Constraints on the age and duration of the last interglacial period and on sea-level variations

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The relation between height and age of shorelines formed during the last interglacial period, as revealed by coral reefs, cannot be related directly to changes in ocean volume because of the effect of isostatic uplift in response to changes in ice-sheet loading. Sea-level changes at sites near the melting ice sheet, such as Bermuda and the Caribbean islands, differ from those along the Australian margin. Modelling of these differences constrains the times of onset and termination of the last interglacial, which are at variance with those deduced from oxygen-isotope studies of deep-sea cores.

THE existence of elevated coral reefs and other marine shorelines of last interglacial age at many locations around the world[1-3] has generally been interpreted as evidence for a larger ocean volume during oxygen isotope substage 5e (refs 4, 5) than today[6]. This evidence is not without ambiguity, because shoreline elevations cannot be directly equated with ocean volumes unless the glacio-hydro-isostatic rebound effects are first evaluated. Also, because of these rebound effects, the ages of formation of the shorelines do not provide a direct measure of the age and duration of the substage. As for the Late Holocene sea-level models and observations[7,8], the last interglacial levels can be expected to vary not only with time but also with location, depending on position relative to the former ice sheets. Height-age relations of Late Interglacial shorelines along the Australian margin are therefore predicted to be distinctly different from those for locations nearer to the former ice load, such as Bermuda and the Caribbean islands, and these differences can be used to constrain the times of onset and termination of the 5e substage as well as the ocean volume at that time.

When compared with late interglacial sea-level observations from these two regions, the glacio-hydro-isostatic models lead to the conclusions that (1) ocean volumes during the oxygen isotope substage 5e did not exceed their Late Holocene volume, (2) these volumes had been reached by ~135 kyr BP and possibly earlier and (3) the volumes remained at this level until at least 120 kyr BP.

Shoreline evidence

Figure 1 summarizes the observed height-age relations of 5e shorelines for two regions: the tectonically stable margins of Western Australia far from the former ice sheets, and the islands of the Caribbean and Bermuda within the sphere of rebound influence of the former North American ice sheet. The Western Australian observations are from three locations where stratigraphic relationships between sea level and *in situ* corals have been established. The results for both Pelsaert[9] and Rottnest[10] represent lower limits, whereas the Cape Cuvier result[11] represents a measure of the height range occupied by sea level during substage 5e. All heights refer to mean low water, the upper limit of present coral growth. The age determinations at the three localities are based on conventional uranium-series dating methods, and the precisions are relatively low. The Cape Cuvier result, including the Lake MacLeod and Cape Range localities, is based on the weighted mean of 11 samples from five different reefs whose individual ages range from 116 ± 6 to 138 ± 7 kyr BP. For all reefs the results are based on a small number of dated samples, and the ages therefore represent a lower limit estimate of the interval in which sea levels were near or above their present level. Taken together, the Western Australian continental margin observations suggest that sea levels reached their present level by about 135 kyr BP and possibly earlier, and that they remained there until at least 120 kyr BP and possibly as late as 115 kyr BP.

The Caribbean observations illustrated in Fig. 1*b* are from islands that are believed to be tectonically stable. They include the results from two Bahaman islands, San Salvador and Great Inagua, for which a high-precision uranium-thorium age control is available[12]; from the Cayman Islands where the result represents a lower limit[13]; from the Yucatan Peninsula, where the result is based on samples from several locations[14]; from the 'Pleistocene tide gauge' island of Bermuda[15]; from northern Bahaman islands on the Great and Little Bahama Banks[16]; and from the Lesser Antilles islands of Curacao[17,18] and La Blanquilla[17] which lie furthest from the former ice sheet. The weighted mean ages for all except San Salvador and Great Inagua are illustrated in Fig. 1*b* (with weights inversely proportional to the published age variance). The Curacao observation is based on conventionally dated samples from five locations[17] and mass-spectrometrically dated samples from three of the same sites[18]. Individual ages range from 141 ± 8 to 123 ± 7 kyr BP. Except for the Lesser Antilles results, the observations indicate shorelines that lie a few metres above the present levels, but the height uncertainties are large. The ages of these reefs all fall within a time interval of ~132–120 kyr BP although, with the exception of the San Salvador and Great Inagua results, the ages are of low precision.

Evidence from rapidly uplifting coastlines is also helpful in defining the interval in which sea levels were near or at their present value. Conventional and high-precision mass-spectrometric ages for the Barbados corals, for example, indicate that sea levels here were near their present levels by 130 kyr BP and remained there until ~122 kyr BP[19-21]; similar results for the raised terraces of western Haiti[22] indicate an age range of 132 ± 5 to 122 ± 1 kyr BP. Preliminary high-resolution data from the Huon Peninsula of Papua New Guinea suggests that here the interval may have been longer (~135–120 kyr BP) although not necessarily continuous[23].

With the exception of the mass-spectrometric ages, the ages have low accuracies. Moreover, each reef is represented by only a few samples so that the results may not be representative of the time interval in which the reefs formed. A broader search for the oldest and youngest coral ages in the elevated reefs is desirable for establishing improved constraints on the duration of the interglacial interval.

Glacio-hydro-isostatic rebound models

Figure 2 illustrates the sea-level curve corresponding to the model proposed by Shackleton[4] from observations of oxygen isotope anomalies in deep-sea cores. These equivalent sea levels $\Delta\zeta_e$ are defined as (change in ocean volume relative to present volume)/(ocean surface area). According to this model, sea levels reached their present height at ~124 kyr BP and fluctuated about this level until 117 kyr BP, attaining a maximum height of +6 m, although a simplified model (I-2) has been adopted in which the high-frequency oscillations in the interval 124–117 kyr BP have been replaced by a zero equivalent sea level. Here we adopt an approximate model for the period before the penultimate glacial maximum at 140 kyr BP. Extensive numerical tests have shown that this model is adequate for describing sea-level change during the interglacial interval. The ice model corresponding to this equivalent sea-level function is similar to the ice-volume changes after 18 kyr BP which were used in previous glacial rebound modelling[24]. The formulation for the response of the Earth to this ice and associated water load fluctuation has been previously described[24,25], and the Earth model adopted is one that has been found to give a good description of Holocene sea-level change for the same regions[26]. This model is characterized by density and elastic moduli profiles consistent with seismic models, with a 100-km-thick high-viscosity lithosphere, an upper-mantle viscosity of 3×10^{20} Pa s down to a depth of 670 km and a lower-mantle viscosity of 10^{22} Pa s, but a wide range of plausible models give similar results.

Along the continental margin of Western Australia, far from the former ice sheets, highstands of 4–6 m amplitude are predicted to occur early in the interglacial interval (Fig. 3*a*) because of the adjustment of the Earth to the redistribution of surface loads that occurred immediately before substage 5e. Generally, the predicted amplitudes are comparable to the reported values, demonstrating that observed Late Interglacial highstands do not necessarily imply that the ocean volume at that time exceeded the present volume, but that they may be, just as the Holocene highstands are, a consequence of glacio-hydro-isostatic rebound. Like the far-field Holocene highstands, the amplitudes of these interglacial highstands vary along the coastline, in part because of ocean geometry and distance of the site from the open sea, and in part because of different distances from the ice sheets. This is illustrated in Fig. 3*a* for the offshore Rottnest Island, the coastal Cape Cuvier site and the site of Lake MacLeod now 70 km inland. For most plausible combinations of Earth and ice models, however, this variation is predicted to be ~1.5–2.0 m and is unresolvable with the available data.

Figure 3*b* illustrates predictions for three intermediate-field locations: Bermuda, Barbados and San Salvador (Bahamas). At none of these sites does the ice model I-2 produce significant highstands, because the glacio-hydro-isostatic deformation here is dominated by the glacial unloading, which is negative in this region, with the result that sea levels are predicted to lie below their present value. The predictions do indicate that at all sites the highest levels occur at the end of the interglacial interval, when the glacial unloading contribution has partly relaxed and before the lowering of sea level by renewed glaciation becomes significant. The predicted absence of a highstand is most pronounced at Bermuda where no plausible Earth model used in conjunction with the ice model I-2 produces a highstand similar to that observed (Fig. 1*b*). Significant tectonic uplift of this island is improbable, for if any vertical movement has occurred in the past 100 kyr, it is likely to have been one of slow subsidence[27]. If the ocean volumes during substage 5e are increased in the model so as to raise equivalent sea level by 5–7 m, then the shorelines in the Caribbean and Bermuda approach the observed levels but the predicted far-field highstands become excessively high. Alternatively, higher interglacial sea levels can be achieved if the duration of the 5e interval is lengthened so that there is greater relaxation of the glacial unloading effect before ocean volumes again decrease. Thus the amplitude of substage 5e highstand at these intermediate-field locations is a function of both the ocean volume and the duration of the substage, with the maximum elevations occurring late in the interglacial interval. Both the San Salvador and Great Inagua observations support the predicted trend of a rising sea level during substage 5e (Fig. 1*b*). In contrast, at the far-field continental margin sites the amplitude is primarily a function of the ocean volume during this stage with the maximum highstand occurring early in the interglacial interval.

The high-precision observations of reef age from San Salvador[12] establish an upper limit of ~120 kyr BP for the end of the interglacial stage. This is consistent with precise data from Bermuda[15] and other locations throughout the region,

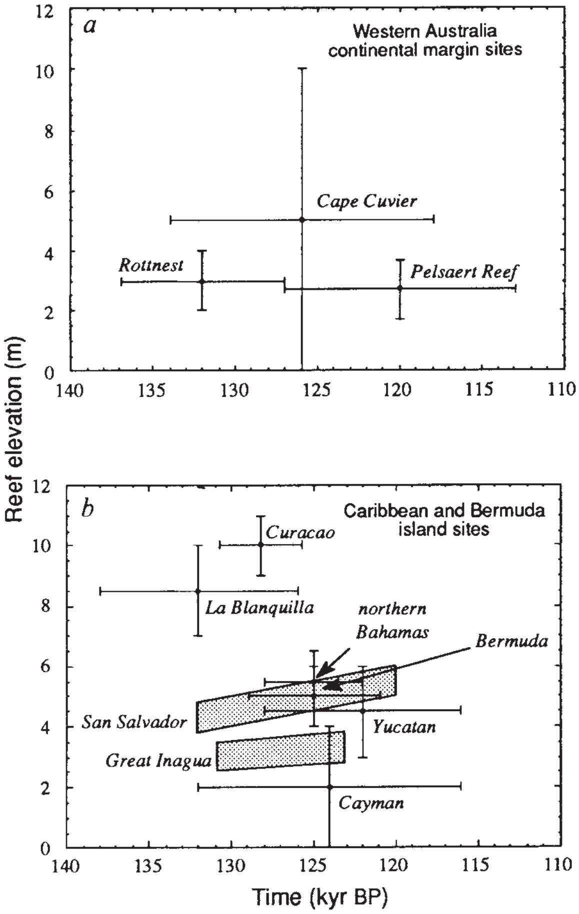

FIG. 1 Observed height–age relationships of elevated reefs along (*a*) the continental margin of Western Australia, and (*b*) at tectonically stable sites in the Caribbean and northwest Atlantic (see text for references).

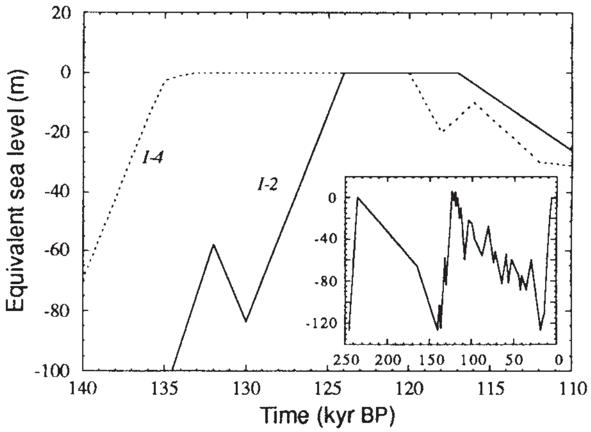

FIG. 2 Equivalent sea-level function for the ice models I-2 and I-4 at the time of oxygen isotope substage 5e and (inset) the Shackleton[4] curve for the interval 140–0 kyr BP and the approximate function from 250 to 140 kyr BP.

suggesting that the end of the interglacial interval in the adopted ice models should be shifted back in time by ~3-5 kyr from that given by the Shackleton-based model I-2. For these models, moreover, the interval in which sea levels at both Bermuda and the Bahaman islands are predicted to lie near or above their present level is less than the duration of the interglacial interval itself, and the local sea-level response lags the equivalent sea-level function by ~5-7 kyr (compare Fig. 3*b* with Fig. 2). The presence of raised coral reefs on San Salvador by 132 kyr BP therefore implies that equivalent sea level approached its present level considerably earlier, possibly by ~139-137 kyr BP.

Comparison with observations

In the ice model I-4 (Fig. 2) the ocean volume is assumed to have reached its present value at 135 kyr BP and remained at this level until 120 kyr BP. Sea-level changes before 135 kyr BP are the same as in model I-2 except that all ages have been translated by 11 kyr. Melting of the earlier ice sheet did not cease abruptly as in model I-2, and the final few metres of equivalent sea level are assumed to have been added over a period from 135 to 133 kyr BP, similar to that proposed for the final decay of the last ice sheet in mid-Holocene time[28]. From the evidence of sea levels at San Salvador and Great Inagua near or just above the present level as early as 132 kyr BP, the model I-4 must be considered to be a minimum duration model for substage 5e. Figure 4 illustrates the corresponding predicted sea levels for the two regions. The maximum highstand amplitudes reached in the far-field at Rottnest (Fig. 4*a*) are typically 3-5 m for a range of plausible Earth models. The oldest corals above present sea level are predicted to be ~135 kyr BP, and corals at or above this level can be expected to span an age range of 135-120 kyr BP. Similar results are predicted for all far-field sites including ocean islands.

The predictions for the intermediate field sites in the Caribbean and Bermuda are illustrated in Fig. 4*b*. Now, other than for the more distant sites of Barbados or the Lesser Antilles, the local sea levels do not reach their present value until ~127 kyr BP, after which, and until the end of substage 5e, sea levels increase with time. The maximum attained amplitudes of the highstands are predicted to increase from north to south. The predictions are generally consistent with the observed trends of substage 5e observations across the region. The only large discrepancy with observation occurs for the Lesser Antilles islands of Curacao and La Blanquilla for which the predictions are similar to those for Barbados and where no Earth model predicts the observed highstands of 7-10 m (ref. 17). Thus a tectonic uplift of 0.05-0.10 mm yr^{-1} must be assumed to have occurred if the observations are correct.

Implications

On the basis of these comparisons of the observed sea levels in substage 5e with the models of glacio-hydro-isostatic rebound, our conclusions are that the ocean volume during this substage was similar to the present volume, and that the substage started by or before 135 kyr BP and lasted until at least 120 kyr BP. Both conclusions are relevant to important issues in Quaternary science. For example, several terrestrial, marine or glaciological indicators[5,29-31] indicate that regional warming may have occurred during the last interglacial relative to the Late Holocene, although evidence for global differences between the two periods remains scant[5]. If, as often assumed, ocean volumes were greater during substage 5e than during the Late Holocene, this suggests

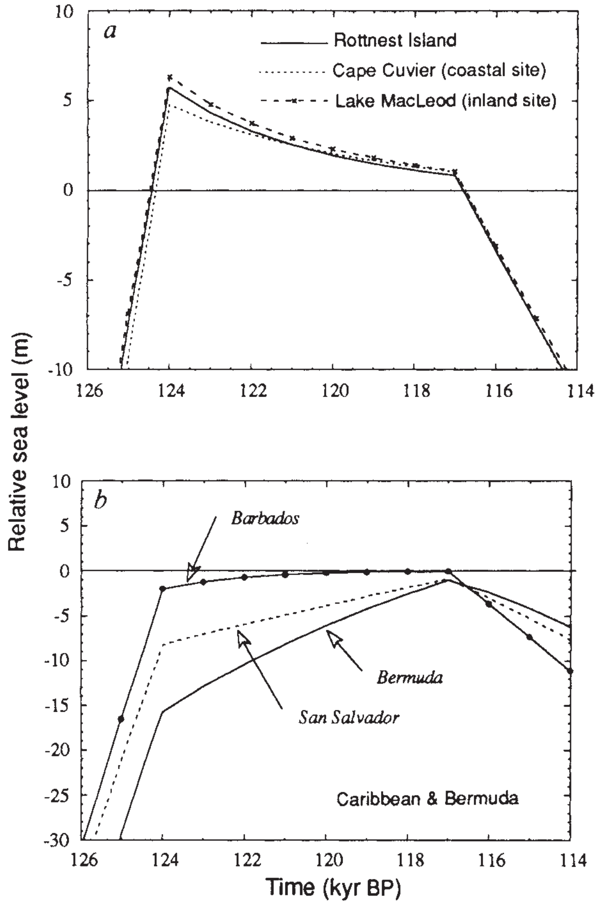

FIG. 3 Predicted sea levels based on the ice model I-2 for (*a*) sites along the Eastern Australian margin, and (*b*) sites in the Caribbean region and Bermuda.

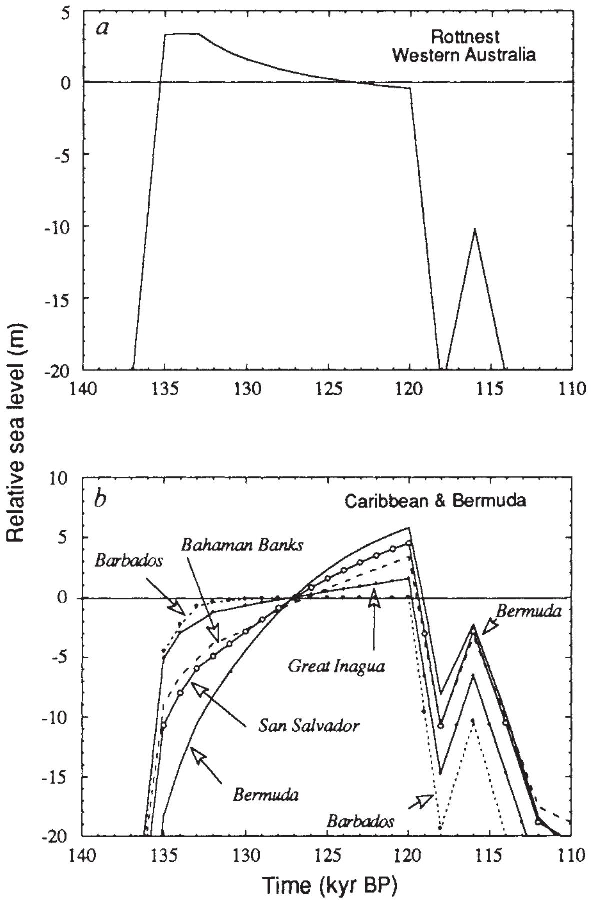

FIG. 4 Predicted sea levels based on the ice model I-4 for (*a*) Rottnest Island, and (*b*) Caribbean islands and Bermuda.

that the remaining ice sheets (such as that of the West Antarctic) must be sensitive to minor climate warming. But the models for the glacio-hydro-isostatic adjustment of the Earth remove the principal argument for larger ocean volumes at that time, so that if the climate was indeed warmer during substage 5e then these residual ice sheets must be relatively stable in the presence of small temperature increases.

Another issue raised is the duration of the interglacial interval. The evidence from raised reefs is that sea levels were near their present level from at least 135 to ~120 kyr BP, an interval longer than the 7-12-kyr interval inferred from the oxygen isotope record from deep-sea cores and scaled by astronomical motions[4,5]. It has been usual to ascribe the discrepancy to inaccurate dating of the reefs, but even with recent improvements in uranium-series dating, ages as old as 130-132 kyr BP are still indicated for some Caribbean corals; because of the glacio-hydro-isostatic adjustments of the Earth at these localities, the ocean volumes would have reached their present value earlier than this, possibly by 135-137 kyr BP. Improved age constraints on interglacial reefs at or above present sea level, particularly from better sampling of the individual reefs, coupled to glacio-hydro-isostatic rebound models, should contribute considerably to resolving this apparent conflict of the evidence for the onset and duration of the last interglacial interval. □

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ATP-dependent recognition of eukaryotic origins of DNA replication by a multiprotein complex

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A multiprotein complex that specifically recognizes cellular origins of DNA replication has been identified and purified from the yeast *Saccharomyces cerevisiae.* We observe a strong correlation between origin function and origin recognition by this activity. Interestingly, specific DNA binding by the origin recognition complex is dependent upon the addition of ATP. We propose that the origin recognition complex acts as the initiator protein for *S. cerevisiae* origins of DNA replication.

THE complex process of eukaryotic chromosomal replication must be carefully regulated throughout the cell cycle. It is likely that much of this regulation occurs at the level of the initiation of DNA synthesis. Studies of *Escherichia coli* chromosomal, bacteriophage, and eukaryotic viral DNA replication have resulted in a paradigm for the initiation of bidirectional DNA replication[1,2]. For each of these organisms, the first step is the sequence-specific recognition of the origin of DNA replication by an initiator protein. Binding of the initiator causes partial untwisting of the double helix adjacent to the recognition site and the subsequent action of a helicase leads to further unwinding of the DNA duplex. This unwound DNA structure serves as a template for the initiation of DNA synthesis. Although protein factors likely to be involved in the unwinding and elongation stages of eukaryotic chromosomal DNA replication have been described[3,4], proteins involved in the initial stage of eukaryotic origin recognition have not been identified.

The availability of short well characterized chromosomal origins of DNA replication derived from the yeast *S. cerevisiae* make it a particularly useful organism to study the earliest steps of eukaryotic DNA replication. Originally identified as chromosomal sequences able to confer high frequency of transformation on plasmid DNA[5], a subset of these autonomous replication sequences (ARS) were subsequently shown to act as true origins of replication in the chromosome[6-9]. Sequence comparison of numerous ARS elements led to the identification of an 11-base-pair sequence that is conserved across all ARS elements and is referred to as the ARS core consensus sequence (ACS)[10,11]. Studies of the sequences required for ARS function have found that although the ACS is necessary, sequences 3′ to the T-rich strand of the ACS also are required for ARS function[11]. A detailed analysis of *ARS1* identified four *cis*-acting elements that constitute this chromosomal origin of DNA replication[12]. In addition to an essential A element containing the ACS, three distinct elements within the 3′ region, B1, B2 and B3, are required for efficient *ARS1* function. One of these elements, B3, is a