Age accuracy and resolution of Quaternary corals used as proxies for sea level

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Abstract

The accuracy of global eustatic sea level curves measured from raised Quaternary reefs, using radiometric ages of corals at known heights, may be limited by time-averaging, which affects the variation in coral age at a given height. Time-averaging was assessed in uplifted Holocene reef sequences from the Huon Peninsula, Papua New Guinea, using radiocarbon dating of coral skeletons in both horizontal transects and vertical sequences. Calibrated 2σ age ranges varied from 800 to 1060 years along horizontal transects, but weighted mean ages calculated from 15–18 dates per horizon were accurate to a resolution within 154–214 yr. Approximately 40% of the variability in age estimate resulted from internal variability inherent to ^{14}C estimates, and 60% was due to time-averaging. The accuracy of age estimates of sea level change in studies using single dated corals as proxies for sea level is probably within 1000 yr of actual age, but can be resolved to ≤250 yr if supported by dates from analysis of a statistical population of corals at each stratigraphic interval. The range of time-averaging among reef corals was much less than that for shelly benthos. Ecological time-averaging dominated over sedimentological time averaging for reef corals, opposite to patterns reported from shelly benthos in siliciclastic environments.
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1. Introduction

Quaternary eustatic sea level records are derived empirically from two major sources: direct dating of Quaternary fossil coral reefs and isotopic analysis of microfossils in deep-sea sediment cores, e.g. [1,2]. Sea level curves are derived from reef sequences by measuring radiometric age of one or several corals at each

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horizon through a stratigraphic section e.g. [3–7] or core of coral reef, e.g. [8,9]. The two basic assumptions for this approach are that (1) the dated corals grew at or close to sea level and (2) the age determination is representative of the horizon from which the coral was sampled. Much attention has been focused on the relationship between a given coral and actual sea level at the time the coral grew, which is inferred from the known depth range of the coral species [3,10–12], except for microatolls, which necessarily grew at sea level [13,14]. However, the second assumption inherent in these sea level estimates, that corals at a given horizon all represent the same age, has not previously been tested. Here we address the reliability of age estimates from corals in Holocene raised reef sequences from the Huon Peninsula, Papua New Guinea (PNG), and assess the magnitude of temporal resolution that can be observed from fossil coral reefs, by examining time-averaging.

Time-averaging refers to the temporal mixing of different cohorts in fossil assemblages. It is pervasive in most depositional environments, and places fundamental constraints on the precision with which the fossil record, and the sedimentary record, can be interpreted [15]. Sedimentological time-averaging stems from vertical mixing of fossils through unconsolidated sediments, and ecological time-averaging stems from spatial or temporal mixing of patches of organisms that occupied the same location at different points in time [15,16] into a single deposit [16–19].

Carbonate environments, such as coral reefs, generally experience a lesser degree of time-averaging than siliciclastic environments [20], for two reasons. First, sedimentation rates, and especially rock accumulation rates, tend to be higher in reefs than in siliciclastic-dominated environments [20,21]. Second, carbonate sediments, especially reefs, are dominantly composed of bioclasts, such that the accumulation of sediment and the accumulation of fossils necessarily occur at the same rates [22]. Ecological time-averaging in coral reefs results in fossil reef assemblages represented by a combination of different coral morphologies that grow, and accumulate carbonate sediment, at different rates [23,24]. By way of contrast, shallow marine siliciclastic deposits containing shelly fossils such as bivalves [25,26] or brachiopods [27] typically preserve a biological record spanning several hundreds to a few thousands of years [15,16]. Vertical mixing of shells into and out of the taphonomically active zone (TAZ) extends the age range of shells sampled at the surface to several thousands of years [16,25,28]. Age distributions in typical shelly fossil deposits are young-skewed (right-skewed) with most samples young and a small number of older shells, displaying an age distribution approximating exponential decay [15,25–28].

Our goal is to better constrain age estimates for sea level curves based on shallow water corals, and to assess the temporal resolution of the paleoecological record in fossil reefs. Here we directly measure the range and
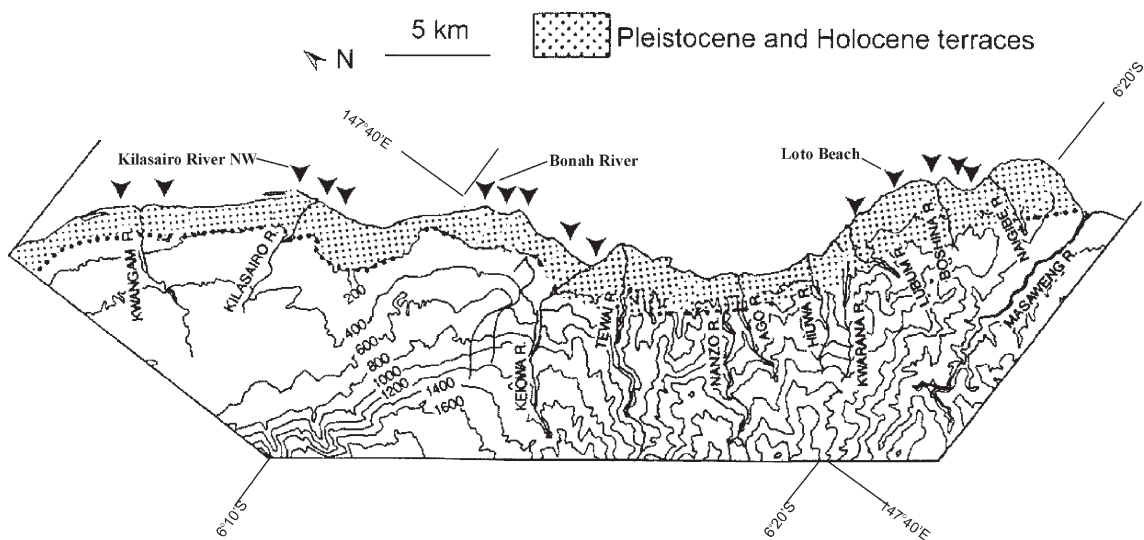

Fig. 1. Location of stratigraphic sections studied at Loto Beach, Bonah River, and Kilasairo River NW, along the Huon Peninsula coastline, Papua New Guinea. Locations of all other sections measured in broader paleoecology studies [30], are indicated by unlabeled triangles. Tectonic uplift rates generally increase from northwest to southeast.

nature of time-averaging in raised Quaternary reefs using radiocarbon dates of fossil corals from the exquisitely-preserved Holocene reef section of the Huon Peninsula, PNG. We show that accuracy for the timing of sea level curves increases with the number of different corals dated within a sampling horizon, and we make explicit the temporal resolution expected as a function of degree of accuracy and sample size. Thus, we offer a roadmap for the sample size of dated corals needed to afford meaningful interpretation of paleoecological and sea-level data. We found no relationship between reef accretion rates and the extent of time-averaging, suggesting an inherent style of preservation very different from better studied siliciclastic environments.

2. Materials and methods

2.1. Geologic setting

We surveyed multiple seacliff sections of the tectonically uplifted Holocene terrace using galvanized steel scaffolding along 29 km of the Huon Peninsula, Papua New Guinea (Fig. 1), in an area of low historical and present human population. The present climate is relatively uniform, with a seasonal sea surface temperature range of about 2 °C around a mean of about 29 °C, few major storms and no cyclones. The climate during the Holocene was broadly similar to present, although inter-annual variability related to the El Niño Southern Oscillation was reduced [29]. Shallow water reef deposits exposed in uplifted seacliffs up to 24 m high contain reef coral assemblages that grew between about 11 000 and 6400 cal years (ybp) during the sustained sea-level rise of the last deglaciation [30]. Most corals accumulated in place (upright, whole and in life position), preserving both their former biological inhabitants' paleoecological histories and physical environments. Holocene reefs from the Huon Peninsula grew as keep-up reefs, matching post-glacial sea level rise [31–33]. We sampled primarily the shallow reef crest environment. Comparison of the associated coralline algal assemblages with modern depth profiles of living corallines revealed that the Holocene reef deposits represent water depths between 2 and 6 m [34].

2.2. Sites

Three sections were chosen for horizontal and vertical dating profiles to assess time-averaging within fossil reef deposits (Fig. 1). The Loto Beach, Bonah River, and Kilasairo River sections occur in the Hubegong, Kanomi, and Sialum portions of the field area, respectively (Table 1).

Table 1
Location and characteristics of each section

Site	Location (lat/long)	Total section height (m)
Loto beach	6°17.2063 S 147°45.3676′ E	9.5
Bonah river	6°10.4598 S 147°40.0110′ E	7.3
Kilasairo river NW	6°7′31.20″ S 147°37.7388′ E	9.5

These areas experience different average tectonic uplift rates [3,33,35,36].

2.3. Sampling

In order to assess reef age variation within horizons at each reef, we sampled 15–20 corals, mostly whole and in life position, continuously along a horizontal transect from 15–40 m in length. Horizontal transects were laid in areas where there were no observable breaks in sedimentation, for example, well above disturbance horizons [30]. Transects were sampled continuously until 20 corals or molluscs had been sampled, hence transect length was not equivalent in the three sections. Mollusc dates were excluded from the present analysis, as were corals that displayed evidence of recrystallization. The horizontal profiles at the Kilasairo River and Bonah River sections were measured approximately 1 m above a disturbance interval, while the Loto Beach horizontal profile was measured 5 m above a disturbance interval. Transects did not follow observed paleotopography within the fossil reef, because no disconformities or paleotopography were observed.

In order to assess reef accretion rates at each of the three sections, we collected one to three corals, usually whole and in life position, from 25 m long transects at 1 m vertical intervals up the fossil reef exposure. Detailed 3–5 m vertical profiles were also measured at the three sections, from which every coral was sampled and subsequently dated. These detailed profiles served to constrain vertical mixing and apparent age reversals.

2.4. Radiocarbon analysis methods

Ages of corals were determined by ^{14}C age dating using accelerator mass spectrometry [37,38]. The site-specific ^{14}C reservoir effect for Papua New Guinea, calculated as 490±7 yr [39], was subtracted from the conventional (δ^{13}C-corrected) ^{14}C ages; the values were then converted to calendar years (1950) using the Intcal04.14c calibration dataset [40] via the OXCAL

v. 3.10 program (http://c14.arch.ox.ac.uk/oxcal.php). Although regional variation in reservoir effect may affect absolute age, it will have negligible effect on the extent or pattern of time-averaging. Individual coral ages are reported as 2σ ranges (yr), within which median age is plotted only for corals with anomalous ages. [14]C age, calibrated age, sample position and coral species identification of all samples are listed in the background dataset.

2.5. Data analysis

Average age, median age, age range, and age standard deviation were measured for each horizontal profile [27]. Age range within each horizontal profile is reported as the range of calibrated 2σ ranges, from the oldest age estimate for the oldest coral to the youngest age estimate for the youngest coral. Age histograms were calculated, and average age and median age within each horizontal transect compared, to assess whether age distributions were clearly non-normal, and if so, whether they were old-skewed (left-skewed) or young-skewed (right-skewed). Histograms of mean calibrated coral ages for all corals within each horizontal transect were constructed using 50-year bins. Completeness, or the percentage of the age range within a horizontal transect actually represented by individual fossils, was calculated as the percentage of 50-year age bins represented by corals [15,18].

Weighted average calibrated age for each horizontal profile was calculated according to the treatment of Bevington [41], and Ward and Wilson [42]. Weighted average age calculations used the median calibrated age estimate for each individual coral and the 1σ error estimate associated with that median age. Median age of each coral was defined as the midpoint between the maximum and minimum calibrated age estimate for that coral derived from the OxCal ^{14}C calibration, while the 1σ standard deviation estimate was defined as half of the range between the maximum and minimum calibrated age estimates. Weighted averages were calculated with the equation:

$$\mu \cong \mu' = \sum (x_i/\sigma_i^2) / \sum (1/\sigma_i^2) \qquad (1)$$

where μ' is the weighted average, x_i are the individual measurements, and σ_i are the radiocarbon measurement 1 standard deviation (S.D.) uncertainties in the individual measurements. Weighted average age calculation weighted each point inversely by its variance, and allowed separation of statistical S.D. (σ_{st}, within sample age estimate variation) and scatter S.D. (σ_{sc}, between

sample variation). Statistical standard deviation, σ_{st}, was calculated as [41]:

$$\sigma_{st} = \sum (1/\sigma_i) \qquad (2)$$

while scatter standard deviation, σ_{sc}, was calculated as:

$$\sigma_{sc} = \sum [(w_i'(x_i - (x))]/(N-1) \sum w_i', \qquad (3)$$

where $\langle x \rangle$ is the average value, N is the number of measurements in the average and w_I' is the individual weighting factor, defined as $w_i' \equiv 1/\acute{o}_I'$, and $\acute{o}_i'$ is the relative statistical standard deviation in the sample, determined from the radiocarbon measurements directly [41,42].

The ratio of σ_{sc}/σ_{st} estimates the relative importance of intrinsic and extrinsic variability [41,42], representing here the proportion of age uncertainty stemming from radiometric measurement error (intrinsic, σ_{st}) and the proportion stemming from time-averaging (extrinsic, σ_{sc}).

Average reef accretion rates for each reef were calculated using least-squares linear regression. Median age of each dated coral within each section was measured against the stratigraphic height of each coral sample. Average accretion rates, measured as the slope of the linear regression line, are expressed in vertical m of reef exposure per thousand years (m/kyr).

The probability of estimating a date with a resolution of 1000, 500, 250, 100 and 50 yr was calculated depending on the number of samples dated using power analysis [43]. Firstly three sets of random dates were generated for each site using the observed sample dates. Then power curves were constructed for each site using the average power of these three sets for each effect size (1000, 500, 250, 100 and 50 yr).

The uses of *a priori* power analysis to determine the required sample size given a desired effect size and power have been criticised since the analysis assumes that the variance of the real sample is the same as the variance obtained in the pilot study [60]. In this study we adopted two measures to minimize this effect. First we randomized three times the order in which the samples where chosen for the calculation; by doing so we increased the representativeness of the results. Additionally, we analysed sets of up to 18 samples which is higher than the number required to obtain an accurate estimation for most of the time intervals studied (1000, 500, 250, and 100 yr). It has been suggested that if the number of samples used for the power calculation is similar to or higher than the number required for the actual analysis, the probability of obtaining a misleading result is

minimized [44]. The power threshold selected for the recommended minimum sample size (80%) is standard for ecological applications [45] and for environmental monitoring [46].

3. Results

3.1. Age ranges and age variation within horizontal transects

Horizontal transects differed considerably in their age ranges and age distributions. The 2σ age range from oldest estimate of the oldest coral to youngest estimate of the youngest coral within each horizontal transect was between 810 and 1060 yr. The 2σ range of the weighted average age of each transect was between 144 and 214 yr (Table 2).

The Loto Beach horizontal transect had a total age range of 9050–8010 ybp. This horizontal profile contained one large columnar coral, *Acropora palifera*, which was older than all other corals sampled in that horizon (Fig. 2a). All other corals sampled in this horizontal transect had ages falling between 8550 and 8010 yr. Weighted average age (8349 ± 80.28 yr, 2σ range) and mean age (8349 ± 63 yr, 2σ range) were identical, and median age (8340 yr) was only slightly younger than mean age (Table 2). The ratio of extrinsic variability to intrinsic variability (σ_{sc}/σ_{st}) at the Loto Beach section was 1.56 (Table 2). Age distributions were slightly young-skewed in the Loto Beach horizontal transect (Fig. 3a). Completeness for the Loto Beach transect was the lowest observed, at 53% (see background dataset, Table S1).

The Bonah River horizontal profile contained whole and broken corals, and coral rubble (Fig. 2b). The ages of whole corals and broken corals within this profile were not distinct, and all fell within an age range of 9000–8190 cal BP. No single coral had greater age than other corals in the sample, and there were no major gaps within the age distribution (Fig. 2b). Weighted average age (8552 ± 107 yr, 2σ range) was considerably younger than mean age or median age, which were nearly identical, indicating that the older corals tended to have greater measurement uncertainty in their ages than did the younger corals. The ratio of extrinsic variability to intrinsic variability (σ_{sc}/σ_{st}) at the Bonah River section was 1.69 (Table 2). Age distribution within the Bonah River horizontal transect was slightly old-skewed (Fig. 3b). Completeness was the highest observed, at 85% (see background dataset, Table S1).

The Kilasairo River NW horizontal profile contained the greatest age range for most samples, spanning 9000 to 7940 yr (Fig. 2c). One sample, a 1 m diameter *Diploastrea heliopora*, was considerably older than the others, and had a much higher error associated with its age estimate than the other corals. All other corals were aged between 8550 and 7940 yr, with an age range equivalent to that observed at the other two sites. Weighted average age and mean age were identical, while median age was only slightly younger than these two (Table 2), The ratio of extrinsic variability to intrinsic variability (σ_{sc}/σ_{st}) at the Kilasairo River section was 1.45, the lowest observed among the three sections (Table 2). Age distributions within the Kilasairo River horizontal transect approximated a bell curve (Fig. 3c). The completeness value for the Kilasairio River transect was 77% (see background dataset, Table S1).

3.2. Average accretion rates and deviations from linear trends

Vertical age profiles for each reef showed consistent rates of accretion through time at the Loto Beach and Kilasairo River sections, but uneven rates of accretion at the Bonah River section (Fig. 4). The average reef accretion rate was highest at the Loto Beach section, where average accretion was 5.5 m/kyr (95% confidence limits 3.6 to 7.1 m/kyr). Average accretion was lowest at

Table 2
Calibrated age distributions of 3 horizontal transects from the Holocene of the Huon Peninsula, Papua New Guinea

Site	N corals	Mean age	Median age	S.D.	2σ Age range (yr)	Weighted mean age ±2σ (yr)	σ_{st}	σ_{sc}	σ_{sc}/σ_{st}
Loto beach	18	8349	8340	31.52	8010–9050	8349±80	15.69	24.45	1.56
Bonah river	15	8621	8603	38.25	8190–9000	8552±107	19.89	33.59	1.69
Kilosairo river NW	16	8339	8313	27.71	7940–9000	8335±72	14.64	21.27	1.45

σ_{st} statistical standard deviation, represents radiocarbon age uncertainty within each coral, while σ_{sc}, scatter standard deviation, represents age estimate variation among corals, hence time averaging. 2σ for weighted mean$=2(\sigma_{st}+\sigma_{sc})$. The ratio σ_{sc}/σ_{st} indicates the proportion of age uncertainty stemming from each source, i.e. age variation from time-averaging was 45–69% greater than age variation from radiocarbon uncertainty.
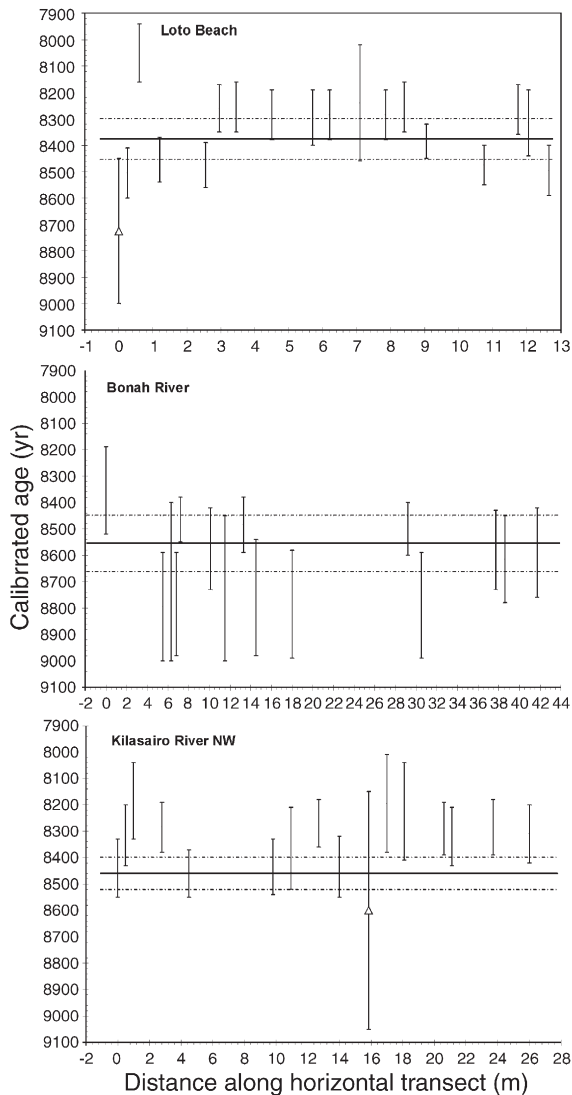
Fig. 2. Horizontal age transects. X-axis: distance along transect, starting from end of accessible outcrop or end of scaffolding. Y-axis: calibrated age (years). All ages are calibrated 2σ ages. a. Loto Beach: Anomalously old coral is 1 m tall *Acropora palifera*. b. Bonah River. c: Kilasairo River NW: Anomalously old coral is 1m diameter domal *Diploastrea heliopora*. Weighted mean age indicated by solid horizontal line, with 2σ upper and lower limits indicated by dashed lines above and below solid line. Weighted mean age ±2σ range indicates the most probable actual age of the stratigraphic horizon measured. Total range of time-averaging extends from the oldest age for the oldest coral to the youngest age for the youngest coral.

regressions of accretion versus time were highly significant ($p < 0.001$) and more than 50% of the variance was explained (Table 3).
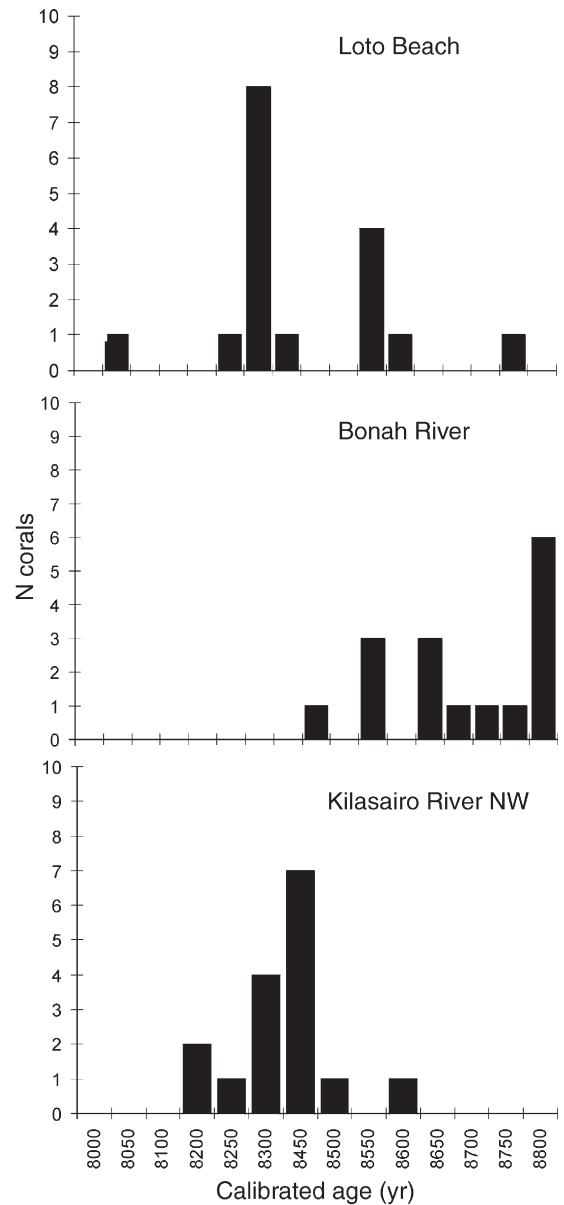

Fig. 3. Age histograms for horizontal transects. a. Loto Beach, b. Bonah River. c: Kilasairo River NW. Bars represent the number of corals with median ages falling into each 50-year age bin. Bins labels represent youngest age within bin. Age histograms are consistent with normal or uniform time averaging, in contrast to the exponential time-averaging usually observed among shelly fossils in siliciclastic environments. Completeness, calculated as the number of 50-year bins between the oldest and youngest corals that are represented by corals [18], was 53% at Loto Beach, 85% at Bonah River, and 77% at Kilasairo River NW.
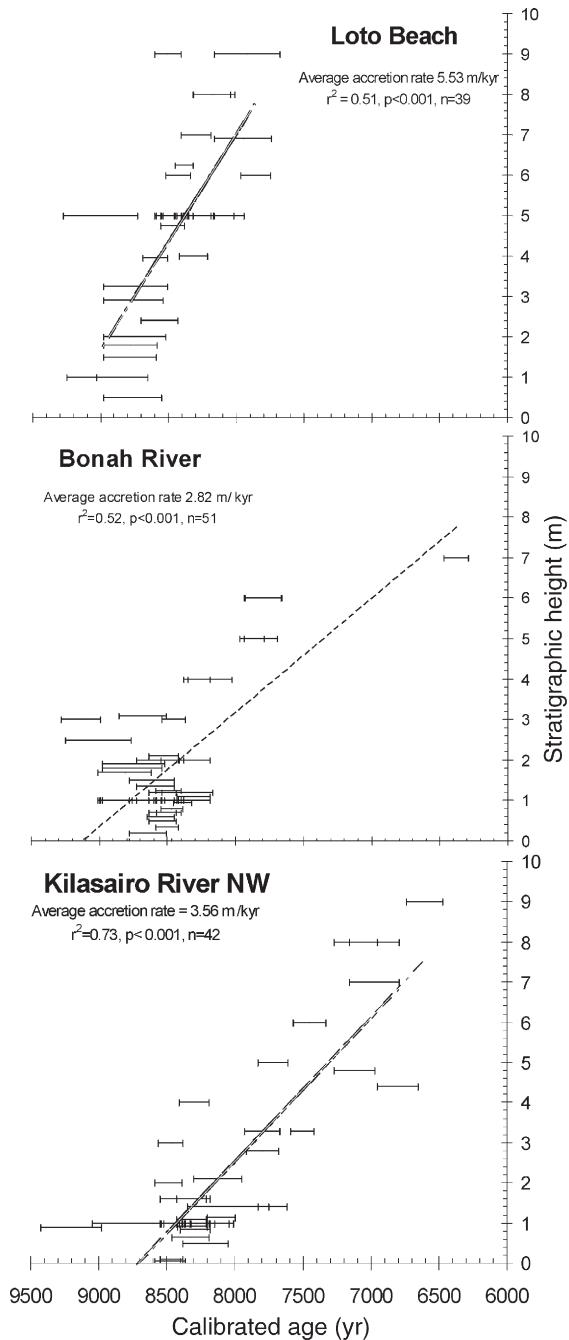
the Bonah River section (2.8 m/kyr, 95% confidence limits 2.1–3.6 m/kyr). Average accretion rate at the Kilasairo River section was intermediate between the other two sections (3.6 m/kyr, 95% confidence limit 2.9–4.3 m/kyr; Table 4). In all three cases, linear

Fig. 4. Vertical age profiles and average reef accretion rates. A. Loto Beach, B. Bonah River. C: Kilasairo River NW. All ages are calibrated ages (years) expressed as 2σ range. Average reef accretion rates determined by least squares linear regression plotted as dashed lines. Bonah River section displays evidence of age reversals in the bottom 2.5 m, and an average accretion rate of 1.8–2.3 m/kyr in the upper 4.5 m of the section.

No evidence for age reversals was encountered at the Loto Beach or Kilasairo River sections, but apparent age reversals were observed in the bottom 2–3 m of the Bonah River section. The bottom 3 m of the section had no significant age trend ($r^2 = 0.12$, $p > 0.05$, $n = 25$, while the top 4.5 m (from 2.5 to 7 m stratigraphic height) of the section had a slow but uniform accretion rate (1.8 m/kyr, 95% confidence limit range 1.2–2.4 m/kyr, $r^2 = 0.83$, $p < 0.001$, $n = 11$). Because the youngest coral in the section appeared anomalously young, the accretion rate was re-calculated from 2.5 to 6 m stratigraphic height, again yielding a slow but uniform accretion rate of 2.3 m/ky, 95% confidence limit 2.4–3.2 m/kyr, $r^2 = 0.81$, $p < 0.001$, $n = 10$).

3.3. Power of obtaining a specific time resolution depending on the number of corals dated

The power (accuracy) of estimating an expected time resolution increased by increasing the number of samples dated from a sample horizon (Fig. 5). At each of the three study sites, between three and four samples were needed to obtain at least an 80% power for a resolution of 1000 to 500 yr. To obtain a resolution of 250 yr, five to seven samples were needed. On the other hand, at least 15 samples (for one of the sites and more than 18 for the other two) appeared to be necessary to date the horizons with a resolution of 100 yr. Beyond this point (a resolution of 50 yr) the total number of samples analysed in this study generated a maximum power of only 41% (Table 4).

4. Discussion

4.1. Age accuracy for sea level reconstruction

Our results are encouraging for the ability to construct Quaternary sea level curves with error ranges ≤1000 yr (2σ age range, Table 2), or even more precise if multiple dates per horizon are possible (weighted mean age ±2σ, Table 2). Sea level curves derived from raised reef sequences typically contain error estimates based on coral radiometric age uncertainty, which we term intrinsic variability in age estimate. Estimating extrinsic variability allows another estimate of uncertainty in sea level curves, relating to the nature of the coral reef stratigraphic record. Extrinsic variation in coral ages in our data was 1.45 to 1.7 times greater than intrinsic variation, suggesting that the majority of the age variation among fossil corals at a given stratigraphic position stems from time-averaging, rather than intrinsic variation related to dating method or radiocarbon plateaux (a period of time in which the radiocarbon year — calendar year calibration curve is flat,

Table 3
Average reef accretion rates for each site

Site	Height range (m)	Median Age range (yr)	Section average accretion rate (m/kyr)	r^2	Significance	Area average accretion rate (m/kyr) [33]
Loto beach	8.5 m	9000–7860	5.5	0.51	$p < 0.001$	8.2
Bonah river	7 m	9135–6380	2.8	0.52	$p < 0.001$	5.1
Kilasairo river NW	8.95 m	9205–6605	3.6	0.73	$p < 0.001$	4.7

Median age ranges reported as ranges between individual coral median ages (years), rather than limits of 2σ coral ages. Section average accretion rate measured as slope of least-squares linear regression line through median ages within the stratigraphic section. Area average accretion rates (m/kyr) represent the empirically derived average accretion rates from several stratigraphic sections in the same portions of the Huon Peninsula as the sections we measured, reported by Ota and Chappell [33]. Loto Beach: Ago–Bobongara area; Bonah River: Kanzarua area; Kilasairo River: Kwambu–Kilasairo area (see Section 4.2).

causing poor resolution of calendar years from radiocarbon years [40]. Sea level curves in which age control is based on Uranium-series dates or electron spin resonance (ESR) should be subject to approximately the same degree of time-averaging as those derived from ^{14}C dates, even though intrinsic variation is lower [47,48].

Our results emphasize the need to date multiple corals at each horizon in a fossil reef sequence, particularly in cases where rapid sea level changes are suspected [4,6,12,49–52] or any instances where episodic growth is observed which may have more to do with tectonics than sea level [5,35,36]. Sea level curves calculated with 3–4 coral ages per stratigraphic horizon, including calculation of weighted average ages, can constrain the error associated with each age-height data point to ≤ 500 years (Table 4), with increased precision requiring a greater number of ages per stratigraphic unit. Extensive lateral sampling, such as that conducted here, is much easier in outcrop than in core. Replicate coring may achieve the same result when dating submerged reefs, although paleotopography, reef facies geometry, and variable porosity place limitations on the ability to accurately correlate replicate samples from the same core depth [8,53].

The high variability associated with the estimation of age from reef deposits (as demonstrated by the low power associated with low sample size, Fig. 5) emphasizes the risk associated with dating horizons using few samples. With the construction of sea level curves, this risk is maximized if sea level variability for the specific time studied is high or unknown. Considering the cost associated with multiple dating and the results of the power analysis, we recommend the use of at least 3 samples for a 1000 yr resolution, at least 4 samples for
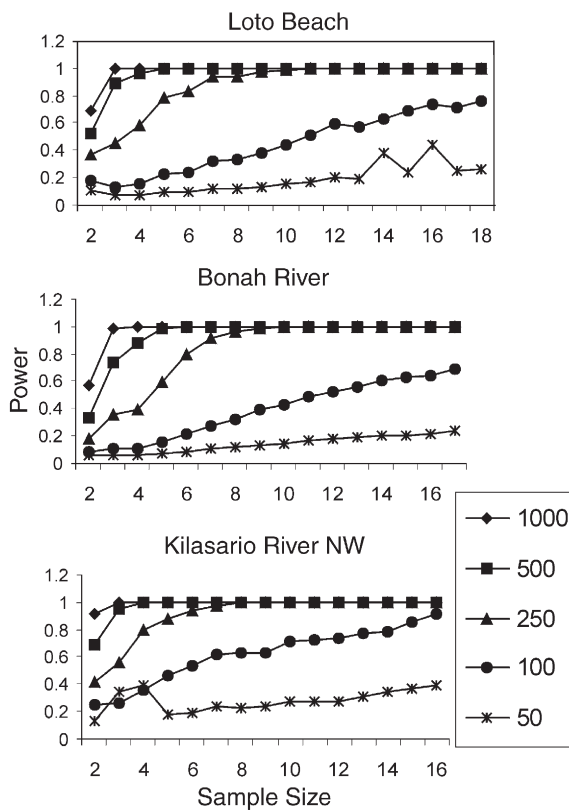

Fig. 5. Power curves. Accuracy (power) of age dating depending on the number of samples used. Each line represents the average values for three random sample sets per site. The accuracy of age dating is dependent upon both the number of samples and the desired resolution (1000, 500, 250, 100, and 50 yr).

Table 4
Number of samples required to achieve 80% power depending on the temporal resolution (years), deduced by power analysis

Site	Temporal resolution				
	1000 yr	500 yr	250 yr	100 yr	50 yr
Loto beach	3	3	6	>18	≫18
Bonah river	3	4	7	>17	≫17
Kilasairo river NW	2	3	5	15	≫16

Three replicate corals were sufficient to measure within 1000 yr resolution in all cases, while resolution of 250 yr was achieved with 5–7 corals. Resolution less than 100 yr was not usually reached, and resolution of 50 years or less was beyond the capabilities of ^{14}C AMS dating.

500 yr resolution and at least 7 samples for 250 yr resolution. Trying to get a higher resolution (100 or 50 yr) may be prohibitively expensive in terms of the number of samples required and in any case beyond the physical resolution of the ^{14}C dating technique (though perhaps not for other dating methods such as U-series TIMS).

The sample size proposed here for the different time intervals is specific for the three sites studied and must not be considered a general rule for studies carried out elsewhere. However, given the high cost associated with radiometric dating and the consistency in the number of samples required across our three sites, these numbers should be considered as guidelines for future (and past) studies. In any case, we recommend the use of *a posteriori* power analysis as a requirement for validating any study that attempts to date coral reef horizons with a resolution below 500 yr.

4.2. Comparability of accretion rates

Rock accretion rates measured in this study from single outcrops, and calculated using a least-squares regression, were lower than average accretion rates compiled from multiple sections in the same portions of the Huon Peninsula (Table 3, final column). As in previous studies, highest reef accretion rates were measured in the southeast portion of the Huon Peninsula (Loto Beach, Ago-Bobongara portion). Accretion rates reported in this study are necessarily lower than in previous studies because least squares regression calculates an average accretion rate line, with approximately half of all corals lying "above" that line (i.e. they would have grown above mean sea level, according to the line, whereas most sea-level studies derive an empirical sea-level curve that would have accounted for all corals measured). While we used least-squares regression to achieve a uniformly calculated measure of reef accretion rate for this study, we do not advocate regression analysis for calculating sea level curves.

Accretion rates measured here are not directly comparable with sea level curves. Nonetheless, accretion rates measured in this study are roughly comparable with a regional average sea level curve for the period 8.50 to 6.50 ka reported in a regional compilation study [33], in which corals lying below the keep-up reef envelope were considered catch-up reefs (see [33] Fig. 7). Evidence from species composition of corals and calcareous algae collected in outcrop during this study, however, convincingly shows that reefs studied were matching sea level (i.e. demonstrating keep-up growth, rather than catch-up growth) [30,34]. Instead, the reef accretion rates measured in this study may

represent keep-up reef growth between major coseismic events that account for much of the uplift on the Huon Peninsula [33,35,36].

4.3. Magnitude of time-averaging

The degree of time averaging observed among the Huon Peninsula fossil corals, with 2σ age ranges of 800–1000 yr, was relatively small compared to the several hundreds to several thousands of year range reported from shelly fossil assemblages [20,25–28]. Furthermore, the degree of time-averaging, proportional to the age of coral, was much smaller than that reported for shelly fossils [15]. The shallow reef front stout branching corals we sampled here, mainly *Acropora palifera*, *A. hyacinthus*, and corals from the *Acropora humilis* group, probably grew for 20–80 yr each, based on the sizes observed in the field, and growth rates of other *Acropora* species observed elsewhere (e.g. *A. palifera* [54], *A. formosa* [55], *A. valenciennesi* [56]). By contrast, the shelly fossils sampled in previous studies of time-averaging generally lived 3–5 yr (molluscs, [26]) or up to 10 yr (brachiopods, [27]). Coral age range estimates from weighted mean age are ≤215 yr, only 2.5–10 times the 20–80 yr lifespan of the dominant fossils recorded. This low magnitude of time-averaging, proportional to organism lifespan, suggests that most laterally adjacent whole upright corals in fossil reefs probably co-existed in life, and is encouraging for efforts to reconstruct ecological dynamics on fossil reefs [57–60].

4.4. Age distributions and completeness

We did not observe the exponential decay in ages typical of modern or Quaternary level-bottom shelly fossils [25–28]. Median ages and mean ages were generally consistent, with the former only slightly younger than the latter. Age histograms did not show strong or consistent patterns among sections (Fig. 3).

Our data suggest normal or uniform, rather than exponential, age distributions, for fossil corals on reefs (cf. [15]), although the number of corals sampled per horizontal transect is not sufficient to distinguish among various forms of symmetrical age distributions. Exponential age distributions, as observed among most shelly fossils, indicate a dominant role for sedimentological time-averaging, as shells are cycled into and out of the taphonomically active zone (TAZ), and are removed by burial below the TAZ or by complete destruction at the surface by durophagy or bioerosion. Shell destruction or removal from the TAZ proceeds at a more or less constant rate, yielding an exponential decay in shell number

versus age, similar to a shell half-life [27,28]. Normal or uniform age distributions by contrast, indicate dominantly ecological time-averaging, as a given stratigraphic horizon contains shells in proportion to their actual abundance throughout the duration of the time represented by that bed [15].

The age patterns observed in the Loto Beach and Kilasairo River horizontal transects are consistent with ecological time-averaging, as described for Holocene reefs from lagoon environments near Madang, Papua New Guinea [23]. In two of the three sections sampled, some of the largest corals (large columnar *A. palifera* at Loto Beach, *Diploastrea heliopora*, at Kilasairo River) were considerably older than all other corals in the horizontal profile. These corals may have been exposed dead at the surface at the time the other corals surrounding them grew. Whether alive or dead, the larger, older corals probably formed small topographic highs around which other corals grew and deposited sediment, but no disconformity surface was visible surrounding either of these corals in outcrop. When attempting to reconstruct ecological dynamics from fossil reefs, average lifespans of different morphological groups of corals should be considered.

By contrast, the Bonah River horizontal transect did not contain any corals that were clearly older than all other corals, but did display an age range > 800 yr. The vertical profile showed evidence of age reversals, with no net change in coral age within the bottom 2.5–3 m of the outcrop, and the bottom 3 m having an apparent accretion rate radically different from the remainder of the section. The horizontal transects at both the Kilasairo River NW section and the Bonah River section were located 1 m above a disturbance interval, but only the Bonah River section displayed possible influence of the disturbance in the form of age reversals. The Bonah River section may show evidence of sedimentological time-averaging, as a result of an underlying disturbance event [30].

Completeness values in two of the three reef sections were considerably higher than completeness values for shelly fossils in siliciclastic environments, which are typically in the 50–70% range, but completeness values in the Loto Beach section (53%) were on par with those from typical molluscan assemblages [15]. Given the small sample sizes, the high completeness values in the Bonah River (85%) and Kilasairo River (77%) sections may be statistically indistinguishable from 100% completeness [15,25]. The higher completeness values than for shelly fossils in siliciclastic sediments suggest continuous (ecological) time-averaging, and probably result from the nature of reef growth, and fossil deposition within reefs.

4.5. Reef growth and the nature of time-averaging on reefs

Magnitude of time-averaging can be influenced by the balance between rates of sediment accumulation and rates of biological change, such that expanded sections (with high accretion rates) should experience less time-averaging than condensed sections (with low accretion rates) [18]; that is, rock accretion rate and magnitude of time-averaging should be inversely correlated. Magnitude of time-averaging observed on our rapidly accreting fossil reefs was less than that observed for shelly fossils in most siliciclastic environments [15,20,25–28]. The only study that explicitly compared molluscan time-averaging in reef, carbonate sediment, and siliciclastic sediment found highest time-averaging in nearshore siliciclastic sediments, intermediate in carbonate sediment, and lowest on reefs, even though sedimentation rate was estimated to be higher in the siliciclastic sediments than in the carbonate sediments [20]. Within our data, however, magnitude of time-averaging was approximately equal in all three sections, despite variation in reef accretion rates (Fig. 6). The lack of a clear relationship
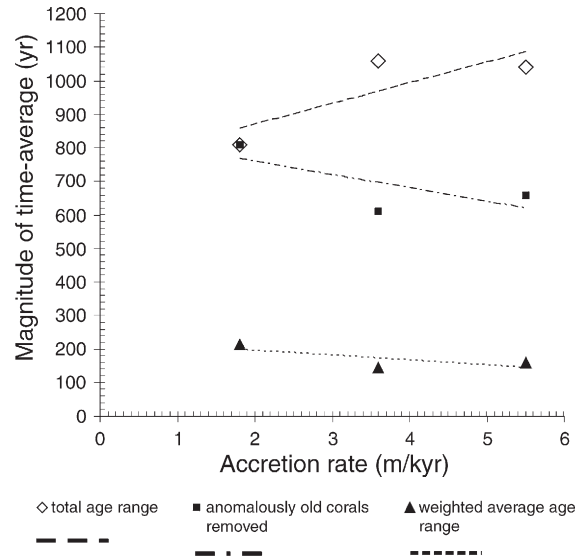

Fig. 6. Relationship between reef accretion rate and magnitude of time-averaging. Magnitude of time-averaging (in years) estimated for the three reef sections, measured as total 2σ age range, 2σ age range without anomalously old corals, and 2σ variance around weighted average age. Among the three reef sections, there was no clear relationship between magnitude of time-averaging and reef accretion rate: none of the three trend lines have slope significantly different from zero. Accretion rate for the Bonah River section was determined from the upper 4.5 m of the section, above the zone of reworking, in which age reversals were apparent.

between reef accretion rate and extent of time-averaging suggests that the relatively narrow range of time-averaging observed depends more on the way reefs grow, in which sedimentation is dominantly biogenic, than on the balance between reef rock accumulation and fossil accumulation. Because the dominant organisms, corals, also are the dominant sediment producers, sediment (rock) accumulation and biological change necessarily proceed together, rather than being balanced against each other as in siliciclastic environments. The apparent lack of relationship between accretion rate and magnitude of time-averaging observed here could be tested by measuring extent of time-averaging on fossil reefs that grew after Holocene sea levels stabilized, i.e. Indo-Pacific fossil reefs younger than 3–5 ka [2,7].

A fundamental difference between time-averaging of corals on reefs, as opposed to shelly fossils in siliciclastic environments, may be the relative importance of sedimentological and ecological time-averaging. Most corals on reefs are sufficiently large that they are unlikely to be moved vertically within reef sediment more than a few centimetres, except in storm deposits, where the corals *and* the reef sediments are all removed and re-deposited *ex-situ*. Rather, dead corals at the reef-water interface are likely to remain exposed for longer periods of time than is typical of shelly fossils, suffering taphonomic alteration only in dead portions that are exposed [61–64]. Under normal fair-weather conditions, if buried corals are exhumed, they are likely to be exhumed by erosion of sediment, rather than bioturbation and actual movement of corals. This style of exhumation would not mix corals of older ages upward to younger horizons as effectively as bioturbation or reworking would mobilize shelly fossils [28]. In the absence of disturbance events, sedimentological time-averaging on reefs probably occurs mainly as younger corals fall downward into cavities among older corals exposed dead at the reef surface. Only major disturbances would be able to produce significant upward mixing of buried dead corals, similar to the sedimentological time-averaging experienced by shelly fossils in siliciclastic environments under normal conditions.

5. Conclusions

Our results are encouraging for sea level reconstructions, because they imply that continuous fossil reef sequences accurately record time at high resolution. High resolution sea level curves from reef sequences should be constructed with multiple coral ages per stratigraphic horizon, with finer temporal resolution requiring a greater degree of replication. Sea level events as recorded through radiometric age dating of individual corals in Quaternary reef deposits may be accurate at time scales> 1000 yr, but weighted average ages of 5–7 corals may yield more precise age estimates, on the order of 250 yr. Abrupt climate change events <500 yr in duration may not be well represented in the coral reef sea level record without extensive replication, but most intermediate (1000 yr) to longer-term (several thousands of years) events will be accurately represented by individual corals or a small number of coral samples per horizon. Multiple samples per horizon dramatically increase the accuracy of temporal estimates, no matter what the dating technique, and regardless of whether samples are taken from cores or outcrops.

Our results are encouraging for studies of reef paleosynecology, and suggest that most laterally adjacent fossil corals likely co-occurred in life. Time-averaging of weighted average Holocene fossil coral assemblages occurred on the scale of 215 yr or less. Proportional to the lifespan of the organisms, time-averaging was one to two orders of magnitude less extensive than that observed among shelly fossils in siliciclastic environments. Extent of time-averaging was not clearly related to reef accretion rate. Corals on fossil reefs experience ecological time-averaging, but probably do not experience extensive burial-exhumation cycles, at least under 'keep-up' reef growth conditions. Time-averaging on reefs differs qualitatively and quantitatively from time-averaging in siliciclastic environments.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.epsl.2006.10.014.

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