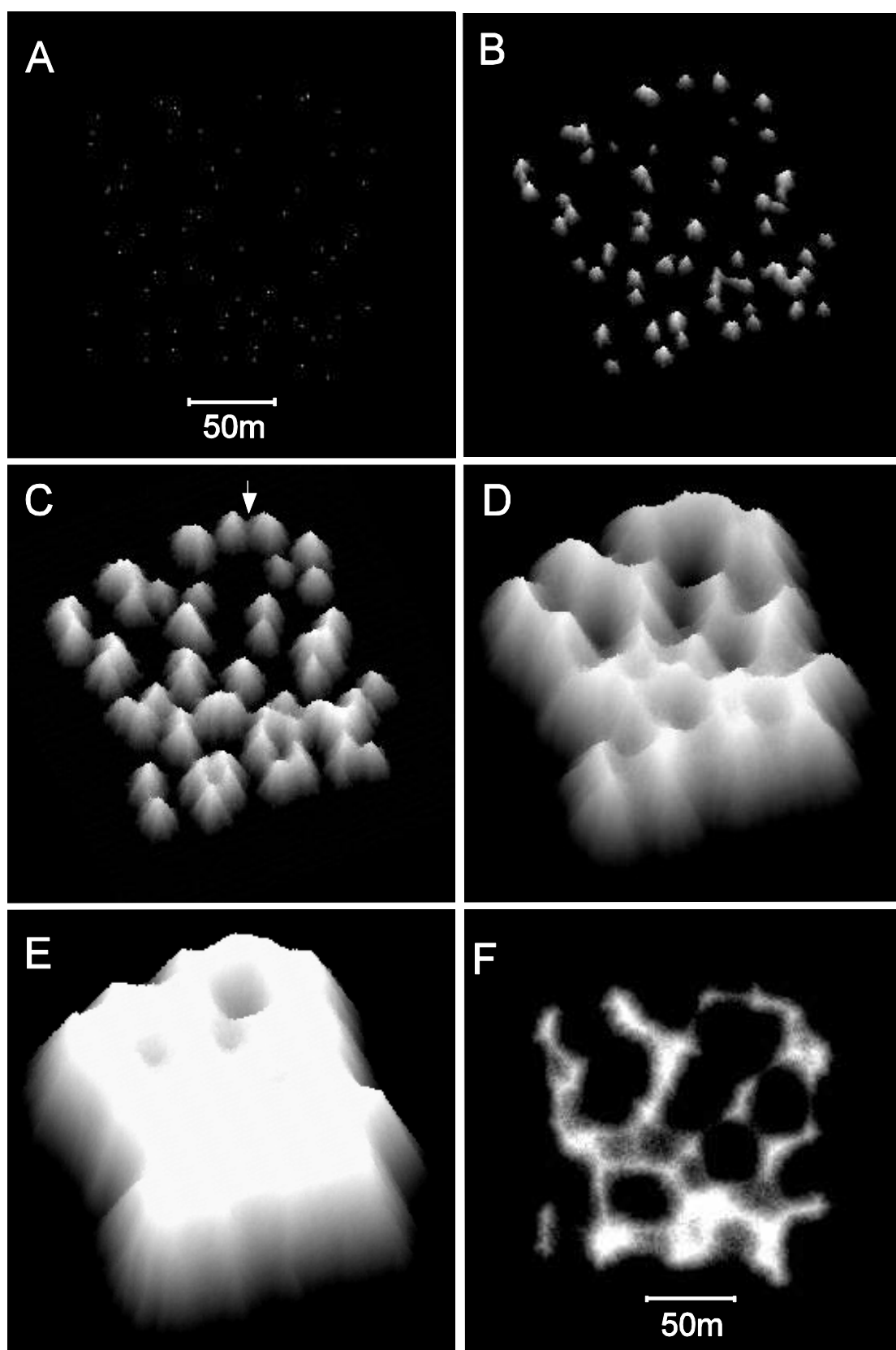
Figure 11. Sequential stages in the development of model branching coral reefs. **A**) The
set of 64 randomly spaced seed corals from which the model reefs developed. The seed
coral configuration is the same as that used to create the model reefs in Fig. 8C and D. **B**)
After 25 iterations the seed corals have developed into cone-shaped patch reefs with 45°

slopes. **C**) After 50 iterations the patch reefs have enlarged and many have merged. When patch reefs meet, the valleys between them grow upward rapidly to become saddle-shaped ridges (arrowed). **D**) After 100 iterations some of the reef tops have reached sea level and the system of ridges has developed to enclose and isolate depressions, producing egg-carton morphology. **E**) After 150 iterations an extensive sea level platform has developed, and most of the depressions have filled. **F**) Plan view showing the uppermost 10m of the reef in D, simulating an aerial view with 10m water visibility.
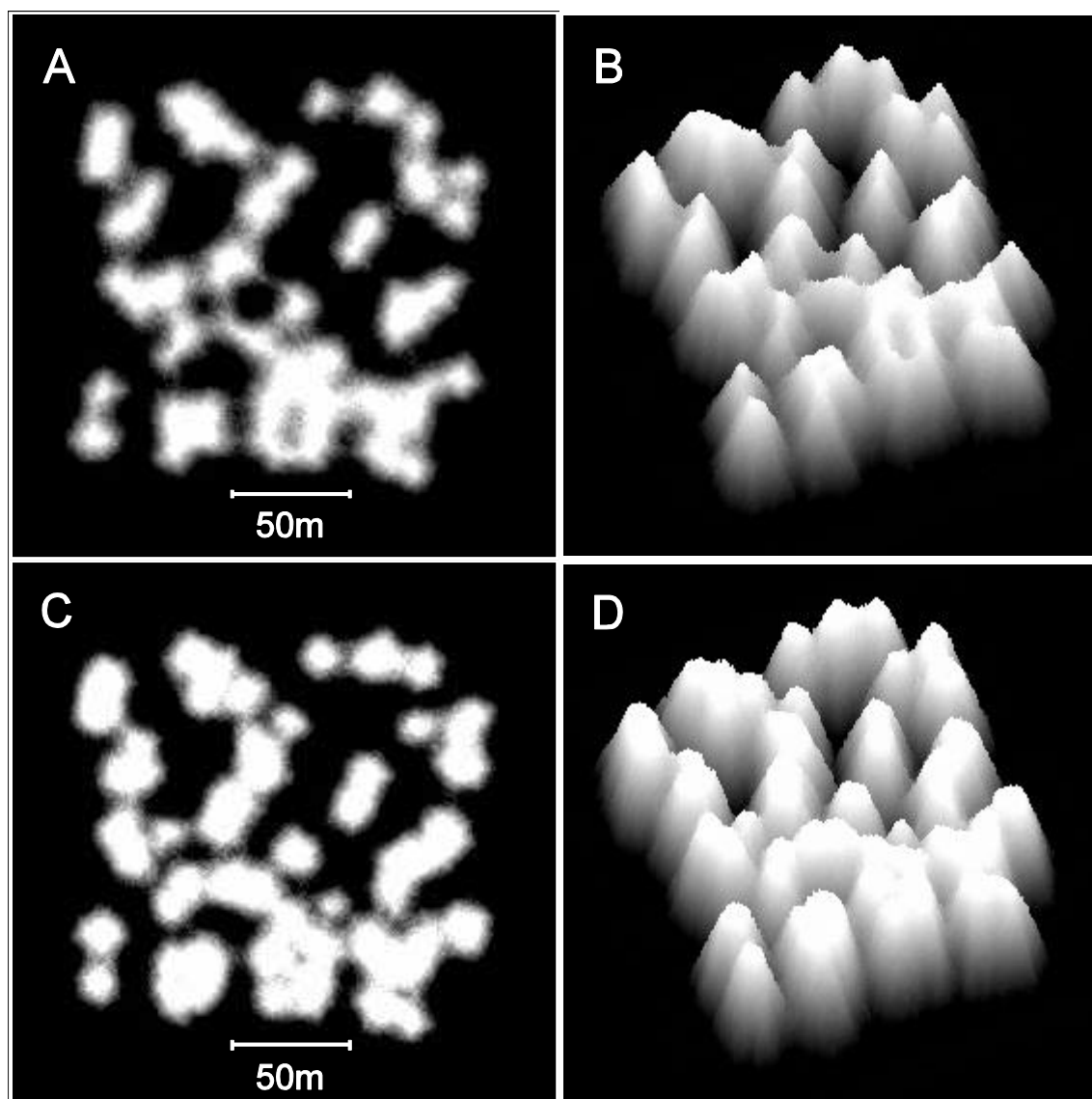

Figure 12. A) Plan view, 0-10m depth, of model reef with a 3m collapse limit after 90 growth iterations. **B**) Oblique view of the model reef in A. The reef slopes are approximately 55°. **C**) Plan view, 0-10m depth, of model reef with a 4m collapse limit after 85 growth iterations. **D**) Oblique view of the model reef in C. The reef slopes are approximately 60°.
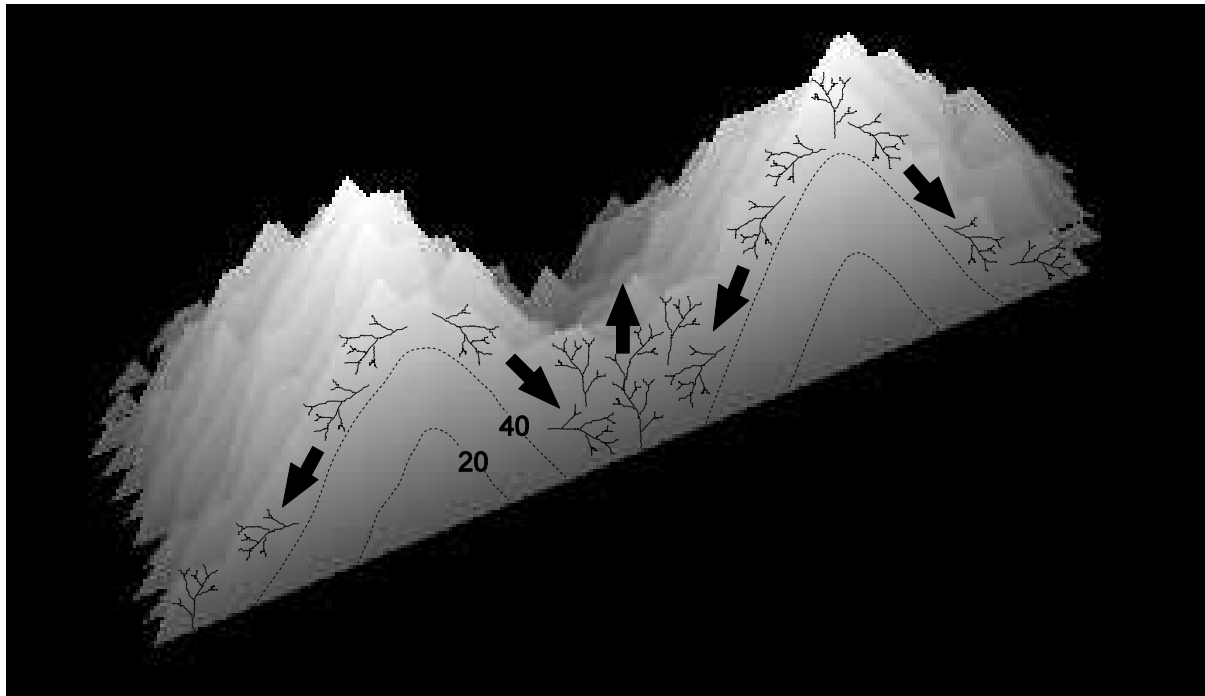
Figure 13. Schematic diagram illustrating the proposed mechanism of ridge formation derived from the branching coral model. The diagram shows a cross-section through two patch reefs after 50 iterations (the patch reefs at the top of Fig. 11C). Isochrons at 20 and 40 iterations show that the patch reefs were initially conical, and that the valley between them has accreted rapidly since the patch reefs merged.

Figure 14. Coalescing nodular patch reefs exposed on a low spring tide at Cockatoo Island, Western Australia. These are 'true' nodular reefs, consisting of massive and encrusting corals and having a steep-walled columnar form (D. Blakeway, pers. obs.). Photograph by John MacFadyen.

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