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Quaternary corals from reefs in the Wakatobi Marine National Park, SE Sulawesi, Indonesia, show similar growth rates to modern corals from the same area

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ABSTRACT: We have used digital photography, image analysis and measurements in the field to determine the growth rates of Quaternary corals in the Wakatobi Marine National Park, Indonesia, and compared them to growth rates of similar corals in the same area. In the Quaternary deposits it was possible to measure the growth rates of two massive coral genera *Porites* and *Favites*. For each genus, the corals reworked from better-illuminated upslope environments had higher growth rates than the *in situ* fossil corals. The calculated radial growth rates for the *in situ Porites* are slightly lower than, but of the same order of magnitude as, the modern *Porites* growing in 10 m water depth at Hoga (10.04 ± 3.34 mm yr^{-1} ± 1 s.d.; $n = 3$) and Kaledupa (15.26 ± 4.83 mm yr^{-1} ± 1 s.d.; $n = 3$).

Sedimentation rates and underwater visibility are inferred to have been similar in the fossil site to that at the modern Kaledupa site. Decreasing light penetration due to increased water depth is inferred to have been a major influence on growth rates. The *in situ* massive corals with good growth banding are inferred to have grown in a comparable environment to modern Kaledupa and Hoga. The study highlights that it is possible to compare coral growth rates, and their influencing parameters, from modern and well-preserved ancient examples. Copyright © 2006 John Wiley & Sons, Ltd.

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KEYWORDS: coral growth rates; growth banding; fossils; sedimentation; visibility; videophotography; transects.

Introduction

While there have been many studies of coral growth rates (e.g. Hubbard and Scaturo, 1985; Crabbe *et al.*, 2002; Crabbe and Smith, 2002, 2003; Crabbe, 2003), the intercorrelation of modern and Quaternary environmental effects on growth is often hindered as data are not available from the same area (Pandolfi, 2002).

The Wakatobi Marine National Park is situated in the Tukang Besi archipelago, a remote island group of about 200 000 hectares off SE Sulawesi in Indonesia (Figs 1 and 2) (Elliot *et al.*, 2001). Using digital videophotography and computer image analysis, as well as physical measurements, we have surveyed the reefs near the island of Hoga, where a Marine Research Station, run by Operation Wallacea, is situated. For modern reefs, we have concentrated on three different reef sites in the Park, each separated by about 1.5 km. One has high turbidity and experiences high human activity (Sampela), another has low turbidity and little human activity (Kaledupa), and the third has intermediate water clarity and human use (Hoga) (Crabbe and Smith, 2002, 2003, 2005, 2006; Crabbe *et al.*, 2004).

A Quaternary coral-rich limestone, up to 400 m thick, is exposed onshore around the margins of the islands of the Tukang Besi Group (Koswara and Sukarna, 1994). Preliminary study of these limestones on Hoga and the neighbouring island of Kaledupa revealed that these deposits accumulated in reefal and reef-associated environments comparable to those seen offshore today. In a quarry section on Kaledupa (Figs 3 and 4) massive corals are preserved with growth banding picked out by differential erosion (Fig. 5(a)–(c)). The quarry is a perpendicular cut through a reef front, and in this exposure it is possible to infer some of the environmental parameters that influenced the massive corals during their growth.

The Quaternary site

Since the quarry on Kaledupa is a perpendicular cut through reefal and forereef deposits it is possible to measure directly

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Figure 1 Map of SE Sulawesi and the Tukangbesi archipelago, showing the area of the Wakatobi Marine National Park in the boxes

parameters such as water depth, facing direction and slope angle. Other past parameters such as temperature, salinity, water clarity, nutrient conditions and depositional energy cannot be measured directly. However, through study of the preserved biota and the associated sediments it is possible to make inferences about these conditions during the time of coral growth.

The quarry walls, and rocks exposed in the hillside above, preserve an excellent near perpendicular cut through a reef crest and its forereef deposits with the original aragonite-secreting reefal biota preserved in life position or sometimes toppled. The strata of the forereef deposits are composed of lithified carbonate sand with the original depositional layering preserved (Fig. 4). There is minimal evidence of compaction features in these forereef deposits, based on petrographic study of thin sections. The inclination of the sedimentary layers is inferred to be very close to the original slope angle. The measured forereef slope angle is between 30° and 42° and dips towards the NNW (Fig. 4). The massive corals with growth banding preserved grew on and colonised the lower parts of this forereef slope and some are in growth position (Fig. 5). Others have been reworked from higher up the slope. The vertical height difference between where the massive corals are preserved and the very gently inclined reef crest to reef flat deposits is 22 to 25 m (cf. Perrin *et al.*, 1995; Perrin, 2000). The reef crest and flat deposits are dominated by *in situ* colonies of branching *Acropora*, consistent with their development in very shallow waters. Unfortunately it was not possible to observe growth banding in the branching *Acropora* since they have been totally leached out and only moulds remain.

The lithologies of the forereef deposits are composed of medium- to coarse-grained carbonate grains with only traces of finer clay-grade material and less than 2% non-carbonate material. The size fraction of grains present would have meant that any sediment entrained within the water column by waves or storms would have rapidly settled out of suspension. Water clarities similar to those on the modern reefs at Kaledupa, where the sedimentation rate is 5.35 ± 0.68 g dry weight

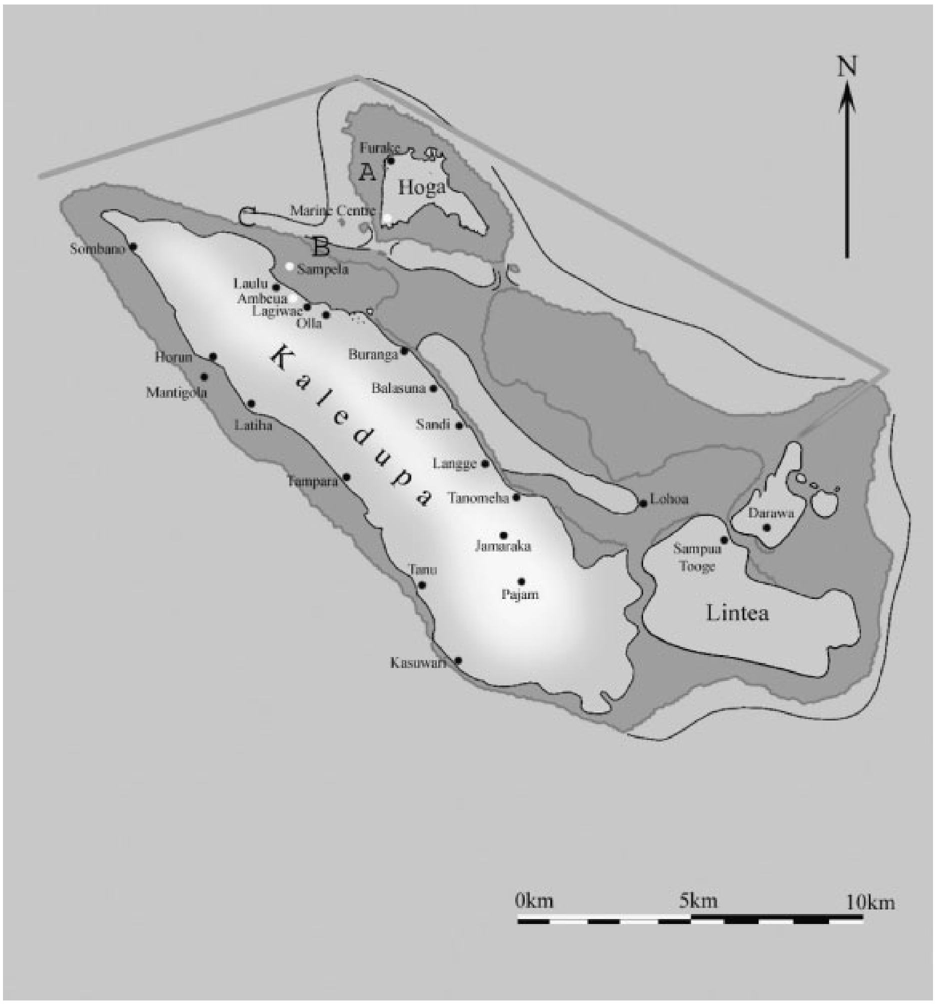

Figure 2 Diagram showing the sites studied in the Wakatobi Marine National Park. A, Hoga site; B, Sampela site; C, Kaledupa site. The quarry is close to the town of Ambeua on the NE coast of Kaledupa

Figure 3 The quarry close to Ambeua on Kaledupa. Figure in the centre for scale. This figure is available in colour online at www.interscience.wiley.com/journal/jqs

Figure 4 Exposure in quarry looking west showing dipping deposits of forereef sediment. The rock face is 10 m high. This figure is available in colour online at www.interscience.wiley.com/journal/jqs

$m^{-2} d^{-1}$ (Crabbe and Smith, 2002; Crabbe *et al.*, 2004) are therefore inferred for this site based on the rapid settling of grains and lack of organic material or land-derived terrigenous grains. The wide diversity of fossil corals and associated biota, such as giant clams, in the Quaternary deposits is comparable with the modern deposits. Similar marine salinities and temperatures to the present day are inferred for the Quaternary reefs. Much of the original aragonitic skeletal material of the corals has been replaced by calcite. It was therefore not possible to obtain independent isotopic evidence from the corals to corroborate past temperatures. Specific larger benthic foraminifera, such as *Calcarina*, are adapted to inhabit high wave

(a)

Figure 5 Growth banding in fossil corals. (a) Growth banding in *Porites* (coral 1). Tape measure is 4.6 cm across. (b) Growth banding in *Favites* (coral 4). (c) Growth banding in *Porites* (coral 2). This figure is available in colour online at www.interscience.wiley.com/journal/jqs

(b)

(c)

Figure 5 (*Continued*)

energy environments (Hallock and Glenn, 1986) and are common in the oceanic-facing, wave-influenced modern site at Kaledupa. These foraminifera are present in lesser amounts at Hoga and more rarely at Sampela, which are both sites influenced by less wave activity. The amounts of *Calcarina* present in the fossil reef deposits are intermediate between the amounts found in the modern deposits at Kaledupa and Hoga and moderate wave energies are inferred.

Measurement of Quaternary coral growth rates

Many of the corals exposed in the quarry walls had been cut through parallel to their growth direction, and differential leaching during weathering highlights growth banding. In some of the corals, preserved in growth position or reworked, up to

70 growth layers were observed. Growth banding has commonly been observed in modern and fossil corals due to changes in skeletal precipitation associated with variable growth rates. When growth rates are low, dense skeletal frameworks result, whereas more open skeletons are secreted when growth rates are high (cf. Tomascik *et al.*, 1997). In the fossil corals, it is the less densely calcified skeletons formed during high growth rates that are preferentially leached out to reveal the growth banding. Individual growth bands in modern and fossil corals are commonly interpreted as annual growth bands (cf. Tudhope *et al.*, 1995, 2001; Klein *et al.*, 1997). It is likely that the growth bands seen in the Quaternary corals on Kaledupa are recording yearly growth increments. This is because the monsoonal climate, which results in the annual changes in growth rates in the modern corals was already developed in the area during the Miocene (Morley, 2000).

Incremental growth band thicknesses, on a millimetre-scale accuracy, were recorded along transects through the corals in outcrop. Measurements were taken along multiple transects to record lateral variations in numbers of growth bands and their thickness. Numbers of bands in each coral were between 14 and 26. Digital image analysis (Crabbe and Smith 2002, 2003) was used as well as *in situ* measurements on bands. Care was taken always to record the thickness perpendicular to the growth band surface. The corals were photographed and the images studied to avoid missing any growth banding that may have been overlooked while measuring along individual transects.

Measurement of modern coral growth rates

Surface areas of non-branching corals were calculated as described previously (Crabbe *et al.*, 2002; Crabbe and Smith, 2003) from the largest diameter of the coral head, measured with a flexible tape or with vernier callipers, and the diameter at 90° to that. Colonies of a single species that were close together (< 5 cm) or touching were avoided, to minimise age discontinuities through fission (Hughes and Jackson, 1980). Radial growth rates of coral colonies were calculated from increases in overall surface areas, with four individual measurements being made throughout the year on each colony. Statistical values represent means ± SE, with probabilities calculated by one- or two-factor ANOVA (Crabbe and Smith, 2002, 2003)

Results and discussion

In the Quaternary deposits it was possible to measure the growth rates of two massive coral genera (*Porites* and *Favites*), each with examples of *in situ* and reworked corals (Table 1). For each of the genera the reworked corals had higher growth rates than the *in situ* corals. The calculated radial growth rates for the *in situ Porites* are slightly lower than, but of the same order of magnitude as, the modern *Porites* growing in 10 m water depth at Hoga (Table 2).

Table 1 Radial growth rates of non-branching corals from the Pleistocene site on Kaledupa (05°29.95′S, 123°44.69′E) formed at an inferred water depth of 22–30 m

	In situ or reworked	Growth rate (mm/band and SD)
Porites	*In situ*	Coral 1: 10.2 ± 5.8
Porites	*In situ*	Coral 2: 9.1 ± 3.9
Porites	*In situ*	Coral 5: 9.7 ± 3.7
Porites	Reworked	Coral 7: 11.3 ± 4.7
Favites	*In situ*	Coral 4: 8.2 ± 1.8
Favites	Reworked	Coral 6: 11.1 ± 1.9

Table 2 Radial growth rates of non-branching corals. Modern corals (*Porites lutea*, *Montipora* sp. and *Favia* sp.) are at 10 m depths at Sampela, Hoga and Kaledupa. $n = 3$ at each site. Growth rates are given ± 1 SD

Coral	Site		
	Sampela	Hoga	Kaledupa
Porites lutea	3.98 ± 1.32	10.04 ± 3.34	15.26 ± 4.83
Montipora sp.	1.75 ± 0.7	9.23 ± 1.1	9.74 ± 1.2
Favia sp.	2.86 ± 2.5	9.23 ± 1.3	12.73 ± 4.1

It is difficult to ascertain the rugosity of the Quaternary slope deposits since the best exposures in the quarry walls are cut parallel to the downslope direction. From study of the more poorly exposed southern back face of the quarry, which is a cut through parallel to the original slope contours, it is inferred that the rugosity was of the order of 35–40 (Crabbe and Smith, 2003). Underwater visibility is inferred to have been similar to that at the modern Kaledupa site, and the corals on the Quaternary slope may have been growing towards the base of the depth range. It is possible to infer rough rates of carbonate sedimentation accumulating adjacent to some of the *in situ* massive corals. Sedimentation rates of around 5–10 mm yr^{-1} are inferred from the growth shapes and patterns of lateral termination of individual growth bands towards the coral margins. Those are approximately the rates currently experienced at Hoga and Kaledupa, while the rates at Sampela (20.16 ± 1.71 g dry weight $m^{-2} d^{-1}$) are significantly greater (Crabbe and Smith, 2002, 2005). However, it is stressed that since factors other than smothering by sediment can cause demise of the living coral at its margins these are very rough estimates of sedimentation. It is difficult to make meaningful comparisons between the modern and ancient sedimentation rates owing to the different ways the data are collected, as the sediment traps used in the modern systems are 'closed' pots that do not allow further downslope sedimentation or resuspension of grains. As a consequence, the modern traps record sedimentation at a point, but not the actual sediment that would naturally accumulate and be preserved in the fossil record.

Our study highlights that it is possible to compare coral growth rates, and their influencing parameters, from modern and well-preserved ancient examples. Combined study of modern and Quaternary deposits from the same area was seen as directly complementary. Study of the fossil record allowed evaluation of growth rates over a longer timescale than in the modern. Although general environmental conditions could be inferred for the Quaternary, it was not possible from these deposits to evaluate annual changes in local conditions and their effect on growth rates, which can be done on modern reefs (Crabbe and Smith 2002, 2005, 2006).

Evidence for incident light being an important influence on coral growth and calcification rates was found in the Quaternary examples. The *in situ* massive corals with good growth banding are inferred to have grown in a comparable environment to modern reefs at Kaledupa and Hoga, but possibly at deeper water depths. Accurate determination of depth would require more extensive studies linking depth and growth rates

(Bosscher, 1992), such as those on the Huon Peninsula of Papua New Guinea (Pirazzoli *et al.*, 1991; Galewsky, 1998). The reef we sampled may be from one of the interstadial reef-building still-stands recorded on the Huon Peninsula and elsewhere in Indonesia (Pirazzoli *et al.*, 1991).

It is inferred that as a consequence of reduced light penetration into deeper waters, genera such as *Porites,* had lower growth rates than in the modern clear, but shallower, water study sites. In clear water sites from the South China Sea Titlyanov and Latypov (1991) noted that incident light irradiance at 18–20 m water depth was about half that at 9–11 m. This decrease in light intensity is the preferred explanation for the growth rates in the Quaternary *Porites* formed at >20 m water depth being nearly half that of modern corals growing in water depths of 10 m at Kaledupa. However, it is important to note that coral growth appears to be related to total net photosynthetic active radiation (PAR) rather than instantaneous values, and shading by land masses is a potentially important factor (Kleypas, 1997).

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