Are catch-up reefs an artefact of coring?

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ABSTRACT

Drill cores through modern coral reefs commonly show a time lag in reef initiation followed by a phase of rapid accretion to sea level from submerged foundations - the so-called 'catch-up response'. But because of the difficulty of drilling in these environments, core distribution is usually restricted to accessible areas that may not fully represent reef history, especially if the reef initiated in patches or developed with a prograde or retrograde geometry. As a consequence, core data have the potential to give a misleading impression of reef development, particularly with respect to the timing of initiation and response to sea-level rise. Here, we use computer models to simulate keep-up reef development and, from them, quantify variations in the timing of reef initiation and accretion rate using mock cores taken through the completed simulations. The results demonstrate that cores consistently underestimate the timing of reef initiation and overestimate the reef accretion rate so that, statistically, a core through a keep-up reef will most likely produce a catch-up pattern – an initiation lag followed by a phase of rapid accretion to sea level. This implies that catch-up signatures may be an artefact of coring and that keep-up reefs are significantly more common than previous core studies claim.

Keywords Computer simulation, coral reef, ecological succession, Holocene, Indo-Pacific, sea level, time lag.

INTRODUCTION

With the application of portable drilling rigs in the mid-1970s, the investigation of Holocene reef development and its response to the rapid deglacial sea-level rise has progressed steadily. Although some early studies concentrated on a detailed core analysis of individual reefs (e.g. Easton & Olson, 1976, Macintyre & Glynn, 1976; Shinn *et al.*, 1982a), others preferred a less detailed, but more regional analysis of reef systems in the hope of seeing a larger and more significant picture (Adey & Burke, 1977; Davies & Hopley, 1983; Davies *et al.*, 1985; Montaggioni, 1988; Cabioch *et al.*, 1995). The view that emerged in the Indo-Pacific was that early Holocene reef cores apparently showed a widespread and significant lag in reef initiation after insular shelves were flooded by rising seas (Davies & Hopley, 1983; Davies et al., 1985; Marshall, 1988; Montaggioni, 1988). Similarly, in the Caribbean, cores seemed to indicate that abrupt shelf flooding killed off any established reef growth and prevented subsequent recolonization for thousands of years (Adey et al., 1977; Lighty et al., 1978; Macintyre, 1988). In both areas, a large proportion of cores showed an upward-shallowing sequence terminated by reef-flat or crest facies. It was claimed that this sequence was a result of the lag, which left most reef systems to initiate in deeper water and 'catch up' after water conditions returned to normal and/or sea level had slowed or reached its present position (Macintyre, 1988; Hopley, 1994).

These early drilling results were influential and not only spawned new ideas on the fundamental

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controls on reef development (Schlager, 1981; Hallock & Schlager, 1986), but also provided the basis for a conceptual model of how reef systems respond to sea-level rise (Davies et al., 1985; James & Macintyre, 1985; Neumann & Macintyre, 1985). This model proposed three basic responses to sea-level rise: (1) 'keep-up' reefs initiated as soon as substrates were flooded and accreted at the same rate as sea-level rise; (2) 'catch-up' reefs showed a significant lag in initiation of up to several thousand years and then accreted rapidly to sea level from submerged foundations; (3) and 'give-up' reefs apparently failed to accrete normally and were 'drowned' by rising seas (Davies et al., 1985; Neumann & Macintyre, 1985; Montaggioni, 1988). Assigning a reef to either of the first two categories involved constructing a reefaccretion curve from coring and dating, then comparing that accretion curve to an independent regional sea-level curve (e.g. Marshall & Davies, 1982; Montaggioni, 1988; Macintyre & Adey, 1990). But categorising an entire reef in this way requires the assumption that core data are representative and complete, and that all stages of the reef's development have been sampled. Detailed studies using one or two transects of closely spaced cores are clearly the optimal method of ensuring that such data are representative. But where core distribution has a more limited coverage or is restricted to specific reef zones, the assumption of representativeness may not be valid. Indeed, it can only be justified where reef development is homogeneous and has a simple vertical accretion axis (Fig. 1A). If reef development were more heterogeneous and accretion axes were inclined, cores could show significant variation over relatively short distances and individually may not record the complete developmental sequence (Fig. 1B).

Most detailed drilling studies indicate that Holocene reef development has in fact been heterogeneous. Transects of closely spaced drill cores encompassing both submerged and exposed zones of several modern reefs show either prograde or retrograde geometries where the accretion axis is inclined and the initiation point is offset from the present reef-crest position (Easton & Olson, 1976; Macintyre & Glynn, 1976; Shinn *et al.*, 1982b; Takahashi *et al.*, 1988; Blanchon & Perry, 2003). These accretion patterns have also been confirmed directly by excavations into Holocene reefs (Lighty *et al.*, 1978; Lighty, 1985; Kan *et al.*, 1997).

Such heterogeneous accretion patterns have two obvious consequences for interpretations of reef history based on limited core data. First, a core that penetrates a reef where the accretion axis deviates from vertical will probably miss early stages of reef development and therefore record an apparent time lag in reef initiation. The



Fig. 1. Schematic cross-sections of two superficially identical reef complexes with different accretion histories. Section A shows a homogeneous accretion history with simple 'layer-cake' isochrons (dashed lines) and vertical, uniform accretion axes (arrows). In this case, a single core would recover a complete history of reef development. In contrast, section B shows a heterogeneous accretion history with offset isochrons and inclined accretion axes. In this case, a single core would recover an incomplete history of reef development; only a transect of cores across the crest and reef-front would give a complete history. Both sections show heterogeneous colonization typical of reef systems in general. The scale of cross-sections is arbitrary but intended to be within the range of 10–50 m in height and 50–200 m in width.

core will also show a shallowing-up sequence and a falsely enhanced rate of vertical accretion – or a catch-up signature. Here, we use computer simulations of spatially heterogeneous reef development to quantify the potential magnitudes of these coring artefacts. By comparing these simulation results with data from actual reefs, we are better able to assess the validity of time lag in reef initiation and the catch-up signature of reefs that has been so widely reported in the literature.

COMPUTER SIMULATION

The approach used is to simulate keep-up reef development through a transgression and highstand, then plot initiation times and accretion curves from numerous mock cores 'drilled' through the simulated keep-up reefs. The intention is not to produce an ultrarealistic model incorporating the multitude of different controls on reef development, but rather to generate a basic model that simulates simple examples of keep-up reefs, with heterogeneous colonization and accretion patterns, and then use it to determine how representative core data are of these patterns. In order to do this, two different simulations are used, one to examine the effect of variation in colonization rate on the timing of reef initiation in core and one to examine the effect of a variable accretion rate on reef-accretion curves generated from cores. It is important to note that the concept of keep-up reef growth is not one in which the entire reef keeps pace with sea level. Instead, it is envisaged that the first-colonized areas of reef keep pace with sea level, and the remainder fills in later.

Colonization simulations

The model used for the colonization simulations, described by Blakeway (2000), is a stochastic cellular automaton of 250×250 cells, each representing a square metre of sea floor. Reef development is initiated by seeding the central 160×160 m of sea floor with randomly spaced corals, each 1 m^3 in size. Additional corals colonize the sea floor in each iteration of the model. Corals can grow upwards and outwards in 1 m increments per iteration. Coral growth translates directly to net reef accretion – the model does not incorporate factors such as physical or biological erosion, sedimentation or compaction. These factors are not critical for the simulation, given that the goal is to quantify the effect of

colonization rate on the apparent timing of reef initiation in core. Each iteration of the model represents 100 years, giving a maximum reef accretion rate of 10 m ka⁻¹ (average accretion rates in real reefs commonly exceed 10 m ka⁻¹, and maximum rates are up to 30 m ka⁻¹; e.g. Macintyre *et al.*, 1977; Chappell & Polach, 1991; Blanchon & Shaw, 1995). Sea level rises by 1 m per iteration (10 m ka⁻¹) until it is 30 m above the sea floor, and then remains constant during subsequent iterations. Two runs of the model were carried out with differing colonization rates. In the 'high' rate, 50 corals were added per iteration and, in the 'low' rate, five corals were added per iteration.

As programmed, initial patch reefs in both runs of the simulation kept pace with sea-level rise and began to develop reef flats after sea level stabilized. New reefs added at each iteration grew at the same rate as the initial reefs, and therefore caught up with sea level later. After reaching sea level, they continued to expand laterally, eventually coalescing into a continuous platform after 5000 years in the high colonization reef (Fig. 2) and 6000 years in the low colonization reef (Fig. 3).

Reef accretion curves constructed from mock cores 'drilled' through the two platforms show significant offsets from the sea-level curve (Figs 4A and 5A). The offset for each curve indicates the lag period between substrate submergence and reef initiation at that particular core site. Lag periods typically fell between 1000 and 2000 years in the high colonization reef (Fig. 4B) and between 1000 and 3000 years in the low colonization reef (Fig. 5B). The probability of intersecting any of the initial patch reefs with a single core was extremely low, $\approx 0.2\%$ in the high colonization reef and 0.02% in the low colonization reef. These values represent the respective probabilities of recording a zero lag period, i.e. obtaining the correct keep-up accretion curve.

The gradient of the accretion curves is similar or identical to that of the sea-level curve because of the model's invariant accretion rate at all depths and its inability to allow coral to project over open space and create overhangs. These restricted accretion parameters mean that the colonization model cannot simulate lateral or vertical variations in accretion rate.

Accretion rate simulations

Although many factors influence accretion rate in modern reefs (e.g. Grigg, 1982, 1998; Vecsei,



Fig. 2. Oblique views of the high colonization reefs after (A) 10 iterations (1000 years), (B) 20 iterations (2000 years), (C) 30 iterations (3000 years) and (D) 50 iterations (5000 years). The grid overlay in (D) shows the locations of the 16 mock cores from which the reef accretion curves in Fig. 4A were derived.

2001), perhaps the most important for reef development is the negative gradient in light availability with depth (Chalker *et al.*, 1988; Bosscher & Schlager, 1992). To account for this gradient and simulate accretion patterns better, graphic software (Macromedia Freehand) was used to generate a two-dimensional simulation of a single patch reef. In this simulation, it was assumed that the primary control on coral growth and hence reef-accretion rate is light availability. Other parameters such as physical or biological erosion, sedimentation and variation in photosynthetic potential between different species were ignored because they are unnecessary as we are not making a comparison of absolute accretion values. The effects of light attenuation are represented by reducing the accretion rate linearly with depth to 50% of the surface rate at 30 m. Apart from this, other parameters for the accretion simulation correspond to the colonization simulations – the reef grew from a 1 m diameter seed coral, sea level rose uniformly to a height of 30 m in 30 iterations then remained constant, and the maximum accretion rate (perpendicular to the reef surface) was 1 m per iteration.



Fig. 3. Oblique views of the low colonization reefs after (A) 10 iterations (1000 years), (B) 20 iterations (2000 years), (C) 30 iterations (3000 years) and (D) 60 iterations (6000 years). The grid overlay in (D) shows the locations of the 16 mock cores from which the reef accretion curves in Fig. 5A were derived.

The simulation produced a dome-shaped patch reef that kept pace with sea level, and developed a reef flat after sea level stabilized at 30 iterations (Fig. 6). The reef walls steepened to vertical at ≈ 40 iterations and subsequently overturned. The simulation was stopped after 60 iterations, representing 6000 years. Accretion curves were then constructed from 16 mock cores 'drilled' through the reef (Fig. 7). As in the colonization simulation, the only core to indicate the correct timing of reef initiation, and the correct keep-up accretion curve, is that intersecting the initial nucleus of the patch reef.

Unlike the colonization simulation, the gradients of the accretion curves progressively deviate from the linear sea-level curve, eventually reaching a point where they slope in the opposite direction (i.e., become negative). Accretion rates calculated from the cores exceed the actual rate, with the error increasing in proportion to the distance from the initial patch reef. Apparent accretion rates recorded by the cores increase to a maximum of nearly 7 m per iteration (or 70 m ka^{-1}) before becoming 'negative' in the cores that penetrated the overhanging reef wall. In other words, cores offset from the reef nucleus

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Fig. 4. (A) Accretion curves from 16 cores spaced on a 50 m grid across the reef shown in Fig. 2D. (B) Frequency histogram of lag periods between submergence and reef initiation for all 22 500 cells within the 150 m \times 150 m grid shown in

Fig. 5. (A) Accretion curves from 16 cores spaced on a 50 m grid across the reef shown in Fig. 3D. (B) Frequency histogram of lag periods between submergence and reef initiation for all 22 500 cells within the 150 m \times 150 m grid shown in



Fig. 6. (A) Cross-section of a simulated patch reef. Sea level rose uniformly to a height of 30 m in 30 iterations, then remained constant for a further 30 iterations. The reef grew from a 1 m diameter seed coral, with a maximum accretion rate of 1 m per iteration, corresponding to 10 m kyr⁻¹. Numbers to the left of centre indicate the position of the reef surface at 10 iteration (1000 years) intervals. Arrows show the progressive deviation of the reef accretion axis. Vertical bold lines to the right of centre represent the 16 mock cores from which the reef accretion curves were derived. (B) Sixteen accretion curves from the cores in (A), showing progressively later initiation and greater accretion rates with increasing distance from the reef nucleus. Age reversals occur in the cores that penetrate the overhanging reef wall.

clearly show an artificial exaggeration in vertical accretion rates.

DISCUSSION

The simulations of keep-up reef development used here are 'stripped down' to consider only

primary parameters affecting all reefs and purposely ignore secondary factors that do not constitute prerequisites for reef development (e.g. antecedent topography, storm impact, wave-induced zonation, etc.). As a result, the simulations are highly simplified representations of reef development and sea-level change. But, provided that their main assumptions are accep-



Fig. 7. Catch-up signatures predominate when reef-accretion curves constructed from radiocarbon-dated reef core data are compared with regional coral-based radiocarbon sea-level curves (all sea-level curves except the Caribbean are corrected for 13 C content, but none is corrected for ocean reservoir or secular variation; all accretion curves use uncorrected dates to facilitate comparison). (A) Accretion curves for South Pacific reefs (Montaggioni, 1988; Montaggioni *et al.*, 1997). (B) Accretion curves for the Great Barrier Reef (Marshall & Davies, 1982; Davies & Hopley, 1983; Davies *et al.*, 1985). (C) Accretion curves for New Caledonian fringing reefs (Cabioch *et al.*, 1995). (D) Accretion curves for Indian Ocean reefs (Montaggioni, 1988). (E) Accretion curves for Hawaii (Easton & Olson, 1976). (F) Accretion curves for the Caribbean (Macintyre & Glynn, 1976; Shinn *et al.*, 1982; Macintyre & Adey, 1990). Regional sea-level curves: Huon Peninsula, Papua New Guinea (Chappell & Polach, 1991); Houtman Abrolhos Islands, southwestern Australia (Eisenhauer *et al.*, 1993); Tahiti, south Pacific (Bard *et al.*, 1996); western Atlantic and Caribbean (Lighty *et al.*, 1982; Blanchon & Shaw, 1995). Grey shading shows depth–time variation between different sea-level curves.

ted – that heterogeneous colonization and accretion are inherent reef characteristics – then the conclusions drawn from the simulations can be applied to real reefs. These are that both the timing of reef initiation and the reef-accretion rate are liable to be consistently misrepresented in

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core. The timing of reef initiation indicated in core will be equal to or later than the real timing, and the accretion rate indicated in core will be equal to or more than the real rate. Only wellplaced cores or closely spaced core transects that intersect the reef-accretion axis and the earliest stage of reef development will give correct accretion curves and initiation ages.

The number and location of cores in real reef studies is, however, commonly less than ideal. Cores are commonly restricted to accessible zones such as lagoon, reef-crest and flat because of the difficulty of drilling in submerged or high-energy reef front slope zones (e.g. Marshall & Davies, 1982; Davies & Hopley, 1983; Montaggioni, 1988; Cabioch et al., 1995; Montaggioni et al., 1997). In spite of this restriction, many have interpreted reef development without considering how representative such core data are of the accretion history of the reef and, specifically, whether these data include artefacts induced by inadequate sampling. In fact, several important concepts based on these studies may be suspect because of their reliance on these data (Kendall & Schlager, 1981; Davies et al., 1985; James & Macintyre, 1985; Neumann & Macintyre, 1985; Marshall, 1988; Hopley, 1994). In this discussion, we concentrate on the most important of these concepts: the postulated lag in Holocene reef initiation and the catch-up response of these reefs to sea-level rise.

Artefact 1: time lag in reef initiation

The phenomenon of late initiation, or 'apparent lag', in the reef colonization simulations is conceptually similar to the lag in carbonate platform sedimentation modelled by Tipper (1998). The key point made by both models is that the lag phenomenon is an artefact of patchy colonization and not related to environmental suppression. The duration of the apparent lag depends inversely on the colonization density. This relationship is not one-to-one, however, and a 10-fold increase in colonization density only reduces the apparent lag by approximately half (Figs 4 and 5). By extension, it can be inferred that significant apparent lag will remain even at extremely high colonization densities. Apparent lag can only be eliminated if the entire substrate is colonized immediately and completely.

Many of the lags reported in published research that are based on absence of evidence may well be artefacts of the type described above. In a review of reef development across the Great Barrier Reef, Davies & Hopley (1983) and Davies et al. (1985) reported a time lag in early Holocene reef initiation of a few hundred to several thousand years based on the lack of ages > 8 ka. As more drilling took place, both Marshall (1988) and Montaggioni (1988) claimed that this lag was more widespread and that no reef growth occurred in the Indo-Pacific reef province before 8.5 ka BP, even though substrate was available. It was widely accepted that this lag in reef initiation was real and that it resulted from the intensified circulation patterns that existed during glacially lowered sea level. These patterns supposedly prevented reef initiation by reducing water quality and preventing the dispersal of coral larvae from their glacial refuges (Davies et al., 1985; Marshall, 1988; Montaggioni, 1988).

Several factors indicate, however, that this widespread Indo-Pacific lag may be more apparent than real. The suggestion by Davies et al. (1985) that a consistent lag period in multiple cores strengthens the case for a genuine lag is not supported by the simulations presented here. These findings show that apparent lags tend to cluster within a relatively narrow period, significantly later than the actual timing of reef initiation (Figs 4B and 5B). This period indicates a mode in the apparent lag rather than in the first appearance of reefs. In addition, all these Indo-Pacific studies were reconnaissance in nature and only recovered a limited number of cores from accessible reef environments on any given reef (i.e. submersible drills were not used). Little consideration was apparently given to the possibility that the cores may not have sampled all stages of reef development. Instead, it was tacitly assumed that the reef initiated directly below the location of the cores and that its accretion axis was vertical (e.g. Fig. 1A). No cores were taken from submerged reef zones to test for reef initiation further downslope, and few cores were taken laterally in the same environments to test for internal consistency in the data (all probably for reasons of limited accessibility).

Although these factors cast doubt on the Indo-Pacific data, they do not completely rule out the possibility of a genuine widespread lag in reef initiation during the early Holocene. That possibility has been ruled out, however, in other more thoroughly sampled regions. In the Caribbean– Atlantic reef province, for example, drilling and excavations in submerged areas of the outer shelves has shown widespread reef development during the earliest Holocene. Along the Florida shelf, there was no lag in Holocene reef initiation and extensive reef development occurred between > 9.5 and 7.1 ka BP (Lighty *et al.*, 1978). Similarly, no lag was encountered off the Barbados shelf where 16 cores drilled by Fairbanks (1989) not only documented early Holocene reef development between > 9.5 and 6.8 ka BP but also continuous backstepping reef development during the entire deglacial sequence (Blanchon & Shaw, 1995). Lowered sea level and attendant changes in oceanic circulation apparently did not suppress reef development in this case.

Several workers have claimed that subsequent shelf flooding degraded water quality, which killed off these early Holocene reefs and prevented recovery and further reef initiation for several thousands of years (Adey et al., 1977; Adey, 1978; Lighty et al., 1978; Lighty, 1985; Macintyre, 1988). A more thorough analysis of these and subsequent data has shown, however, that most early Holocene reefs died out at the same time as modern reefs were establishing further upslope (i.e. backstepping), indicating that the data can also be explained by jumps in sea level (Blanchon & Shaw, 1995; Blanchon et al., 2002). Regardless of the interpretation, Caribbean data clearly show continuous (albeit backstepping) reef development during the Holocene and do not support a widespread lag in modern reef initiation.

In the absence of support from other areas, the validity of the lag concept as it relates to reefs rests or falls on the adequacy of data from the Indo-Pacific. Based on the simulations presented here, it is argued that these Indo-Pacific data probably represent an 'apparent lag' in reef initiation because the initiation point of the reef was probably not sampled. Some support for this claim comes from Tahiti where more core data have been collected recently (Montaggioni *et al.*, 1997). These new data show that there was no lag in Holocene reef initiation in this area, with shallow reefs initiating as soon as the substrate was flooded.

Artefact 2: catch-up response

The second aspect of reef history that is liable to be misrepresented in cores is the reef-accretion rate and consequently its interpreted response to sea-level change. Our simulations of keep-up reefs show that only a core that intersects the initial reef nucleus will produce the correct keepup accretion curve (Fig. 6). Cores offset from the reef nucleus show an initiation lag and then a catch-up response resulting from the artificial exaggeration of vertical accretion rates. In such cases, cores present a biased view of reef response to sea-level rise by over-representing catch-up accretion signatures.

This artefact of coring, like the initiation lag, will be prevalent in reefs that developed heterogeneously and are incompletely sampled. It is not surprising to find, therefore, that reef studies with limited core coverage show a predominance of catch-up signatures (Fig. 7). Of the 17 reefs on the Great Barrier Reef where accretion data have been reported, 15 were classified as having catch-up accretion responses to sea-level rise (Fig. 7B). Similarly, of the 13 Indo-Pacific reefs with limited core data, 11 have been described as 'catch-up reefs' (Fig. 7A and C-E). In fact, the alleged catchup response was so common that Davies et al. (1985) identified several subtypes on the Great Barrier Reef (Fig. 8A). A 'type 1' catch-up response was interpreted to occur when a reef initiated and caught-up before sea level stabilized close to its present position (in the Indo-Pacific, stabilization occurred between 6600 and 3000 ¹⁴C years BP; Fig. 7F). A 'type 2' catch-up response was interpreted to occur when a reef initiated before sea level had stabilized but only caught up after stabilization, and a 'type 3' catch-up response occurred when the reef initiated and caught up after sea level had stabilized. Although catch-up reefs in the Caribbean could not be subdivided in this way because of the late stabilization of sea level (Fig. 7F), all three catch-up responses were subsequently identified in other areas of the Indo-Pacific (Montaggioni, 1988).

The catch-up response of whole reef systems to sea-level rise was widely accepted and subsequently used to develop detailed conceptual models of Holocene reef development (Davies & Montaggioni, 1985; Davies *et al.*, 1985; James & Macintyre, 1985; Neumann & Macintyre, 1985; Hopley, 1994; Montaggioni, 2000). But, as with the initiation lag, little consideration was apparently given to the possibility that cores drilled on the crest or flat of a modern reef may not fully represent the accretion history of that reef and may have missed early developmental stages.

Indeed, three factors support our claim that the proposed catch-up response of whole reef systems to sea-level rise may simply be an artefact of coring. First, our simulations of keep-up reef accretion replicated all three of the main types of catch-up curves, thereby demonstrating that these responses could also be artefacts of coring (Fig. 8B).



Fig. 8. (A) Classification of accretion curves derived from empirical reef core data. 1. Curve showing a keep-up response. 2. Curve showing a 'type 1' catch-up response interpreted to occur where a reef initiates and catches up before sea level stabilizes. 3. Curve showing a 'type 2' catch-up response interpreted to occur where reef initiates before sea level stabilizes but only catches up after stabilization. 4. Curve showing a 'type 3' catch-up response interpreted to occur where the reef initiates and catches up only after sea-level has stabilized. 5. Curve showing a give-up response. (B) Selected accretion curves taken from the simulation of keep-up reef development. Note that the keep-up simulation produced all three types of catch-up curve in addition to a keep-up curve. It also produced catch-up curves with negative gradients, which have also been found in Great Barrier Reef cores with the most detailed chronologies (cf. Fig. 7B). This implies that all types of catch-up curves can be artefacts of coring.

Second, all reefs in which the full reef profile was sampled (using either closely spaced cores or excavations) clearly show an initiation point that is offset from the present reef-crest position and/ or an inclined accretion axis. The extent of the offset or inclination varies from ≈ 50 m to 400 m and is either progradational and oversteps reeffront deposits (Easton & Olson, 1976; Macintyre & Glynn, 1976; Takahashi et al., 1988) or retrogradational and oversteps backreef deposits (Lighty et al., 1978; Shinn et al., 1982b; Lighty, 1985). The extent of heterogeneity in these reefs supports our simulations and clearly shows that: (1) the chances of sampling the initiation stage of a reef from a core on the crest is extremely low; and (2) that omission will automatically produce a catch-up accretion signature.

Third, incompletely sampled reefs can show contrasting accretion signatures within the same area, and even along different parts of the same reef tract (Davies & Hopley, 1983). On the southern Great Barrier Reef, for example, three reefs within 30 km of each other showed three distinct accretion signatures: One Tree Reef to the north showed a classic catch-up pattern; Fitzroy Reef only 15 km further south was a classic keep-up reef; whereas Fairfax Reef some 30 km further south had a keep-up windward side and a catchup leeward side (Davies & Hopley, 1983). This variability led Davies *et al.* (1985) to conclude that: '...local factors, whether substrate, nutrient availability, or biological cussedness may be more important than the rate of sea-level change in determining the character of reef growth' (Davies *et al.*, 1985, p. 102). And yet even such inconsistency in local data did not raise the suspicion that perhaps it was incomplete sampling that produced such signatures rather than the true response of the reefs themselves. Certainly, the simulations presented here indicate that inadequately sampled keep-up reefs with slightly varying degrees of heterogeneity could give accretion curves that ranged from keep-up to catch-up, even within the same reef system.

Although data supporting a catch-up response of whole reef systems are dubious, there is better evidence supporting the catch-up response on a more local scale in protected patch-reef settings where their development occurs behind linear keep-up reef systems (e.g. Aronson *et al.*, 1998). On these reefs, isolated cores do show a succession of shallowing-upward coral communities as the surface caught up with sea level, but estimating the timing of patch-reef initiation and actual accretion patterns from such isolated cores will still be subject to the same artefacts described here.

CONCLUSIONS

The main implication of the coring artefacts simulated in this study is that catch-up curves are likely to be over-represented in reef cores, and keep-up curves may be correspondingly underrepresented. Our simulations show that, statistically, a core through a keep-up reef is most likely to produce a catch-up signature: an apparent lag in reef initiation of up to several thousand years, followed by a phase of rapid accretion to sea level. This potential for over-representation of catch-up signatures should be taken into account in future core-based studies of reef history. Before invoking environmental 'suppression and release' mechanisms to explain lags and catch-up accretion, the possibility that these phenomena are sampling artefacts must be considered. If the results of this study apply to actual reefs - and existing reef data indicate that they do - then keep-up reefs may be significantly more abundant than previous drilling results have indicated.

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