Hypoxia shapes coral reefs

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Abstract

The three-dimensional form of a coral reef emerges from thousands of years of ecological interactions between reef-building organisms and their environment. Time integrates those interactions, such that the predominant ecological processes are distilled into reef form, often as striking geometric patterns. Several of these patterns have a fractal appearance, exhibiting nested, scale-invariant structure. Cellular reefs are one fractal reef morphotype, characterised by the presence of subcircular, bowl-shaped, depressions (‘cells’) within a reef network. Cell diameters range from approximately 10 metres to 1 kilometre, the larger cells being compound structures containing multiple smaller cells. The common attribute shared by cellular reefs of all scales is an abundance of staghorn *Acropora*. Staghorn’s fast growth, fuelled by a correspondingly fast metabolism, allows them to rapidly fill lagoons, but leaves them vulnerable to reduced water flow as their own growth begins to impede lagoonal circulation. This article outlines a conceptual model of multi-scale cellular reef development, based on water quality and coral distribution data from the cellular reefs of Western Australia’s Houtman Abrolhos Islands. The key process in the model is density-stratification of the water column during extended periods of warm, calm, weather. Warm water in the shallows traps stable pools of cooler and denser water at depth. The trapped water is rapidly depleted of oxygen, which causes extensive mortality among staghorn colonies. This initiates a negative feedback process in which ongoing growth of colonies above the stratification boundary further reduces water circulation at depth, such that subsequent stratification events kill increasingly larger areas of the reef, eventually producing massive, stagnant cells in which few corals can survive. Investigating the many other reef patterns may provide similar insights into the predominant natural ecological processes occurring on those reefs.

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Introduction

Many coral reef lagoons exhibit striking geometric patterns when viewed from above. A common pattern is that of a network—a configuration termed reticulate reef, after the Latin *reticulum*: a network or net-like structure (Stoddart 1969; Woodroffe 2011). The network theme, however, encompasses a broad spectrum of reef forms. Considered solely as biological patterns, without reference to their scale or context, subtypes within the spectrum bear an intriguing resemblance to the microscopic networks created by cells, capillaries and neurons (Fig. 1). Like those microscopic networks, reticulate reefs often exhibit scale-invariant, nested structure (e.g. Fig. 2; Fig. 3), an apparent manifestation of fractal behaviour (c.f. Kaandorp 1994; Purkis, Riegl & Dodge 2006; Schlager & Purkis 2013). These reef patterns are entirely natural, having developed over millennia with no human influence. Understanding the mechanisms that generate such regular and globally-consistent spatial patterns in coral reefs can potentially deepen our understanding of both modern and ancient reef ecology: modern ecology because those mechanisms are likely to be ongoing and influential, but perhaps not always fully appreciated, on today's living reefs (Hopley, Smithers & Parnell 2007), and ancient ecology because modern pattern/process relationships can be applied to better understand ancient reefs, in which morphological patterns are preserved long after the reef-building organisms have become extinct (Purkis, van de Koppel & Burgess, 2016).

Self-organization

The contemporary view of reticulate reefs is that they are self-organized: i.e. their large-scale structure emerges spontaneously from the local-scale behaviour of their components (Reitkerk & van de Koppel 2008; Blanchon 2011; Schlager & Purkis 2015; Blakeway & Hamblin 2015; Purkis, van de Koppel & Burgess 2016). Because the components of coral reefs are living or once-living organisms, the self-organized perspective implies that reticulate reefs are essentially expressions of life at the local scale, such that each reef pattern in Figure 1 potentially symbolises some aspect(s) of the biology and/or ecology of individual reef-building organisms. This greatly simplifies the search for mechanisms of pattern formation in reticulate reefs, because any consistent correlation between pattern and organism implies causality: if a specific pattern is invariably associated with a specific organism, it is likely that the pattern somehow emerges from the intrinsic traits of that organism. If such associations can be reliably established, several questions typically applied at organism scale can validly be applied at reef scale. From a morphological perspective, two fundamental questions are:

1. To what extent is reef morphology inherent to the organism versus shaped by its environment?
2. What is the natural ontogeny (morphological progression) of the organism through its sea-level-controlled lifespan?

Addressing these questions can potentially contribute to reef conservation and management, by increasing the ecological information that can be extracted from remotely-sensed images (cf. Hamylton, Andréfouët, & Spencer, 2012), and by improving our understanding of the natural changes that occur on reefs as they progress through juvenile, mature, and senile configurations (Maxwell 1968; Hopley 1982; Hopley, Smithers & Parnell 2007).

Cellular Reefs

One apparently consistent correlation between reef pattern and organism is that between cellular reefs and staghorn *Acropora* (Blakeway & Hamblin 2015). Cellular reefs (terminology after Hoskin 1963) are defined by Blakeway & Hamblin (2015) as reticulate reefs in which the ‘cells’ within the reef network are approximately circular in plan view (e.g. Fig. 1a & 1b). Based on surveys in the ‘Maze’ reefs of Western Australia’s Houtman Abrolhos Islands, and published coral community data from other cellular reefs worldwide, Blakeway & Hamblin (2015) observed that cellular reefs invariably seem to be dominated by staghorn *Acropora*. Coring and seismic data from the Maze show that the abundance of staghorn extends throughout the Holocene (Collins, Zhu & Wyrwoll 1996; Collins, Zhu & Wyrwoll 1998). The staghorn-dominated sequence of the Maze is 40 m thick, initiated approximately 10.5-11 kyr BP (thousand years before present), and overlies a uniformly flat last Interglacial grainstone (Collins, Zhu & Wyrwoll 1996; Collins, Zhu & Wyrwoll 1998). These findings clearly imply that cellular reefs are a natural growth form of staghorn *Acropora*, and are therefore of significant interest as a potential type example of self-organized, trait-based, reef geomorphology.

A possible mechanism of cellular reef development in the Maze was provided by Blakeway & Hamblin (2015), who used cellular automata simulations to show that Maze-like morphology can develop through growth and coalescence of *Acropora* patch reefs. The essential trait generating cellular morphology in the model is the well-documented propensity of staghorn *Acropora* colonies for fragmentation (Maragos 1972, Bak 1976; Gilmore & Hall, 1976; Tunnicliffe, 1981; Bothwell, 1982; Highsmith, 1982). Due to this trait, expanding *Acropora* patch reefs behave essentially as sandpiles, or 'haystacks' (Kinzie 1973), their slopes constantly oversteepening and collapsing to maintain the angle of repose. This behaviour changes when adjacent patch reefs meet, however, because each patch reef then supports the other, such that collapse rarely occurs in the merging zone between the patch reefs. The retention of *in-situ* growth in the merging zones increases their accretion rate, which links the patch reefs together into the characteristic cellular structure. Enclosed cells are initially stellate (star-shaped) in plan view, but become circular over time as staghorn growth and fragmentation fills and smooths their irregularities (see Fig. 11 and Fig. 15 in Blakeway & Hamblin 2015).

The model accurately reproduces the small-scale cellular morphology of the Maze, and the model's fragmentation-based mechanism is supported by field observations in the Maze (Blakeway & Hamblin 2015). In the wider context, however, the model only provides a partial explanation of cellular reef development, because it cannot reproduce the compound cells-within-cells morphology of medium- and large-scale cellular reefs (Fig. 2; Fig. 3). While it does produce a few compound cells, they are relatively small (approximately 100 metres across), and distinctly multi-lobed, not circular (see Fig. 10 in Blakeway & Hamblin 2015). This limitation suggests that the model's simplified representation of staghorn *Acropora*, based solely on fragmentation, lacks the additional trait(s) and/or process(es) that generate medium- and large-scale cellular morphology in real reefs. A more comprehensive explanation of cellular reefs clearly requires an understanding of how medium and large-scale cells develop, and what they signify.

Self-limitation

An influential process occurring in real cellular reefs, and not represented in the model, is the progressive restriction of water circulation caused by reef growth; a process termed 'self-limitation' by Blanchon (2011). In the Abrolhos Maze, self-limitation operates through stratification of the water column within the cells, and the consequent restriction of live *Acropora* to relatively shallow depths on the cell walls (Wyrwoll et al., 2006; Blakeway & Hamblin 2015). Self-limitation appears to have significantly slowed the infilling of the Maze through the mid to late-Holocene, thereby maintaining its cellular structure to the present, nearly 11,000 years since its inception. This contrasts strongly with the model reefs, which indicate that, in the absence of self-limitation, the Maze would have become completely infilled by *Acropora* within approximately 7,000 years.

The apparent influence of self-limitation in the Abrolhos Maze, and the likelihood that self-limitation is a general phenomenon in cellular reefs worldwide (Blanchon 2011), make it a strong candidate as a potential process generating compound medium and large-scale cells in real reefs. Drawing from the information outlined above, the working hypothesis evaluated in this article is that compound medium and large-scale cells emerge sequentially from small-scale cells as lagoonal circulation declines. Small-scale cells are considered the fundamental form of staghorn *Acropora* patch reef systems, emerging solely from colony growth and fragmentation, whereas medium and large-scale cells are derivations of the fundamental form, emerging through a self-limiting feedback between reef accretion and water circulation. Staghorn *Acropora*'s rapid growth is a central aspect of the hypothesis, because it has allowed them to quickly expand into newly-available lagoon habitat during deglacial sea level rise (Renema et al. 2016), and to substantially fill the accommodation space in those lagoons, thereby restricting water circulation and leading to self-limitation.

Hypoxia

An additional aspect of staghorn *Acropora*'s growth, critical with respect to self-limitation, is that its fast growth is underlain by a correspondingly fast metabolism (Smith, 1981). This creates a significant vulnerability for staghorn *Acropora*: because they depend on water flow for the delivery of essential chemicals and the removal of metabolic byproducts, they risk rapid depletion and/or buildup of these materials when flow is reduced or halted (Dennison & Barnes, 1988). Dissolved oxygen is likely to be a critical limiting resource in these situations, for three main reasons: first, oxygen, and other gases, diffuse so slowly through water (< 1 mm/hour) that transport by diffusion is negligible at all but the smallest scales (Verwey 1931). Second, the metabolic oxygen requirements of staghorn *Acropora* are remarkably high; so high, in fact, that early experimental estimates of oxygen consumption in *A. muricata* (Mayer 1918) and *A. hebes* (synonym *A. aspera*; Verwey 1931) were considered unreliable, on the basis that they were equivalent to those of mobile animals such as fishes (Yonge, 1957, p. 437). Recent, well-controlled, experiments in *A. yongei* have, however, demonstrated a low-tolerance threshold for dissolved oxygen of approximately 4 mg/L (Haas et al. 2014), which is indeed equivalent to that of most fishes (Vaquer-Sunyer & Duarte, 2008). The third reason is that, because the decay of dead organisms by aerobic bacteria consumes oxygen, any reef mortality event in a low-flow environment, whether initiated by oxygen depletion or not, has the potential to become an oxygen crisis through runaway feedback, as observed in staghorn-dominated lagoons by Simpson et al. (1993) and Hobbs & Macrae (2012). These two observations are part of a wider set of suspected hypoxia-related mass mortality events involving a variety of reef communities and occurring in a variety of reef settings, the common attribute being stagnation of the water column, generally induced by warm, calm weather (Kinsey 1979; Delesalle 1985; Adjeroud, Andréfouët, & Payri 2001; Hobbs & McDonald 2010; Altieri et al. 2017; Gajdzik & DeCarlo 2017; Baird et al. 2018). Altieri et al. (2017) reviewed recent literature to make a convincing case that similar hypoxic events frequently occur on coral reefs worldwide, but, due to their intermittent and short-lived nature, have been significantly under-reported. In reef environments prone to stagnation, hypoxia is potentially a dominant ecological influence, as recognised by Altieri et al. (2017), and the other researchers cited above, but also much earlier by Verwey (1931). In addition to his oxygen consumption experiments in corals and algae, Verwey (1931) undertook comprehensive dissolved oxygen measurements on multiple reefs in Batavia (Djakarta) Bay, Indonesia, concluding that (p. 178): "*...the quantity of oxygen, present in the water, must often be the limiting factor in reef growth*."

Based on the foregoing information, hypoxia must be considered a likely agent of self-limitation in cellular reefs. This article examines dissolved oxygen dynamics and coral distribution in the cellular reefs of the Maze, and uses the results to provide a testable model of the emergence, through self-limitation, of medium and large-scale cellular reefs from small-scale cellular reefs.

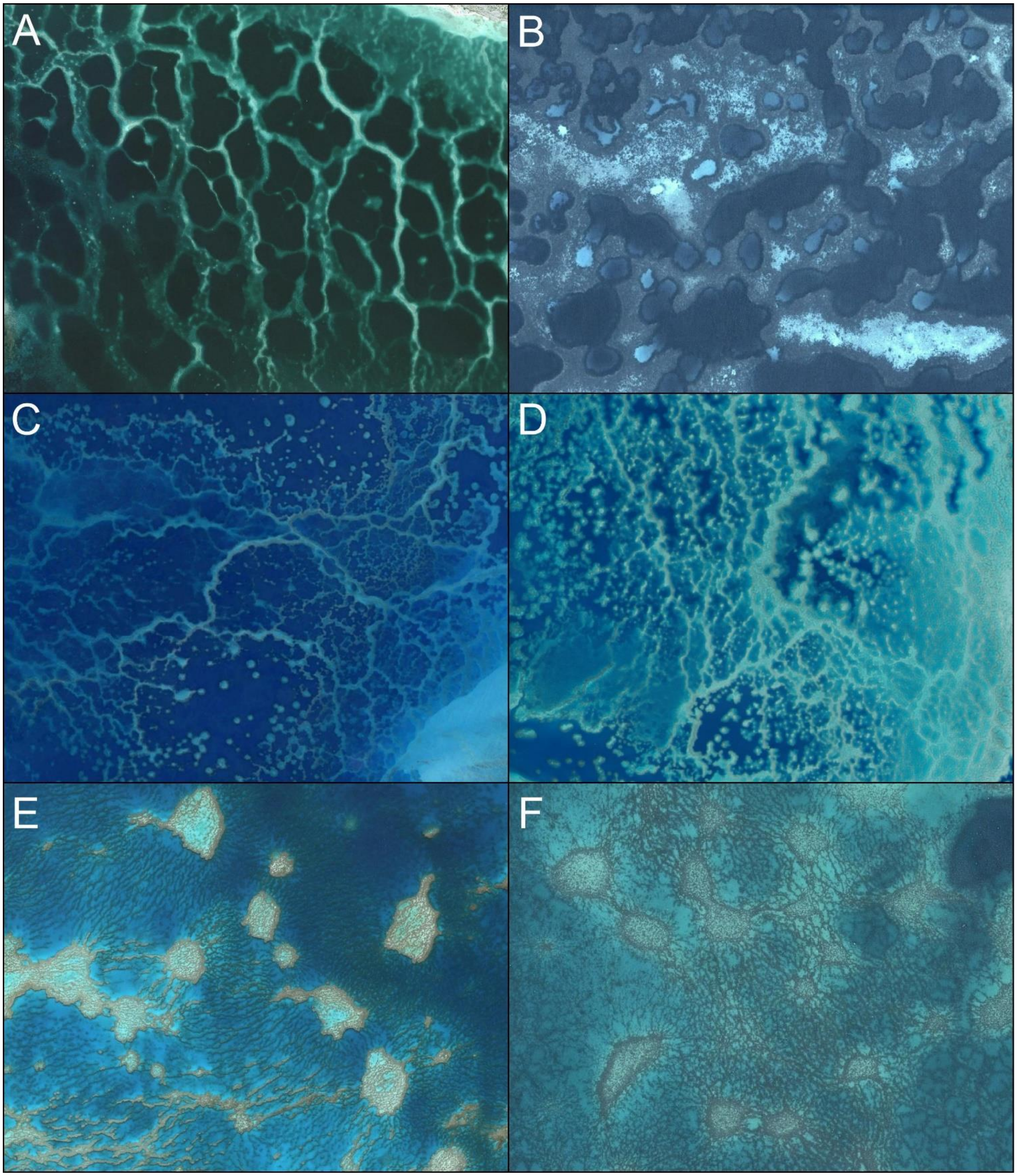

Figure 1. Reticulate reef subtypes. A & B: cellular structure in the reticulate reefs of Kanton Atoll, Kiribati (2.81°S, 171.68°W) and the Houtman Abrolhos Islands, Western Australia (28.68°S, 113.824°E). C & D: capillary-like structure in the reticulate reefs of Pearl and Hermes Atoll (27.867°N, 175.812°E).) and Alacrán Reef, Yucatán, Mexico (22.46°N, 89.67°W). E & F: neuron-like structure in the reticulate reefs of Hardy Reef, southern Great Barrier Reef (19.755°S, 149.232°E) and Selakan Bank, Semporna, Malaysia (4.589°N, 118.664°E). Images: Google, Digital Globe.

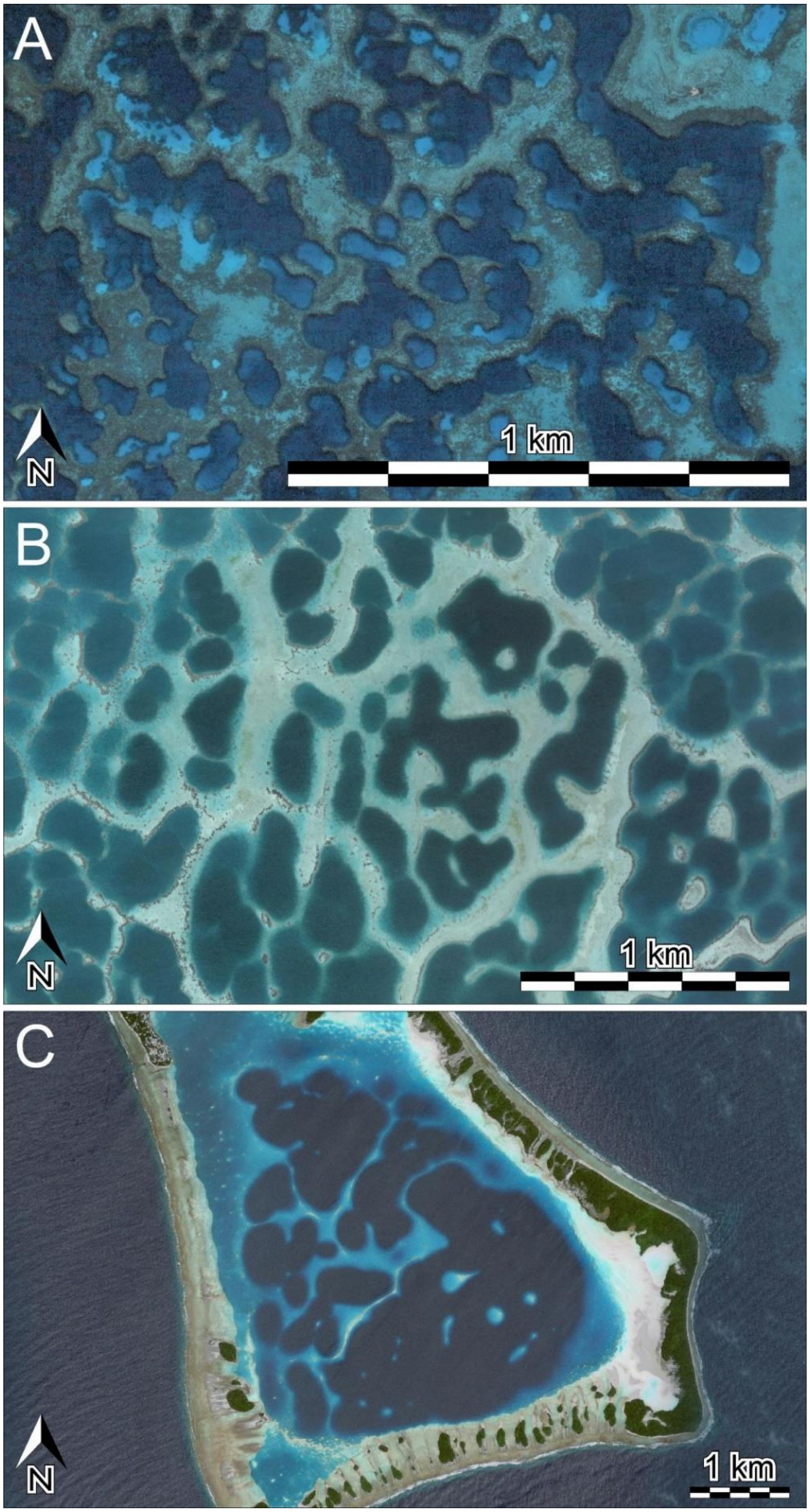

Figure 2. Cellular structure at successively larger scales: (A) ‘The Maze’, Houtman Abrolhos Islands, Western Australia (28.676°S, 113.819°E), (B) Mataiva Atoll, Tuamotu Archipelago (14.882°S, 148.668°W), and (C) Atafu Atoll, Tokelau (8.56°S, 172.494°W). Images: Google, Digital Globe.

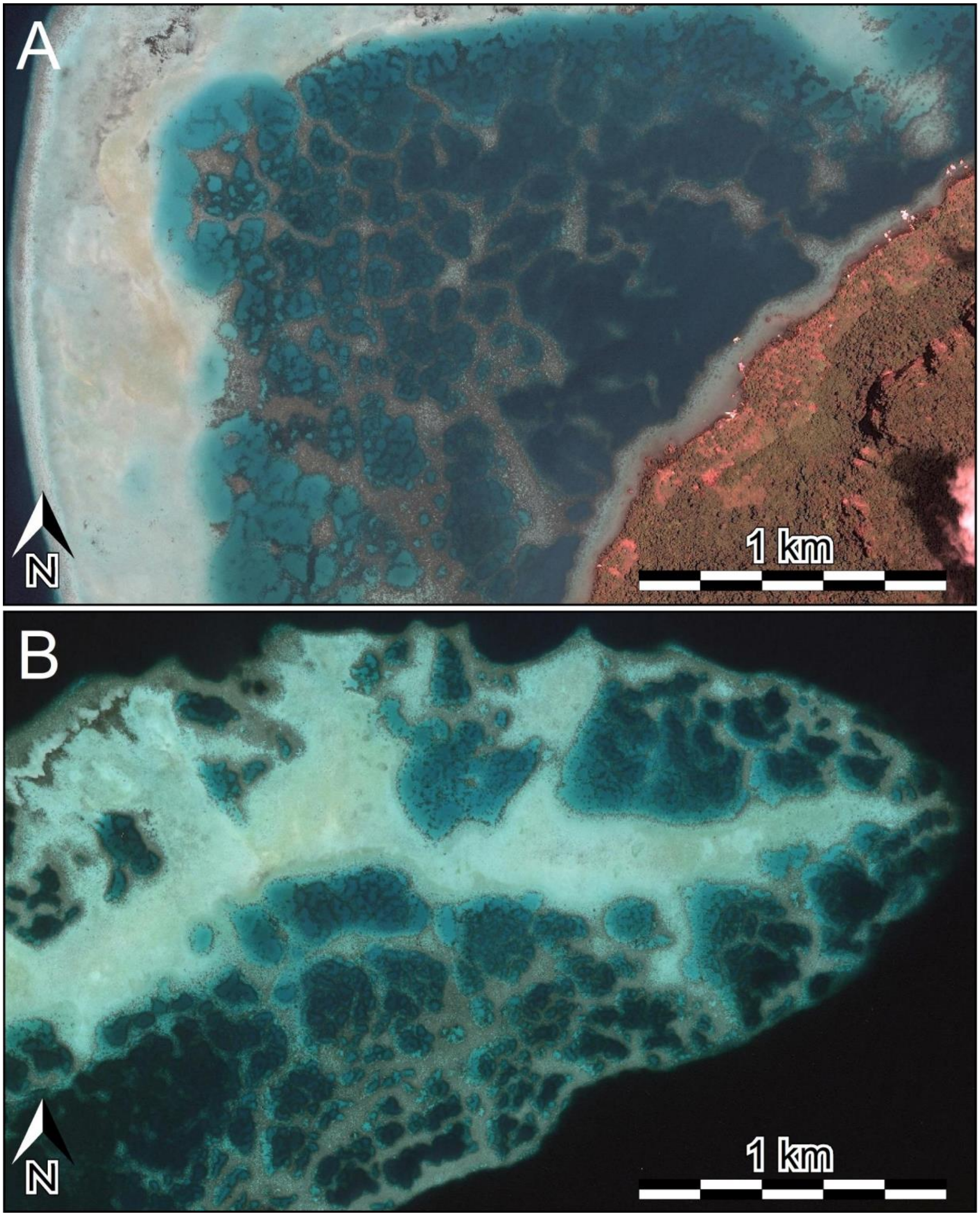

Figure 3. Nested cellular structure in reticulate reefs of (A) Gaya Bank, Semporna, Malaysia (4.623°N, 118.723°E) and (B) xxxx Bank, East Kalimantan (1.599°N, 118.486°E). Images: Google, Digital Globe.

Methods

Water quality

Depth profiles of dissolved oxygen, pH, temperature, and salinity were recorded from multiple cells within the Maze in the autumn (March-April) and spring (October) of 1996 and 1997, using a Hydrolab Instruments H_20 probe. Measurement of all parameters involved taking a surface reading at 0.5m depth, a second reading at 2m depth, and subsequent readings at 2m intervals to the seafloor. The most comprehensive records were collected within 'cell O', a 50-metre-wide and 14-metre-deep cell on the southwestern edge of the Maze (Fig. 4).

Coral depth distribution

Coral depth distribution within cells was quantified from four video belt transects per cell, oriented to the cardinal directions, and running upslope from the base of the cell to the surrounding reef flat. The transects were filmed from 0.5 m above the substrate, giving a field of view of approximately 0.5 x 0.3 m. Tide-corrected depth was recorded at one metre intervals along each transect, and benthic substrate composition was determined by point counting sequential non-overlapping still images, using five fixed points per image (English, Wilkinson & Baker 1997) and 25 substrate categories (see Data S1 in Blakeway & Hamblin 2015).

Coral transplants

Two coral transplant experiments were carried out to examine coral survival within cell O. In the first experiment, in April 1996, 18 branches of 20 to 30 cm length were collected from a thicket of *Acropora muricata* at 12m depth outside cell O to the south. Twelve branches were transplanted inside the cell: six at 12 m depth and six at 3 m depth. The remaining six branches were returned to their original site as handling controls. In the second experiment, in October 1996, six *Acropora* branches (nominally *A. abrolhosensis*), six small *Favia speciosa* colonies of 10 to 15 cm diameter, and six small *Nephthea* soft coral colonies of 10 to 15 cm expanded height were transplanted from 6 m depth to 12 m depth within cell O. Because the *Favia* and *Nephthea* colonies had grown on dead *Acropora* branches, they were readily transplanted with no apparent handling damage.

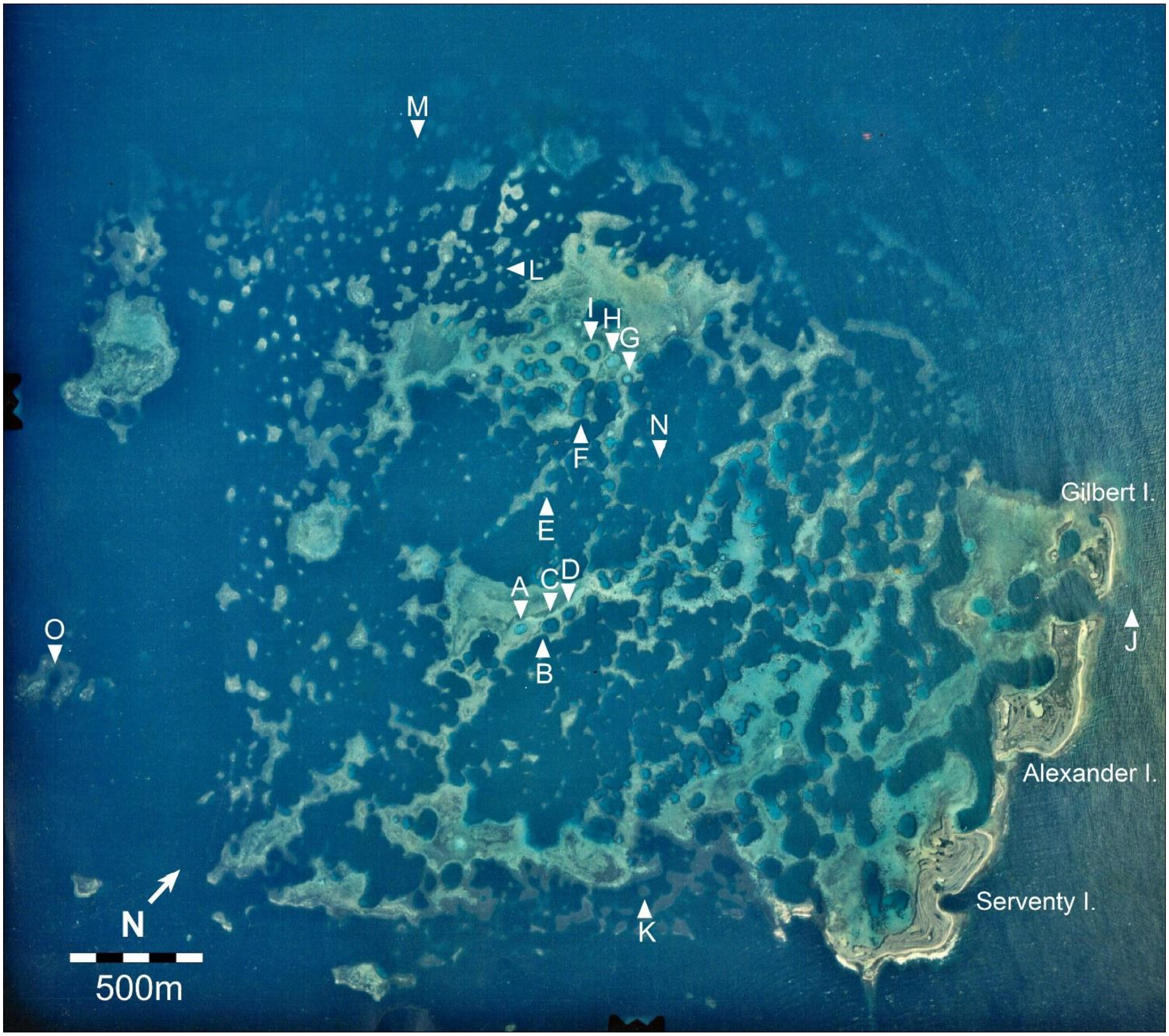

Figure 4. ‘The Maze’ in the Easter Group of the Houtman Abrolhos Islands, showing the study cells labelled A to O. Image: Google, Digital Globe.

Results

Water quality

Stratification of the water column, in all measured parameters, was prevalent in the Maze cells. Stratification was correlated with cell depth: cells less than approximately five metres deep were rarely stratified, cells between five and 15 metres deep were intermittently stratified, and cells more than 15 metres deep were almost always stratified (Fig. 5). The water column on the surrounding shelf was unstratified (Fig. 6). The most variable parameters were dissolved oxygen and pH, which were always strongly positively correlated. The variability in dissolved oxygen concentration in moderately-deep cells is illustrated by the cell O profiles in Fig. 7, which show frequent, often multi-layered, stratification of the water column, particularly during autumn (April). Visually, the stratification was evident as a hazy appearance within the lower strata, and a refractive lensing effect when crossing stratification boundaries. Stratification was strongest during the prevailing warm and relatively calm weather in autumn, and weakest during the colder and more windy weather in spring. Significant deviations from these patterns occurred on the 14/10/96, 7/4/97, the 21/10/96, and the 22/10/97 (Fig. 7). In each case, the deviations coincided with periods of unseasonal weather; the stratified conditions in October followed warm and calm weather, and the unstratified conditions in April followed cold and windy weather.

Coral depth distribution

The zonation of the benthic community on the internal slopes of cell O is compressed and sharply defined, with each zone occurring as a band at consistent depth around the cell. Tabular and staghorn *Acropora* occupy the upper 2m of the slopes, thickets of staghorn *Acropora* occur to 7m, a mixed coral assemblage consisting primarily of faviids extends to about 10m, *Nephthea* soft corals to 11m, and the macroalgae *Lobophora variegata* to 12m (Fig. 8). Below 12m, dead coral colonies and staghorn rubble are covered by epilithic turf algae and/or coralline algae. Many of the dead colonies are upright and in-situ, indicating that the base of the cell was once a living reef (Fig 9).

Zonation within the other surveyed cells in the Maze is neither as vertically-compressed nor sharply-defined as that within cell O, but shows the same general patterns of greatly reduced live coral cover at depth, and a consistently depth-banded benthic community (Blakeway & Hamblin 2015).

Coral transplants

In the April 1996 transplant, all six *A. muricata* branches transplanted to 12 m depth inside cell O bleached severely after one to three days, then began to shed tissue (Fig. 9), and died within a week. The six branches transplanted to 3 m depth inside cell O survived, although two branches bleached slightly before recovering. All six handling control branches survived apparently unaffected.

In the October 1996 experiment, the transplanted branches and colonies were first examined eight days after being moved. At that time, four of the *A. abrolhosensis* branches were bleached in patches, but the *Nephthea* and *Favia* appeared healthy. When they were next examined in January 1997, three months after being transplanted, only five *Nephthea* and three *Favia* colonies remained alive. By April 1997, after six months, all had died.

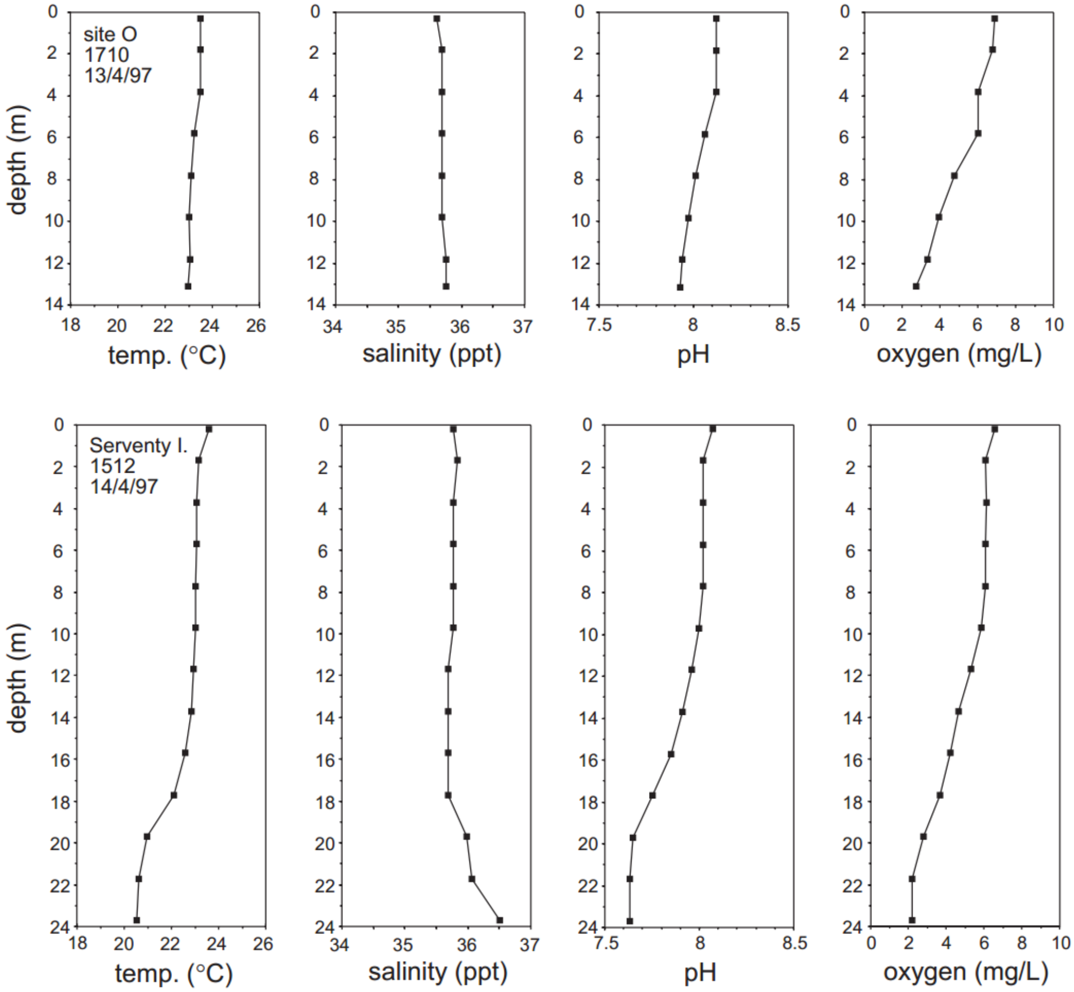

Figure 5. Water quality profiles from cell O and the Serventy Island cell in April 1997 (cell O: 28.7016°S, 113.7971°E; Serventy Island: 28.6818°S, 113.8344°E).

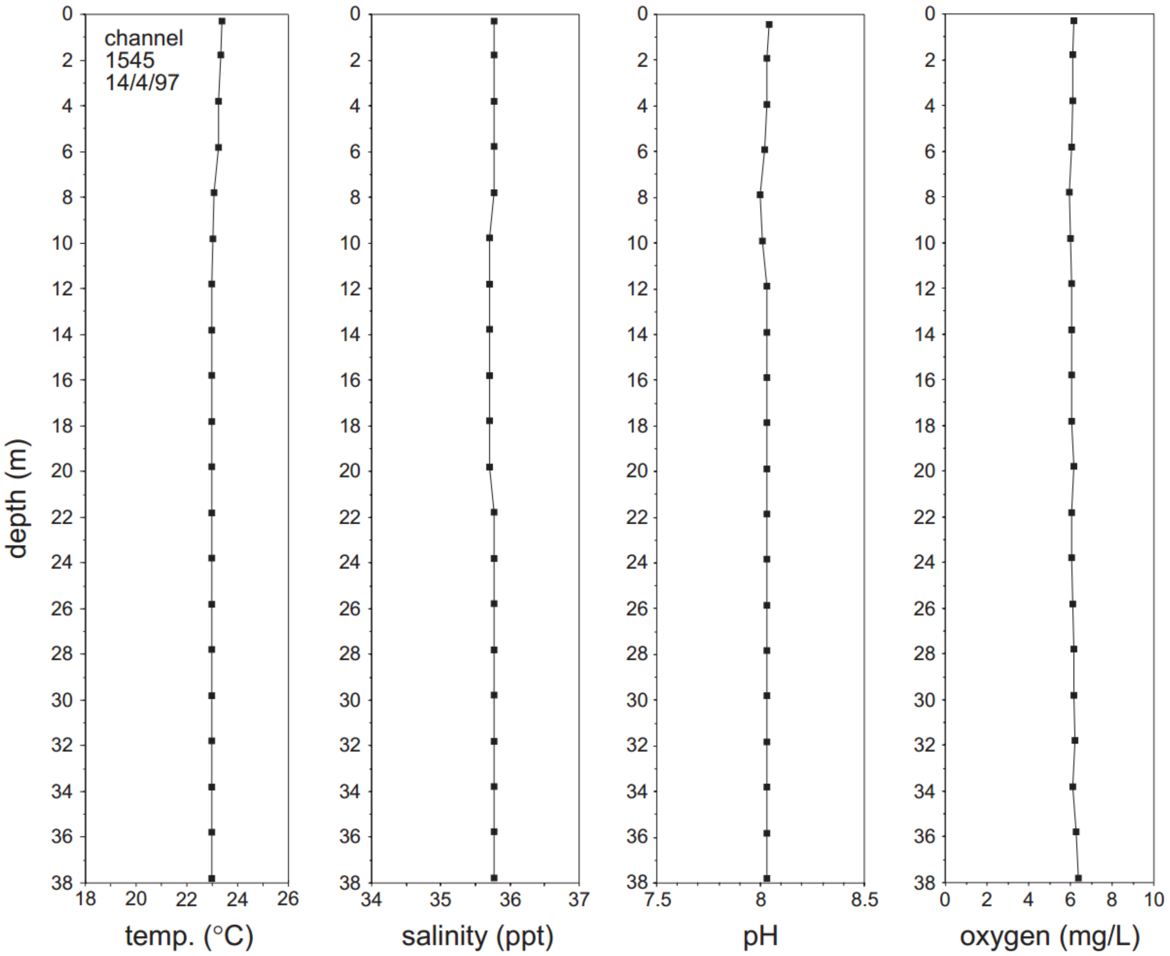

Figure 6. Water quality profile from the open shelf east of the Maze in April 1997 (28.68°S, 113.84°E).

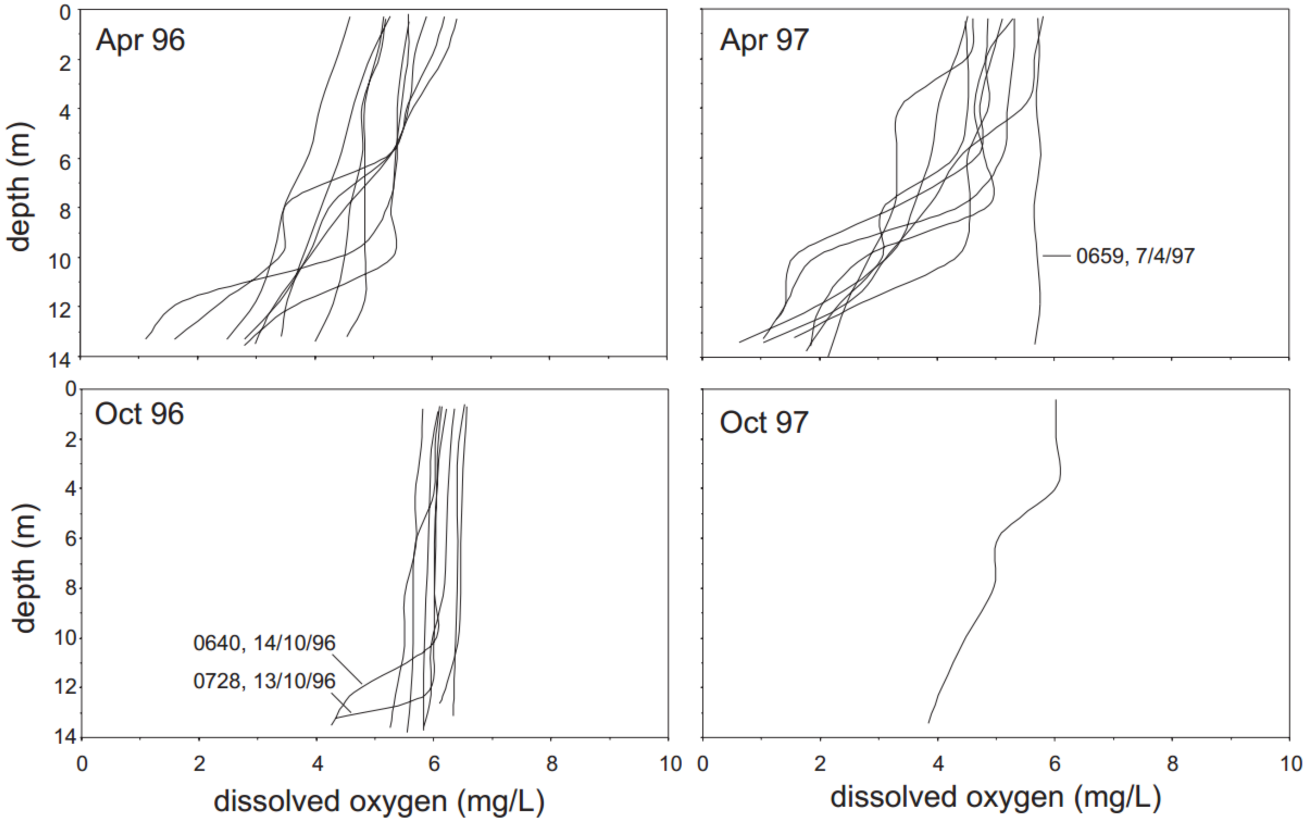

Figure 7. Early morning (6 to 9 am) dissolved oxygen profiles from cell O in autumn (April) and spring (October) 1996 and 1997.

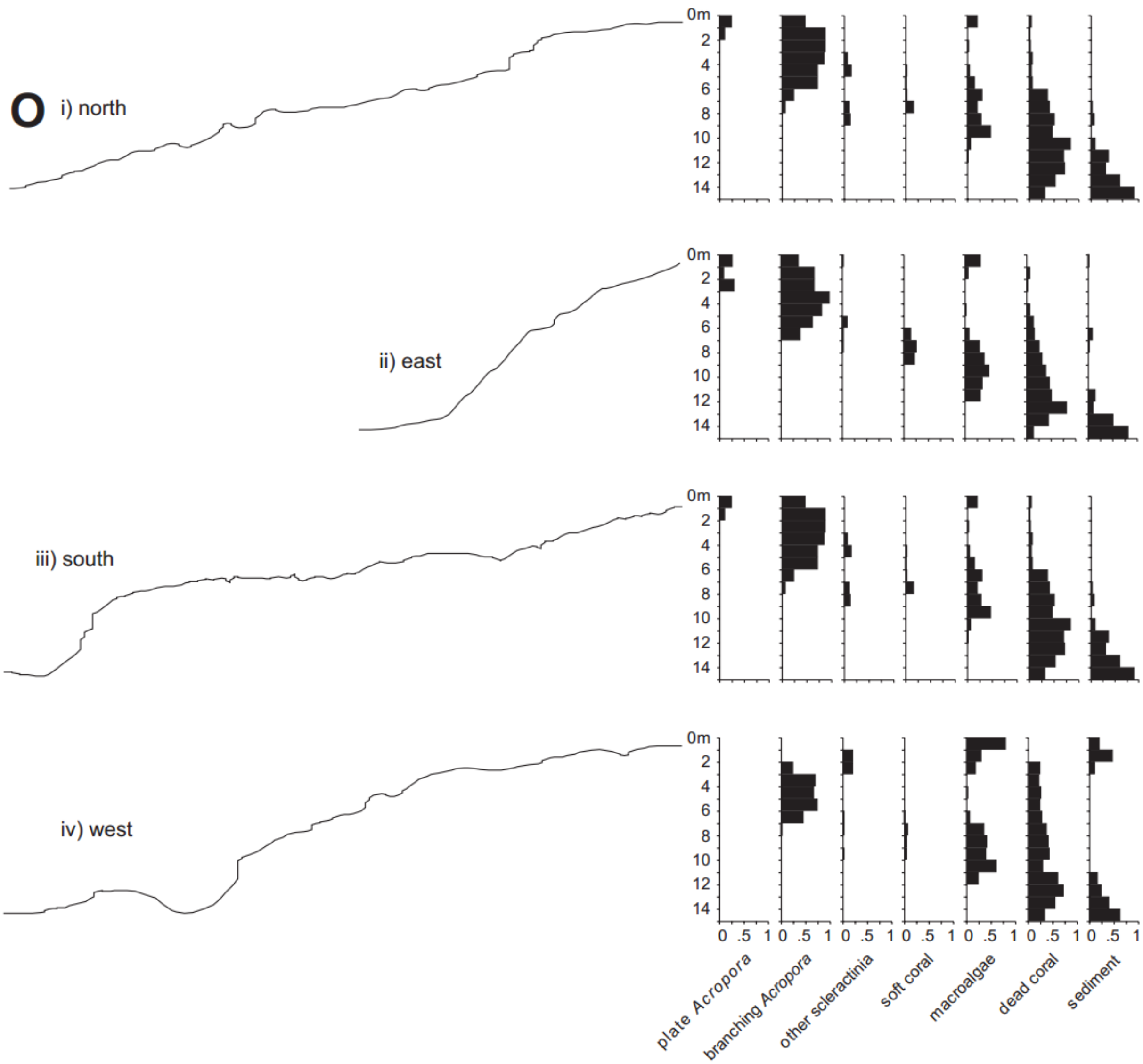

Figure 8. Bathymetric profiles (left) and depth-zoned benthic community graphs (right) within cell O.

Figure 9. In-situ dead *Acropora* and *Montipora* colonies at 10m depth on the north slope of cell O in April 1996. The only living scleractinian corals at this depth are small faviid colonies (arrowed). The scale bar is marked in 10cm intervals.

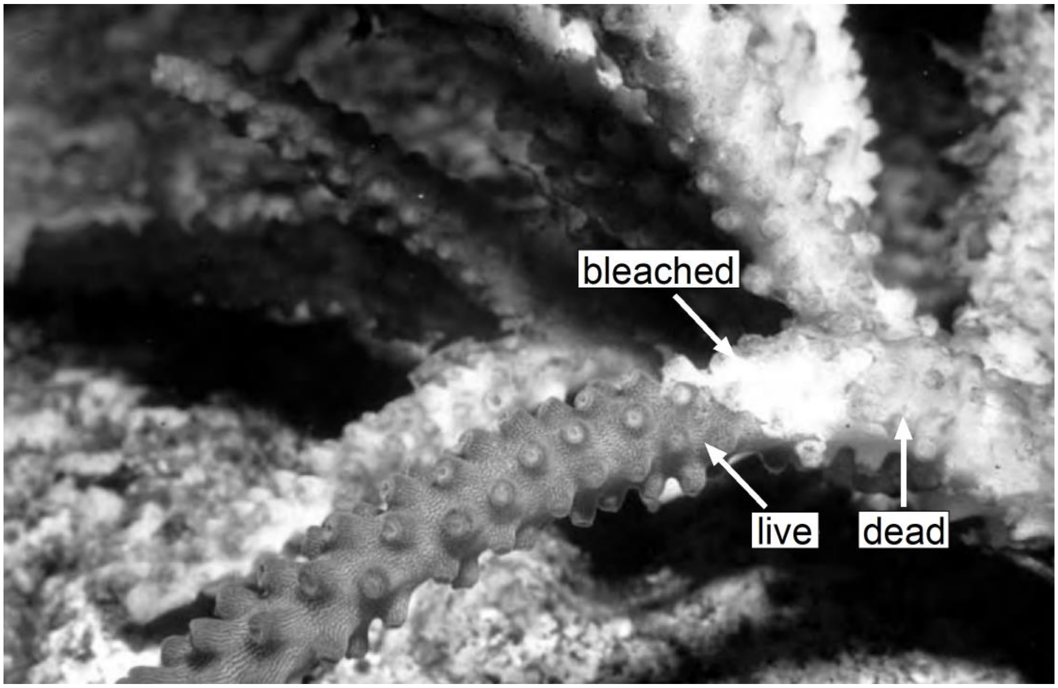

Figure 9. Bleached and dying *Acropora abrolhosensis* branch after being transplanted from 6 m to 12 m depth in cell O, October 1996.

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Discussion

Considered jointly, the water quality profiles, benthic community distribution, and coral transplant results provide strong circumstantial evidence that dissolved oxygen concentration controls coral depth zonation within cell O, and, by extension, all enclosed cells in the Maze. The 7 m lower depth limit of live staghorn *Acropora* in cell O is particularly compelling, because it coincides with the depth at which the autumn dissolved oxygen concentration typically falls below 4 mg/L, the experimentally-determined low-tolerance limit of staghorn *Acropora* (Haas et al. 2014). Further circumstantial evidence linking staghorn mortality to oxygen depletion in cell O is the sequence and timing of bleaching, tissue necrosis, and death of staghorn branches transplanted to 12 m depth in autumn, which corresponds exactly to that of staghorn branches subjected to hypoxia by Haas et al. (2014). The sequentially deeper lower limits of other scleractinians and *Nephthea* soft corals in cell O may be similarly constrained by dissolved oxygen availability, based on their sequentially higher tolerance to transplantation.

Stratification

Consistent with the inferred sequence of events initiating hypoxia on reefs elsewhere (Kinsey 1979; Adjeroud, Andréfouët, & Payri 2001; Hobbs & McDonald 2010; Gajdzik & DeCarlo 2017; Baird et al. 2018), hypoxia in cell O appears to be initiated by density-stratification of the water column during warm, calm weather. Density-stratification can develop quickly (< 1 day), and strengthens if the warm, calm weather prevails. The main driver of density-stratification seems to be surface water heating, with a secondary influence of salinity. In cell O, and other cells of less than approximately 15-20 metres depth, density-stratification can be broken down by strong wind alone. Deeper cells appear to remain stratified throughout most of the year, only overturning when surface water cools during winter.

Once density-stratification develops, biological activity within the trapped strata drastically reduces dissolved oxygen and pH. Microbial respiration within the water column, rather than respiration of benthic organisms, appears to be the main driver of oxygen depletion at present, because oxygen depletion is horizontally consistent within each layer. The energy source for microbial respiration is presumably dissolved organic matter derived from the surrounding reefs, although no sampling was undertaken to examine this aspect.

Present conditions at depth within cell O are clearly unsuitable for corals. However, the area was, until recently, a living staghorn/*Montipora* reef (Fig. 10). How recently is unknown, but the condition of the dead corals suggests perhaps only a decade or so. The most likely explanation for this situation is that growth of the surrounding reef has progressively reduced water circulation within cell O, leading to stratification, hypoxia, and coral mortality. A significant consequence of this process is that, as the surrounding reef grows upward, the mean depth of the stratification boundary will also migrate upward, such that corals once safely above the stratification boundary will be killed as it migrates upward. This progressive shallowing of the stratification boundary is likely to occur in all cellular reefs, and is a potential mechanism for the emergence of medium and large-scale cells, as outlined below.

Conceptual model

Because the conceptual model outlined here considers small-scale cellular reefs to be the precursors of medium and large-scale cellular reefs, the development of the Abrolhos Maze is an informative starting point for the model. The Maze grew on a flat and featureless last Interglacial grainstone, in the lee of a barrier reef and a chain of emergent last Interglacial islands to the southwest (Collins et al. 1998; Wyrwoll et al. 2006). Staghorn *Acropora* colonised the seafloor immediately it was submerged in the early Holocene (Collins et al. 1998; see Fig 10, section A). The distribution of the initial staghorn patch reefs appears to have been random, based on modelling described in Blakeway & Hamblin (2015). As the patch reefs enlarged and coalesced, their small-scale cellular morphology developed, as a consequence of fragmentation (Blakeway & Hamblin 2015; see Fig. 10 section B). Intermittent stratification within the developing cells probably began at this stage, due to their restricted water circulation (Fig 10., section D). Stratification reduced coral cover within the cells, keeping them open as the surrounding reefs grew upward. Thus, the small-scale cellular structure of the Maze arose as a primary growth pattern, with the stratification being consequential (Blakeway & Hamblin, 2015). The reason the Maze did not progress to medium and large-scale morphology, according to the conceptual model, is that, compared to most other cellular reefs, the Maze is a relatively open and well-flushed system. In more enclosed lagoons, where water residence times are significantly higher, stratification and hypoxia are likely to be even more prevalent and influential (Adjeroud, Andréfouët, & Payri 2001; Andréfouët et al. 2015). In cellular lagoons, the most restricted of all, this could result in stratification emerging as the dominant geomorphological process, with occasional severe stratification events capturing multiple adjacent small-scale cells within large pools of hypoxic bottom water (Fig 10, section E). Subsequent growth of shallow corals would tend to further restrict circulation and raise the stratification boundary, such that ensuing stratification events may capture additional cells (Fig 10, section F). While Figure 10 shows the sequence ending at that point, as the reefs attain sea level, the sequential-capture mechanism has the potential to generate significantly larger, hierarchically-structured, cells, particularly in deeper lagoons such as that of Atafu (Fig. 2c). Detailed bathymetric maps of Atafu and other large-scale cellular lagoons, such as Fakaofo (9.38°S, 171.22°W), and Manihiki (10.42°S, 161°W), would constitute a good test of the model, particularly if combined with depth-integrated water quality logging and benthic habitat mapping (cf. Andréfouët et al. 2015). Simulation could clearly also contribute to model development and evaluation.

Application to ecological theory

Research on cellular reefs, and other patterned reefs, can potentially contribute to ecological theory, particularly with respect to the relationships between process, form and scale in natural patterns (e.g. Pringle & Tarnita 2017). For example, although stratification-induced hypoxia is inferred to be the process controlling the sequentially larger scales of cellular reefs, the cells' circularity probably arises from the same process that generates circularity in small-scale cells: the filling and smoothing influence of *Acropora* fragmentation and collapse (Blakeway & Hamblin 2015). The transition from small to medium and large-scale cellular morphology therefore appears to be an additive process, progressing from an initially very pure system in which reef morphology is generated solely by *Acropora* growth and fragmentation, to a more complex system in which hydrodynamic self-limitation becomes increasingly important, but the signature of fragmentation remains. Feedbacks within the system also appear to be additive. The fundamental feedback mechanism is a self-regulating oscillation of reef slopes around their angle of repose, due to the oversteepening and collapse of *Acropora* colonies (cf. Bak, Tang, & Wiesenfeld, 1987). The onset of stratification and hypoxia provides an additional feedback mechanism, creating ever-larger compound cells, but not overriding the original self-regulating feedback, which continues to maintain all reef slopes at the angle of repose.

Further research on process/form/scale relationships in other examples of scale-invariant reef morphology would provide interesting counterpoints to the cellular reef example. The classic anastomosing reticulate reefs of shallow lagoons (Woodroffe 2011; see Fig. 1B, Fig. 1C) are especially interesting in this regard, as they consistently exhibit smaller-scale anastomosing structures on their sandy platform tops (e.g. Alacrán Reef at 22.422°N, 89.678°W). Purkis, van de Koppel & Burgess (2016) provide a plausible model for the development of Alacrán’s reticulate reefs, based on reef response to water flow and sedimentation. Modelling by Mistr & Bercovici (2003) also highlights the potential role of water flow in generating reef patterns at multiple scales. Intuitively, it seems reasonable that the anastomosing alignment of the capillary-like reticulate reefs is somehow related to flow. The bizarre neuron-like structures of Hardy Reef (Fig. 1E) and Selakan Bank (Fig. 1F), on the other hand, are perplexing. Given their appearance and shallow-water setting, they are almost certainly constructional, self-organized features. Although it is difficult to envisage a process that could produce their forms, this difficulty is perhaps largely due to our preconceptions, in that we automatically tend to seek a cause at the scale of the effect. Self-organization suggests that we should instead look much closer, onsite and underwater, for mechanisms operating at the scale of the reef-building organisms themselves, via their structural, physiological, and behavioural traits, their interactions with their surroundings, and the events occurring in their lives. Virtually all traits, interactions, and events have the potential to influence reef morphology, directly or indirectly, in emergent and unpredictable ways. Determining causality may therefore be complex. However, under the assumption that the best-defined reef patterns are generated by the most influential processes, field studies investigating local reef-building processes within distinctly-patterned reefs—the neurons and others—have the potential to provide many fundamental insights into reef ecology.

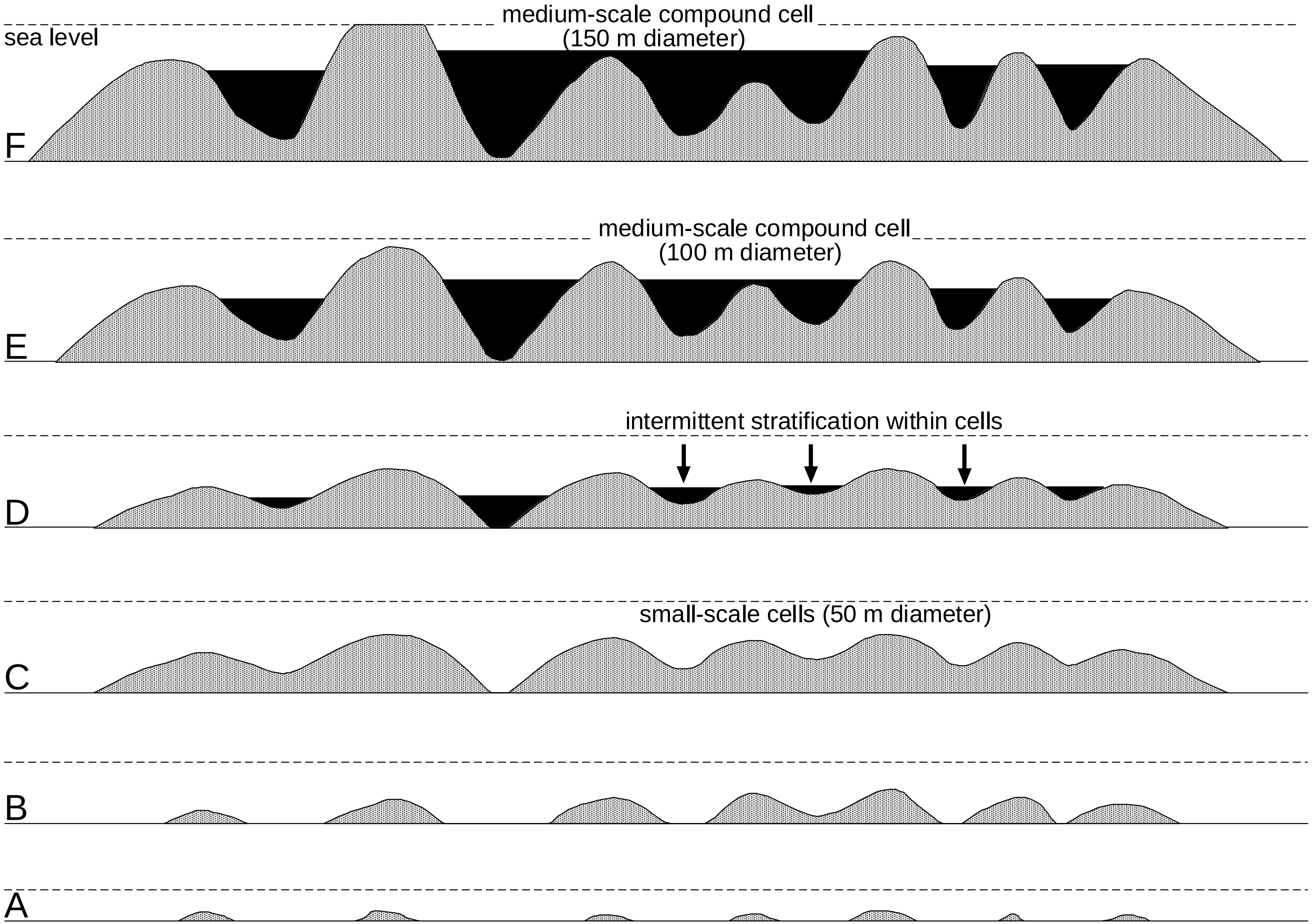

Figure 11. Hypothetical sequence of reef cross-sections, labelled A to F, depicting the sequence of events in the proposed mechanism of medium-scale cell development. (A) *Acropora* patch reefs colonise a flat pre-Holocene substrate as sea level (dashed line) rises onto the shelf in the early Holocene. (B) Patch reefs enlarge. (C) Patch reefs merge to generate cellular structure (see Fig. 11 in Blakeway & Hamblin, 2015). (D) The cellular structure restricts circulation, trapping density-stratified pools of hypoxic bottom water (black) during intermittent stratification events. (E) Accretion within the cells is retarded, amplifying the reef topography, raising the stratification boundary, and resulting in the capture of adjacent small-scale cells during a subsequent stratification event. (F) Process continues, capturing an additional cell.

References

Adjeroud M, Andréfouët S and Payri C. 2001. Mass mortality of macrobenthic communities in the lagoon of Hikueru atoll (French Polynesia). *Coral Reefs* 19: 287–291

Altieri AH, Harrison SB, Seemann J, Collin R, Diaz RJ, Knowlton N. 2017. Tropical dead zones and mass mortalities on coral reefs. *Proceedings of the National Academy of Sciences*. 114:3660–3665. https://doi.org/10.1073/pnas.1621517114

Andréfouët, S, Dutheil, C, Menkes, CE, Bador, M & Lengaigne, M. 2015. Mass mortality events in atoll lagoons: environmental control and increased future vulnerability. *Global Change Biology* 21: 195-205

Baird AH, Keith SA, Woolsey E, Yoshida R, Naruse T. 2018. Rapid coral mortality following unusually calm and hot conditions on Iriomote, Japan. *F1000Research* 6

Bak RPM. 1976. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. *Netherlands Journal of Sea Research* 10(3):285-337

Bak P, Tang C, Wiesenfeld K. 1987. Self-organized criticality: An explanation of 1/f noise. Physical Review Letters 59: 381-384

Blakeway, D, Hamblin MG. 2015. Self-generated morphology in lagoon reefs. PeerJ, 3: e935 https://doi.org/10.7717/peerj.935

Blanchon P. 2011. Geomorphic zonation. In: Hopley D, ed. *Encyclopedia of modern coral reefs: structure, form and process*. Dordrecht: Springer. 469-486

Bothwell AM. 1982. Fragmentation, a means of asexual reproduction and dispersal in the coral genus *Acropora* (Scleractinia: Astrocoeniida: Acroporidae)—a preliminary report. In: *Proceedings of the 4th International Coral Reef Symposium, vol. 2*. Penang. Reefbase Project. 137-144

Collins LB, Zhu ZR, Wyrwoll K-H. 1996. The structure of the Easter Platform, Houtman Abrolhos reefs: Pleistocene foundations and Holocene reef growth. *Marine Geology* **135**:1-13

Collins LB, Zhu ZR, Wyrwoll K-H. 1998. Late tertiary-quaternary geological evolution of the Houtman Abrolhos Carbonate Platforms, Northern Perth Basin. In: Purcell R, Purcell P, eds. *The sedimentary basins of Western Australia 2*. Perth: Petroleum Exploration Society of Australia. 647-663

Delesalle B. 1985. Environmental survey of Mataiva Atoll, Tuamotu Archipelago, French Polynesia. *Atoll Research Bulletin* **286**:1-42

Dennison WC, Barnes DJ. 1988. Effect of water motion on coral photosynthesis and calcification. *Journal of Experimental Marine Biology and Ecology* 115:67–77

English S, Wilkinson C, Baker V, eds. 1997. *Survey manual for tropical marine resources* (Second edition). Townsville: Australian Institute of Marine Science.

Gajdzik, L, DeCarlo TM. 2017 The perfect calm: Reoccurring mass die-offs on a remote coral atoll. *Matters* 3 (9), e201707000003

Hamylton, S., Andréfouët, S. & Spencer, T. 2012. Comparing the information content of coral reef geomorphological and biological habitat maps, Amirantes Archipelago (Seychelles), Western Indian Ocean. *Estuarine, Coastal and Shelf Science*. 111 151-156

Gilmore MD, Hall BR. 1976. Life history, growth habits, and constructional roles of *Acropora cervicornis* in the patch reef environment. *Journal of Sedimentary Petrology* 46(3):519-522

Haas AF, Smith JE, Thompson M, Dehyn DD. 2014. Effects of reduced dissolved oxygen concentrations on physiology and fluorescence of hermatypic corals and benthic algae. *PeerJ* 2:e235 https//doi.org/10.7717/peerj.235

Highsmith RC. 1982. Reproduction by fragmentation in corals. *Marine Ecology Progress Series* 7:207-226

Hobbs J-PA,McDonald CA. 2010. Increased temperature and decreased dissolved oxygen triggers fish kill at the Cocos (Keeling) Islands, Indian Ocean. *Journal of Fish Biology* 77: 1219–1229

Hobbs J-PA, Macrae H. 2012. Unusual weather and trapped coral spawn leads to fish kill at a remote coral atoll. *Coral Reefs* 31:961-961

Hopley D. 1982. *The geomorphology of the Great Barrier Reef: quaternary development of coral reefs*. New York: Wiley-Interscience.

Hopley D, Smithers SG, Parnell KE. 2007. *The Geomorphology of the Great Barrier Reef: Development, Diversity and Change*. Cambridge: Cambridge University Press.

Hoskin CM. 1963. Recent carbonate sedimentation on Alacrán Reef, Yucatán, México. *National Academy of Science National Research Council, Foreign Field Research Program*, Publication 19

Kaandorp, J. **1994**. *Fractal* Modelling: *Growth and Form in Biology*. Berlin: Springer Verlag

Kinsey DW. 1979. Carbon turnover and accumulation by coral reefs. *D. Phil. thesis*, University of Hawaii

Kinzie RA. 1973. The zonation of West Indian gorgonians. *Bulletin of Marine Science***23**(1):93-155

Mayer, A. G. 1918. Toxic effects due to high temperature. *Carnegie Institute of Washington Publications* 252, 175-178.

Maragos JE. 1972. A study of the ecology of Hawaiian corals. *D. Phil. thesis*, University of Hawaii, Honolulu

Maxwell WGH. 1968. *Atlas of the Great Barrier Reef*. New York: Elsevier

Mistr S, Bercovici D. 2003. A theoretical model of pattern formation in coral reefs. *Ecosystems* **6**:61-74

Pringle RM, Tarnita, CE. 2017. Spatial self-organization of ecosystems: integrating multiple mechanisms of regular-pattern formation. *Annual review of Entomology* 62: 359-377 https://doi.org/10.1146/annurev-ento-031616-035413

Purkis, SJ, Riegl, B, Dodge, RE. 2006. Fractal Patterns of Coral Communities: Evidence from Remote Sensing. *Arabian Gulf, Dubai, U.A.E. Oceanography Faculty Proceedings, Presentations, Speeches, Lectures* 13

Purkis S, Casini G, Hunt D, Colpaert A, 2016. Morphometric patterns in Modern carbonate platforms can be applied to the ancient rock record: Similarities between Modern Alacranes Reef and Upper Palaeozoic platforms of the Barents Sea. *Sedimentary Geology* 321, 49-69

Purkis SJ, van de Koppel J, Burgess PM. 2017. Spatial self-organization in carbonate depositional environments. In SEPM Special Publication 106. *Autogenic Dynamics in Sedimentary Systems*, eds DA Budd, E Hajek, SJ Purkis, pp. 53-66. Society for Sedimentary Geology

Renema, W, Pandolfi, J Kiessling, W, Bosellini, F, & Klaus, J, Korpanty, C, Rosen, B, Santodomingo, N, Wallace, C, Webster, J, Johnson, K. 2016. Are coral reefs victims of their own past success? *Science Advances*. 2. e1500850-e1500850. 10.1126/sciadv.1500850.

Rietkerk M, van de Koppel J. 2008. Regular pattern formation in real ecosystems.*Trends in Ecology & Evolution* **23**:169-175

Rogers, J. S., Monismith, S. G., Koweek, D. A., Torres, W. I. and Dunbar, R. B. 2016. Thermodynamics and hydrodynamics in an atoll reef system and their influence on coral cover. *Limnology and Oceanography* 61: 2191–2206. doi:10.1002/lno.10365

Schlager W, Purkis SJ. 2013. Bucket structure in carbonate accumulations of the Maldive, Chagos and Laccadive archipelagos. *International Journal of Earth Sciences* 102:2225-2238

Schlager W, Purkis S. 2015. Reticulate reef patterns: antecedent karst versus self-organization. *Sedimentology* **62**(2):501-515

Simpson, C.J., Cary, J.L. & Masini, R.J. 1993. Destruction of corals and other reef animals by coral spawn slicks on Ningaloo Reef, Western Australia. *Coral Reefs* 12: 185-191. doi:10.1007/BF00334478

Smith, S.V., 1981. The Houtman Abrolhos Islands: carbon metobolism of coral reefs at high latitude. *Limnology and Oceanography* 26: 612-621

Tunnicliffe V. 1981. Breakage and propagation of the stony coral *Acropora cervicornis*. *Proceedings of the National Academy of Sciences of the United States of America* 78(4):2427-2431

Vaquer-Sunyer R, Duarte CM, 2008. Thresholds of hypoxia for marine biodiversity

Proceedings of the National Academy of Sciences 105 (40): 15452-15457

Verwey, J, 1931. Coral reef studies. II. The depth of coral reefs in relation to their oxygen. consumption and the penetration of light in water. *Treubia*, 13(2): 169-198

Woodroffe, CD. 2011. Reticulated Reefs. In: Hopley D, ed. *Encyclopedia of modern coral reefs: structure, form and process*. Dordrecht: Springer. 931-933

Wyrwoll K-H, Zhu ZR, Collins LB, Hatcher BG. 2006. Origin of blue hole structures in coral reefs: Houtman Abrolhos, Western Australia. *Journal of Coastal Research* 22:202-208

Yonge, CM. 1957. Symbiosis. In: Hedgepeth JW, Ladd HS eds. Treatise on Marine Ecology and Paleoecology. *Geological Society of America Memoirs* 67(1): 429-442