Coral indicators of past sea-level change: a global repository of U-series dated benchmarks

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Abstract

Fossil corals provide valuable data for reconstructing past sea levels, as they are often well preserved in the fossil record and can be dated with U-series methods. Here we present a global and internally consistent database of U-Th dated fossil coral sea-level indicators, including full consideration of all (known) associated uncertainties (both vertical and chronological). We include carefully determined taxon-specific depth distributions, rather than blanket depth uncertainty terms as used in most previous work. This is based on a synthesis of extensive modern ecological information on depth ranges. These ranges are found to be spatially variable (between ocean basins, between regions, and on sub-regional scales) because depth itself is not limiting – instead, depth distributions arise from complex physical, chemical, and biological interactions with coral-reef growth, distribution, and composition. One of the main causes for recognition of the greater depth-variability of coral taxa has been the routine inclusion of deep-diving and ROV surveys in coral ecological studies over the past few decades, which has broken through the “shallow-water” bias of early surveys by adding frequent observations on deeper occurrences (although more are needed). It is also clear from our assessment that coral habitat-depth distributions must be determined on the species level to reduce uncertainties in reconstructions of past sea levels, and that application to sea-level studies then requires these studies also to identify fossil corals to the species level. Most existing data were determined only to the genus level, which gives rise to wide uncertainties in habitat depth and, hence, sea level. Our database contains extensive metadata to assist evaluations of dating quality, as well as geomorphic and stratigraphic metadata. We demonstrate with examples how such metadata can help to evaluate sea-level reconstructions, for example by identifying outlier points. One example discusses the Last
Interglacial (LIG), where we use the available data with their uncertainties to assess probabilistically the time at which local sea levels exceed that of the present, which yields a mean age of 124.6 ka with 95% probability bounds at 118.5 and 129.5 ka. We conclude with identification of key outstanding issues relating to: (i) current incomplete understanding of tectonic setting (including the current lack of independent verification of uplift/subsidence rates and reliance of somewhat unsatisfactory, and circular, use of the elevation of Last Interglacial deposits); (ii) the depth-distributions of coral taxa and; (iii) the complete documentation of stratigraphic, geomorphological information and other contextual information, with suggestions for strategies to address these issues.
1. INTRODUCTION

Fossil corals have provided valuable insights into past changes in sea level, from the early studies that tested Milankovitch pacing of glacial-interglacial cycles (e.g., Broecker et al., 1968; Mesolella et al., 1969), to more recent work on detailed, high-resolution reconstructions of past sea levels (e.g., Deschamps et al., 2012) that provide constraints for investigations of past ice-sheet dynamics (e.g., Clark et al., 2002; Stanford et al., 2011; Lambeck et al., 2014).

Fossil corals offer distinct advantages for reconstructing past sea levels, principally their good preservation potential, and the potential for obtaining precise, numerical ages using U-series dating. They also have a wide distribution in the topical/subtropical regions and many of these sites are far-field (i.e. far away from the centres of the former ice sheets), where glacio-isostatic adjustment (GIA) influences are minimised (e.g. Clark et al., 2002; Bassett et al., 2005). However, the coral data distribution is heterogeneous in space and time; i.e., they are limited to tropical/subtropical regions and represent periods of reef construction, and provide discrete data points rather than continuous sea-level records. In addition, taphonomic and diagenetic factors influence coral preservation, and the relationship between the present elevation of the fossil coral and former sea levels often remains insufficiently constrained. In this paper, we first review modern ecological studies of the main controls on coral growth, and formulate from this a comprehensive assessment of depth-distributions. Thereafter, we present and discuss a new compilation of U-series dated fossil coral data, which is quality-checked and internally consistent, includes relevant contextual metadata, and gives full consideration of uncertainties.

2. PRINCIPAL CONTROLS ON REEF DEVELOPMENT AND DISTRIBUTION

Sceleractinian (‘hard’) corals are composed of polyps that secrete an aragonitic skeleton using calcium and carbonate ions precipitated from seawater. Zooxanthellate sceleractinian corals have endosymbiotic photosynthetic algae. Scleractinian corals may take various growth forms (branching, massive, encrusting, solitary, free-living i.e. not attached to the substrate etc.) and in this review we concentrate on the reef-forming (hermatypic) corals.

Coral reefs are complex structures that consist of both primary (skeletogenesis) and secondary (e.g., marine (re)cementation) structures with a potential for significant biomineralisation (e.g., Barnes and Devereux, 1984). The exact mechanisms of calcification and the role of symbionts remain debated, and - despite considerable progress in recent decades (e.g., Cohen and McConnaughey, 2003) - understanding of how major and trace elements are incorporated into the coralline aragonite remains
incomplete (Allemand et al., 2004, 2011). The principal components required for coral growth are:
light, carbon dioxide and inorganic nutrients for photosynthesis; organic food for organic tissue and
organic matrix synthesis; and calcium and carbonate ions for skeleton formation.

Coral reefs can be separated into three main geomorphological zones: (i) the back-reef and reef flat
zone; (ii) the reef crest, and (iii) the fore-reef (which includes the reef slope), within which different
benthic assemblages make statistically distinct contributions to reef framework construction (e.g.,
Hopley et al., 2007; Woodroffe and Webster, 2014). The back-reef zone is a low-energy zone with
lagoons featuring sea-grass beds, patch reefs and sand plains. The reef flat and reef crest (or algal
ridge where encrusting coralline algae replace corals in the highest wave-energy settings) is formed
from consolidated calcareous material, corals, and coralline algae. This is a high-energy zone with
potential for breakage, desiccation through exposure at low tide, and ultra violet (UV) light stress. The
fore-reef continues seaward of the reef crest to depth. This lower-energy zone has steep gradients in
light and temperature, with the greatest coral diversity typically at intermediate depths of 15 to 30 m
(e.g., Burns, 1985; Huston, 1985; Cornell and Karlson, 2000) and decreasing with increasing depth. We
refer the reader to Woodroffe and Webster (2014), Kennedy and Woodroffe (2002) and Montaggioni
and Braithwaite (2009) for detailed considerations of reef morphology.

The interplay of physical, biological and chemical factors (e.g., substrate, incidence of severe storms,
predation, disease, etc.) determines the structure and composition of coral reefs, including their
growth form, taxonomic composition, distribution, and their preservation potential within the fossil
record. These factors operate on a variety of geographic scales: some affect the global distribution of
reefs; others control the dimensions and geometry of individual reefs; yet other factors influence – at
the ecosystem level – the community composition, zonation, and habitat availability (including the
distribution and abundance of populations/taxa); and, finally, several factors combine to affect corals
at the individual level, through recruitment, growth rates, size, form, reproduction, and mortality.

In this section we review the main influences on coral growth (Figure 1), with a focus on the ecological
and hydrological factors.

2.1. Temperature

Sea surface temperature is a major determinant in the growth and distribution of modern coral reefs
(Macintyre and Pilkey, 1969; Andrews and Gentien, 1982; Johannes et al., 1983; Veron and Minchin,
1992), influencing the composition and structure of reef communities, and regulating the aragonite
saturation state of the surface waters (growth is optimal in warm waters that are super-saturated with respect to aragonite; Kleypas, 1997; Kleypas et al., 1999). Temperature also exerts a control on the latitudinal extent (geographical range) of species, and comparison between fossil and modern coral ranges suggests a substantial poleward expansion of the range of many coral taxa during the Last Interglacial (LIG) relative to the present as a result of increased temperatures, although equatorial diversity was reduced (Kiessling et al., 2012). Most modern coral reef growth is limited to waters with temperatures between \(~18\) and \(~31\) °C for most of the year (Hubbard, 1997; Kleypas et al., 2008), but some reef corals are able to tolerate temperatures as low as \(~11\) °C (Veron, 2000). Prolonged exposure to temperatures outside this range may lead to reduced photosynthesis, coral bleaching, and mortality.

Coral reef growth is generally confined to tropical latitudes, although warm surface currents can enable growth outside the tropical latitudes (e.g., Kuroshio, Leeuwin, and Agulhas Currents). In addition, thermal gradients within basins, such as the Red Sea, may determine local/regional coral reef distribution and diversity (Veron, 1995, 2000). Changes in these local or regional conditions or currents and their associated temperature regimes can influence coral distributions resulting in expansion or contraction of the latitudinal range of coral species (e.g., Roberts et al., 1982; Veron, 1992; Abram et al., 2001). For example, Greenstein and Pandolfi (2008) demonstrate a contraction in geographic range and a change in assemblage composition within modern reefs compared to fossil Last Interglacial reefs of Western Australia, in response to decreased temperatures from a weakened Leeuwin Current, given that this current brings warm equatorial waters to higher southern latitudes. Similarly, Muhs et al., (2002a, b, 2006) use molluscs and corals as part of the wider reef assemblage, to infer changing thermal and ocean current changes (for California, Hawaii and Bermuda).

### 2.2. Salinity

Corals are generally thought to be tolerant of salinity variations, generally growing within a range of 30 to 38 psu with some species tolerating salinities of \(~40\) psu. Extended exposure to low-salinity waters may reduce growth rates, reproductive success, photosynthesis, and respiration (Coles and Jokiel, 1992; Muthiga and Szmant, 1987; Richmond, 1993; Moberg et al., 1997; Porter et al., 1999; Lirman et al., 2003) although the effects are often species dependent. Past changes in sea surface salinities (e.g., due to altered precipitation regimes associated with changing monsoon dynamics) are relatively poorly constrained, but salinity changes since the Last Glacial Maximum (LGM) are not thought to have been a limiting factor on subsequent coral reef development (Montaggioni, 2005).
2.3. Nutrient Availability

Coral reefs are often found in what are considered to be nutrient-poor regions where an increase in nutrient availability can increase macro-algal growth, which increases competition for space within the reef system. In addition, the often-associated phytoplankton blooms increase water turbidity and decrease light penetration (Hallock, 1988; Hallock and Schlager, 1986; Chazottes et al., 2002; Sanders and Baron-Szabo, 2005).

In detail, the situation is more nuanced: coral reefs span a wide range of nutrient levels (Kleypas et al., 1999, Atkinson et al., 1995), and nutrient flux affects coral zonation in multiple ways. Upwelling as well as terrestrial and riverine inputs affect coral distribution via the transport of nutrients to sites (e.g., Maxwell and Swinchatt, 1970; Andrews and Gentien, 1982; D’Elia and Wiebe, 1990; Leichter et al., 2003). Increased nutrient supply can be beneficial (promoting reef growth or enhancing calcification) as well as deleterious – reducing rates of skeletonogenesis (Marubini and Davies, 1996), and/or increasing bioerosion (Hallock, 1988; Hallock and Schlager, 1986), and/or increasing the incidence and severity of coral disease (Bruno et al., 2003, 2007). Overall, the resulting changes in coral distribution reflect changing community structures as a whole due to several factors (turbidity, light availability, etc.), rather than just changing nutrient availability (Szmant, 2002).

2.4. Turbidity

Fluctuations in turbidity regimes can occur at the local and/or regional scale, with turbid environments ‘compressing’ the habitable vertical range of corals to a few metres (Veron, 1995). High inputs of sediment can have detrimental effects on reef frameworks, in part through the reduction in light penetration. High sediment environments are often associated with fewer coral species, reduced live cover and growth rates, decreased calcification and net productivity, and reduced rates of reef accumulation (Rogers, 1990). Increased turbidity often coincides with elevated nutrient levels, which result in a further decrease in light penetration (see section 2.5 for impacts of irradiance levels). High sediment inputs also affect reef frameworks through abrasion and particle deposition. This results in changes in reef zonation, growth forms, and rates of mass mortality, through smothering or burial (Loya, 1976; Acevedo et al., 1989; Rogers, 1990; Shin 2000; Montaggioni, 2005). However, some coral species and communities can tolerate a wide range of turbidity and light levels, forming sites of relatively high diversity (Veron, 1995), for example in Jamaica (Mallela and Perry, 2007) and in nearshore turbid zones of the Great Barrier Reef (Woolfe and Larcombe, 1998; Larcombe et al., 2001; DeVantier, et al., 2006; Browne et al., 2012). Thus, some communities can become established and persist in environments dominated by persistent fine-grained sediment deposition (Perry et al., 2008).
Coral polyps themselves can be effective in removing clays and silts (e.g., through ciliary currents, tissue expansion, direct tentacle manipulation and pulsed partial contraction of the polyp; Stafford-Smith and Ormond, 1992). Waves and current action provide an additional means of removing suspended and settled material.

Experiments suggest that some symbiotic corals can alter their balance between autotrophy and heterotrophy, making heterotrophic carbon a significant source of energy when photosynthetic carbon is unavailable due to bleaching events or in deep and/or turbid waters. This allows corals to broaden their ecological niche and tolerate turbid conditions (Anthony and Fabricius, 2000; Anthony and Connolly, 2004). In addition, so-called phenotypic (shape) plasticity enables corals to regulate light capture across a large spectrum of light conditions (Anthony et al., 2005).

Turbidity increases have been implicated as a major factor in the demise of coral reefs in the geological record (e.g., Lighty et al., 1978; Kleypas, 1996), although changing sediment regimes may be only one of a multitude of related influences that led to cessations of reef formation (e.g., Perry and Smithers, 2011).

2.5. Irradiance Levels

The amount of light received by corals varies spatially and temporally, and is influenced by cloud cover, turbidity, tidal changes, reef topography, and depth. The depth of light penetration varies with latitude and distance from the shore (Kleypas et al., 1999), with many coastal reefs receiving reduced light levels due to high turbidity. For example, in the most turbid regions of the Great Barrier Reef, corals are found only within the upper 3 to 4 m of the water column, while on the outer shelf, corals are found to depths up to 100 m (van Woesik and Done 1997, Hopley, 1994, Cooper et al., 2007). At some mid-ocean Pacific atolls, irradiance levels can be compatible with coral growth even at ~160 m depth (Montaggioni, 2005).

Irradiance and coral growth are often positively correlated, with a strong link to calcification in many scleractinian corals (Goreau, 1959; Chalker, 1981; Marubini et al., 2001; Reynaud et al., 2004; Schlacher et al., 2007; Schutter et al., 2008). As stated by Veron (1995), “light, not temperature, is by far the most ecologically limiting of all physical-environmental parameters”. As light intensity and penetration depth decrease, the habitable depth range of many corals becomes compressed and there is a decrease in the depth at which reef building ceases (Hallock and Schlager, 1986, Veron 1995).

For corals with symbiotic algae, production of photosynthates is reduced when irradiance levels are
low (Titlyanov et al., 2001), and a decrease in internal pH may develop due to reduced photosynthesis, which in turn may lead to less favourable conditions for calcification (Schneider and Erez, 2006).

Similarly, the increased energy required to repair light damage may exceed the increase in photosynthetic energy received at high irradiance levels (photoinhibition; Iglesias-Prieto et al., 1992). Corals may adapt to changing light levels by altering their growth form (e.g., from mounds to plates in order to maximise exposure of photoreceptors (Hubbard, 1997), altering the density of zooxanthellae (endosymbionts) or pigment (Titlyanov et al., 2001), or altering the composition of pigment according to the spectrum of the available light (Dustan, 1982). In light-limited conditions, corals will rely on heterotrophy for their energy needs, to compensate for reduced photosynthetic activity (Anthony and Fabricius, 2000; Antony, 2006).

2.6 Substrate availability and antecedent topography

The availability of suitable substrate is “the most biogeographically limiting of all physical-environmental parameters” (Veron, 1995). The eastward attenuation of coral species richness across the Pacific is considered to be primarily due to substrate availability coupled with the survival and dispersal capacity of recruits (Veron, 1995). Substrate type can also influence coral distributions, with colonisation occurring preferentially on karst or rough lava flows, whereas unconsolidated or smooth surfaces are less favoured sites for coral growth (Cabiocch et al., 1995). Additionally, highly reflective substrates such as carbonate-rich sands amplify light intensity surrounding coral colonies and increase stress levels, particularly during bleaching events (Ortiz et al., 2009).

Coral recolonisation (e.g., during high sea levels after episodes of low sea level) may be inhibited by the contraction or absence of suitable nurseries (shelf edges, banks, seamounts etc.). These provide potential refugia and centres of dispersal once ocean circulation is conducive to larval transport, e.g., after episodes of lowered sea levels (Montaggioni and Braithwaite, 2009). Topographic highs or other elevated regions offer advantages to coral reef formation, for example by optimising larval recruitment (Hubbard, 1997); the general distribution of such highs can directly constrain reef locations; e.g., for Florida see Lidz et al. (1997), for Belize see Purdy (1974), Gischler and Hudson (2004), and for Palau Islands see Kayanne et al. (2002). However, topographic lows, such as those found in some Hawaiian locations (e.g., a drowned stream valley within a morphologically complex antecedent substrate), provided a refuge for Holocene reef growth in a region of high wave energy that would otherwise limit most Holocene reef growth to a generally thin veneer (Grigg, 1998; Grossman and Fletcher, 2004).
2.7 Hydrodynamics (waves, tides and disturbances)

Wave energy and tidal regimes exert a control on the ecological zonation, habitat availability and morphology of modern reefs (Veron, 2000; Rasser and Riegl, 2002), with disturbances (sometimes catastrophic; e.g., storms, cyclones, hurricanes/typhoons, or tsunamis) altering sedimentary inputs, temperatures, salinity, and hydrodynamic patterns that result in breakage and redistribution of coral debris, in effect remodelling the reef surface.

Waves can promote the exchange of nutrients, larvae, and particulate food (Pineda, 1991). In high-energy environments, the enhanced circulation of nutrients and/or the removal of metabolic waste products can promote coral growth (Atkinson and Bilger, 1992; Atkinson et al., 1994; Hearn et al., 2001), but at higher energy levels, community structure can change toward more stress-tolerant growth forms (e.g., encrusting or massive corals) to compensate for the increased mechanical erosion (Done, 2011). For example, the community structure of modern reefs in Hawaii is primarily a function of wave energy and depth: in wave-exposed environments, coral growth is frequently disturbed by wave-induced breakage, scour, and abrasion, which results in frequent turnover and re-growth of fragmented colonies that are rarely thicker than a single living community (Grigg, 1998).

Tidal regimes impact corals over a wide range of habitats, not just those within the intertidal zone. For example, the reduced tidal range of the open ocean, relative to continental margins, often results in fewer inter-tidal habitats, whereas high tidal ranges generally result in a wider range of habitats and maximise the area available for coral growth (Veron, 2000). Within the tidal zone, there is a potential for periodic subaerial exposure of reefs, strong wave action, large temperature fluctuations, and high solar irradiation, as well as the tidal modulation of currents and waves. However, the reef crest is one of the most biologically productive parts of a coral reef (Chisholm, 2003) and accounts for more than half the species richness (Karlson et al., 2004), which indicates that such extremes in environmental conditions are generally within the tolerance of modern corals (Anthony and Kerswell, 2007). Extreme low tides may, however, lead to coral mortality, particularly when coupled with high irradiance levels (Anthony and Kerswell, 2007). This is not necessarily detrimental, as it helps to maintain high species diversity due to periodic removal of competitive taxa, as also occurs with storm-induced coral mortality (Connell, 1978; Rogers, 1993).

Pulsed upwelling can promote coral growth and diversity (e.g., Leichter and Genovese, 2006; Schmidt et al., 2012). However, in regions of strong upwelling, these positive effects may be counteracted by
low temperatures, low pH, and high nutrient loading, which favour algal rather than coral growth (McCook et al., 2001).

The effect of hydrodynamics on coral distribution and diversity may be local (e.g., wave scour producing resistant reef spurs orientated towards high-energy coastlines; Shinn, 1966), and may extend to the reef/regional scale, with ecological zones dependent upon wave exposure (Geister, 1977) and the tendency for reefs to become more developed on windward as opposed to leeward island aspects (Grigg, 1998; Veron, 2000; Yamano et al., 2001). Storms and/or hurricanes can also change sea surface temperatures and turbidity regimes (potentially leading to coral mortality), or cause clearing of reef surfaces that then become available for re-colonisation (e.g., Scoffin, 1993). Finally, changing hydrodynamics can alter the accommodation space available for reef growth (Grossman and Fletcher, 2004).

Within the geological record, one of the most important hydrodynamic influences is breakage and redistribution of debris due to permanent wave agitation (Hughes 1999) and major storms, with potential implications for stratigraphic integrity of the fossil reef (Scoffin, 1993). Such events may result in severe modification of the reef by mechanical destruction and reforming surface morphology, displacement of blocks downslope, and/or landward redistribution of sediments from reef margins (i.e., accelerating the process of backreef infilling) (Hubbard, 1992; Scoffin, 1993; Blanchon et al., 1997; Braithwaite et al., 2000; Macintyre et al., 2001; Yamano et al., 2001; Rasser and Riegl, 2002). Reef rubble may accumulate as talus on steep slopes and cause the displacement of material to depth, while on gentle slopes this displacement may result in onshore transport and formation of large piles of rubble (Rasser and Riegl, 2002). Within the geological record, such disturbance events may be recognised by a change in lithology (Dunham, 1962; Insalaco, 1998), although there may be a permanent cycle of destruction and regeneration of coral leading to a constantly reworked substrate (Blanchon et al., 1997) and reef interiors that are “more garbage pile than an in-place assemblage of corals, cemented together into a rigid framework” (Hubbard et al., 1990).

Storms or other hydrodynamic disturbances may be evident within the fossil record. For example, an ‘extreme wave event’, probably as a result of a tropical cyclone or tsunami, is thought to be responsible for the abrupt infilling of the Paraoir reef (Philippines) by reef rubble and bioclastics (Gong et al., 2013). Recognition of such acute disturbances within the geological records can only be achieved by thorough examination of stratigraphic (i.e., consistency within each stratigraphic unit), geomorphic, lithologic, and geochemical (i.e., petrography of the reef structure) information (for a
review, see Scoffin, 1993), as well as detailed consideration of the coral assemblages themselves. For example, some Pleistocene terraces of Barbados contain distinct ~2 m high *in-situ Montastraea annularis* colonies separated by piles of *Acropora* debris. Although the coeval growth of both species on the reef is possible, growth considerations suggest that *Acropora* only existed for a relatively short period time, or else the massive *M. annularis* forms would have been unable to reach their large dimensions due to shading effects (Scoffin, 1993). More extreme hydrodynamic origins (a tsunami or large wave) have been controversially suggested for the elevated (at ~ +20 m) boulders of Eleuthera Island (Bahamas) (Hearty, 1997), although these may also have resulted from cliff erosion or be relict features associated with karst towers (Panuska et al., 2002; Mylroie, 2007). Tsunami or giant wave origins have also been suggested for deposits on Hawaii (~ +190 m deposits of coral and coralline algae fragments) (Moore and Moore, 1984, 1988), but again there are alternative explanations for the origin of these deposits (e.g., lithospheric deformation) (Keating and Helsley, 2002).

### 2.8 Population dynamics, predation, competition and disease

Coral reproduction may occur through broadcast or brooding behaviour. Broadcast spawning releases eggs and sperm in mass spawning events and fertilisation occurs within the water column. The gametes may remain within the water column for several weeks and can distribute offspring over a wide geographic area (Veron, 2000). In coral brooding reproduction, fertilisation and embryogenesis occur internally and the larvae may be ready for settlement immediately. Once settled on a suitable substrate, coral growth is rapid in order to avoid overgrowth by algae or burial by sedimentation (Barnes and Hughes, 1999). Reproduction may also occur asexually through budding (i.e., division into clones; Sumich, 1996) and fragmentation, where such fragments may attach and develop into new colonies.

Larval recruitment influences both distribution and diversity of coral populations, reflecting variations in stock size, larval survival, and settlement behaviour (Hughes and Tanner, 2000; Hughes et al., 2003). Macroalgae and cyanobacteria (Kuffner et al., 2006) can have a detrimental impact on coral recruitment and survival of juvenile corals (Tanner, 1995; Jompa and McCook, 2002), as well as on the growth, reproduction, and survival of established corals (Kuffner et al., 2006, Burkepile and Hay 2006, 2008; Carpenter, 1986, Williams and Polunin, 2001; Hughes et al., 2007), and on the prevalence of coral disease (Nugues et al., 2004). Along with availability of suitable substrates, limits on survival and dispersal capacities are thought to account for the eastward attenuation of coral species diversity across the Pacific (Veron, 2000; Montaggioni, 2005).
Biological interactions govern the population density of coral species (Montaggioni and Braithwaite, 2009). Examples include: (a) grazing influences on the diversity and growth of coral (Burkepile and Hay, 2010; Bellwood et al., 2004), and on the establishment and maintenance of coral-dominated communities by removing competitively ‘superior’ macroalgae (Birkeland, 1977; McClanahan and Muthiga, 1988; Burkepile and Hay, 2006); (b) bioerosion controls on reef dynamics by reshaping reef topography and/or weakening colony structures of live branching corals (Hutchings, 1986, Sammarco, 1996); (c) predation impacts on coral fitness and rates of coral decline (Knowlton et al., 1990; Rotjan et al., 2006), and on coral colony growth and survival (including reproductive potential) (Veghel and Bak, 1994; Rotjan, 2007; Rotjan and Lewis, 2008); and (d) coral disease, which can change the community structure of a reef (Willis et al., 2004; Page and Willis, 2008; Haapkyla et al., 2011). Stress factors, such as increased temperature, nutrient inputs, etc., may both increase the prevalence of coral pathogens, and weaken coral resistance to disease (Aronson and Precht, 2001). Increased ocean temperature is thought to be a main driver of the incidence of coral disease (Harvell et al., 2002, 2007; Rosenberg and Ben-Haim, 2002; Bruno et al., 2003, 2007; Miller et al., 2009). Coral disease may impair zooxanthellae cell division (e.g., yellow band disease), result in tissue necrosis and/or depression of the colony surface (e.g., dark spot disease) (Cervino et al., 2001), and cause weakening of skeletons (Aronson and Precht, 2001).

2.9 Depth

Most species of zooxanthellate corals are generalists; they can occupy a wide range of habitats, reef and non-reef, with vertical ranges from sub-tidal to substantial depths (Veron, 1995). The influence of biotic factors on reef zonation is highly complex, and there is no simple relationship with bathymetry (Perrin et al., 1995). There is relatively little published research on the direct relationship between coral distribution and depth; instead coral diversity and/or distributions are assessed in terms of factors such as light, temperature, and nutrient availability, for which depth may often serve as a (rough) proxy.

The literature suggests that corals are “depth-generalists” that occur in both shallow and deep water, with most species occurring within very shallow to -40 m water depth (Carpenter et al., 2008). Indeed, based on the International Union for the Conservation of Nature (IUCN) Red List data (currently the most comprehensive global compilation of the depth distribution of coral species), the maximum global coral species occurrence was at mean depth of -27 ± 17 m (Carpenter et al., 2008). Coral diversity generally peaks at intermediate depth (-15 to -30 m) (Burns, 1985; Huston, 1985; Cornell and Karlson, 2000). Most studies, however, do not directly investigate coral distribution and depth.
Surveys are generally undertaken to monitor/ascertain coral reef ‘health’ in terms of community composition, and any change through time. Typically, such surveys are undertaken by divers, although in recent years there has been an increasing use of autonomous underwater vehicles, which – coupled with technological improvements in diving – have allowed greater depths to be reached (approx. -150 m depth; Hinderstein et al., 2010). This has enabled more extensive investigation and documentation of deeper-living coral species, including a burgeoning literature on mesophotic reefs. These are defined as deep fore-reef communities that occur in low-light habitats and are composed of zooxanthellate and azooxanthellate scleractinian corals, macroalgae and sponge communities (Lesser et al., 2009). They typically have a depth range of -30 to -40 m, and can extend to over -150 m in tropical and subtropical regions, depending on water quality, light penetration, etc. (Hinderstein et al., 2010; Kahng et al., 2010). Mesophotic reefs are considered extensions of shallow reef ecosystems (with biological, physical and chemical connectivity with these reefs and communities; e.g., Bongaerts et al., 2010; Bridge et al., 2012), although they have coral assemblages that are generally of lower diversity (Liddell et al., 1997; Jarrett et al., 2005; Armstrong et al., 2006; Hinderstein et al., 2010). The genetic and ecological linkages between shallow and deeper reefs remain unclear (Van Oppen et al., 2011). Mesophotic reefs are thought to have acted as refuges during past instances of environmental disturbance (e.g., Bongaerts et al., 2010), but they are poorly documented within the fossil record and potentially difficult to recognise without precise dating and a comprehensive assemblage approach (e.g., Abbey et al., 2013).

Technological advancements are extending the maximum documented depth for many species of zooxanthellate corals. For example: Agaricia grahamae was documented at -119 m in the Caribbean (Reed, 1985), Leptoseris fragilis at -145 m in the Red Sea (Fricke et al., 1987), and Leptoseris sp. at >-100 m in the Indo-Pacific (e.g., Kahng and Kelley 2007; Maragos and Jokiel 1986; Fricke et al., 1987), with observations of the latter reaching 153 m in Hawaii (Kahng and Maragos, 2006) and including abundant cover at -90 m depth on the Great Barrier Reef (GBR; Hopley et al., 2007). Also notable is the documentation of coralline algae at -268 m in the Bahamas (Littler et al., 1985, 1986), given that association of coralline algae with corals is increasingly being used in sea-level reconstructions (Cabioch et al., 1999; Iryu et al., 2010; Camoin et al., 2012; Deschamps et al., 2012).

The vertical ecological zonation of corals is well documented (e.g., for the Atlantic see Goreau, 1959; Mesolella 1967; Lighty et al., 1982; for the Pacific see Maragos, 1974; for the Indian Ocean see Loya, 1972) and is a function of intrinsic and extrinsic factors, and their interactions. In addition, morphological variation can occur across a depth range. Again this variation is correlated with...
environmental conditions (light depth, wave energy, etc.) rather than depth sensu stricto (Veron, 1995). Such community structure and species diversity can be retained in the fossil record (e.g., Mesolella 1967; Lighty et al., 1982; Edinger et al., 2001; Pandolfi and Jackson, 2006), although the accuracy and resolution of fossil corals for sea-level reconstructions may be limited by time-averaging (i.e., temporal mixing of different coral cohorts within the fossil coral assemblage; see section 1.1.12 for further discussion) (Edinger et al., 2007).

Changes in accommodation space (the vertical and lateral space available for coral reef growth) occur through processes such as tectonic movements (uplift/subsidence, etc.) and sea-level changes that alter the water depth above a reef. With an increase in accommodation space, reef growth may fill the space (i.e., ‘keep up’ or ‘catch up’ depending upon the rate of relative sea-level rise; Neumann and Macintyre, 1985), but local processes (e.g., larval supply and survival, hydrodynamics, sediment supply) may prevent reef growth from filling any additional space (e.g., the high wave energy settings of Hawaii; Grigg, 1998). A modern example from Heron Island, Australia, demonstrates the ability of coral reefs to respond to changes in accommodation space in response to rising sea levels and other, coincident hydrodynamic factors (Scopélitis et al., 2011). Reef growth may also ‘turn off’ when the increase in accommodation space ceases and vertical accumulation reaches dynamic equilibrium with other factors (wave energy, disturbances, etc.). In some instances, growth may be arrested and ‘drowning’ occurs as vertical accretion can no longer track the increasing water depth and concomitant decrease in light, temperature, etc. (i.e., ‘give up’ response, cf. Neumann and Macintyre, 1985).

These different responses to changing accommodation space have been identified within the fossil record. For example, Holocene sea-level stillstands have been inferred from the elevation of upper (dead) surfaces of micro-atolls (e.g., Smithers and Woodroffe, 2001; Kench et al., 2009; Yu et al, 2009), while instances of ‘keep up’ reef growth and limited aggradation due to accommodation-space reduction (e.g., Strasser et al., 1992; Braithwaite et al.; 2000; Grossman and Fletcher 2004), as well as reef ‘drowning’ (e.g., Ludwig et al., 1991; Blanchon and Shaw 1995; Webster et al., 2009) have been inferred from changes in sedimentary facies and benthic communities. Rather than relating to depth per se, the effect on coral growth and diversity reflects instead the changing physio-chemical conditions brought about by external factors (sea-level change, tectonic subsidence, etc.). The following sections (2.10 and 2.11) present further discussion of the impacts of sea-level change and tectonics.
2.10 Sea-level change

High species diversity within the central Indo-Pacific is thought, in part, to be due to the interaction of long-term tectonic activity and changes in sea level. Bathymetry of this region was such that, even though reefs were repeatedly aerially exposed during Pleistocene sea-level lowstands, the complex coastline and creation of diverse shallow habitats in close proximity to deep (>150 m) waters meant that there was minimal broad-scale species dislocation during intervals of rapid sea-level change (Veron et al., 2009).

Changes in sea level may lead to severe (or catastrophic) ecological disruption; e.g., via changing sedimentary regimes, loss of accommodation space (a lack of accommodation space being a limiting factor for reef growth in some instances, Kennedy and Woodroffe, 2002), and disruption of coral dispersal due to changing oceanographic patterns. In addition, the rate of sea-level change may affect the composition of coral reefs; Neumann and Macintyre (1985) suggest that reef growth is a balance between rate of sea-level rise and the ability of the reef to keep pace. The differing responses proposed (“keep-up”, “catch-up and “give-up”) should be recognisable within the fossil record: (i) “keep-up”, where reefs maintain crests at or close to sea level, are preserved as shallow-water growth forms; (ii) “catch-up” – where reef growth initially occurs in deeper water as the rate of sea-level rise exceeds the rate of growth and where reefs later caught up, often due to a decrease in the rate of sea-level rise – produces a successive change from deeper to shallower water assemblages; and finally (iii) the “give-up” scenario, where there is a sudden cessation in growth possibly due to a sudden rise in sea level or a sudden change in environmental or oceanographic conditions and accretion can no longer keep pace, ‘drowning’ the reef.

In the fossil record, the successive highstand reefs of the Huon Peninsula (Papua New Guinea) were found to have similar coral taxonomic composition and species richness, and it was also noted that the spatial differences in community composition within reefs of the same age were greater than between reefs of different ages (Pandolfi, 1996, 1999). In contrast, the lowstand species compositions of the Huon Peninsula reefs look significantly different. This has been ascribed to changes in the relative influence of ecological processes between the highstands and lowstands, or community response to changed environmental conditions (Tager et al., 2010).

2.11 Tectonics

The tectonic history of a region may have a profound influence on the diversity and distribution of modern coral species. This may occur through: subsidence (e.g., Darwin, 1874); folding and faulting
In tectonically unstable regions, coral reefs may suffer repeated environmental perturbations, which can create a variety of coral habitats and high species diversity (Pandolfi, 1992; Veron, 1995; Wilson and Rosen, 1998; Veron et al., 2009). Tectonic uplift (subsidence) can also decrease (increase) the accommodation space available for coral growth (see section 1.1.9). The very high species diversity of the "coral triangle" (a region of the western Pacific stretching from the Philippines to the Solomon Islands in which over 600 species of reef-building coral species have been recorded) is the product of interplay between repeated tectonic and environmental disturbance, and sea-level variations (e.g., Keith et al., 2013). Specifically, proximity of deep refugia and complex island shorelines meant that a diversity of habitats was available for recolonisation, and ensured minimal dislocation during rapid sea-level change, thus forming a geographic location that promotes larval recruitment and favourable environmental conditions (Veron et al., 2009).

Exposure of fossil reef material to enhanced diagenetic effects may occur through tectonic uplift (i.e., exposure of the uplifted coral terrace to percolating waters; e.g., Hamelin et al., 1991, Henderson et al., 1993), with sustained and prolonged uplift further increasing the potential for diagenetic alteration. These diagenetic effects are further discussed below (section 2.12).

### 2.12 Taphonomy and Diagenesis of coral reefs

The fossil record represents past reef communities after significant modifications. The two main issues to be considered are potential non-preservation, and selective removal or alteration of material by physical, chemical, or biological processes.

Reefs are complex systems that comprise primary and secondary growth frameworks, marine cementation, mechanical and biological erosion, and post-depositional diagenesis. Their complex structure may result in differing susceptibility of the coral reef and individuals within the reef to diagenesis, time averaging and transport of material, and the potential for preferential preservation of certain species or adults/size classes within species. For example, dense fine-grained coral skeletons
are most physically durable (Chave, 1962; Brett, 1990), and corals with a branching linear growth form such as *Acropora cervicornis* are more susceptible to storm damage than massive head corals such as *Montastraea annularis* (Scoffin, 1992).

Fossil coral reef frameworks typically comprise *in situ* corals and coral rubble bound by calcareous encrusters and cements. Skeletons are frequently reworked in reef settings, with selective destruction of certain growth forms, individuals and age-classes, as well as a mixing of successive generations (also known as time averaging) (Scoffin, 1992; Pandolfi and Greenstein, 1997a; Greenstein and Pandolfi, 2003). Ecological time averaging is the spatial or temporal mixing of organisms that occupied the same location at different times into a single deposit (Kowalewski and Bambach, 2003; Kidwell and Holland, 2002; Kidwell and Flessa, 1995; Kowalewski 1996). This accumulation and mixing of successive cohorts (Scoffin, 1992; Edinger et al., 2001) directly constrains the temporal resolution achievable from fossil coral reef records, especially given that geological sections rarely provide full 3-dimensional information of coral reef structure.

Moreover, the fossil record may not be a faithful representation of the living coral assemblage (Pandolfi and Michin, 1995; Greenstein and Pandolfi, 2003). For example, rare or slow-growing corals may be under-represented in the fossil record due to dilution by other fast-growing taxa or rubble inherited from the death assemblage. This loss in fidelity was highlighted by comparison of raised Pleistocene reefs with their modern counterparts in Barbados, which indicated that the fossil corals confirmed to be in growth position represented less than a quarter of the primary reef framework visible in their modern equivalents (Stearn et al., 1977; Scoffin et al., 1980).

Finally, post-depositional alteration can significantly alter the chemical characteristics of the fossil coral (e.g. the replacement of aragonite with calcite by subaerial weathering, freshwater leaching or percolation through the reef of waters supersaturated with CaCO$_3$). For example, exposed fossil reefs (e.g., uplifted coral terraces) are prone to diagenesis and loss of sample integrity through contact with meteoric waters. The rate of alteration is dependent upon: the composition of the interstitial waters; the permeability of the framework; and the potential for complex interplay between meteoric, vadose, and phreatic waters with mixing of fresh- and seawater. The latter is governed by *inter alia*: permeability; oxidation of organic matter; and surface and subsurface hydrogeology. These effects are not necessarily confined to exposed corals and long-term submergence is not a guarantee against alteration or dissolution (e.g., Sherman et al., 1999; Montaggioni and Braithwaite, 2009).
### 2.13 Summary and implications

Within coral reefs, the interactions between physical, chemical and biological factors are numerous and complex, which can hinder the identification of straightforward cause and effect relationships. Coupled with the fact that most coral species are generalists (i.e., they can occupy a wide range of diverse habitats and vertical ranges; Veron, 1995), this leads to heterogeneous reef structures and spatial variations in their distribution and composition (Figure 2).

These complications can be compounded in the fossil record, where additional processes (taphonomy and diagenesis, etc.) along with a limited 2-dimensional (section) or 1-dimensional (drill-core) perspective may render physical, chemical, and biological relationships virtually indistinguishable from one another. That is they fail to fully capture the heterogeneous reef structure evident in most modern coral reefs.

When reconstructing past sea levels from fossil coral reefs, the relationship between sample elevation and the position of sea level at the time of growth is a fundamental parameter. Unfortunately, modern ecological studies suggest that there is no direct relationship between coral growth and depth *per se*. Instead, depth can be considered a proxy for a multitude of factors that determine both species diversity and distribution. Sea-level reconstructions commonly also assume that the modern depth distribution is stable/constant through time. Given the spatial and temporal variability evident in modern coral communities, this assumption requires further testing.

### 3. CORAL DISTRIBUTION AND DIVERSITY

Variations in coral communities between different geographic regions (e.g., variations in coral diversity, growth forms, species composition, spatial coverage, etc.) result in local and regional coral-community zonation. These zones result from factors discussed in the preceding sections, which induce variations ‘within species’ (i.e., morphological changes, often in response to environmental gradients and which can lead to the emergence of geographic subspecies), and ‘between species’ (e.g., presence/absence of species, or lack of common species between regions) (Veron, 1995). These variations in coral communities reflect, in the broadest sense: (i) the degree of geographic separation (e.g., the evolutionary history and degree of genetic connectivity, as well as changes in oceanic circulatory regimes, or the degree of dispersal success by coral species); (ii) latitude-correlated environmental changes (e.g., temperature gradients); and (iii) the degree of isolation and size of each distinct region (Veron, 1995). Additionally, the generalist nature of most corals means: (a) that a species commonly found in one type of habitat in one region may be absent from similar habitats in
another, or found in completely different habitats; and/or (b) that species that in one region occupy a wide range of habitats may be confined to just one particular habitat type elsewhere (Veron, 1995).

Attempts to delineate modern faunal distributions (Wallace, 1863; Wells, 1954; Stehli and Wells, 1971; Veron 1993, 1995) have resulted in a variety of biogeographic maps. A recent update of these yields a comprehensive evaluation of species distribution (Veron, 2000; Veron et al., 2009), in which 141 coral ‘ecoregions’ were defined (Figure 3). Below, we discuss relevant aspects for key regions covered by our coral sea-level database.

3.1. Caribbean

In high to moderate wave-energy settings, robust, branching Acropora palmata is the primary framework builder (reef-crest and upper-reef zones), while Acropora cervicornis dominates in more protected environments (fore- and back-reef settings) (Montaggioni and Braithwaite, 2009). The table- and plate-forms of Acropora palmata in the Caribbean are particularly well suited to rapid exploitation of a wide range of environments as growth rate, substrate coverage, and exposure to sunlight are maximised (Veron, 1995). Montastraea annularis is the third of the principal species; it exhibits a high degree of phenotypic plasticity and a wide depth distribution (Knowlton and Jackson, 1994).

The biogeographic distribution of corals in the Caribbean is fairly uniform relative to that in the Indo-Pacific, which may reflect good connections between locations and generally uniform environmental conditions (e.g., generally low terrigenous inputs) (Veron 1995), although local variations are evident in the ecoregions identified by Veron et al. (2009). From comparison with Pleistocene reefs, the structure of Caribbean coral communities appears, in general, to have changed little through the Pliopleistocene (e.g. Budd et al., 1994, 1996; Mesolella, 1967, 1968; Jackson, 1992; Budd, 2000), with only five species becoming extinct in the Caribbean during the past 1.5 million years (Budd et al., 1994).

Notable examples are the once common and widely distributed Pocillopora cf. palmata and Montastraea nancyi. M. nancyi was once as abundant and as widely distributed throughout the Caribbean region as other species of the M. annularis complex for the half a million years before its extinction at ca. 82 ka (Pandolfi et al., 2001; Pandolfi 2007). The general similarity of Caribbean Pleistocene reef communities suggests a degree of community stasis despite repeated sea-level oscillations (Hunter and Jones, 1996; Greenstein et al., 1998a, b; Pandolfi and Jackson, 2007).

3.2. Indo-Pacific
Species diversity is approximately an order of magnitude greater in the Indo-Pacific than in the Caribbean (Veron, 2000). However, reef growth and carbonate production are similar between the two regions (Dullo, 2005), which highlights that diversity is not a control on reef growth. Latitudinal attenuations in species distributions are evident along the coastline of east Africa, both eastern and western Australia, northward along the Japanese coast, and northeast towards Hawaii (Figure 3). In high-latitude areas, species composition is primarily controlled by boundary currents, which determine the thermal regimes and create a ‘one-way genetic connectivity’ with upstream (tropical) communities (Veron, 1995).

Within the Indian Ocean, species diversity is fairly uniform with distinct longitudinal variations only in the eastern Indo-Pacific region. The central equatorial Indo-Pacific exhibits the highest species diversity and has been named the ‘coral triangle’ (605 zooxanthellate coral species, representing approx. 76% of the global complement; Veron et al., 2009). Reasons for this high species diversity include the complex interplay between repeated environmental perturbations, habitat complexity (and assumed evolutionary change) created by the unstable tectonics of the region, and the influence of repeated Pleistocene sea-level changes, as well as patterns of coral larval dispersion and oceanographic regimes (Veron et al., 2009). In contrast, the Hawaiian and far eastern Pacific are somewhat peripheral regions of species diversity. Persistence of taxa and coral community composition also characterise the fossil coral communities of the Pacific (Pandolfi, 1996, 1999; Webster and Davies, 2003). As mentioned in section 2.10, Pandolfi (1996) demonstrated greater diversity within fossil coral sites of the same age from the Huon Peninsula, than between reefs of different ages, which suggests that local environmental conditions exert a greater influence on diversity than differences in global factors such as sea level and atmospheric CO₂ concentrations between successive highstands (Pandolfi, 1999).

4. CORALS AS INDICATORS OF PAST SEA LEVELS

4.1 Objectives

Here, we compile a comprehensive fossil coral database, to facilitate evaluation of the data in a ‘holistic’ manner that spans all major geological and ecological aspects that affect the use of coral benchmarks in studies of past sea level. Thus, the benchmarks possess well-expressed and substantiated uncertainties.

This effort is needed to address current problems within Quaternary science (e.g. the relationship between sea level, ice sheets and changes in climate; the variability, rates and magnitude of sea-level
change; the evidence and implications of a potential two-stage highstand during the last interglacial),
which cannot be thoroughly addressed by looking at a single study, or a handful of studies, in isolation.
Note that when this database is used, the contributions of the original authors should also be given
due credit (e.g., Düsterhus et al., 2016).
Our overall aim is to create one harmonised (i.e., all data treated in a similar way) resource that serves
not only to support sea-level reconstructions, but also highlights the state of the art and the remaining
challenges, and so foster in-depth discussions about strategies to address the challenges. To achieve
this, our specific objectives are:
1. to facilitate assessment of available U-series dated coral sea-level markers within their proper
   uncertainties;
2. to improve and widen access of user groups to the currently available coral data (and sea-
   level reconstructions); and
3. to flag outstanding issues, illustrated with examples.
In order to reconstruct past sea levels using fossils corals, there are four main requirements:
   i) preservation within the fossil record (preferably with stratigraphic and geomorphological
      context);
   ii) determination of the modern elevation of the fossil (including any uplift corrections);
   iii) precise dating of the fossil coral (with due consideration of the diagenetic history of the
      sample); and
   iv) understanding the relationship between the likely position of the fossil and the sea surface at
      the time of its growth (i.e., the palaeo-water depth).
The latter term is critically important for refining sea-level reconstructions, in addition to properly
accounting for all (known) uncertainties. However, the relationship between the modern distribution
of corals and the depths at which they occur is far from straightforward. As seen in section 2, modern
ecological studies suggest that depth by itself exerts little direct control on the distribution of coral
taxa. Instead, other biotic and abiotic factors influence modern coral distributions, and some of these
factors vary with depth. Furthermore, the depth relationships vary spatially, and possibly also
temporally. Nonetheless, information on the depth-distribution of the fossil coral taxa is fundamental
to the calculation of past sea levels and their uncertainties. We therefore identify from modern census
studies the species-level (where possible) depth distributions for use in our sea-level calculations. We
thus assess the available geological data within a well-documented modern biological/ecological
context.

We ensure that all appropriate fields within the database are ‘harmonised’ (i.e., treated the same
throughout), so that they are internally consistent. Examples of such harmonisation are: (1) the single
approach applied to all locations (where possible) for deriving the appropriate regional uplift term
(any exceptions are clearly indicated); and (2) the recalculation of radiometric ages using the same
decay constants for all samples, while also noting the originally determined values in the database.

Although we inspect the degree of coherence in reconstructed sea-level records between sites (within
uncertainties), we refrain from making glacio-isostatic adjustments (this is not a trivial exercise, and is
being addressed in a separate study).

Section 4.2 briefly outlines the main parameters within the fossil coral database. It builds upon the
compilations of Dutton and Lambeck (2012) and Medina-Elizalde (2012), and currently contains
>2,500 data points (a greater than three-fold increase on both compilations) from 37 locations (Figure
4). Data from the sources involved in these previous compilations are incorporated in our database,
but we have recalculated: the ages; corrected coral position \(Z_{cp}\); and the reconstructed relative sea-
level probabilities \(P_{RSL}\) following our harmonisation. Our \(P_{RSL}\) reconstructions include the re-
evaluated taxon-specific habitat-depth distributions from section 4.2.4.

We highlight that comparison of U-Th ages for a given sample between the three databases (i.e.,
Dutton and Lambeck, 2012; Medina-Elizade, 2012; this study) may reveal some age differences. Also,
ages in the databases may not be the same as those originally reported in the primary source. These
discrepancies arise for two reasons: (1) the use of different decay constants for \(^{230}\text{Th}\) and \(^{234}\text{U}\); and (2)
the consideration (or lack thereof) of the method of spike calibration during recalculation of the ages.

Differences between this study and the Dutton and Lambeck (2012) compilation can be attributed
solely to the current application of updated decay constants for \(^{230}\text{Th}\) and \(^{234}\text{U}\) by Cheng et al. (2013)
versus previous use of earlier decay constants after Cheng et al. (2000). The difference in absolute
value of these decay constants is very small and in many cases has a negligible effect on age, but the
precision is greatly improved in the most recent generation of decay constants (Cheng et al., 2013).

Differences between the Medina-Elizade (2012) and Dutton and Lambeck (2012) compilations arise
because the method of spike calibration was not considered by Medina-Elizade (2012). This has an
effect on isotope activity ratios, and hence calculated age, when a gravimetric standard was used to
calibrate the isotopic spike. Our recalculated ages also include the decay constant error within the final age uncertainty.

As a rule, we use only published information to compile our database (to date, only data published prior to January 2014 are included). We include only information readily available within the published literature and include the following studies within the database: Andersen et al., 2008, 2010a,b; Ayling et al., 2006; Bard et al., 1990a, b, c, 1996a, b, 2010; Blanchon and Eisenhauer, 2001; Blanchon et al., 2002, 2009; Bruckner and Radtke, 1989; Cabioch et al., 2003, 2008; Camoin et al., 1997, 2001, 2004; Chappell et al., 1996; Chen et al., 1991; Chiu et al., 2005; Cobb et al., 2003a; Collins et al., 2003, 2006; Colonna et al., 1996; Coyne et al., 2006; Cutler et al., 2003, 2004; Delanghe et al., 2002; Deschamps et al., 2012; Dia et al., 1992, 1997; Edwards et al., 1987b, 1993, 1997; Eisenhauer et al., 1993, 1996; Esat and Yokoyama, 2006; Esat et al., 1999; Fairbanks et al., 2005; Frank et al., 2006; Frujtier et al., 2000; Galewsky et al., 1996; Gallup et al., 1994, 2002; Grün et al., 1992; Hamelin et al., 1991; Hearty et al., 1999, 2002, 2007; Israelson and Wohlfarth, 1999; Kennedy et al., 2012; Ludwig et al., 1996; McCulloch and Mortimer, 2008; McMurtry et al., 2010; Montaggioni and Hoang, 1988; Muhs et al., 2002a,b, 2006, 2011, 2012a,b; Multer et al., 2002; Nunn et al., 2002; O’Leary et al., 2008a,b, 2013; Peltier and Fairbanks, 2006; Pirazzoli et al., 1993; Potter et al., 2004; Riker-Coleman et al., 2006; Schellmann et al., 2004; Scholz et al., 2009; Sherman et al., 1999; Speed and Cheng, 2004; Stein et al., 1993; Stirling, 1996; Stirling et al., 1995, 1998, 2001; Sun et al., 2005; Szabo et al., 1994; Thomas et al., 2009, 2012; Thompson and Goldstein, 2005; Thompson et al., 2003, 2011; Toscano and Lundberg, 1999; Toscano et al., 2012; Vezina et al., 1999; Walter et al., 2000; White et al., 2001; Yokoyama et al., 2001; Zazo et al., 2007; Zhao and Yu, 2002; Zhu et al., 1993.

Most of the data within our fossil coral database are from the last deglacial interval (~20%) and the last interglacial (~30%). Obtaining reliable age determinations becomes increasingly difficult the further back in time, due to the lack of well-preserved specimens and the influence of diagenetic processes. Theoretically, the U-Th method enables age determinations of up to ~600 ka but in practice there are few coral data older than about 200 ka. Improvements in analytical techniques (in particular the increased precision and accuracy offered by TIMS and MC-ICP-MS techniques over α-counting techniques) have enabled local sea-level reconstructions on millennial rather than just orbital timescales. Uncertainties increase with increasing age, so that in older periods, millennial-scale sea-level reconstructions are not possible for comparison with those of the last deglaciation. However, the older data remain valuable, for example, for the distinction of older interglacial periods.
This presents a first step toward a comprehensive database of all coral U-Th data generated on mass spectrometers (excluding alpha-counting data) that both legacy data and future data can be added to. Alpha analyses tend to have larger uncertainties and are not included in the current version of the database but are nonetheless valuable and will be incorporated into future versions. The database presented here incorporates all available metadata (e.g., contextual information on geomorphology, taxonomy and stratigraphy of the sample) to enable users to assess the reliability of each sample for reconstructing past sea level. In section 4.3, we evaluate some of the major implications of the collated information in more detail.

4.2 Principal database parameters

4.2.1 Sample identifiers and location

Each data point has been assigned a unique identifier within the database, along with the original sample identifier by which it was first published. Sample locations are as originally reported, with the proviso that many of the original publications lack detailed sample location information so that latitude and longitude are estimated.

4.2.2 Tectonic setting (and uplift/subsidence rate)

We initially intended to find independent estimates of uplift/subsidence rates for each location that requires a tectonic correction. Unfortunately, it was not possible to obtain such independent estimates for the vast majority of sites. One way to perform this correction would be to obtain a GIA prediction of relative sea level at each site in the database for the LIG and use this value in combination with the age and elevation of peak sea level for each site to calculate an uplift rate (e.g., Creveling et al., 2015). In the absence of GIA modelling in this paper, we use a simple approach using the age and elevation of the LIG terrace, which is less desirable as it is both circular and it ignores that geographic variability in sea level that is due, in part, to GIA effects. We recalculated all regional uplift/subsidence rates using the maximum elevation given for the LIG terrace at each site, and assuming a LIG sea level of 6.6 ± 2 m (Kopp et al., 2009, 2013) and an age of 125 ± 5 ka (equation 1). Where no elevation was given for a regional last interglacial terrace, we have used uplift rates as presented in the original publication (while ensuring that a consistent value is used for all data from such a site) (Table 1). We calculate uplift rates (in m/ka) as follows:

\[
\frac{\Delta H}{\Delta t} = \frac{H_{\text{loc}, \text{LIG}} - H_{\text{LIG}}}{t_{\text{LIG}}}
\]

(Equation 1)

where
\[ H_{\text{LocLIG}} = \text{maximum elevation of the local LIG terrace (in m, relative to modern sea level; + is above modern sea level)}; \]

\[ H_{\text{LIG}} = 6.6 \pm 2 \text{ m (Kopp et al., 2009, 2013); and} \]

\[ t_{\text{LIG}} = 125 \pm 5 \text{ ka.} \]

This approach assumes that uplift/subsidence has been linear through time, although we recognise that this assumption may not hold for all locations or time periods (cf. Schellman and Radtke, 2004).

Additionally, although internally consistent, our procedure remains open to considerable uncertainties (cf. Creveling et al., 2015) and introduces additional uncertainties to any sea level reconstruction. It does, however, enable a first-order estimation of sea-level but it is an unsatisfactory approach for studies that wish to precisely constrain the position of sea levels through time. Little or no independent information exists to verify the uplift/subsidence rates – this remains one of the most important parameters to require further attention.

4.2.3 Sample elevation and stratigraphic context

We record the method that was used to determine the present elevation of the sample (GPS, levelling, or interpolation from map contours), and assign elevation uncertainty where none was specified in the original publication; for example, all drill-core samples are assigned a 1 m elevation uncertainty. We could not correct elevations to any specific datum (e.g., mean high water) because there commonly is insufficient information to do so (i.e., no information on the datum relative to which elevation was measured). Also, we could not (yet) confidently determine past tidal ranges at each location. To date, only few models offer estimates of local or regional variations in palaeo-tidal range (e.g., Hinton 1996; Uehara et al., 2006; Hill et al., 2011). Instead, we provide (modern) indicative ranges (Table 2) from a global tidal model.

Geological and geomorphological context details were obtained from source publications, when reported (e.g., facies information, details of whether the sample is in situ or displaced, etc.). Terrace designation is that of the original authors (where reported) with any subsequent reanalysis or change in accepted local nomenclature also noted. Incorporating these metadata allows assessment of the stratigraphic integrity of sample series. For example, it allows evaluation of whether sample ages obtained from within a stratigraphic unit are consistent with each other (including data from multiple studies). However, note that – unlike sediment layers – coral reefs grow in 3-dimensions, so that a prograding reef may contain a wide range of ages along the same elevation (or terrace). Such age structure has been reported, for example, for Holocene growth on the Great Barrier Reef (Marshall
and Davies, 1982). The implication is that data should not be rejected where multiple ages are observed for a single elevation. Likewise, age inversions that are identified on the basis of age and elevation data alone should not be rejected out of hand because such relationships may be entirely consistent with 3-dimensional development of the reef.

4.2.4 Taxonomic identification and depth distribution

The identification of coral is as given in the original papers; identification to species level is available in ~60 % of the total fossil data, while ~34 % is identified to genus level only, and 6 % is unidentified. Many previous studies tended to assume a 6 m depth habitat for many species (e.g., Lighty et al., 1982; Toscano and Macintyre, 2003; Gischler and Hudson, 2004; Peltier and Fairbanks, 2006; Medina-Elizalde, 2012). Some studies use a local modern analogue (i.e., incorporating the characteristics of the modern coral assemblage at a site) to constrain the depth preference of fossil corals (e.g., Montaggioni et al., 1997; Cabioch et al., 1999, Webster et al., 2009; Deschamps et al., 2012). Apart from such local studies, however, there is sparse published research on the direct relationship between coral distribution and depth. As discussed in section 2, corals are “depth-generalists”, with most species occurring within very shallow waters down to depths of as much as 40 m (Carpenter et al., 2008). Other controls such as temperature, salinity, nutrients, predation, and local environmental and substrate conditions, were found to exert a greater influence on the depth limit of species than irradiance levels or depth per se (section 2). In addition, depth zonations for coral taxa are less well defined in the Indo-Pacific than in the Caribbean (Woodroffe and Webster, 2014). In the Indo-Pacific, coral assemblages and associated coralline algae assemblages may give better indicators of depth (Pandolfi, 1996; Montaggioni and Braithwaite, 2009).

It is therefore difficult to justify a blanket assumption that past sea level stood 6 m above the elevation of the coral for all taxa at all locations. This is reflected in the increasing use of coral or coral/coralline-algal assemblages (cf. Cabioch et al., 1999; Pandolfi and Jackson, 2001; Webster and Davies, 2003; Webster et al., 2004; Abbey et al., 2011; Deschamps et al., 2012) to refine depth relationships.

Here we use data from modern ecological studies to assign modern depth relationships to each fossil coral sample identified to genus or species level. Specifically, we use information from the Ocean Biogeographical Information System (OBIS) (OBIS, 2014; a full list of extracted data and references can be found in online supplementary material) and assign a median depth habitat and uncertainties based on the modern depth distributions of each genus and species, respectively. The modern
ecological data within OBIS are derived from credible and authoritative biological research initiatives and have passed internal quality control measures prior to release (e.g., verification of species name). The database contains over 700 datasets and more than 22 million records of marine life. For this study, we have extracted only coral depth data for species currently included in the fossil sea-level database (the exercise may be expanded for any new species added to the reconstructions). The modern studies include information from both shallow and deep (diver/automated underwater vehicle) surveys, often spanning several years.

We use only direct observations with a vertical precision ≤0.25 m in our analyses. Examples of the modern depth distributions of the main coral taxa used in sea-level reconstructions are given in Figure 5. The depth distributions are clearly variable, and tend toward skewed distributions (i.e., a long tail to greater depths). There are significant differences between species, with some resembling a lognormal distribution while others exhibit bi- or multi-modal distributions (e.g., *Montastraea annularis*). For each species, we derive an estimate of the median water depth in which the species lives using all locations available. We have chosen the median rather than the mean because the depth distributions are not Gaussian or symmetrical (Figure 5), and because the mean is more sensitive to outliers. The lower and upper bounds of the 95 and 68 % confidence intervals were also determined using the 2.5, 97.5, 16 and 84 percentiles, respectively (Table 3, depth distributions can be found in the online supplementary material).

For some species, no or very limited observational data were available. In these instances, we have used the genus relationship (e.g., *Acropora danai*, *Favia speciosa*, *Pocillopora guadalupensis*) (marked with an asterisk in Table 3). However, the number of fossil corals from these groups is small in our database. We highlight in Table 3 those depth relationships that are based on relatively few (<300) observations (e.g., *Alveopora* sp., *Gardinerosis planulata*), and we recommend increased caution when using these in sea-level reconstructions. For *Oculina* sp. and *Oulophyllia* sp., there were insufficient observational data to determine a robust depth relationship (33 and 183 observations, respectively). In these two instances only, we relaxed the acceptable depth precision of the modern observations to ≤ 5 m and included data derived from museum specimens (this increased the number of data to 287 and 240 for *Oculina* sp. and *Oulophyllia* sp., respectively). There are no direct observations and only few museum specimens available for the solitary coral *Balanophyllia elegans* (n = 88) and we therefore use data from the study of Gerrodette (1979) for this species. It should be noted that most *B. elegans* specimens are from Californian emerged, erosional terraces (e.g. Muhs et al., 2002b, 2006, 2012b) and are are not in growth position, which results in spurious relationships
between fossil elevation and former sea levels (and so this depth distribution is not use in our
reconstructions). The authors use shoreline angles etc. to constrain the vertical position of past sea
levels for these locations (see sections 5.1.2 and 5.3.1 for further discussion).

Using our synthesis of modern, ecologically derived, and species-specific depth distributions, we have
evaluated the relationship between each modern coral taxon and its modern habitat-depth
distribution. For example, species of the genus Acropora have been observed in water depths ranging
from 0 to -91 m: A. cytherea was observed at a depth of -91 m in the Pacific (CRED Rapid Ecological
Assessments of Coral Population in the Pacific Ocean 2007-2010) and down to depths of -55 to -60 m
on the Great Barrier Reef (Bridge et al., 2012; Abbey et al., 2013). Our analysis suggests that most
(95% probability) Acropora sp. live between -0.5 and -16.4 m (Figure 5, Table 3). Within the genus,
Acropora cervicornis has a wider depth range (-0.2 to -48 m) (Figure 5, Table 3): it was observed at -
48 m in Puerto Rico (La Parguera, Puerto Rico Benthic Composition and Monitoring Data, 2002 -
Present); at -35 m in St Croix (St. Croix, USVI Benthic Composition and Monitoring Data, 2002 - Present)
and at -21 m in Cuba (Atlantic and Gulf Rapid Reef Assessment – Benthic; Marks, 2007). Acropora
palmata is generally found between -0.35 and -9.4 meters water depth (95 % confidence limits)
(Figure 5, Table 3)), with a maximum observed depth of -22 m at St Croix, US Virgin Islands (St. Croix,
USVI Benthic Composition and Monitoring Data, 2002 - Present), but this increases to a maximum of
-41 m at this location if we allow depth precision of the observations ≥0.25 m (St. Croix, USVI Benthic
Composition and Monitoring Data, 2002 - Present). This accords with the compilation in Lighty et al.
(1982), which suggested a narrow range of <-1 m to -5 m for this species in the Caribbean (note that
most studies used in Lighty et al. (1982) occurred prior to the advent of routine deep-water surveys),
and with the range of -0.1 to -40 m from the more recent IUCN Red List (Carpenter et al., 2008) (Table
3). Comparisons of our depth relationships with previous assessments (e.g., Carpenter et al., 2008;
Bridge et al., 2013) are shown in Figure 6 and Table 3.

Most of the depth distributions (this study and Carpenter et al., 2008, Figures 5 and 6, Table 3)
corroborate the “depth generalist” tendency of most coral species, with the majority confined to the
upper ~20 m water depth, and a few species extending to depths of >50 m (e.g., Siderastrea radians).
This has implications for the sea-level precision achievable from fossil corals. For example, use of a
fossil Acropora palmata sample, which has a vertical range of ~ 9 m (95% probability range from -0.4
to -9.4 m, median depth of -1.5 m), will result in smaller uncertainties than use of Montastraea
annularis, which has a ~16 m range (95% range from -1.1 to -17 m, median depth -9.7 m). This is not
a new finding, but it is here more precisely quantified by synthesis of the – as yet – most complete
biological/ecological database. Also, our synthesis emphasises that depth ranges are much wider and more complex than commonly assumed in fossil coral-based sea-level studies.

Some species are not well constrained by modern observations (e.g. Oculina sp.) and caution should be used when using these corals for sea level reconstructions. Oculina includes both zooxanthellate and azooxanthellate species, but the two groups are not morphologically distinct (Veron, 1995). Three species of Oculina are considered to be facultative symbiont bearers (Cairns, 1999). In Florida, Oculina reefs have been identified at depths of -50 to -60 m (Reed, 2002, 2006) and O. varicosa was observed at -50 to -152 m (Reed, 1980, 2006). On the Flower Garden Banks (Gulf of Mexico), O. diffusa has been observed at -95 m (Sammarco et al., 2014). The present lack of depth constraints for this species (given its wide depth distribution), in conjunction with the lack of distinguishable morphological feature for the facultative species (Veron, 1995), implies that Oculina is unsuitable for precise relative sea level (RSL) reconstructions from fossil corals.

Our synthesis gives a ‘maximum’ species depth preference that applies when considering points without further context; the vertical uncertainties may be reduced where stratigraphic, geomorphic, or other biological information exists. For example, a fossil coral sample that can be firmly associated with reef crest facies will have a much narrower vertical range than a coral of the same species without a reef facies context. Unfortunately, records within our modern synthesis (and many fossil records) have not differentiated between the different reef environments/facies.

Starting from section 4.3, we apply the new depth-distributions and their uncertainties in sea-level reconstructions. This includes further assessment of habitat-depth complexities, in particular the substantial habitat-depth differences that appear to exist within single taxa on a variety of local (reef), regional, and inter-oceanic scales. Prior to such applications, however, we must highlight some caveats to our assessment of habitat-depth preferences. First, the information is limited to regions where modern ecological surveys have been undertaken, and which have been included in the OBIS database. Second, we are constrained by survey-methodologies included in the OBIS database, many of which remain strongly focussed on the uppermost water column. Third, there are limited observations in OBIS for some species (for example, there are no observations of the solitary coral Balanophyllia elegans within the OBIS database, although it is an important species in fossil studies, represented by 274 samples in our database, although the majority of these are not in growth position, see section 5.1.2 for further discussion of the utility of these fossils for sea level reconstructions). Finally, we note that results may be refined as further information becomes available.
in OBIS, or through the addition of other studies, but care must be taken to avoid duplication when combining other studies along with the OBIS compilation, as that would bias the statistics.

4.2.5 Sample age

Comprehensive reviews of U-Th dating systematics in corals are available elsewhere (Edwards et al., 2003a; Stirling and Andersen, 2009; Dutton, 2015). All U-Th geochemical data reported in the initial publications are included in the database, including $^{238}\text{U}$ and $^{232}\text{Th}$ concentrations, $^{230}\text{Th}/^{232}\text{Th}$ activity or atomic ratios, and activity ratios of $^{230}\text{Th}/^{238}\text{U}$ (or $^{230}\text{Th}/^{234}\text{U}$) and $^{234}\text{U}/^{238}\text{U}$. Uncertainties are included where possible. We record the instrument used for analysis, decay constants used, and method of spike calibration. Where available, we also note the calcite content and the methodology used for this determination. Wherever possible, missing data not included in the initial publications were obtained from the original authors.

Activity ratios were recalculated using the Cheng et al. (2013) decay constants for $^{234}\text{U}$ and $^{230}\text{Th}$ in cases where we were able to establish that the spike was calibrated gravimetrically. All ages and initial $\delta^{234}\text{U}$ values were recalculated using Isoplot version 3.5 (Ludwig, 2003) assuming closed-system behaviour and using the decay constants of Cheng et al. (2013). The reported uncertainties include the error associated with the decay constants.

$$1 - \left[\frac{^{230}\text{Th}/^{238}\text{U}}{^{238}\text{U}}\right]_{\text{act}} = e^{-\lambda_{230}T} - \left(\frac{\delta^{234}\text{U}(\text{meas})}{1000}\right) \left(\frac{\lambda_{230}}{\lambda_{230} - \lambda_{234}}\right) \left(1 - e^{(\delta^{234}\text{U} - \lambda_{230})T}\right)$$

(Equation 2)

where

$\left[\frac{^{230}\text{Th}/^{238}\text{U}}{^{238}\text{U}}\right]_{\text{act}}$ is the $^{230}\text{Th}/^{238}\text{U}$ activity ratio;

$\lambda_{238}$, $\lambda_{234}$, $\lambda_{230}$ are the decay constants of $^{238}\text{U}$, $^{234}\text{U}$ and $^{230}\text{Th}$ respectively (Cheng et al., 2000, 2013);

$\delta^{234}\text{U}(\text{meas})$ is the measured value of the activity ratio of $^{234}\text{U}/^{238}\text{U}$ relative to secular equilibrium in per mille ($\delta^{234}\text{U} = (\frac{^{234}\text{U}}{^{238}\text{U}} - 1) \times 1000$); and

$T$ is the age of the sample in years.

The initial value of $^{234}\text{U}$ at the time that the coral grew is calculated by:

$$\delta^{234}\text{U}_{\text{initial}} = (\delta^{234}\text{U}_{\text{measured}}) e^{(\lambda_{234}T)}$$

(Equation 3)
We include ages reported in the original sources for comparison, as well as the originally reported isotope ratios and associated geochemical data, to enable users to perform their own calculations, if desired. The potential for open-system behaviour (i.e., remobilisation of nuclides) is recognised as a major limitation of the U-series dating method with the accuracy of ages limited to a greater degree by diagenetic effects than by analytical precision (Bard et al., 1992; Stirling et al., 1995). The potential for open-system behaviour increases with age (e.g., with exposure), but has been recognised even in younger samples that appear to be well preserved at the macro- and micro-scopic level (e.g. Henderson et al., 1993; Andersen et al., 2008). Diagenetic alteration may be episodic or occur over a prolonged period; it can occur upon deposition or at some interval later (e.g. upon exposure) with potentially multiple and differing modes of alteration (post-depositional gain and/or loss of U and or Th) even within the same fossil coral (e.g., Scholz et al., 2009) (Figure 7).

Methods have been proposed to correct for open-system behaviour (e.g., Thompson et al., 2003; Vilmant and Feuillet, 2003; Scholz et al., 2004). However, there is debate within the community regarding how and when such models may be appropriately applied to fossil coral U-Th data (e.g., Stirling and Andersen, 2009). The ages listed in the database are all closed-system ages. However, some of these corals have experienced open-system behaviour of the U and/or Th isotopes. To detect and remove samples which have been altered, a variety of screening criteria can be used (Section 5). The disadvantage of screening out these altered data is that it produces a much smaller pool of samples from which to make interpretations. Another approach would be to evaluate the open-system behaviour of corals study by study (site by site) and use an open-system model such as that of Thompson et al. (2003) to make corrections to a subset of the data in cases where it is appropriate.

There are at least two pre-requisites to applying an open-system model to correct U-Th ages (Dutton, 2015). The first of these is whether the coral(s) have been modified in a way that is consistent with the geochemical array predicted by the the open-system model (compare diagenetic trends in Thompson et al., 2011 with Scholz et al., 2009). If subsamples of the coral or multiple corals from the same outcrop display an array of $^{230}$Th-$^{234}$U-$^{238}$U compositions that are consistent with the pattern predicted by the open-system model, this would provide some justification for an open-system modelling approach. In contrast, applications of the model to isolated data points (e.g., single analyses of corals or where the digenetic pattern has not been established) are dubious and become misleading for corals that have been altered along a different diagenetic pathway. The second pre-requisite is that the initial value of seawater $\delta^{234}$U is known (for the time when the coral grew); as this seawater
value is an input parameter that defines the point at which the model ‘stops’ and calculates an age, the accuracy of the seawater value will directly translate into the accuracy of the interpreted age.

In reality, determining whether application of an open-system model is even more complicated. For example, there are cases where the geochemical array of data produced be comparing the U and Th isotope compositions between coral heads follows the slope predicted by an alpha-recoil mechanism such as that of the Thompson et al. (2003) model, but the array of subsamples within each coral does not (e.g., Thompson et al., 2011). It is not clear that averaging the subsamples from each coral and then applying the model is appropriate if each individual data subsample has been affected differently. Also, rates and mechanisms of open-system alteration will be a function of climate hydrology, lithology, taxon (and related porosity and thickness of skeletal elements), as well as other site- or sample-specific factors. The overall implication is that a one-size-fits all open-system model is unlikely to capture all the observed modes of open system alteration in corals. For this reason, we explicitly discourage any attempt to apply an open-system model to the database as a whole.

4.2.6 Reconstructed sea level and uncertainties

In the above, we ensured consistency of the four principal parameters by: (1) assigning appropriate uncertainties to the modern elevation of each sample; (2) applying empirically derived species-specific depth-distributions and their associated uncertainties (note, we use only the taxon-specific depth-distributions not palaeo-water depths derived from, for example, assemblage information); (3) determining uplift/subsidence rates for each geographical region using the same assumptions; and (4) recalculated all ages using the same procedure and decay constants. This allows us to recalculate both a corrected coral position ($Z_{cp}$) and past sea levels with full consideration of the associated uncertainties.

In order to reconstruct past sea levels, we must consider the relationship between the position of the coral and the position of sea level at the time of coral growth. Without this, we only have a (tectonically) corrected coral position ($Z_{cp}$) and associated uncertainties.

$$Z_{cp} = H_{sam} - (\Delta H/\Delta t)*t_{sam}$$

(Equation 4)

where

$Z_{cp}$ is corrected coral position (in m, negative values are below sea level);
$H_{sam}$ is the modern elevation of the sample (in m, positive is above and negative values are below sea level);

$\Delta H/\Delta t$ is the recalculated (equation 1) uplift/subsidence rate (in m/ka, increasing positive ages in kilo-years before present); and

$t_{sam}$ is the recalculated conventional age of the sample (in ka, increasing positive ages in kilo-years before present).

To reconstruct past sea level, we must also consider the relationship between the position of the coral and the position of sea level at the time of coral growth (i.e., where the coral was living the the water column). In order to do this, we need to change the frame of reference from mean sea level (i.e. the modern elevation at which the coral is measured with respect to mean sea level) to the position of the fossil coral (i.e., we know the present elevation of the coral but want to determine past sea levels) (Figure 8). For example, a living *Acropora palmata* coral occurs at a depth of -1.5 m below present mean sea level (i.e., we know the depth of the coral relative to sea level), so that sea level is +1.5 m above the position of the coral. In the fossil record, we know the elevation of the coral (corrected for any tectonic change), but we do not know the position of sea level at the time of its growth. Instead we can reconstruct the probability of sea level at the time the coral was living ($P_{RSL}$) by assuming that the coral occurs at the median depth (i.e., that the elevation of the coral, $Z_{cp}$, occurs at the median of the modern depth distribution) and combining the corrected coral position ($Z_{cp}$) uncertainties with the inverted depth probability distribution (Figure 8). We combine these using a Monte Carlo approach of 350,000 simulations to derive a probability maximum ($P_{RSL}$) associated with each coral position ($Z_{cp}$) and an uncertainty distribution around that point. For each coral, we obtain a set of randomly sampled values from the corrected coral position ($Z_{cp}$) uncertainty, and a set of randomly sampled values from the modern taxon depth distribution and sum across the two errors. For each individual coral, we then have multiple instances across a combined error distribution. From this set we can generate the probability distribution, and extract a probability maximum and the (usually asymmetrical) associated 1-, 2- and 3- sigma equivalent levels (68%, 95%, and 99% probability intervals).

The result is a probability distribution of relative sea level ($P_{RSL}$) for each coral, which represents the local sea level position and comprises both a eustatic and local glacio-isostatic component. As we include a more comprehensive suite of input uncertainties (most notably the depth-distribution ranges as derived from modern studies), our new $P_{RSL}$ calculations come with increased total vertical uncertainties relative to those in previous compilations (cf. Dutton and Lambeck 2012; Medina-Elizalde 2012). Our calculation of $P_{RSL}$ results in a probability distribution of past sea level (through
which a line can be drawn); this is in contrast to all previous calculations where the depth-distribution
term was not included (i.e., the output was in terms of tectonically corrected elevations, and the
position of former sea levels was estimated to be above these).

The inclusion of detailed metadata in our database allows users to assess for themselves the ‘most
reliable’ age determination and sea-level reconstructions. It also facilitates an assessment of the
available U-series dated corals within both their geological and ecological settings, and a first order
assessment of the degree of coherence of reconstructed sea levels within a site, as well as between
sites. Again, we emphasise that we have not incorporated GIA-corrections (e.g., Farrell and Clark,
1976; Milne and Mitrovica, 1998; Lambeck and Chappell, 2001; Mitrovica and Milne, 2003; Peltier,
2004) in the database. This means that the data should not be expected to directly overlap, since GIA
effects will cause site-specific sea-level data to depart from the eustatic signal. In the remainder of
this paper, we briefly explore the general features of RSL variations in the database, and assess its
utility for interrogating data relative to one another to highlight some outstanding (and solvable)
limitations to sea-level reconstructions.

5. INTERPRETATION AND SCREENING OF DATA

Obtaining a reliable and precise RSL reconstruction from the numerous fossil samples requires choices
by the user (i.e. what screening criteria are most appropriate to the question they wish to investigate).
For example, for regional RSL it may be more appropriate to use regional subsets rather than the
global dataset (and there will also be fewer GIA concerns), whereas a global dataset is needed for
eustatic sea level (ESL) estimation, where GIA corrections become more important. Other
considerations include: how well constrained the tectonic history of a site is; the sensitivity of sites,
especially in the near-field, to glacio-isostatic processes (with uncertainties); the reliability of age
determinations; how well constrained the modern coral depth-distribution is for the location(s)
studied; and whether metadata such as facies or stratigraphic constraints can inform screening
choices. The following section outlines such criteria and their impacts upon the data.

5.1. Location: tectonic and depositional setting

5.1.1 Tectonic setting and uplift rate constraints

In regions of high uplift/subsidence, the record of changing sea levels becomes expanded in the
vertical, which facilitates high-resolution studies. On stable margins, no correction for uplift is
required, but stable margins present a superimposition of successive sea level variations and coastal
processes (e.g. erosion and post-depositional diagenesis) that complicates interpretation.
The tectonic setting of many sites is complex and often imperfectly described. For example, the islands of Vanuatu are the product of island-arc volcanism with a complex uplift history. Tasmaloum has experienced subsidence (~4mm/yr for ~220 to 130 ka) followed by uplift (3 mm/yr), while Urelapa has been uplifting at a mean rate of 1.9 mm/yr since 130 ka (Taylor et al., 2005 and references therein). These phases of uplift and subsidence have been attributed to pinning of submarine features during subduction (Taylor et al., 2005). Similarly, Barbados (where 85% of the island is covered by a Pleistocene coral reef limestone cap) evolved as an accretionary prism. Anticline warping and episodic uplift (i.e., non-uniform rates of uplift) have been documented (e.g. Donovan and Harper, 2005), leading to locally different uplift rates (Schellmann and Radtke, 2004; Radtke and Schellmann, 2006). Any such uncertainties in our (and all preceding) assumptions for calculating uplift rates for the various locations would lead to vertical inaccuracies in RSL. Complex tectonic histories are not limited to uplifting or subsiding sites; tectonic warping has been documented for the Perth and Carnarvon Basins of Western Australia (e.g. Hocking et al., 1987; Whitney and Hengesh, 2015). Coseismic events (e.g. Ota et al., 1993; Ota and Chappell 1996; Tudhope et al., 2000; Sieh et al., 2008) are also problematic for palaeo-RSL reconstructions.

One distinct advantage afforded by sites that are rapidly uplifting or subsiding is that the spacing and ages of individual terraces may provide the potential to identify short-term sea-level oscillations that are not well-expressed on stable coastlines due to overprinting and lack of accommodation space. Unfortunately, tectonically affected sites are not well suited for reconstructing the absolute position of sea level in the past. Due to a lack of independent estimates of uplift/subsidence, we have recalculated rates using the highest elevation of the regional LIG terrace and assumed LIG age and eustatic sea level values (equation 1). Although this offers a consistent application of uplift/subsidence rates for each site, it remains distinctly unsatisfactory: the values for both the age and LIG eustatic component are ill defined (and most likely incorrect), partly due to spatial and temporal variability between sites arising from site-specific GIA effects. Additionally, there is an inherent circularity to using the elevation of the LIG corals to determine an uplift rate that is subsequently used to calculate \( P_{RSL} \). The advantage of this approach is that it allows for an approximation of relative sea-level changes from tectonically affected sites, though the uncertainty may be significantly larger than quoted in the database. In addition, the pragmatic but unlikely assumption that uplift/subsidence rates were constant through time (cf. Schellmann and Radtke, 2004; Taylor et al., 2005; Radtke and Schellmann, 2006) further complicates any tectonic correction required for reconstructing past sea levels (Creveling et al., 2015). Clearly there is an urgent need for independent verification of
uplift/subsidence rates, especially because age determinations and their uncertainties interact with uplift/subsidence rates and their uncertainties, to produce complex RSL reconstructions.

5.1.2 Constructional versus erosional marine terraces

Fossil corals contained within emergent, primarily erosional, marine terraces have been used to provide information on past sea levels. These environments, such as the coasts of California (e.g., Muhs et al., 2006, 2012), Bermuda (e.g., Vacher and Hearty, 1989; Ludwig et al., 1996; Muhs et al., 2002a; Rowe and Bristow, 2015), Japan (e.g., Radtke et al., 1996), and the Mediterranean region (e.g., Brancaccio et al., 1978; Poole et al., 1990; Leeder et al., 2003; Muhs et al., 2014, 2015), are generally high energy environments and, in contrast to many constructional reefs, the terraces are formed by erosional processes. The fossils within these deposits are generally poorly sorted and are rarely in growth position; consequently they cannot, in themselves, provide information on past sea levels. Rather, they provide information on the age of the deposit, and past environmental conditions (i.e. from their faunal composition). Former sea levels can be reconstructed from these environments only with additional information, such as the elevation of the terrace shoreline angle or other such feature, where a sound relationship to sea level can be established. Where no such information is available, the corrected elevation ($Z_{cp}$) of the fossil provides a minimum estimate of former sea levels (i.e., sea level must have been at, or above $Z_{cp}$).

Constructional and abrasional terraces may both be present in the landscape. For example, Speed and Cheng (2004) emphasised the role of marine erosion in the deposition of carbonates in Barbados. In Japan, emerged marine terraces were found to be of both erosive and biological construction (Ota et al., 1983). In Hawaii, Muhs et al (2002a) highlight that for some locations, reef facies are absent and replaced by coral-basalt conglomerate resting on shore platforms cut into Tertiary basalt. Hence, thorough and complete documentation of the sample context is essential in establishing the fidelity of the fossil record for reconstructing past sea levels.

Emerged marine terraces of California

In California, flights of emerged marine terraces are preserved (e.g., Alexander, 1953, Vedder and Norris, 1963), documenting past sea levels superimposed on tectonic uplift. These erosional landforms develop in high energy environments and usually retain a veneer of marine sands and gravels that often contains molluscs and solitary corals (e.g. *Balanophyllia elegans*), which can be used to date the deposit (and constrain the timing of past sea level fluctuations; e.g., Muhs and Szabo, 1982; Stein et al., 1991; Muhs et al., 1994, 2002a, 2012). These fossil corals cannot be used to reconstruct sea levels.
as few, if any, remain in growth position, so that the relationship between coral elevation and sea level is ‘lost’. Instead, the elevation of past sea levels can be derived from the elevation of shoreline angles, or other such geomorphological features (e.g. Muhs et al., 2012b).

**Emerged marine deposits of Bermuda**

The surficial deposits of Bermuda consist of Quaternary carbonates, mostly eolianite with isolated sublittoral marine and beach deposits (e.g., Vacher et al., 1989). Hermatypic corals are presently found, due to the influence of the Gulf Stream, but only limited emergent fossil patch reefs have been documented (e.g., Harmon et al., 1983) and “their existence has subsequently been difficult to verify” (Rowe et al., 2014). The higher than present fossil corals contained in the marine littoral deposits from the high energy, south shore environment (e.g., Fort St Catherine) sparked considerable debate regarding the processes governing their formation, with implications for their utility for reconstructing former sea levels. Both storm processes (e.g., Harmon et al., 1983) and higher than present sea levels (e.g., Vacher and Hearty, 1989; Ludwig et al., 1996) have been invoked. The first naturally renders these fossils unusable for reconstructing past sea levels. The relatively few, *in situ* patch reefs and lack of in growth position fossils coupled with the modern high energy environment suggest that the poorly sorted marine fossils of Bermudan sublittoral deposits are useful for temporal constraints and palaeozoogeography, but less useful for reconstructing sea levels. However, additional geomorphological evidence (tidal notches, shoreline angles etc.) with a clear relationship to sea level, would enable past sea levels to be reconstructed. In the absence of such a clear relationship between the fossil/feature and sea level, the information remains limited.

5.2 Determining reliable ages – chemical screening

The effect of diagenesis can be significant, resulting in erroneous age and hence, RSL reconstructions. There are several screening criteria often applied to identify corals that have been geochemically altered and to additionally identify those that suffer from contaminating effects of detrital Th ($^{232}$Th).

Geochemical alteration, also referred to in the U-series literature as open-system behaviour, can be recognised by: (1) conversion of coralline aragonite to calcite; (2) anomalous $^{238}$U concentration (or other trace elements that indicate partial conversion to calcite such as Sr/Ca or Mg/Ca ratios), and; (3) $^{234}$U$_{initial}$ which is back-calculated from the measured $^{234}$U ratio and the age of the coral to determine the $^{234}$U value of the coral at the time it grew (Equation 3). Anomalous $^{230}$Th concentrations may also be an indicator of open-system behaviour; expected $^{230}$Th concentrations are a function of prior knowledge of age of the sample, and; Th is less mobile in oxidising solutions such as groundwater or seawater, so is considered unlikely to experience significant loss or gain in the way
that the more soluble U may behave. To monitor for the contaminating effects of initial $^{230}$Th in the coral, $^{232}$Th concentration is also typically measured when U-series measurements are made. Pa-Th dating is another cross-check that can be used to determine the age of the coral, but is less commonly applied owing to the more difficult laboratory procedures involved. Here we explore the basis for each of these criteria and discuss issues involved with applying them to a dataset. We also refer the reader to several in-depth reviews of the systematics of U-series dating of corals (Edwards et al., 2003a; Edwards et al., 2003b; Stirling and Andersen, 2009; Dutton, 2015).

5.2.1 Mineralogy

Coralline aragonite is metastable and hence prone to conversion to calcite over time. This conversion will be a function of the water/rock ratio, the porosity of the coral taxa, temperature, exposure history, as well as other factors. During conversion to calcite, some of the primary U-Th geochemistry may be altered. For this reason, it is good practice to screen all coral samples for even trace amounts of calcite that may bias the calculated U-Th age of a sample. Recently, X-ray diffraction (XRD) techniques have been applied with increasing resolution and detection limits for trace amounts of calcite (e.g., Sepulchre et al., 2009) to screen corals prior to radiometric dating. Calcite conversion is also associated with changes in Sr/Ca (lower) and Mg/Ca (higher) (e.g., McGregor and Gagan, 2003) but has been less commonly applied to screen corals prior to U-series measurements.

5.2.2. Anomalous $^{238}$U concentration

The measured concentration of uranium ($[^{238}U]$) in a fossil can be used as an additional age reliability screening criterion (cf. Broecker and Thuber, 1965; Thompson et al., 2003; Scholz and Mangini, 2006). In principle, the addition/loss of uranium since the time of formation may be detected by comparing the concentration of uranium in a fossil coral to its modern counterpart (i.e., if there has been no addition/loss of uranium, then the uranium concentration of the fossil should be similar to that in modern corals of the same species). In modern corals, the concentration of uranium is species dependent (e.g., Cross and Cross, 1983) and its distribution is heterogeneous within the coral skeletal structure (e.g., Schroeder et al., 1970; Robinson et al., 2006). The incorporation of uranium into the skeleton may also vary seasonally as U/Ca is correlated with sea surface temperatures. For example, concentrations of uranium within a single coral can vary by around 20 % (e.g., Shen and Dunbar, 1995; Min et al., 1995). $^{238}$U concentration is routinely measured during U-series measurements, but this parameter is not always used for screening purposes. There are relatively few studies that report the uranium concentration of modern corals (data for modern and young (<1 ka) fossil corals is compiled in Table 4). We recommend the use of modern uranium concentration data as an additional screening
criterion, although we recognise that the data on modern corals is limited at present and should be addressed by the community.

5.2.3. Initial uranium isotope composition ($\delta^{234}U_{\text{initial}}$)

Corals are thought to precipitate their skeletons with no fractionation of $^{234}$U relative to $^{238}$U, and hence should record the same $\delta^{234}$U value as that of ambient seawater at the time of growth (e.g., Edwards et al., 2003a). In contrast, corals that have behaved as open-systems tend to display elevated values of $\delta^{234}$U and anomalously old ages (e.g., Bard et al., 1991, Hamelin et al., 1991, Henderson et al., 1993). This pattern was systematically described by Gallup et al. (1994), although other forms of open-system behaviour may produce different geochemical arrays and even anomalously low $\delta^{234}$U values (see discussion in Stirling and Andersen, 2009). Laser ablation mass spectrometry methods are showing promise as a rapid, first indicator of open system behaviour (as the $\delta^{234}U_{\text{initial}}$ of a sample may be determined rapidly, Spooner et al., 2016). However, the precision and accuracy of this method are currently lower than for conventional TIMS or MC-ICPMS methods, (e.g., Eggins et al., 2005; Hoffmann et al., 2009; McGregor et al., 2011).

As seawater $\delta^{234}$U ($\sim$147 ‰) was thought to be homogenous in the open ocean and relatively invariant across the timescales relevant to U-series dating, the $\delta^{234}U_{\text{initial}}$ value of corals became widely used as a screening parameter to reject altered corals if the value was significantly different from that of modern seawater. We note that the accepted value for seawater $\delta^{234}$U has been revised several times, in part related to the revision of the decay constant of $^{234}$U (Cheng et al., 2000; Cheng et al., 2013). The most recent, and most precise, determination of seawater $\delta^{234}$U was performed by Andersen et al. (2010b), who reported a seawater value of 146.8 ± 0.1 ‰ (2σ). As these data were calculated relative to a secular equilibrium standard, the seawater $\delta^{234}$U does not need to be revised, despite subsequent revision of the $^{234}$U decay constant (Cheng et al., 2013). Using this benchmark, coral U-series data are often screened for compliance with a $\delta^{234}U_{\text{initial}}$ value of 147 ‰ (i.e. within the range of values consistent with modern seawater and living corals), though the tolerance for the magnitude of departure from the seawater value varies between publications.

One potential complication of this approach is the assumption that seawater composition has remained the same over the last several 100,000 years. It has been proposed that seawater $\delta^{234}$U may vary on glacial-interglacial timescales (on the order of $\sim$10-15 ‰, Henderson, 2002; Robinson et al., 2004; Esat and Yokoyama, 2006), with lower than modern values (by 7 to 10 ‰) during the last glacial (Cutler et al., 2004; Esat and Yokoyama, 2006; Durand et al., 2013) meaning that screening of corals
using a narrow range around modern seawater may reject some high quality data, if seawater $\delta^{234}$U has indeed varied in the past. On the other hand, using a range that is too wide will increase the inclusion of altered samples that will bias the analysis. One option is to use a scheme similar to that developed by the radiocarbon IntCal working group, which has defined a seawater $\delta^{234}$U screening value for the last glacial period that is lower (142 ± 8‰, Reimer et al., 2013) and use a value more similar to the modern value of 147‰ for the interglacial periods. If $\delta^{234}$U has varied on glacial-interglacial timescales, it would be inappropriate to apply a constant value for screening the data if the seawater composition is temporally variable. Unfortunately, the precise evolution of seawater $\delta^{234}$U and the magnitude of the possible changes are still debated, making it difficult to derive a robust screening approach that would capture such variability.

5.2.4. Detrital Th ($^{232}$Th)

The use of detrital Th as a screening criterion relies on the fact that $^{232}$Th is virtually absent from seawater, but is sometimes found in very small concentrations within coral skeletons during growth if there is detrital contamination (Edwards et al., 1987; Chen et al., 1991). As all isotopes of Th have identical chemical properties, if $^{232}$Th is present, then some amount of $^{230}$Th is likely to have also been introduced. The amount of this $^{230}$Th contamination is a function both of the concentration of $^{232}$Th and the $^{230}$Th/$^{232}$Th composition of the contaminating source. This allows an assessment of the initial $^{230}$Th of the sample, as the assumption of ingrowth of $^{230}$Th is the basis for the U-Th dating method. Most modern corals have low to negligible initial $^{230}$Th concentrations (e.g., Edwards et al., 1987; Cobb et al., 2003a) although values up to ~7 ppb have been reported for modern corals from the Bahamas (Robinson et al., 2004) and Sumatra (Zachariasen et al., 1999). During diagenesis, voids within the coral skeleton may be filled with detrital material, thereby adding extraneous $^{230}$Th, $^{234}$U, $^{238}$U and $^{232}$Th to the coral system.

Initial $^{230}$Th can have a significant effect on the age determination of young corals, but less impact on samples older than a few thousand years. For example, coral samples with a $^{232}$Th concentration of 1 ppb (and assuming a bulk crustal value for $^{230}$Th/$^{232}$Th of 2.0 x $10^{-5}$) would require an adjustment of up to ~40 years, which is significant for very young corals, but only a <1% error for a 5,000-year old coral (Cobb et al., 2003a). In previous studies, low $^{232}$Th concentrations such as <2 ppb is considered acceptable (cf. Dutton and Lambeck, 2012) due to the relatively small error this introduces when dating corals older than a few thousand years. The $^{232}$Th concentration, however, is not always reported so this criterion cannot always be applied. We note that it is preferable to use the $^{230}$Th/$^{232}$Th activity ratio, as this parameter can be better applied to screen out samples with $^{232}$Th contamination.
where the influence of this contamination is effectively scaled to its age (the $^{230}$Th activity). In this way, corals with a similar $^{230}$Th/$^{232}$Th activity ratio can be considered to have a more comparable influence on the age of the sample, even across a dataset with corals that have a wide range of ages. This parameter, however, is even less frequently reported than $^{232}$Th. In our compiled database, we have back-calculated the $^{230}$Th/$^{232}$Th activity ratio wherever possible so that this parameter can be used to screen for detrital Th contamination in the future instead of $^{232}$Th concentration. As this parameter is not reported as often (<25% of samples in the database report this parameter whereas ~87% of samples have reported $^{232}$Th concentration), a well-defined, accepted value to use for screening the corals is currently lacking. However, we note that lower values of $^{230}$Th/$^{232}$Th represent more significant age biases introduced by detrital Th contamination.

5.2.5. Pa-Th dating

Another method for detection of post-depositional alteration combines U-Th dating with $^{231}$Pa/$^{235}$U dating, which is based on the decay of $^{235}$U to $^{231}$Pa assuming, (i) the initial $^{231}$Pa/$^{235}$U ratio is zero and, (ii) that the changes in the $^{231}$Pa/$^{235}$U ratio occurs only through radioactive ingrowth and decay. If the system has remained closed since the time of formation, combining $^{231}$Pa/$^{235}$U and U-Th methods, the ages obtained by each technique should agree within analytical precision (as both methods rely upon the assumption of changes in the ratio results only from radioactive ingrowth and decay). In addition, using concordia plots enables some constraints on the nature of diagenetic process and the possibility of obtaining the ‘true’ age (e.g., Rosholt, 1967; Szabo and Vedder, 1971; Edwards et al., 1997; Gallup et al., 2002; Cutler et al., 2003). The combination of the two methods is perhaps the most robust method for assessing if the system has remained closed since the time of formation. However, practically, the $^{233}$Pa spike required for $^{231}$Pa/$^{235}$U dating is more difficult to handle and to calibrate.

5.2.6 Implications of chemical screening choice

Although these screening criteria may successfully remove a subset of altered samples from further consideration, the signature of carbonate diagenesis may be subtle and not fully captured by this approach. In particular, the $\delta^{234}$U$_{initial}$ value appears to be a more sensitive indicator of open-system behaviour than X-ray diffraction assessments of mineralogy (% calcite) or other geochemical indicators of carbonate diagenesis. As such, this parameter has been heavily relied upon to screen out altered coral samples. However, corals may undergo subtle diagenetic alteration that results in erroneous ages without apparent disturbance to the $\delta^{234}$U$_{initial}$ ratio, or undergo variable degrees of alteration (causing shifts to both lower and higher $\delta^{234}$U$_{initial}$ within the same sample; Henderson et al., 1993, Scholz et al., 2009).
The choice of screening criteria has a large effect upon the number of samples available for further analysis (Dutton and Lambeck, 2012; Medina-Elizalde, 2012) (Figure 9). Placing tight limits on the acceptable $\delta^{234}\text{U}_{\text{initial}}$ values is effective only if there is sufficient precision in the measurement of $\delta^{234}\text{U}$. Modern corals display some variability around the mean open-ocean seawater value, so that overly tight screening may reject high-quality data. In addition, if seawater $\delta^{234}\text{U}$ has varied through time, use of a constant range of ‘acceptable’ values may exclude samples that are ‘reliable’ (i.e., have not experienced open system behaviour or post depositional diagenesis).

Hence, screening data will successfully remove some, but not all, of the altered samples. This is where additional criteria can help, such as reproducibility of measurements for corals that have been measured multiple times or stratigraphic relationships that can be used to evaluate relative ages (see discussion in Dutton, 2015). Users of the database may assess the data with respect to the replication of analyses within a coral, where replicate analyses that are consistent in terms of both their calculated age and their calculated $\delta^{234}\text{U}_{\text{initial}}$ values are considered most reliable.

### 5.2.7. Replicate age determinations

Ages that have been affected by open-system remobilisation of U and/or Th isotopes can have a significant impact on subsequent sea-level reconstructions. For example, a large proportion of the Scholz et al. (2009) report data from Barbados based on multiple dates from the same coral specimen, as well as from multiple short cores in close proximity to one another from the same stratigraphic unit. The authors demonstrate the effects of U-redistribution within these samples, even though they would pass a screening criteria of $\delta^{234}\text{U}_{\text{initial}}$ within 5‰ of modern, ≤2% calcite and $^{232}\text{Th}$ concentrations ≤2 ppb and similar screening criteria employed by Dutton and Lambeck (2012) and Medina-Elizalde (2012). Of the 54 samples dated in this study, 15 would even pass a stricter criteria ($\delta^{234}\text{U}_{\text{initial}} = 147 \pm 1$‰ and ≤2% calcite), and these samples also have $^{232}\text{Th}$ concentrations <2 ppb, similar to those found in some modern corals; cf. Chen et al., 1986; Muhs et al., 2002a; Robinson et al., 2004; Stirling and Andersen, 2009). The screened data appear as a linear trend in the reconstructed Barbados P$_{\text{RSL}}$ record (Figure 10), even though all are from the same stratigraphic unit, the Last Interglacial/Rendezvous Hill Terrace (some separated by only 30 cm). The expectation would be that ages for each coral from within this single unit (and especially the replicates of single coral specimens) yield closely replicating U-Th ages and hence a close cluster of tectonically corrected coral positions ($Z_{\text{cp}}$) after multiplication with the site’s uplift rate. However, the samples instead show a spread of ages, which through multiplication with the site’s uplift rate result in a linear trend of tectonically
corrected coral positions ($Z_{cp}$) (Equation 4). Averaging all the measurements for one coral head would be one way to overcome this, but is not warranted if the initial measurements are not within analytical error of each other. Another reason that averaging the data is not recommended is that the average of a diagenetic trend may represent the average composition of alteration whereas one end member is more likely to be a better indication of the primary geochemistry.

Where many replicates are available, outlier analysis can be undertaken and an average age provided (e.g., ADU-3, xA4-2 and BB02-5-1; Figure 10). Unfortunately, this is not an appropriate procedure for most of the replicate analyses in the database, especially when only a few ‘survive’ the initial geochemical screening (only a few repeat analyses are consistent i.e., with some overlap of their 2σ ranges). Where only two replicates pass the initial screening, both should be excluded if age and $\delta^{234}U_{\text{initial}}$ are inconsistent (at a 4σ distance) because one, or both, of the ages are clearly incorrect but we cannot determine which one. Further refinements of past sea-level records from fossil corals may be achieved through agreement on a statistically sound method for dealing with replicates to reduce the instances of several (different) $P_{\text{RSI}}$ values for the same sample, and eliminate the spurious linear trends from the plots. Clearly, meticulous inclusion of contextual metadata is essential.

5.2.8 Example of chemical screening approach

Here we introduce an example application of how the database can be screened, as described in the following, but emphasise that this is an example only and that there are multiple ways to screen the data as previously discussed. The data were screened for reliability using the commonly applied $\delta^{234}U_{\text{initial}}$, % calcite, and $^{232}$Th concentration criteria. As noted previously, it would be preferable to also include a screening criterion for $^{238}$U concentration, which may be a tractable solution for a site-specific study with a limited number of taxa with known modern $^{238}$U baselines, but was not feasible in this example. We do not exclude data from our analysis on the basis of $^{238}$U, rather we highlight (circled in the figures) samples that have uranium concentrations outside the modern range of modern corals of the three genera with the most modern $[^{238}\text{U}]$ determinations: 2 to 4 ppm for Acropora sp., 2 to 3.5 ppm for Montastraea sp. and, 2 to 4 ppm for Porites sp. As previously mentioned, use of the $^{230}\text{Th}/^{232}\text{Th}$ activity ratio is probably preferable to use of the $^{232}\text{Th}$ concentration, which is now possible using the back-calculated $^{230}\text{Th}/^{232}\text{Th}$ values provided in the database. We opted to use three different $\delta^{234}U_{\text{initial}}$ screening criteria to account for the possibility of variations in seawater composition on glacial-interglacial timescales. For interglacials, we use the modern $\delta^{234}U_{\text{initial}}$ value of 147 ± 5 ‰, and for glacial intervals we follow the IntCal Working Group (Reimer et al., 2013) recommendation of $\delta^{234}U_{\text{initial}}$ values of 142 ± 8 ‰. The IntCal Working Group (Reimer et al., 2013) use this lower value for
samples older than 17 ka but do not define an older age limit (because the radiocarbon timescale does not extend past the last glacial period). We use the LR04 (Lisiecki and Raymo, 2005) age of the transition from Marine Isotope Stage (MIS) 5 to MIS 4 (71 ka) as the transition between glacial and interglacial screening criteria (i.e. between 71 and 130 ka, a screening criterion of $147 \pm 5 \%$ is used).

For samples older than 130 ka (age of the transition from MIS 6 to 5 defined in LR04; Lisiecki and Raymo, 2005), we use a value of $147 +5/-10 \%$ in order to account for possible variations in seawater (Figure 9).

Further to this, we opted to exclude data with a reported calcite percentage $>2 \%$ or when this information has not been reported. This particular cut off has been used is some previous studies either due to detection limits (where % <2 could not be evaluated) or because more outliers appear when values above 2% are used. In theory, there is no percentage of calcite that is “ideal”. The effect of recrystallization on the age will depend on many site-specific factors, including the age of the coral, so a 5 % calcite coral may have an age that is as robust as a 1 % coral at another location. We also chose to exclude data where the $^{232}\text{Th}$ concentration is $>2 \text{ppb}$ or where this has not been reported.

Despite these screening criteria, we emphasise that multiple diagenetic episodes, such as the exposure of uplifted reef terraces to meteoric waters (with potentially varying effects; i.e., the addition or loss of nuclides) may not necessarily be recognisable using the $\delta^{234}U \text{ initial}$ and percentage calcite screening criteria (Scholz et al., 2009). We have used our screening criteria in such a way as to retain samples with most likely reliable ages, while also retaining a reasonable number of samples for further analysis; this resulted in a 70 % reduction in the number of samples relative to the full database.

After screening ($\delta^{234}U \text{ initial}, \text{calcite} \leq 2 \%, ^{232}\text{Th concentration} \leq 2 \text{ppb}$) ~750 samples remain from the original database (for which we can calculate $Z_{\text{cp}}$ and $P_{\text{RSL}}$) representing 31 locations, both near-field sites (proximal to former ice sheets, where influence of glacio-isostatic adjustment (GIA) processes on RSL records is large) and far-field sites (far from former ice sheets and where GIA influences are smaller): Bahamas (Chen et al., 1991); Barbados (Edwards et al., 1987; Gallup et al., 1994, 2002; Cutler et al., 2003; Thompson et al., 2003; Bard et al., 1990a,b,c; Hamelin et al., 1991; Blanchon and Eisenhauer, 2001; Peltier and Fairbanks, 2006; Fairbanks et al., 2005; Potter et al., 2004; Scholz et al., 2009; Andersen et al., 2010a); Bermuda (Ludwig et al., 1996; Muhs et al., 2002a); southern China (Zhao and Yu, 2002); Comoro Islands (Camoin et al., 2004); Curacao (Muhs et al., 2012a); Mururoa atoll, French Polynesia (Camoin et al., 2001); Tahiti (Thomas et al., 2009; Yokoyama et al., 2001; Deschamps et al., 2012; Bard et al., 1996b); Haiti (Bard et al., 1990a); Sumba Island, Indonesia (Bard et al., 1996a);
Madagascar (Camoin et al., 2004); Yucatan Peninsula (Blanchon et al., 2009); Huon Peninsula, Papua New Guinea (Yokoyama et al., 2001; Esat and Yokoyama, 2006; Cutler et al., 2004; Bard et al., 1996b; Cutler et al., 2003; Stein et al., 1993); Henderson Island (Pitcairn Islands) (Anderson et al., 2010; Stirling et al., 2001); Seychelles (Israelson and Wohlforth, 1999; Camoin et al., 2004); Hawaii (Muhs et al., 2002; Szabo et al., 1994); Vanuatu (Edwards et al., 1987b; Taylor et al., 1985; Cutler et al., 2004); and Western Australia (Stirling et al., 1995, 1998, 2001; Zhu et al., 1993; Eisenhauer et al., 1996; O’Leary et al., 2008; Collins et al., 2006) (Figure 11). Only these data are used in subsequent analyses. Most data are concentrated within the last deglacial and the LIG periods, with relatively few samples older than >200 ka passing our screening (note that the choice of screening criteria has a dramatic influence upon the number of samples available for subsequent analysis, Figure 9).

5.2.9. Overview of reconstructed sea levels using screened data

Despite some degree of scatter in the data, the various records provide, in general, a consistent (i.e., within 95% bounds of one another) picture of sea level during the last deglacial and interglacial periods (see also, for subsets of the data: Stanford et al., 2011; Medina-Elizalde, 2012; Dutton and Lambeck, 2012) (Figure 11). The principal difference between our compilation and previous efforts is the greater vertical uncertainty associated with the sea-level reconstructions, which in our case are based on a synthesis of extensive modern ecological surveys.

While there is general agreement between \( P_{RSL} \) records from the various sites, some significant differences are also evident. For example, data from the far-field site Mururoa atoll (French Polynesia; Camoin et al., 2001) between \(~15.5\) and \(18\) ka appear ‘anomalously’ low, relative to other records for this interval, although the youngest Mururoa samples overlap with the Tahiti dataset within their respective vertical uncertainties (Figure 11). The \( P_{RSL} \) values from both Vanuatu and Tahiti agree well (within uncertainties) with \( P_{RSL} \) values from Barbados in this time interval even without incorporating corrections for GIA effects at each site. These differences will reflect in part GIA influences (cf., Dutton and Lambeck, 2012), but the magnitude of the observed differences (Figure 11) is often greater than the size (and uncertainty) of typical GIA corrections (Figure 12). Figure 12 was generated using a version of the ICE-5G ice history (Peltier, 2004) extended to cover two glacial cycles with a 4 ka duration interglacial at near present day ice volume, and a VM2-like earth model. We model sea level in multiple locations using a GIA model based on principles detailed in Kendall et al., (2005), which incorporate variations in sea-level resulting from changes to the Earth’s rotation vector, and time dependent shorelines. These are plotted with reference to a global mean sea level. These should not
be interpreted as "the" glacial isostatic correction for these points in time, but they serve to illustrate the variability in local relative sea levels that is possible.

For the Holocene, values of $P_{\text{RSL}}$ sit a few metres (+1.5 for Western Australia and +0.7 m for New Caledonia) above 0 m (Figure 11). This can be accounted for by: (i) the tidal component of RSL at each location - as the modern elevation of the sample was measured to mean sea level (see Table 2 for estimated ranges for these sites) - and; (ii) glacio-isostatic processes (where the correction is on the order of 1 to 2 m).

A striking difference between the corrected coral position ($Z_{\text{cp}}$) and our reconstructed sea level probabilities are the large vertical uncertainties associated with the latter (compare Figures 11a, c with Figures 11b, d). The majority of this vertical uncertainty derives from our updated taxon-specific depth distributions.

Aside from habitat-depth uncertainties and GIA effects, vertical uncertainties and differences in RSL reconstructions between sites may result from an incomplete understanding of influences such as local and regional tectonic histories, and from insufficient application of contextual information from geology, stratigraphy, and geomorphology. There also remain considerable dating uncertainties in many cases, and these affect $Z_{\text{cp}}$ and $P_{\text{RSL}}$ through interaction with uplift/subsidence rates. Important improvements in the vertical resolution of sea-level reconstructions may be achieved by comprehensively addressing these issues. The following sections use examples from the database to illustrate the extent and importance of these issues.

5.3. Stratigraphic and sedimentological constraints

In addition to age, the facies and stratigraphic context of samples provides vital information for RSL assessments. Our fossil coral database incorporates fields that indicate whether the original authors assessed the sample to be in growth position and/or in situ. Coral fragments and rubble are included in the database and can provide bounding ages on deposits but unlike the in situ samples, they are not, in themselves, reliable indicators for past sea level. Regardless, they can provide valuable information where additional, complementary data, such as the elevation of shoreline angle associated with these deposits is available (section 5.1.2). Stratigraphic constraints can also help reduce the vertical uncertainty that applies to sea-level trends reconstructed for sites that are stratigraphically coherent (section 5.2.4).
5.3.1. In situ samples

A simple means for refining RSL records could be to include only in situ or in growth data. Classically, in situ relates to material found in the geological unit in which they formed or were deposited whereas in growth means that the fossil coral as remained in the same position as it was in life. An in growth designation means the fossil coral is in situ but in situ does not necessarily mean that the fossil is in growth position. For reefs, these are complicated issues. Reefs are complex structures that comprise both primary growth frameworks and coral rubble, with variable degrees of reworking (section 2.12). Ascertaining if a fossil coral remained in the same position as at the time of growth (e.g., by a lack of severe surface abrasion/rounding; orientation of well-preserved corallites; orientation of branches; orientation of encrusting algae on the upper surface of the coral; geopetals or other ‘way up’ structures) is key for establishing if a faithful record of elevation has been retained, which is required for reconstructing Zcp and PRSL. However, in some erosional settings/high wave energy settings such as the marine terraces of California and Bermuda, fossil corals rarely remain in life or growth position but they are still in situ, i.e., they are found within the unit formed at the time of their growth and death. The nature of these deposits renders the fossil coral elevation unreliable and additional sources of information are needed to reconstruct past sea levels (section 5.1.2), but as they are in situ, ages derived from these fossils provide temporal constraints. In growth position designation therefore provides further clarification on the stratigraphic integrity of the fossil coral. It should be noted that this distinction is not always made the literature (in situ and in growth position have been used interchangeably). Within the database, we have noted both in situ and in growth position designations and, for primarily constructional reef environments, assumed that these are synonymous (note, a sample is labelled as in situ or in growth only where this was explicitly stated by the original authors).

5.3.2. Samples from the reef crest (or close to)

Some studies explicitly state that they targeted (close to) the reef crest during sampling (e.g. Dodge et al., 1983; Chen et al., 1991; Gallup et al., 1994; Potter et al., 2004. However, in some cases apparent contradictions between the reconstructed coral position (Zcp) and this stratigraphic constraint are evident. For example, reef-crest samples from Barbados of similar age have Zcp values (coloured symbols; Figure 13a) that are separated vertically by approximately 30 m at ~104 ka. The samples concern different taxa; those with Zcp of -15 to -23 m are A. palmata, except for one Montastraea sp. sample. The samples at -43 to -53 m are Montastraea sp., which has a much wider modern depth distribution than A. palmata. Interestingly, the samples have overlapping reconstructed PRSL values (within uncertainty) (Figure 13b). This suggests that: (i) the Montastraea sp. samples were misdiagnosed as reef crest, given that identification was to genus level only, and that no other
assemblage information was given; (ii) there is an artefact due to reef heterogeneity; (iii) the samples are not in situ (only the A. palmata samples from Barbados were confidently determined as in situ by the original authors); (iv) the ages of the samples are incorrect, which results in erroneous reconstructions due to the age-dependent uplift correction; or (v) a combination of some or all of these.

5.3.3. Other stratigraphic constraints: Drill cores and vertically coherent sections

Vertically coherent stratigraphic sequences (e.g. sections, vertical transects or drill cores) allow the age-elevation relationship of a set of samples to be interrogated. For example, one can test whether, for the same stratigraphic unit, all ages and reconstructed sea levels are consistent. However, note that ages from a single stratigraphic unit may reflect variability within the reef structure as well as changes in prevailing environmental (including sea-level) conditions. Coral reefs do not grow as continuous horizontal layers; they have 3-dimensional structures. Hence, a given elevation is not indicative of a certain age. Caution is therefore needed, as reversals in the age-depth relationships may occur due to: (i) erroneous age determinations; (ii) inherent complexity of a reef structure and the multitude of factors influencing coral zonation and formation; (iii) taphonomic processes (e.g. vertical/time averaging etc.; section 2.12); or (iv) a combination of some or all of these. In summary, age reversals within a core do not invalidate the data, because of the 3-dimensional structure of reefs. Hence, age-elevation relationships can only be used where there is evidence that one coral nucleated directly on top of another.

Several key RSL records were obtained by drilling (e.g., Barbados: Bard et al., 1990a, c; Fairbanks et al., 2005; Peltier and Fairbanks, 2006; Chiu et al., 2005. Tahiti: Bard et al., 1990b, 2010; Thomas et al., 2009, 2012; Deschamps et al., 2012) and the inherent stratigraphic constraints offer valuable information for refining RSL records. However, while drill cores provide useful stratigraphic ordering, they may lack other contextual information. For example, it may be difficult to assess if the samples are in situ in growth position, and the restricted dimensions of cores can also make palaeo-assemblage and facies description more difficult. In addition, there are potential difficulties in resolving notoriously complex reef structures using drill cores (and even using 2-dimensional sections), particularly when drilling is at an angle, or where backstepping reef architecture dominates.

Stratigraphic information has the potential to provide valuable constraints on the vertical uncertainties associated with reconstructed $P_{RSL}$, especially in a relative sense between consecutive samples. The stochastic component of the $P_{RSL}$ uncertainty, in particular the depth-distributions, can
be modified by such contextual constraints. Unfortunately, information on the stratigraphic ordering of samples is not available for all samples (and all sites), and – as yet – inclusion and subsequent modification of the vertical error terms would therefore introduce undue bias between the various sites in the database. We invite authors to submit to us scans of contextual field notes for inclusion into the database.

As yet, drill-core results offer the best examples of stratigraphic constraints to larger numbers of samples. For the last deglaciation, a large proportion of the data derives from Barbados and Tahiti drill cores. When identified by core, the Barbados data (Figure 14) are remarkably consistent both within each core and between cores, and a coherent temporal evolution is evident. For Tahiti, the P<sub>RSL</sub> records are highly consistent within cores between 14 and 9 ka (cores P6 to P9, Figure 15). For the older portion of the Tahiti records, some discrepancies appear between the various cores, but robust P<sub>RSL</sub> inflections seem to be visible in the sequences of several cores between 16 and 14 ka. Offsets between the different cores reflect changes in assemblages and the depth-distributions of the various taxa (Deschamps et al., 2012). Discrepancies may also have arisen from variable hydrodynamic and oceanographic conditions between the southwestern and northeastern sides of the island, due to different levels of turbidity and seawater chemistry) (Abbey et al., 2011), and/or progressive flooding of the shelf and increasing accommodation space (i.e. the sequential drowning of corals in cores from the outer to the inner reefs) (Camoin et al., 2012). Figure 15(c) reveals a ‘line’ of maximum probability, and a ‘ghost maximum’ above it. This ‘ghost’ is directly caused by the use of many observations that are identified only to the genus-level, which leads to bimodal habitat-depth distributions. For the Tahiti data presented here, detailed coral assemblage information is available, which allowed the authors to provide a palaeowater depth estimates based on modern analogues (resulting in uncertainties that are much smaller than those plotted here). This example is intended only to show the result of using depth distributions strictly limited to taxonomic identification of the coral (without consideration of assemblage or stratigraphic information), which in some cases is only to the genus level. This example is not intended to be a new reinterpretation of the Tahiti dataset.

Identification of corals to species level as well as inclusion of site-specific depth-distributions (e.g. from modern assemblage studies) would help to reduce uncertainties around the main reconstructed level. Where possible, P<sub>RSL</sub> reconstructions need to include not only the data and uncertainties, but also the more qualitative of contextual constraints. Going forward, statistical treatment of the data will also need to deal with such more qualitative knowledge.
5.4 Palaeodepth

The vertical resolution and precision achievable in determining past relative sea level from fossil corals depends upon several conditions. Foremost among these is the need for identification to species level and the application of appropriate depth-habitat ranges. For example, the median depth of growth for a taxon with genus-only identification is inevitably a reflection of many different species (e.g. *Acropora* sp. has a median depth of -2.4 m, whilst *A. palmata* and *A. cervicornis* have median depths of -1.5 m and -4.6 m respectively). Similarly, at the genus level, the total depth-distribution incorporates species with narrow and large depth ranges (e.g. *Acropora* sp. has a depth range of 0 to -18 m, whilst *A. palmata* and *A. humulis* have ranges of -0.4 to -9.4 m and 0 to -40 m respectively).

Hence, using habitat-depth data for exactly the right species will increase both accuracy and precision of the calculated RSL.

Additional constraints to the depth-habitat values used can come from modern assemblage analogues that can be derived, for example: from the composition and vertical zonation of corals, corals and coralline algae (coralgal associations), and foraminifera; or from the presence/absence of indicator taxa (for example, vermetid gastropods: Morton and Chalis, 1969; Safriel, 1974; Antonioli et al., 1999; Cabioch et al., 1999; Schiaparelli et al., 2008). It requires an adequate assemblage description of the fossil record, which may be difficult given sampling constraints, such as drill cores, or limited exposures. Unfortunately, relatively few studies in the database undertook a local, modern assemblage survey at their study location but some considered palaeo-depth of samples by applying local and/or regional (i.e., from the same ocean basin) modern analogues to their palaeo-assemblage, zonation, or species (e.g. Bard et al., 1996b, 2010; Yokoyama et al., 2001; Deschamps et al., 2012).

Given the current paucity of local modern analogue studies, we have adopted a uniform approach of describing the depth-distribution of the commonly used taxa from a synthesis of modern data (OBIS, 2014; for a full list of extracted data and references, see online supplementary material). As noted in section 4.2.4, there are gaps in the spatial coverage (e.g., Western Australia) and possibly also with depth due to methodological limitations and focus on the upper water column. As yet, this precludes the incorporation of the well-documented variations in coral composition and distribution both within and between ocean basins (see section 5.3.2), as well as variations on local scales that arise from differences in sediment load, temperature, etc. However, as further modern ecological information becomes available, our ‘global’ depth-distributions will likely change, and regional and/or local depth ranges will eventually become available for all sites and species found in the fossil database. Of course, the use of local, modern assemblage data is preferable, as these generally best describe the modern
vertical zonation of the reef under consideration. One caveat to this is recent human influence; in Barbados the modern fringing reefs (Tomascik and Sander, 1987) are dominated by *Porites astreoides*, with very little *Acropora palmata* cover (<1%), even though branching *Acropora* corals dominated the tropical western Atlantic for the last 500 ka (Geister, 1977; Pandolfi and Jackson, 2006). Recent human influence has changed the coral community structure of Barbados reefs in ways that have not been observed in the last ~ 200 ka (Pandolfi and Jackson, 2006).

In the following sections we consider examples of how our ecologically derived depth-distributions compare with those accounting for assemblage information, and how this may offer improvements to RSL calculations.

5.4.1. Comparison of the ecologically derived depth distributions with assemblage palaeo-depths:

*A. palmata* is the most frequent taxon within the fossil database (accounting for ~20% of all samples). This species is highly characteristic of reef environments in the Caribbean with a common depth range of -0.5 to -5 m (Goreau and Wells, 1967; Lighty et al., 1982), but it is also found at depths up to -40 m (Carpenter et al., 2008). Our synthesis of ecological (depth) data gives similar values with 68% of OBIS observational data (OBIS, 2014) between -0.7 and -3 m (95% between -0.4 and -9.4 m) (Figure 5a). The increase in the reported vertical range of *A. palmata* between older surveys and more recent work reflects methodological developments, with ROV and diving improvements extending depths at which observations have been made.

For *Porites* sp., our synthesis of depth distributions indicates that most specimens are found in the uppermost water column (Figure 5) but that there is a significant proportion of observations at depth as well (median depth -4 m; 68% between 0 and -45 m, 95% between 0 and -71 m). Carpenter et al (2008) give a range of 0 to -50 m, but the depth range of some species remains unknown. Studies within the fossil database report a variety of palaeodepths for this genus, including: < 5 m (Comoro Islands; Camoin et al., 2004); 0 to -35 m (with ‘most likely’ 0 to -20 m, Mururoa Atoll; Camoin et al., 2001); >-20 m, 0 to -25 m and 0 to -6 m depending upon assemblage (Tahiti: Thomas et al., 2009, with palaeodepths derived from Montaggioni, 2005); -2 to -5 m, or 0 to -15 m (Huon Peninsula: Chappell et al., 1996; Yokoyama et al., 2001 citing Pandolfi and Chappell, 1994). The most recent Tahiti dataset (Deschamps et al., 2012) assigns a palaeodepth to *Porites* sp. of -5 to -25 m, 0 to -20 m and -5 to -15 m dependent upon coralgal assemblage. Fossil assemblages used were after Camoin et al. (2007), Abbey et al. (2011), and Camoin et al. (2012), with depositional environments inferred from modern studies from Tahiti (Sugihara et al., 2006; Montaggioni et al., 1997; Camoin et al., 1999; Cabioch et al.,
and other Indo-Pacific reefs (Camoin et al., 1997, 2004; Montaggioni and Faure, 1997; Cabioch et al., 1999; Sagawa et al., 2001).

Our depth distributions – which do not take into account the assemblage information, and which are based on global data – adequately capture the majority of assigned palaeodepths within the literature, albeit with larger vertical uncertainties. As Porites sp. is determined only to the genus level, the median depth and vertical uncertainties are increased relative to other assessments (cf., Deschamps et al., 2012). These vertical uncertainties may be substantially reduced if new identifications could reduce it to the species level (Figure 5), and if stratigraphic ordering of samples is taken into account (section 5.2.4). Still, the somewhat narrow depth-distribution uncertainties allowed in some of the cited palaeo-studies seem to be at odds with the wide range of depth habitats for Porites sp. in modern ecological data.

The third most common species in the fossil database is Montastraea annularis (~ 9% of all samples). Unfortunately few of the original studies included consideration of the modern (or palaeo) depth range for this species (e.g., Shinn et al., 1989; Muhs et al., 2011). Other studies calculated RSL for these specimens with only a ‘generic’ depth uncertainty applied, if at all, and should therefore be treated with caution. Our recalculation specifically accounts for the depth-distribution within both the calculated $P_{\text{RSL}}$ and the vertical uncertainties.

5.4.2 Global, regional, and local variations in depth habitat

Modern coral distributions (e.g. ‘ecoregions’ of Veron 2000, Veron et al., 2009) vary at both the inter- and intra-ocean basin scales. Hence, we might expect differences in both the regional and local drivers of species diversity and distribution between locations to be reflected in the depth-distribution of each coral species (see Figure 3, section 3). In this section, we evaluate this expectation.

Variation at the genus level: an example from the Pacific

Differences in coral community composition and zonation result from the complex interplay of biological and environmental factors (section 3). These modern faunal distributions (cf. Veron et al., 2009) reflect the generalist nature of most corals; for example, a species may occupy a wide range of habitats in one region, and be confined to a specific habitat elsewhere, or be absent entirely (Veron, 1995). From detailed scrutiny of modern depth ranges, we observe that the depth-distribution of single taxa can differ between ocean basins. For example, on a global scale, Porites sp. observations are concentrated within the uppermost few metres for all species (except P. asteroides for which a
The genus *Acropora* shows strikingly different depth distributions between the NW Pacific (multi-modal with large numbers close to the surface and at ~40 m), the Great Barrier Reef (skewed distribution with a long tail to greater depths), and three central Pacific regions (similar to NW Pacific but with fewer observations at depth) (Figure 17). Even within the central Pacific, there are distinct differences between the three sub-regions, with the most southerly region 3 (Figure 17) possessing a substantial number of *Acropora* observations at depths of -50 m. We observe similar variability in the depth distributions of *Porites* (Figure 16). There are very few recorded observations for *Acropora* sp. and *Porites* sp. below about -11 to -15 m on the Great Barrier Reef (Figures 16b and 17b).

The observed differences may be due to different species compositions within each genus at the various sites (which is why a strict species-specific approach would be vital), but it may also include a component of truly contrasting depth preferences of individual species between sites. To test this, we investigate the sub-regional depth-distribution variability within a single species at an even finer (sub-regional) scale.

**Variation at the sub-regional scale: a species-specific example from the Caribbean**

Intra-species variation is well illustrated by the modern depth distribution of *A. palmata* within the wider Caribbean (including Florida and Gulf of Mexico). We assigned the modern synthesis data to one of ten geographic regions (Figure 18) and determined *A. palmata* depth preferences for each separate sub-region. *A. palmata* is found within the upper 3 m in the Caribbean region (excluding the...
Gulf of Mexico and Florida regions; median depth of -1.5 m; 95% range of -0.35 to -9.4 m) which accords with Lighty et al. (1978, 1982). Around Florida, A. palmata is not recorded in the upper 2.5 m, but is mostly confined to the 0 to -4 m depth. The Gulf of Mexico is represented by too few observations in our modern synthesis to make a significant case (n = 12). The Bahamas and Cuba share similar depth profiles, with most A. palmata within the upper 5 m of the water column and with limited numbers at -5 to -15m (median depths of -1.5 and -1 m respectively) (Figure 18). This contrasts with the Cayman Islands and the Puerto Rico to Virgin Islands sub-regions, where A. palmata tends towards greater depths (median depths of -7 m and -4 m respectively).

Such local variations in the depth distribution of a single species (A. palmata) could cause bias of the order of several metres when applied to fossil coral-based \( P_{\text{RSL}} \) reconstructions (Figures 18 and 19). In Figure 19, we investigate how calculated \( P_{\text{RSL}} \) values (and uncertainties) would change if such sub-regional (or local) depth-distributions were used rather than global depth-distribution. For the Bahamas and Yucatan Peninsula (Chen et al., 1991 and Blanchon et al., 2009 respectively), using the sub-regional depth distribution does not alter calculated \( P_{\text{RSL}} \) values, but it does alter the size of the vertical uncertainties (95% bounds). These ‘offsets’ in \( P_{\text{RSL}} \) uncertainties are not trivial, and the complexity of reconstructed \( P_{\text{RSL}} \) is best highlighted when full consideration of the modern depth-distribution is incorporated into our \( P_{\text{RSL}} \) reconstructions (Figure 19). Still, we have not been able to systematically apply such sub-regional depth-habitat corrections in the fossil coral database, because modern habitat constraints remain insufficiently documented for many areas.

5.3.3. Palaeodepth summary

Using a few key examples, we have found that there is excellent scope for improving RSL reconstructions by further documentation of modern species-specific depth distributions at regional to sub-regional scales. To avoid “shallow-water” bias, such new ecological survey work should include deep-diving and ROV surveys.

Unfortunately, there is a more fundamental hurdle to overcome for coral-based RSL reconstructions than regional depth-preference variability within single species. This obstacle relates to the identification of corals to the species level: many taxonomic determinations in fossil coral-based sea-level studies remain limited to the genus level. Genus-level assessment of the modern distribution data yields much broader depth distributions than species-specific assessment, and genus-level results may become skewed by particular species that may or may not be present at all sites (also, there is scope for sampling bias when some areas have fewer observations than others). So, while
improved modern species-level depth-habitat assessments will undoubtedly help to minimise
certainties in past RSL reconstructions, this can only be effectively applied in sea-level studies if
those follow a similarly strict species-specific approach.

We find that improvements in RSL reconstructions may be achieved by: (1) using identifications to the
species level; (2) using coral depth-distributions and an assemblage approach that are location-
specific; (3) inclusion of a greater number of cores/sections to more fully assess the complex reef
geometry; and (4) optimisation of the use of stratigraphic constraints within the calculations.

6. EXAMPLE APPLICATION OF THE FOSSIL CORAL DATABASE

Here we provide an example of how the database can be used, in this case to assess the age range of
samples in our database where local sea level exceeds present during the LIG period. This age range
may not be equivalent to the actual timing of the global mean sea level highstand, due primarily to
the influence of GIA effects at each of the sites and also due to biases in the sample collections
represented in the database (e.g., Dutton and Lambeck, 2012).

Using ages and uncertainties from the screened fossil coral database ($\delta^{234}$U$_{\text{initial}} = 147 \pm 5 \%$, $\leq 2 \%$
calcite and $^{232}$Th concentration $\leq 2$ ppb), we can approximate in a Monte-Carlo approach the median
age and 95% confidence bounds for the last interglacial (LIG) (Figure 20). For the purposes of this
exercise we define the LIG as being where local sea levels are at or above 0 m, which is significantly
different to a LIG defined by global ice volume or global mean sea level. We acknowledge that the
duration of the last interglacial may be amplified or reduced by isostatic influences depending on the
locations that the sample data are taken from (cf. Dutton and Lambeck, 2012; Figure 12), hence our
estimates relate only to a definition of a local interglacial period, defined by local relative sea levels
being above 0 m. Additionally, any statistical analysis of the dataset will be to some degree affected
by sampling biases, for example where only particular portions of the reef were sampled due to
access/exposure/recovery issues.

The analysis further illustrates the impact of screening choices, not only on the data available but also
the outcome. We consider only data with a reconstructed $P_{\text{RSL}} \geq 0$ m. First, we use samples that pass
our screening criteria from tectonically stable locations ($n=51$: Chen et al. 1991; Muhs et al. 2002a;
O’Leary et al. 2008) and use a Monte-Carlo style (350,000 simulations per coral sample) approach to
account for age and vertical (elevation measurement uncertainties and taxon-specific depth
distributions) uncertainties to produce an estimate of periods of time where it is more likely than not
(probability > 50 %) that relative (i.e. local) sea level ($P_{RSL}$) exceeds 0 m (Figure 20a). This exercise
suggests a median LIG age (i.e. $P_{RSL} \geq 0$ m) of 125.3 ka with 95 % bounds of 113.2 ka and 138.1 ka. For
comparison, we repeated the exercise using all data passing the ‘chemical’ screening ($\delta^{234}$U$_{initial}$ = 147
± 5 ‰, ≤ 2 % calcite and $^{232}$Th concentration ≤ 2 ppb) with the additional constraint that samples must
have been described as in situ or in growth position in the original publications, and relaxing the stable
tectonic criterion (n=57: Chen et al. 1991; Muhs et al. 2002a; Blanchon et al. 2009; Stirling et al 1995;
Stirling et al. 1998; Zhu et al. 1993; Eisenhauer et al. 1996; O’Leary et al. 2008). In this instance, we
also account for the time varying tectonic correction of each uplifting or subsiding sample. Note that
these adjusted criteria exclude some data from the Yucatan Peninsula (Blanchon et al., 2009) and
Bermuda (Muhs et al. 2002a), with significant impact upon our analysis, effectively removing the tails
of the distribution and producing a median LIG age of 124.0 ka and 95 % bounds at 118.1 ka and 130.3
ka (Figure 20b). This again highlights that the use of data from our database in subsequent analysis is
highly sensitive to the screening criteria that are applied. Hence, this illustrates the need for clear and
transparent description of the definitions, selection criteria, and procedures used in interpretations.

7. OUTSTANDING ISSUES AND WAYS FORWARD

The compilation of U-series dated fossil coral indicators presented here enables an evaluation of the
fossil coral sea-level index points within their proper uncertainties via: harmonisation of the fossil
coral data; a thorough assessment of all uncertainties; and inclusion of full metadata. There remain,
however, outstanding issues that limit the ability of these data to provide robust sea-level
reconstructions aside from issues expected due to glacio-isostatic adjustments. Principal among these
are the relatively large vertical uncertainties that are driven especially by the application of our new
ecology-based taxon-specific depth-distributions, and by the fact that many fossil coral data points
have been identified only to the genus level. While these vertical uncertainties are large, they derive
from extensive biological/ecological surveys, and we therefore consider them be a more realistic (if
conservative) representation of the errors associated with $P_{RSL}$ reconstructions from fossil corals. The
current database combines data with little to no prior information about palaeodepth with data that
contains more detailed palaeodepth information. Going forward, reconstructions may be refined by
designing methods for objectively implementing a more structural use of diverse palaeodepth
information.

Significant advances (e.g., technological advances increasing the precision of age determinations,
accuracy of elevation measurements etc.) have been made in the last few decades that have facilitated
millennial-scale sea-level reconstructions for several locations (e.g., Barbados and Tahiti). There remain, however, three principal outstanding issues that currently hamper our ability to reconstruct precise and accurate past sea levels from fossil corals.

The first issue concerns the frequently incomplete understanding of the (often complex) vertical displacement (tectonic or otherwise) of many sites. This comprises: (a) current inability to adequately describe the often complex tectonic history of many sites; (b) use of the dated corals themselves to derive uplift/subsidence rates, coupled with assumptions regarding the age of the last interglacial and its sea-level position to calculate uplift rates; (c) the assumption of constancy of those uplift/subsidence rates through time (e.g., Schellmann and Radtke, 2004); and (d) insufficiently quantified effects of dynamic topography that become more important with increasing age (Moucha et al., 2008). These need to be revisited as a matter of priority, through independent verifications of uplift and subsidence rates.

The second outstanding obstacle to obtaining precise sea-level reconstructions concerns the vertical uncertainties associated with species- and region-specific depth relationships. RSL reconstructions rely upon understanding of the relationship between the elevation of the fossil coral and sea level at the time at which the coral was growing. Thus, robust estimates of these species-specific depth relations are a prerequisite for coral reconstructions of sea level. Significant progress has been made (e.g., the use of modern, local biological assemblages and the association with vermetid gastropods and coralline algae), and this study seeks to extend this progress by evaluating fossil data within the context of modern ecological studies. On that basis, we recommend: (1) the use of modern, ecologically derived depth distributions in palaeo-sea-level reconstructions; (2) that these are applied at the species level rather than the often used genus level; (3) that (sub-) regional ecological surveys are conducted to determine accurate depth-distributions for the appropriate specific species in the vicinity each fossil coral site; (4) that the surveys mentioned in (3) include extensive deep-diving and ROV deployments to avoid “shallow-water bias” in the modern habitat characterisations; and (5) optimisation of the promising approach of using assemblages of reef biota (e.g., coral, coralline algae, vermetid gastropods, and encrusting foraminifera) and use of coral micro-atoll data to obtain independent constraints on growth position relative to sea level. As suggested by Camoin and Webster (2014), additional novel approaches to provide tighter constraints on palaeowater depth should also be pursued (e.g., endolithic microboreters or carbon isotopes).
These five key measures to improve the base-information that goes into RSL reconstructions can be further strengthened by addressing the third outstanding issue mentioned above. This concerns the need for complete and routine inclusion of stratigraphic and geomorphological (reef architecture) data including pictures and outcrop or drill-core descriptions (see also Medina-Elizalde, 2012). This context, when provided, is extremely important in making interpretations about sea-level behaviour (e.g., Speed and Cheng, 2004; Blanchon et al., 2009). Given the importance of these metadata, we have added this information into the fossil database, so that users may assess the coherency of samples from the same stratigraphic unit, identify those samples explicitly identified as in situ, etc. A remaining limitation is that geological sections and drill cores rarely provide the complete desired 3-dimensional information of coral reef structure. This could be addressed by obtaining a greater number of drillcores/sections to more fully describe reef architecture.

8. DATABASE RECOMMENDATIONS AND MANAGEMENT

At present, there is no centralised online repository for the combination of data assembled here, though preliminary steps are underway to develop a means of archiving both the geochronological data as well as the associated sample metadata. This will be achieved, in part, through existing open-access, online data repositories that operate under the umbrella organization of Integrated Earth Data Applications (IEDA, http://www.iedadata.org/). EarthChem, and eventually GeoChron, will be able to archive the U-series geochronological data, provided that all samples are given an International GeoSample Number (IGSN) through the System for Earth Sample Registration (SESAR, http://www.geosamples.org/). Software is presently being developed to recalculate ages from archived data, as well as to develop publication-quality tables and plots such as evolution diagrams. What remains to be developed in terms of the cyberinfrastructure is a way to integrate these archived data with the sample metadata required to make sea-level interpretations, as well as a means to incorporate other types of sea-level proxies into the database.

The incomplete reporting of data, and a lack of standardised practices for the reporting of data, hinder syntheses of data such as that shown here. We provide a brief summary of the minimum suggested data requirements that will facilitate future incorporation of data into the database and improve the quality and longevity of the data.

With respect to the U-series data, all geochemical parameters measured should be reported with their associated uncertainties (i.e., $^{238}$U and $^{232}$Th concentration, $^{230}$Th/$^{238}$U and $^{234}$U/$^{238}$U activity or molar ratios), including the decay constants used, the method of spike calibration, instrumentation and
analytical methodology. In particular we note that it is critical to report both isotope ratios (i.e., $^{230}\text{Th} / ^{238}\text{U}$ (or $^{230}\text{Th} / ^{234}\text{U}$) and $^{234}\text{U} / ^{238}\text{U}$) so that ages can be calculated (and re-calculated) and assessed for open-system behaviour based on the back-calculated initial $\delta^{234}\text{U}$ value.

Reported elevations should also include uncertainty and a description of the methodology used for surveying as well as the method used to tie the measurements to a tidal benchmark. All samples should be assigned an IGSN identifier available through SESAR to ease online cataloguing of geochemical data and associated metadata.

Complete descriptions of sample location and context within the reef and/or drill core are also strongly recommended to improve the level of interpretations that can be made, including species-level identification and reef biota assemblage information, if possible.

This database will be maintained and periodically updated by FDH (updates accessible on http://www.highstand.org/erohling/ejrhome.htm via the link “CORAL SEA-LEVEL DATA”. The version of the database used in this paper is archived by British Oceanographic Data Centre (BODC; www.bodc.ac.uk) doi: xxx. To contribute data, please contact FDH to discuss format requirements and release information – note that the underlying philosophy is one of complete open access. Updates will be released periodically.

Acknowledgements

We thank the editors at QSR for inviting this review, Dan Muhs and Anthony Dosseto for their thoughtful reviews that improved the manuscript, Belinda Dechnik for the photographs (Figure 2) and colleagues for fruitful discussions at PALSEA2 conferences. This work was supported by NERC Consortium Grant iGlass: Using Interglacials to Assess Future Sea Level Scenarios (NE/I009906/1) and 2012 Australian Laureate Fellowship FL120100050 to EJR, and NSF grant 1443037 to AD.
Figure captions:

**Figure 1:** Principal influences on coral reef distribution and development (adapted from Harriott and Banks, 2002; Montaggioni and Braithwaite 2009)

**Figure 2:** Variation of *Isopora* (highlighted by red boxes) coral morphology from One Tree Reef, One Tree Island (southern Great Barrier Reef): (a) encrusting *Isopora* from the windward, shallow slope (2 m water depth) (very high energy margin); (b) columnar, low branching *Isopora* from the shallow leeward slope (2 m water depth) (low energy margin); (c) robust, branching *Isopora* from the deep leeward slope (9 m water depth) (low energy, deeper environment). Photographs courtesy of Belinda Dechnik, Geocoastal Research Group, The University of Sydney.

**Figure 3:** Spatial distribution of zooxanthellate coral species richness (after Veron et al., 2009).

**Figure 4:** Map of fossil coral locations contained in the fossil database.

**Figure 5:** (a) Modern depth distributions for the 8 most frequently identified coral taxa within the fossil database. See Table 3 for the modern depth range, median depth, and 95% and 68% confidence intervals. (b) Cumulative distribution functions for the 8 most frequently identified coral taxa within the fossil database.


**Figure 7:** Schematic for the effects of the main diagenetic processes on the isotopic composition of fossil corals (after Scholz et al., 2009).
Figure 8: schematic of relationship between, and uncertainty propagation for, corrected coral position (Z_{cp}) and RSL probability (P_{RSL}).

Figure 9: Effect of screening criteria upon the number of samples available for subsequent analysis. Shaded boxes denote the range of acceptable $\delta^{234}$U_{initial} values used, grey crosses are all unscreened data in the database (0 to 350 ka), blue filled squares are samples passing all screening criteria (i.e. acceptable $\delta^{234}$U_{initial} % calcite and $^{232}$Th concentrations); yellow box - ‘interglacial’ screening of $\delta^{234}$U_{initial} = 147 ± 5 % (ages > 17 ka and 71 to 130 ka); blue box – ‘glacial’ screening of $\delta^{234}$U_{initial} = 142 ± 8 % (ages 17 to 71 ka) and; grey box – ‘older than 130 ka’ screening of $\delta^{234}$U_{initial} = 147 +5/-10 % (ages > 130 ka). Red dashed line is the modern $\delta^{234}$U_{initial} of 147 %.

Figure 10: (a) Samples that pass our initial chemical screening (grey crosses) and replicate analyses (blue dots). Yellow dots are the consistent multiple analyses from core BB02-5-1 (Barbados, Scholz et al., 2009).

Figure 11: Reconstructed relative sea levels for fossil corals, without GIA correction, from both near and far-field locations that pass an initial screening ($\delta^{234}$U_{initial} Calcite ≤ 2 % and $^{232}$Th concentration ≤ 2 ppb) with their respective uncertainties intervals (95%). Age and RSL recalculated from data contained in the following studies: Bahamas (Chen et al., 1991), Barbados (Gallup et al., 1994; 2002; Cutler et al., 2003; Thompson et al., 2003; Bard et al., 1990a; Hamelin et al., 1991; Blanchon and Eisenhauer, 2001; Peltier and Fairbanks, 2006; Fairbanks et al., 2005; Potter et al., 2004; Bard et al., 1990b,c; Scholz et al., 2009) Bermuda (Muhs et al., 2002), southern China (Zhao and Yu, 2002), Comoro Islands (Camoin et al., 2004), Curacao (Muhs et al., 2012a; Vezina et al 1999), Mururoa atoll (French Polynesia) (Camoin et al., 2001), Tahiti (Thomas et al., 2009; Yokoyama et al., 2001; Deschamps et al., 2012; Bard et al., 1996b), Indonesia (Sumba Island) (Bard et al., 1996a), Madagascar (Camoin et al., 2004), Yucatan Peninsula (Blanchon et al., 2009), Huon Peninsula (Papua New Guinea) (Yokoyama et al., 2001; Esat and Yokoyama, 2006; Cutler et al., 2004; Bard et al., 1996b; Cutler et al., 2003; Stein et al., 1993), Henderson Island (Pitcairn Islands) (Anderson et al., 2010; Stirling et al., 2001), Seychelles (Israelson and Wolfrath, 1999; Camoin et al., 2004), Hawaii (Muhs et al., 2002; Szabo et al., 1994), Vanuatu (Edwards et al., 1987; Taylor et al., 1985; Cutler et al., 2004) and Western Australia (Stirling et al., 1995, 1998, 2001; Zhu et al., 1993; Eisenhauer et al., 1996; O’Leary et al., 2008; Collins et al., 2006).

Figure 12: A demonstration of the geospatial variability of relative sea-level (RSL) predictions with global mean (eustatic) for (a) the last deglacial and (b) the last interglacial periods for an ice history incorporating a 4 ka interglacial period, using one earth model. For any ice history, the choice of earth model affects both the timing and the amplitude of a sea-level peak, highstand or low stand.

Figure 13: (a) Reconstructed corrected coral position (Z_{cp}) for Barbados samples that pass our initial chemical screening (grey crosses), and those with reef-crest designations (coloured). Age and vertical uncertainties are plotted at the 2σ (95%) interval. (b) As (a) but reconstructed P_{RSL} (with their 95% uncertainties).

Figure 14: (a) Reconstructed corrected coral position (Z_{cp}) for drill-core samples from Barbados that pass our initial chemical screening. Age and vertical uncertainties are plotted at the 2σ (95%) interval. (b) As (a) but reconstructed P_{RSL} (with their 95% uncertainties). (c) Reconstructed P_{RSL} for the last deglaciation using Monte-Carlo style simulation of samples. Coloured shading indicates the 99th (pale blue), 95th (yellow), 85th (orange), 70th (red) and 50th (black) percentiles.
Figure 15: (a) Reconstructed corrected coral position ($Z_{cp}$) for drill-core samples from Tahiti that pass our initial chemical screening. Note, we have also plotted the Papeete Harbour samples for comparison, although no $^{233}$Th data are available for these samples (and these therefore do not strictly meet our screening criteria). Age and vertical uncertainties are plotted at the 2σ (95%) interval. (b) As (a) but reconstructed $P_{RSL}$ (with their 95% uncertainties) calculated using only taxonomic depth distributions derived (Note, assemblage derived palaeo-water depths estimates are available and that this example is intended only to show the result of using depth distributions strictly limited to taxonomic identification of the coral) (c) Reconstructed $P_{RSL}$ for the last deglaciation using Monte-Carlo style simulation of samples (excluding the Papeete Harbour samples) using only the taxonomic depth distributions (not original palaeo-water depth estimates). Coloured shading indicates the 99th (pale blue), 95th (yellow), 85th (orange), 70th (red) and 50th (black) percentiles. This example is not intended to be a new reinterpretation of the Tahiti dataset.

Figure 16: (a) Map of Porites sp. observations from the Pacific and the Atlantic (OBIS, 2014; see online supplementary material for references and datasets used). (b) Histograms of the depth distributions for: all OBIS observations (‘Porites sp. – ALL’); the Atlantic and Pacific basins; and regional subsets of the Pacific.

Figure 17: (a) Map of Acropora sp. observations from the Pacific and the Atlantic (OBIS, 2014; see online supplementary material for references and datasets used). (b) Histograms of the depth distributions for: the Atlantic; a subset of Caribbean data and Florida data; the Pacific basin; and regional subsets of the Pacific.

Figure 18: (a) Map, histogram and cumulative frequency distribution of Acropora palmata in the Caribbean (OBIS, 2014; see Appendix A for references and datasets used). (b) Histograms of A. palmata depth-habitat distributions in Caribbean sub-regions. (c) Cumulative frequency distributions of A. palmata depth-habitat distributions in Caribbean sub-regions.

Figure 19: Example of the effect of applying sub-regional, taxon-specific depth distribution to calculate $P_{RSL}$ (Chen et al., 1991; Blanchon et al., 2009 using the depth distributions derived for A. palmata for the Caribbean (i.e. ‘global’), Bahamas and Yucatan Peninsula regions) (a) reconstructed coral position ($Z_{cp}$) with 2σ uncertainties (b) $P_{RSL}$ calculated using the A. palmata depth-distributions. (i) using the ‘global’ depth-distribution (ii) as in (i), but $P_{RSL}$ calculated using sub-regional (Bahamas and Yucatan Peninsula) depth-distributions. Note the smaller vertical uncertainties for the Bahamas samples (vertical uncertainties are plotted at the 2σ (95%) interval). (iii) calculation of $P_{RSL}$ using a Monte-Carlo style simulation of the same samples. Coloured shading (red, Bahamas; blue, Yucatan Peninsula) indicates the 99th, 95th, 85th, 70th and 50th percentiles. All data plotted pass our initial chemical screening.

Figure 20: Monte-Carlo style simulation (350,000 simulations per coral sample) estimate of periods of time where it is more likely than not (probability > 50 %) that relative (i.e. local) sea level ($P_{RSL}$) exceeds 0 m (a) histogram for data from stable regions only (n=51) (b) as in (a) but with additional constraint that samples must be in situ or in growth position and the tectonically stable location criterion relaxed (n=57). All data plotted pass the initial interglacial screening criteria.
Table captions:

Table 1: Recalculated uplift/subsidence rates used in the fossil database. Uplift/subsidence rates were recalculated assuming a LIG sea level of 6.6 ± 2 m (Kopp et al., 2009, 2013) and an age of 125 ± 5 ka.

Table 2: The modern tidal range for sites in the fossil database (for simplicity the minimum and maximum tidal ranges for a location are listed here). The modern tidal range was estimated from a global tidal model (i.e. the difference between the maximum and minimum tides predicted from the location).

Table 3: Summary of empirically derived global depth distributions for coral in the fossil coral database. Only modern observational data with a depth precision ≤0.25 m were used to derive the depth-habitat distributions (OBIS, 2014; a full list of datasets and references can be found in the online supplementary material).

Table 4: Compilation of modern (and fossils < 1 ka) $^{238}$U concentrations from the literature.

Supplementary Materials (online):
1. Fossil coral database.
2. Depth distributions (for each taxa) derived from OBIS (2014).
3. OBIS (2014) data sources listed by genus and references
Table 1:

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<td>† uncertainty derived from mapping (i.e., half contour spacing) and assigned ±1 m measurement uncertainty</td>
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<td>* assigned ±1 m uncertainty (none quoted in original reference)</td>
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<td>§ elevation uncertainty derived from half the elevation range plus an assigned ±1 m measurement uncertainty (as this was not given in the original reference)</td>
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<tr>
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<td>Southern Huon Gulf</td>
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<td>USA (California)</td>
<td>~ +7 to +8</td>
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<td>Point Loma</td>
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<td>Muhs et al., 2002b</td>
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<td>San Clemente Island</td>
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<tr>
<td></td>
<td>~ +33</td>
<td>(northern, northeastern and eastern side of the island, to +36 (near Viscaino Point)</td>
<td>Muhs et al., 2006</td>
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<tr>
<td>Green Oaks Creek area, San Mateo County</td>
<td>n/a</td>
<td>Shoreline angles elevation</td>
<td>Bradley and Griggs, 1976; Muhs et al., 2006</td>
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<td>Palos Verdes Hills, Los Angeles County</td>
<td>+70 to +80 (Gaffey terrace)</td>
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**Notes:**
- Values are given in meters.
- Some values are inferred or estimated.
- References are cited for each location.
- The table includes sites such as Nanda, Sialum, Drill core, Henderson Island, and others, along with their respective elevations and methods of measurement.
- The table also includes references to scientific studies and literature for further context.

---

**References:**
- Chappell, 1973
- Chappell and Polach, 1991
- Edwards et al., 2008
- Galewsky et al., 1996
- Riker-Coleman et al., 2006
- Blake, 1995
- Andersen et al., 2008
- Muhs et al., 2002b
- Muhs et al., 2006
- Muhs et al., 2012b

---

**USA (Hawaii):**

**Locations:**
- Cayucos Pt
- Point Loma
- Point Arena
- San Clemente Island
- San Nicholas Island
- Green Oaks Creek area, San Mateo County
- Palos Verdes Hills, Los Angeles County

**Elevations:**
- ~ +7 to +8
- ~ +23 to +24
- ~ +40 to +45
- ~ +21 (Eel terrace aka terrace 2b)
- ~ +34
- ~ +33 (northern, northeastern and eastern side of the island, to +36 (near Viscaino Point)
- n/a
- 6°
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<td>-0.028 to +0.052</td>
<td>(based on +8.5 m elevation of growth position corals of Waimanalo deposits at Mokapu Point)</td>
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<tr>
<td></td>
<td>+0.02 to +0.028</td>
<td>(based on submerged reef terraces)</td>
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<td>+0.06 to +0.001</td>
<td>(rate over the last 500 ka from emerged reef elevation of +21 m and mean U-series age of 335 ± 22 ka)</td>
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<tr>
<td></td>
<td>+1.5 ± 0.3</td>
<td>(mean late Holocene rate)</td>
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<tr>
<td></td>
<td>-0.02 to -0.1</td>
<td>(east to west)</td>
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<td>USA (Oregon)</td>
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<td>Coquille Point</td>
<td>n/a</td>
<td>Used estimate from literature (Bloom et al., 1978; Edwards et al., 1987a)</td>
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<tr>
<td></td>
<td>+0.45 to +1.05</td>
<td>(based on the elevation of the Whiskey Run terrace, corrected for landward tilt; an age of 80 ka and assumptions regarding sea level at 80 ka)</td>
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<td>West End</td>
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<td>Mapped beach facies</td>
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<td>Hubbard et al., 1989</td>
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<td>-0.04</td>
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<td></td>
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<td>Toscano et al., 2012</td>
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<td>-7.75</td>
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<td></td>
<td>+1</td>
<td></td>
</tr>
<tr>
<td>Espiritu Santo Island</td>
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<td>+4.6</td>
<td>(no details on derivation provided)</td>
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<td>Tengoa</td>
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<td>Not reported</td>
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<td>+3.4</td>
<td>(no details on derivation provided)</td>
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<td></td>
<td>+3 ± 0.3</td>
<td>(mean late Holocene rate)</td>
</tr>
<tr>
<td></td>
<td>~ +2.5</td>
<td>(average for last 100 ka based on dating of terraces)</td>
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<tr>
<td>Island</td>
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<td>n/a</td>
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<td>--------------</td>
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<td>Araki Island</td>
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2144
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<tr>
<th>Location</th>
<th>Site(s)</th>
<th>Modern tidal range (min and max) (m) (3dp)</th>
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<tbody>
<tr>
<td>Bahamas</td>
<td>Abaco, Great Inagua and San Salvador Islands</td>
<td>1.005 to 1.284</td>
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<tr>
<td>Barbados</td>
<td>various</td>
<td>0.906 to 1.29</td>
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<tr>
<td>Bermuda</td>
<td>various</td>
<td>1.249 to 1.258</td>
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<tr>
<td>China</td>
<td>Leizhou Peninsula</td>
<td>4.628</td>
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<tr>
<td>Comoro Islands</td>
<td>Mayotte Island</td>
<td>4.160</td>
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<tr>
<td>Curacao</td>
<td>various</td>
<td>0.450 to 0.501</td>
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<td>Eritrea</td>
<td>Red Sea coast</td>
<td>1.391</td>
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<td>French Polynesia</td>
<td>Mururoa atoll</td>
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<td>Tahiti</td>
<td>0.394 to 0.427</td>
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<td>Grand Cayman</td>
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<td>0.441 to 0.443</td>
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<tr>
<td>Haiti</td>
<td>N.W. Peninsula</td>
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<td>Indonesia</td>
<td>Sumba Island</td>
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<td>Madagascar</td>
<td>Toliara</td>
<td>3.289</td>
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<tr>
<td>Mexico</td>
<td>Baja California: various</td>
<td>0.958 to 2.710</td>
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<tr>
<td>Mexico</td>
<td>Yucatan Peninsula</td>
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<td>New Caledonia</td>
<td>Amdee Inlet</td>
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<td>Niue Island</td>
<td>1.276 to 1.542</td>
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<td>Huon Peninsula: various</td>
<td>1.186 to 1.225</td>
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<td>Henderson Island</td>
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<td>Seychelles</td>
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<td>1.554 to 1.787</td>
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<tr>
<td>USA</td>
<td>California: various</td>
<td>2.667 to 2.876</td>
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<td>Florida: various</td>
<td>0.737 to 1.129</td>
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<td>Hawaii: various</td>
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<td>Vanuatu</td>
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<td>Western Australia</td>
<td>various</td>
<td>0.897 to 2.097</td>
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Table 3:

* too few modern observations (<50) to enable a depth preference to be assigned – used genus information (where available; fossil database;
† depth preference based on few (<200) observations – treat with caution
# widened depth precision (depth precision ≤ 5m)
‡ no modern observations (but some museum collection specimens); used the study of Gerrodette, 1979
§ numbers in brackets are the number of species used to determine the genus depth range
ζ Maximum depth observed from study of Muir et al., 2015 using the Worldwide Acropora Collection, Queensland Museum collection comprises 23,000 specimens and included SCUBA collection (to base of reef or the regulating diving limit)
<table>
<thead>
<tr>
<th>Gordinieroseras sp.*</th>
<th>2</th>
<th>28*</th>
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<td>Gordinieroseras planulata*</td>
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<td>27*</td>
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<td>Goniastrea pectinata</td>
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<td>Goniastrea retiformis</td>
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<td>Gonipora sp.</td>
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<td>15*</td>
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<td>Hydnophora exesa</td>
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<td>Montastraea cavernosa</td>
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<td>(16)</td>
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<td>Pacillipora verrucosa</td>
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<td>Parestes sp.</td>
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<td>Parietea magnifica#</td>
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<td>Parietea solidida#</td>
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<td>Sympatryia sp.</td>
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<td>0 to -45 (7)</td>
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<td>0 to -45 (7)</td>
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**Depth range unknown**
Table 4

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<th>Species</th>
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<th>References</th>
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<tr>
<td>Acropora cervicornis (a)</td>
<td>3</td>
<td>3.27 to 5.8 $^{(a)}$</td>
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<tr>
<td>Acropora cuneata</td>
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<td>Acropora palmata</td>
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<td>Flor and Moore, 1977; Cross and Cross 1983; Hamelin et al., 1991;</td>
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<td><em>ibid</em>, Veeh and Turekian, 1968; Gwirtman et al., 1973; Zhu et al., 1993;</td>
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<td>Schroeder et al., 1970; Cross and Cross, 1983; Muhs et al., 2011; Romaniello et al., 2013;</td>
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<td><em>ibid</em>, Vanuatu, Christmas Island, Tuamotu</td>
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<td><em>ibid</em>, Henderson et al., 1993.</td>
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<td>Schroeder et al 1970.</td>
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<td><em>ibid</em>, Edwards et al., 1987b</td>
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<td>Vietnam</td>
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<td><em>ibid</em>, Gvirtman et al., 1973, Szabo et al., 1994, Zhao and Ku, 2002, Lazar et al., 2004, Scholz et al., 2004, Cabioch et al., 2008</td>
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<td>Broecker, 1963; Broecker and Thuber, 1965; Friedman, 1968; Livingston and Thompson, 1971; Amiel et al., 1973; Gvirtman et al., 1973; Cobb et al., 2003b</td>
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<td>1.28 to 12.5</td>
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La Parguera, Puerto Rico Benthic Composition and Monitoring Data (2002 - Present) (NOAA-CCMA). National Oceanic and Atmospheric Association (NOAA)-National Ocean Service (NOS)-National Centres for Coastal Ocean Science (NCCOS)-Centre for Coastal Monitoring and Assessment (CCMA)-Biogeography Team Publication_Date: 200703 Title: La Parguera, Puerto Rico Benthic Composition and Monitoring Data (2002 - Present) Publication Information: Publication Place: Silver Spring, MD Publisher: NOAA's Ocean Service, National Centers for Coastal Ocean Science (NCCOS)


Sackett and Portratz, 1963. Dating of carbonate rocks by ionium-uranium ratios. USGS Prof Papers No 260-BB.


Sugihara, K., Yamada, T., Iryu, Y. 2006. Contrasts of coral zonation between Ishigaki Island (Japan, northwest Pacific) and Tahiti Island (French Polynesia, central Pacific), and its significance in Quaternary reef growth histories. SEALAIX'06 Meeting. (eds G. Camoin, A. Droxl, C. Fulthorpe, & K


Dispersion

Coral recruitment

Physiological tolerances and symbiosis

Coral disease

Coral species diversity

Coral reef accretion

Disturbance

Sea level

Tectonics

Antecedent topography

Water turbulence

Hydrodynamics

Reproduction and fecundity

Nutrients

Predation

Light

Turbidity

Competition (e.g. for space, light, etc.)

Substrate availability and habitat area

Coral growth and calcification

presence/absence of key reef building species

Aragonite saturation

Species saturation

Coral cove

Coral reef accretion
Species Number (see legend for details)

modern depth preference
modern depth limits
(95% confidence limits) (this study)
IUCN Red List; Carpenter et al., 2008)
234U and 238U gain with δ²³⁴U > δ²³⁴Ucorr
230Th and 234U gain or 238U loss
234U loss

(234U / 238U)

100 ka closed-system isochron

230Th or U loss

234U and 238U gain with δ²³⁴U < δ²³⁴Ucorr

(234U / 238U)
**MODERN:**

1. Modern coral elevation (datum = mean sea level)

2. Modern taxa depth distribution

**PAST:**

1. Corrected coral position

2. Probability of RSL ($P_{RSL}$) = Combination of elevation error AND depth distribution
   (frame of reference = coral position)
All data

Data passing all screening

(δ²³⁴U_initial : % calcite; ²³³Th concentration)

'interglacial' (δ²³⁴U_initial = 147 ± 5‰)

'glacial' (δ²³⁴U_initial = 142 ± 8‰)

'>130 ka' (δ²³⁴U_initial = 142 ± 5/-10‰)
Corrected coral position (Zcor) (m)

Age (ka)

- Samples passing $^{234}U_{\text{nat}}$, % calcite, $^{232}Th$ concentration screening
- Replicate samples passing screening
- Scholz et al., 2009 samples passing screening
A\text{ge (k}\text{a})

Z_{cp} (m)

\begin{align*}
&\text{AllBarbados samples passing screening} \\
&\text{(\textsuperscript{234}U_{total}, \% calcite, \textsuperscript{230}Th concentration)}
\end{align*}

\begin{align*}
\text{Reef crest - A. palmata} \\
\text{Reef crest - Diplovia sp.} \\
\text{Reef crest - Montastera sp.} \\
\text{Reef crest - Siderastrea sp.}
\end{align*}
Barbados samples NOT passing screening
(\(^{234}\)U\(_{\text{initial}}, \% \text{calcite}, \(^{232}\)Th concentration)
Barbados samples passing screening -
NO stratigraphic constraints

Drill core samples:
- RGF 7
- RGF 9
- RGF 12
- RGF 13
- RGF 15
- RGF 16

\(\delta^{234}\text{U}_{\text{initial}}, \% \text{calcite}, \(^{232}\)Th concentration)
Tahiti samples NOT passing screening

Samples passing screening

(\(^{234}\)U\(_{\text{initial}}\%\) calcite, \(^{232}\)Th concentration)

Papeete harbour
(note, no \(^{232}\)Th concentrations listed for these samples)

Faaa
M0020A

Tiaeri
M0009A-6R
M0009B
M0009C
M0009D
M0009E
M0023A
M0023B
M0024A
M0025A
M0025B
M0026A

Maraa
M0005C
M0005D
M0015A
M0018A

99% probability interval
95% probability interval
80% probability interval
70% probability interval
50% probability interval
(A) \( Z_{cp} \)

(B) \( R_{\text{RSL}} \)

(i) 'global' depth distribution

(ii) 'sub-regional' depth distribution

(iii) 'sub-regional' depth distribution

- Bahamas
- Yucatan Peninsula

99% probability interval
95% probability interval
80% probability interval
70% probability interval
50% probability interval

Age (ka)
Stable sites only

(A)

In situ samples only

(B)