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Self-generated morphology in lagoon reefs

The three-dimensional form of a coral reef develops through interactions and feedbacks between its constituent organisms and their environment. Reef morphology therefore contains a potential wealth of ecological information, accessible if the relationships between morphology and ecology can be decoded. Traditionally, reef morphology has been 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. 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. The purest reef growth forms arise in sheltered lagoons dominated by a single type of reef builder, as in the branching *Acropora*-dominated lagoons of the Abrolhos. In these situations reef morphology can be considered a phenotype of the predominant reef building organism. The capacity to infer coral type from reef morphology can potentially be used to identify and map specific coral habitat in remotely sensed images. More generally, identifying ecological mechanisms underlying other examples of self-generated reef morphology can potentially improve our understanding of present-day reef ecology, because any ecological process capable of shaping a reef will almost invariably be an important process in real time on the living reef.

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13

14 **Introduction**

15 Coral reefs are large organic structures created over centuries to millennia by relatively small
16 individual organisms. The anatomy of coral reefs varies along a continuum from ‘framework’ reefs
17 consisting of coral skeletons in growth position (Lowenstam 1950; Fagerstrom 1987) to ‘garbage piles’
18 of toppled corals, coral fragments and sediment (Hubbard, Miller & Scaturro 1990; Blanchon, Jones &
19 Kalbfleisch 1997). The three-dimensional form of a reef, particularly a framework reef, is a potential
20 repository of ecological information, because it represents a long-term integration of interactions and
21 feedbacks between the reef-building organisms and their physical, chemical and biological
22 environment (Roberts et al. 1975; Hopley, Smithers & Parnell 2007; Perry 2011). Reef form can
23 perhaps also be considered a distillation of those interactions and feedbacks, in that the most influential
24 processes in the history of the living reef could be expected to leave the greatest imprint on its
25 morphology. Investigating the ecological mechanisms underlying aspects of reef morphology can
26 therefore help provide a context for interpreting present-day ecological processes on reefs (Hopley,
27 Smithers & Parnell 2007).

28
29 The primary influences on reef morphology differ across spatial scales, from the inherent forms of
30 reef-building organisms at the small scale to the configuration of continental shelves at the large scale.
31 Over intermediate scales (metres to kilometres) reefs exhibit a great diversity of forms, reflecting the
32 multitude of interacting processes affecting them. But within the diversity is a subset of globally
33 recurring forms, indicating that there are some consistent influences governing reef morphology
34 worldwide (Wells 1957, Stoddart 1969; 1978; Goreau, Goreau & Goreau 1979; Blanchon 2011;
35 Schlager and Purkis 2015). Traditionally, these influences have been envisaged as external controls
36 operating at or above the scale of the morphological features, for example substrate topography
37 (MacNeil 1954, Purdy 1974; Choi & Ginsburg 1982) or the wave field (Munk & Sargent 1954; Roberts
38 1974). While these factors are undoubtedly responsible for many aspects of reef morphology, they
39 raise an interesting question: what would reefs look like in the absence of such external influences?
40 This question brings the focus down to the reef-building organisms themselves. Because these
41 organisms cumulatively become the reef, there is significant potential for behaviour and events at their
42 scale to be expressed in reef morphology at the intermediate scale. Such ‘emergence’ of self-organised
43 patterns from small scale processes is ubiquitous in physical and biological systems (Nicolis and
44 Prigogine 1977; Camazine et al. 2001). While it is recognised that coral reefs are likely to exhibit this

45 trait (Drummond and Dugan 1999; Mistr and Bercovici 2003; Rietkirk and van de Koppel 2008;
46 Blanchon 2011; Schlager and Purkis 2015), it has not been directly demonstrated.

47

48 Lagoons are the most likely setting for inherent reef growth forms to arise, as they are generally flat-
49 floored and sheltered. Several characteristic lagoon reef forms are repeated worldwide, ranging from
50 simple mound-like patch reefs to complex cellular¹ reef networks (Fig. 1; Stoddart 1969; Hopley 1982;
51 Blanchon 2011). Patch reef development can be readily visualised in terms of expansion from a
52 nucleus, and this mode of growth has been demonstrated repeatedly, from various nuclei including
53 topographic highs in underlying limestones (Halley et al 1977; Mazzullo et al. 1992), sedimentary
54 structures (Perry et al. 2012; Novak et al. 2013), or early-colonising corals (Jones 1977; Crame 1981).
55 Cellular morphology, in contrast, is not an intuitive growth form. Cellular reefs distinctly resemble
56 negative landforms, particularly karst terrains (terrestrial erosion landforms created in limestone
57 through dissolution by rainwater). Based on this resemblance, and the recognition that the foundations
58 of most reefs have been exposed to at least 100,000 years of weathering during Interglacial periods,
59 cellular reef morphology has long been interpreted as an inheritance from underlying karst (Fairbridge
60 1948; Purdy 1974; Guilcher 1988; Searle 1994; Macintyre, Precht & Aronson 2000; Purkis et al. 2010;
61 Kan et al. 2015). However there has always been an opposing view attributing cellular morphology to
62 reef growth (Dakin 1919; GIE Raro Moana 1985; Collins et al. 1993; Wyrwoll et al. 2006; Barott et al.
63 2010; Blanchon 2011; Schlager and Purkis 2015). The growth alternative is gradually gaining
64 acceptance, having been confirmed for the cellular reefs of Mataiva Atoll in French Polynesia (GIE
65 Raro Moana 1985; Rossfelder 1990) and the Houtman Abrolhos Islands in Western Australia (Collins
66 et al. 1993; Collins, Zhu & Wyrwoll 1996; 1998; Wyrwoll et al. 2006). Seismic surveys and coring at
67 Mataiva showed the Holocene reef to be 10 to 20 m thick and demonstrated that, although the reef is
68 underlain by a karst Tertiary limestone, the karst features are relatively small-scale and were infilled
69 before submergence, such that the present reef morphology is independent of the substrate (Rossfelder
70 1990). Similarly, seismic and coring in the Abrolhos lagoons recorded a Holocene reef thickness of 40
71 m over a flat Last Interglacial grainstone, again demonstrating independence from the substrate
72 (Collins et al. 1993; Collins, Zhu & Wyrwoll 1996; 1998).

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, the term reticulate has been applied to a variety of lagoon reef forms that probably develop through different mechanisms (Schlager and Purkis 2015). Therefore we consider cellular reefs to be a subdivision of reticulate reefs, distinguished by subcircular depressions as shown in Fig. 1.

73

74 While the seismic and coring work has proven beyond reasonable doubt that the cellular reefs of
75 Mataiva and the Abrolhos have grown into their present configuration, it has not provided a generally
76 accepted growth mechanism. Four alternative mechanisms have been proposed. The first, developed
77 independently by GIE Raro Moana (1985) at Mataiva and Barott et al. (2010) at Millenium Atoll, is the
78 colonisation of the lagoon floor by networks of massive corals, which are subsequently colonised by
79 other corals and grow upward to the surface. The second, proposed by Wyrwoll et al. (2006) for the
80 Abrolhos, is growth to sea level of isolated branching *Acropora* pinnacles and stellate (star-shaped)
81 reefs, which subsequently extend laterally and coalesce to surround enclosed depressions. The third,
82 proposed by Blanchon (2011), is a self-limitation mechanism based on negative feedback between reef
83 growth and water circulation—reef growth reduces water circulation which reduces reef growth, such
84 that the cellular depressions become self-reinforcing as the surrounding reefs grow. The fourth
85 mechanism, proposed by Schlager and Purkis (2015) is biological self-organisation through short-range
86 support and long-range inhibition, conceptually based on Turing's (1952) reaction-diffusion
87 mechanism of natural pattern formation.

88

89 The alternative mechanisms outlined above are hypothetical and have not been comprehensively
90 evaluated on real cellular reefs. In this article we use field observations and reef growth simulations to
91 examine the process of cellular reef development in one of the type examples of cellular reefs
92 mentioned above, those of the Houtman Abrolhos Islands. These reefs are an ideal case study site due
93 to their flat pre-Holocene substrate, known accretion history and very pure reef-building community—
94 cores through the Abrolhos cellular reefs consist almost entirely of branching *Acropora*, with a few
95 tabular *Acropora* appearing as the reefs approached sea level (Collins et al. 1993; Collins, Zhu &
96 Wyrwoll 1996; 1998). Furthermore, an apparent sequence of cellular reef development is evident in the
97 Abrolhos lagoons (Wyrwoll et al. 2006), progressing from pinnacle reefs to stellate reefs surrounding
98 semi-enclosed depressions to a reef platform surrounding enclosed depressions. Under the assumption
99 that these are sequential stages of reef development, surveys of the pinnacle-stellate-platform sequence
100 represent surveys through time. Space-for-time substitution (Darwin 1842; Maxwell 1968; Hopley
101 1982) can therefore be applied to describe the evolution of the Abrolhos cellular reefs and, potentially,
102 to reveal their formative mechanism.

103

104 **Reef survey**

105 **Methods**

106 We examined replicate sites of each stage in a 15 km² cellular reef complex known as the Maze in the
107 Easter Group of the Abrolhos (Fig. 2; 28°41'S, 113°49'E). We surveyed fifteen sites in detail and many
108 more in brief visits, including some in the Pelsaert Group to the south and the Wallabi Group to the
109 north. At each of the fifteen Maze sites we established four transects oriented to the cardinal directions,
110 running upslope from the deepest to shallowest habitat. Transects varied in length from 5 m at site A
111 (maximum depth 3 m), to 75 m at site K (maximum depth 30 m). We constructed a topographic profile
112 of each transect by recording tide-corrected depth at one metre intervals, and quantified substrate
113 composition by filming each transect and point counting sequential still images, using five fixed points
114 per image (English et al. 1976) and 25 benthic substrate categories (Data S1). The twenty five substrate
115 categories were condensed into seven categories for graphical representation: tabular *Acropora*,
116 branching *Acropora*, massive and encrusting coral, soft coral, macroalgae, dead coral, and sediment.

118 **Results**

119 Underwater observations show that the different reef stages are joined in a continuous reef blanket with
120 a distinctive undulating form, resembling the 'egg box' structure described by Kan et al. (2015) in the
121 cellular reefs of Nagura Bay, Japan. The relationship between the shapes of the different stages can be
122 envisaged by imagining sequentially deeper horizontal slices through a solid egg box. The initial slices
123 contact the peaks, producing circular shapes. These reefs correspond to Wyrwoll et al.'s (2006)
124 pinnacles but we subsequently refer to them as haystacks, based on earlier descriptions of similar
125 *Acropora*-dominated reefs in the Caribbean (Goreau 1959; Kinzie 1973). Deeper slices reach the ridges
126 between adjacent peaks, producing stellate shapes. Subsequent slices produce a platform surrounding
127 enclosed depressions and eventually a solid platform. Below we describe the sequence in the three
128 idealised stages: haystack, stellate and platform. However it should be noted that the sequence is a
129 continuum and that sites within each stage may have features of earlier and/or later stages. Fig. 3 shows
130 representative transect profiles from each stage and Fig. 4 is a schematic block diagram incorporating
131 the main features of the three idealised stages.

133 **Haystacks**

134 Haystack reefs occur around the margin of the Maze (e.g. sites K and M; Fig. 2). The reef surface at
135 these sites has a sinusoidal profile, curving up over dome-shaped reef tops then descending into bowl-
136 shaped depressions (Fig. 3). The wavelength and amplitude of the profile vary within ranges of
137 approximately 40-100 m and 15-30 m respectively. Like the haystacks of the Caribbean (Goreau 1959;
138 Kinzie 1973), the Abrolhos haystacks consist of loosely interlocked branching *Acropora* colonies, most
139 in growth position but many collapsed and overturned. Adjacent haystacks are linked by saddle-shaped
140 ridges of branching *Acropora*. The predominant *Acropora* species on the haystack reefs and ridges are
141 *A. formosa/muricata* and *A. abrolhosensis*. Tabular *A. spicifera* is abundant at site M on the exposed
142 northern margin of the Maze but absent from the more sheltered site K to the south. Live *Acropora*
143 cover is 60-100% on the reef tops and ridges at both sites, decreasing to approximately 30% within the
144 site M depressions and 0% within the more enclosed and restricted site K depressions. Dead *Acropora*
145 branches at depth are occupied by macroalgae at both sites, predominantly *Sargassum* spp. at site M
146 and *Lobophora variegata* at site K. Beyond the outermost haystacks, the reef surface slopes down to a
147 flat sandy seafloor at 35 m without breaking into isolated patches (Fig. 4). Corals on these outer slopes
148 are predominantly branching and tabular *Acropora* to approximately 25 m depth (Wilson & Marsh
149 1979). Below 25 m the coral community is more diverse, with a high proportion of foliose genera,
150 particularly *Leptoseris* and *Pachyseris*.

151
152 Three islands of storm-deposited *Acropora* rubble line the eastern margin of the Maze (Collins, Zhao
153 & Freeman 2006), and a series of submerged east-west trending linear reef banks occur on the northern
154 margin of the Maze. Two banks can be seen in Fig. 2 and two deeper banks lie beyond them. The bank
155 crests are 2 to 15 m deep, sloping downward to U-shaped troughs at 20 to 30m. The outermost bank
156 reaches the seafloor at 35m. Coral cover and zonation on the banks is equivalent to that of the haystack
157 reefs.

158

159 **Stellate reefs**

160 In the stellate stage the haystack reef tops and ridges reach sea level, producing a network of flat-
161 topped star-shaped reefs (sites B, E, F, J, L, N). Water circulation within the intervening depressions is
162 further reduced and the water column is often stratified and stagnant. Live coral is consequently
163 restricted to shallow depths, often less than 15 m in the more enclosed depressions. The shallow
164 subtidal reef slopes and ridges remain dominated by live branching *Acropora* (Fig. 5) and occasional

165 foliose *Montipora*. Dead *Acropora* branches at depth are colonised by *Nephthea* soft corals and
166 *Lobophora variegata*, and fine sediment accumulates in the bases of the depressions.

167

168 A distinct shallow coral community begins to appear in the stellate reefs, consisting of diverse massive
169 and encrusting corals, the most abundant genera being *Montipora*, *Goniastrea*, *Favia*, *Favites*,
170 *Merulina*, *Astreopora*, *Montastrea*, *Mycedium*, *Echinophyllia*, *Cyphastrea*, *Alveopora* and *Lobophyllia*.

171 Several apparent developmental stages of this community are present, initiating as a discontinuous
172 cover of small colonies on dead *Acropora* branches (Fig. 6A) and culminating in vertical or
173 overhanging walls descending from the surface to as deep as ten metres, but typically between two and
174 eight metres (Fig. 6B).

175

176 **Reef platform with enclosed depressions**

177 In the platform stage (sites C, D, I, O) the trends in water quality and coral distribution that were
178 established in the stellate reefs develop further: most depressions are rimmed by vertical walls of
179 massive and encrusting coral, live *Acropora* cover below the walls declines rapidly with depth, the
180 water column is usually stratified, and the depressions typically have a deep sediment fill. Late-stage
181 enclosed depressions (A, G, H) gradually fill with sediment to the level of the surrounding reef flat. As
182 they fill, the fringe of live *Acropora* beneath the vertical walls migrates upward, eventually
183 overgrowing the walls and encroaching over the depression floors.

184

185 **Model**

186 **Rationale**

187 Based on the survey results described above, the Abrolhos cellular reefs appear to exhibit a
188 straightforward developmental sequence. However they provide little direct insight into the origin of
189 cellular morphology because the cellular form is already present at the haystack stage. Given the high
190 coral cover on the haystack reef tops and ridges, subsequent growth will inevitably enclose the
191 depressions. Although the haystacks must have progressed through earlier stages to reach their present
192 configuration, the existing space-for-time sequence does not extend back to the earlier stages,
193 presumably because coral colonisation of the Last Interglacial surface ceased when it became deeply
194 submerged and covered by sand in the mid Holocene. If this is the case, even the youngest haystacks
195 probably initiated more than 4000 years ago. Several processes appear to be suppressing live coral

196 cover, and therefore accretion, within the present-day haystack reef depressions, including reduced
197 water circulation and macroalgal colonisation. But in the absence of earlier stages in the space-for-time
198 sequence it is impossible to determine whether these processes could have initiated the depressions or
199 whether they are consequential. In this situation computer simulation provides a potential means of
200 investigating the early stages of reef development.

201

202 **Methods**

203 The model we describe below is configured as a cellular automaton: an array of identically-
204 programmed interacting cells (Ulam 1962; von Neumann 1963; Data S2). This structure is well-suited
205 to simulating reef growth because each cell in the array can be considered to represent a square metre
206 of seafloor, and reefs can grow on the seafloor as three-dimensional stacks of cubic ‘corals’. Using this
207 approach, we simulate lagoon reef development as the growth and coalescence of patch reefs from
208 individual coral recruits on a flat seafloor. We first describe a basic model in which colonisation and
209 growth is essentially random and unconstrained except by sea level, and subsequently introduce a
210 parameter representing branching *Acropora*.

211

212 **Basic model**

213 The basic model is initialised by defining the seafloor depth, the array dimensions, and the number of
214 coral recruits. We used a default configuration of 30 m depth (static, i.e. no sea level variation), a 160 x
215 160 cell array (representing 160 x 160 m, or 2.56 hectares, of seafloor), and 64 randomly-spaced coral
216 recruits, occupying 0.25% of the array. The 160 x 160 m recruitment array was centred within a larger
217 array of 250 x 250 m, giving the reefs a 45 m margin for lateral growth. We chose 30 m as the default
218 depth, rather than the 40 m of the Maze, because cellular reefs elsewhere appear to be thinner than the
219 Maze; those at Mataiva for example are only 10 to 20 m thick (Rossfelder 1990). The horizontal
220 dimensions of the array were selected to minimise computation time while still allowing adequate
221 spatial representation of reef morphology. The colonisation density was selected such that the resulting
222 patch reefs were close enough to eventually coalesce but not so close as to immediately coalesce. We
223 examined variations to the default configuration, including sea level rise, and describe them later under
224 ‘additional modifications’.

225

226 Growth from the initial coral recruits is effected by assigning two growth probabilities to each cell in
227 the array in each iteration: a vertical probability representing the likelihood of the cell growing upward
228 itself and a neighbour probability representing the likelihood of the cell being overgrown by a
229 neighbouring coral (Fig. 7). The vertical probability of vacant seafloor cells is zero and the vertical
230 probability of coral-filled cells is random. The neighbour probability of each cell is the product of a
231 random number between zero and one and a 'neighbour value' that depends on the state of the eight
232 surrounding cells. Cells with no shallower neighbours are assigned a neighbour value of zero;
233 otherwise the cell's neighbour value rises incrementally for each shallower neighbour. If a cell
234 becomes surrounded by shallower neighbours it is guaranteed to be overgrown. Otherwise growth is
235 determined by comparing the cell's vertical and neighbour probabilities against two random numbers
236 between zero and one. If either or both probabilities exceed their respective random numbers, the cell
237 grows by one metre when the array is updated prior to the next iteration. Vertical accretion is halted at
238 sea level but lateral accretion continues. The time represented by each iteration is arbitrary but we
239 consider it to be 100 years, giving a mean vertical reef accretion rate of 7 mm/yr (the theoretical
240 maximum rate of 10 mm/yr is not achieved because corals do not grow in every iteration).

241 **Branching *Acropora* model**

242 Representation of branching *Acropora* was guided by the output of the basic model (Fig. 8). The basic
243 model reefs have an irregular 'spiky' surface, with corals projecting up to four metres above the
244 surrounding reef. Such projections cannot occur on real branching *Acropora* reefs because, due to their
245 'brittle tree' morphology, any branching *Acropora* colonies that grow more than a metre or two above
246 their surroundings will inevitably collapse (Maragos 1972; Bak 1976; see Fig. 5B). This is not
247 necessarily a disadvantage. Because broken fragments can survive and grow to form new colonies,
248 collapse and fragmentation is recognised as an inherent and significant mode of reproduction and short
249 range dispersal in branching *Acropora* (Gilmore and Hall 1976; Tunnicliffe 1981; Bothwell 1982;
250 Highsmith 1982). Collapse is represented in the branching *Acropora* model by imposing a maximum
251 height differential between neighbours (hereafter termed collapse limit) of two metres, such that corals
252 growing to project two metres above any neighbouring cell are prevented from growing upward until
253 the deeper cell grows. Although they cannot grow upward, projecting corals contribute to the growth
254 probability of neighbouring cells in two ways: first, they 'support' neighbouring corals, ensuring they
255 are unrestricted by the collapse limit, and second they may 'collapse into' deeper neighbouring cells
256 (i.e. they increase the neighbour probability of those cells). Although this representation of collapse

257 involves no subtraction of height from the collapsing colony, it remains valid because it is equivalent to
258 the projecting colony growing a metre then collapsing back a metre during the iteration. Because the
259 imposition of the collapse limit slows reef growth, the time represented by each iteration is reduced to
260 40 years. This gives a mean vertical reef accretion rate of 9 mm/yr, approximating that of the Abrolhos
261 cellular reefs (Eisenhauer et al. 1993, Collins et al. 1993).

262

263 **Additional modifications**

264 We examined the effects of increasing the collapse limit, altering water depth, altering colonisation
265 density, and periodically adding new coral recruits. We also simulated sea level rise and depth-
266 dependent growth, using a simplified linear sea level rise of 10 mm/yr, stabilising at 30 m depth, and a
267 simplified linear reduction of the coral growth rate to 10% of the surface rate at 30 m.

268

269 **Results**

270 **Basic model**

271 Patch reefs created with the basic model appear approximately circular in plan view and steeply conical
272 in oblique view (Fig. 8A and B). The individual patch reefs maintain their conical form as they enlarge
273 and coalesce with neighbouring patches (Fig. 8C and D). We use the term ‘nodular’ to describe the
274 shapes and forms generated by the basic model. While the nodular reefs resemble many natural patch
275 reefs (e.g. Fig. 9), they bear little resemblance to cellular reefs. In fact their shapes are the inverse of
276 cellular reefs; nodular reefs appear convex and subcircular in plan view whereas cellular reefs are
277 concave and stellate, surrounding subcircular depressions. However, the basic model is generic and
278 does not intentionally represent any particular coral type.

279

280 **Branching *Acropora* model**

281 Reefs created with the branching *Acropora* model closely resemble the Abrolhos cellular reefs (Fig.
282 10). The model reproduces the characteristic egg box form of the real reefs and all its corollaries
283 including haystack reefs, stellate reefs with radiating ridges, reef platforms enclosing bowl-shaped
284 depressions, scalloped platform margins and the presence of multiple small depressions within larger
285 multi-lobed depressions. The 45° slopes of the model reefs are steeper than the mean of the real
286 *Acropora* slopes (37° ± SD 6°) but within their recorded range. Fig. 11 and Movie 1 show sequential
287 stages in the development of the branching *Acropora* reefs, demonstrating the emergence of their egg

288 box morphology. The key process is the formation of ridges between adjacent patch reefs. This process
289 begins when the patch reefs meet, whereupon the valleys between them grow rapidly upward to
290 become saddle-shaped ridges (Fig. 11C and D). The depressions surrounded by the reefs and ridges are
291 initially irregular in outline but are progressively smoothed to subcircular shapes as the surrounding
292 reef grows. Eventually the depressions become completely enclosed within the reef platform and
293 infilled by coral (Fig. 11E).

294

295 **Additional modifications**

296 Increasing the collapse limit was the most influential of the additional modifications. Progressively
297 increasing the collapse limit beyond the two metres of the branching *Acropora* model produces a
298 transition from cellular to nodular reef forms. A three metre collapse limit creates reefs with weakly
299 developed subcircular depressions (Fig. 12A and B) and a four metre collapse limit creates reefs with
300 very few depressions (Fig. 12C and D). Collapse limits of more than four metres produce nodular reefs
301 equivalent to those of the basic model.

302

303 Varying water depth also significantly influences reef morphology. Reducing depth reduces reef
304 thickness, which constrains the morphological expression of the collapse limit such that the appearance
305 of the branching *Acropora* reefs transforms from cellular to nodular as depth decreases (Fig. 13A and
306 B). In the extreme case of reefs growing in only one or two metres water depth, where the collapse
307 limit has no effect, all variants of the model produce identical nodular reefs. Increasing depth, by itself,
308 has little influence on reef morphology (Fig. 13C and D). However, more realistic representations
309 incorporating sea level rise and depth-dependent growth cause reef slopes to steepen significantly as
310 depth increases (Fig. 13E and F). Variations in colonisation density and timing have relatively little
311 effect on reef morphology, besides the expected crowding of patch reefs at high density (Fig. 14).

312

313 **Discussion**

314 **Model**

315 The resemblance in shape and form between the model reefs and real reefs suggests that the model
316 adequately represents reality. This interpretation is supported by the model's simplicity: it has only one
317 rule—collapse if too steep—which is intuitively reasonable and supported by field observations. Model

318 reef morphology is hyper-sensitive to that rule, running through a nodular to cellular spectrum as
319 permissible steepness is reduced and collapse becomes more frequent.

320

321 The nodular reefs produced by the basic model appear straightforward and visually ‘correct’ as growth
322 forms, because the individual patch reefs maintain their forms as they grow and merge. This
323 straightforward morphology is indicative of pure in-situ (in place) growth. Cellular reefs are more
324 complex because the patch reefs transform as they merge, eventually becoming linked by a network of
325 ridges. This transformation results from the high frequency of collapse in the branching *Acropora*
326 model. However, it is not simply the frequency of collapse that produces ridges; more important is the
327 distribution of collapse. Because the valleys between merging patch reefs are low points in the reef
328 structure, coral colonies in the valleys are less likely to project above their neighbours than corals
329 elsewhere. Consequently, they are relatively unrestricted by the collapse limit and are therefore more
330 likely to remain in place as they grow, and less likely to collapse, than colonies elsewhere (Fig. 15).

331 The retention of in-situ colonies transforms the V-shaped valleys into U-shaped ridges that grow to sea
332 level, enclosing depressions (Fig. 11C and D, Movie 1). The subcircular shapes of the depressions arise
333 through the same non-uniform distribution of collapse. Colonies in the re-entrant concavities of early-
334 stage depressions are supported by neighbours and therefore tend to remain in place while those on
335 projecting convexities tend to collapse. Over time this creates smooth rounded shapes, the ultimate
336 smooth shape being a circle.

337

338 **Abrolhos cellular reefs**

339 The foregoing descriptions of the model branching *Acropora* reefs provide two testable predictions
340 regarding real cellular reefs. First, their slopes should have consistent and relatively low gradients,
341 representing the angle of repose (maximum slope stability angle) of branching *Acropora*. Second, the
342 proportion of collapsed colonies should be lowest in the valleys and ridges and highest on reef slopes.
343 Both predictions are supported in the Abrolhos, where *Acropora* slopes average $37^\circ \pm \text{SD } 6^\circ$ (Fig. 3)
344 and *Acropora* colonies in valleys and ridges are generally upright (Fig. 5A, see Fig. 10 for photo
345 location) while those on reef slopes are often overturned (Fig. 5B). We conclude that the Abrolhos
346 cellular reefs have developed according to the model and that Fig. 11 closely describes their
347 morphological progression.

348

349 One significant difference between the real and model reefs is the reduced accretion rate of the real
350 reefs once they reach sea level. Model branching *Acropora* reefs reach sea level from 30 m depth in
351 approximately 90 iterations (3600 years) and only require 70 more iterations (2800 years) to
352 completely fill the platform, whereas the Maze reefs, in 40 m depth, reached present sea level in
353 approximately 4500 years (Eisenhauer et al. 1993; Collins et al 1993) but still have not filled the
354 platform 7000 years later. The reduced accretion of the real reefs probably results from two factors not
355 represented in the model. The first is the reduction of *Acropora* cover and vitality at depth as water
356 circulation is restricted by the enclosure of the depressions (Wyrwoll et al. 2006). This is an example of
357 self-limitation through negative feedback between reef growth and water circulation (Blanchon 2011).
358 Self-limitation is therefore a significant influence on the Abrolhos cellular reefs, but operates primarily
359 on their accretion rate not their morphology. The second factor is the colonisation of upper reef slopes
360 by relatively slow-growing massive and encrusting corals. The steep walls created by these corals
361 effectively exclude branching *Acropora*, because any branching *Acropora* that colonise the walls are
362 likely to break off once they grow too large to be supported at their base. By ‘engineering’ steep walls
363 (*sensu* Jones, Lawton & Shachak 1994), massive and encrusting corals are able to monopolise—for
364 thousands of years—prime shallow subtidal habitat that would otherwise be occupied by fast-growing
365 branching *Acropora*. The combination of reduced water circulation at depth and steep walls in the
366 shallows restricts live *Acropora* to a fraction of their previous distribution, significantly slowing the
367 overall reef accretion rate. Model cellular reefs, in contrast, rapidly fill the platform because ‘live’
368 *Acropora* occupy all habitats including the depression slopes and floors.

369

370 Another significant difference between the real and model reefs is the series of linear reef banks on the
371 northern margin of the Maze. We interpret these as early to mid Holocene wave-deposited structures,
372 resulting either from storms, cyclones (Scheffers et al. 2012) or tsunamis (Scheffers et al. 2008).

373

374 **Application to other reefs**

375 The morphology of cellular reefs elsewhere appears similar enough to the Abrolhos reefs to suggest
376 they have developed the same way, an inference supported by the abundance of branching *Acropora* in
377 documented examples (Alacran Reef: Hoskin 1963; Solomon Islands: Morton 1974; Tétambia Reef: de
378 Vel and Bour 1990; Cocos-Keeling Atoll: Williams 1994; Pelican Keys: Aronson et al. 1998; Elizabeth
379 Reef: Woodroffe et al. 2004; Pohnpei: Turak and DeVantier 2005; Tun Sakaran: Montagne et al. 2013;

380 Nagura Bay: Kan et al. 2015). At least two of these examples, the Solomon Islands (Morton 1974) and
381 Nagura Bay (Kan et al. 2015), exhibit vertical walls of massive and encrusting corals above the
382 *Acropora* zone, suggesting they have undergone the late-stage shallow coral community succession
383 observed in the Abrolhos.

384

385 We have separated Mataiva Atoll from the list above as *Porites* is abundant there and has been
386 considered responsible for the cellular morphology (GIE Raro Moana 1985; Delesalle 1985). However,
387 branching *Acropora* are also abundant at Mataiva (Delesalle 1985; Rossfelder 1990). We suggest that
388 branching *Acropora* are the primary reef-builders at Mataiva and *Porites* are colonisers of the
389 *Acropora* reef, not framework builders. Another possible exception to the rule of *Acropora* dominance
390 is the 'Type-1' reticulate reef of the Red Sea (Purkis et al. 2010), where *Porites* is also abundant
391 (Bruckner 2011). However, we would not classify all Type-1 Red Sea reefs as cellular because,
392 although deep, the depressions are not always circular; more often resembling the transitional
393 depressions produced by intermediate collapse limits (see Purkis et al.'s Fig. 2). Some Red Sea reefs
394 are distinctly cellular and we predict those to be *Acropora*-dominated (e.g. 27°57'N, 35°13'E). Closer
395 examination of these and other cellular reefs is required to determine whether the predominance of
396 branching *Acropora* is universal, and whether the reef slope gradients and the distribution of collapsed
397 colonies conform to the Abrolhos example.

398

399 We have not classified the previously-mentioned Millenium Atoll with the cellular reefs listed above
400 because the scale of the cellular morphology at Millenium and in many other Pacific atoll lagoons is up
401 to an order of magnitude larger than the Abrolhos. While the large-scale cellular reefs also seem to
402 consist predominantly of branching *Acropora* (Roy and Smith 1971; Grovhoug and Henderson 1973;
403 Valencia 1977; Barott et al. 2010), we do not believe our model applies directly to them because it
404 cannot produce cells of their dimensions unless it is scaled up massively, to unrealistic depths of at
405 least 100 m. We are currently investigating the large-scale cellular morphology.

406

407 The transitional and nodular shapes produced by increasing the collapse limit in the model also occur
408 in real reefs (e.g. Fig. 9). The simplest interpretation of these shapes is that they indicate coral types, or
409 mixtures of coral types, progressively less prone to collapse than branching *Acropora*. In this
410 interpretation, transitional shapes represent reef builders that occasionally collapse, such as foliose and

411 tabular corals, and nodular shapes represent reef builders that rarely collapse, such as massive and
412 encrusting corals or coralline algae. The nodular reefs of Cockatoo Island in Fig. 9 appear to conform
413 to this interpretation, as they consist of massive and encrusting corals cemented by coralline algae (D.
414 Blakeway, pers. obs.). However, the model indicates that transitional and nodular reef shapes are not
415 necessarily diagnostic of coral type, because branching *Acropora* patch reefs appear nodular (i.e.
416 circular in plan view) before they merge with adjacent patch reefs, and transitional to nodular after they
417 merge in shallow water (Fig. 13A). This suggests that additional information on water depth, reef
418 thickness and reef slope gradients will be required to reliably infer coral type from reef morphology in
419 transitional and nodular reefs. Such three-dimensional data are becoming increasingly available
420 through reef-oriented remote sensing (Zawada & Brock 2009; Zieger, Stieglitz & Kininmonth 2009;
421 Goodman, Purkis & Phinn 2013 and references therein; Leon et al. 2013; 2015). In two-dimensional
422 aerial images, however, the only diagnostic morphology is cellular—signifying relatively thick (>10m)
423 reefs constructed by collapse-prone organisms.

424

425 **Branching *Acropora***

426 The default collapse-prone reef builders on modern reefs are branching *Acropora*. While it seems
427 possible for other branching coral genera or other calcareous branching invertebrates (e.g. *Millepora*)
428 to create cellular reefs, observations worldwide (listed above) suggest it is almost exclusively
429 *Acropora*: *A. cervicornis* in the Atlantic and multiple species in the Indo-Pacific. This is probably
430 because branching *Acropora* have the ultimate strategy for rapid pre-emption of space in lagoon
431 environments. *Acropora* branches not only grow quickly (up to 19 cm/yr in the Maze; Blakeway 2000),
432 they regularly develop new branches which themselves branch and rebranch, giving them the potential
433 for exponential expansion (Shinn 1976). Constant growth, branching and collapse produce an open
434 three-dimensional structure that rapidly fills lagoons (Davis 1982). Our model indicates that, given
435 adequate depth, cellular reefs are the inevitable result. Cellular reefs are essentially a phenotype of the
436 branching *Acropora* genome(s), emerging from the innate behaviour of branching *Acropora* colonies
437 just as colony morphology emerges from the innate behaviour of polyps.

438

439 If the relationship between cellular reef morphology and branching *Acropora* holds, the distinctive
440 shapes of cellular reefs in remotely sensed images can potentially be used to identify and map
441 branching *Acropora* habitat. This could be useful in reef conservation, as the sensitivity of branching

442 *Acropora* to environmental conditions makes them something of a canary in the coral reef coalmine
443 (Marshall & Baird 2000; Loya et al. 2001; ABRT 2005; Roth & Dehyn 2013). However, assessing
444 anthropogenic impacts in apparently degraded *Acropora*-dominated lagoons will rarely be
445 straightforward, because natural self-limitation and community succession can drastically reduce
446 *Acropora* cover and vitality in the mid to late stages of reef development. Aronson et al. (1998),
447 Aronson (2011) and Perry & Smithers (2011) highlight the value of documenting and understanding
448 such intrinsic trends, generated by the reef itself, before attempting to evaluate the effects of extrinsic
449 influences imposed from outside the reef, including anthropogenic stresses.

450

451 **Conclusions**

452 Our simulations indicate that reef morphology is fundamentally determined by the extent to which reef
453 building organisms either remain in place or collapse. This control is best expressed in lagoons, where
454 diminished hydrodynamic and substrate influences allow reefs to grow into their inherent forms. The
455 purest growth forms arise in sheltered lagoons dominated by a single type of reef builder, as in the
456 cellular reefs of the Abrolhos. In these situations reef morphology can be considered a phenotype of the
457 predominant reef building organism.

458

459 While the propensity for collapse appears to explain the nodular to cellular spectrum of lagoon reef
460 morphology, many more relationships between reef morphology and ecology remain to be discovered.
461 Many of the recurrent patterns in reef morphology are likely to be ecological phenomena (Blanchon
462 2011; Schlager and Purkis 2015). Quantifying these patterns and identifying their underlying
463 mechanisms can potentially improve our understanding of present-day reef ecology, because any
464 ecological process capable of shaping a reef will almost invariably be an important process in real time
465 on the living reef. Investigation of the relationships between reef morphology and ecology is benefiting
466 from advances in the availability, resolution and processing of remotely sensed imagery. However, the
467 single most important research technique remains careful and objective underwater observation. Any
468 consistent correlations between reef morphology and underwater survey data, such as coral type, can be
469 considered potential causal relationships warranting closer examination.

470

471 In surveying modern reefs it should be recognised that a reef's current state may not represent its
472 formative state, particularly if the reef has reached sea level. While seismic and coring can access the

473 history stored within such reefs, both techniques are logistically demanding and expensive. The
474 complementary methods we employed in the Abrolhos, space-for-time substitution and computer
475 simulation, are relatively simple and inexpensive but can provide a comprehensive reconstruction of a
476 reef's history and a sound basis for extrapolating its future development.

477

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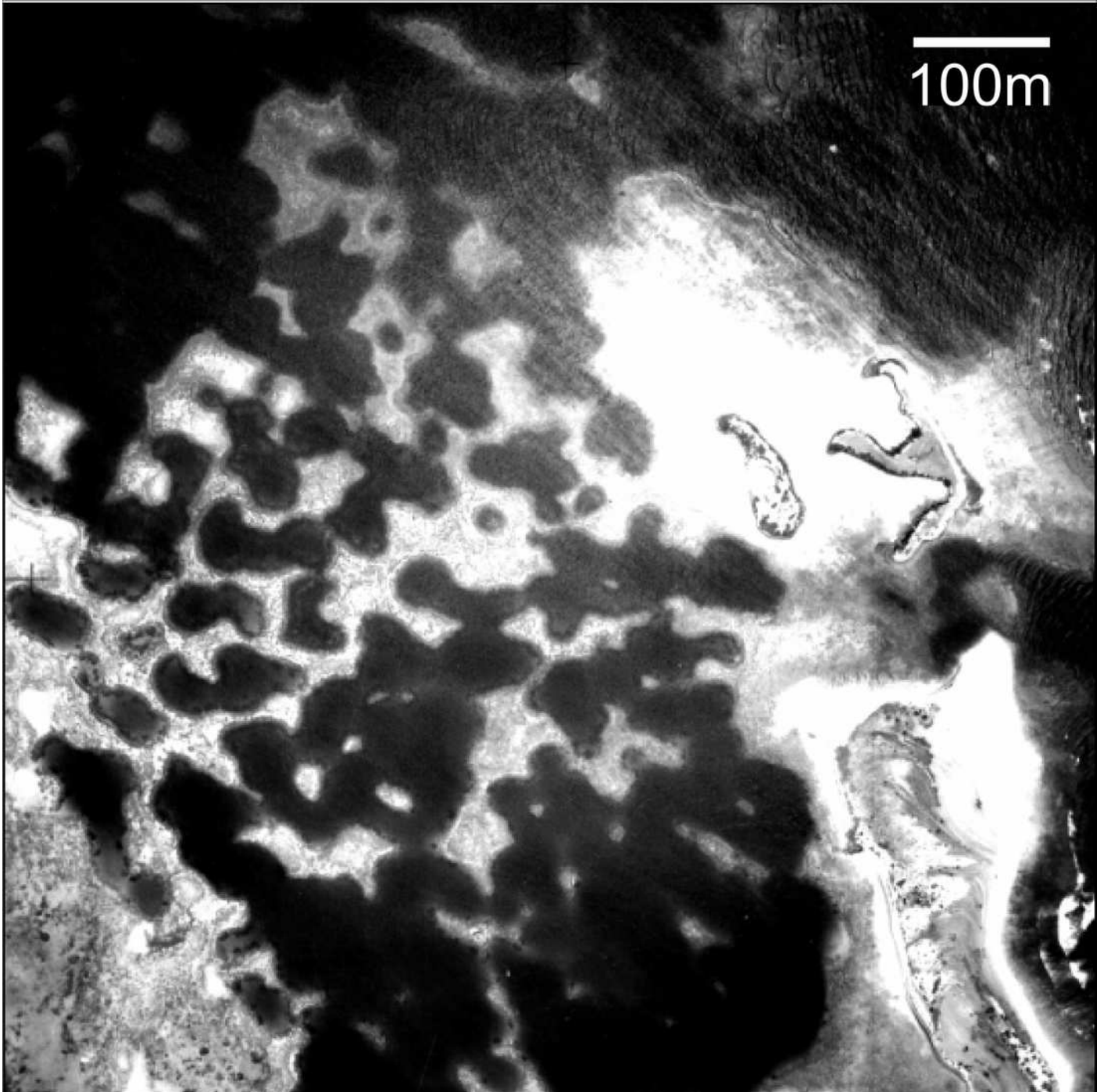
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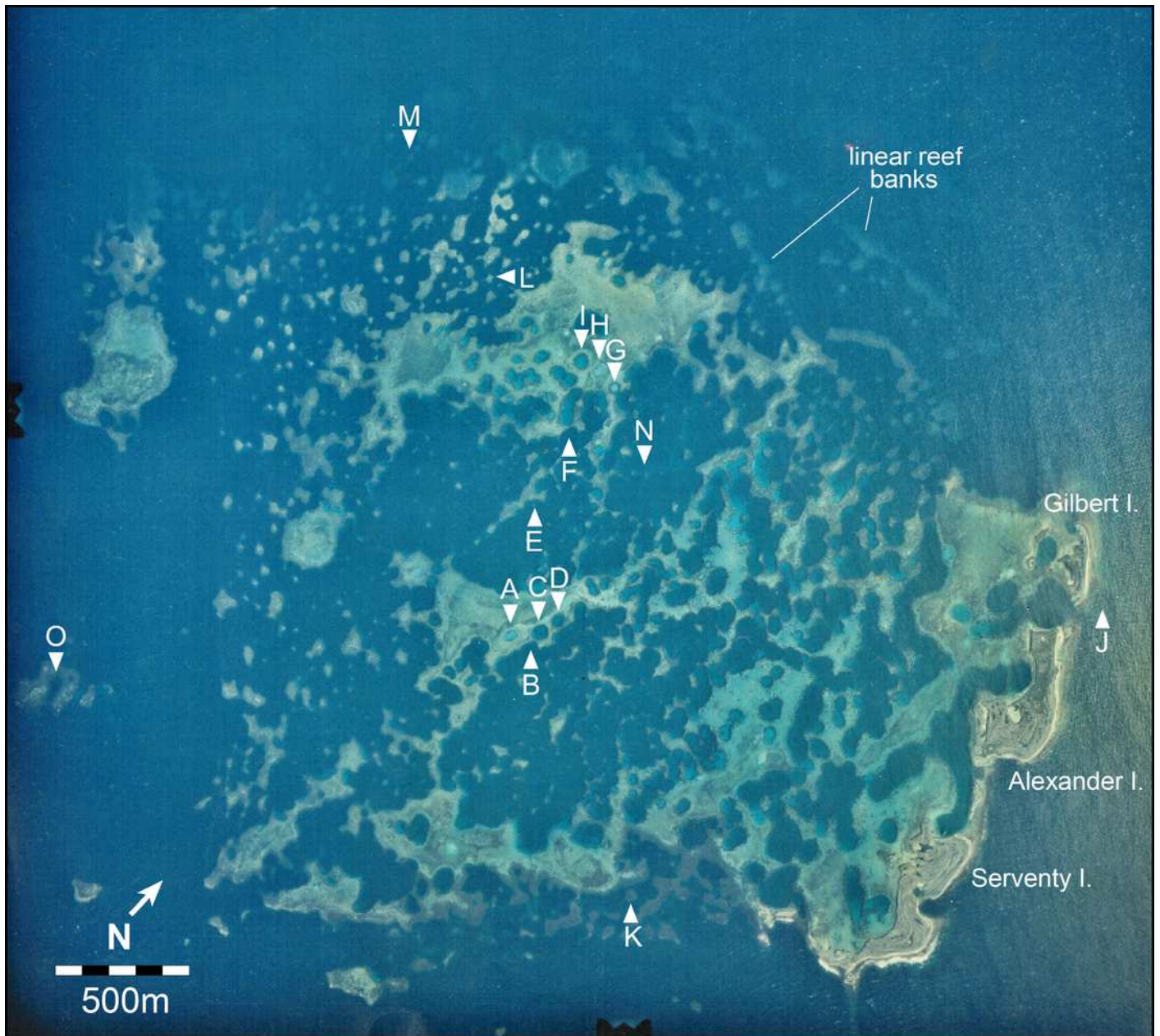
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1

Cellular reefs in the Pelsaert Group lagoon, Houtman Abrolhos Islands, Western Australia (28°54'S 114°E).

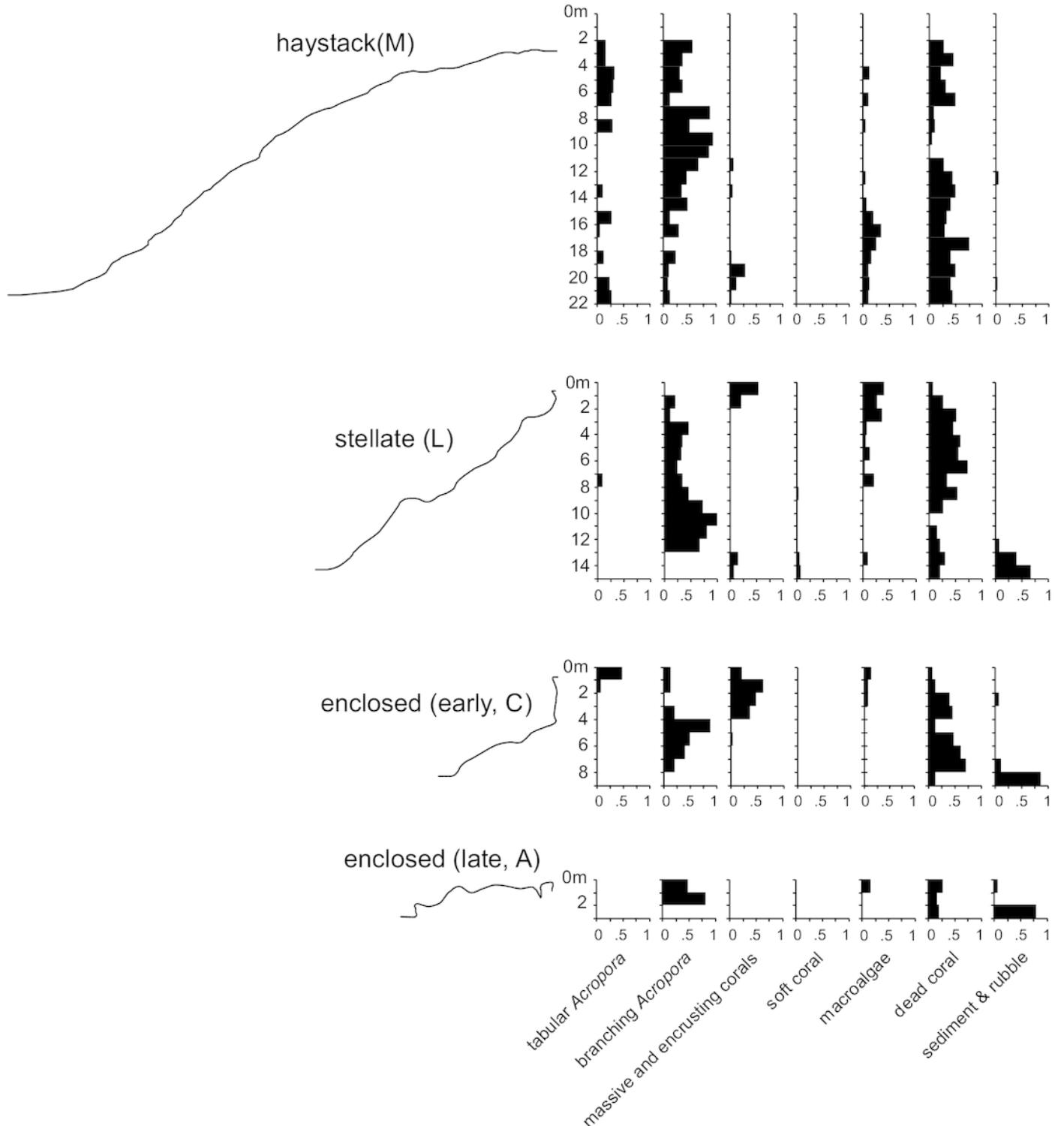


Aerial photograph of the Maze in the Easter Group of the Houtman Abrolhos Islands (28°41'S 113°49'E) showing the 15 survey sites labelled A to O.



3

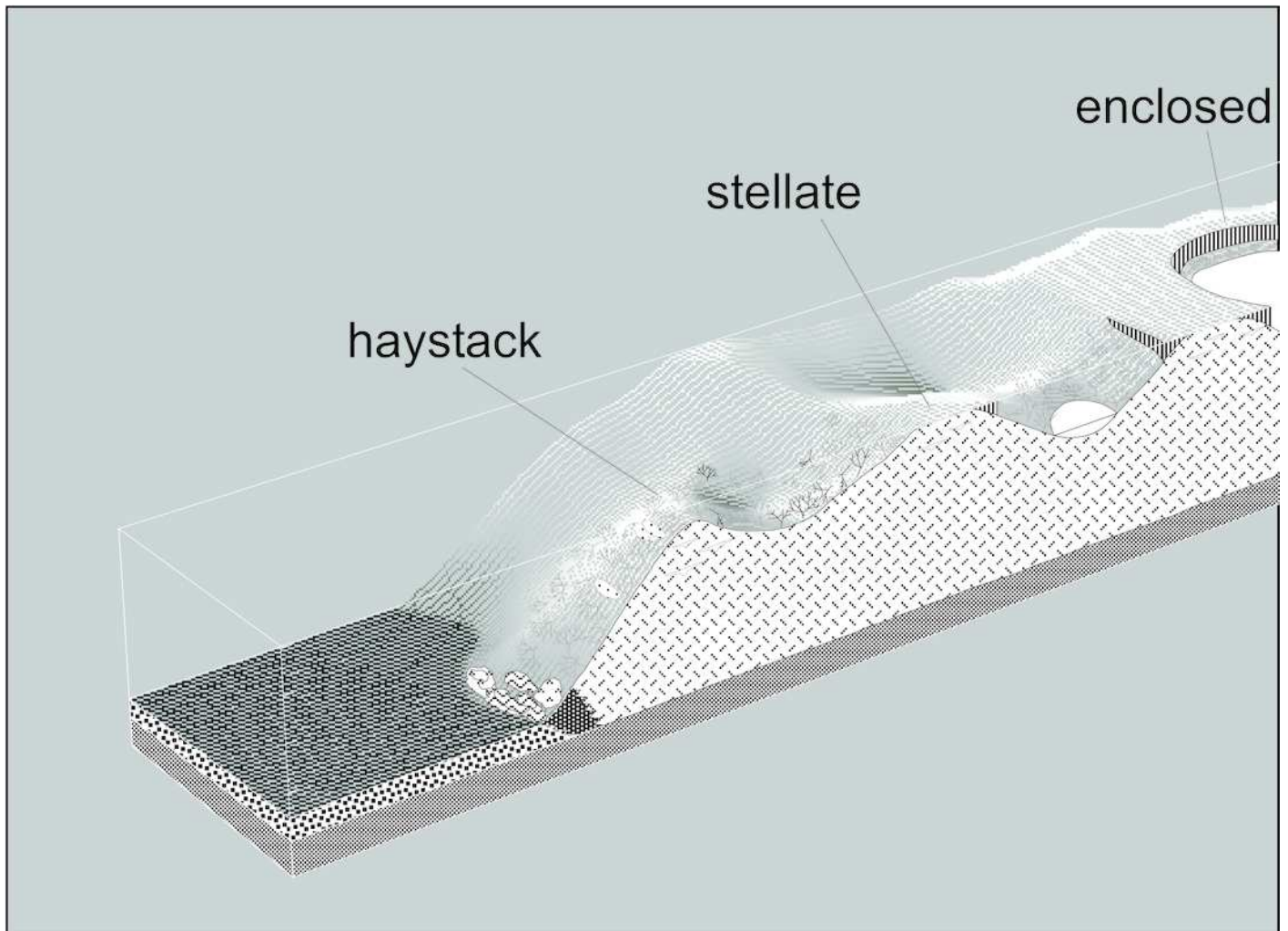
Representative transect profiles and graphs of benthic substrate composition from haystack, stellate and enclosed sites in the Maze.



4

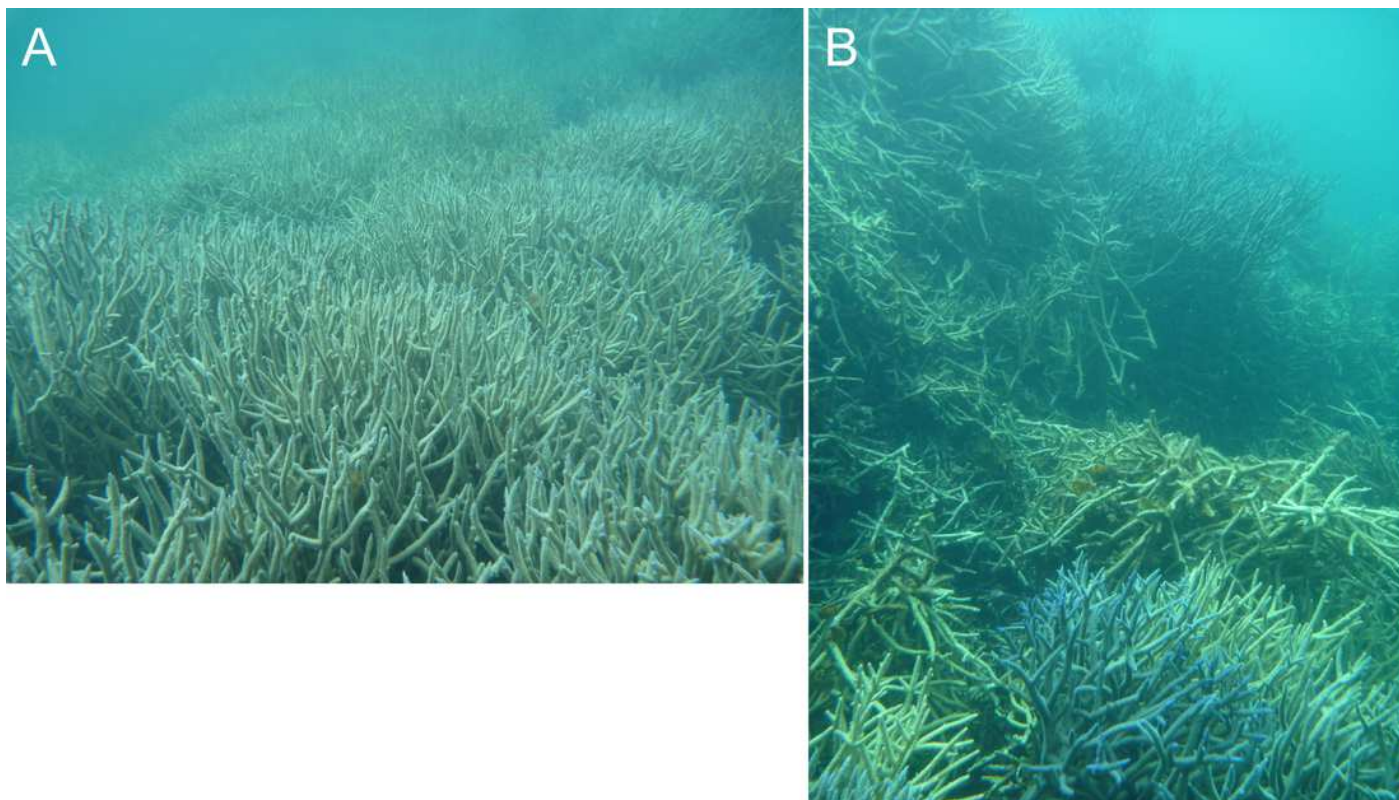
Block diagram illustrating the Maze's egg-box topography and the three idealised stages of cellular reef development.

The cross-section is hypothetical but consistent with seismic and core data.



5

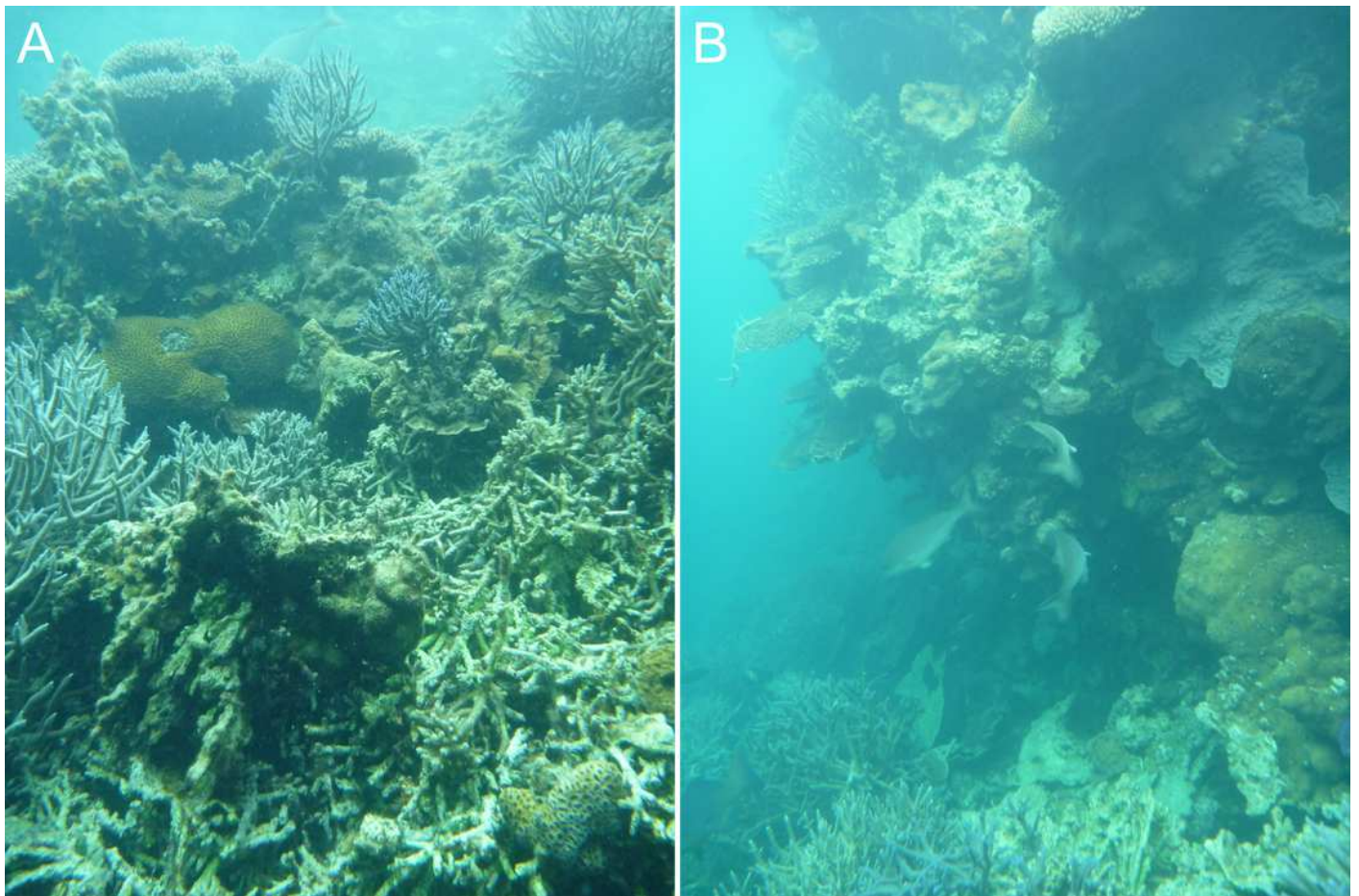
Dense in-situ (A) and collapsed (B) *Acropora* colonies on a stellate reef in the Pelsaert Group lagoon.



6

Inferred early (A) and late (B) stages of reef wall development in the Pelsaert Group lagoon.

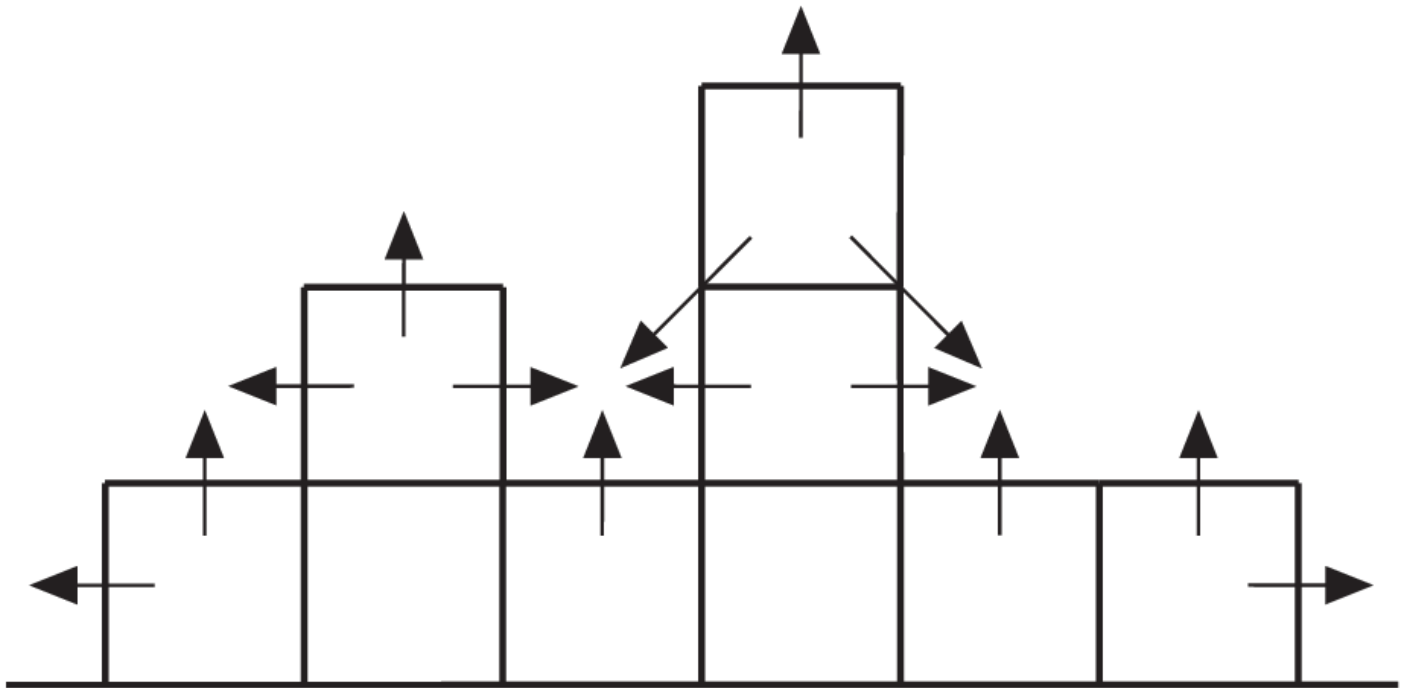
The walls appear to initiate through the colonisation of dead *Acropora* branches by massive and encrusting corals (A), and subsequently grow to become vertical or overhanging (B).



7

Cross-section through a hypothetical model reef.

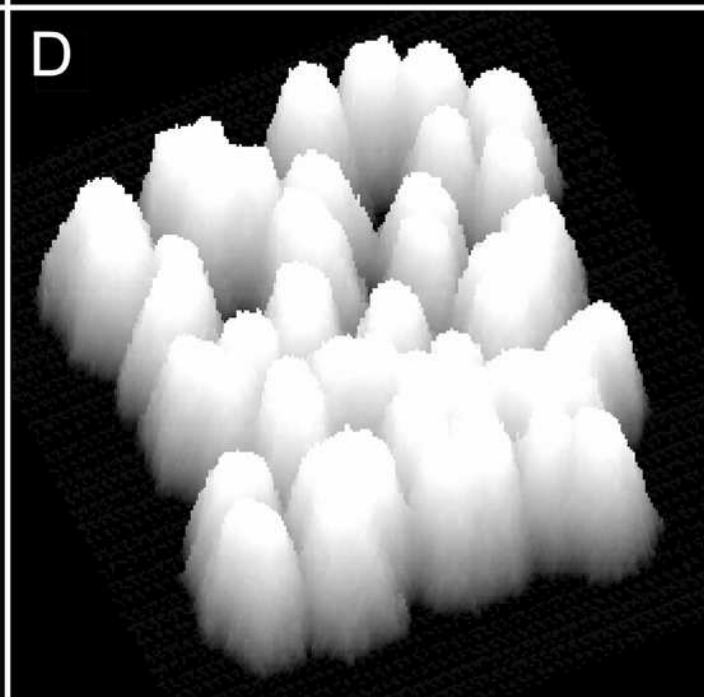
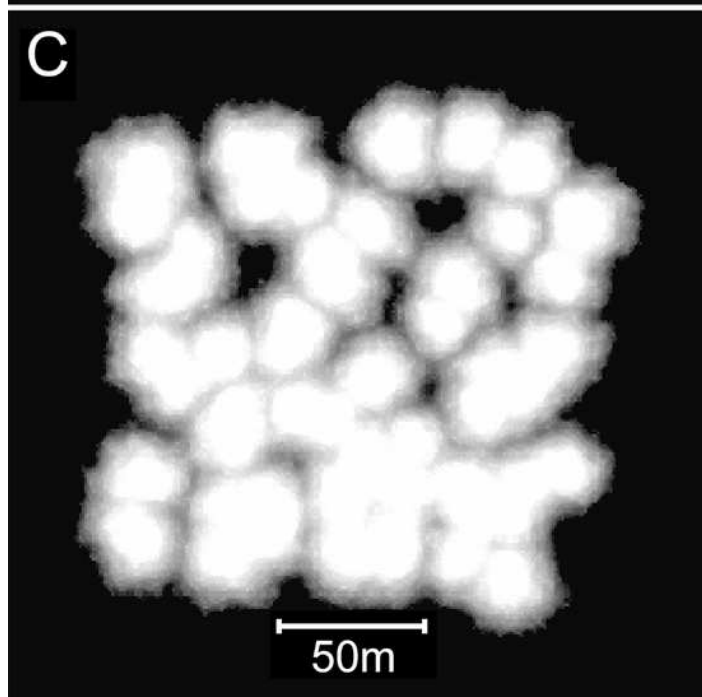
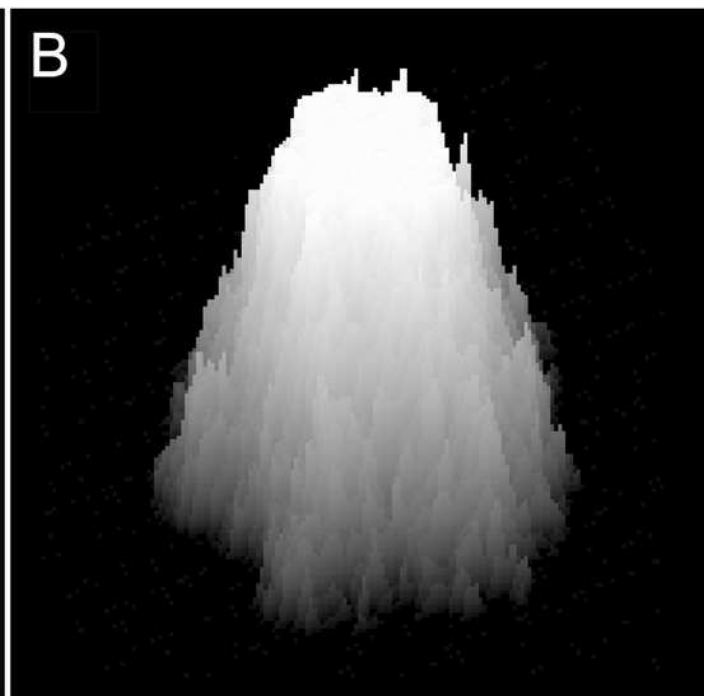
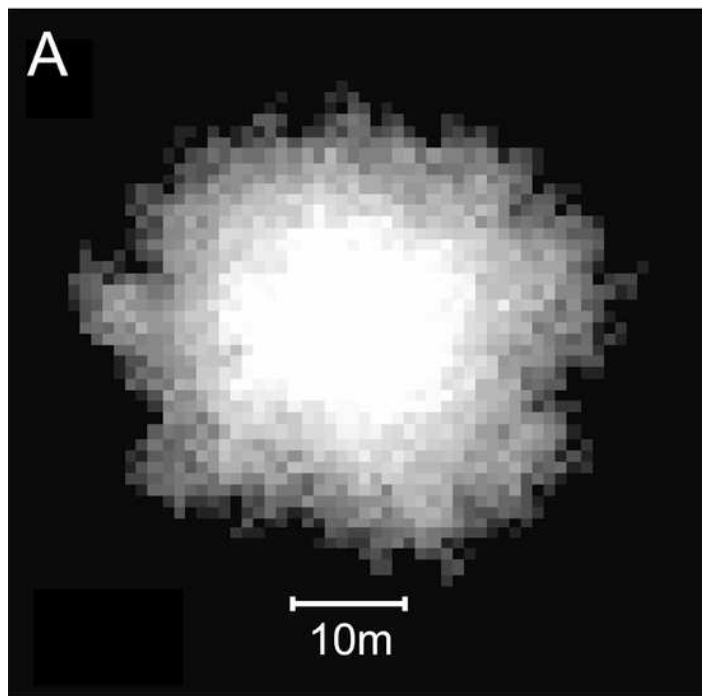
Upward-pointing arrows indicate vertical growth directions, horizontal and diagonal arrows indicate neighbour growth directions.



8

Reefs generated by the basic model.

- A) Two-dimensional plan view of a patch reef after 80 iterations (8000 years) of growth from a single seed coral. 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 (4500 years), and by 80 iterations has developed a 15m wide reef flat. B) Three-dimensional oblique view of the patch reef in A, showing the irregular surface morphology caused by projecting corals. The reef slopes are approximately 65° . C) Two-dimensional plan view of a coalescing patch reef system after 80 iterations. 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.



9

Coalescing nodular patch reefs exposed on a low spring tide at Cockatoo Island, Western Australia, 16°4.8'S 123°35'E.

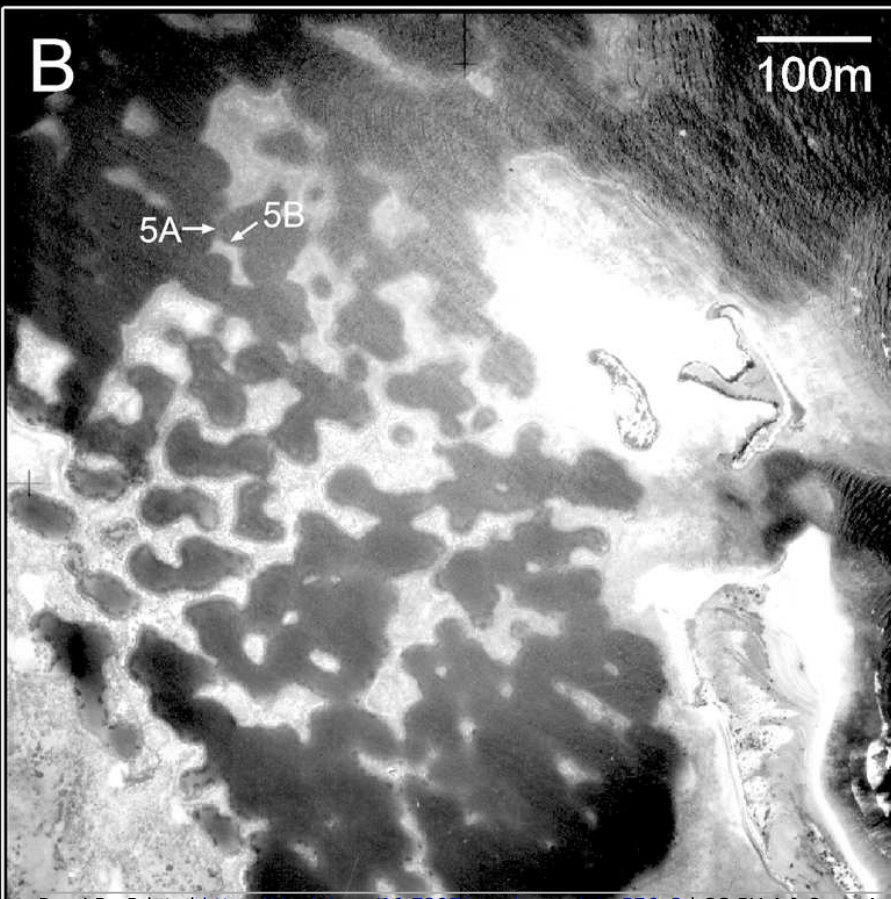
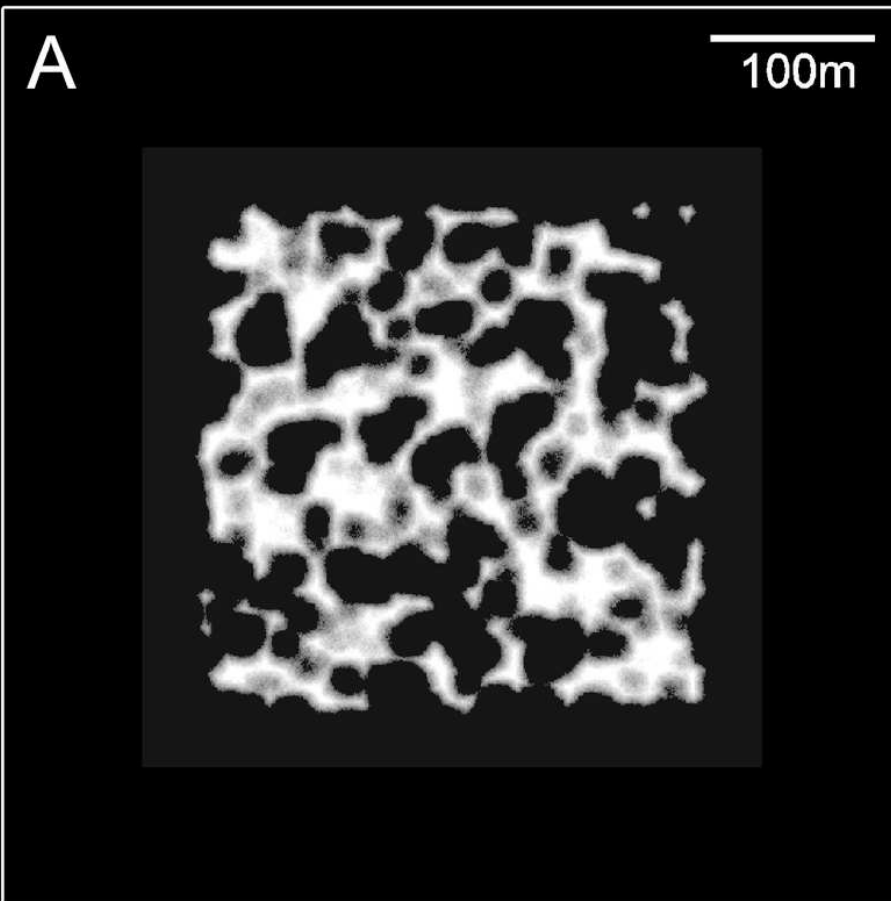
Photograph by John MacFadyen.



10

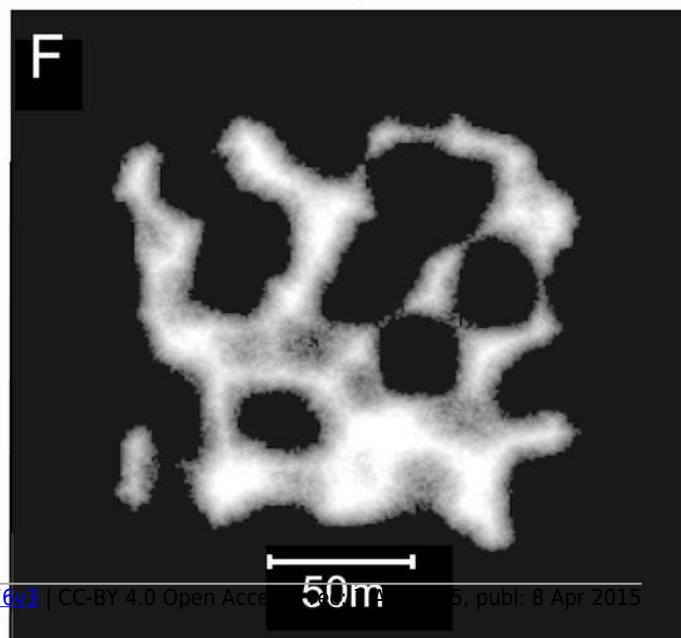
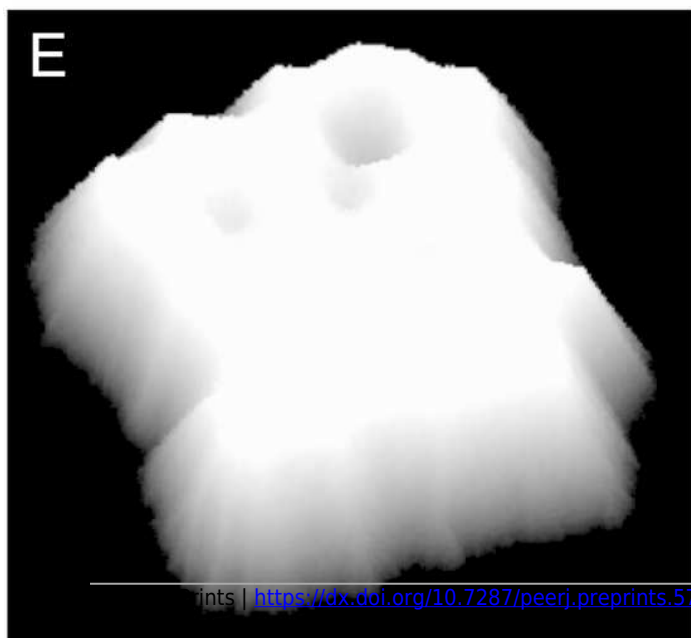
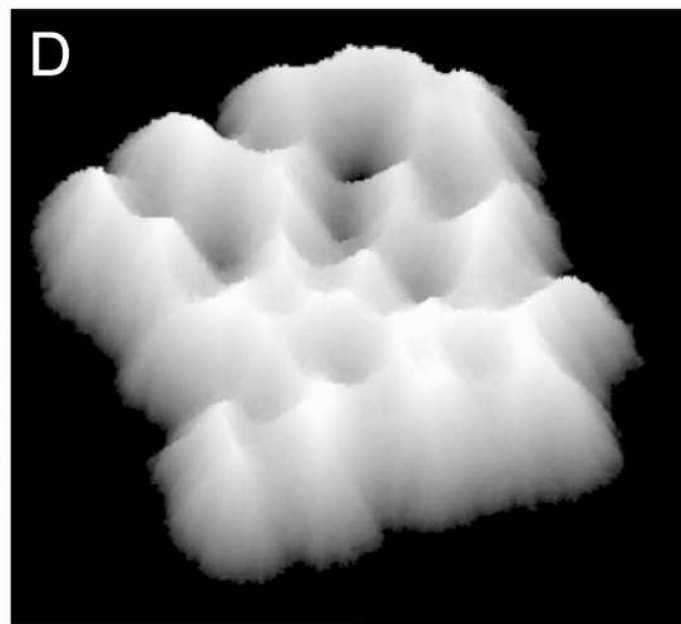
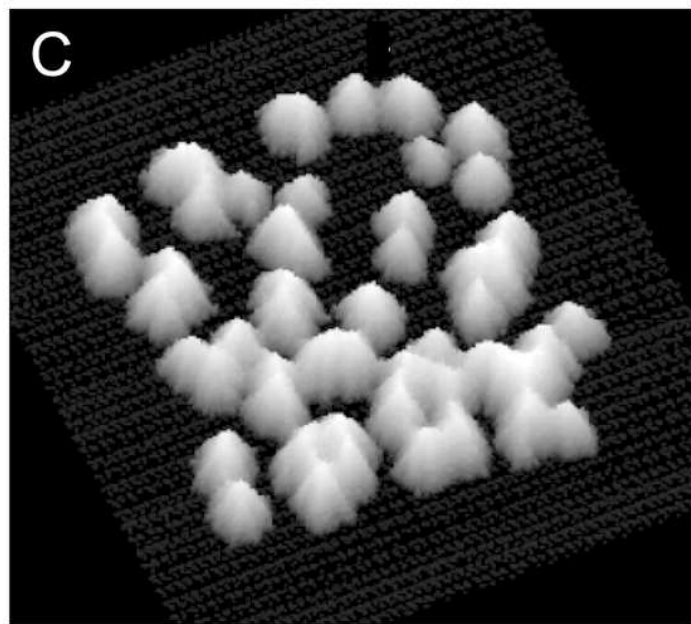
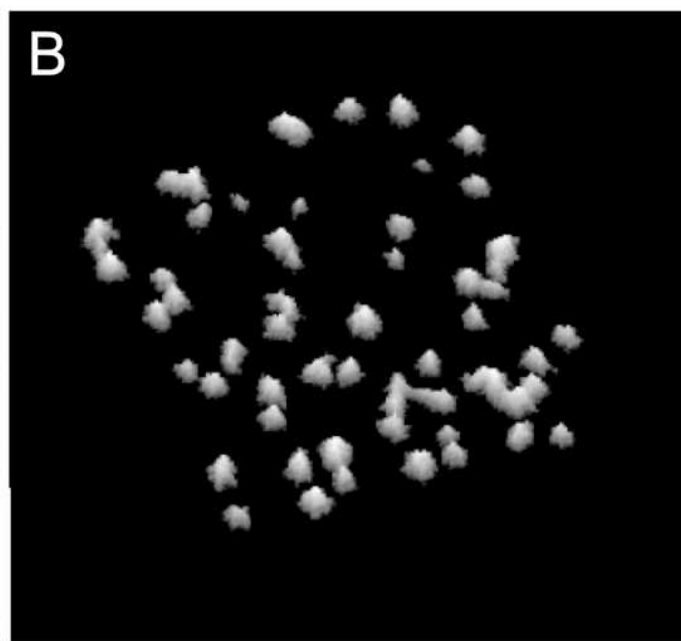
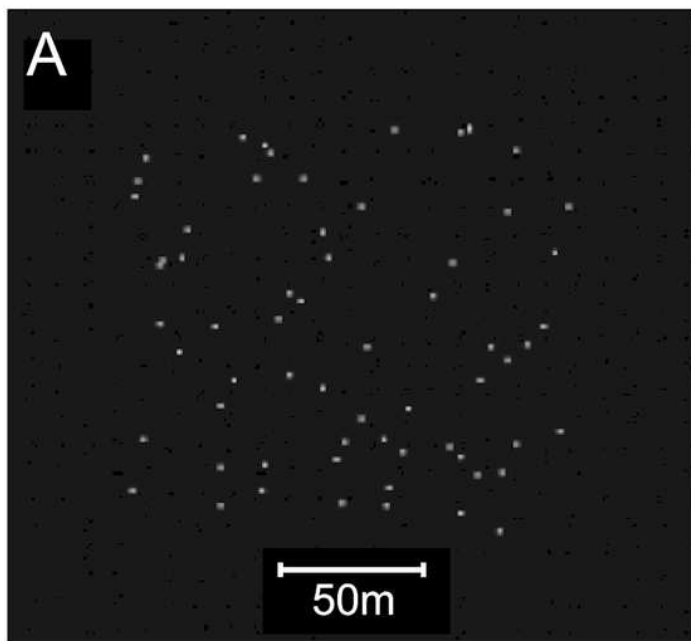
Plan view of model (A) and real (B) branching *Acropora* reefs.

Only the uppermost 10m of the model reef is shown, simulating an aerial view with 10m water visibility. This reef grew in 100 iterations (4000 years) from 225 corals seeded at the default colonisation density (0.25%) in a 300 x 300m array. The real reefs shown in B are those from Figure 1, in the Pelsaert Group of the Abrolhos.



Sequential stages in the development of model branching *Acropora* 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 basic model reefs in Fig. 8C and D. B) After 25 iterations (1000 years) the seed corals have developed into conical patch reefs with 45° slopes. C) After 50 iterations (2000 years) 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 (4000 years) some of the reef tops have reached sea level and the system of ridges has developed to enclose and isolate depressions, producing egg-box morphology. E) After 150 iterations (6000 years) 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.



12

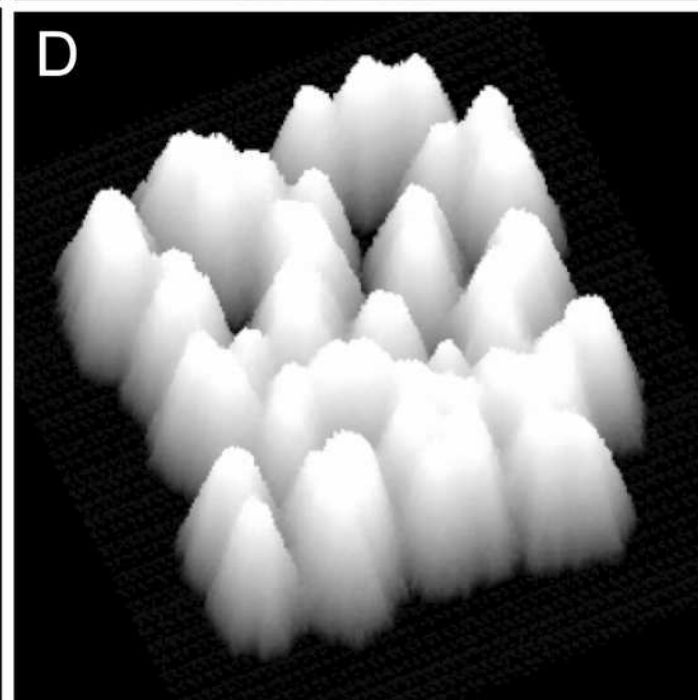
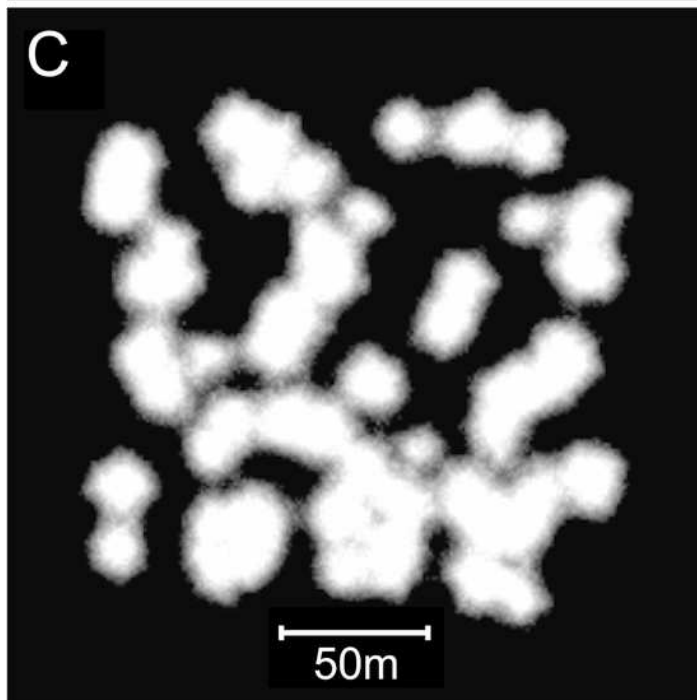
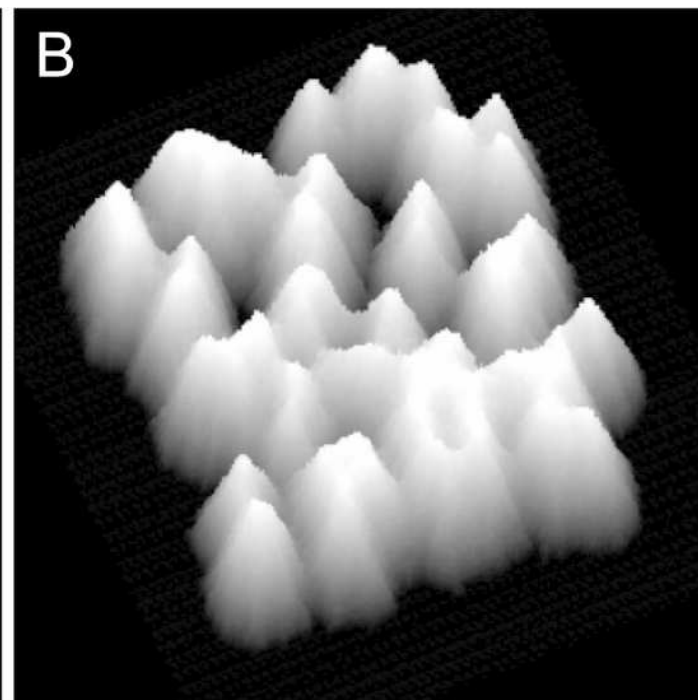
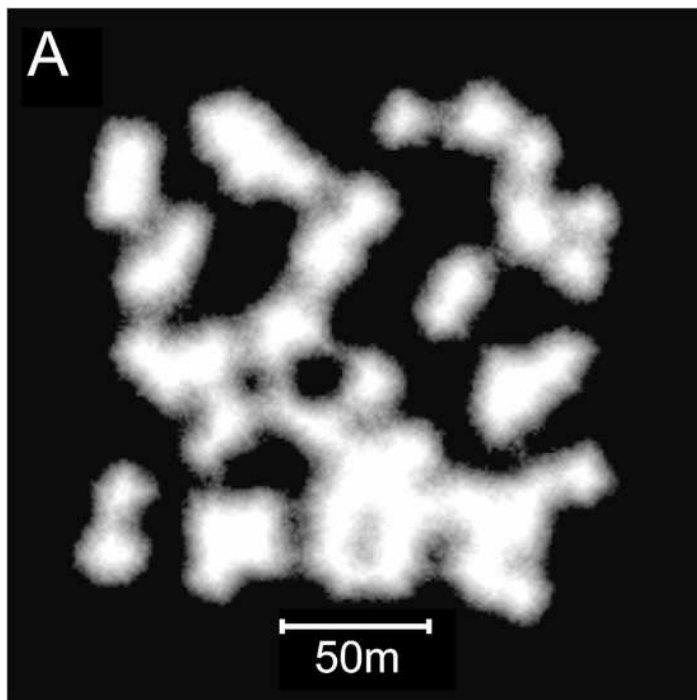
Influence on model reef morphology of increasing the collapse limit.

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.

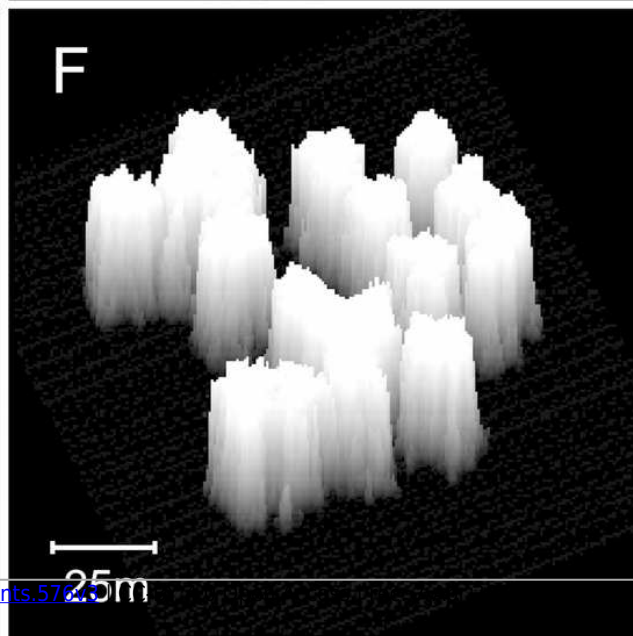
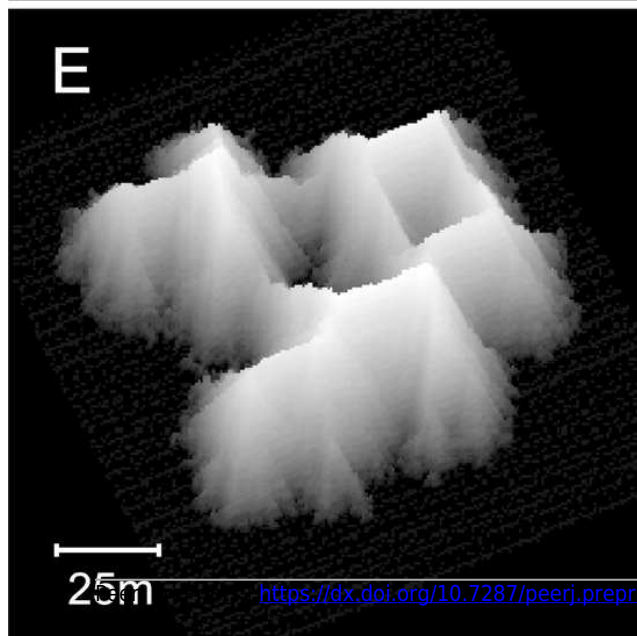
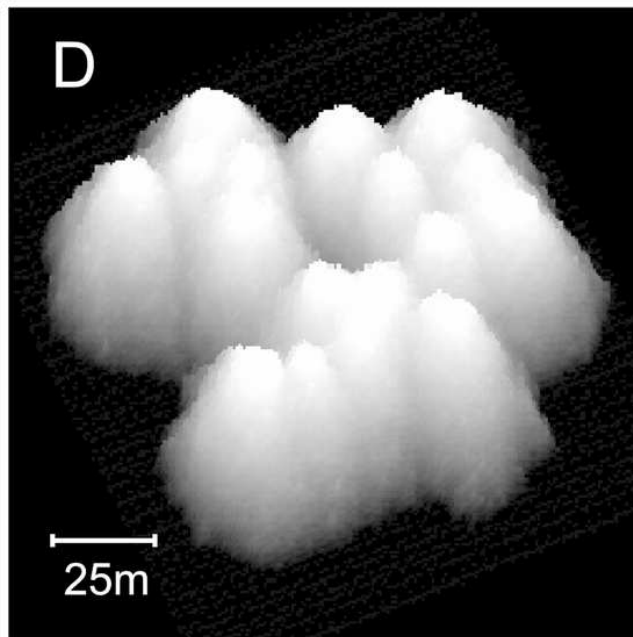
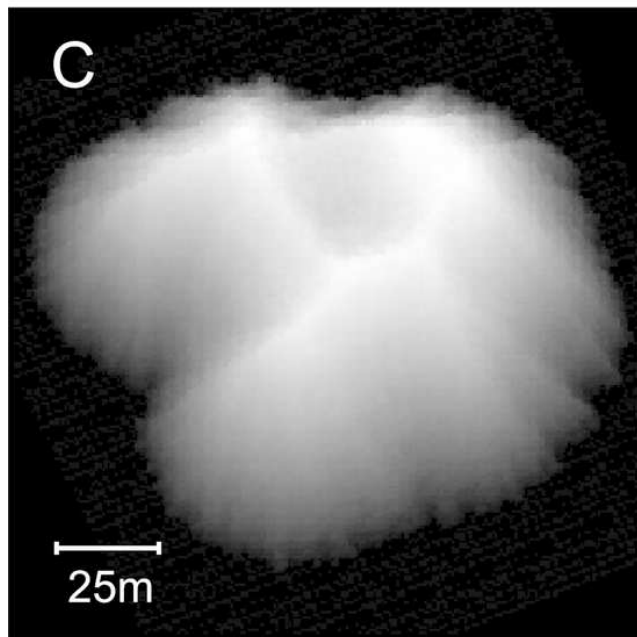
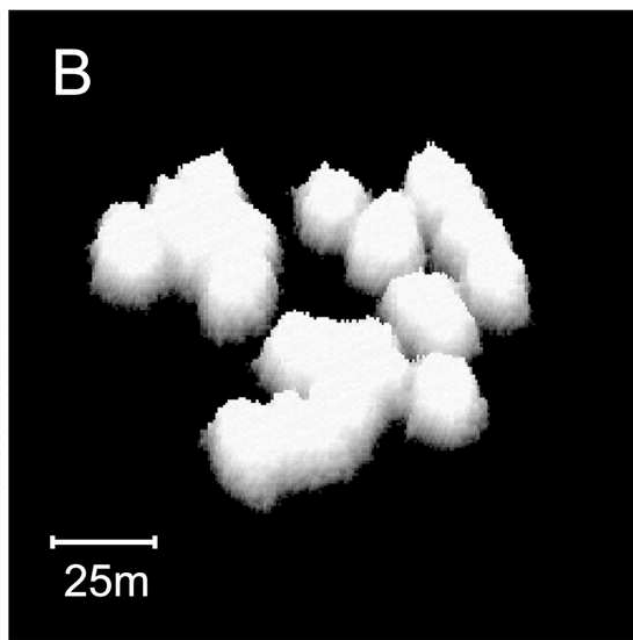
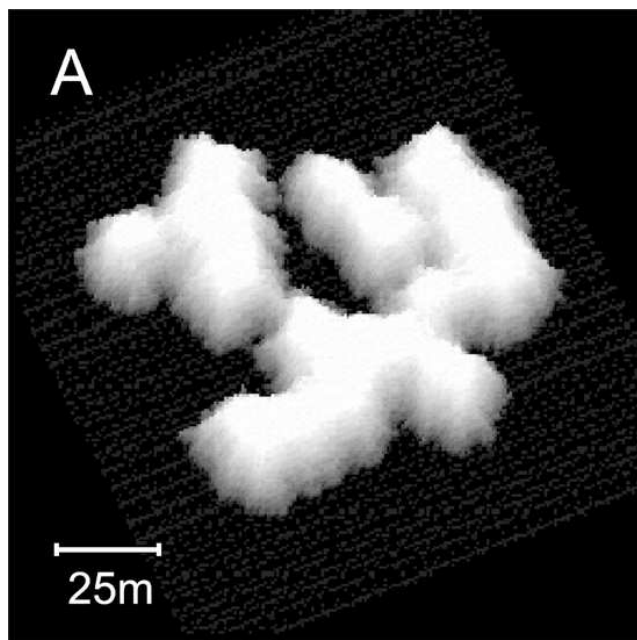
D) Oblique view of the model reef in C. The reef slopes are approximately 60° .



13

Influence of water depth on the morphology of reefs created with the branching *Acropora* model (A, C, E) and the basic model (B, D, F).

These modifications were undertaken in a smaller (90 x 90 m) array, but maintained the default 0.25% colonisation density. A) Branching *Acropora* reefs grown in 10 m depth exhibit a transition toward the nodular forms of the basic model reefs shown in B). C) Branching *Acropora* reefs grown in 50 m depth retain their cellular morphology. D) basic model reefs grown in 50 m depth retain their nodular morphology. E) Branching *Acropora* reefs incorporating sea level rise and depth-dependent growth steepen to approximately 60°. The blocky appearance of these reefs is a consequence of being forced to their maximum slope, which overrides the model's randomness. F) Basic model reefs incorporating sea level rise and depth-dependent growth steepen to approximately 85°.



14

Influence on model reef morphology of varying the colonisation density and timing.

These plan view images show the effects of decreasing the recruitment rate from the default 0.25% to 0.125% (A —branching *Acropora* reef, 100 iterations, B —basic reef, 80 iterations), increasing the recruitment rate to 1% (C —branching *Acropora* reef, 90 iterations, D —basic reef, 60 iterations), and periodically adding new recruits during reef growth (E —branching *Acropora* reef, 100 iterations, F —basic reef, 70 iterations).

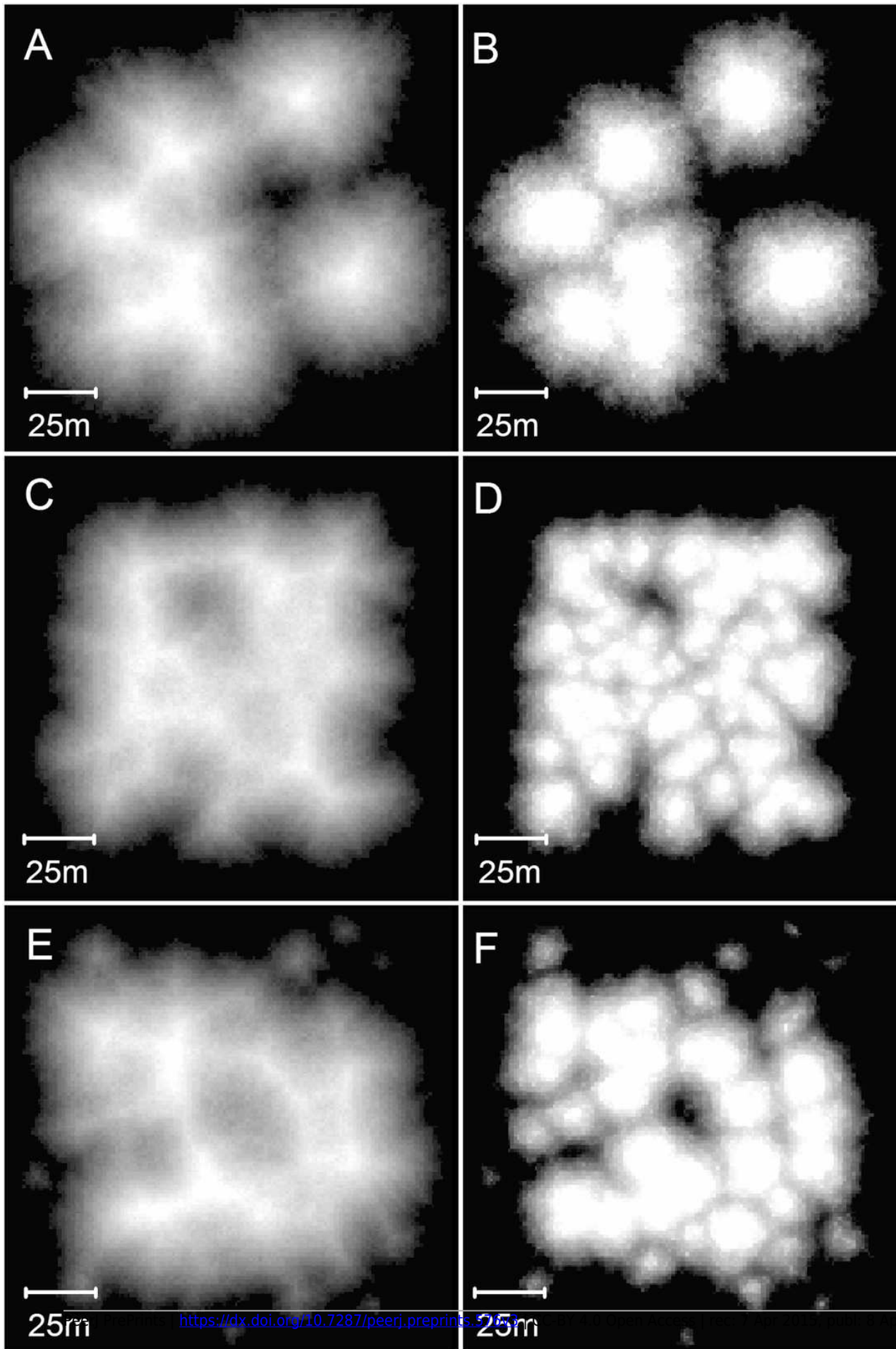


Diagram illustrating the proposed mechanism of ridge formation derived from the branching *Acropora* model.

The diagram shows a cross-section through two merging patch reefs after 50 iterations (the patch reefs arrowed in 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. Rapid accretion is attributed to the tendency for colonies in valleys to remain in place and colonies on reef slopes to collapse.

