

Depth-related and species-related patterns of Holocene reef accretion in the Caribbean and western Atlantic: a critical assessment of existing models

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ABSTRACT

Reef-accretion rate was measured in 151 core intervals from 12 Caribbean and western Atlantic locations. Palaeowater depth for each core interval was determined by comparing its position to the curve of Lighty *et al.* (1982), based on calendar years before 1950. While the majority of the data points fell within the upper 15 m of the water column, no clear depth-related pattern of reef accretion emerged. This is in sharp contrast to the widely held assumption that reef accretion will decrease exponentially with water depth at rates approximately an order of magnitude below the corresponding rates of coral growth at the same depths. Similarly, reef-accretion rates from facies dominated by branching *Acropora palmata* (3.83 m kyr^{-1}) versus those associated with massive corals (3.07 m kyr^{-1}) were not significantly different ($\alpha = 0.05$), owing to high variance across all water depths. Reef accretion showed a tendency to increase at higher rates of sea-level rise, but that relationship was also non-significant.

It is proposed that the known depth-related decrease in carbonate production may be offset by a parallel drop in bioerosion. While available data generally support this hypothesis, quantitative verification must await careful measurements of both biological degradation and transport along a depth gradient. Nevertheless, bioerosion appears to not only play an important role in creating reef fabric, but to perhaps affect patterns of reef accretion as much as initial calcification. Regardless of the cause, the patterns revealed by this study fly in the face of the assumptions that underlie our most widely accepted Holocene reef models. Clearly new ones are needed that emphasize the varying contribution of biological material to what is largely a process of physical aggradation – in short reef corals grow, coral reefs accrete.

Keywords Reef accretion, Caribbean, Holocene, bioerosion, sea level, *Acropora*.

INTRODUCTION

What emerges from the myriad definitions of reefs is that they are resistant structures that stand above their surroundings, thus exerting some degree of influence over local circulation. Reefs can be built by organisms as large as modern corals or Cretaceous rudists, or as small as Precambrian microbes. They might emerge as fringing and barrier reefs or form submerged features along shelf margins (Macintyre *et al.*, 1981; Hubbard *et al.*, 1997, 2005), or even in very deep water well below the photic zone (Fosså *et al.*, 2002; Reed *et al.*, 2005). Disagreements focus on how resistant these features need to be and what is responsible for that rigidity. Throughout most of the twentieth century, descriptions of modern reefs emphasized the constructive role of corals,

corallines and other organisms that secrete calcium carbonate and 'build reefs'. Mention is made of physical damage and bioerosion by grazers and infauna (e.g. Ginsburg, 1958; Scoffin, 1992) but the role of construction was until recently perceived as overwhelmingly dominant. As a result, discussion of reefs throughout the later twentieth century focused on reef 'framework' as the architect of this rigidity (Lowenstam, 1950; Newell *et al.*, 1953) and the importance of 'large, colonial or gregarious, intergrown skeletal organisms in general growth position' in creating it (Fagerstrom, 1987).

More recently, the interiors of some Caribbean coral reefs have been likened to 'garbage piles' that comprise as much sediment and toppled corals as in-place or interlocking organisms (Hubbard *et al.*, 1990). These ideas challenge the primacy

of biological production in coral-reef assembly. It is ironic that as early as 1888, Johannes Walther (translated in Ginsburg *et al.*, 1994) noted a dominance of detrital material in Quaternary reefs exposed along the Sinai Peninsula. This idea was apparently ignored in favour of more-popular 'framework' models derived from the discussions of Lowenstam and Newell, despite an apparent recantation by the latter in Newell 1971. As we swim over a modern reef, there is little disagreement over its status. Less readily apparent is the fact that the interiors of many (or possibly most?) of these structures contain less than 30% recognizable coral, with only a portion of that in place (Conand *et al.*, 1997; Hubbard *et al.*, 1998). The remainder is sand and rubble caused by ubiquitous bioerosion plus void space. In as much as this composition probably cannot by itself create the rigidity that is the hallmark of 'true reefs', the roles of encrustation and cementation must rise to equal those of initial calcification and subsequent bioerosion.

How are coral reefs built?

The symbiotic relationship between many corals and their endolithic zooxanthellae, leads to calcification being strongly dependant on light intensity and character ('photosynthetically active radiation' occurs at the red end of the spectrum). This relationship and the maximum depth for corals have been generally understood since the nineteenth century (Quoy & Gaimard, 1825). Light and, therefore, photosynthesis decrease exponentially with depth. Accordingly, the ratio between light intensity (I) at any depth and the light-saturating intensity (I_k : the amount of light that will result in maximum photosynthesis) for a particular coral species also drops. Chalker (1981) proposed that photosynthesis by scleractineans can be approximated by this ratio and the hyperbolic tangent function. Bosscher (1992) showed that such relationships could be used to predict the growth rate of corals with increasing depth (Fig. 1).

It has been generally assumed that reef accretion is a biological process that is dominated by the growth of corals that are largely in place or at least have not been moved far from where they grew. While it has been long understood that post-mortem degradation of corals is commonplace, it has been largely assumed that much of the detritus from bioerosion will stay within the reef, and that the depth-related pattern

of coral growth will be reflected in trends in reef accretion along the same gradient. Schlager (1981) summarized available data for reef aggradation relative to sea-level rise and coral growth (Fig. 2). While accretion was an order of magnitude slower in his model, it generally mimicked the rapid decrease of coral growth with depth. Citing anecdotal data from other studies, it was argued that most reefs in shallow water have been capable of building at rates greater than the maximum rate of glacio-eustatic sea-level rise during the Holocene (*c.* 7 mkyr⁻¹). Based on this, it was suggested that drowned reefs (or platforms) in the ancient record represent a 'paradox' that can be resolved only by invoking extreme and short-lived conditions associated with either rapid (and probably tectonically induced) sea-level rise or degraded environmental conditions (e.g. 'inimical bank waters' or larger-scale marine 'crisis events').

These concepts represent the foundation upon which most current models of Holocene reef development are based (Adey, 1978; Schlager, 1981; Macintyre, 1988). Linear-extension rates of corals in shallow water can exceed 10 cm yr⁻¹, but coral growth generally ranges from around 10 mm yr⁻¹ in shallow water to less than 1 mm yr⁻¹ at depth (for an excellent compilation, see Dullo, 2005). Reefs are thought to build at a rate roughly an order of magnitude slower (Schlager, 1981; Bosscher, 1992) but still following the general depth-related pattern of coral growth (Fig. 3). From this, it may be deduced that areas dominated by branching coral will build faster than those inhabited by slower-growing massive species (Adey & Burke, 1976), while reefs in shallow water will build faster than their deeper counterparts (Schlager, 1981; Bosscher, 1992).

Despite the overwhelming acceptance of these axioms, they have never been systematically tested. This paper attempts to quantify depth- and species-related patterns of Caribbean and western Atlantic reef accretion using a preliminary survey of information from the literature as well as unpublished core data. It attempts to convince the reader that the relationship between coral growth and reef accretion is not as has been generally assumed. More specifically, it is proposed that the pattern that emerges from systematic analyses of existing core data is controlled no more by coral growth than by the myriad physical and biological processes that come afterwards. If this is the case, then it will have significant bearing on existing models of coral-reef accretion.

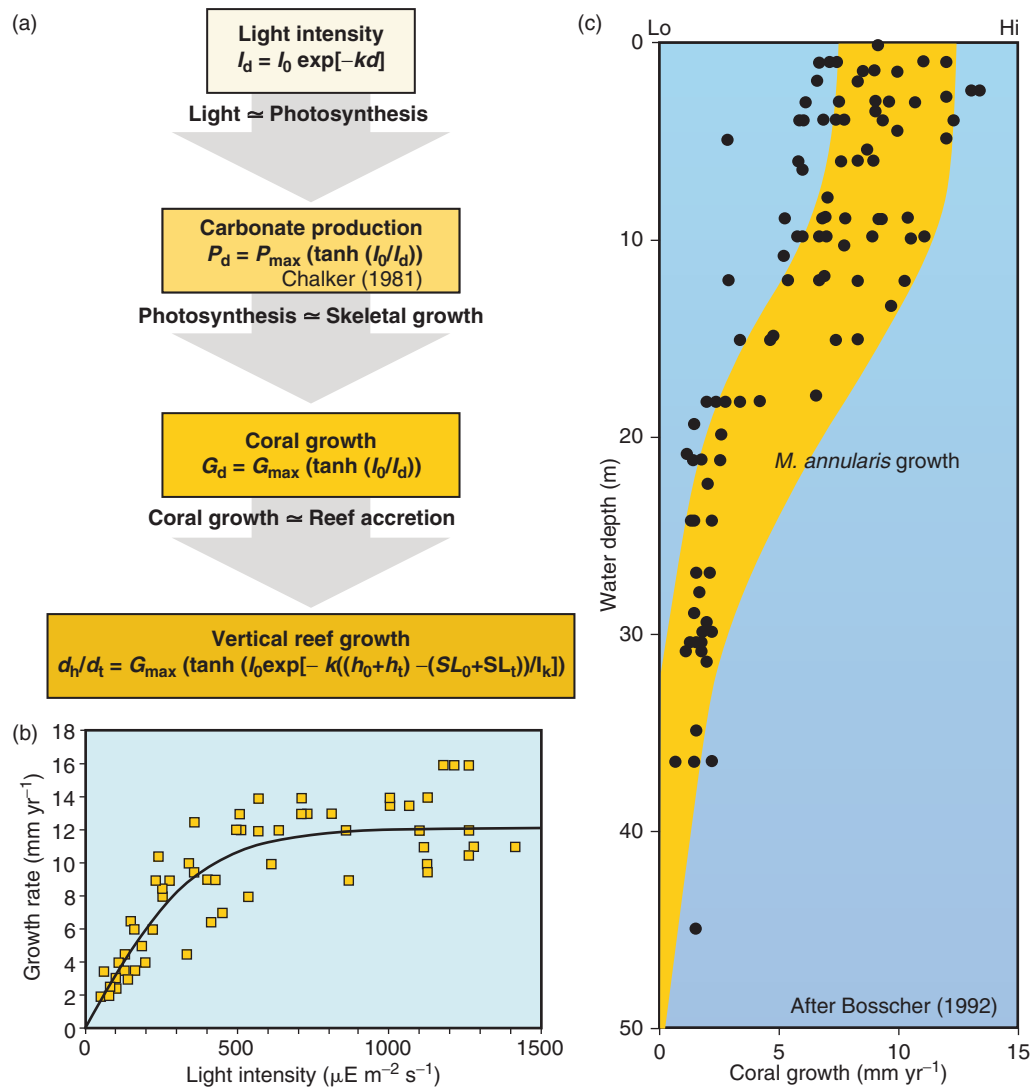


Fig. 1. (a) Summary of a quantitative model to predict coral growth and reef accretion with depth. (b) Growth rate for the *Montastraea annularis* complex versus light intensity (measured in microEinsteins). The best-fit line mimics the hyperbolic tangent function, as predicted by Chalker (1981). (c) The relationship between coral growth and water depth. Circles are actual growth rates determined by X-radiography of modern colonies. The shaded area is the predicted range of coral-growth rates based on A and B. It has been generally assumed that while reef accretion will proceed at rates an order of magnitude slower than coral growth, a similar depth-related trend (i.e. exponentially decreasing) is present. All after Bosscher (1992).

METHODS

Reef accretion is generally defined as vertical aggradation over time. This is in part an artefact of the vertical orientation of cores from which measurements are made. However, it also stems from the realization that coral growth is strongly controlled by light from the surface. While reefs may build horizontally, this is generally held to be the lateral expression of largely upward extension. In this study, accretion rates were calculated

using all data that could be recovered from the literature as well as unpublished information in the author's archives. In the literature, each sample was reported by species, depth below present sea level and radiometric age. The analyses discussed below compare accretion rates for reef intervals dominated by *Acropora palmata* (Lamarck) versus massive species across a wide palaeodepth range. Because *A. palmata* is easily distinguished from massive species in cores, no effort was made to check the identifications reported in the

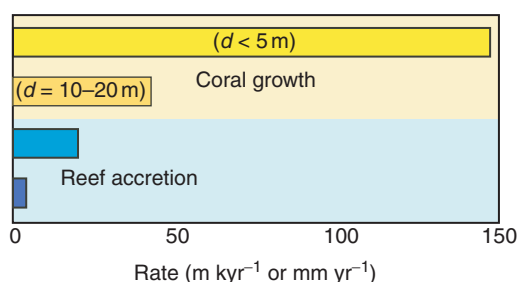


Fig. 2. Reef accretion versus sea-level rise and coral growth (d =water depth). In this scenario by Schlager (1981), shallow reefs (depth less than 5 m) are expected to build an order of magnitude faster than their deeper-water counterparts. This is explained largely by the dominance of faster-growing branching corals in shallow water.

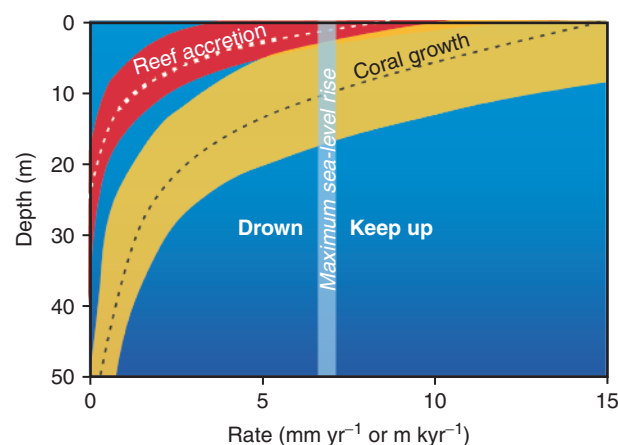


Fig. 3. Summary of presumed depth-related patterns of reef accretion and coral growth. While coral growth (yellow) can exceed 10 cm yr^{-1} in some shallow-water species, it generally drops from a maximum of $c. 10\text{--}20 \text{ mm yr}^{-1}$ in shallow water to less than 1 mm yr^{-1} at depth. Based on rates quoted in the previous literature, reef accretion (red) should decrease following a similar pattern, but at rates an order of magnitude slower. According to Schlager's (1981) 'Drowning Paradox', many shallow-water reefs in the past have built up faster than the highest rates of glacio-eustatic sea-level rise ($\sim 7 \text{ m kyr}^{-1}$; light blue bar). Those reefs should have been able to keep up with rising sea level, while their slower-building cohorts drowned.

literature. The precision of the depth information varied among studies, but errors are most likely random and are not thought to impact the general patterns shown below. Reported radiocarbon ages were calibrated by Beta Analytic, Inc. using the INTCAL-98 data set (Stuiver *et al.*, 1998) and methods similar to those of Talma & Vogel (1993). This transformation takes into account metabolic variations between sample types (i.e. coral vs. shell, wood, etc.), global/local

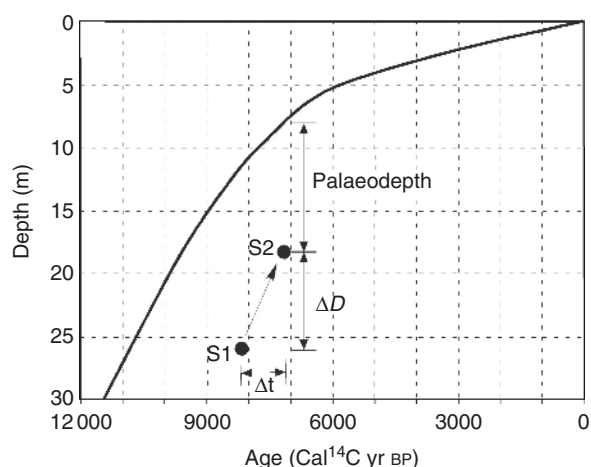


Fig. 4. Illustration of measurements used in this paper. Palaeodepth (D_p) is computed as the difference between the position of a recovered sample and sea level at the time it was deposited. Time of deposition is based mostly on calibrated radiocarbon measurements. Accretion was calculated as $\Delta D/\Delta t$.

reservoir effects, and biological fractionation for marine carbonates using a presumed isotopic value of $\delta^{13}\text{C} \sim 0$, unless otherwise specified. The procedure is similar to that used by the freeware program CALIB, except that it operates on smoothed data by visually scanning for short-term perturbations in the calibration curve (D. Hood, personal communication). U/Th ages were used as reported. Errors in age were typically 100 years or less, and are assumed to be randomly distributed about the reported dates.

Palaeowater depth

Water depth at the time of deposition was calculated as the vertical difference between the present depth of a coral sample and the height of sea level at the time corresponding to its radiometric age (Fig. 4). It is assumed that the recovered coral was either in place or was alive close to the time when it was deposited. Hindcast sea level is based on the corrected Lighty *et al.* (1982) sea-level curve as presented in Hubbard *et al.* (2005). This curve is virtually identical to the curve of Toscano & Macintyre (2003), which used many of the same samples and a nearly identical correction algorithm (i.e. CALIB vs. the proprietary Beta calibration). The rate of accretion was calculated using the formula:

$$A = (\Delta D/\Delta t)$$

where A is the accretion rate (in metres per thousand years), ΔD is the vertical difference between two core samples (in metres) and Δt is the time difference (in thousands of years) between the two samples.

Choosing the right sea-level curve

Recent discussions have challenged the Lighty *et al.* (1982) curve and its subsequent iterations. The objections generally relate to either the validity of the samples used for the curve (Blanchon, 2005) or the occurrence of numerous coral and peat samples, largely from Belize, that sit above it (Gischler, 2006). Figure 5 summarizes the available *A. palmata* data from the Caribbean. It includes all the coral data from Toscano & Macintyre (2003) plus the Belize and Campeche Bank samples of Gischler & Hudson (2004) and Blanchon & Perry (2004), respectively; additional, unpublished data from the Virgin Islands and Puerto Rico are also plotted. The sea-level curve that was used in this paper (from Hubbard *et al.*, 2005) is shown in black. It is virtually identical to the curve of Toscano & Macintyre (2003) (orange), because both are little more than isotopically based corrections of the Lighty *et al.* (1982) curve using either the Beta Analytic algorithm or the similar CALIB routine. A. Conrad Neumann's peat curve from Bermuda (unpublished personal communication), similarly corrected and allowing for differences between coral and peat (*c.* 400 years) is shown in green. Except for minor variations that are probably related to smoothing versus straight-line interpolation, the curves are again identical. The curve proposed by Blanchon (red) displays a series of step-like changes, reminiscent of the 'melt-water pulses' of Fairbanks (1989). Unlike the events proposed for Barbados, no separate isotopic evidence for sudden melt-water releases have been provided for any of the variations from a smooth curve. Coral samples well above his curve during all three proposed steps argue against their existence. In addition, the inflections in the curve are in part based on an interpretation of mangrove peat that is in fundamental conflict with the arguments of Gischler (2006), who argues that the elevated *A. palmata* and peat samples from Belize (plus Jamaica) support a fundamentally elevated Caribbean sea-level curve (blue line).

Verifying that a particular sample is in place has been the fundamental 'Achilles heel' of coral-based sea-level curves. Likewise, discriminating between reef material and allochthonous debris

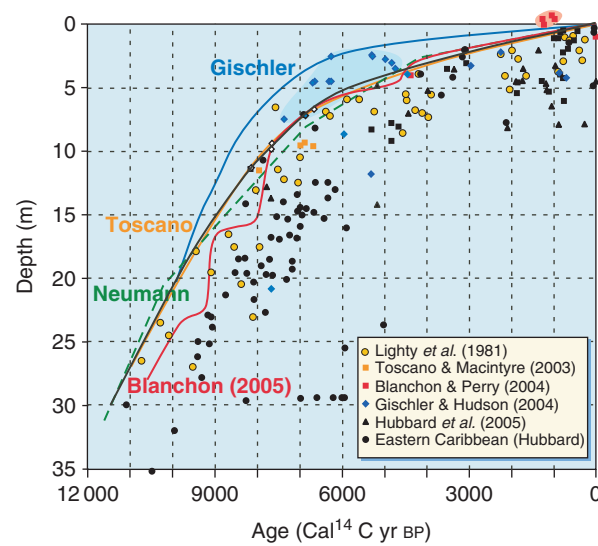


Fig. 5. Variability in proposed Caribbean sea-level curves. The data points represent the radiometric age and vertical position of individual *Acropora palmata* samples from cores throughout the region. The curve used in this paper (black: after Hubbard *et al.*, 2005) is based on both *A. palmata* and peat. This curve and the one by Toscano & Macintyre (2003; orange) are little more than isotopically corrected versions of the one originally proposed in Lighty *et al.* (1982; not shown). Neumann's (unpubl. pers. comm.) curve for Bermuda (dashed green) is based on mangrove peats, and is in general agreement. The stepped curve of Blanchon (2006; red) was not considered because (a) it is inconsistent with the entirety of the data, and (b) no separate isotopic evidence has been provided to support these drastic deviations from a smoothed trend. The curve of Gischler (2006; blue) sits above the calibrated Lighty curve with a maximum deviation of *c.* 3 m. The Toscano & Macintyre curve is based on the assumption that the curve should be placed at the bottom of what they interpreted as intertidal to slightly supratidal peats. Gischler's curve (Gischler & Hudson, 2004) straddles the top of the same peat-coral package.

thrown up onto supratidal storm ridges further complicates the matter. A detailed discussion of these problems and a solid defence of one particular curve over another is beyond the scope of this paper. However, it is worth noting that all the curves follow the same general pattern, and an approximate average of all the curves falls somewhere close to the black line in Fig. 5. The maximum difference between the three more central curves and either of the other two amounts to 3 m. The absolute depth of one particular sample might vary by up to that much, but it seems unlikely that the overwhelming patterns described below could be fundamentally changed. Nevertheless, the general impacts of choosing one curve over another will be discussed later.

Accretion rate

Reef-accretion rates have typically been reported for whole cores or reefs (for an excellent summary, see Dullo, 2005). In this paper, accretion rates from individual intervals (i.e. between two adjacent samples) within cores were chosen over those for whole cores or facies, because palaeowater depth could be more accurately assigned to a shorter time step. Intervals that contained largely mixed coral types or were dominated by detrital deposition were not included. Samples that plotted above sea level or resulted in negative accretion rates (i.e. the lower sample was younger than the upper one) were not used. Finally, rates calculated from closely spaced samples with age differences less than the reported analytical errors were also discarded. Of the 11 discarded accretion calculations, all were faster than 10 m kyr^{-1} . All but three were from palaeowater depths greater than 5 m. Furthermore, these shorter-term rapid rates were invariably contained within longer intervals that reflected much lower net accretion rates.

Separate analyses of reef accretion were run for (A) all corals regardless of species, and (B) a comparison of *A. palmata* versus massive-coral facies. The dominant corals within an interval were determined by examining core logs. The 11 data points from abandoned *A. palmata* reefs off Barbados (Fairbanks, 1989; Bard *et al.*, 1990) were used for the comparison between accretion rates in massive and branching facies only. They were eliminated from the depth-related comparison because no independent verification exists for sea level at the time these deeper reefs were active. All the Belize corals above the curve used in this paper (Fig. 5) occurred within mixed-coral intervals that violated the acceptance criteria. Thus, all the data used from the cores of Gischler & Hudson (2004) fell below the curve.

RESULTS

A total of 151 core intervals met the criteria described above. Of these, 79 were from branching-coral facies, compared with 72 from massive-coral intervals. Samples were recovered from 11 Caribbean and Atlantic locations (and from multiple reefs at many of these), ranging from central Florida in the north to Panama and Belize in the southwest and Antigua/Barbados in the easternmost Caribbean (Fig. 6; Table 1). Present-day environments ranged from emergent barrier and

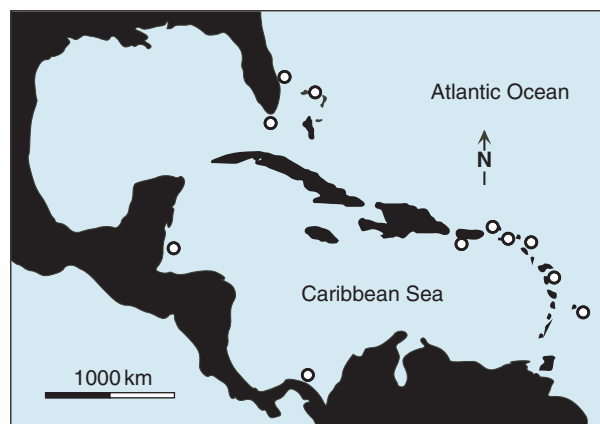


Fig. 6. Map showing the locations of the sites from which core data were derived (open circles).

Table 1. Sources of core data used in this study.

Florida	Lighty <i>et al.</i> (1982), Toscano & Lundberg (1998), Toscano & Macintyre (2003)
Bahamas	Lighty <i>et al.</i> (1982)
Martinique	Lighty <i>et al.</i> (1982)
Puerto Rico	Hubbard <i>et al.</i> (1997, unpublished data), Lighty <i>et al.</i> (1982)
Antigua	Macintyre <i>et al.</i> (1985)
St. Croix	Adey <i>et al.</i> (1977), Burke <i>et al.</i> (1989), Hubbard <i>et al.</i> (1990), Hubbard <i>et al.</i> (2005), Hubbard (unpublished data), Lighty <i>et al.</i> (1982), Macintyre & Adey (1990)
Barbados	Fairbanks (1989)
Panama	Macintyre & Glynn (1976)
Belize	Gischler & Hudson (2004)

fringing reefs to submerged but still active shelf-edge reefs (e.g. Lang Bank and SW Puerto Rico) and abandoned reefs that are now below the depth where accretion can occur (e.g. Barbados). The data are tabulated in Appendix 1.

The majority of the data points fell within the upper 15 m of the water column (Fig. 7). As expected, the fastest accretion rates were derived from core intervals in water <10 m deep at the time of deposition. However, accelerated accretion was evenly split between branching- and massive-coral intervals, and any depth-related coral affinities were weak above 15 m. *A. palmata* clearly thrived at depths much greater than is generally accepted as its maximum, commonly deeper than 10 m and occasionally down to 20 m. More important, they were capable of significant accretion well below the 5-m depth limit proposed by Lighty *et al.* (1982) and Macintyre (1988), among others.

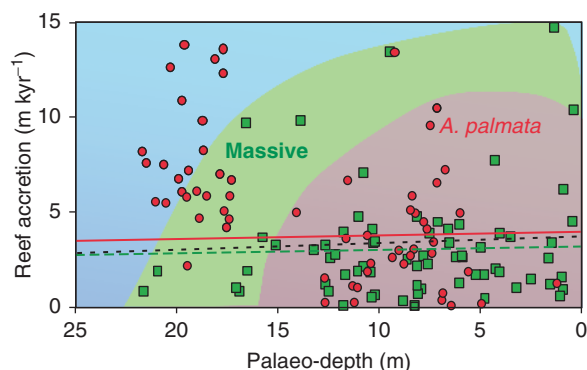


Fig. 7. Reef accretion versus palaeowater depth for branching (red dots) versus massive corals (green squares). Approximate limits for branching and massive facies (shaded) reflect a general overlap in the depth ranges for the two facies, but with a slight tendency for branching *Acropora palmata* to inhabit shallower water than massive species. The linear regression lines for branching (red solid: $y = 0.02x + 3.98 - R^2 = 0.001$), massive (green dashed: $y = 0.02x + 3.20; R^2 = 0.0001$) and all corals combined (black dotted: $y = 0.03x + 3.52; R^2 = 0.003$) show no strong depth-related relationship and R^2 values are very low, reflecting the large variance across all depth ranges (Fig. 8). The difference between the regression lines for branching (solid) and massive corals (dashed) is not statistically significant.

No strong depth-related pattern emerged either by facies type or for all corals combined. The highest R^2 value for linear regression was only 0.003. Exponential and polynomial best-fit lines yielded similarly poor results. The difference between means for shallow- and deep-water accretion ($<1.0 \text{ m kyr}^{-1}$) was lower than standard deviations within 5-m depth intervals (Fig. 8). The mean accretion rate for *A. palmata* intervals was faster than that for massive-coral facies (3.83 vs. 3.07 m kyr^{-1}), but this difference was not significant at $\alpha = 0.05$ using a Student's t -test, owing to these large variances. Additional data could raise the significance levels for this comparison, but the absolute difference would remain small, and certainly not approach the relationship that has been presumed for the two coral types.

Accretion rate was weakly and positively correlated with the rate of sea-level rise, but the R^2 value for the relationship was only 0.015. Only 16 of the measured intervals accreted at rates greater than 7 m kyr^{-1} , the upper threshold for Holocene sea-level rise proposed by Schlager (1981); these were equally distributed between 'deep' and 'shallow' reefs. In all but five cases, the intervals of unusually high accretion were small and were contained within a larger interval over which

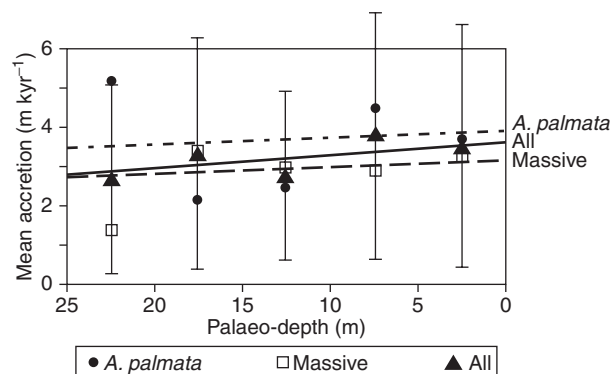


Fig. 8. Reef accretion versus palaeowater depth in 5-m increments. The depth-related trend is weak (lines shown here are based on linear regression) regardless of coral type, and standard deviations are larger than the difference between mean accretion rates at either depth extreme. The anomalously high accretion rate for *A. palmata* between 20 and 25 m is based on only one core interval.

mean accretion rate was below that threshold. Of those five intervals, only one was associated with a vertical section of significant thickness (*A. palmata* facies at $d = -1.4 \text{ m}$).

DISCUSSION

The higher concentration of measured intervals in palaeowater depths less than 15 m is consistent with the presumption that light intensity exerts a primary control on coral growth, and by extension, reef accretion. Also, the tendency for massive-coral intervals to extend into deeper water than branching-coral sections (compare shaded areas in Fig. 7) mimics modern reef zonation. However, neither the species- nor depth-related differences in average accretion rate that are the foundations of most modern-reef models clearly emerge from the data.

Schlager (1981) proposed that shallow reefs (set at $d < 5 \text{ m}$) accrete between 1 and 20 m kyr^{-1} , compared to less than 2 m kyr^{-1} at depths between 10 and 20 m (Fig. 2). The depth-related model of Bosscher (1992; Fig. 1) was built on these assumptions, as are most discussions of reef accretion versus sea-level rise, both past (Macintyre, 1988) and future (Graus & Macintyre, 1999). Figure 9 compares these presumptions to the results of this study. The maximum 'shallow-water' accretion rate (16.6 m kyr^{-1}) was higher than that for 'deep reefs' (9.73 m kyr^{-1}). However, the majority of the accretion rates for the Caribbean cores analysed

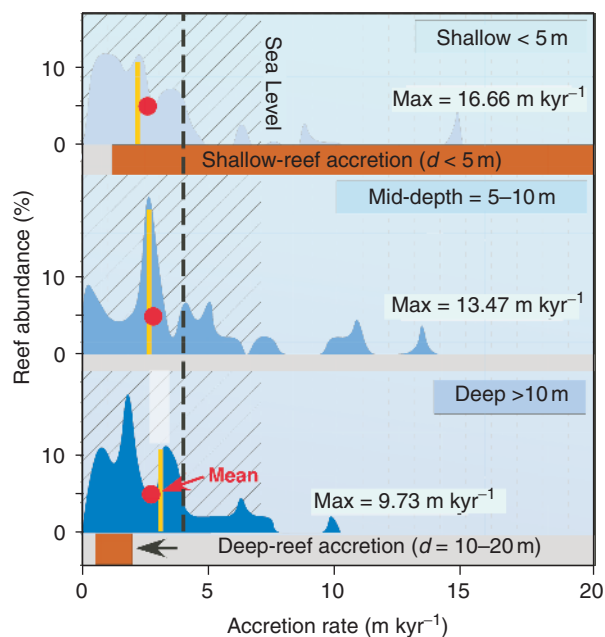


Fig. 9. Depth-related patterns of reef-accretion rates from this study (blue curves), compared with rates suggested by Schlager (1981; brown bars) for reefs in water depths less than 5 m and greater than 10 m (d =depth). Means and medians for each distribution are also shown. The range of Holocene sea level proposed by Schlager (up to 7 m kyr^{-1}) is shown by the diagonal pattern. Maximum accretion rate decreased with depth (16.66 m kyr^{-1} shallower than 5 m; 9.73 m kyr^{-1} deeper than 10 m). However, the primary mode of reef accretion remained below 4 m kyr^{-1} (dashed black line) for all depths. Mean (large red dots) and median accretion rates (yellow lines) for the three depth ranges are nearly identical for all three depth ranges.

for this study fell below 4 m kyr^{-1} , regardless of palaeowater depth. Moreover, mean accretion rates for the three depth intervals were virtually identical, as were the medians and the positions of the primary modes.

If these patterns are representative of what is actually happening on a larger scale, then we are faced with a number of questions. What is responsible for this surprising and seemingly counter-intuitive finding? How do we explain a system in which branching corals grow faster than their massive counterparts, but where a depth-related decrease in accretion is clearly absent? Can reefs in water depths greater than 10 m actually keep pace with those in shallow water where light intensity and coral growth are at least an order of magnitude higher? And, if so, how? Finally, what are the implications for reefs keeping up or being left behind by the sea-level rise in the distant past, or the near future?

It comes as no surprise that reef-accretion rates are significantly below the rate of coral growth.

Coral cover is rarely 100% on any reef. It has been long understood that bioerosion and physio-chemical damage occur on reefs (Grant, 1826), and can easily reduce 70% of the carbonate produced in a reef to sediment (Stearn & Scoffin, 1977; Hubbard *et al.*, 1990; Conand *et al.*, 1997). Much of this is exported from the reef, especially by storms (Woodley *et al.*, 1981; Hubbard, 1992), leaving only a portion of the original carbonate fixed by coral, corallines and other calcifiers within the reef edifice. What is surprising is the apparent disconnection between the depth-related patterns of coral growth and reef accretion that has emerged from these analyses. The presumption that the dominance of light-mediated calcification will remain as the fundamental underlying control of reef accretion has been widely held. The results of this synthesis indicate otherwise.

Possible sources of error

As in any budgeting exercise, an unexpected result begs for consideration of two possibilities: (1) the measurements are incorrect or somehow inappropriate, or (2) some factor may have been omitted from consideration. There are numerous sources of inaccuracy in the data used for the calculations. Precisely determining the position of a sample within a core can be difficult, and surely some of these reported values are less than totally accurate. However, these are undoubtedly evenly distributed around the true values and would logically cancel out one another. Also, palaeowater depth is based on a sea-level curve that is by necessity generalized, and represents a regional average. As discussed above, honest disagreements persist over the details of the Caribbean sea-level curve over the past 12,000 years. Some of this stems from different interpretations of the same data. Toscano & Macintyre (2003) chose to place their curve above the majority of the *A. palmata* and below the mangrove peats from Florida, Jamaica and Belize. Gischler (2006) argued that the curve should be placed over both. One might reasonably argue that there is some validity in both arguments and that the truth lies somewhere in between. If this is the case, then the maximum variation from the curve used here would be in the order of 1.5 m. The curve used in this paper (from Hubbard *et al.*, 2005) is based on both mangrove peat (Florida and Bermuda) and *A. palmata*. In that case, the vertical variation of the peat, which was short-rooted, was small and agreed with the line skirted over

the top of the coral package (with the exception of the 11 samples from Belize and the four young samples from Campeche Bank that plot above present sea level). If this agreement in any way validates the curve, then the possibility that the difference seen in the Belize samples represents local tectonic differences cannot be ruled out. The point in all of this is that the actual depth values assigned to any individual coral based on using the 'wrong' sea-level curve might be in error by 1–3 m. It will be left to the reader to decide if this sort of difference could be used to explain the lack of variability in reef accretion seen in this compilation over a depth range of some 22 m.

Another source of possible error is related to the assumption that recovered corals were either in growth position or ultimately came to rest close to the place where they lived. This lay at the core of the argument between Toscano & Macintyre (2003) and Blanchon (2005) over whether there are 'good' and 'bad' corals, and which should and should not be used to reconstruct sea level. The Faustian bargain of Lighty *et al.* (1982) was to lay a curve over the top of the 'coral envelope', assuming that the occasional upward deviants represented rubble tossed up on beaches or storm ridges. However, another reliable independent data source (e.g. peat) is required to support or refute this approach.

The identification of basal coral attachments strongly argues for a colony being in place. Convex upward coral-growth bands similarly lend credibility to a colony in growth position, albeit with less confidence. Unfortunately, the likelihood of encountering either in a core with any regularity is small. Coral-growth rates consistent with the hindcast depth can be useful (Hubbard *et al.*, 1986), but this will not resolve issues related to *A. palmata*. It has been proposed that the differences between polyp structure on the top and bottom of *A. palmata* branches can be used to divine orientation, and that 'right-side-up' branches reflect colonies in growth position. However, measurement of over 500 broken and in-place branches from the same localities reveals no statistical difference (D.K. Hubbard, unpublished data).

It is necessary to consider *in situ* colonies – those that are either in growth position or have not moved significant distances from where they grew. While great strides have been made in identifying taphonomic signatures associated with different styles of coral deposition (Perry,

1999, 2000, 2001; Blanchon & Perry, 2004), this is not yet a panacea. When available, the greatest assurance can be derived from either direct observation in submarine outcrop/excavation or reconstructing topography using multiple cores along transects. The data from northern Florida (in Lighty *et al.*, 1982; Toscano & Macintyre, 2003) were from excavations where the in-place nature of the sampled corals could be directly observed. The samples from Hess Ship Channel (Adey *et al.*, 1977) similarly benefited from direct observation (W. Adey, personal communication). Samples in the parent study from Buck Island (BI and BB in Appendix 1), Lang Bank (LB) and SW Puerto Rico (PAR) were all collected from cores aligned in transects where time lines could be used to reconstruct palaeotopography. In all these cases, the samples were recovered from either the apex of the topographic surface or along a broad horizontal bank. The result is that there was no shallower site from which to derive the samples. Also, these features were of sufficiently limited lateral extent that any disrupted sample had only limited space to be moved from where it grew. Similar reconstructions can be made from the well-constrained transects at Galeta Point, Panama (Macintyre & Glynn, 1976). Even if it is assumed that all the remaining studies suffered from dramatic downward transport of samples, the patterns reflected in the curves of Lighty *et al.* (1982), Toscano & Macintyre (2003), and Hubbard *et al.* (2005) remain.

This is not to say that any of these curves are a perfect representations of Holocene sea-level rise. Certainly, the package of mangrove and coral data above the curve that fueled the debate between Toscano & Macintyre (2003) and Gischler (2006) cannot be ignored. However, the author has not examined any of these samples and is, therefore, not in a position to comment (for example, are the peats short-rooted? What are the species, and what is their relationship to sea level? What is the condition of the corals and what evidence is there that might be used to reconstruct palaeotopography?). Nevertheless, the bulk of the data available support the curve used in this paper as a realistic approximation of sea level over the past 12,000 years. Even if this position were abandoned, the maximum spread among all the curves is less than 3 m, a value that is not likely to reconcile the trends shown in Fig. 7 with present models based on an order-of-magnitude decrease in reef accretion between the sea surface and a depth of 20–30 m. It is worth noting

that using the same method and the uppermost Belize curve as a datum, Gischler found that reef accretion increased significantly with depth, and intervals dominated by massive corals accreted faster than those dominated by branching acroporids (E. Gischler, personal communication, 2006).

A final possibility relates to the way in which the data were collected. Existing models are more often based on generalized patterns seen throughout a core or along an entire reef over its lifetime. In contrast, the measurements reported here are from discrete intervals within single cores. Furthermore, the data do not include intervals with a mixture of branching and massive corals or a predominance of detritus. This approach was chosen to (1) allow for a more accurate characterization of average palaeowater depth across a single accretionary interval, and (2) address the presumption that branching-coral reefs in shallow water will accrete much faster than their massive counterparts at depth. What effect might this have on the data, and would it be sufficient to explain the difference between the expected depth- and species-related patterns and those seen here?

Reefs do not accrete evenly, either spatially or temporally. Using each interval between dated samples adds variability and undoubtedly contributed to the high variance seen in Fig. 8. However, when the patterns from a particular reef system were examined (Fig. 10a), wholesale accretion rates between coral types and with increasing depth remained similar, both to one another and to the average rates for smaller intervals reported above. For example, *A. palmata* reefs from the shelf edge off both St. Croix and Puerto Rico accreted at rates similar to those from massive-coral reefs in deeper water, at the same place and time. Similarly, branching- and massive-coral reefs near Buck Island (St. Croix) accreted at similar rates, regardless of the dominant coral type. Whole cores showed the same pattern; cores from the same time frame within a single reef yielded accretion rates similar to each other and to the averages reported above for smaller intervals regardless of depth or facies (Fig. 10b).

The possible role of bioerosion

References to biological destruction of substrate date at least to Grant's 1825 description of temperate species of *Cliona*, and were more formally recognized when Neumann (1966) introduced the term 'bioerosion'. More recently, Scoffin *et al.*

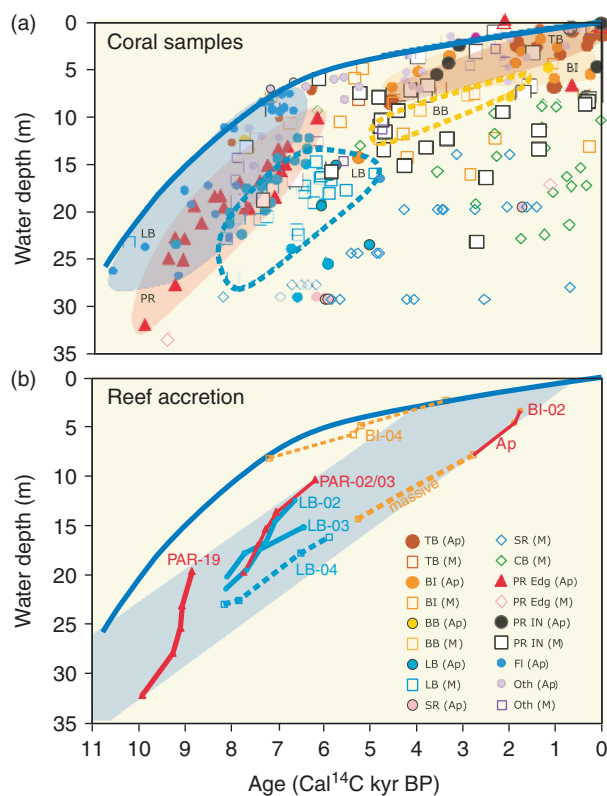


Fig. 10. (a) Ages versus water depths of all samples examined for this synopsis. The coloured envelopes delineate samples grouped by species for six reefs on St. Croix and Puerto Rico. The general trend of each envelope is interpreted as the overall rate of reef building by that species in a single reef. Earlier reefs accreted at the same rate regardless of species (filled = *Acropora palmata*; open = massive) or water depth. Similar parity existed in later reefs, except they built at slower rates. (b) Reef accretion pathways for selected cores examined for this study. Note that, with the exception of the massive-coral interval constrained by accommodation space (BI-04) and one deep reef (PAR-19), accretion rates were similar. *Acropora palmata* intervals are shown by solid lines; massive intervals are dashed. LB = Lang Bank (E St. Croix, US Virgin Islands); BI = Buck Island (N St. Croix), PAR = La Parguera (SW Puerto Rico). The shaded blue band corresponds to the mean accretion rate for this study (3.45 m kyr^{-1}).

(1980) concluded that, 'the internal structure of the reef is controlled not only by the nature of the dominant builders but also by the type and rates of bioerosion'. Chazottes *et al.* (1995) proposed that the greatest substrate loss off Morea was due to grazing fish and urchins ($2.33 \text{ kg m}^{-2} \text{ yr}^{-1}$), followed by macroborers (e.g. molluscs, worms: $0.20 \text{ kg m}^{-2} \text{ yr}^{-1}$) and microborers (algae, fungi: $0.009: 2.33 \text{ kg m}^{-2} \text{ yr}^{-1}$). A similar hierarchy has been proposed for the Great Barrier Reef (Kiene &

Hutchings, 1994; Tribollet *et al.*, 2002), and the Caribbean (Stearn & Scoffin, 1977).

A quantitative assessment of bioerosion rates across the full depth range of modern reefs is not available. However, anecdotal information is available that may allow at least a qualitative characterization of depth-related patterns. In shallow water off Barbados, Scoffin *et al.* (1980) noted increased bioerosion in shallower water, owing to a greater abundance of *Diadema antillarum Philippi* closer to shore. Steneck (1994) reported *Diadema* populations of 16 individuals per square metre at a depth of 3 m in Jamaica, compared with 2 individuals/m² and <1 individual/m² at depths of 10 m and 20 m, respectively. Kiene & Hutchings (1994) measured grazing rates of 0.30–1.96 kg m⁻² yr⁻¹ in shallow to mid-range depths off Lizard Island, Australia compared with only 0.08–0.29 kg m⁻² yr⁻¹ in deeper water on the forereef; a similar but variable trend was reported for total bioerosion. Off Bonaire, Steneck & McClanahan (2004) measured a 75% decrease in bite density and size on naturally occurring flora between shallow water and 30 m depth.

Data for infaunal boring are less clear but, on balance, infer a depth-related decrease in substrate destruction. By inference, the increased bioerosion by sponges within the wave-cut notches of Bermuda (Neumann, 1966) argues for greater sponge density close to sea level. Kiene & Hutchings (1994) measured higher rates of boring in shallower water, but the differences were not statistically significant. This is supported by data from Moore & Shedd (1977), who reported a consistent, depth-related decrease in sponge boring on three Jamaican reefs (8–80% decrease between 15 m and 27 m; 65% decrease between 27 m and 40 m). Vogel *et al.* (2000) reported a consistent decrease in microboring off Lee Stocking Island (Bahamas), from 0.2 kg m⁻² yr⁻¹ at 2 m to 0.1 kg m⁻² yr⁻¹ at 10 m and 0.01 kg m⁻² yr at 30 m. Highsmith (1980) proposed that the abundance of boring bivalves is proportional to primary productivity, which should be higher in shallow water where light intensity is greater. By contrast, Macdonald & Perry (2003) noted an increase in bioerosion with depth within the lagoon of Discovery Bay, Jamaica (8–10% loss shallower than 16 m; 18% below 16 m). However, they also noted heavy nutrient inputs from surrounding development that, in this restricted environment, could exert a control that overwhelms depth-related patterns. Goreau & Hartman (1963) cited a higher density of sponge boring at depths of 30 m

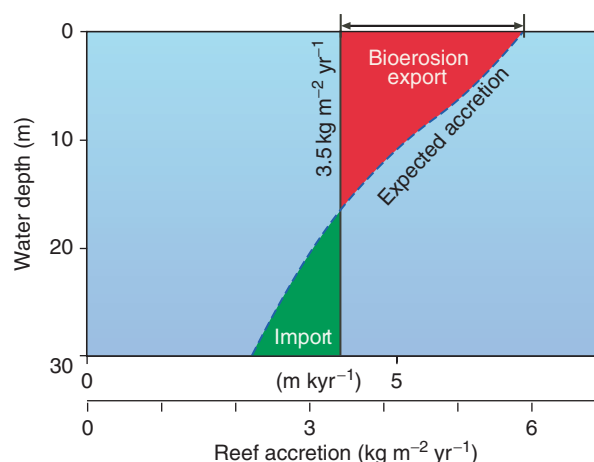


Fig. 11. Stylized model explaining depth-related differences between expected reef accretion based on prevailing models and the results of this study. The lower portion of the ‘expected accretion’ curve ($d > 10$ m) is based on the measured growth rates and species mix at Cane Bay Virgin Islands) and an assumed total-coral abundance of approximately 50%. Accretion rates in water shallower than 10 m were increased to allow for the greater accretion assumed to be associated with branching *Acropora palmata*. In this scenario, bioerosion decreases from a maximum rate of *c.* 2.5 kg m⁻² yr⁻¹ in shallow water to 0.7 kg m⁻² yr⁻¹ at a depth of 25 m, based on data from the literature cited in this paper. The remainder of the offsetting difference is related to sediment that is transported downslope but stays within the reef.

or more, but this was in very slow-growing plate corals. No actual bioerosion rates were reported, and this may have reflected low calcification rates rather than high infaunal excavation.

Figure 11 compares the depth-related trend in accretion from this study to a stylized carbonate-production curve based in part on data from Cane Bay in the US Virgin Islands (Hubbard *et al.*, 1990). In this scenario, increased bioerosion in shallow water (2.0–2.5 kg m⁻² yr⁻¹) offsets higher calcification rates. With increasing depth, both calcification and bioerosion decrease on parallel tracks, resulting in the loss of a strong depth-related change in reef accretion. It must be kept in mind that bioerosion by itself cannot create the depicted result. Accretion will be affected only to the extent that the sediments produced by bioerosion are exported down the reef front. In this scenario, the apparent homogenization of depth-related accretion patterns also reflects material produced in shallow water being shifted into deeper environs but remaining within the reef.

This exercise makes a significant assumption in creating a stylized production curve from a single location and utilizing depth-related

bioerosion data that are scant at best. While none of the values are inconsistent with those found in the literature, this cartoon is neither a quantitative treatment nor a proof that the proposed relationship actually exists. This must await more careful measurement of depth-related bioerosion and sediment-export patterns. It nevertheless highlights the potential importance of bioerosion as something more than a secondary control of reef accretion and architecture. It may ultimately prove to be as important as calcification by corals in determining the rates at which reefs are built.

The ‘drowning paradox’?

Based on an assumption that ‘many Holocene reefs can be shown to have outpaced even the fastest sea-level rise’, Schlager (1981) proposed that reef drowning presents a paradox that can be resolved only by extreme events such as sudden and rapid sea-level rise or degraded oceanic conditions that severely compromise the accretionary capacity of a reef or platform. Based on the results of this study, reefs that accrete at rates in excess of 7 m kyr^{-1} are in fact rare. Only one out of 151 intervals exceeded that threshold and was not part of a slower, long-term aggradational history. Given this, the drowning of a reef or platform seems much less surprising. Parts of reefs are capable of extraordinary ‘sprints’, but reef accretion is generally slower and sea level largely exerts the dominant control. At the average rate of reef accretion proposed by this study ($3\text{--}4 \text{ m kyr}^{-1}$; blue band in Fig. 10b), reefs would have lagged behind rising sea level prior to 7000–6000 years ago when the rate of sea-level rise slowed below this value. After this time, most Caribbean reefs were able to catch up in the absence of some environmental stress that severely compromised the ability of reef biota to make carbonate.

Significance to existing models

Two fundamental principles that underlie our existing Holocene coral-reef models are:

- (1) reefs in shallow water (i.e. $<5 \text{ m}$) build an order of magnitude faster than their deeper-water counterparts (i.e. $>10\text{--}15 \text{ m}$);
- (2) reefs dominated by branching corals accrete much faster than those primarily inhabited by slower-growing, massive species.

This study has shown that in the Caribbean and western Atlantic these relationships have not been as strong over the past 10–12,000 years, as has been assumed. It is not clear whether this pattern holds for other oceans or other time periods. Dullo (2005) has provided an excellent synthesis of coral growth and reef accretion in the Caribbean versus the Indo-Pacific, and has proposed that the early plateau in sea level *c.* 6000 years ago restricted reef-building and resulted in slower rates of reef accretion in the latter. A more-detailed look at shorter-term accretion within individual reefs (and cores) would provide an excellent comparison to this study and could serve to broaden our understanding of the role of sea-level rise and accommodation space in a pattern that seems considerably different than has been taught.

Whether or not something akin to the scenario depicted in Fig. 11 ultimately emerges as the correct explanation, the lack of a substantial decrease in reef accretion according to either depth or species cannot be ignored, and may have profound implications for models of coral-reef accretion over the past 10,000 years, and perhaps longer. At the very least, these findings reinforce the idea that reefs do not grow in the organic sense, rather they build or accrete as largely physical structures in which biological processes make varying contributions. Thus, although impossible, it would be fortuitous indeed if it were possible to simply strike the phrase ‘reef growth’ from the literature. While ‘growth’ in the strictest sense is not incorrect, the phrase ‘reef growth’ makes a strong inference of biological primacy that would not be of concern when discussing, for example, ‘delta growth’ or ‘fault growth’.

In the absence of oceanographic stresses that limit calcification as a supplier of raw material for reef building, the rate of sea-level rise emerges as the primary determinant of whether or not a reef will “keep up” or “give up” (*sensu* Neumann & Macintyre, 1985). Prior to 7000 cal. yr BP, sea-level rose at a rate exceeding 5 m kyr^{-1} , faster than accretion in most of the core intervals measured in this study. After 6000 cal. yr BP, this rate dropped below 1 m kyr^{-1} , and virtually every reef shallower than 25 m was capable of keeping pace or exceeding on rising sea level. In some instances, accretion in reefs closer to sea level was probably constrained by a lack of accommodation space. While this undoubtedly skewed the pattern of shallow-water accretion rates reported in this study, its

effect was not sufficient to return shallow-water accretion to a position of primacy.

It is interesting to note that a weak but positive correlation was found between the rates of sea-level rise and accretion. Again this was probably influenced by a lack of accommodation space for shallow-water reefs during intervals of slowed sea-level rise. However, the higher rates of accretion during periods of rapidly rising sea level were not found at mid-depths but rather in some of the deepest calculated palaeowater depths. Core PAR-19 (Fig. 10b) built at an average rate exceeding 9 mkyr^{-1} . Despite starting off in 15 m of water, a depth generally considered too deep to allow significant accretion by branching corals, this *A. palmata* reef was actually catching up with rapidly rising sea level when accretion suddenly stopped *c.* 9000 years ago; it was in water only 5 m deep by that time. Similarly, the submerged reefs off Barbados cored by Fairbanks (1989) accreted at rates higher than 6 mkyr^{-1} during perhaps the most rapid sea-level rise in the Holocene. All of this suggests reconsideration of existing Holocene reef models, which are based largely on strong depth- and species-dependant accretion.

CONCLUSIONS

The findings of this study appear to conflict with two of the most basic rules of Holocene coral-reef accretion. There are undoubted inaccuracies in the methods used to log the cores and the assumptions used in analysing the data from the literature. However, it is difficult to imagine any combination of factors that, if changed, could make the pattern seen in Figs 7–10 look like those in Figs 2 and 3. The next step is to revisit the studies from which the existing concepts were developed, and determine whether the reef-wide patterns that they examined were actually different than those shown here or whether the models derived from them were simply a very good explanation of what was known at the time, but now need to reconsider. Similarly, the results reported above should be used to resolve how such different conclusions can be reached and whether these should be used to formulate new models.

Based on the findings discussed above, the following conclusions are offered.

- 1 No strong depth-related decrease in reef-accretion rate was found in cores from reefs that built in water depths between 0 and 25 m.
- 2 The decrease in average accretion rate from 3.58 mkyr^{-1} in shallow water to 2.76 mkyr^{-1} between depths of 20 and 25 m was less than the standard deviations measured at any depth ($2.20\text{--}3.13\text{ mkyr}^{-1}$), and was not statistically significant.
- 3 Average accretion rates in reefs dominated by branching *A. palmata* (3.83 mkyr^{-1}) were not statistically different than those from intervals of massive species (3.07 mkyr^{-1}).
- 4 Bioerosion and export of detritus into deeper reef environs undoubtedly exert some control on this pattern. Whether they can make up the difference between previously assumed trends and those shown here awaits further study. Nevertheless, the role of bioerosion emerges as a factor that is quantitatively important in not only influencing the character of internal reef fabrics, but also affecting the rate at which reefs build as well.
- 5 Few reefs have built faster than the rate of sea-level rise in the early and mid-Holocene. Therefore, drowned reefs should be more expected than has been suggested by Schlager's (1981) 'drowning paradox'. This has an important bearing on understanding the relationship between reef accretion and rising sea level, both past and future.
- 6 Coral reefs are structures that are built as much by physical sedimentation as by calcification by corals, coralline algae and other large calcifiers. In short, reef corals grow; coral reefs accrete.

ACKNOWLEDGEMENTS

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Finally, individuals like Bob Ginsburg who asked the questions that have directed us for the three decades since our first holes were drilled with those crude, portable units ultimately set the stage for a new science that was to follow. The session in which this contribution was presented reflects the high esteem in which we hold, not only Bob, but all of those individuals who propose ideas that force us to abandon comfortable dogmas.

APPENDICES

Appendix 1. Data used for analyses discussed in this paper.

St. Croix (USVI)					
Sample	SL [m]	Wtr D [m]	Accretion rate [m kyr ⁻¹]		Site (source)
			<i>Acropora palmata</i>	Massive	
BI 01-02	-2.2	-1.7	2.3		Buck Island (Hubbard <i>et al.</i> , 2005)
BI 01-13	-2.8	-2.7	2.9		
BI 01-24	-3.4	-3.8	1.7		
BI 01-40	-6.8	-4.2		2.0	
BI 02-01	-1.0	-2.4	10.0		
BI 02-05	-1.2	-3.4	3.7		
BI 02-27	-2.0	-5.9		2.6	
BI 02-43	-3.2	-8.6		2.5	
BI 03-05	-0.1	-0.4	1.3		
BI 03-16	-0.8	-1.3	2.0		
BI 03-37	-3.3	-5.2		1.7	
BI 04-02	-2.4	0.0		1.4	
BI 04-14	-4.0	-0.9		6.3	
BI 04-21	-4.4	-1.6		1.3	
BI 05-24	-0.6	-5.6	1.9		
BI 05-40	-1.0	-6.2		2.7	
BI 07-07	-0.3	-7.6		2.3	
BI 07-20	-1.5	-10.8		7.1	
BB 01-02	-0.8	-4.3	3.8		BI Bar (Hubbard <i>et al.</i> , 2005)
BB 01-11	-1.3	-6.9	0.8		BI Bar (Macintyre & Adey, 1990)
BB 02-01	-1.2	-4.8		1.7	
BB 02-02	-2.0	-6.0		1.3	
BB 02-03	-2.8	-6.5		3.4	
CB 01-05	0.0	-10.4		0.6	Cane Bay (Hubbard <i>et al.</i> , 1990)
CB 01-11	-0.9	-10.2		0.7	
CB 02-01	-0.3	-15.1		3.3	
CB 02-07	-0.5	-16.9		0.9	
CB 03-01	-0.8	-8.2		0.1	
CB 04-03	-0.2	-7.9		1.0	
CB 04-09	-0.9	-8.1		0.7	
CB 04-16	-1.6	-8.1		1.2	
CB 04-23	-4.3	-8.8		0.4	
CB 05-15	-0.9	-12.5		0.8	
CB 05-23	-1.6	-12.7		1.3	
CB 06-02	-0.5	-20.9		1.9	
CB 06-07	-0.9	-21.6		0.9	
CB 07-02	-0.2	-17.0		1.1	
LBE 06-06	-3.8	-12.2		2.8	Lang Bank (Hubbard, unpublished data)
LBE 06-18	-4.5	-13.2		3.0	
LBE 06-30	-5.3	-14.1	5.0		
LBE 07-02	-4.1	-19.4	2.2		
LBE 07-18	-5.0	-20.5	5.5		
LBN 01-06	-5.5	-9.5		13.5	

Appendix 1. Continued.

St. Croix (USVI)

Sample	SL [m]	Wtr D [m]	Accretion rate [m kyr ⁻¹]		Site (source)
			<i>Acropora palmata</i>	Massive	
LBN 02-05	-6.5	-6.0	5.0		
LBN 02-18	-7.5	-7.1	10.5		
LBN 02-30	-8.0	-8.8	2.3		
LBN 02-41	-8.0	-11.3	1.2		
LBN 05-25	-5.5	-13.9		9.9	
LBN 05-53	-6.1	-16.6		9.7	
LBN 08-02	-5.8	-6.7	7.3		
LBN 08-22	-6.4	-8.5	5.1		
LBN 08-36	-7.7	-9.2	13.4		
LBN 09-03	-6.0	-7.7	4.2		Lang Bank (Hubbard, unpublished data)
LBS 03-03	-5.9	-9.3	2.6		
LBS 03-11	-8.5	-10.2		3.5	
LBS 03-15	-9.3	-10.5	3.8		
LBS 03-19	-11.0	-10.6	1.9		
LBS 04-04	-4.9	-11.2	0.3		
LBS 04-08	-5.0	-11.7		1.8	
LBS 04-14	-6.1	-11.7		4.0	
LBS 04-21	-8.2	-12.6		3.3	
LBS 04-34	-10.0	-12.7	1.6		
LBS 06-39	-6.4	-15.8		3.7	
S Lang Bk	-4.8	-10.3		3.4	Lang Bank (Adey <i>et al.</i> , 1977)
S Lang Bk	-6.4	-11.0		4.8	
S Lang Bk	-5.3	-11.1		1.9	
S Lang Bk	-10.0	-11.1	1.0		
Tague Bay	-1.0	0.0	2.9		Tague Reef (Burke <i>et al.</i> , 1989)
Tague Bay	-5.8	-1.4	4.4		
Tague Bay	-0.1	-1.5	6.0		
Tague Bay	-1.3	-1.6		2.6	
Tague Bay	0.0	-1.6	0.9		
Tague Bay	-2.5	-4.8		0.5	
<i>Puerto Rico</i>					
PAR 01-02	0.0	-5.0	0.2		Parguera (Hubbard <i>et al.</i> , 1997)
PAR 01-07	-2.8	-3.0	8.8		
PAR 01-11	-3.0	-5.0		3.2	
PAR 01-27	-3.9	-7.1		4.5	
PAR 01-39	-5.0	-10.8		2.2	
PAR 02-06	-7.0	-8.4	5.9		
PAR 02-13	-9.6	-10.4	2.3		
PAR 03-10	-7.1	-7.4	2.9		
PAR 03-12	-7.9	-7.5	9.6		
PAR 03-20	-8.9	-8.2	4.9		
PAR 05-03	0.0	-0.1	0.8		
PAR 05-09	-2.3	-0.5	8.5		
PAR 05-20	-2.5	-2.1	3.4		
PAR 05-29	-3.2	-4.3		7.7	
PAR 05-40	-3.8	-7.8		2.7	
PAR 05-53	-6.5	-10.4		1.9	
PAR 06-01	-0.4	-0.3	0.4		
PAR 06-11	-3.1	-0.9		1.0	Parguera (Hubbard <i>et al.</i> , 1997)
PAR 06-22	-3.9	-4.1		1.9	
PAR 07-05	-2.0	-1.4		14.7	
PAR 08-06	-1.0	-2.5	1.5		
PAR 08-18	-2.9	-4.0		3.9	
PAR 08-25B	-3.5	-5.9		2.7	
PAR 09-09	-0.2	-8.2		4.8	
PAR 09-11	-0.2	-8.5		2.7	
PAR 09-29	-1.0	-12.5		2.6	

(Continued.)

Appendix 1. Continued.

Sample	SL [m]	Wtr D [m]	Accretion rate [m kyr ⁻¹]		Site (source)
			<i>Acropora palmata</i>	Massive	
PAR 10-19	-1.0	-6.0		4.4	
PAR 10-25	-1.2	-6.6		4.1	
PAR 10-35	-1.4	-8.1		2.2	
PAR 10-63	-2.9	-10.3		4.2	
PAR 10-81	-3.4	-11.8		0.1	
PAR 11-11	-7.0	-9.0	3.0		
PAR 11-29	-11.5	-8.3	3.1		Parguera (Hubbard <i>et al.</i> , 1997)
PAR 12-01	0.0	-0.4	9.8		
PAR 12-17	-0.5	-6.4	0.1		
PAR 12-24	-4.3	-3.2		1.1	
PAR 17-09	-0.7	-16.6		2.0	
PAR 19-55	-13.7	-7.8	4.5		
PAR 19-87	-16.4	-11.5	6.7		
PAR A-02	-9.9	-7.3	3.4		
PAR A-14	-11.7	-6.9	0.4		
VH1-C1	-0.1	-1.1		0.6	Vieques (Lighty <i>et al.</i> , 1982)
<i>Florida</i>					
Sand Key	-7.1	-2.2	2.0		Toscano & Macintyre (2003)
Fla-SeqA-01	-10.4	-7.1	6.6		Lighty <i>et al.</i> (1982)
Fla-SeqB-01	-3.9	-12.7	0.3		
Fla-SeqB-02	-13.1	-4.5	4.4		
Fla-SeqC-01	-15.6	-2.5	7.1		
Fla-SeqD-01	-11.4	-11.6	3.6		
<i>Panama</i>					
H03C02 5/5	-2.0	0.2	1.4		Galeta (Macintyre & Glynn, 1976)
H03C06 2/2	-4.8	-1.2	1.3		
H03C7 2/3	-6.0	-0.8	9.3		
H06C01 3/3	-1.5	-0.1	2.0		
H10C04 1/7	-3.0	-2.5	2.3		
H11C01 4/4	-3.2	-0.6	3.2		
H11CC06 4/5	-4.6	-3.5		3.7	
<i>Antigua</i>					
N2-07	-1.6	-1.5		3.4	Nonesuch Bay (Macintyre <i>et al.</i> , 1985)
N2-38	-3.8	-7.5		3.9	
N4-04	-0.3	-1.0		1.6	
N5-05	-3.3	-0.5		4.5	
<i>Belize</i>					
BBR-4	-7.6	-0.4	3.1		Belize (Gischler & Hudson, 2004)
BBR-5	-7.0	-4.1		4.4	
BBR-6	-4.2	-1.9	3.2		
BBR-7	-4.2	-0.2	2.4		
BBR-8a	-6.0	-2.5	6.3		
BBR-8b	-5.5	-6.3		4.3	
BBR-9a	-2.5	-8.3		2.8	Belize (Gischler & Hudson, 2004)
BBR-9b	-5.2	-9.4		4.4	
<i>Barbados</i>					
RGF12-16-5	n/a	n/a	5.7		Deep Reefs (Fairbanks, 1989)
RGF12-21-10	n/a	n/a	0.5		
RGF12-6-7	n/a	n/a	4.1		
RGF12-9-5	n/a	n/a	9.5		
RGF7-12-2	n/a	n/a	10.8		
RGF7-16-2	n/a	n/a	8.1		
RGF7-4-2	n/a	n/a	1.0		
RGF7-5-5	n/a	n/a	7.4		
RGF9-21-11	n/a	n/a	4.6		
RGF9-32-4				2.8	
RGF9-8-2	n/a	n/a	11.1		

REFERENCES

- Adey, W.H.** (1978) Coral reef morphogenesis: a multidimensional model. *Science*, **202**, 831–837.
- Adey, W.H.** and **Burke, R.B.** (1976) Holocene bioherms (algal ridges and bank barrier reefs) of the eastern Caribbean. *Geol. Soc. Am. Bull.*, **87**, 95–109.
- Adey, W.H., Macintyre, I.G., Stuckenrath, R.** and **Dill, R.F.** (1977) Relict barrier reef system off St. Croix: its implications with respect to late Cenozoic coral reef development in the western Atlantic. *Proc. 3rd Intl. Coral Reef Symp.*, **2**, 15–21.
- Bard, E., Hamelin, B., Fairbanks, R.G.** and **Zindler, A.** (1990) Calibration of the ^{14}C timescale over the past 30,000 years using mass spectrometric U–Th ages from Barbados cores. *Nature*, **345**, 405–410.
- Blanchon, P.** (2005) Comments on ‘Corrected western Atlantic sea-level curve for the last 11,000 years based on calibrated ^{14}C dates from *Acropora palmata* framework and intertidal mangrove peat’. *Coral Reefs*, **24**, 183–186.
- Blanchon, P.** and **Perry, C.T.** (2004) Taphonomic differentiation of *Acropora palmata* facies in cores from Campeche Bank Reefs, Gulf of Mexico. *Sedimentology*, **51**, 53–76.
- Bosscher, H.** (1992) *Growth Potential of Coral Reefs and Carbonate Platforms*. Proefschrift Vrije Universiteit Amsterdam, Utrecht, Netherlands, 157p.
- Burke, R.B., Adey, W.H.** and **Macintyre, I.G.** (1989) Overview of the Holocene history, architecture, and structural components of Tague Reef, St. Croix, U.S.V.I. In: *Terrestrial and Marine Geology of St. Croix, U.S. Virgin Islands* (Ed. D.K. Hubbard), *West Indies Laboratory Special Publ.*, **8**, 105–110.
- Chalker, B.E.** (1981) Simulating light-saturation curves for photosynthesis and calcification by reef-building corals. *Marine Biol.*, **63**, 135–141.
- Chazottes, V., Le Champion-Alsumard, T.** and **Peyrot-Clausade, M.** (1995) Bioerosion rates on coral reefs: interactions between macroborers, microborers and grazers (Morea, French Polynesia). *Paleogeogr., Paleoclimatol., Paleoecol.*, **13**, 189–198.
- Conand, C., Chabanet, P., Cuet, P.** and **Letourneur, Y.** (1997) The carbonate budget of a fringing reef in La Reunion Island (Indian Ocean): sea-urchin and fish bioerosion and net calcification. *Proc. 8th Int. Coral Reef Symp.*, **1**, 953–958.
- Dullo, W.-C.** (2005) Coral growth and reef growth: a brief review. *Coral Reefs*, **51**, 33–48.
- Fagerstrom, A.J.** (1987) *The Evolution of Reef Communities*. John Wiley & Sons, New York, 600 p.
- Fairbanks, R.G.** (1989) A 17,000 year glacio-eustatic sea level record: influence of glacial melting rates on the Younger Dryas event and deep-ocean circulation. *Nature*, **342**, 637–642.
- Fosså, J.H., Mortensen, P.B.** and **Duevick, D.M.** (2002) The deep-water coral *Lophelia pertusa* in Norway waters: distribution and fishery impacts. *Hydrobiologia*, **47**, 1–12.
- Ginsburg, R.N.** (1958) Early diagenesis and lithification of shallow-water carbonate sediments in south Florida. *SEPM Spec. Publ.*, **5**, 80–100.
- Ginsberg, R.N., Gischler, E.** and **Schlager, W.** (1994) Johannes Walther on reefs. *Comparative Sedimentology Laboratory, University of Miami, Geological Milestones*, Vol. II, 141 p.
- Gischler, E.** (2006) Comments on ‘Corrected western Atlantic sea-level curve for the last 11,000 years based on calibrated ^{14}C dates from *Acropora palmata* framework and intertidal mangrove peat’. *Coral Reefs*, **25**, 273–279.
- Gischler, E.** and **Hudson, J.H.** (2004) Holocene development of the Belize barrier reef. *Sedimentary Geol.*, **164**, 223–236.
- Goreau, T.F.** and **Hartman, W.D.** (1963) Control of coral reefs by boring sponges. In: *Mechanisms of Hard Tissue Destruction* (Ed. R.F. Sogannaes), *AAAS Publ.*, **75**, 25–54.
- Grant, R.E.** (1826) Notice of a new zoophyte (*Cliona celata* Gr.) from the Firth of Forth. *Edinburgh. New Philos. J.*, Apr–Oct, 78–81.
- Graus, R.R.** and **Macintyre, I.G.** (1999) Global warming and the future of Caribbean coral reefs. *Carbonates Evaporites*, **13**, 43–47.
- Highsmith, R.C.** (1980) Geographic patterns of coral bioerosion, a productivity hypothesis. *J. Exp. Mar. Biol. Ecol.*, **46**, 177–196.
- Hubbard, D.K.** (1992) Hurricane-induced sediment transport in open-shelf tropical systems – an example from St. Croix, U.S. Virgin Islands. *J. Sedimentary Petrol.*, **62**, 946–960.
- Hubbard, D.K., Burke, R.B.** and **Gill, I.P.** (1986) Styles of reef accretion along a steep, shelf-edge reef, St. Croix, U.S. Virgin Islands. *J. Sedimentary Petrol.*, **56**, 848–861.
- Hubbard, D.K., Burke, R.B.** and **Gill, I.P.** (1998) Where’s the reef: the role of framework in the Holocene. *Carbonates Evaporites*, **13**, 3–9.
- Hubbard, D.K., Gill, I.P., Burke, R.B.** and **Morelock, J.** (1997) Holocene reef backstepping – southwestern Puerto Rico Shelf. *Proc. 8th Int. Coral Reef Symp.*, **2**, 1779–1784.
- Hubbard, D.K., Miller, A.I.** and **Scaturro, D.** (1990) Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, U.S. Virgin Islands): applications to the nature of reef systems in the fossil record. *J. Sedimentary Petrol.*, **60**, 335–360.
- Hubbard, D.K., Zankl, H., van Heerden, I.** and **Gill, I.P.** (2005) Holocene reef development along the north-eastern St. Croix shelf, U.S. Virgin Islands. *J. Sedimentary Res.*, **75**, 97–113.
- Kiene, W.E.** and **Hutchings, P.A.** (1994) Bioerosion experiments at Lizard Island, Great Barrier Reef. *Coral Reefs*, **13**, 91–98.
- Lighty, R.G., Macintyre, I.G.** and **Stuckenrath, R.** (1982) *Acropora palmata* reef framework: a reliable indicator of sea level in the western Atlantic for the past 10,000 years. *Coral Reefs*, **1**, 125–130.
- Lowenstam, H.A.** (1950) Niagaran reefs of the Great Lakes area. *GSA Memoir*, **67**, 215–248.
- Macdonald, I.A.** and **Perry, C.T.** (2003) Biological degradation of coral framework in a turbid lagoon environment, Discovery Bay, Jamaica. *Coral Reefs*, **22**, 523–535.
- Macintyre, I.G.** (1988) Modern coral reefs of western Atlantic: new geologic perspective. *AAPG Bull.*, **72**, 1360–1369.
- Macintyre, I.G.** and **Adey, W.H.** (1990) Buck Island Bar, St. Croix, USVI: a reef that cannot catch up with sea level. *Atoll Res. Bull.*, **336**, 1–7.

- Macintyre, I.G.** and **Glynn, P.W.** (1976) Evolution of modern Caribbean fringing reef, Galeta Point, Panama. *AAPG Bull.*, **60**, 1054–1072.
- Macintyre, I.G., Burke, R.B.** and **Stuckenrath, R.** (1981) Core holes in the outer fore reef off Carrie Bow Cay, Belize: a key to the Holocene history of the Belizean barrier reef complex. *Proc. 4th Int. Coral Reef Symp.*, **1**, 567–574.
- Macintyre, I.G., Multer, H.G., Zankl, H.L., Hubbard, D.K., Weiss, M.P.** and **Stuckenrath, R.** (1985) Growth and depositional facies of a windward reef complex (Nonsuch Bay, Antigua, W.I.). *Proc. 5th Int. Coral Reef Symp.*, **6**, 605–610.
- Moore, C.H.** and **Shedd, W.W.** (1977) Effective rates of sponge bioerosion as a function of carbonate production. *Proc. 3rd Int. Coral Reef Symp.*, **2**, 499–505.
- Neumann, A.C.** (1966) Observations on coastal erosion in Bermuda and measurements of the boring rates of the sponge *Cliona lampa*. *Limnol. Oceanog.*, **11**, 92–108.
- Neumann, A.C.** and **Macintyre, I.** (1985) Reef response to sea-level rise: keep-up, catch-up, or give-up. *Proc. 5th Int. Coral Reef Symp.*, **3**, 105–110.
- Newell, N.D., Rigby, J.K., Fischer, A.G., Whiteman, A.J. Hickox, J.E.** and **Bradley, J.S.** (1953) *The Permian Reef Complex of the Guadalupe Mountains Region, Texas and New Mexico: a Study in Paleocology*. W.H. Freeman, San Francisco, 236p.
- Perry, C.T.** (1999) Reef framework preservation in four contrasting modern reef environments, Discovery Bay, Jamaica. *J. Coastal Res.*, **15**, 796–812.
- Perry, C.T.** (2000) Macroboring of Pleistocene coral communities, Falmouth Formation, Jamaica. *Palaios*, **15**, 483–491.
- Perry, C.T.** (2001) Storm-induced coral rubble deposition: Pleistocene records of natural reef disturbance and community response. *Coral Reefs*, **20**, 171–183.
- Quoy, J.R.** and **Gaimard, J.P.** (1825) Memoire sur l'accroissement des polyps lithophytes consider e geologiquement. *Annales Sci. Naturelles*, **6**, 373–390.
- Reed, J.K., Shepard, A.N., Koenig, C., Scanlon, K.M.** and **Gilmore, R.G. Jr.** (2005) Mapping, habitat characterization, and fish surveys of the deep-water *Oculina* coral reef Marine Protected Area: a review of historical and current research. In: *Cold-Water Corals and Ecosystems* (Eds A. Freiwald and J.M. Roberts), Springer-Verlag, Berlin-Heidelberg, pp. 443–465.
- Schlager, W.** (1981) The paradox of drowned reefs and carbonate platforms. *GSA Bull.*, **92**, 197–211.
- Scoffin, T.P.** (1992) Taphonomy of coral reefs: a review. *Coral Reefs*, **11**, 57–77.
- Scoffin, T.P., Stearn, C.W., Boucher, D., Frydill, P., Hawkins, C.M., Hunter, I.G.** and **MacGeachy, J.K.** (1980) Calcium carbonate budget of a fringing reef on the west coast of Barbados. *Bull. Mar. Sci.*, **30**, 475–508.
- Stearn, C.W.** and **Scoffin, T.P.** (1977) Carbonate budget of a fringing reef, Barbados. *Proc. 3rd Intl. Coral Reef Symp.*, **2**, 471–476.
- Steneck, R.S.** (1994) Is herbivore loss more damaging to reefs than hurricanes? Case studies from two Caribbean Reef Systems (1978–1988). *Proc. Colloq. on Global Aspects of Coral Reefs, Miami*, 220–226.
- Steneck, R.S.** and **McClanahan, T.** (2004) *A Report on the Status of the Coral Reefs of Bonaire with Advice on the Establishment of Fish Protection Area.*, Univ. of Maine, Walpole, ME, 89 pp.
- Stuiver, M., Reimer, P.J.** and **Braziunas, T.F.** (1998) High-precision radiocarbon age calibration for terrestrial and marine samples. *Radiocarbon*, **40**, 1127–1151.
- Talma, A.** and **Vogel, J.** (1993) A simplified approach to calibrating C14 dates. *Radiocarbon*, **35**, 317–322.
- Toscano, M.A.** and **Lundberg, J.** (1998) Early Holocene sea-level record from submerged fossil reefs on the southeast Florida margin. *Geology*, **26**, 255–258.
- Toscano, M.A.** and **Macintyre, I.G.** (2003) Corrected western Atlantic sea-level curve for the last 11,000 years based on calibrated ¹⁴C dates from *Acropora palmata* framework and intertidal mangrove peat. *Coral Reefs*, **22**, 257–270.
- Tribollet, A., Decherf, G., Hutchings, P.A.** and **Peyrot-Clausade, M.** (2002) Large-scale spatial variability in bioerosion of experimental coral substrates on the Great Barrier Reef (Australia): importance of microborers. *Coral Reefs*, **21**, 424–432.
- Vogel, K., Gektidis, M., Golubic, S., Kiene, W.E.** and **Radtke, G.** (2000) Experimental studies on microbial bioerosion at Lee Stocking Island: Bahamas and One Tree Island, Great Barrier Reef, Australia – implications for paleoecological reconstructions. *Lethaia*, **33**, 190–204.
- Woodley, J.D., Chornesky, E.A., Clifford, P.A., Jackson, J.C.B., Kaufman L.S., Knowlton, N., Land, J.C., Pearson, M.P., Wulff, J.L., Curtis, A.S.G., Dallmeyer, M.D., Jupp, B.P., Koehl, M.A.R., Neigel, J.** and **Sides, E.M.** (1981) Hurricane Allen's impact on Jamaican coral reefs. *Science*, **214**, 749–755.