M

MACNEIL, F. STEARNS (1909–1983)

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Darwin's 1842 model for atoll development provoked numerous alternative ideas including antecedent platforms, eustatic sea level oscillations, and integrated hypotheses. Japanese researchers were the first to consider that modern reefs are growing on limestone platforms exposed to sub-aerial weathering during lower sea level periods of the Pleistocene (Asano, 1942; Yabe, 1942; Tayama, 1952). Their papers, however, were largely ignored or dismissed (e.g., Umbgrove, 1947) until the ideas were redeveloped in the American literature. Initially Stearns (1946) believed that variations in sea level were major factors in producing the relief of atolls and in particular, internal unconformities where the reef limestone was eroded or exposed during low sea levels.

However, the paper published in 1954 by F. Stearns MacNeil of the US Geological Survey has become the most widely quoted source of the hypothesis of an inheritance from sub-aerial forms for the shape of atolls. Interestingly, MacNeil notes that Hoffmeister and Ladd (1944) had previously concluded that the saucer shape of many uplifted Pacific limestone islands was due to solution, and not to the fact that they were raised atolls, yet they did not develop the argument in their exposition on antecedent platforms. MacNeil's theory recognized the importance of organic growth during periods of submergence but placed at least equal importance on the role of solution in fashioning the lagoonal depressions and anular rims of atolls. Case-hardening and development of underground drainage systems were seen as important factors in the development of the sub-aerially exposed limestone surface. MacNeil, in the introduction to his 1954 paper, stated:

> Though it is true that most authors have sought to explain barriers and atolls as the ultimate forms of reefs, the inclusion of all reef hypotheses under one heading implies more conflict than really exists. Generally no distinction is made between theories dealing mainly with the foundation of reefs, and the shape of reefs. There is a general feeling among investigators at present that atolls are not always formed the same way, and therefore no one theory can explain atolls.
>
> and later:
>
> It would seem that each atoll should be studied as an individual and it is not thought that the present hypothesis, believed to be true for the oceanic atolls of the mid Pacific, is necessarily true for the atolls (*sic*) of the Great Barrier Reef.
>
> *MacNeil*, 1954. pp. 402–403

It is possible here that MacNeil was too conservative in his application of his hypothesis, for Purdy (1974) has greatly extended the antecedent karst model to explain the configuration of all reefs by means of preferential reef accretion on topographic highs in underlying subaerially weathered surfaces. However, MacNeil's statements implying that the coral reef problem has been largely a matter of confusing structure and surface morphology, and of assuming that all reefs have a similar evolution, are an illumination of the problem not previously considered. It is from about the time of his paper that general models of reef evolution have become unfashionable, a trend that is noticeable within geomorphology generally, as indicated by Higgins (1975). Higgins attributes this decline in landscape models to a change in the intellectual climate resulting from increasing quantification and interest in process, which in turn have suggested that complex landforms may be explained by more than one hypothesis.

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Cross-references

Antecedent Platforms
Atolls
Darwin, Charles (1809–1882)
Glacial Control Hypothesis
Solution Unconformities
Subsidence Hypothesis of Reef Development

MAKATEA

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Definition

Makatea is defined originally as an elevated (uplifted) rim of coral reef limestone wholly or partly surrounding a volcanic island. Makatea islands refer to composite islands according to Nunn (1994) as they possess three distinct geomorphic features from the shoreline inwards: a makatea limestone, a depression with swamps and streams, and an exposed volcanic core.

Etymology: The term *makatea* was originally defined and used in the southern tropical Pacific (Cook Islands). It derives from the Polynesian language, probably from two words: maka (slingstone) and tea (white).

Origin: The makatea limestone consists usually of Cenozoic reef material, locally with peripheral fringes of Quaternary reef terraces deposited before island uplift (see Montaggioni and Camoin, 1997; Vacher and Quinn, 1997 for reviews). The morphology of makatea islands frequently resembles that of modern barrier reefs or almost-atolls in which topography is believed to be inherited from pre-existing karstic relief. In most cases, the depression behind the reef rim is the result of subaerial solution by freshwater (Purdy and Winterer, 2006). The final landscape is typified by upland depression-and-rim reliefs and coastal cliffs. The volcanic core has been built by different mechanisms in relation to lithospheric plate tectonics, e.g., hotspot, arc volcanism, and volcanism at or close to divergent plate boundaries. Similarly, uplifting has been controlled by a variety of regional tectonic processes.

Parent feature: The island of Makatea in the northwesten Tuamotus (French Polynesia) is a high carbonate, atoll-shaped structure, generally not regarded as a typical makatea island because of the lack of exposed volcanics in its central part. However, its present-day morphology has been produced by uplift of a Cenozoic reef tract, followed by subaerial, karstic erosion. The name of makatea island therefore is suggested to be used in a wider sense and thereby applied to any tropical Pacific island typified by uplifted reefal limestone severely karst-eroded.

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Cross-references

Diagenesis
Emerged Reefs
Solution Processes/Reef Erosion

MALDIVES

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Definition

Maldives: The Republic of Maldives is an archipelago of coral atolls and reef platforms located in the central Indian Ocean.

Introduction

The Maldives archipelago comprises a chain of coral reefs and reef islands situated 700 km southwest of Sri Lanka and positioned between the Lakshadweep Islands (to the north) and Chagos Islands (to the south). The archipelago extends 868 km from Ihavandhippolhu in the north (6°57′N) to Addu atoll (0°34′S) just south of the equator. Comprising 2,041 reefs the archipelago is globally unique in biological diversity, the diversity of reef structures it possesses, and their mode of evolution. The reef system is host to approximately 1,190 low-lying reef islands. As one of only four atoll nations, the Maldives is commonly regarded as extremely vulnerable to future sea-level and climatic change.

Early exploration

Earliest scientific investigations of the Maldives involved detailed hydrographic observations of the archipelago by Commander James Moresby 1835–1838. This work produced detailed hydrographic charts of the reef system, which were used by Charles Darwin in constructing his global synthesis of reef evolution, and which remain the most accurate records of bathymetry in the archipelago. At the end of the nineteenth century and beginning of the twentieth century a number of scientific expeditions were undertaken to the Maldives to document the taxonomy and biogeography of reef biota and make observations of oceanographic conditions. Most notable were the expeditions of James Stanley Gardiner in 1899–1900 who undertook the first detailed descriptions of marine and terrestrial fauna and flora as well as reef structures (Gardiner, 1903). Shortly thereafter, Alexander Agassiz also visited the archipelago in 1901–1902 and undertook sampling and description of biological aspects of the reefs (Agassiz, 1903). Seymour Sewell led the "John Murray" expedition to the Maldives (1933–1934) in which Sewell undertook detailed geomorphic observations of a number of atoll islands (Sewell, 1936a, b).

In 1957–1958 the "Xarifa" expedition undertook detailed investigations of the sub-littoral ecology and structure of reefs in many atolls in the archipelago (Hass, 1965). Introducing new systematic survey techniques, this expedition was notable for its taxonomic investigation of faunal and floral communities, identification of high species diversity, and establishment of baseline monitoring locations for future reference of reef community dynamics (Wallace and Zahir, 2007). British scientists also studied the marine and terrestrial geomorphology and ecology of Addu atoll (Stoddart, 1966).

Since these early expeditions the research effort in the Maldives can be described as sparse and narrowly focused on specific aspects of reef ecology, geology, and management. As a result large gaps exist in scientific knowledge and many atolls have not been visited by scientists since Gardiner and Sewell.

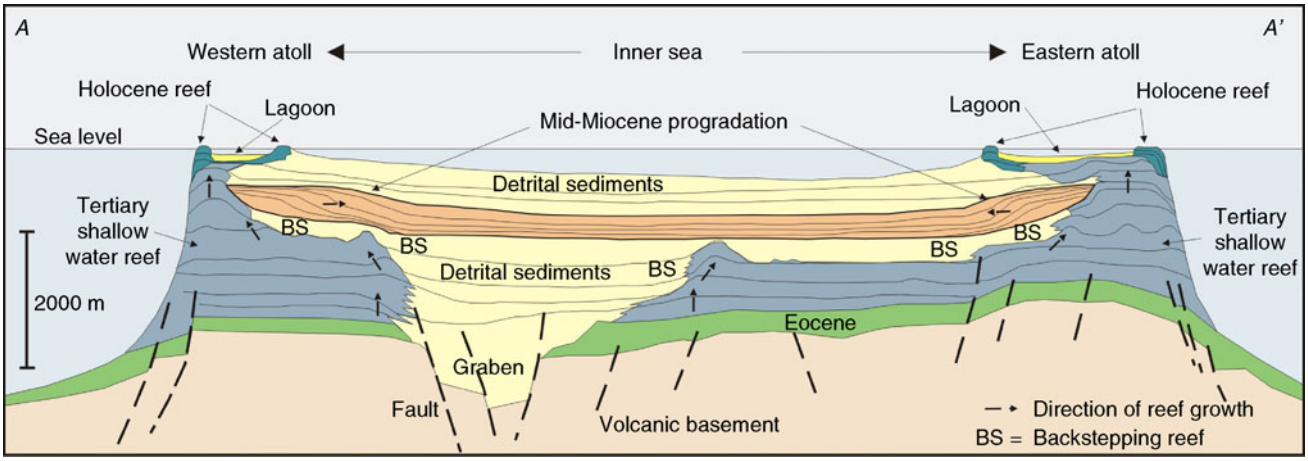
Geologic history

The Maldives constitute the central section of the Laccadives – Maldives – Chagos submarine ridge, which in turn is part of a larger feature that stretches from the early Tertiary Deccan Traps of India to the volcanically active zone of Reunion. The Deccan Traps were the first manifestation of the stationary mantle hotspot that subsequently produced the volcanic ridge underlying the Maldives. Northward drift of the Indian Plate and northeastward motion of the African plate has resulted in northward age progression along this ridge (Duncan and Pyle, 1988; Duncan and Hargreaves, 1990; Tiwari et al., 2007).

The history of formation of the Maldivian atoll systems differs from the subsidence model proposed by Darwin (1842). Rather, carbonate accumulation through the Tertiary was controlled by phases of aggradation and progradation modulated by large oscillations in sea level (Aubert and Droxler, 1992; Purdy and Bertram, 1993; Belopolsky and Droxler, 2003). The basement rocks underlying the Maldives are Eocene volcanics (55 million years old). These basement volcanics are capped by up to 3,000 m of limestones. Carbonate banks were initiated in the Eocene on topographic highs of the faulted volcanic basin (Figure 1). A number of NNE-SSW oriented grabens acted as channels that became filled with sediments shed from surrounding carbonate banks. The Oligocene to early Miocene were characterized by aggradation of carbonate banks and backstepping in response to sea level rise. An elevated outer rim developed and provided the antecedent structure for the double chain of atolls separated by an inner sea basin that characterizes the central section of the contemporary archipelago (Figure 2). The mid-Miocene (15–10 million years ago) was dominated by lateral progradation from the outer margins of the twin atoll chain toward the inner sea forming a shallow carbonate platform. This period of lateral progradation was followed in the late Miocene and Pliocene by flooding of the platforms and backstepping of the carbonate banks to the periphery of the platform. These peripheral platforms were exposed to karstification during the Plio–Pleistocene sea level minima.

During the Quaternary, the dominant mode of reef development has been vertical coral reef growth on top of these karstified remnants. This vertical reef growth is a consequence of high-amplitude sea-level fluctuations during the Pliocene–Pleistocene, producing alternate periods of exposure and submergence. The Holocene is the last of these reef growth phases.

The contemporary surface morphology of the Maldivian reefs is the result of coral reef growth over the past 10,000 years upon Pleistocene foundations. The Holcoene reef growth history of the Maldives has only recently been resolved in detail based on drill cores from Ari and South Maalhosmadulu atolls with the Holocene reef thickness ranging from 12 to 14 m (Gischler et al., 2008; Kench et al., 2009). These studies show the Holocene reef growth initiated approximately 8,100 years ago as sea level flooded the Pleistocene surface. Vertical reef growth occurred at around 7 mm/year for the period 8,100–6,500 years ago and subsequently slowed to 1 mm/year thereafter. Evidence suggests the final stages of reef accretion in the late Holocene exhibited local variations. In situ reef deposits located above sea level on some reefs show



Maldives, Figure 1 Schematic of the geological structure and evolution of the Maldives archipelago along a west to east transect through the central archipelago. Representative location of transect shown in Figure 2 (after Belopolsky and Droxler, 2003).

vertical reef accretion to a mid-Holocene highstand of approximately 0.5 m above present 2,500 years ago (Kench et al., 2009), where elsewhere the lack of higher sea level evidence suggests reef accretion may have lagged other sites (Gischler et al., 2008).

Reef structure

The Maldivian archipelago consists of 2,041 individual reefs with a total reef area of 4,513 km^2 (Naseer and Hatcher, 2004). This complex network of reefs is organized into a number of distinct atoll and reef types. There are 21 atolls and 4 oceanic reef platforms.

Atolls can be divided into two types based on their broad physiographic characteristics. *Open atolls* are the dominant atoll type (16 in total) and are characterized by heavily dissected atoll rims, which in planform appear as a sequence of individual reef platforms enclosing a central lagoon. Passages provide free connection between the lagoon and waters of the surrounding ocean and inner sea. Open atolls are large structures ranging from 290 to 3,790 km^2 in area, that contain numerous lagoonal reefs and collectively account for 99.5% of all Maldivian reefs. A striking feature of the open atolls is the presence of faros, ring-shaped coral reefs located within broader atoll lagoons. Globally faros are scarce, yet they are abundant in the Maldives where their formation has yet to be resolved. *Closed atolls* have a near-continuous reef rim that enclose their lagoons, and have limited number of passages connecting the lagoon and surrounding oceanic water. There are only five closed atolls in the archipelago, which are much smaller in area than open atolls, ranging from 47 to 143 km^2.

Four oceanic reef platforms also occur in the archipelago. These reef platforms are individual reefs that emerge from the inner sea or ocean basin and have no structural connection with neighboring atolls. Oceanic reef platforms are small in area ranging from 4.4 to 10.2 km^2 and have no lagoon that connects to the open ocean. Vegetated islands occupy a large proportion (16–50%) of the reef platforms.

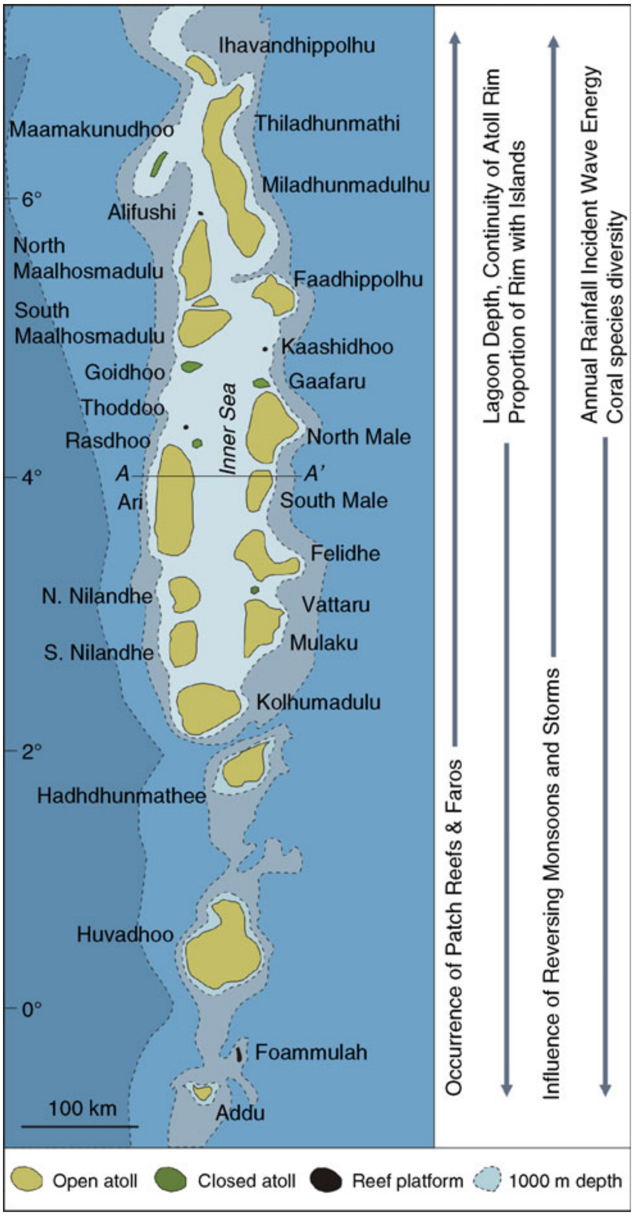
Latitudinal gradients in atoll characteristics and processes

The physical characteristics of atolls in the Maldives show marked spatial variations along the north-south gradient (Figure 2). Northern atolls are characterized by a heavily dissected atoll reef rim, numerous lagoonal patch reefs and faros, and moderate lagoon depths (40–50 m). Reef islands are located on the peripheral and lagoonal patch reefs. Toward the south, atolls are characterized by more continuous atoll reef rims, a higher proportion of peripheral reef rim containing islands, deeper lagoons (70–80 m), and fewer lagoonal patch reefs.

Latitudinal variations in atoll morphology have been attributed to broad north-south gradients in climate and oceanographic conditions. Annual rainfall reduces from south to north along the archipelago (Figure 2). Over the longer-term this rainfall gradient has influenced solutional lowering of lagoons during Quaternary glacial periods. The archipelago is subject to monsoon conditions that switch from the west to northeast in a predictable fashion and influence wave and current patterns. The intensity of oscillating monsoon conditions increases to the north. In contrast, incident wave energy reduces in magnitude in the northerly direction. This energy gradient influences contemporary coral reef growth and island building processes.

Reef ecology and biodiversity

The central Indian Ocean location of the Maldives places the archipelago close to the mid-point between the reef faunas of the east and west margins of the ocean basin.



Maldives, Figure 2 Configuration of the Maldives archipelago, central Indian Ocean showing atoll types, names, latitudinal gradients in climate, oceanography, physical atoll characteristics, and coral species diversity.

This geographic position and the fact that the faunal characteristics of the Maldives reefs have close affinities with the Indonesian high diversity reefs and east African reefs is indicative of the archipelago's important role as a biogeographic stepping stone in the so-called "Chagos stricture." As a consequence, the Maldives has high coral diversity with approximately 250 species of scleractinian corals recorded (Pichon and Benzoni, 2007; Wallace and Zahir, 2007). There are also more than 1,200 reef and reef associated fish species (Rajasuriya et al., 2004). Of note, coral diversity increases southward along the archipelago.

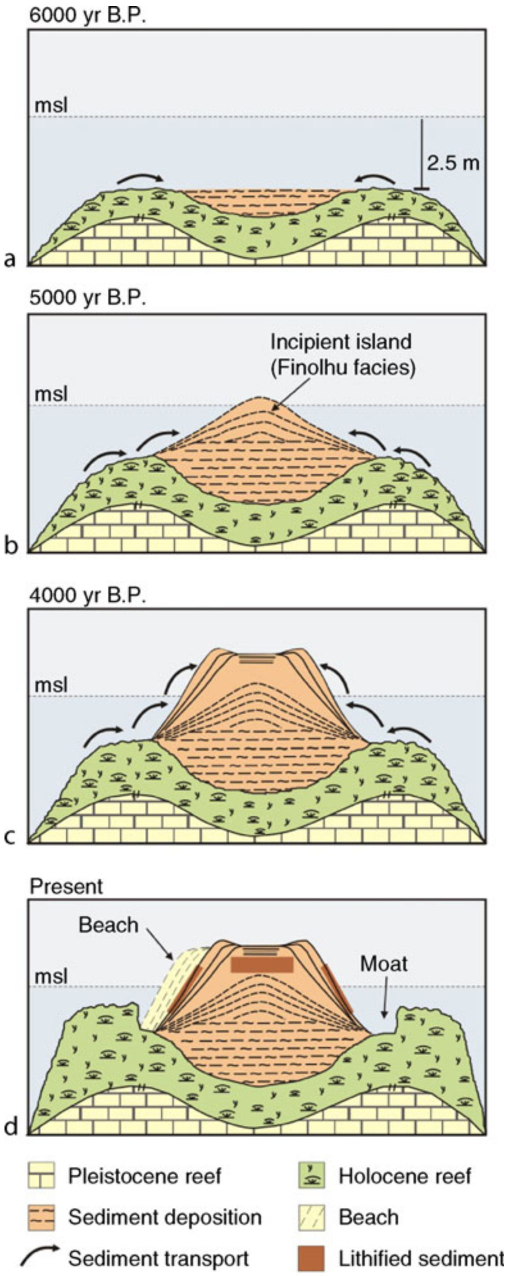
The health of the Maldivian reefs is of critical importance for the maintenance of land, provision of resources (fisheries and aggregates) and economic earnings (tourism). The reef systems are vulnerable to the impact of anthropogenic stresses and global environmental change. Of note, the Indian Ocean-wide bleaching event of 1998 is estimated to have killed upward of 90% of living coral. This observation is based on the monitoring of limited shallow water reef locations (Rajasuriya et al., 2004). Despite localized coral recovery, global climate change and associated sea level rise, increased ocean temperatures and ocean acidification all pose severe threats to reef health in the near future.

Reef islands

The Maldives contains 1,190 reef islands perched on top of reef surfaces, 200 of which are inhabited. The islands provide the only living space for the Maldivian population of approximately 330,000. Islands are found on peripheral and lagoonal reefs with larger islands located on the peripheral rims of closed atolls. Composed entirely of carbonate sand and gravels derived from the surrounding reef, the islands are typically small and have a mean elevation of less than 1 m above sea level.

Detailed reconstructions of island formation show that the islands are mid-Holocene in age, forming as reefs reached the latter stage of vertical growth through the infill of shallow lagoons (Kench et al., 2005, Figure 3). A major phase of island building occurred 5,500–4,000 years ago across infilled lagoons with islands remaining relatively stable over the past 3,500 years. Following the phase of island building the outer reef has continued to grow, in final stages of catch-up, forming a moat around island shorelines. Although islands are composed largely of skeletal materials derived from the surrounding reef, cemented sediments can occur on the perimeter of islands (beachrock) and in the island core (cay sandstones and phosphate rocks). These lithified sediments indicate a degree of stability to the island core.

The reef islands have been found to exhibit a high degree of short-term variability in response to seasonal climate patterns and extreme events. Island shorelines exhibit rapid morphological adjustments in response to monsoonal reversals in wind and wave patterns (Kench and Brander, 2006). Situated outside the zone of cyclone-genesis, the archipelago and its islands are not subject to extreme storms. However, the archipelago was affected by the passage of tsunami waves as a consequence of the December 2004 Sumatran tsunami. While this event promoted a small amount of island erosion, tsunami waves inundated islands and allowed the transfer of sediments from beaches to island surfaces. This process of overwash was able to vertically build the margins of reef islands by up to 0.3 m providing further



Maldives, Figure 3 Summary model of the formation of reef platform islands in the Maldives (after Kench et al., 2005).

evidence that the reef islands are morphologically dynamic features on reef surfaces (Kench et al., 2006).

Summary

Located in the central Indian Ocean the Maldives is one of the largest and most geologically complex mid-ocean atoll chains in the world. The archipelago possesses high biological diversity, a unique geological history, and contains a diverse range of reef structures and atoll types. The reefs are also host to a large number of vegetated reef islands. However, despite the aerial extent and unique aspects of reef and island diversity, structure and evolution, the Maldives remain one of the least studied reef systems in the world.

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Cross-references

Atolls
Coral Cay Classification and Evolution
Faroes Reefs
Gardiner, John Stanley (1872–1946)
Indian Ocean Reefs

MANGROVE ISLANDS

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Definition

"Mangrove islands" is a descriptive term applied usually to overwash banks or outcrops vegetated notably by mangrove plants (cp. Woodroffe, 2002). Considering the geological definition of islands, mangrove islands are atypical since they lack a terrestrial land mass surrounded by water. In the absence of mangrove plants, the base geomorphic feature would be described as a mud bank or sand cay. Therefore, it is the mangroves themselves that give mangrove islands their island-like appearance. The term is sometimes applied more broadly, however, to include other "low" islands with relatively small terrestrial parts amongst the mangroves.

Mangrove islands are a distinct type of island where the bulk of land area, if not all, is below tidal high water. Since mangrove islands depend on mangrove presence, their occurrence is restricted, as are mangroves, to the tropics and subtropics where sea temperatures rarely drop below 20°C, except in Australia and New Zealand (see *Mangroves*). In addition, the substrate of mangrove islands varies widely, including banks of fine estuarine mud, peat, sheltered sandy berms, rocky outcrops, and coral reef enclaves (e.g., see, Hopley, 1982; Duke et al., 1998; Macintyre et al., 2004). While mangroves favor soft sediments and nutrients in sheltered conditions, they can be very adaptable, clinging tenaciously to hard or soft substrate in periodically exposed locations.

The biodiversity and structural complexity of vegetation on mangrove islands is influenced by global and regional factors (Duke et al., 1998). Overall, mangrove assemblages are comprised chiefly of downstream marine species: in the Indo-West Pacific (see Duke and Larkum, 2008) – *Aegialitis annulata*, *Avicennia marina*, *Bruguiera gymnorhiza*, *Lumnitzera racemosa*, *Osbornia octodonta*, *Pemphis acidula*, *Rhizophora stylosa, Rhizophora mucronata*; and in the Atlantic East Pacific (see Tomlinson, 1986) – *Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*, *Rhizophora mangle*. Specific diversity depends on terrigenous catchment and annual rainfall, reflecting the importance of fresh water. In general, the larger the catchment water supply, the greater the number of mangrove species. So, larger islands often have greater numbers of mangrove species.

There are two predominant types of mangrove islands, as distinct from continental or oceanic islands. Mangrove islands are influenced by sea level, substrate type, and geomorphic setting, to form as either: (1) reefal mangrove islands based on carbonate or peat sediments (Hopley, 1982; Macintyre et al., 2004), clear waters, and low nutrients; or (2) river mouth mangrove islands (Duke et al., 2005) based on fine terrigenous sediments, turbid waters, and runoff nutrients. Both settings are characterized by active processes where over time the tidal banks are continually formed, eroded, and reformed. Reefal mangrove islands form when mangroves grow on coral reef flats or behind shingle ramparts. Low energy conditions may arise within exposed locations. On Australia's Great Barrier Reef, "low wooded islands" with mangroves (Hopley, 1982), like Low Isles (Figure 1), often occur behind shingle ramparts on windward, southeastern shores of reefs. Mangrove islands form Montgomery Island in northern Western Australia, and they show that tidal range can be extreme, to 10 m. Overall, the height of mangrove stands on coral reefs is usually modest to low, below 5 m. River mouth mangrove islands form when mangroves occupy depositional banks downstream in the mouths of river-influenced estuaries. Low energy conditions occur during seasonal lulls in river flow and storms. Mangroves readily colonize fine deltaic sediments, rich in organic matter, washed in nutrient-loaded river runoff. The height of resulting mangrove trees is maximal, in some cases attaining 50 m; for example, at the mouth of the Mahe River, Darien, Pacific coast of Panama, and Central America. Because these mangrove islands are formed from riverine sediments, their number and size have expanded greatly following the clearing and disturbance of catchment vegetation, as seen in the Fitzroy River estuary northeastern Australia (Duke et al., 2005; see Figure 2).

Mangrove islands provide valuable structure and habitat, plus areas of respite and refuge, for key groups of

Mangrove Islands, Figure 1 Expanding mangrove island on the coral reef of Low Isles, northeastern Australia, in 2008 – home to threatened Torres Strait Pigeons.

Mangrove Islands, Figure 2 Mangrove islands double in area over the last three decades in the river mouth of the Fitzroy River, northeastern Australia, in 2004.

displaced coastal fauna, including: insects, fish, crustaceans, molluscs, birds, flying foxes, and other bats. In northeastern Australia, river mouth mangrove islands are the last refuge for flying fox colonies (Hall and Richards, 2000). In the same region, Torres Strait pigeons take refuge on the reefal mangrove island at Low Isles (Crome, 1975; Frank and Jell, 2006).

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MANGROVES

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Synonyms

Mangrove forest; Mangrove swamp; Mangrove trees; Sea trees; Tidal forest; Tidal swamp; Tidal wetland

Definition

Mangroves. A tidal habitat comprised of salt-tolerant trees and shrubs. Comparable to rainforests, mangroves have a mixture of plant types. Sometimes the habitat is called a tidal forest or a mangrove forest to distinguish it from the trees that are also called mangroves.

Mangrove. A tree, shrub, palm, or ground fern, generally exceeding 0.5 m in height, that normally grows above mean sea level in the intertidal zone of marine coastal environments and estuarine margins.

Tidal salt marsh. Small shrubs or herbaceous plants, generally less than 0.5 m in height, that normally grow above mean sea level in the intertidal zone of marine coastal environments and estuarine margins.

Tidal salt pan. Flat areas of fine sediments lacking macrophyte vegetation above mean sea level in the intertidal zone of marine coastal environments and estuarine margins.

Tidal wetlands. The combination of mangroves, tidal salt marsh, as salt pan, as habitats distinctly occurring between mean sea level and the highest tides. In arid and cooler settings, mangroves share this tidal niche, or are replaced with diminutive halophyte cousins, the tidal saltmarsh, and flat salt pan expanses with their remarkable microalgal carpet.

Introduction

Mangroves are one of the world's dominant coastal ecosystems comprised chiefly of flowering trees and shrubs uniquely adapted to marine and estuarine tidal conditions (Tomlinson, 1986; Duke, 1992; Hogarth, 1999; Saenger, 2002; FAO, 2007). They form distinctly vegetated and often densely structured habitat of verdant closed canopies (Figure 1) cloaking coastal margins and estuaries of equatorial, tropical, and subtropical regions around the world (Spalding et al., 1997). Mangroves are well known for their morphological and physiological adaptations coping with salt, saturated soils, and regular tidal inundation, notably with specialized attributes like: exposed breathing roots above ground, extra stem support structures (Figure 2), salt-excreting leaves, low water potentials and high intracellular salt concentrations to maintain favorable water relations in saline environments, and viviparous water-dispersed propagules (Figure 3).

Mangroves have acknowledged roles in coastal productivity and connectivity (Mumby et al., 2004), often supporting high biodiversity and biomass not possible otherwise. Mangrove ecosystems are key sources of coastal primary production with complex trophic linkages (Robertson et al., 1992), as nursery and breeding sites of marine and arboreal life (Figure 4), and as physical shelter and a buffer from episodic severe storms, river flows, and large waves.

In tropical waters, mangrove stands are often sandwiched between two of the world's iconic ecosystems of coral reefs and tropical rainforests. Biota-structured ecosystems, like these, play a unique role in coastal ecosystem processes via a combination of well-developed linkages, coupled with transient biota uniquely adapted to unusual and often dramatic physico-chemical gradients. Linked and dependent relationships developed over millennia have become vital to the survival of each biome. Colonial corals flourish in shallow warm seas of coasts where mangroves buffer and protect them from land runoff. Mangroves absorb unwanted nutrients and turbid waters stabilizing otherwise smothering water-borne sediments and depositional shorelines. These specialized plant assemblages provide important ecosystem services along with additional acknowledged roles of highly productive habitat and nursery sites. The consequences in disturbing these habitats is likely to have unexpected and far-reaching impacts on neighboring ecosystems and dependant biota (Duke et al., 2007).

Uniquely mangrove origins and vulnerability

Mangroves are a unique ecological assemblage (Duke et al., 1998), remarkable for their relatively small number of widely distributed flowering plants – evolved mostly post-Cretaceous over the last 60–100 million years. The relatively recent evolution of these plants may explain

Mangroves, Figure 1 Sinuous channels and tidal wetlands of Missionary Bay, northeastern Australia. Amongst the wide mangrove zones are bare saltpans with saltmarsh patches.

Mangroves, Figure 2 A forest of exposed, above-ground stilt roots of *Rhizophora apiculata*, Daintree River estuary, northeastern Australia.

Mangroves, Figure 3 Mature, viviparous propagules of a *Bruguiera gymnorhiza* tree, near Dumbea, New Caledonia.

their comparatively low diversity, but this feature is arguably also related to the harsh environmental conditions defining the niche. Today's mangrove flora includes representatives of at least 21 plant families, testament to the adaptive success of various phylogenetic lineages venturing into the intertidal zone from upland rainforest ancestors. This small group of highly specialized plants tap rich estuarine nutrients with characteristically shallow

Mangroves, Figure 4 A cormorant makes use of an eroding edge tree of *Sonneratia caseolaris*, in the upper Daintree River estuary, northeastern Australia.

arrays of below-ground roots bearing distinctively vascular, air-breathing anatomy. Specialized above-ground roots and buttresses further provide exposed air-breathing surfaces and physical support, as well as significant habitat amongst their structure – a characteristic shared with adjacent upland forests and reefal corals.

Ancestral mangrove plants are believed to have reinvaded marine environments in multiple episodes from diverse angiosperm lineages culminating in today's mangrove flora (also Saenger, 2002). Their appearance and evolution appears constrained by key functional attributes essential to their survival in saline, inundated settings where isotonic extremes, desiccation, and hydrologic exposure combine as uniquely harsh constraints on organisms living in the tidal zone, and estuaries. The land–sea interface is a dynamic environment, where subtle changes in climate, sea level, sediment, and nutrient inputs have dramatic consequences for the distribution and health of mangroves. Adding to these, direct human disturbance of mangroves include: eutrophication, dredging/filling, overfishing, and sedimentation. The combined pressures, coupled with global climate change and sea level rise, have led to many healthy mangrove areas becoming endangered communities (Duke et al., 2007). Various rehabilitation projects have shown further that it is extremely difficult to achieve effective, large-scale restoration. Urgent protective measures need to be implemented to avoid further mangroves losses and further degradation of coastal ecosystems.

Rich and diverse

Mangroves are a diverse group of predominantly tropical trees and shrubs growing in the upper half of the intertidal zone of coastal areas worldwide (Duke, 1992). They are often mistakenly thought of as a single entity. But, like coral reefs, healthy mangroves are functionally diverse and complex. They also provide essential structure and habitat for a host of marine and intertidal species (Figure 5), comprised of both: residents amongst their dense forest of stems and complex roots, and as visitors with each flooding tide. Mangroves are analogous to tropical rainforests also, where they have foliage canopy habitat for birds, mammals, insects, and other invertebrates. Shared ancestral links underlie many similarities between these plant-structured habitats.

Mangroves are not a genetic entity, but an ecological one (Duke et al., 1998). Mangrove vegetation includes a range of functional forms, including trees, shrubs, a palm, and ground fern. The only plant families comprised exclusively of mangrove taxa are Avicenniaceae and Sonneratiaceae, although this continues to be debated. In Table 1, 77 species of mangrove plants are listed for the world. This number however, is not fixed, and varies with different authors since there are a number of subjective and influential factors, including: doubts surrounding the definition of mangroves; whether to include saltmarsh plants; whether to include mangrove associates; and inconclusive taxonomic description of all taxa.

Amongst the 21 flowering plant genera found in mangroves, there is a relatively high degree of specialization for the tidal wetland habitat. Twelve angiosperm genera are exclusively mangrove while ten others include non-mangrove species. This latter group includes: *Aglaia*, *Barringtonia*, *Cynometra*, *Diospyros*, *Dolichandrone*, *Excoecaria*, *Heritiera*, *Mora*, *Pemphis*, *Tabebuia*, and

Mangroves, Figure 5 Terebralia gastropods devouring a fallen mangrove leaf, near Koumac, New Caledonia.

Xylocarpus. For *Pemphis*, this genus has only one upland species located inland as an isolated population on the island of Madacascar. Others show different degrees and types of variation. For instance, distinct hybrids are reported in four genera including *Bruguiera*, *Lumnitzera* (Figure 6), *Sonneratia*, and *Rhizophora* (in Table 1, see species prefixed with "X"). Overall, the diversity of species in these genera is often relatively low, being one or two. These relatively low measures of diversity are believed to be the result of harsh growth conditions present in intertidal habitats. Local and regional environmental factors are believed to play a key role in defining the ecological entity that is mangrove habitat. *Rhizophora* species, the most diverse and dominant genus, often occur at the front of mangroves, fronting the sea or channel, and associated with moderate salinities but not extremes. *Avicennia* species, having a wider salinity tolerance, are notably variable occurring in both frontal and upland stands in the Indo-West Pacific.

Structural diversity

Mangrove plants characteristically range from trees (like species of *Avicennia* (Figure 7), *Rhizophora* (Figure 2)), to shrubs (species of *Aegiceras*, *Aegialitis*, *Pemphis*, and *Conocarpus*), to the trunkless palm (*Nypa fruticans* (Figure 8)), and ground fern (*Acrostichum*). Trees and shrubs vary further where they might be columnar and erect (*Pelliciera rhizophorae* (Figure 9), *Bruguiera parviflora*), to spreading, sprawling (*Acanthus* spp., *Scyphiphora hydrophylacea*), and multiple-stemmed (*Ceriops decandra*). Growth form might also vary within the same species (*Lumnitzera littorea* and *Rhizophora*), having both an erect tree form, and low tangled thicket forms. In general, edge plants (both waterfront and landward) have more lower limbs and foliage, and their stems are laterally sprawling and sinuous, rather than erect and straight. Some species typically form combined closed canopies (*Avicennia marina*, *Rhizophora apiculata*, *Bruguiera parviflora*, *Bruguiera gymnorhiza*, *Camptostemon schultzii*, *Xylocarpus* spp.), while others are commonly found as undercanopy plants beneath the closed canopy (like species of *Aegiceras*, *Cynometra*, *Acanthus*, *Acrostichum*, and *Ceriops decandra*).

Mangroves have notable above-ground breathing roots and shallow below-ground anchoring roots, because their soils are usually saturated and airless. The trees have broad support structures, such as buttresses and sturdy prop roots, because soils are often soft and unconsolidated. Root structures above ground include four types: (1) pneumatophores – pencil-like (*Avicennia* (Figure 7)), erect conical (*Xylocarpus moluccensis*), thinly conical (*Sonneratia alba*), and elongate conical (*Sonneratia caseolaris* (Figure 4) and *Sonneratia lanceolata*); (2) knee roots – thick and knobbly (*Bruguiera*) and thin and wiry (*Lumnitzera littorea*); (3) stilt roots (*Rhizophora* (Figure 2)); and (4) buttresses – sinuous planks (*Xylocarpus granatum*, *Heritiera littoralis*, and *Ceriops* spp., *Pelliciera rhizophorae*), and erect "fins" (*Bruguiera* X *rhynchopetala*, *Xylocarpus moluccensis*). Roots are used by various fauna, but most notably by burrowing shipworms, mollusks, termites, and crabs.

Factors influencing mangrove distributions

Mangroves have evolved and flourished in their dynamic setting. While mangroves collectively have specialized morphologies and physiologies, these attributes have limits that vary with individual species. The distributional range of each mangrove species reflects its response to the dominant influencing factors at global, regional, and local scales (Duke et al., 1998).

Where mangroves inhabit tropical and subtropical regions of the world, their presence in higher latitudes is generally constrained by the 20°C winter isotherm in the respective hemispheres (Figure 10). Exceptions to this pattern mostly correspond to the paths of oceanic circulation currents where mangrove distributions are broader on eastern continental margins and more constrained on the west. Present day distribution patterns depend on specialized, water-buoyant propagules of mangroves. Their dispersal is constrained by wide bodies of water and continental land masses. Four major barriers restrict dispersal of warm coastal marine organisms (including mangroves) around the world today, namely: the continents of (1) Africa and Euro-Asia; plus (2) North and South American continents; and the oceans of (3) the North and South Atlantic; plus (4) the eastern Pacific. The relative effectiveness of each of these barriers differ, depending on its

Mangroves, Table 1 Mangrove species of the world. Families and genera with zero 'Non-mangrove' are exclusively mangrove (modified from Duke et al., 1998)

Families with mangroves	Family relatives of mangrove taxa	Family genera	Mangrove genera	Non-mangrove	Mangrove spp.	Species of mangroves
Acanthaceae	Black-eyed Susan, Shrimp plants	250–300	*Acanthus*	30	3	*Acanthus ebracteatus* *Acanthus ilicifolius* *Acanthus volubilis*
Arecaceae	Palms	200	*Nypa**	0	1	*Nypa fruticans+*
Avicenniaceae (ex Verbenaceae) (or Acanthaceae)	Grey mangroves	1	*Avicennia*	0	8	*Avicennia alba* *Avicennia integra* *Avicennia marina* *Avicennia officinalis* *Avicennia rumphiana* *Avicennia bicolor* *Avicennia germinans* *Avicennia schaueriana*
Bignoniaceae	Trumpet-tulip tree, Jacarandas	120	*Dolichandrone*	9	1	*Dolichandrone spathacea*
			Tabebuia	245	1	*Tabebuia palustris*
Bombaceae (or Fabaceae)	Baobab, Balsa, Kapok, Durian	31	*Camptostemon*	0	2	*Camptostemon philippinense* *Camptostemon schultzii*
Caesalpiniaceae (or Fabaceae)	Cassia, Tamarind, Legume	150	*Cynometra*	70	1	*Cynometra iripa*
			Mora	19	1	*Mora oleifera*
Combretaceae	Combretum, Quiqualis	20	*Lumnitzera*	0	3	*Lumnitzera littorea* *Lumnitzera racemosa* *Lumnitzera* X *rosea*
			Laguncularia	0	1	*Laguncularia racemosa*
			Conocarpus	0	1	*Conocarpus erectus*
Ebenaceae	Ebony, Persimmons	3	*Diospyros**	400	1	*Diospyros littorea*
Euphorbiaceae	Castor oil, Spurges	300	*Excoecaria*	35–40	2	*Excoecaria agallocha* *Excoecaria indica*
Lecythidaceae	Brazil nuts	15	*Barringtonia**	40	1	*Barringtonia racemosa*
Lythraceae	Crepe Myrtle, Henna, Cuphea	25	*Pemphis*	1	1	*Pemphis acidula*
Meliaceae	Mahogany, Rosewood	50	*Aglaia*	100	1	*Aglaia cucullata*
			Xylocarpus	1	2	*Xylocarpus granatum* *Xylocarpus moluccensis*
Myrsinaceae	Turnip-wood, Mutton-wood	35	*Aegiceras**	0	2	*Aegiceras corniculatum* *Aegiceras floridum*
Myrtaceae	Eucalyptus, Bottlebrush, Guavas	80–150	*Osbornia*	0	1	*Osbornia octodonta*
Pellicieraceae	Tea, Camellia, Franklinia	1	*Pelliciera*	0	1	*Pelliciera rhizophorae*
Plumbaginaceae	Sea lavender, Thrifts	10	*Aegialitis**	0	2	*Aegialitis annulata* *Aegialitis rotundifolia*
Pteridaceae	Ferns	35	*Acrostichum*	0	3	***Acrostichum aureum*** *Acrostichum speciosum* *Acrostichum danaeifolium*
Rhizophoraceae	Crossostylis, Cassipourea	16	*Bruguiera*	0	7	*Bruguiera cylindrica* *Bruguiera exaristata* *Bruguiera gymnorhiza* *Bruguiera hainesii* *Bruguiera parviflora* *Bruguiera* X *rhynchopetala* *Bruguiera sexangula*

Mangroves, Table 1 (Continued)

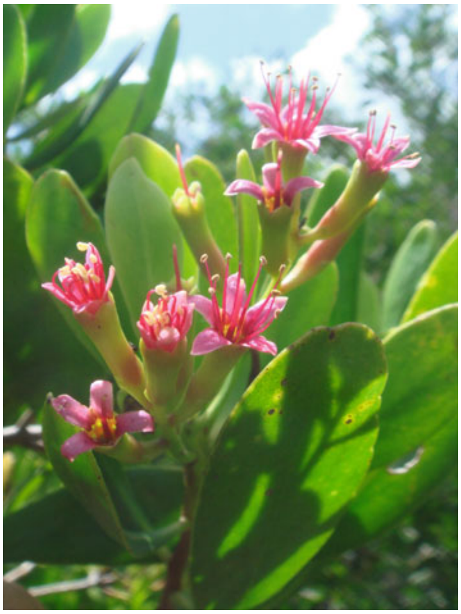
Families with mangroves	Family relatives of mangrove taxa	Family genera	Mangrove genera	Non-mangrove	Mangrove spp.	Species of mangroves
			Ceriops	0	4	*Ceriops australis* *Ceriops decandra* *Ceriops tagal* *Ceriops zippeliana*
			Kandelia	0	2	*Kandelia candel* *Kandelia obovata*
			Rhizophora	0	11	*Rhizophora* X *annamalayana* *Rhizophora apiculata* *Rhizophora* X *lamarckii* *Rhizophora mucronata* ***Rhizophora samoensis*** *Rhizophora* X *selala* *Rhizophora stylosa* *Rhizophora* X *tomlinsonii** *Rhizophora mangle*+ *Rhizophora racemosa* *Rhizophora X harrisonii*
Rubiaceae	Coffee, Gardinia, Quinine	500	*Scyphiphora*	0	1	*Scyphiphora hydrophylacea*
Sonneratiaceae (or Lythraceae)	Duabanga	2	*Sonneratia*	0	9	*Sonneratia alba* *Sonneratia apetala* *Sonneratia caseolaris* *Sonneratia griffithi* *Sonneratia* X *gulngai* *Sonneratia X hainanensis* *Sonneratia lanceolata* *Sonneratia ovata* *Sonneratia* X *urama*
Sterculiaceae (or Malvaceae)	Cocoa, Kola, Bottle trees	70	*Heritiera*	29	3	*Heritiera fomes* *Heritiera globosa* *Heritiera littoralis*

Genera marked with an asterisk have been classified previously comprising their own family, named: Diospyraceae, Barringtoniaceae, Aegicerataceae, Nypaceae, Aegialitidaceae, and Pellicieraceae, respectively. Species region codes: regular font refers to those from the Indo-West Pacific; underlined names occur in the Atlantic East Pacific; **bold underlined** occur naturally in both; + indicates species introduced to, and established in, the other region
*See Duke (2010)

geological history, dispersal/establishment ability, and the evolutionary appearance of respective species.

Regional distribution patterns of mangroves are further influenced by habitat availability and local environmental factors such as rainfall, estuary size, and tides. In Australia (Duke, 2006), two major environmental factors, temperature and rainfall, largely explain regional distributions where low temperatures limit the latitudinal extent of species – affecting the pool of available species. The relative number of species is also highest in areas of higher rainfall. Species richness declines generally with increasing latitude on north-south coastlines and groupings of islands. In general, species diversity in mangrove stands of equal size is greatest in wet equatorial areas. However, where rainfall is comparable, species diversity is higher in longer estuaries with larger catchments. The influence of rainfall, therefore, not only comes from rain falling directly on mangrove stands, but also as it influences runoff volume from upstream catchments.

At the local scale, individual mangrove species usually occupy only part of an estuary from sea mouth to tidal limit upstream (Duke et al., 1998). Species generally display a preferred estuarine range based on the overall salinity tolerance. For instance, species like *Avicennia marina*, *Rhizophora stylosa*, and *Sonneratia alba* commonly occur in downstream locations. By comparison, *Rhizophora mucronata*, *Sonneratia caseolaris*, and *Bruguiera sexangula* are found upstream in larger,



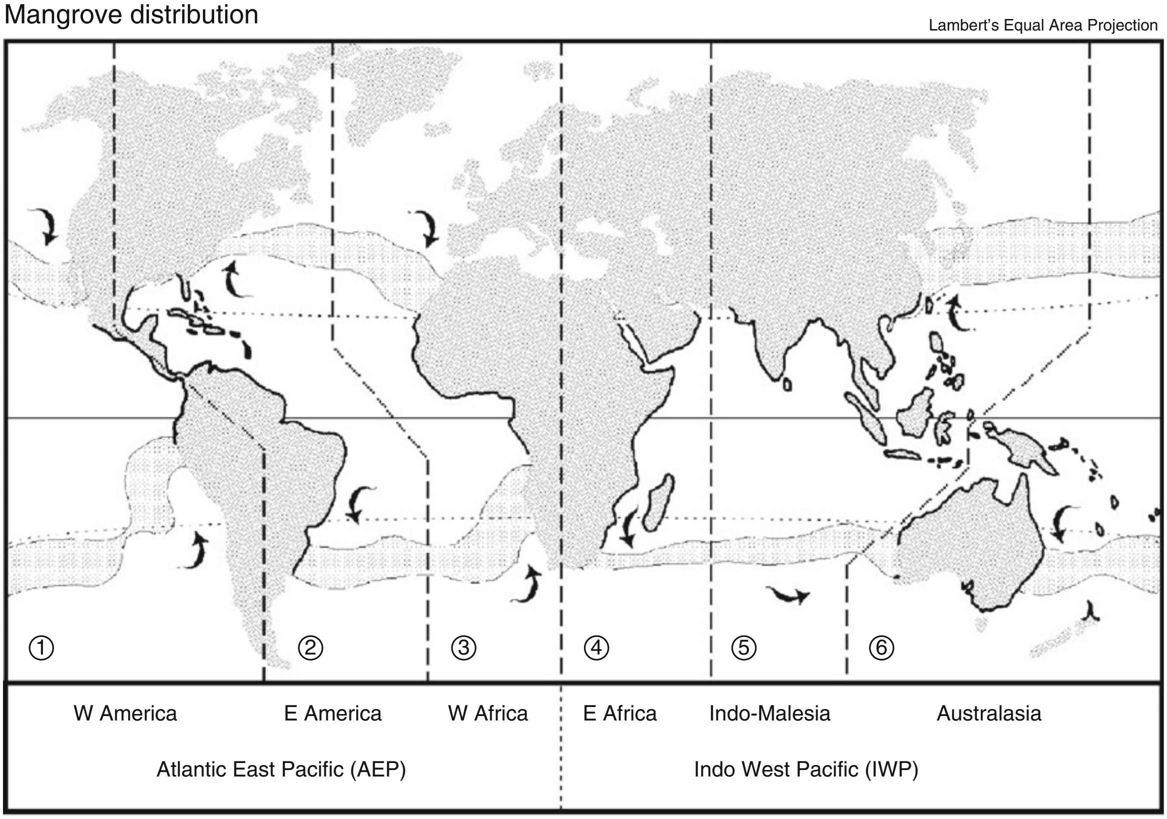
Mangroves, Figure 6 Delicate pink flowers of the rare hybrid shrub, *Lumnitzera rosea*, Le Cap River, New Caledonia.

Mangroves, Figure 7 Sizing up an ancient tree of *Avicennia germinans*, near Braganza, Amazonian Brazil.

freshwater-dominated estuaries. Furthermore, at this local scale, respective species occupy distinct parts of the tidal profile above mean sea level. Characteristic zonation bands of different mangrove assemblages indicate the pronounced influences of inundation frequency and tidal elevation. For example, species like *Avicennia integra*, and *Sonneratia alba* commonly occupy low intertidal positions. By comparison, *Heritiera littoralis*, *Xylocarpus granatum*, and *Lumnitzera racemosa* are found in high intertidal positions. Some species, such as *Avicennia*

Mangroves, Figure 8 Erect fruiting bodies of the striking mangrove palm, *Nypa fruticans*, Kien Giang Province, Vietnam.

Mangroves, Figure 9 Attractive flowers of *Pelliciera rhizophorae* support hummingbirds, near Diablo on the Pacific coast of Panama, Central America.



Mangroves, Figure 10 World distribution of mangroves (*dark line* along coastal margins) showing global regions and subregions with ocean zone limits at the seasonal 20°C isotherm (*source*: Duke et al., 1998).

marina, *Acanthus ilicifolius*, and *Aegiceras corniculatum*, are observed at high and low intertidal positions.

Conclusion

Mangroves and tidal wetlands are essential to the sustainability of highly productive natural coastal environments. However, these ecosystems and their dependant biota (Figures 4, 5, and 9) are under serious threat from the escalation this century of large-scale land clearing and conversion of coastal forested wetlands (including mangroves) with the development of coastal lands for agricultural, aquaculture, port, and urban and industrial use (Field, 1995; Duke et al., 2007). In populated areas, key coastal rivers have become little more than drains transporting eroded mud and effluent to settle in downstream estuarine reaches, as well as in shallow embayments and inshore coral reefs. Remaining mangroves have become depauperate, poorly functional vestiges with relatively low resilience. Where healthy, mangrove-lined estuaries had once offered respite and critical dampening of land runoff, in recent years these bastions of coastal buffering and filtering – dubbed "coastal kidneys" – are not responding well to expanding human activities. Efforts to remediate these impacts is being undertaken in many ways with international and regional partnerships, but more is needed as the full impact of global climate change and sea level rise begin to take effect.

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Cross-references

Coral Cay Classification and Evolution
Low Wooded Islands
Mangroves

MARIANA ISLANDS, CORAL REEF GEOLOGY

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Definition

The Mariana Islands are an arch of volcanic islands stretching ~500 miles from Guam to Uracas. Coral reefs occur only in the volcanically inactive southern part (Figure 1). Most of the human population lives on Guam and Saipan and the political organization is split into the U.S. Territory of Guam and the Commonwealth of the Northern Mariana Islands.

The Marianas are part of the Izu-Bonin-Mariana (IBM) arc system, stretching ~2,800 km from Japan to south of Guam. Modern reef building occurs exclusively in the southern Marianas from Guam to Farallon de Medinilla (Figure 1). Corals also occur in the northern arc but no extensive framework production is reported, likely due to a combination of high latitude and relative tectonic instability. In the southern Marianas, temperatures are tropical and ideal for reef-building organisms. Mean annual air temperatures in Guam are 27°C, with ~6°C variations between daily maxima and minima (Figure 2). Relative humidity ranges 65–80% by day and 85–100% by night (Mink and Vacher, 1997). Long-term annual SST means vary between 28°C and 29°C. Tinian has a mean tidal range of 45 cm and a spring tide range of 65 cm (Doan et al., 1960). Rainfall averages at Guam 85–115 in./year (Gingerich, 2003), at Tinian 43–97 in./year (Gingerich, 2002), and at Saipan 34–145 in./year (Carruth, 2003). Wet and dry seasons are well developed with ~70% of total annual rainfall from July–December. Seasonally pulsed rainfall in combination with steep slopes, lateritic soils and deforestation led to runoff and sedimentation problems on coral reefs (Wolanski et al., 2003, 2004). The Marianas are influenced by the ENSO, and coral records indicate an ~0.75°C warming over the past two centuries (Asami et al., 2005).

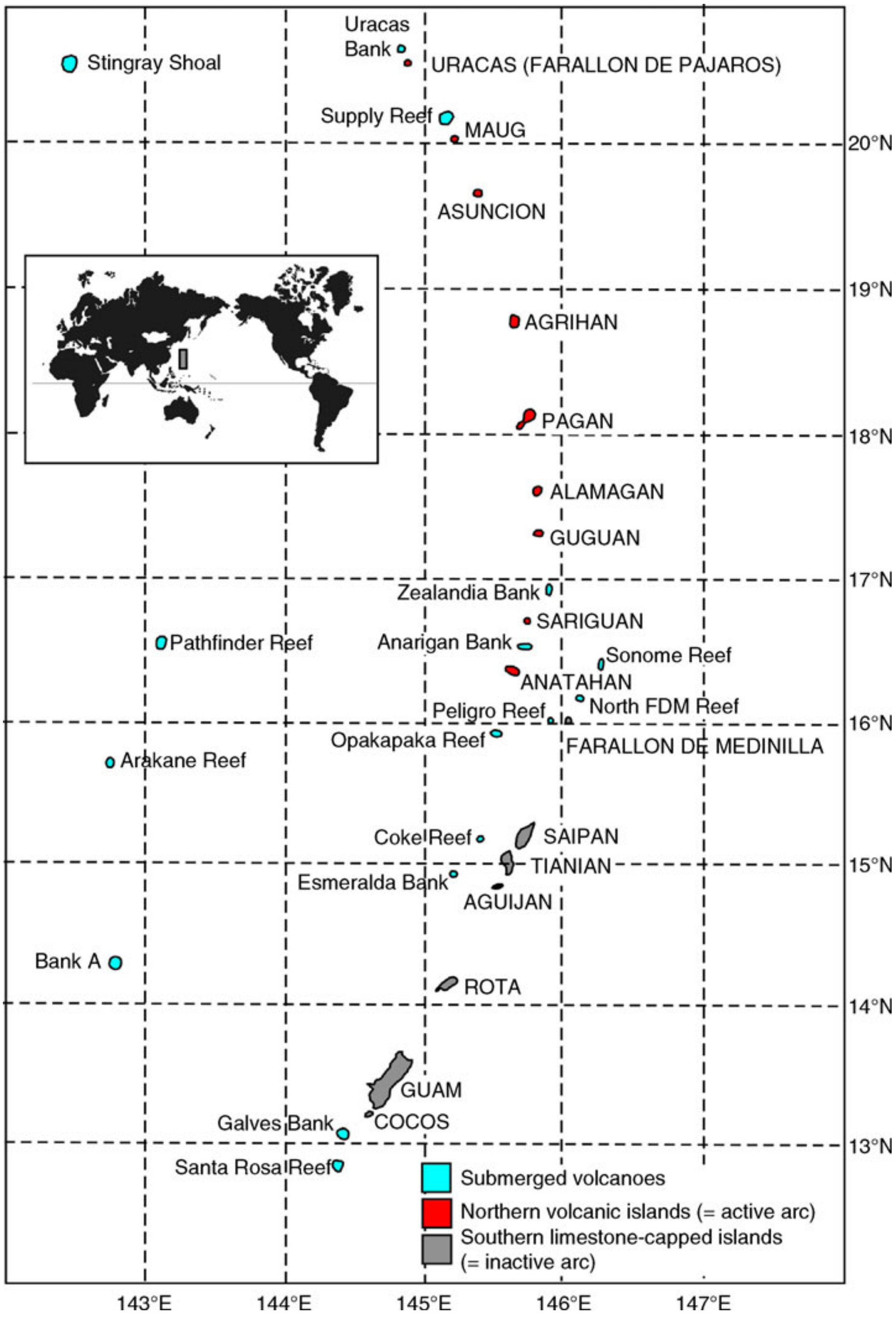
Holocene coral reefs in the southern Marianas

Two major Holocene reef-building episodes are known in the southern Marianas. An early Holocene episode is found in the Merizo (Guam), Milencatan (Rota) and Tanapag (Saipan) Limestones, and the modern reef (Siegrist et al., 1984b). Present-day coral frameworks are mostly narrow and of the fringing type, their morphology often clearly influenced by underlying morphology. In Guam, many small bays are reef-fringed with rivers entering. In such cases, reefs are discontinuous at the rivermouths and increase in thickness and coral cover away from the rivers (Wolanski et al., 2003, 2004). Two notable exemptions to the general pattern of narrow fringing reefs hugging the islands' shorelines exist in Cocos Lagoon (Guam) and Tanapag Lagoon (Saipan), where barrier reefs occur. Development of these lagoons is structurally controlled. Additionally, fringing reefs are developed along the shorelines inside the lagoons (Emery, 1962; Randall, 1979). Also Tinian had a small section of barrier reef that was filled and dredged into a port during World War II.

Four distinct coral habitats (Figure 3), of which only one involves an actively growing reef, occur in the Marianas (Randall, 1985):

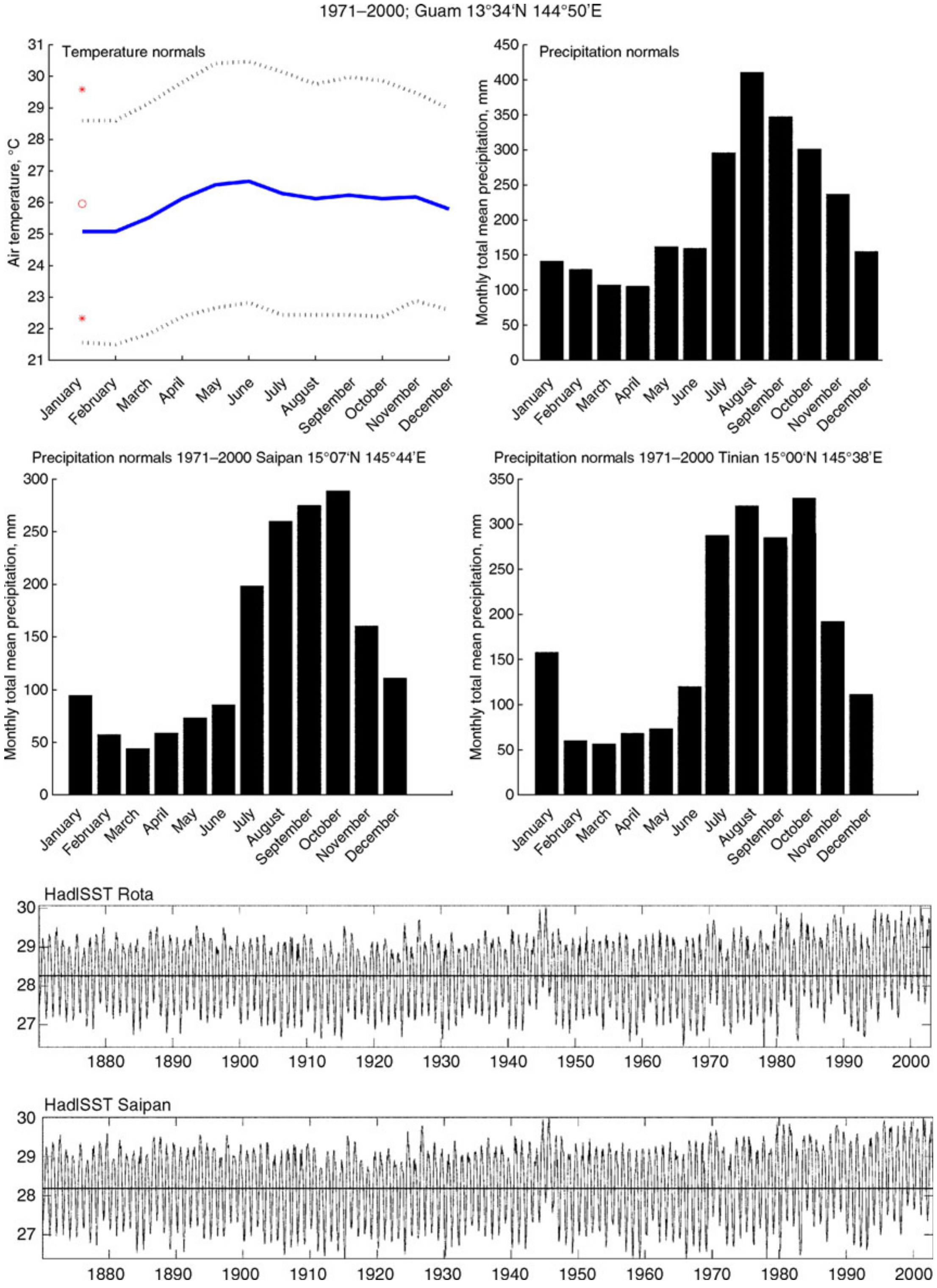
- Habitat I consists of *in situ* reef frameworks, with well-developed buttress and channel system (Pagan, Anatahan, Saipan, Aguijan, Rota, Guam).
- Habitat II occurs among volcanic boulders, *in situ* frameworks are absent or only thin veneers (Pagan, Guguan, Anatahan).
- Habitat III exists primarily between old limestone rocks and boulders, *in situ* frameworks are absent (Aguijan).
- Habitat IV occurs along limestone slopes with few boulders, *in situ* frameworks are absent (Saipan, Rota, Guam).

Underlying, and determining the position of late Holocene reef growth are the early Holocene Merizo Limestone (also called "2 m limestone") on Guam, the Milencatan Limestone on Rota, and the Tanapag Limestone on Saipan. These limestones represent the first phase of reef building in the early Holocene from the post-Wisconsin transgression through the mid-Holocene highstand at ~4,000 year B.P. (before present). They contain beautifully preserved, emergent reef facies in the low supratidal to shallow subtidal and are exposed to about 2–4 m. The emergence of these early Holocene reefs is likely due to tectonic factors (Kayanne et al., 1993; Siegrist and Randall, 1992). Thickness on Guam varies between 5 and 1 m (Siegrist and Randall, 1992). The limestones are coral-dominated and contain virtually all genera that are found in the modern reefs. Growth history on Rota is as follows (Bell and Siegrist, 1988): at 5,500 year B.P. sea level flooded an older, bioclastic facies of the already

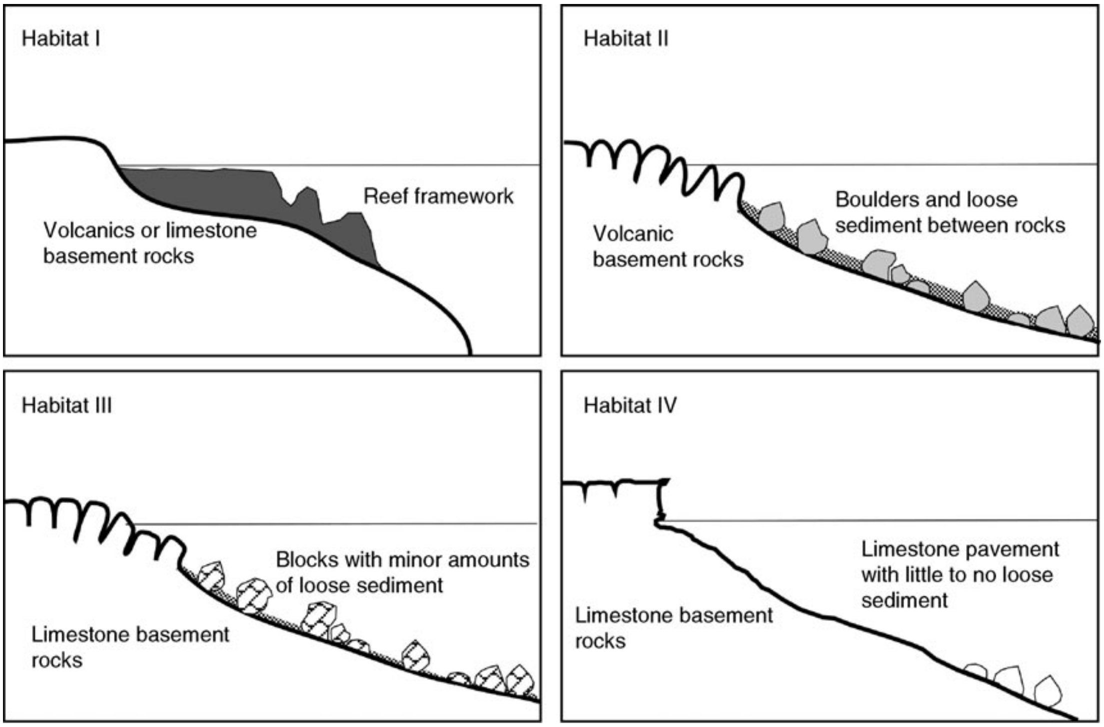


Mariana Islands, Coral Reef Geology, Figure 1 The Mariana Islands, consisting politically of Guam and the Commonwealth of the Northern Mariana Islands, the westernmost territories of the USA.

existing Milencatan Limestone and corals settled on preexisting highs about 80 m behind today's reef margin. Between 5,500 and 4,700 year B.P. corals accreted primarily under rising sea-level conditions and produced high buttresses dominated by corymbose *Acropora* and thick algal crusts. Large *Porites* mounds occurred in protected areas. Around 4,700 year B.P. sea-level rise slowed and the reefs caught up to the surface (then around +2.5 to 3 m above present sea level; Bell and Siegrist, 1988). Maximum sea level was at ~4,200 year B.P. on Rota and Guam (Kayanne et al., 1993; Pirazzoli and Montaggioni, 1988; Dickinson, 2000). Coral frameworks were then encrusted by digitate coralline algae, which Bell and Siegrist (1988) and Kayanne et al. (1993) interpret as



Mariana Islands, Coral Reef Geology, Figure 2 Atmospheric temperature record and precipitation at Guam, precipitation only at Saipan and Tinian (National Climatic Data Center, NOAA). Normals are uninterrupted measurements for three consecutive decades. Original data were transformed into metric units. Red circle = annual mean; red stars = minima and maxima. Lower two panels: Hadley Center's synthetic HadISST data for Rota and Saipan, as representatives of the southern and northern limestone islands. Lower two panels: Monthly temperature mean, and trend line.



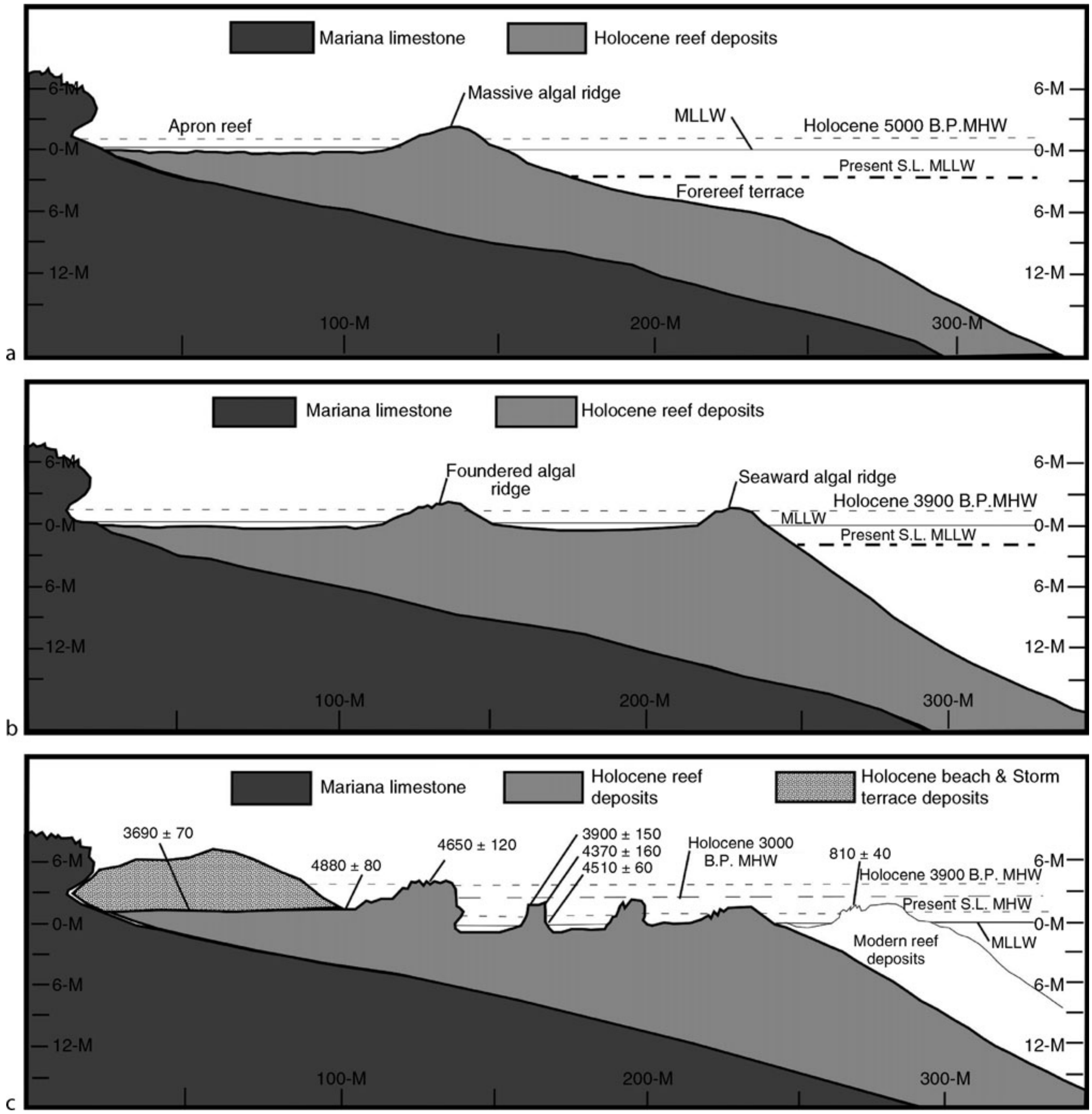
Mariana Islands, Coral Reef Geology, Figure 3 Generalized vertical profiles of coral habitats. (Modified from Randall [1985] and Siegrist et al. [1991].)

shallow, relatively high-energy facies, that can still be found in the same area today. Between 4,700 and 2,900 yr B.P. sea level fell, exposing the buttresses, and by 2,850 year B.P. corals settled on the present reef flat and the algal ridge began to develop (Figure 4). A total of 45 species, which still occur in the area, are recorded in the Merizo Limestone (Siegrist et al., 1984a; Randall et al., 1984). The dominant corals were corymbose *Acropora* which fueled the rapid growth and aggradation of the reefs. Similar facies were also described from Rota (Bell and Siegrist, 1988): (1) coral framestone facies of corymbose *Acropora* (primarily *A. humilis*; Kayanne et al., 1993) and in leeward settings of *Porites* mounds, considered to be the catch-up phase of reef growth; (2) algal bindstone facies, which are interpreted as the keep-up algal ridge; and (3) detrital facies at the leeward margin of the reef. High-magnesium cements were common besides aragonite cements.

On Guam and Rota, the early Holocene fringing reef (Merizo Limestone on Guam and Milancatan Limestone on Rota) displaced later Holocene reef growth seaward (Kayanne et al., 1993). Early Holocene limestones are well eroded, in particular, in the softer landward, detrital facies behind the corymbose coral facies (Siegrist et al., 1984a), in which deep lagoons can develop. The present-day reef frequently grows in form of well-developed groove-and-spur buttresses. Also the Merizo and Milencatan reefs had well-developed buttresses and it is unclear whether these reflect forcing by antecedent topography and/or wave energy. Morphology in deeper water frequently is also highly convoluted and in many areas it is evident that the modern reef is forced into its shape.

There are not only similarities in morphology between the early and late Holocene reefs, but also in the distribution and composition of the primary calcareous reef-builders. The same coral species, as listed by Siegrist and Randall (1985) and Randall et al. (1984), for the early Holocene occur today. Modern buttresses on the reef slope are primarily built by corymbose *Acropora* and deeper on the reef slope or in more sheltered areas, large *Porites*- or *Goniastrea*-built buttresses occur. Shallowest and highest energy parts of the reef edge, when not occupied by calcareous algae, show local dominance by *Pocillopora*. The shallowest reef environments in the Merizo and the present-day reefs are covered by a densely calcified algal ridge. Landward of this algal ridge, another zone of corymbose *Acropora* can be found. In lagoons that are eroded into the Merizo or Milancatan Limestone, typically good growth of *Heliopora coerulea* is found in well-drained areas, large stands of open-arborescent *Acropora* occur alongside *Porites* micro-atolls.

A similar zonation is found across the lagoons of Saipan and Guam. The biotic zonation described by Cloud (1959) at Tanapag lagoon is still recognizable despite significant reduction in space covered by corals and sea grasses (Houk and van Woesik, 2008). A reef slope with variable coral cover and groove-and-spurs abuts a well-cemented reef crest that slopes lagoonward and is



Mariana Islands, Coral Reef Geology, Figure 4 Stages of Holocene reef growth on Guam from Randall and Siegrist (1988). It is clearly visible how strongly the morphology of present-day reef growth is determined by early Holocene reef growth.

densely overgrown with massive corals and corymbose *Acropora*. Areas with large thickets of *Acropora formosa* still occur but cover is dramatically reduced since the 1940s (about 20% of the lagoon shifted from coral and sea grass cover to sand, Houk and van Woesik, 2008). Toward the center of the lagoon, coral growth becomes increasingly sparse as cover by sandy sediment increases. Rocky outcrops with low coral cover and increasingly high algal cover toward the land as well as small patch reefs occur irregularly in the lagoon. Dense sea grass beds have also been reduced in size (Houk and van Woesik, 2008).

General geology of the southern Marianas – volcanics and limestones

Guam, at the southwestern end of the West Mariana Ridge, was volcanically active from 32 to 20 Ma

(= million years) and 9 to 5 Ma (Reagan and Meijer, 1984). Rifting of the West Mariana Ridge created the Mariana Trough and the Mariana Ridge. Volcanic activity resumed ~1.3 Ma in the active, northern, ridge. The main volcanic basement of Guam resulted from the first volcanic phase and is evidenced in the middle Eocene Facpi Formation (~200 m thick boninite lavals with some limestone infills) and the Eocene to early Oligocene Alutom Formation (~400 m thick, tuffaceaous shales, sandstones, volcanic breccias, lapilli conglomerates, pillow lavas, tubidites, some calcareous shales in the Mahlac member, and some coral-rich floats, Schlanger, 1964). Serious carbonate sedimentation began in the upper Oligocene/lower Miocene as Maemong Limestone, a member of the Umatac Formation which is of shallow-water origin and consists of mud- to wackestones with coral (*Porites* and *Acropora*) rudstones and intermixed volcanic detritus. Reefal organisms such as corals, *Tridacna*, *Halimeda*, and crustose algae are common, but *ex situ* and no reef edifice is known. This episode represents a shallowing with carbonate precipitation around three volcanic highs on Guam. The Miocene Bonya Limestone contains deeper-water facies with reef coral and coralline algae detritus but no reefs are preserved, so deposition was likely on a seaward slope between volcanic cones. The Miocene Alifan Limestone contains mudstones that grade to sparry packstones with well-preserved reef fauna and flora (*Porites*, *Acropora*, and *Halimeda*). The smallest limestone unit on Guam is the Tortinian and Pontian Janum Limestone consisting of deep fore-reef to basinal facies (Siegrist and Randall, 1992). The Mio/Pliocene Barrigada Limestone is a chalky foraminiferal-algal wackestone with some corals (*Porites*, and *Astraeopora*). While essentially all limestones show reefal fauna among their components, no Miocene reefs crop out in Guam or anywhere in the Mariana Islands (Siegrist and Randall, 1992).

The most widely distributed limestone is the Plio-Pleistocene Mariana Limestone, the dominant carbonate on Guam, Rota, Aguijan, Tinian, and Farallon de Medinilla (Siegrist and Randall, 1992; Randall, 1995) and also of great importance on Saipan. It contains well-developed reefal and peri-reefal facies. On Guam, it can reach a thickness of 175 m. Reef margin facies generally crop out as the most seaward facies and coincide often with the edges of terraces. Rocks are coralline and coralgal boundstones, coarse grainstones, packstones, and wackestones. Branching and massive corals occur *in situ* and in growth position and Siegrist and Randall (1992) report a rich fauna, reminiscent of the situation in modern reefs (*Acropora*, *Favia*, *Goniastrea*, *Leptoria*, *Platygyra*, *Pocillopora*, *Porites*, *Stylophora*, *Symphyllia*, and *Turbinaria*). Detrital facies are common and contain benthic foraminifera, corals, mollusks, oysters, snails, and *Halimeda*. The Mariana Limestone has thoroughly altered porosity and mineralogy and displays many karst features (Siegrist and Randall, 1992).

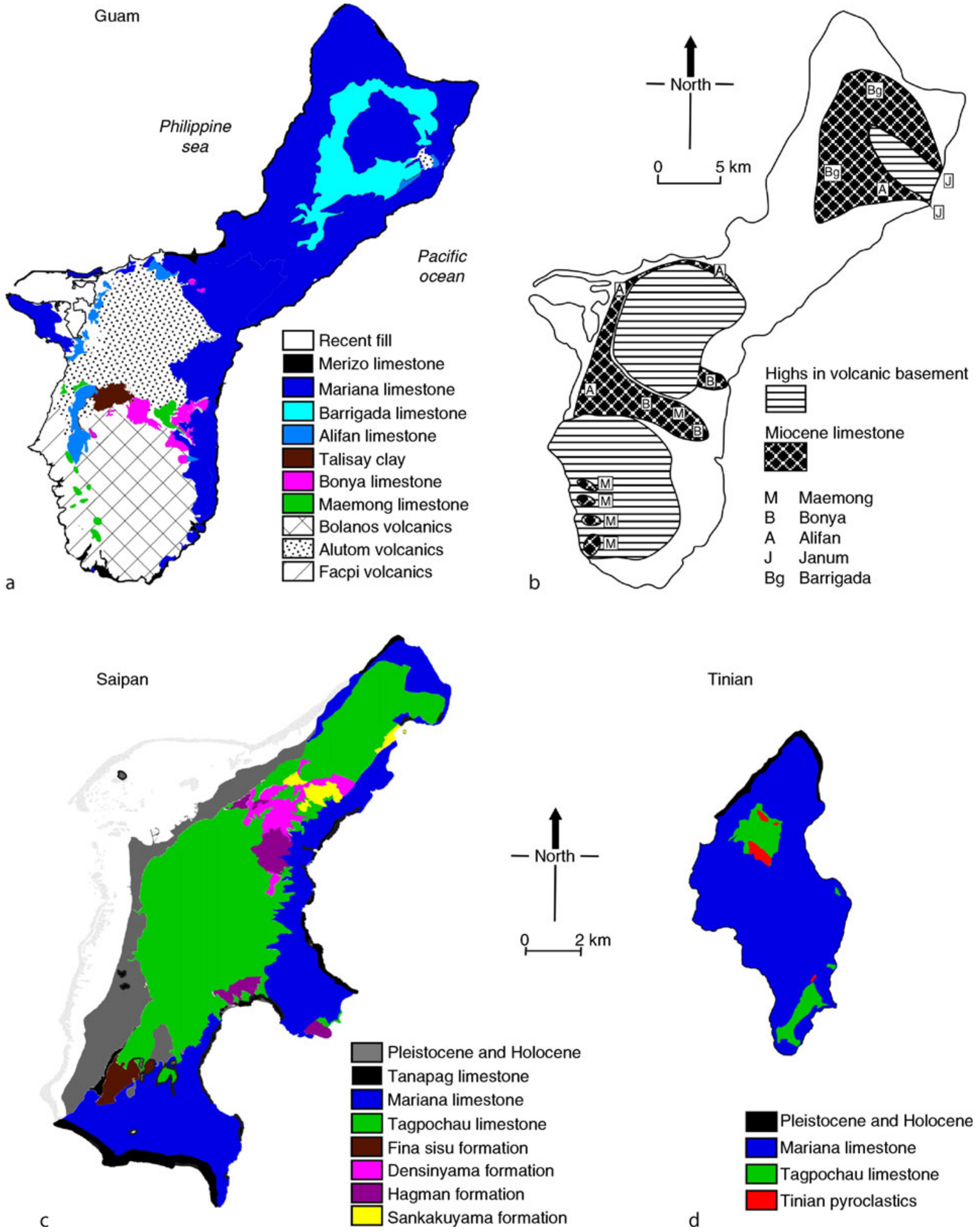
Rota shares many rock units with Guam but is primarily (>90%) covered by carbonates, mainly Mariana Limestone (Carruth, 2005; Figure 5). Near the shoreline, exposures of the Milencatan Limestone occur (Sugawara, 1934; Kayanne et al., 1993 refer to it as Milencatan while Bell and Siegrist (1988) refer to it as Mirakattan Limestone), which are an important sea-level indicator (Easton et al., 1978; Randall and Siegrist, 1988; Bell and Siegrist, 1988; Siegrist and Randall, 1992; Kayanne et al., 1993; Dickinson, 2000).

Saipan, the largest of the CNMI (48 sq. miles), consists of an andesitic-dacitic volcanic core (Sankakuyama Formation) overlain by sandstones, conglomerates, and breccias (Hagman, Desinyama, Fina Sisu Formations) which are capped by limestones covering about 95% of the island's surface (Figure 5). Volcanism on Saipan probably ceased in the Oligocene, after which marine deposition produced thick limestone sequences.

The Matansa Limestone is an upper Eocene carbonate bank deposit (Cloud et al., 1956). Saipan's center is covered by the early Miocene Tagpochau Limestone, a complex of calcareous clastic rocks. Saipan's eastern side is Pliocene Mariana Limestone, as found on Guam and Rota. It is reefal with argillaceaous rubbly facies (Carruth, 2003) and differs from the Tagpochau Limestone in the abundance of corals and the modern aspect of its fossil assemblage. Mariana Limestone does not occur along the entire western coast but disappears under Tanapag lagoon (Figure 5). Thus, the structural control of the lagoon rim (= barrier reef) is probably determined by the course of the Mariana Limestone. Lagoon and the coastal lowlands seaward of the Tagpochau Limestone are probably fill, overlying the Mariana Limestone. The Tanapag Limestone is a Pleistocene to Holocene raised reef limestone, well indurated and porous with well-preserved coral heads and mollusk shells (Cloud et al., 1956). It formed as fringing reefs on an emerging surface with maximum thickness <20 m. Its younger, Holocene, parts are correlative to the Merizo Limestone of Guam and the Milencatan Limestone of Rota (Dickinson, 2000) and occur along the steep eastern shoreline of Saipan.

In Tinian, which is situated 5 km south of Saipan, the oldest rocks belong to the Eocene Tinian Pyroclastics (Doan et al., 1960), exposed in the central highlands and the island's southern section (Figure 5). The rest of Tinian is covered by limestones. The same Miocene Tagpochau Limestone as on Saipan is exposed on about 15% of the island. Pliocene Mariana Limestone covers the majority of Tinian (~80% of its surface and thickens from 0 to 150 m in all directions from near the Tinian Pyroclastics; Doan et al., 1960; Gingerich, 2002). Like on Saipan, the limestones on Tinian are heavily faulted and karstified. Recent alluvium and colluvium reaches thicknesses up to 13 m.

Farallon de Medinilla is the northernmost of the calcareous Marianas and is also mostly covered by Mariana Limestone (Randall, 1995). North of Farallon de Medinilla, the Mariana Islands bear no limestone caps and are volcanically active. This active island arc stretches from Anatahan to Uracas (Meijer and Reagan, 1981).



Mariana Islands, Coral Reef Geology, Figure 5 (**a**) Surficial geology of Guam (Modified from Gingerich [2002]). (**b**) Early Miocene volcanic highs in relation to Miocene carbonates show that the latter formed primarily as ramp facies on and around the volcanic cones (Siegrist and Randall, 1992). (**c**) Surficial geology of Saipan (Modified after Carruth [2003]). (**d**) Surficial geology of Tinian (Modified after Doan et al. [1960] and Gingerich [2002]).

Conclusions

- Reef building in the Mariana Islands is confined to the inactive southern Arc from Guam to Farallon de Medinilla.
- The dominant coral reef type in the Marianas is fringing reefs, with barrier reefs only at Guam (Cocos Lagoon) and Saipan (Tanapag Lagoon).
- The northern Marianas are volcanically active and corals occur there, but tectonic instability and volcanic activity have precluded reef building.
- Reef building in the southern Marianas likely dates back to the Miocene, but no reef edifice has yet been found (corals and reefal fragments only).
- Late Holocene reef building in the southern Marianas is constrained by the presence of an early Holocene reef episode (Merizo Limestone on Guam, Milencattan Limestone on Rota, and younger part of Tanapag Limestone on Saipan) that clearly shows a mid-Holocene sea-level overshoot.

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Cross-references

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MASS EXTINCTIONS, ANOXIC EVENTS AND OCEAN ACIDIFICATION

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Introduction

The five great mass extinction events that have greatly influenced paths of evolution of life on Earth have attracted a wide range of speculation about original causes and ultimate effects. In this context, reefs are among the most widely studied of marine communities, partly because carbonate platforms are so enduring, but also because the fossil record of corals is relatively well known in terms of abundance and distribution. The marine tropics in general and reef taxa have been particularly targeted in mass extinctions. In each case, they have taken many millions of years to recover, intervals of time known as "reef gaps." Many authors have speculated on the causes of mass extinctions and reef gaps, the outcome being a wide array of hypotheses involving climatic upheavals of both terrestrial and extraterrestrial origin. This article reviews these proposals and examines them in the light of the biology of extant corals and their Pleistocene history.

Mass extinctions, corals, and reef gaps

Mass extinction events are characterized by fundamental changes in plant and animal diversity as many high-level taxonomic groups go extinct over the same geological time interval. They are also characterized by very slow recovery, led by the evolution of new species rather than recolonization by survivors.

The five great mass extinction events occurred at widely spaced intervals, each at or near the end of major divisions in Earth history. Of these, extinctions at the Permian and Cretaceous were so profound that they respectively mark the end of the Palaeozoic and Mesozoic eras. However, present interest in mass extinctions is not so much in their geological timing, but in their cause, for they illustrate outcomes of extreme environmental upheavals and are thus worst-case scenarios of climate change.

Mass extinctions are usually perceived as dramatic catastrophes inflicted on an otherwise peaceful Earth, but this is not the case. There were actually many minor or background extinction events at other times that left clear marks in the fossil record – no fewer than 27, according to a particularly detailed study (Raup and Sepkoski, 1986; Sepkowski, 1995). Although not global, some background extinctions were just as catastrophic as mass extinctions for particular ecosystems or particular places, and many had major impacts on coral reefs. Reefs, more than any other major type of ecosystem, leave a geological record that tracks such events (e.g., Sepkowski, 1995; Wood, 1999; Stanley, 2001). On an Earth history scale, this record does not show a process of gradual evolutionary development or improvement, but rather a stop-start response to a succession of environmental upheavals. Reefs are actually uncommon throughout the Phanerozoic and appear to have a "boom or bust" existence (Veron, 2008a and Kiessling, 2009). Environmental conditions that lead to reef proliferation are generally well understood; it is those which lead to their demise that are addressed below.

The end Ordovician mass extinction

The first great mass extinction "event" took place at the end of the Ordovician, a time when, according to the fossil record, 26% of all families and 60% of all genera of both terrestrial and marine life worldwide were exterminated (Hallum and Wignall, 1997). This extinction occurred at the end of a period of high mean global temperatures, probably caused by global greenhouse stability, a condition that seems to have prevailed since the end of Cambrian 70 million years earlier. The extinction, however, was not just one "event." It took place over a very long time span, perhaps several million years, and appears to have been the cumulative outcome of a succession of disasters. Possible causes that have been suggested include major fluctuations in sea level, multiple short-lived polar glaciations, and changes in ocean temperature, circulation, and chemistry. The extinction was particularly disastrous and long lasting for reefs (Webby, 1992; Copper, 2001). Extreme levels of carbon dioxide have been recently implicated (Berner, 2006). Although some individual rugose and tabulate coral taxa survived, living reefs disappeared from the face of the Earth and did not reappear for another 4–6 million years, long after the climate had returned to preextinction conditions. This is the first true "reef gap," meaning a gap in the geological record of reefs.

The late Devonian mass extinction

The Late Silurian to Late Devonian period – 75 million years or so of more or less global greenhouse conditions with high temperatures set between ice ages – probably included all-time peaks of Palaeozoic reef development (Copper, 2002). Sea levels were mostly high, so that seas flooded extensive areas of continents, forming epicontinental seas. However, despite the apparent proliferation of reefs, their development was intermittent, with major periods of worldwide expansion, especially during the

Middle Silurian to Late Devonian interspersed with periods of apparent collapse (Copper, 1994).

The world's Devonian reefs may have been every bit as well formed and biologically diverse as today's reefs and, with an estimated area of 5×10^6 km^2 (including inter-reef areas), may have been as much as twice as extensive (Copper, 1994). The Late Devonian mass extinction, like that at the end of the Ordovician, has been linked to multiple causes. Many bolides may have struck the Earth around this time (McLaren and Goodfellow, 1990 and others), although this is unlikely to be linked to the extinction (reviewed by Racki, 2005). A precipitous drop in atmospheric carbon dioxide owing to uptake by vascular plants, low global temperatures, and wildly fluctuating sea levels have all been blamed (Copper, 2001). The extinctions appear to have varied geographically, although they primarily affected marine life: reef development ceased almost completely. Some corals and stromatoporoid sponges lived on, but there was no recovery for the vast coral-sponge reef-building communities anywhere in the world. Instead, the survivors were microbes. These continued to build carbonate structures, but these have none of the characteristics of "reef" or "coral reefs" built by skeleton-secreting organisms.

Reefs – although still not structures comparable to today's coral reefs – existed sporadically during much of the Carboniferous and Permian – through times of oscillating temperatures and sea levels, including the periodic development of polar ice caps. Some of these reefs, especially those of the Late Permian, were very extensive. Their fossil content indicates that they were exceptionally diverse relative to their forebears, for they contained extensive arrays of all of the major marine groups, especially molluscs, echinoderms, and crustaceans, as well as rugose and tabulate corals.

The end Permian mass extinction

The fossil record of the end Permian mass extinction reveals a staggering loss of life: 82% of all genera and perhaps 80–95% of all marine species went extinct (Sepkowski, 1995, 2002; Erwin, 2006). All rugose and tabulate corals and most other calcifying organisms ceased to exist. The cause of this catastrophe was one of the foremost questions in palaeontology a century ago, and it remains so today. At one point or another, wildly fluctuating temperatures in response to sharp increases in atmospheric carbon dioxide, acid rain, and lack of oxygen in shallow waters after protracted times of plenty have all been held responsible. The oceans are widely believed to have turned anoxic and to have contained free hydrogen sulphide (Wood, 1999). Recent studies using biomarkers and isotopic data (Grice et al., 2005) are particularly revealing, one study suggesting that hydrogen sulphide generated by bacteria in deoxygenated oceans was so abundant that they released enough hydrogen sulphide to drive terrestrial extinctions (Ward, 2008). Other studies suggest that a sudden release of methane occurred at this time (Ryskin, 2003; Erwin, 2006). Recently, a comprehensive palaeophysiological study clearly implicates carbon dioxide (Knoll et al., 2007), perhaps associated with the Siberian Traps, the biggest volcanic outpouring of all time. Whatever the cause (reviewed by Knoll et al., 2007), the impact on reefs was sudden by geological standards and devastating. Some members of most marine phyla survived, yet reefs did not reappear for about 10 million years, the greatest hiatus in reef building in all of Earth history. What emerged in the Middle Triassic was the Scleractinia in place of their Palaeozoic predecessors. There is much in common between the ancient reefs of the mid-Palaeozoic and the first scleractinian reefs that took their place, not so much in the animals that built them, but in the stop-start nature of their intervals of growth, their biodiversity, and the sheer size of the structures they formed.

The end Triassic mass extinction

For 20 million years Triassic scleractinian corals, in concert with calcifying sponges and algae, went on to build some of the most spectacular reefs of all time. There was another substantial extinction of corals early in the Late Triassic, followed by a brief interval of dramatic recovery. Then, once again, the Earth plunged into a full-scale mass extinction. The end Triassic mass extinction (Stanley, 1988, 2001) – the fourth in the history of reefs – is estimated to have claimed about half of all marine invertebrates. The main taxa affected were conodonts (all), ammonites (almost all), and bivalves and gastropods (over half of all species). One-third of all scleractinian families went extinct and fewer than 25% of all genera are known to have survived (Beauvais, 1984). Nevertheless, this mass extinction, like its predecessors, was not only marine; perhaps 80% of all land quadrupeds also went extinct. The cause, again, has been much debated without a clear outcome (Wood, 1999; Flügel and Senowbari-Daryan, 2001). Atmospheric carbon dioxide reached extreme levels for the Mesozoic (perhaps eight times today's level) (Hautmann, 2004; Hautmann et al., 2008), and high greenhouse temperatures certainly resulted. Short-term sea-level fluctuations and various changes in ocean chemistry have been implicated by several palaeontologists, although none gives convincing evidence. The extinction was relatively abrupt (in geological time), making the reason for it particularly obscure. Whatever the cause, reefs again remained rare or absent throughout the world for a vast amount of time, perhaps 6–8 million years.

The end Cretaceous mass extinction (K/T)

K/T has been extensively studied because of its indelible association with the demise of the dinosaurs. However, many well-known animal groups besides the dinosaurs went extinct at the K/T boundary. Virtually no large land animals survived. Plants were also greatly affected, although this is less clearly documented. Once again tropical marine life was decimated, including a high proportion of calcifying organisms. All remaining ammonites and belemnites went extinct, as did a high percentage of bivalves, gastropods, and echinoids, as well as almost all Foraminifera. Many other unicellular organisms including radiolarians were also severely affected. However, most other major taxa – including freshwater fish, amphibians, turtles, crocodiles, snakes, and lizards – appear to have been almost unaffected, as were placental mammals.

Criteria used in extant coral taxonomy suggest that one-third of all families and 70% of all genera went completely extinct. Of the extant families, the Faviidae retained six of its original 16 genera; the others survived with only one or two. At least that is what the fossil record appears to say Veron (1995). However, that record is poor (Rosen and Turnšek, 1989; Kiessling, 2001) partly because sea levels were high during most of the Cretaceous and reefs were eroded away as the seas receded. Importantly, no branching corals appear to have survived, thus the habitats maintained by branching corals – those that provide shelter for algae-grazing fish – would have completely disappeared. On a taxonomic level, there are differences of opinion based primarily on what are considered to be valid records. Veron (1995) found that azooxanthellate corals were affected to the same degree as zooxanthellate corals, whereas Kiessling and Baron-Szabo (2004) on other criteria found that they were less affected. There are also differing views as to whether there was a reef gap or not. What is beyond dispute is that the fossil record is poor and few details been gleaned from it (Rosen, 2000).

Globally averaged atmospheric temperatures at the time of K/T have been estimated to be 6–14°C higher than at present (Barron, 1983), ranging from a few degrees' difference at the equator to as much as 20–40°C at the poles (Barron and Washington, 1985). Estimates of carbon dioxide levels vary greatly; however, the data for K/T are more reliable than those for more ancient extinctions. By the end Cretaceous carbon dioxide levels were at least five times, and perhaps as much as ten times, those of today (Berner, 1994; Tajika, 1999; Gale, 2000; Johnson et al., 2002).

A bolide hitting the Earth near the Yucatán Peninsula of southeast Mexico was widely thought to have caused the K/T extinctions (Alvarez et al., 1980). This theory, however, is highly controversial: over 2,000 books and articles were published about it within a decade of the original publication (Glen, 1990); the consensus now being that the bolide was not the primary cause of the extinction. The impact itself and the outpourings of the shock-induced volcanoes are widely believed to have created a stratospheric dust cloud that would have plunged the whole of the Earth into a cold, interminable night. Certainly acid rain (including nitric acid generated from heat-induced fusion of nitrogen and oxygen), high levels of carbon dioxide released from the impact site and from volcanic eruptions everywhere, and high concentrations of methane released from continental slopes would have combined to create intense greenhouse warming. However, the timing of the ultimate extinction of different animal groups, the time taken for many to go extinct, and the age of the bolide debris do not correlate well. Some animal taxa became extinct within an apparently brief period, whereas others, including the dinosaurs, took hundreds of thousands of years, and their decline started long before the bolide's impact.

Causes of mass extinctions

Extrapolations from today's knowledge of coral biology to past environments must be cautiously made, especially as the Scleractinia of today have been in existence for only two mass extinctions (the end Triassic and K/T). However, just as a number of physical parameters have remained effectively constant throughout the Phanerozoic, some physiological processes, while they may vary in detail over time, would in general have been applicable to the Scleractinia throughout their existence.

The causes of mass extinctions are divisible into two classes; those that do not involve the carbon cycle and those that do (Veron, 2008a, b).

Causes independent of the carbon cycle

Reef development has three prerequisites: (1) corals (and/or other calcifying organisms) must exist in environments that are favorable for calcification, (2) the resulting calcium carbonate must be consolidated into reefs, and (3) the rate of erosion must be less than the rate of accretion. Mass extinctions and reef gaps might occur whenever calcification is decreased, or there is a breakdown in the mechanisms of consolidation, or there are factors that increase the erosion or dissolution of calcium carbonate. In the case of K/T, where there was a simultaneous extinction of both zooxanthellate and azooxanthellate coral species, any explanation of extinction must span wide depth ranges as well as broad spatial scales.

Direct physical destruction from bolides

A bolide many kilometers across could possibly cause massive destruction of reefs along the exposed side of an area the size of a continent; however, it beggars belief that such an effect, from a single point source, could envelop the whole Earth (Toon et al., 1997). Nor is there any way that azooxanthellate species would be equally affected or that surviving reef corals would take millions of years to recommence reef building. Be that as it may, the Earth has several large and well-known craters (13 of which date to the early Mesozoic or later) (Jablonski, 1986), and many studies, motivated by the discovery of the K/T bolide, have sought to establish these as the primary cause of extinction events. Yet credible links have not emerged (Rothschild and Lister, 2003). Indirect effects of bolides are another matter.

"Nuclear Winter" induced by dust clouds

Bolides are presumably capable of creating dust clouds that may have enveloped the Earth for weeks or months, creating devastating darkness and (for terrestrial life) cold.

Survival estimates for corals under conditions of very low light vary from death in just a few weeks to survival of at least parts of colonies for six months or more. Significantly, this strongly suggests that, if today's reef-building species were suddenly subjected to conditions of very low light for periods of years rather than weeks or months, 99% of species would go extinct. No such extinction has ever happened to the Scleractinia. The proportion of zooxanthellate corals that went extinct at K/T is not on its own sufficient to explain the end of reef building or the reef gap that followed: (1) Many taxa that survived, including members of the Poritidae and Faviidae, are among the best reef builders (Veron, 1995). (2) Azooxanthellate taxa fared no better than zooxanthellate taxa. (3) The K/T mass extinction caused a much higher rate of extinction in corals than in many other photosynthetic organisms, notably terrestrial vascular plants, which would have been more vulnerable to prolonged darkness.

From a biological point of view, it can be concluded that very low light, even if maintained for months, is exceedingly unlikely to have been the principal cause of the K/T mass extinction event. The dust cloud created by the K/T bolide would also have caused atmospheric temperatures to plunge, but only for as long as the cloud persisted. The thermal inertia of the oceans would have protected marine environments from significant temperature change.

Sea-level changes

The major sea-level changes throughout Earth's history have been due to plate tectonics. These are very different from the sea-level changes that occurred during the Pleistocene, primarily in being much slower and of immensely longer duration. During the last glacial cycle, the sea level dropped 130 m (Lambeck and Chappell, 2001; Siddall et al., 2003). This fall is more than the depth range of all but a few deepwater zooxanthellate corals, which means that almost all corals had to relocate. Throughout the Pleistocene, such falls were repeated many times, yet only about 10% of all corals went extinct over this entire interval (Veron and Kelly, 1988). This is no more than a background extinction rate. Thus sea-level changes of any kind, let alone those resulting from tectonic movements, can be discounted as a primary cause of coral species extinctions.

Loss of area during sea-level regression

Loss of reef area during sea-level changes of the past has been suggested as a cause of coral extinctions, but the Pleistocene history of modern corals offers a number of reasons why this would not be so. There were major losses of reef area during the last glacial cycles; however, these had no significant effect on today's coral diversity. At the opposite extreme, small areas may have most of the species complement of an entire province. The great dispersal capabilities of corals would ensure that recolonization would take place swiftly from surviving niches. Area loss is thus highly unlikely to have been a primary cause of any extinction. Furthermore, azooxanthellate species would have been unaffected by a loss of reef area.

Loss of biodiversity as a cause of reef gaps

Reef building does not depend on high species diversity. Many of the corals that survived K/T belonged to genera well able to build reefs in the absence of any other coral species. We can therefore discount loss of biodiversity as a primary cause of reef gaps.

It has also been suggested that reefs do not reestablish until peak evolution rates of new species are reached (Jablonski, 1986). Although this may have been true after some mass extinctions (there is no evidence either way), it was certainly not the case after K/T as coral diversity remained low long after widespread reef building had reestablished.

Low temperatures

Conceptually, low temperatures could explain reef gaps and coral extinctions, but the data available for global temperatures give no credence to this. During the K/T extinction, ocean temperatures were at or above, rather than below, present levels. Furthermore, the suite of reef-building genera that survived indicates no selection for cold tolerance. Nor does low temperature explain why azooxanthellate species were lost. Even during a full glacial cycle, the world's oceans cool only around 6°C, and less than this at the equator. Although temperature reductions of this extent would be enough to contract the latitudinal range of species today, such a decrease could not have initiated extinctions in equatorial regions on the scale of any mass extinction.

High temperatures

Elevated temperatures can cause mass bleaching of corals, creating widespread devastation when reef ecosystems become so degraded that they are taken over by macroalgae and bacterial slime. However, mass bleaching only occurs in zooxanthellate organisms as it is due to an overproduction of photosynthetic oxygen. Over geological time, corals growing under such conditions have the evolutionary option of avoiding the issue by becoming azooxanthellate. In such circumstances, any reduced capacity for calcification would be in part offset by the effects of temperature. Furthermore, a mass extinction from temperature would require that such temperatures extend to highest latitudes. This would never have been possible, even under the most extreme conditions. High temperatures cannot explain the extent or global nature of mass extinction events, nor can they account for the species that survived K/T, nor the loss of azooxanthellate taxa.

Salinity

Corals, and by extension reefs, are adversely affected by low salinity and low salinity may well have been a major cause of regional extinctions at various times, especially in partly landlocked regions such as the epicontinental seas of the Super-Tethys and North Africa during the Cretaceous. However, it is inconceivable that any continental landmass could hold enough fresh water to cause a global mass extinction.

Disease and toxins

There is strong evidence today that stresses such as mass bleaching, hyposaline influxes, and a wide range of other ecological imbalances can greatly increase the incidence of diseases in corals. Combinations of stresses from high temperature, high light levels, and disease might lead to major regional losses of corals for as long as those stresses persist. These would have to be very widespread and affect deepwater and nearshore corals equally. The Earth has no toxins in such quantities, nor any that can exist both on land and in the oceans.

Extraterrestrial events

Extraterrestrial events apart from bolides have commonly been suggested as causal factors in extinctions. Episodes of ultraviolet or cosmic radiation from solar flares or supernovas (which may be capable of stripping away the ozone layer, allowing high levels of ultraviolet radiation to reach terrestrial life) can be discounted as causes of mass extinctions because the deep ocean would have shielded bottom-dwelling communities, and these were not shielded. There is also the often-mentioned finding that extinctions follow a 26-million-year periodicity, implying an overriding extraterrestrial "supercycle" of unknown origin. The database of fossils referred to above presents an avalanche of statistics in support of this conclusion (Raup and Sepkoski, 1986); nevertheless, although this long periodicity does not look entirely random, it does not look distinctly cyclical either, so this concept remains enigmatic and without a plausible mechanism.

Links between mass extinctions and the carbon cycle

If the above causes of mass extinctions and reef gaps are discounted as primary factors, there remains an array of further possibilities that have one aspect in common: they are either part of the carbon cycle or closely linked to it. This is hardly surprising, for of all the great matter cycles of the Earth, the carbon cycle is by far the most important.

The chemical impacts discussed below are all directly or indirectly linked to the carbon cycle. Severe environmental degradation can occur rapidly in response to bolide impacts and some geological events such as larva flows (traps) or supervolcanoes. They may also occur in response to slower processes created by gases release from volcanic chains as a result of seafloor spreading and other tectonic movements. Although slow, these processes may lead to relatively abrupt extinctions through cumulative outcomes and synergies.

Importantly, small changes in the concentration of atmospheric gases can lead to major changes in global environments, potentially affecting both marine and terrestrial life. These gases include major components of our atmosphere, notably oxygen and water vapor, as well as those that are only present in trace amounts. The latter include the gases that control the atmosphere's greenhouse warming of which carbon dioxide and methane being the most important.

Peripheral links to the carbon cycle are considered here first.

Acid rain

High levels of atmospheric carbon dioxide produce carbonic acid, and high levels of sulphur dioxide produce sulphuric acid. These substances, together with nitrous oxide from industry and the draining of tropical marshlands, are the main sources of acid rain today. Carbon dioxide and sulphur dioxide are released in massive amounts from some volcanoes, traps (notably the Deccan Traps of India at the time of K/T) and other sources, both terrestrial and marine, both to be ultimately neutralized by ocean buffers. Although sulphur dioxide and nitrous oxide do not contain carbon, by the time their products reach the oceans they do, and thus they are inextricably linked to the carbon cycle. It is not quantitatively possible for acid rain to be a primary cause of an extinction event; however, acid rain may well have acted in synergy with other causes to create extreme environmental degradation.

Hydrogen sulphide

Hydrogen sulphide is another gas released in large quantities into the oceans and atmosphere from volcanoes or from sulphur-rich geysers and the like. It also has biological origins, which is why it regularly occurs in anoxic waters of all types, ranging from aquaria to atoll lagoons. As with sulphur dioxide, although it does not contain carbon, it is inextricably linked to the carbon cycle and could, in terms of quantity, have been a significant contributor to an environmental upheaval in synergy with other gases.

Oxygen and anoxia

In a nitrogen-dominated atmosphere, oxygen and carbon dioxide have an additive relationship, an increase or decrease of the one creating a parallel effect in the other, all else being equal. However, all else may sometimes not be equal, and there may have been conditions, perhaps the end Permian and K/T, where ocean anoxia may have been created by primary productivity decrease (through phytoplankton depletion) as a result of acidification. By this simple mechanism, high levels of atmospheric carbon dioxide can work synergistically with low levels of atmospheric oxygen to create ocean anoxia. Whether or not this has actually happened is not known.

Methane

Methane from geological sources, plant respiration, and some animal life exists in minute amounts in the atmosphere (currently 1.8 ppm). However, it occurs in much greater quantities in permafrost, in tropical marshlands, and in vast quantities as icelike solids (clathrates or hydrates) that are stable only under pressure and at low temperatures on continental shelves. The volume of these solids is unknown, although it is of the same order of magnitude as the Earth's total quantity of fossil fuels. Methane leaks into the ocean and atmosphere naturally, for example, as marsh gas. However, if it were released into the atmosphere in substantial quantities, perhaps as a result of a bolide impact or a buoyancy change in the methane ice (for which there are many possible causes), there could be serious environmental consequences. It would have a major greenhouse effect (methane has 22 times the potency of an equal volume of carbon dioxide) and would also be converted to carbon dioxide by microbes and chemical oxidization, causing the same adverse effects characteristic of high levels of carbon dioxide.

Carbon dioxide

Both increasing and decreasing carbon dioxide levels have been proposed as major contributors to mass extinction events in the past. Over geological time scales, carbon dioxide has varied from levels much lower than the 387 ppm of today up to perhaps ten times today's level (depending on the reliability of studies of a small number of fossil soils and whether or not results from single points in time are representative of longer time intervals). The effects of high levels of atmospheric carbon dioxide are pursued below.

Ocean chemistry and pH

This subject can only reliably be assessed via the chemistry of contemporary oceans. Increased atmospheric carbon dioxide leads to greater amounts of the gas dissolving in the oceans, which directly reduces pH. This, in turn, alters the proportions of different forms of inorganic carbon (CO_2, H_2CO_3, HCO_3^-, and CO_3^{2-}) in the ocean (Buddemeier et al., 2004; Kleypas and Langdon, 2006). Increasing the concentration of carbon dioxide in the ocean alters the proportion of the other three forms of carbon. Calcifying organisms use carbonate and/or bicarbonate ions to build skeletons, and thus a decrease in their availability slows the calcification process. The proportions of each of these carbon components are sensitive to temperature and pressure, and thus to latitude and depth.

Acidification affects zooxanthellate corals and most azooxanthellate corals by different paths. The former are sensitive to acidification of surface waters by atmospheric carbon dioxide directly; the latter are sensitive to having their depth range reduced by shallowing of $\Omega_{\text{aragonite}}$. These surface and deep layers directly influence each other at high latitudes where temperature gradients are weak and mixing occurs relatively easily. However, they are well separated in the warm tropics, especially at the thermocline, and interact primarily via the sinking of carbonate skeletons of surface-dwelling plankton.

Shallow oceans are currently supersaturated with carbonates, allowing zooxanthellate corals to calcify. However, as $\Omega_{\text{aragonite}}$ decreases, calcification requires increasing amounts of energy. The same applies to azooxanthellate corals, although here the process depends on the depth of the aragonite saturation horizon, which, in turn, varies with temperature as well as chemistry: as changes in water temperature and chemistry cause the horizon to rise, the depth range of azooxanthellate corals shallows.

Acidification

The dependence of calcareous algae on high-magnesium calcite, the most soluble of all calcium carbonate skeletons, makes them particularly vulnerable to acidification (Kiessling et al. 2008, Veron, 2008b). Since these algae are critical to reef consolidation, their removal would, in the past, reduce the net accretion of reefs before the rate of coral calcification became limiting. With further decrease in pH, aragonitic organisms including Scleractinia would become increasingly affected, further tipping the balance in favor of reef erosion. Since acidification from elevated atmospheric carbon dioxide affects oceans on a global scale, the effects on reefs would be worldwide, although influences from temperature and surface water mixing would create local variations both geographically and with depth. In equatorial regions, adverse changes in carbonate/bicarbonate ion availability as a result of decreasing pH would be exacerbated by lack of mixing between the warm, shallow, carbon dioxide-enhanced surface layers, and the buffers of cool, deeper ocean water. Acidification could thus have a devastating effect on reef development, leading initially to widespread inhibition of reef growth and eventually to reef erosion and dissolution.

The first impact will be on azooxanthellate taxa, which would be to displace them from deeper oceans as the $\Omega_{\text{aragonite}}$ horizon shallows. This effect is greatest at high latitudes (Guinotte et al., 2003; Turley et al., 2007). Two recent studies point toward acidification as the primary cause of coral extinctions and the reef gaps, despite deficiencies in the fossil record. (1) Late Cretaceous azooxanthellate corals of the caryophylliid genus *Coelosmilia* have been found to have calcitic skeletons rather than skeletons of the more soluble aragonite as have today's Scleractinia (Stolarski et al., 2007). (2) Two Mediterranean corals, *Oculina patagonica* and *Madracis pharensis* which were placed in acidified aquaria gradually lost their skeletons, then regrew them after being returned to normal seawater (Fine and Tchernov, 2007).

Unlike the alternative causes of extinctions noted above, acidification can explain why both azooxanthellate and zooxanthellate species were affected at the time of K/T. It can also explain the loss of reefs both locally and globally, as well as account for the existence of long-lasting reef gaps. Although acidification may be difficult to initiate because of ocean buffers, once achieved it will persist as long as atmospheric carbon dioxide remains high. Furthermore, the oceans would remain acidified for tens of thousand years after carbon dioxide levels had declined, that being the time required for normal alkalinity to be restored. This would be an interval long enough for corals to initiate an evolutionary recovery. Under such a recovery sequence, reef gaps in the past of millions of years would be a plausible consequence, depending primarily on the endurance of atmospheric carbon dioxide and the rate of evolutionary accommodation to it.

Low levels of carbon dioxide

Low levels of carbon dioxide may result in low levels of photosynthesis, leading to low levels of oxygen and eventually ocean anoxia. This might have triggered the Late Devonian mass extinction event; the evidence is inconclusive.

Conclusions

The foregoing discussion argues that ocean acidification and anoxia as a mechanism explains mass extinctions better than other mechanisms that have been offered. However, studies of ancient environments also suggest that similar atmospheric carbon dioxide levels may have occurred at times when reefs actually proliferated rather than declined. One explanation may lie in the interpretation of information from ancient times for carbon dioxide data are very uncertain for most of geological time as it is based on a small number of point samples from widely different geological intervals. In contrast, as seen in ice core records and contemporary measurements, carbon dioxide levels can fluctuate substantially over intervals as short as millennia. Many possibilities present themselves. (1) Reefs may not have proliferated at all during carbon dioxide highs; they only appear to have survived because they were able to resume growth when levels fell (the boom or bust observation made above). (2) The high apparent carbon dioxide levels of ancient times may be an artifact of a lack of data and measuring methods, which currently produce very conflicting results. (3) Corals and other taxa may have become partly or completely askeletal (as noted above) during times of adverse ocean chemistry. (4) Corals may have had calcitic skeletons during such times and the calcifying process may have been more physiologically isolated from ocean pH than it now is. These options can only be guessed; there may have been many aspects of coral biology that allowed ancient corals to tolerate water chemistries that are lethal to today's taxa.

Although these deliberations about possible causes of mass extinction events have highlighted acidification as the most probable cause of both coral extinctions and reef gaps, it would be misleading to consider this as the only cause. Indeed, all mass extinctions appear to be the outcome of several different influences acting synergistically. Acidification may well have been a primary mechanism by which marine ecosystems were affected; however, low light, bleaching, deteriorating water quality owing to acid rain or anoxia, mechanical damage, and disease would all have played their parts. Although the time frames of bolides do not always fit the facts as a singular cause of extinction, bolides or traps or volcanic chains may have created severely adverse conditions that became "the straw that broke the camel's back."

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Cross-references

Aragonite
Carbon Fluxes of Coral Reefs
General Evolution of Carbonate Reefs
Ocean Acidification, Effects on Calcification
Scleractinia, Evolution and Taxonomy

MAYOR, ALFRED GOLDSBOROUGH (1868–1922)

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Born in Frederick, Maryland, on 16 April 1868, Alfred Goldsborough Mayer (spelling changed to Mayor in 1918) was the son of Alfred Marshall Mayer, a noted American physicist. Although an excellent student of mathematics and physics, young Alfred preferred zoology as his field of study. However, as his strong-minded father wanted his son to pursue a career in the physical sciences, Alfred majored in engineering at the Stevens Institute of Technology, in Hoboken, New Jersey, from which he graduated in 1889. He began advanced work in physics soon thereafter, but decided to enter the graduate program in zoology at Harvard University in 1892, where he came to the attention of Alexander Agassiz, a prominent marine zoologist and director of Harvard's Museum of Comparative Zoology (MCZ). Agassiz soon placed Mayor in charge of the MCZ's division of coelenterates and other radiate species.

Mayor collected specimens for the MCZ in various locations on the east coast of America and around the Dry Tortugas, in the Gulf of Mexico. Between 1896 and 1900, he also accompanied Agassiz on three major collecting expeditions in the South Pacific Ocean. Mayor received the Ph.D. degree in 1896, but continued in his position at the MCZ until 1900, when he left to become curator of zoology in the Brooklyn Museum.

In 1903, the Carnegie Institution of Washington (CIW) approved Mayor's proposal for establishing a tropical marine laboratory on Loggerhead Key, in the Dry Tortugas, and made him director of the new station, which opened in 1904. During the early years of the Laboratory, Mayor worked mainly on jellyfish taxonomy, and, in 1910, completed the monumental three-volume work titled *Medusae of the World*. Two years later, he published *Ctenophores of the Atlantic Coast of North Atlantic*, a standard work on the comb jellies.

Influenced by the studies of the prodigious coral geologist Thomas Wayland Vaughan, who conducted considerable research at the Tortugas Laboratory, Mayor began around 1913 to focus his attention on the stony corals. In the waters of the Florida Keys and later those of the South Pacific, Mayor concentrated on the ecology of coral reefs, and produced a number of pioneering studies on the growth-rate of corals and the effects of temperature, light, water depth, wave action, fresh water, and silt on coral development. In 1917, he began to use a diving helmet to further his studies, thus becoming one of the first biologists to conduct underwater explorations of reefs. Mayor was elected to membership in the National Academy of Sciences in 1916.

By the time of his premature death on 24 June 1922, on Loggerhead Key, Mayor had achieved international acclaim for his pioneering work in jellyfish and comb jelly taxonomy and on coral-reef ecology. A monument in his memory was erected on Loggerhead Key in 1923.

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Agassiz, Alexander (1835–1910),
Vaughan, Thomas Wayland (1870–1952)

MEGABLOCKS

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Synonyms

Boulder or megaboulder deposits; Coral boulders; Coral megablocks; Erratic coral boulders

Definition

Megablocks. Intact blocks or boulders, often composed of coral and occasionally with dimensions of 10 m or greater, situated well apart from (as much as 100–500 m) and sometimes well above (up to 30 m) their original formation sites.

Introduction

Coral megablocks are large erratic boulders detached from the reefs or paleoreefs where they formed, and presently situated in the surf zone, along the beach, or still further inland. We distinguish megablocks from sea stacks, which are coral formations that may be similar in size and location to megablocks but are still in growth position, attached at their bases. Megablocks as discussed here are also distinct from tectonic segments or arc segments, often described along subduction zones, which are tectonic blocks with horizontal dimensions up to tens of km or greater that undergo coherent lateral or vertical motions distinct from the motions of adjacent blocks or segments. There is also a vast literature describing ice-rafted or glacier-deposited boulders composed of materials other than coral; for example, glacier-transported boulders reported in Tierra del Fuego by Charles Darwin (1842) are still being studied today (Kaplan et al., 2007).

Scientific interest in megablocks, whether composed of coral or otherwise, often focuses on determining the mechanism and timing of their emplacement. Where coral megablocks may have been emplaced by prehistoric storms or tsunami waves, analysis can provide information about potential hazards from natural events too rare to be represented in the historical record.

Examples

Erratic megablocks often occur near and below sea cliffs. Although the specific mechanism of transport may be uncertain, in most cases a plausible explanation is that the blocks separated from the cliff due to the action of surf, biological activity, earthquakes, or weathering, and subsequently were transported downhill via mass wasting.

However, coral megablocks also occur where sea cliffs are absent, and may lie well above their original sites of formation (Scheffers and Kelletat, 2003). To emplace these, storm or tsunami waves are the most credible mechanism (e.g., Zhao et al., 2009), especially as some such emplacements have occurred historically. The 26 December 2004 Indonesian tsunami deposited hundreds of meter-sized coral boulders in the intertidal zone along Pakarang Cape, Thailand (Goto et al., 2007), including some with estimated weights up to 40 tons (Kelletat et al., 2007). On 27 August 1883 the island of Krakatau in Indonesia experienced a huge explosive eruption; at Anyer beach at a distance of 40 km, this produced a tsunami with a reported height of 36 m that moved coral megablocks distances up to 240 m. The largest transported megablock had a reported volume 317 m^3 and an estimated mass of 600 tons (see picture in Simkin and Fiske, 1983).

A third well-studied historical example of megablock emplacement is on the island of Ishigaki, in the Okinawa group, offshore Japan. Here in April 1771, a tsunami accompanying an earthquake killed some 12,000 island residents and also displaced numerous coral boulders, some with dimension ~5 m (Imamura et al., 2008). Controversies surrounding this incident concern (1) whether an earthquake rupture on any regional fault was alone sufficient to generate the tsunami, or whether the earthquake triggered an undersea landslide (Nakamura, 2006); (2) the height of the tsunami, variously reported as 30–85 m, and the geographic extent of its runup; and (3) whether the 1771 tsunami alone emplaced the megablocks, or instead they were emplaced by previous storms or tsunamis and simply moved again in 1771 (Suzuki et al., 2008).

There are no historical records of emplacement for many megablocks. Frohlich et al. (2009) studied coral megaboulders along the western coastline of Tongatapu in the southwest Pacific. The largest stone (see Figure 1) is situated ~10 m above present sea level and 130 m from the present shoreline. It is one of seven similar megablocks found along a 3-km arc 100–400 m from the present shoreline. The blocks contain well-preserved corals demonstrating that the stones are no longer in growth position. All these stones are the highest features locally. Frohlich et al. (2009) concluded that these megablocks were emplaced by a tsunami, generated probably by explosive volcanism along the Tofua arc ~30 km west of Tongatapu, or possibly by an undersea landslide just offshore. Other examples of exceptionally large coral megablocks occur in the Bahamas (Hearty, 1997), and in the Tuomotu Islands (Bourrouilh-Le Jan and Talandier, 1985).

Origin and mechanism of transport: Tsunamis or storms?

In coastal environments, elucidating the circumstances of megablock emplacement provides crucial information about rare but very severe natural hazards, especially as the historical record in many locations covers only the past century or two. However, there is often controversy about whether storms or tsunamis emplaced the megablocks (e.g., Nott, 2004). This is partly because historically documented storms have displaced some rather large boulders, and partly because distinguishing the characteristics of tsunami-emplaced vs storm-emplaced deposits is a still-developing field (Morton et al., 2007). For example, Noormets et al., (2002) describe a 96 ton megablock emplaced by the 1946 tsunami and since twice moved by storm waves on Oahu in Hawaii.

The largest historically documented storm-emplaced stones displaced vertically upward and moved distances exceeding a few meters have average dimensions smaller than ~5 m and masses less than 100 tons (Nott, 2004); we conclude that larger megablocks are probably tsunami-emplaced as it is likely that the historical record includes storms having near-maximum possible intensities. Wind speeds, wave heights, and storm surge characteristics correlate roughly with the diameter of the

Megablocks, Figure 1 A large coral megablock on the island of Tongatapu, southwest Pacific. This block has dimensions of 15 m × 11 m × 9 m and sits with its base 10 m above sea level and ~130 m from the present shoreline; it is one of seven megablocks that form a group on western Tongatapu.

storm's circulation pattern, and the historical record includes storms such as 1979 typhoon Tip in the western Pacific which had a diameter of 2,200 km (Dunnavan and Diercks, 1980). This is larger than the Gulf of Mexico, the Caribbean, or the Mediterranean; it is difficult to imagine sustaining a significantly larger storm. There has been discussion that sea surface temperatures exceeding 36°C might generate 'hypercanes', storms much stronger than any observed historically (Parks Camp and Montgomery, 2001). However, no one has yet suggested that such conditions occurred within the past several million years.

Tsunamis may be generated by several different natural phenomena, including earthquakes, undersea landslides, subaerial landslides that reach the sea, undersea volcanic eruptions or flank collapses, and meteoroid impacts. Although tsunami hazard analyses focus principally on earthquake-induced tsunamis, the largest tsunami waves are generated by other causes. For example, two of the highest historical tsunami waves were generated by a subaerial landslide (wave runup to 520 m elevation, Lituya Bay, Alaska, 1958; see Mader and Gittings, 2002) and a volcanic eruption (~36 m waves, Krakatau, Indonesia, 1883; see Simkin and Fiske, 1983).

Evaluating megablock occurrence may help quantify hazards and occurrence rates for undersea landslides. This is important because several investigations conclude that giant-to-moderate (100–10 km^3) submarine slope failures may cause exceptionally large tsunamis (Ward and Day, 2001). Sometimes undersea landslides accompany or are triggered by earthquakes and produce tsunamis much larger and more devastating than those attributable to the earthquake alone (e.g., the 18 November 1929 Grand Banks earthquake; see Fine et al., 2005; and the 17 July 1998 New Guinea earthquake; see Heinrich et al., 2001; Satake and Tanioka, 2003). In many coastal locations even a cursory evaluation of offshore bathymetry demonstrates that undersea landslides have occurred.

Dating the emplacement of megablocks

During the past 400 ky, sea level has only been at or above its present only during interglacials. Interglacial highstands typically occur at intervals of about 100,000 years and have durations of ~10,000 years. The two most recent highstands are the past 7,000 years and 120–130 ka; thus these are the most plausible times of emplacement for large megablocks presently situated at elevations near or above their sources. Generally the more recent interval is likely because exposed coral limestone dissolves with rainfall, destroying megablocks over time. During subsequent highstands, sea level returns to near the level of paleomegablocks and they are destroyed by bioerosion. And of course, any that were deposited during lower sea levels are now underwater or had sea level pass over them, thereby eroding them and then burying them under new reef growth. When megablocks contain well-preserved corals, ^{230}Th dating can determine when they lived and thus constrain an earliest credible time for emplacement.

Where megablocks occur as part of a well-preserved stratigraphic sequence emplaced by a storm or tsunami, this may contain mineral or organic material datable using U-series or ^{14}C methods. Where megablocks contain identifiable coral species indicating that the blocks are overturned, it may be possible to use ^{10}Be or ^{26}Al to estimate how long the upper surface has been exposed (e. g., see Nishizumi et al., 1993).

In some environments where erratic megablocks are situated on a raised coral-reef terrace, they are perched on pedestals that have formed beneath the blocks as the adjacent terrace limestone is dissolved by rainfall solution. Matsukura et al. (2007) describe examples of such perched megablocks found on Kikaijima Island in the Ryukyus; they estimate that the dissolution rate of the unsheltered terrace surface is ~205 mm/ky. As many pedestal heights are ~1.0–1.5 m, they conclude that the megablocks were deposited on a reef flat which emerged and began experiencing dissolution about 6,000 years ago. Although it might seem that measuring pedestal heights would provide an accurate way of dating megablock emplacement, at present this is a subject for additional research as reported dissolution rates vary by two orders of magnitude or more and depend on numerous factors including amount of rainfall, whether or not the block is exposed to both rainfall and sea spray, average temperature, and porosity and composition of the terrace surface.

How fast the current? How high the wave?

Wherever large erratic megablocks occur, they provoke the question of how strong a current was required to displace them. If they are situated on land, how high was the storm or tsunami wave that moved them?

A physics-based analysis provides some approximate answers to these questions. In classical hydrodynamics, an object of cross sectional area A in a fluid of density ρ_w streaming at velocity V experiences a drag force of $\frac{1}{2}C_d\rho_w AV^2$, where C_d is a dimensionless parameter known as the drag coefficient which is ~1/2 for objects such as smooth spheres. To displace a megablock with dimension h_b and density ρ_b, the drag force approximately equals its buoyant weight; thus as its cross section is $\sim h_b{}^2$ and its volume is $\sim h_b{}^3$,

$$\tfrac{1}{2}C_d\rho_w h_b^2 V^2 > g(\rho_b - \rho_w)h_b^3 \qquad (1)$$

and

$$V > \sqrt{\frac{2g}{C_d}\left(\frac{\rho_b}{\rho_w} - 1\right)h_b} \qquad (2)$$

If a wave impacts a shoreline, potential energy stored at the wave crest may be converted to kinetic energy, producing a current as the wave breaks and flows onshore. Estimating the height h_w of the wave necessary to displace a boulder depends on various assumptions about the dimensions and hydrodynamic properties of the boulder (e. g., see Nott and Bryant, 2003; Noormets et al., 2004). However, a very crude 'rule of thumb' is that

$$h_w > \frac{\rho_b}{\rho_w} h_b; \tag{3}$$

i.e., the height of a wave necessary to displace a boulder of given density and height is approximately proportional to the product of the boulder's relative density and its linear dimension. This is often an adequate estimate as generally knowledge of the boulder's hydrodynamic parameters and density ρ_b (see Spiske et al., 2008) is highly uncertain.

In practice, the interaction of waves and shorelines is highly nonlinear and depends critically on details of the nearshore bathymetry, and thus computer modeling is required to obtain substantially more accurate results (Mader, 2004). Of practical importance is the observation that boulders entrained in a tsunami tend to saltate, tumbling end-over-end rather than sliding, and thus attention to the dimensions and orientations of megablocks may provide information about the direction of the flow that emplaced them (Imamura et al., 2008).

Summary

Megablocks are erratic coral boulders, some with dimensions as great as 10 m or more, found in and landward of active reef zones. In locations where they can only have been wave-emplaced, they provide important information about the frequency and intensity of rare, very large storms and tsunamis. However, at present identifying the specific characteristics that constrain the features of the waves that emplaced them, or that confirm their origin to be a storm or tsunami, is still a subject of active research.

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Cross-references

Boulder Beaches
Earthquakes and Emergence or Submergence of Coral Reefs
Last Interglacial and Reef Development
Recent Sea Level Trends
Tsunami

MELTWATER PULSES

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Synonyms

Catastrophic [sea-level] rise event; Sea-level jump

Definition

A meltwater pulse is an acceleration in sea-level rise which results from outbursts of pro- or subglacial meltwater and/or surging of ice-streams into the ocean during ice-sheet disintegration. Radiometric ages of coral-reef drowning and back-stepping indicate that rates of sea-level rise during these meltwater pulses were at least 35 mm/yr and may have been as much as 60 mm/yr, and that these rises persisted for 300–500 years.

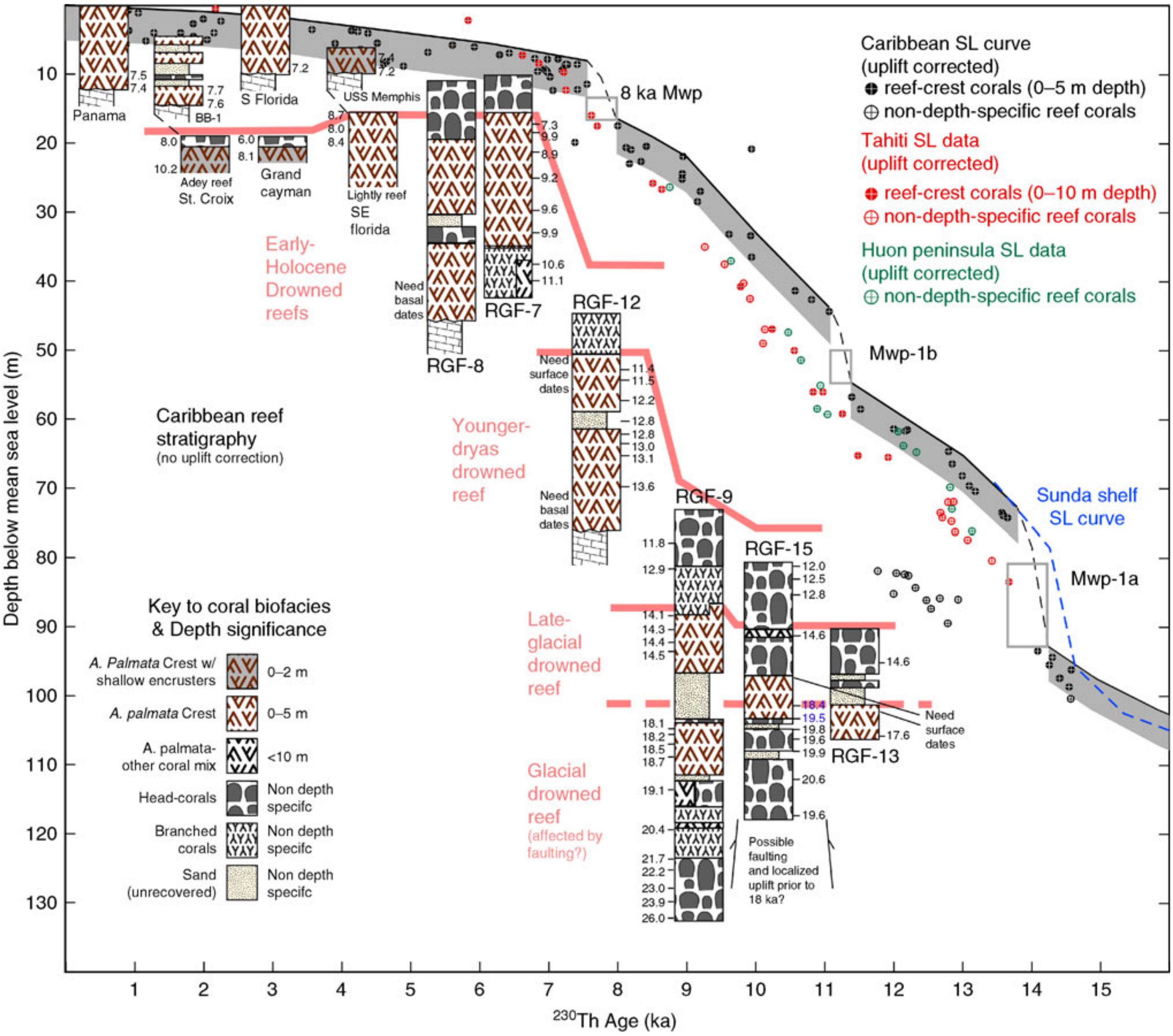
Introduction

Measuring the age and elevation of late Quaternary reef-crest corals has enabled geoscientists to reconstruct the rate and magnitude of relative sea-level rise at several sites and identify global episodes of rapid sea-level rise that resulted from pulses of meltwater or iceburg discharge during the disintegration of ice sheets (Fairbanks, 1989; Blanchon and Shaw, 1995). These reconstructions show that the rate and magnitude of sea-level jumps were truly astonishing. Coastal and shallow marine ecosystems were inundated by rises of as much as 15 m at rates of up to 60 mm/yr. It is no surprise that understanding their causes and consequences has subsequently become the focus of a large multi-disciplinary research effort with particular emphasis on how they may relate to possible future rapid climate and sea-level change.

Glacial Termination I (MIS-2)

Pulses in melt-water discharge during the last deglaciation were first reported by Fairbanks (1989) from an analysis of drowned reef-crest sequences cored off the south coast of Barbados. By plotting age/depth data from the reef-crest coral *Acropora palmata* in these cores and correcting them for tectonic uplift (0.34 mm/yr), he reconstructed sea-level rise during the last deglaciation between 17,100 and 7,800 radiocarbon years ago. From this curve, he identified two "exceedingly rapid" rise events separated by a period of reduced melting, and estimated that the first event, melt-water pulse 1a (Mwp-1a), was a rise of 24 m in less than 1,000 years centered at 12,000 radiocarbon years BP, and the second event, melt-water pulse 1b (Mwp-1b), was a rise of 28 m centered at 9,500 radiocarbon years BP. Fairbanks suggested that these rapid-rise events corresponded to the most intense phases of seasonal melt-water discharge during the disintegration of Northern Hemisphere ice-sheets, and estimated discharge rates of 14,000 km^3/yr and 9500 km^3/yr, respectively. In later studies, he and co-workers re-dated all samples using more precise ^{230}Th ages (Bard et al., 1990; Fairbanks et al., 2005) and produced a curve showing that Mwp-1a was centered at 14,000 years, with a period of reduced melting between 13kyrs and 11 kyrs, and Mwp-1b was centered at 11,000 years BP (Figure 1).

However, these meltwater pulses coincided with gaps between cores which led some to argue that they were artifacts resulting from non-uniform uplift, or from the post-growth collapse of reef deposits themselves (see discussion in Broecker, 1990; Bard et al., 1996; Radtke and Schellmann, 2006). To rule out this possibility, evidence of reef-drowning from other areas was required. That evidence was reported by Blanchon and Shaw (1995) who determined that elevations of drowned *A. palmata* reefs in the Caribbean-Atlantic reef province were consistent with the stepped pattern of sea-level rise identified from Barbados. By combining the previously reported coral ages with stratigraphic data, including the positions of *A. palmata* framework, intervening gaps, and the transitional thickness between units, they further constrained the timing, rate, and magnitude of these melt-water pulses and calculated that Mwp-1a was a 13.5 m rise in 290 years centered at 14,200 years, there



Meltwater Pulses, Figure 1. Three-step model of post-glacial sea-level rise in the Caribbean. Reconstruction of sea-level older than 8 ka uses uplift-corrected elevation and thickness of back-stepping *A. palmata* reef-crest sequences from Barbados (modified from Fairbanks, 1989; Blanchon and Shaw, 1995) and precise ^{230}Th ages from corals in those sequences (Peltier and Fairbanks, 2006). Reconstruction of sea level younger than 8 ka is from stratigraphic sequences and calibrated radiocarbon-ages of relict and active Holocene reefs in tectonically stable areas of the Caribbean (Blanchon et al., 2002; Toscano and Macintyre, 2003). The position of mean sea level is constrained by maintaining coral age/elevation data within a 5 m envelope (shaded) which represents the 0–5 m reef-crest habitat depth zone where *A. palmata* forms a monospecific assemblage mixed with its clasts. Outliers are the result of either up-slope transport during storms or, in other areas, result from deeper habitat ranges for reef-crest corals. Correction for continuous uplift of Barbados is assumed to be 0.34 mm/yr but is ignored for quantification of the rate and magnitude of sea-level jumps that caused episodes of reef-crest drowning and back-stepping. Gray boxes show (non-uplift-corrected) age/elevation data gaps between reef-crest framework that are used to calculate minimum rate and magnitude of sea-level jumps; maximum magnitudes are calculated by assuming that sea-level position was 5 m higher than the base of up-slope reef-crest framework (as required by its 5 m depth habitat) and an increment of 5 m is added to the elevation gaps. Caribbean three-step model is contrasted with data from Tahtit, the Huon Peninsula, and the Sunda Shelf.

was a period of reduced melting between 13kyrs and 11 kyrs, and Mwp-1b was a 7.5 m rise in 160 years centered at 11,000 years (Figure 1). They also identified an additional melt-water pulse event at 7,100 radiocarbon years that drowned early Holocene reefs below the 15 m isobath and led to the initiation of modern reefs above the 10 m isobath. Later calibration of these age data showed that this additional reef-drowning melt-water pulse was centered at 8,000 calendar years (Toscano and Macintyre, 2003) and produced a rise of 6.5 m in <140 years (Blanchon and Shaw, 1995).

Subsequent attempts to test the 3-step model of Caribbean sea-level rise, and corroborate the existence, timing, and magnitude of melt-water pulses, have only been partially successful. The most successful sea-level reconstruction is from the Sunda Shelf between the Indonesian archipelago and the Vietnam peninsula (Hanebuth et al., 2000). Two core transects between the 126 m and 48 m isobaths recovered a transgressive sequence of organic-rich tidal-flat and mangrove-swamp deposits (Hanebuth and Stattegger, 2003). Radiocarbon dating of in-situ organics above the Pleistocene basement allowed the reconstruction of sea level (± 1 m) from 21 to 11 kyrs ago. This high-resolution reconstruction showed that Mwp-1a was recorded as a 16 m rise in 300 years starting at 14.6 calendar kyrs ago, almost identical to the rate and magnitude calculated from the Caribbean drowned reefs (13.5 ± 2.5 m in 290 years; Blanchon and Shaw, 1995). The only difference was the timing: on the Sunda Shelf Mwp-1a occurred 400 years before it did on Barbados (Figure 1). Although there has been considerable argument about which of these is correct (e.g., Weaver et al., 2003; Stanford et al., 2006), the difference in age between these sites may simply be the result of down-slope transport of younger *A. palmata* clasts onto the oldest drowned reef on Barbados seen at the top of core RGF-9 (Figure 1). Such a possibility could easily be tested by dating the lowest section of the up-slope reef (seen at the base of core RGF-12). Down-slope transport would cause an age overlap between the drowned and up-slope reefs.

Less precise reconstructions using corals with larger depth ranges have had more limited success. For example, a single core from the Huon Peninsula of Papua New Guinea recovered an uplifted 52 m thick coral sequence which recorded continuous reef accretion between 11,000 and 7,000 radiocarbon years BP (Chappell and Polach, 1991). All coral samples were later re-dated to obtain more accurate ^{230}Th ages (Edwards et al., 1993) and corrected for tectonic uplift (1.9 mm/yr). The sea-level curve based on these new data showed a distinct period of reduced melting between 12.3 kyrs and 11.0 kyrs, followed by a clear Mwp-1b centered at 11 kyrs (Figure 1). It was claimed that the period of reduced melting prior to the meltwater pulse was shorter than at Barbados, but corals used to identify sea-level position at Huon have larger depth ranges than *A. palmata* and therefore are not as reliable in pinpointing the precise elevation of sea level (Chappell and Polach 1991). Also, the assumption that uplift was uniform in this highly-active neotectonic terrain cannot be confirmed.

Cores recovered from the modern reef-crest around the more tectonically-stable island of Tahiti found a thicker 90 m sequence of continuous reef accretion back to ~13,800 ^{230}Th yrs BP (Bard et al., 1996; Montaggioni et al., 1997). This sequence therefore started accreting immediately following Mwp-1a implying that its effects in Tahiti were the same as in Barbados, and that a rapid sea-level rise had caused reef drowning and up-slope reef back-stepping (Blanchon, this volume). As in the other records, the coral age/depth data, when corrected for subsidence (0.25 mm/yr) showed possible evidence for a period of reduced melting prior to Mwp-1b, but it was significantly shorter (11.5–11 kyrs) than that in either Barbados or PNG. Interestingly, however, the Tahitian corals consistently plot deeper than those at Barbados, indicating that they may not be as precise at indicating sea level as claimed (Blanchon, 1998). This is supported by two observations: the increase in offset of the Tahiti corals through time, and the pattern of shallowing of the cored reef sequence (Figure 1). Both observations indicate that the reef prograded after Mwp-1a so that, in a vertical core, progressively deeper reef-front corals were encountered through time. In other words, Tahitian cores represent deeper-reef accretion when compared to those in Barbados. New cores collected during the IODP-310 Tahiti Leg, should help determine if this offset is indeed the result of deeper coral growth or a function of differing glacio-isostatic-adjustment histories. One preliminary result so far indicates that Mwp-1a at Tahiti has a similar timing to that identified from the Sunda Shelf at 14.6 ka (Deschamps et al., 2009).

In addition to the deglacial events, evidence for a meltwater pulse at 8 kyrs (Mwp-1c) has also been further supported by additional discoveries of drowned reefs from Grand Cayman, southeast Florida and the Gulf of Carpentaria (Blanchon et al., 2002, Banks et al., 2007, Harris et al., 2008). On the east coast of Grand Cayman, a transect of short cores along the reef-front in 20 m of water recovered a submerged *A. palmata* reef-crest whose surface corals returned ^{230}Th ages of between 8.9 kyrs and 8.1 kyrs BP (Blanchon et al., 2002). The depth of this drowned reef also corresponded with an intertidal notch on the western shelf at a depth of 18 m and indicated the establishment of an 18-m shoreline between 8.1 cal and 7.6 cal ka. Comparison of the age/depth data between Grand Cayman and other Caribbean islands, indicated a near synchronous demise and back-stepping of *A. palmata* reefs across the Caribbean around 8 kyrs ago in response to a rapid 6-m jump in sea level (Blanchon et al., 2002). But two potential problems with this jump hypothesis have been raised. The first problem was that back-stepping could only be demonstrated by comparing the age of reef drowning in one location with the age of up-slope reef initiation in another. In other words, there were few sites where clear evidence of both drowning and back-stepping had been reported together. That changed recently with the reporting of new age/depth data from an up-slope reef off the southeast Florida shelf (Banks et al., 2007). Combining the calibrated radiocarbon-age data of this new reef with those from an earlier report of an 8 ka old drowned reef further down-slope (Lighty et al., 1978), confirmed that at this site Mwp-1c at 8 kyrs caused the back-stepping of *A. palmata* reef crests 6–7 m up-slope in less than 580 years (Blanchon, this volume).

The second potential problem with the 8 ka jump was the discovery of a deposit of *A. palmata* off Sand Key, Florida, that apparently filled the elevation gap between drowned and back-stepped reefs (Toscano and Lundberg 1998; Figure 1). This deposit developed between 12.5 m and 9 m below present sea level and contained 9–7 ka old corals. In other words, it developed at the same time as the 8 ka old drowned reef reported 4–7 m further down-slope by Lighty et al., (1978). Given that Banks et al., (2007) confirmed that the down-slope reef morphology is directly analogous to that of modern Florida breakwater reefs, this means that Sand Key deposit further up-slope cannot also be a breakwater reef. This objection is supported by the fact that the deposit not only contains age reversals, but an 86 ka old extra-formational clast reworked from the underlying foundation. The mismatch in elevation with coeval down-slope reefs, together with the evidence of reworking, clearly indicates that the Sand Key deposit is not of reefal origin but is a coastal boulder-rampart deposited by storms and hurricanes. As noted by Blanchon and Perry (2004), such problems highlight the importance of identifying in-place *A. palmata* reef framework using textural and taphonomic criteria in order to differentiate it from either boulder ramparts deposited up to 5 m above present sea-level, or submerged accumulations which can be deposited in much deeper water.

Until recently, there was scant support for reef drowning related to the 8 kyr Mwp-1c outside the Caribbean (e.g., Bard et al., 1996). But in 2008, Harris et al., reported early Holocene reef development in the Gulf of Carpentaria, northern Australia. Multi-beam sonar and short drill cores demonstrated widespread reef development between 23 m and 33 m water depth starting at 10.5 kys and ceasing by 8 kyrs. Unfortunately, the coral sequences were poorly developed and it is unknown if these reefs grew at sea level or were submerged below it. Their surface elevations however are remarkably consistent over wide areas indicating they were likely breakwater reefs. Evidence for the 8 ka Mwp-1c has also been reported from other sedimentary systems, notably deltas and estuaries (Stanley and Warne 1994; Bratton et al., 2003; Hori and Saito 2007) and isolation basins in glacio-isostatic rebound terranes (Yu et al., 2007).

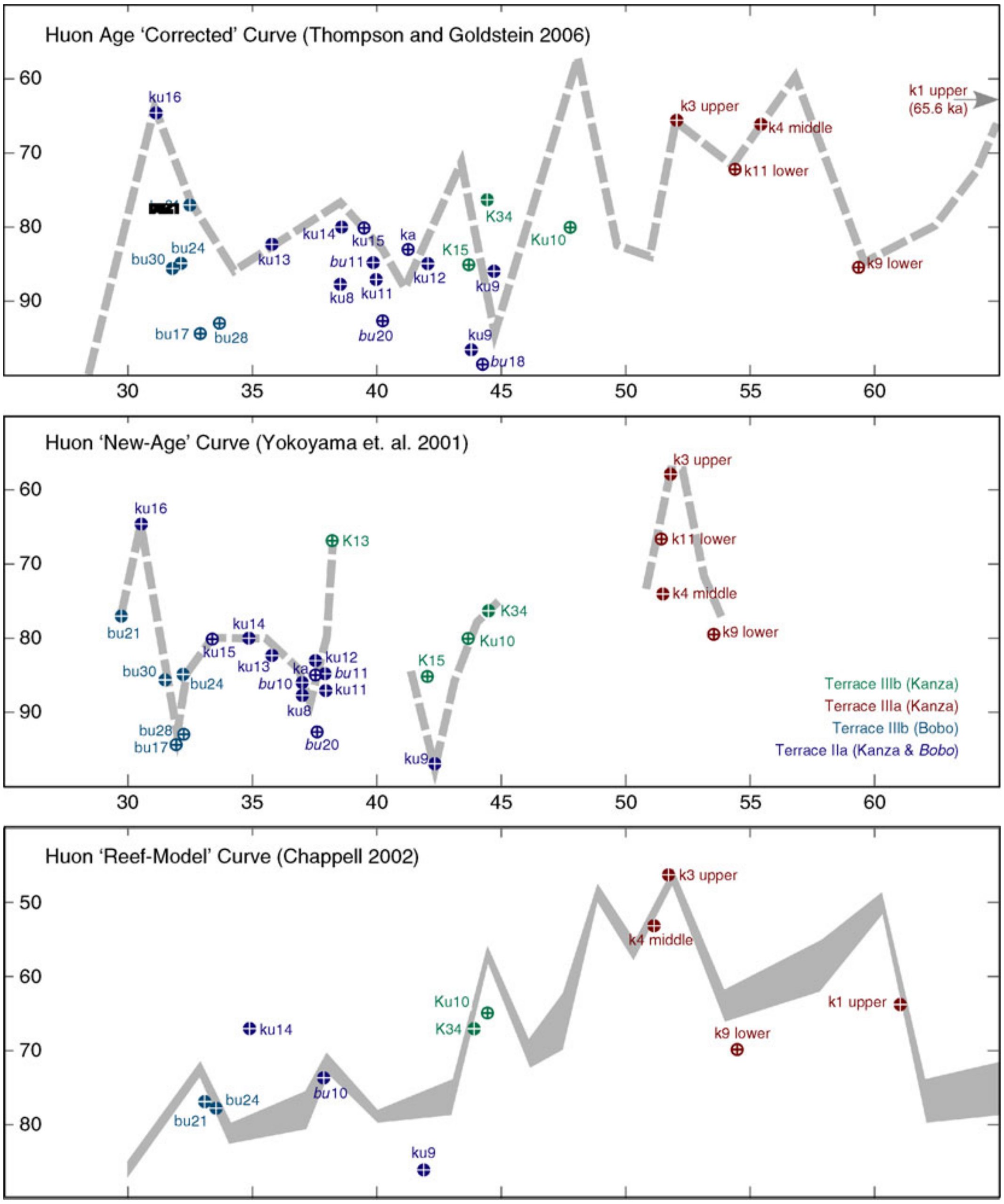
Last glaciation (MIS-3)

Reports of meltwater pulses prior to the last deglaciation are more controversial. For example, there have been multiple claims of melt-water pulses during the last Glacial between 19 ka and 65 ka. The first of these is a proposed melt-water pulse at 19 ka which is based on a core transect across the Bonaparte Gulf, in northern Australia between depths of 147 m and 34 m (Yokoyama et al., 2000). These cores recovered shelf and marginal-marine to brackish-water facies based on the foraminiferal and bivalve assemblages, which were used to radiocarbon date the sequence. Using age/depth data of the transition from the low-stand brackish-water facies into the succeeding marginal-marine facies, it was argued that meter-scale elevation differences between cores was the result of a melt-water pulse centered at 19 cal ka BP. The validity of this sea-level reconstruction, however, has been contested by Shennan and Milne (2003), who highlighted the presence of hiatuses reported in a later study (Yokoyama et al., 2001), inconsistencies between cores, and doubts concerning the depth range of the facies units. As a consequence, the interpretation of a meltwater pulse at 19 kyr is suspect.

The second report of a 19 ka meltwater pulse is from the north-east Irish coast where a presumed fluvial incision was filled by transgressive marine foraminiferal mudstones along a coastal area undergoing active glacio-isostatic uplift (Clark et al., 2004). The uniform age of these deposits and the apparent transgression over a fluvially-incised subaerial surface were interpreted to result from a rapid 10 m rise in sea level at 19 cal ka BP. Unfortunately, alternative interpretations of the origin of the incised valley, such as marine ravinement, cannot be ruled out. In addition, the correction of the ages for marine reservoir has been disputed by Hanebuth et al., (2009). Such problems once again render the interpretation of a meltwater pulse at 19 ka as ambiguous.

Further reports of fully Glacial (MIS-3) stage meltwater pulses have come from the Huon Peninsula. There, the ages of uplifted reef terraces between 30 ka and 65 ka apparently matched rapid climate changes and ice-sheet events seen in Greenland ice and north Atlantic sediment cores (Chappell, 2002). A sea-level reconstruction from these terraces used the thickness and geomorphology of reef-crest and intertidal units to model the relative rate and magnitude of sea-level rise by making assumptions about reef type and accretion rate. Then, these relative rises were used to reconstruct absolute sea-level position using ^{230}Th ages of the reefs and applying uplift corrections (Figure 2). This preliminary reconstruction showed 5 rapid sea-level-rise events of between 10 m and 20 m within duration of 1–2 ka; the timing of some of these rises coincided with rapid-ice loss events from the Laurentide Ice Sheet, known as Heinrich events (Hemming 2004).

Further dating of the Glacial reef terraces on the Huon Peninsula by Yokoyama et al., (2001) attempted to provide an independent sea-level reconstruction and model glacio-isostatic adjustment (Figure 2). Unfortunately, this new reconstruction conflicted in terms of timing, number, and magnitude of rapid sea-level rise events with the reconstruction of Chappell (2002). This is largely because Yokoyama et al., (2001) ignored the problem of true-age variability (Scholtz and Manginni, 2007) and considered all isotopically-reliable ages to be valid sea-level indicators, despite their lack of stratigraphic consistency. These errors were compounded by making an age-dependant uplift correction for every dated coral, rather than making this correction for a core-group of ages that best represented the time-span of individual reef-crest development. Together these errors led to single outlying ages forming the peaks of rapid sea-level-rise events, and



Meltwater Pulses, Figure 2. Three sea-level reconstructions for the Huon Peninsula's Glacial coral-reef terraces (Terraces II and III). Lower reconstruction is based on a model of reef thickness, type, and accretion rate estimates, corrected for uplift using average ^{230}Th age of individual terraces (Chappell, 2002). Middle reconstruction based on new ^{230}Th ages (Yokoyama et al., 2001) with each age corrected for uplift. Upper reconstruction is based on correction of all ^{230}Th ages for open system effects (Thompson and Goldstein, 2005) with each age corrected for uplift. Correcting each age for uplift introduces serious errors and results in single outlying anomalous ages forming the peaks of rapid sea-level-rise events, and neighboring ages from the same reef being placed in different parts of the sea-level curve. In other words, curve position is an artifact of dating which results from true-age variability of samples.

neighbouring ages from the same reef being placed in different parts of the sea-level curve (e.g., ku16 and k13 in Figure 2). In other words, this implies that a single conformable reef unit developed during different stages as sea level returned to the same position over time. Later, Esat and Yokoyama (2006) claimed that this 'disorderly growth conjecture' was a valid explanation of reef development, rather than addressing the more plausible explanation that ^{230}Th ages are difficult to replicate on sub-millennial timescales, as shown by the fact that 50% of ages with pristine isotopic values can have discordant ^{231} Pa ages (Scholz and Mangini, 2007). In addition, disorderly growth is clearly untenable in conformable reef sequences, given that multiple passes of the shore-face would leave significant stratigraphic evidence of marine erosion and/or subaerial exposure.

The problem of true-age variability in the ages of Yokoyama et al., (2001) was partially addressed by Thompson and Goldstein (2005) who recalculated them to correct for bias introduced by open-system diagenesis. Although this reduced the spread of ages from some reef units, it did not significantly alter outlying ages, which remained stratigraphically inconsistent and again plotted in separate parts of the sea-level curve (Figure 2). This failure to address fundamental stratigraphic consistency of these age data and to continue making erroneous age-dependant uplift corrections on every dated coral seriously compromises the Glacial sea-level reconstruction of Thompson and Goldstein (2005) and means that the sea-level peaks are merely dating artifacts.

Glacial Termination II (MIS-6)

Reports of meltwater pulses during the penultimate deglaciation (MIS-6) have also recently been made. On the Huon Peninsula, Esat et al., (1999) reported that a cave exposing the base of the last interglacial terrace (VII) some 90 m below its crest, contained in-situ corals with 1-cm-thick annual bands, implying growth in a shallow-water reef. These corals returned seven isotopically acceptable ^{230}Th ages of between 125.6 ka and 133.7 ka (i.e., a 7.2 ka true-age variation) which were averaged to give an age of 130 ±2 ka (a process which excluded a reliable age of 115 ka). This was compared with a 134 ±2 ka age average from four corals recovered from 5 to 12 m below the reef-crest reported earlier by Stein et al., (1993), but four significantly younger ages at 2 and 16 m were ignored. By comparing average ages and elevations of these two coral groups, Esat et al., (1999) claimed that sea-level fell rapidly at least 70 m from the level of the 134 ka crest group, and then rose rapidly at least 85 m from that of the 130 ka cave group, with both the fall and the rise occurring within the 4 ka difference between the age groups. Unfortunately, the comparison between these two groups is questionable given that it ignores younger ages from both the down-slope cave site and the up-slope barrier site reported earlier by Stein et al., (1993). It is much more likely that the stratigraphic age inversions at both sites reflect true-age variability (Scholz and Manginni, 2007) and that neither may be accurate (Blanchon, this volume). In the absence of reliable ages, the stratigraphy dictates that the cave is simply the oldest part of terrace VII which accreted vertically as sea-level rose. As a result, claims of a rapid 70 m fall and an equally rapid 85 m rise at the Huon Peninsula during the penultimate deglaciation are extreme and poorly supported by the data.

Similar claims of extreme sea-level variability have also been made from IODP-310 cores recovered from the fore-reef slopes of Tahiti (Thomas et al., 2009). In these cores, two corals recovered from 115 to 118 m below present sea level returned reliable ^{230}Th ages of 133 and 137 ka respectively. Both corals are typical of shallow-water reef environments but are separated by a 30 cm section of much deeper-reef framework. This led Thomas et al., (2009) to claim that a rapid deepening event drowned the older coral and produced a limited deep reef before sea-level fell rapidly leading to a resumption of shallow reef development. In other words, the return to shallow reefal environments represented a reversal in the rapidly rising sea level during the penultimate deglaciation. Unfortunately, such an interpretation ignores the more plausible possibility that the shallow-water corals were in fact clasts transported down-slope into deeper water. Examination of the cores in their Figures S2 and 3 supports this shallow-clast interpretation, with the deeper coral at 118 m consisting of a 5 cm diameter coral clast enclosed by other basalt- and coral-clasts (which were even identified as clasts in the log description). The other coral, which sits directly on top of the deeper framework, could also be a clast given its small size (20 cm); the fact that it contains surfaces encrusted by coralline algae, upward growth, and apparently horizontal cavity fills could merely be coincidental, indicating it fortuitously landed with an upright orientation. However, a clast interpretation is supported by the lack of coral microbialites which are typical of deglacial reef-framework of Tahiti (Heindel, 2008). Regardless of the interpretation chosen, such extraordinary claims of extreme sea-level changes are clearly not supported by adequate data. As such, the existence of meltwater pulses during the penultimate deglaciation, although likely, remains to be proven by credible reef data.

Last Interglacial (MIS-5e)

A better supported claim of a more modest meltwater pulse has recently been made from reef development on the Yucatan Peninsula during the last Interglacial (MIS-5e). There, Blanchon et al., (2009) identified an episode of reef-crest demise at +3 m and back-stepping to +6 m. In some parts of the reef, this back-stepping was accompanied by erosion, but in others the sequence between the two reefs was continuous, implying that they grew consecutively on an ecological timescale with no intervening hiatus (Figure 4). In turn, this consecutive development requires that reef-crest back-stepping occurred on an ecological timescale, implying that it was caused by a 2–3 m sea-level jump (Blanchon, 2010). Although the dating precision precluded testing the rise rate, a test of the stratigraphic relations was made by dating samples from both reef-crests. Unfortunately, only the +6 m crest returned strictly reliable ^{230}Th ages which fell between 119.5 ka and 117 ka. However, these ages were younger than well-dated +3 m reefs that had developed in other areas,

Meltwater Pulses, Table 1 Summary of evidence for meltwater pulses, their timing, rate, and magnitude

Mw-event	Site (ref.)	Depth (m)	Adj. depth (m)	Magnitude (m)	Adj. magnitude (m)	Timing (kyrs)	Duration (years)	SL rise rate (mm/yr)
Mwp-1a	Barbados[b]	87 to 76–71	**93 to 78–73**	**11–16**	11–20	14.1–13.7	450	24–36
Mwp-1a[a]	Barbados[b]	90 to 76–71	**95 to 80–75**	**14–19**	15–20	**14.6–14.3**	300	**47–63**
Mwp-1a	Sunda Shelf[c]	96–93 to 80		13–16		14.6–14.3	280	46–57
Mwp-1b	Huon Pen.[d]	32–25	**53–46**	7	**7**	**11.1–10.7**	372	19
Mwp-1b	Barbados[a]	51 to 46–41	**55 to 50–45**	5–10	**5–10**	**11.4–11.1**	314	16–32
Mwp-1b	Tahiti[e]	66–59	**65–59**	7	**6**	**11.5–11.3**	215	28
Mwp-1c	Caribbean[b]	18 to 13–9		5–9		8.0–7.6	400	13–23
121 ka Mwp	NE Yucatan[f]	+3 to +5–6		2–3		121	<100	20–30

[a] excluding upper *A. palmata* unit in RGF-9 due to suspected downslope transport from RGF-12

References for column two: [b] Blanchon (Reef Backstepping, this volume) updated from Blanchon and Shaw (1995), using new data from Toscano and Macintyre (2003) and Peltier and Fairbanks (2006); [c] from Hanebuth et al. (2000) and Hanebuth and Stattegger (2003); [d] Edwards et al. (2003); [e] recalculated from Bard et al. (1996); [f] Blanchon et al. (2009).

both supporting the stratigraphy and constraining the sea-level rise to around 121 ka. To confirm these results however requires replicating the back-stepping reef stratigraphy and obtaining a reliable chronology in other stable areas.

Origin of meltwater pulses

The preceding review of individual claims of meltwater pulses shows that solid geological evidence exists only for the 3 jumps in sea level during the last deglaciation at 14.6, 11.4 and 8 ka. Preliminary evidence also exists for a jump at the end of the last Interglaciation around 121 ka, although this requires support from other stable areas. Tabulation of these data shows that the average rise-rate during these jumps was as much as 63 mm/yr (Table 1). In other words, the jumps represent a rise-rate that is as much as 6 times the background deglacial rise-rate and therefore clearly implicate major rapid ice-loss events resulting from ice-sheet collapse (Blanchon and Shaw, 1995).

Linking the timing of sea-level jumps with climatic evidence of ice-sheet instability, however, is hindered by age biases in both marine-radiocarbon and ice-core chronologies (Skinner, 2008; Druffel et al., 2008). Despite such biases, recent improvements in synchronizing ice-core chronologies indicate that meltwater pulses coincide with or closely follow abrupt climatic warming, which was itself preceded by severe cooling episodes, known as Heinrich events, caused when the Laurentide Ice Sheet extended out to the edge of the continental shelf (see Hemming, 2004). For example, the start of Mwp-1a on the Sunda Shelf and Tahiti at 14.6 ka coincides with or closely follows the abrupt onset of Bolling/Allerod warming in the NorthGRIP ice core at 14.7 ka (Steffensen et al., 2008), which is itself preceded by Heinrich event 1 from 14.5 to 17.5 ka (Skinner, 2008). Similarly, Mwp-1b on Barbados, which starts at 11.4 ka, closely follows the abrupt onset of PreBoreal warming in NorthGrip at 11.7 ka. However, further dating of the base of the reef-crest sequence in RGF-8 might push the onset of Mwp-1b closer to the ice-core timing (Figure 1). Finally, the timing of Caribbean reef demise at ~8 ka closely follows the onset of warming after the 8.2 ka cold event seen in Greenland ice-cores, and the rapid disintegration of the Laurentide Ice-sheet between 8.2 ka and 8.5 ka (Barber et al., 1999; Carlson et al., 2008). If this phasing between rapid sea-level rise events and abrupt climate warming is confirmed, it will have serious implications for the future stability of remaining ice-sheets under the ongoing episode of anthropogenic global warming.

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Cross-references

Back-Stepping
Last Interglacial and Reef Development
Postglacial Trangression

MICRITE

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Synonyms

Microcrystalline calcite

Definition

Micrite is a textural term for microcrystalline carbonates less that 4 μm in size.

Introduction

The term "micrite" is a contraction of the words "microcrystalline calcite" and was introduced by Folk (1959, p. 8) as an aid in the classification of limestones. Initially, Folk applied the term to microcrystalline calcite ooze in the size range of 1–4 μm. Adding a prefix, he coined terms such as "biomicrite" to refer to fossils in a microcrystalline matrix. In 1974, Folk expanded the meaning of the term "micrite" to encompass all carbonate minerals measuring 1–4 μm. He also added a new term "minimicrite" for sizes less than 1 μm.

Bathurst (1966) applied Folk's terminology to refer to the process of grain surface alteration to micrite caused by microborings filled with micrite precipitates as "micritization". However, Friedman (1985) thought that Bathurst and others who used his terminology (e.g., Lloyd, 1971; Gunatilska, 1976; Kobluk and Risk, 1977) were misusing Folk's terminology that simply referred to a microcrystalline ooze matrix.

It was Alexandersson (1972) who suggested that "micrite" should as a textural term to cover all microcrystalline carbonates. Most subsequent studies of grain alteration or submarine lithification use both "micrite" and "minimicrite" as textural terms (e.g., Land and Moore, 1980; Macintyre and Marshall, 1988; Reid et al., 1992; Reid and Macintyre, 1998; Macintyre and Reid, 1995, 1998).

Conclusion

In carbonate petrographic studies, the terms micrite (4–1 μm) and minimicrite (<1 μm) should be used as textural terms to refer to all microcrystalline carbonates.

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Cross-references

Aragonite
Calcite
Platforms (Cemented)
Porosity Variability In Limestone Sequences
Submarine Lithification

MICROATOLL

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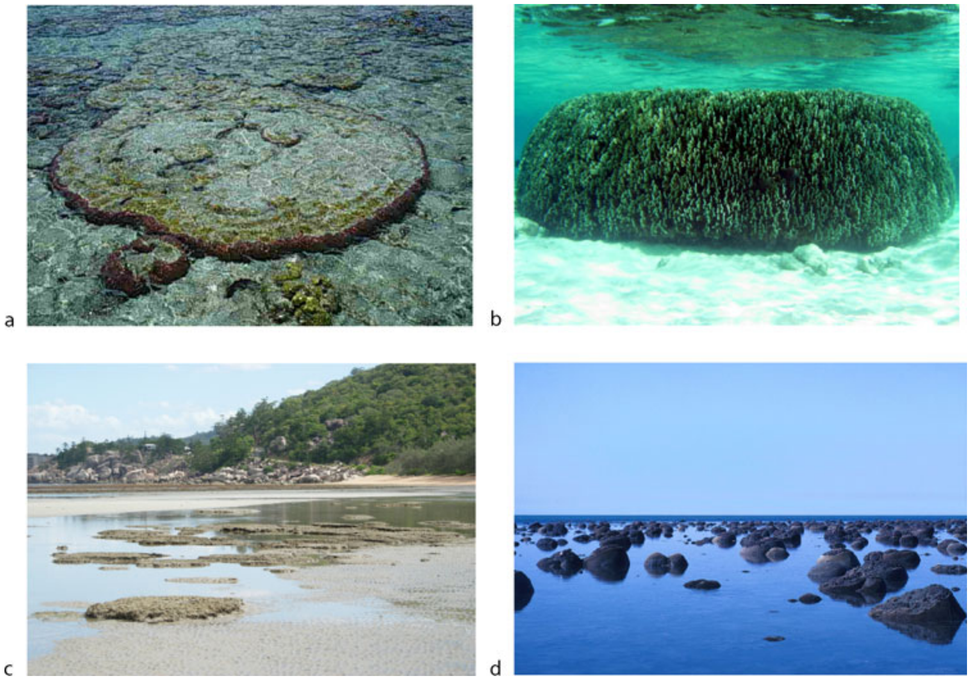
Definition

Microatolls are intertidal coral colonies with dead, relatively flat, upper surfaces surrounded by an annular rim of living coral (Figure 1a,b). They form when upward coral growth is constrained by prolonged exposure near to shallow water, but polyps on the colony sides remain alive and continue to grow laterally (Scoffin and Stoddart, 1978; Stoddart and Scoffin, 1979; Woodroffe and McLean, 1990). Fossil microatolls are microatolls in which no living polyps survive but the colony morphology is preserved (Figure 1c).



Microatoll, Figure 1 (**a**) Living *Porites lutea* microatoll with multiple ringed morphology, reef flat, Cocos Keeling Islands, eastern Indian Ocean; (**b**) *Heliopora coerulea* microatoll, reef flat Mendhoo, Maldives; (**c**) Fossil microatolls 4000–5000 years old, Magnetic Island, GBR, Australia; (**d**) Heliotropic *Goniastrea retiformis* microatolls, Paluma Shoals, GBR, Australia.

Introduction

Darwin (1842) first described coral microatolls, with further accounts by various other early reef scientists (e.g., Dana, 1872; Semper, 1880). Guppy's (1889) description of "miniature atolls" from the Cocos (Keeling) Islands first compared the living coral annulus on microatolls to the circular reef rim of coral atolls, followed by Agassiz (1895) and Krempf (1927) who referred to microatolls as "diminutive atolls" and "dwarf atolls" respectively. The specific term microatoll was coined by Wood-Jones (1910) who argued that microatolls resemble coral atolls and form because sedimentation restricts coral growth to their peripheral rim, as he proposed in his largely discounted theory of atoll formation. Abe (1937) referred to microatolls as "table-forming corals", emphasizing their flat dead tops.

Patch reefs composed of multiple coral colonies with raised rims and sand-filled centres have been referred to as microatolls (e.g., Kornicker and Boyd, 1962; Larkum and Steven, 1994), but are better described as "mini-atolls" (Scheer, 1971). Thirty years ago, Scoffin and Stoddart reviewed "the nature and significance of microatolls" and recommended that only single coral colonies be described as microatolls (Scoffin and Stoddart, 1978; Stoddart and Scoffin, 1979). This has been applied with only rare exceptions. The focus of these earlier investigations was almost entirely on microatolls as high quality sea-level indicators (see Chapter *Sea-Level Indicators*), an application improved further by recent technological advances that have increased the resolution of elevation survey and radiometric dating. Further, exceptional palaeoenvironmental records preserved in the geochemistry and structure of microatoll skeletons are being discovered, and represent exciting new areas for research.

Microatoll description

Most microatolls develop from massive corals; however, branching and foliaceous corals may also adopt this morphology. *Porites* microatolls are particularly common, and intertidal *Goniastrea* and *Platygyra* colonies also form microatolls on many reefs (Figure 1d). They are most abundant on Indo-Pacific reefs but also occur in the Caribbean. In the most detailed survey to date, 43 species from 23 genera were identified as forming microatolls in the northern Great Barrier Reef (GBR) (Rosen, 1978). Microatolls are usually less than 0.5 m high (vertical thickness) but they can be long-lived growing to several meters in diameter. Massive *Porites* grow at rates of around 1 cm per year, so microatolls of a meter in diameter are typically around 40–50 years old. A fossil microatoll exceeding 9 m in diameter and dated at 2195 ± 80 years BP at its centre and 1535 ± 130 years BP on its margin occurs on Pagan in the Mariana Islands (Siegrist and Randall, 1989), with a similarly large fossil *Porites*

(9.6 m diameter, 7009 ± 41 cal years BP at centre) reported from the Leizhou Peninsula, in the southernmost part of Guangdong province in southern China (Yu et al., 2009). *Porites compressa* microatolls 7 m in diameter occur in Kaneohe Bay, Hawaii (Roy, 1970), and fossil *Porites* microatolls 6 m in diameter occur at several locations on the GBR (Hopley and Barnes, 1985; Hendy et al., 2003). Large microatolls demonstrate continuity of growth for several centuries, but most microatolls are < 2 m in diameter. This probably reflects the relatively low probability of extended survival in shallow reef environments where corals are most vulnerable to a range of debilitating conditions. Microatolls on the northern GBR surveyed by Scoffin and Stoddart (1978, p.105) averaged 0.5 m in diameter, although other than stating that they "vary in size from a few centimeters to a few meters" no statistical description of the variance was offered.

Microatoll formation

Corals develop into microatolls when prolonged emergence during low tides kills polyps on a colony's upper surface and constrains subsequent growth to its sides. Tolerances to emergence vary with species; *Goniastrea* and *Platygyra* typically grow higher than *Porites* when they occur on the same reef flat. Other factors have been argued as drivers of upper surface mortality and microatoll formation, including excessive sedimentation (Wood-Jones, 1910), nutrient dynamics, and hydrodynamic stress (Stoddart and Scoffin, 1979); however, the general symmetry developed by individual microatolls and the accordant morphologies developed by neighboring microatolls are difficult to reconcile with these typically and unevenly distributed stresses. Subaerial emergence is clearly the main environmental parameter driving the formation of microatolls in most shallow reef settings, where the absolute elevation of the upper limit to coral growth is a function of the duration of exposure and the intensity of desiccating conditions, which are strongly influenced by elevation relative to a tidally modulated water level. Where microatolls grow in "open water" habitats freely connected to the open ocean, the confining water level is a tidal datum that can be linked to sea level. However, where the ebbing tide is impeded as it drains off the reef, the confining water level is moated above the open water level (see Chapter *Moating*) and thus the upper limit to coral growth is controlled by the height of the moat sill, and is less precisely tied to sea level (Hopley and Isdale, 1977).

The relationship between the upper limit to coral growth and tidal levels may vary with exposure to factors such as wavelet wetting, diurnal, and seasonal tidal patterns, but on the central GBR, where the mean tidal range is 2–3 m, the tops of microatolls within the same field are usually within ±10 cm (Chappell et al., 1983). Smithers and Woodroffe (2000) indicate that even greater uniformity is found where the tidal range is smaller, such as at the microtidal Cocos (Keeling) Islands, although even there microatoll elevations may vary by as much as 40 cm between different habitats (reef flat, intertidal passage, lagoonal) that experience different hydrodynamic conditions. The tops of *Porites* microatolls in open-water habitats on the GBR are usually close to the mean low water spring (MLWS) tide level, but may extend to the mean high water neap (MHWN) tide level in moated habitats (Scoffin and Stoddart, 1978). In the Cocos (Keeling) Islands the tops of open water microatolls are typically elevated approximately midway between MLWS and MLWN.

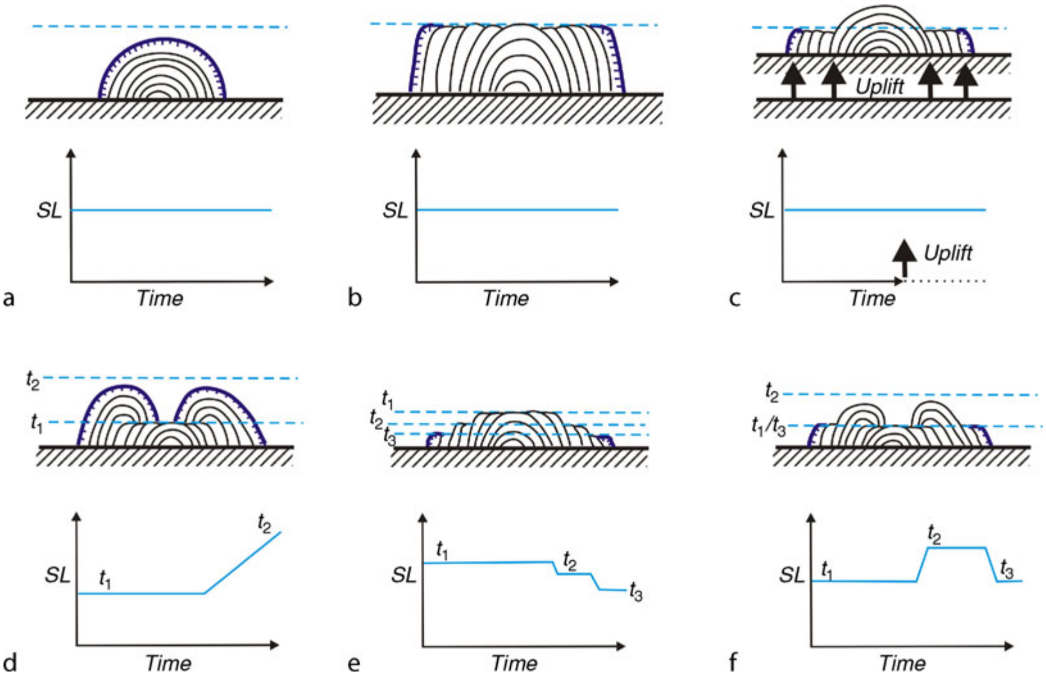
The relatively flat top developed by coral microatolls is referred to as the microatoll plane (Scoffin and Stoddart, 1978). This surface is rarely perfectly horizontal as the water level which confines upward coral growth is seldom absolutely constant through time. As water levels and the upper limit to coral growth fluctuate over a microatoll's lifetime, complex microtopographies composed of concentric ridges and swales can progressively develop across the microatoll plane. Hopley (1982) identified four common microatoll forms:

1. "*Classical*" microatolls are the basic discoidal kind, with a relatively flat microatoll plane formed under relatively stable water level;
2. "*Top hat*" microatolls have an elevated centre and lower outer rims. They form where the upper limit to coral growth is abruptly lowered, for example, where a storm breaches the sill of a pond that holds water over the reef flat at low tide (Hopley and Isdale, 1977);
3. "*Upgrown*" microatolls have low centres encircled by higher living rims. They form where the confining water level has risen, as might occur if falling tides are moated behind a rubble rampart deposited on a reef flat during a storm, or where the reef is subsiding (possibly driven by compaction, or tectonic subsidence);
4. "*Multiple-ringed*" microatolls with concentric undulations across the microatoll plane form when the upper limit to coral growth has oscillated through time, either episodically or dynamically, as may occur where interannual variations in sea level forced by relatively rapidly changing oceanographic and atmospheric conditions – such as ENSO – are experienced.

The progressive development of different microatoll surface morphologies driven by temporal changes in the water level that limits upward coral growth is shown schematically in Figure 2.

Microatolls and sea level

Where the confining water level is an open water level, this relationship means that microatolls, or collections of microatolls, can be used to reconstruct sea-level histories that spatially and temporally augment those available from instrumental records (see Chapter *Sea-Level Indicators* for diagrams). Microatoll derived sea-level records are generally of two main types: (a) records of mid-late Holocene sea level constructed by comparing the elevations of radiometrically dated fossil microatolls to the



Microatoll, Figure 2 Schematic cross-sections through microtolls showing progressive development (rings are annual growth rings with most recent growth at living margins), with water level history below. (**a**) Hemispherical coral as yet unconstrained by emergence at low tide and not yet adopting the microatoll form; (**b**) "Classical" microatoll developed under relatively stable water level; (**c**) hemispherical coral transformed into a microatoll after emergence caused by tectonic uplift; (**d**) "Upgrown" microatoll developed under rising water level conditions; (**e**) "Top hat" or terracetted microatoll recording falls in constraining water level; and (**f**) "Multiple-ringed" microatoll formed by confining water level that fluctuates both upwards and downwards (after Hopley 1982; Woodroffe and McLean, 1990).

elevation of living microatolls at the same location with a known relationship to a tidal datum; and/or (b) records of interannual or decadal sea-level change reconstructed from detailed analyses of the surface topography of long-lived microatolls or microatolls with overlapping lifespans. Both assume that the tidal datum that is the confining water level is unchanged and as sea level varies the absolute elevation of this tidal datum fluctuates.

In many locations, fossil microatolls, often 5,000–6,000 years old, can be readily identified and compared directly with nearby living counterparts that can be surveyed to a tidal datum. Where the tidal curve has not significantly changed, the relative elevations of microatoll tops document the heights of former constraining water levels. Radiometric dating of the fossil microatolls at different heights assigns a chronology to these water levels (see Chapter *Uranium Series Dating*). Where it is confirmed that fossil microatolls were not moated, these histories of water-level change are also excellent records of sea-level change. This approach has been applied to establish mid-late Holocene sea-level histories on the Central GBR (Chappell et al., 1983), in Torres Strait (Woodroffe et al., 2000), the Pacific (e.g., Nunn, 2000; Goodwin and Harvey, 2008), and Indian Oceans (e.g., Woodroffe and McLean, 1990; Kench et al., 2009).

Microtopographic undulations over the upper surfaces of well-preserved microatolls track interannual variations in the elevation of the confining water level (Woodroffe and McLean, 1990; Smithers and Woodroffe, 2001). The internal skeletal structure of massive microatolls contain annual density bands (see Chapter *Sclerochronology*) that can be used to age the upper limit to coral growth over the microatoll's lifetime (preserved as the topography of the microatoll plane), usually by counting back the density bands from the living edge at the time of sampling. Rapid rises that exceed maximum coral growth rates will not be fully recorded, but microatoll microtopographies may yield detailed sea-level records extending back decades and centuries in modern corals (Woodroffe and McLean, 1990; Smithers and Woodroffe, 2001; Spencer et al., 1997), and also in well-preserved fossil microatolls of mid-Holocene age (Yu et al., 2009).

Microatoll records of ENSOs, earthquakes, and other environmental conditions

Microatolls are also excellent archives of a range of other environmental conditions. These include the following:

(a) El-Nino Southern Oscillation (ENSO) events: Sea-level changes accompany shifts from El Nino to La

Nina conditions and associated ENSO cycles, and it has been demonstrated that microatolls in the Pacific Ocean preserve smoothed records of these oscillations across their upper surfaces (Woodroffe and McLean, 1990; Spencer et al., 1997; Woodroffe and Gagan, 2000). The records are smoothed because the record is biologically mediated and only rises in sea level below the coral growth rate (~1–2 cm a year for massive *Porites*) can be completely recorded. Furthermore, in mid-ocean settings changes in sea surface temperature (SST) and salinity (SSS) related to ENSO are documented by the geochemistry of microatoll skeletons (see Chapter *Palaeoclimate from Corals*), with high fidelity between adjacent corals (Woodroffe and Gagan, 2000). Concerns that geochemical records from microatolls may not represent oceanic water conditions appear allayed by studies that demonstrate excellent correlations between these geochemical records and instrumental SST datasets. Narrow stress bands may also be deposited in microatoll skeletons when conditions for coral growth become critical – and these may document the occurrence of past severe ENSO or other stress events.

(b) Tectonic movements and event prediction: Microatolls respond to relative sea level and thus their surface morphologies reflect not only fluctuations in the sea surface but also movements of the substrates on which they grow (see Figure 2c). Microatolls in tectonically active areas have been used to establish histories of subduction or uplift associated with earthquakes or more subtle interseismic crustal deformation processes (Taylor et al., 1987; Zachariasen et al., 2000; Natawidjaja et al., 2004, 2006, 2007; Briggs et al., 2006), to investigate spatial patterns of plate rupture during single and multiple events (Konca et al., 2008), and to calculate the rates of tectonic stress accumulation, the frequency of past tectonic events, and the probability of future tectonic hazards (Sieh, 2006; Sieh et al., 2008). For example, Briggs et al. (2006) used GPS measurements of coral microatolls to establish abrupt coseismic uplift of reefs at Nias by as much as 3 m during the Great 2005 Nias-Simeulue earthquake, which followed decades of strain accumulation and submergence, documented by the development of "upgrown" microatolls.

(c) Other environmental parameters: Coral microatolls confirm that a reef has reached sea level and are critical evidence in geomorphological investigations of reef structure and growth. For example, fossil microatolls across reef flats can reveal reef flat progradation histories (Smithers et al., 2006). Storm histories can also be derived from microatolls, either from upper surface patterns of moated microatolls where moat height or integrity (and thus moated water level) is affected by storms (Hopley and Isdale, 1977) or where storms cause tilting of the microatoll plane (relative to the pre-storm alignment), the timing of which can be derived from the colony's internal structure. Some microatolls grow in areas where tidal conditions only expose the coral during daylight at a particular time of year. For example, on the Central GBR daytime low spring tides only occur during the winter months, when the sun is in the northern sky. As a result, higher growing microatolls, such as those formed by *Goniastrea* and *Platygyra,* develop tilted tops in which the northern, more directly radiated section of the living rim is lower than the "lee" side (Figure 1d). Buskirk et al., (1981) reported similar microatolls with tops dipping towards the sun from Vanuatu. This pattern is usually developed across entire microatoll fields, and where storms have affected these reefs, disturbance of this pattern is conspicuous.

Summary

Coral microatolls are excellent sea-level indicators. Advances in survey and radiometric dating technologies that have improved both elevational and temporal resolution have further enhanced their utility. Furthermore, in recent decades researchers have discovered that microatolls yield excellent data on a broader range of environmental phenomena including atmospheric, oceanic, and tectonic processes. These high-resolution datasets augment more recent and scattered instrumental records both spatially and temporally, improving knowledge of the natural variability and significance of recent changes in these parameters.

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Cross-references

Atolls
Cocos (Keeling) Islands
Earthquakes and Emergence or Submergence of Coral Reefs
El Niño, La Niña, and ENSO
Great Barrier Reef Committee
Moating
Paleoclimate from Corals
Radiocarbon (^{14}C): Dating and Corals
Sea-level Indicators
Sclerochronology
Uranium Series Dating

MICROBES

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Definition

Microbes are microscopic organisms. Many organisms fit into this size category, including, Bacteria, Archaea, Fungi, Protists, etc. The definition provided here uses microbes to describe Bacteria and Archaea. These two groups are unicellular organisms, which do not contain a nucleus and rarely harbor membrane-bound organelles. Both Bacteria and Archaea were classified together as Prokaryotes, but this classification is no longer considered appropriate, because these two groups evolved from separate lineages.

Microbial association with corals: holobiont

Corals exist as a community of multiple organisms that work together, termed the coral holobiont (Knowlton and Rohwer, 2003). These organisms include the coral animal, microbes, Fungi, endolithic algae, and zooxanthellae (Rohwer et al., 2002, Wegley et al., 2004). Microbes associated with corals are diverse, numerous and provide many functions (Kushmaro et al., 1996; Frias-Lopez et al., 2002). Microbes form species-specific associations (Rohwer et al., 2001); however, some taxonomic variation occurs between reefs (Littman et al., 2009).

Functional role of microbes

Metagenomic analysis shows that microbes possess a gene complement that allows them to perform a diverse variety of functions (Wegley et al., 2007). Coral associated microbes have the genes to breakdown complex sugars and proteins, reflecting the types of carbohydrates excreted by the coral animal. Nitrogen fixation, ammonia assimilation, and nitrate/nitrite ammonification are functions that the coral associated microbes can conduct and these would enhance nitrogen recycling with in the holobiont and potentially supplement supplies of nitrogen to the zooxanthellae. Coral associated microbes possessed multiple pathways involved in sulfur cycling. Microbes associated with Dimethylsulfoniopropionate (DMSP) breakdown are also common within the coral holobiont (Raina et al., 2009). Since sulfur is an essential element in the biosynthesis of amino acids, the microbial community maybe playing a pivotal role in the coral growth. Other mutualistic benefits provided by the microbes include, the release of secondary metabolites, such as antibiotics (Castillo et al., 2001).

Microbial role in coral stress

Changes in microbial complement associated with changes in environmental conditions may exacerbate coral stress. Corals exposed to four stressors, including increased organic carbon, inorganic nutrients, temperature, and reduced pH, showed a variation in their associated microbial assemblage. Genes including those associated with virulence, stress response, sulfur and nitrogen metabolism, motility, and chemotaxis increased within the microbial community of stressed corals. The microbial taxonomic component associated with the stressed coral was dominated by species often associated with disease, including many *Bacteriodetes* and *Fusobacteria* (Vega Thurber et al., 2009).

Microbial role in altering environmental conditions

Apart from symbiotic microbes, corals are influenced by the microbes present in their surroundings, such as those in the water column or in the substratum. Microbiolization of the water column was a feature of coral reefs influenced by high levels of human activity (Dinsdale et al., 2008). On a coral reef with little to no fishing or human habitation microbial numbers were low and their gene complement matched that of a balanced autotrophic/heterotrophic community (Dinsdale et al., 2008). On reefs with higher levels of fishing and human population, microbes were highly abundant and dominated by heterotrophic microbes, many of which were similar to known pathogens. The increase in pathogenic-like microbes was correlated with an increase of unhealthy corals (Dinsdale et al., 2008, Sandin et al., 2008).

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MID HOLOCENE

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Definition

The Mid Holocene refers to a period of time between c. 7–5 ka cal BP during which large-scale ice sheet melt ceased. In regions far from former ice sheets, it was the first time in the present interglacial that relative sea level (RSL) reached or passed present levels. The end of ice sheet melt caused a change from rapidly rising RSL during the early Holocene (c. 10–7 ka cal BP) to relatively stable RSL between the mid Holocene and present.

Introduction

The tropical reef environments of the Indo-Pacific and Atlantic have developed in different ways during the Holocene. This is due to the different broad-scale relative sea level (RSL) histories experienced by these two regions through time, particularly during and since the mid Holocene. It is important to understand how global sea level has fluctuated during this period in order to understand how these differences have come about.

The early Holocene period was characterized by a warming climate, which resulted in the complete melt of the Laurentide and Fennoscandinavian ice sheets, and a reduction in the size of the Greenland and Antarctic ice sheets. This large-scale ice sheet melt caused global sea level to rise quickly in far-field, low-latitude locations, which are distant from these ice sheets and are not affected by glacio-isostatic rebound. The rates of RSL rise in some far-field locations exceeded 8 mm/yr during the early Holocene (Sloss et al., 2007). By the mid Holocene, the majority of this melt had ceased; all North American and European ice sheets had disappeared, Antarctica was relatively stable, and the Greenland ice sheet had retreated inside its present margin.

Relative sea level in near and intermediate field locations record the effects of glacio-isostasy (see Chapter entries "*Glacio-Hydro Isostasy*" and "*Postglacial Transgression*"). However, these effects can extend to considerable distances, penetrating well into the tropical waters of the equatorial low latitudes. This is especially so for sites in the Atlantic Ocean which lie within the zone of influence of the former Laurentide Ice Sheet. It is therefore important not to assume that all tropical locations with fringing and barrier reefs lie in far-field locations and are unaffected by glacio-isostasy; tropical reefs in the Caribbean, for example, are not in the far-field zone, whereas the Indo-Pacific region is a genuinely far-field location.

Equatorial ocean siphoning and continental levering

Results of a study combining glacio-isostatic modeling and RSL observations show that the Caribbean is located sufficiently close to the former Laurentide ice sheet to be on its lithospheric forebulge (Milne et al., 2005). The Laurentide ice sheet depressed the crust over North America and this caused displacement of the lithosphere away from the center of load. This caused a rim of crustal uplift outside of the depressed zone. When the ice sheet melted, the lithosphere migrated back to the former center of load and caused the forebulge to collapse. During the early Holocene, the effects of this process were masked by rapidly rising sea level caused by ice sheet melt, but since the mid Holocene this process can be seen in RSL records from both the forebulge region itself, and further away in the far-field.

In tectonically stable locations in the Caribbean, RSL has risen throughout the mid-late Holocene, despite the end of global ice melt c. 7–5 ka cal BP, because of direct crustal subsidence caused by forebulge collapse. In contrast, in the Indo-Pacific region RSL has fallen by a small amount (c. 1–2 m) in the late Holocene, as water has moved from the far-field regions back into space created by crustal subsidence in the forebulge region. This process is known as equatorial ocean siphoning (Mitrovica and Peltier, 1991).

A second process that may be as important as equatorial ocean siphoning in explaining late Holocene RSL fall in the Indo-Pacific region is continental levering. As the underwater shelves around continents were progressively flooded under rising sea level during the early Holocene, they subsided under the increased weight of water on them. Water from the center of large ocean basins (e.g. Indian and Pacific Oceans) flooded into the space created by these subsiding shelves, causing RSL to fall in the center of these ocean basins. Model results suggest that RSL fall in these locations comprises c. 60% due to forebulge collapse and 40% due to offshore subsidence around continental margins (Mitrovica and Milne, 2002).

Effects on reef development

Reef development differences between the Caribbean (forebulge zone) and the Indo-Pacific (far-field), and within the Indo-Pacific region itself (central ocean vs. continental margin sites), have been affected by the two processes described above. In the early Holocene, fast rising sea level in both regions provided accommodation space for reef growth, but after the mid Holocene (c. 7–5 ka cal BP) their broad histories diverge (see Chapter entries *"Holocene Reefs : Thickness and Characteristics"*, *"Sea Level Changes and Effects on Reef Growth"*, *"Reef Classification, Response to Sea Level Rise,"* and *"Reef structure"*).

Caribbean model

Fast rising RSL in the early Holocene allowed high reef accretion rates, particularly in the Caribbean, where the average reef growth rate was c. 6 m/kyr (Dullo, 2005). Caribbean reef-building coral consists primarily of *Acropora cervicornis* (which grows in 5–15 m water depth) and *Acropora palmata* (which grows in <5 m water depth). Therefore, most Caribbean reef growth occurred after RSL rose to within 15 m of present (c. 9 ka cal BP) (Toscano and Macintyre, 2003). The exact timing of reef initiation depends on the depth of the antecedent surface, and can vary by c. 5 ka in locations with different reef-base elevations (Hopley et al., 2007). Caribbean reef-building corals were able to keep pace with RSL rise during the early Holocene (keep-up mode: Neumann and Macintyre, 1985), but as RSL slowed in the mid Holocene, back reef zones developed dominated by unconsolidated sand and rubble, representing a late succession stage of Caribbean reef development (Steneck et al., 1998; Gischler and Hudson, 2004). As RSL continued to rise at a slower rate in the late Holocene, *Acropora palmata* accretion continued to keep pace and slowly developed into framework-coral-covered reef flats.

Indo-Pacific model

In the Indo-Pacific, RSL rose more rapidly in the early Holocene than in the Caribbean, although initial inundation of the −15 m contour occurred at about the same time (c. 9 ka cal BP: Pirazzoli, 1991). Unlike in the Caribbean, reef-building coral (*Acroporids* and *Poritids*) was unable to keep pace with RSL rise, entering instead a 'catch-up' mode where reef accretion lagged RSL rise (McLean and Woodroffe, 1994). As RSL rose to present in the mid Holocene, coral growth caught up with RSL, robust head corals with a dense framework were lain down, and an algal crust developed. The exact timing of reef attaining sea level is dictated by the depth of the antecedent surface and the amount of 'catch-up' it had to undergo, although this age range is much less than in the Caribbean because of the abrupt nature of RSL stabilization in the mid Holocene.

Under stable RSL from the mid Holocene onwards, tectonically stable locations saw lateral reef development as accommodation space for vertical reef growth disappeared. In many oceanic locations, this produced large reef flats and detrital carbonate platforms (Hopley, 1985). As RSL began to fall in the center of the Indo-Pacific ocean basins in the mid-late Holocene, these platforms became emerged at low tide causing any coral living on them to die. There are many examples of coral microatolls from mid to late Holocene time stranded above their growth position on exposed reef flats in the Indo-Pacific region (e.g. Cocos Keeling Islands: Woodroffe, 2005).

These two idealized models of reef development under RSL rise assume no factors other than eustatic sea level affect reef growth. There are, however, some locations in the Indo-Pacific (e.g. Tahiti) where RSL has continued to rise through the Holocene and reef development has followed more closely the Caribbean than Indo-Pacific model. This is due to a variety of factors including volcanic and tectonic subsidence, which have caused continual, gradual submergence of Tahiti as it migrates away from a volcanic hotspot (see Chapter entry *"Volcanic loading and Isostasy"*). Similarly, in the Caribbean there are emerged mid Holocene corals on the island of Barbados, which are evidence of plate tectonic movement in this seismically active zone (Schellmann and Radtke, 2004).

While sea level was an important influence on the growth of coral reefs worldwide during the mid Holocene, other elements of the coral growth environment may also have been different to today's. The period is often referred to as the Holocene Climatic Optimum and in the tropics much of the climatic data comes from the corals themselves (see Chapter entry *"Palaeoclimate from corals"*).

For many areas such as the Great Barrier Reef (GBR), a warmer climate of about 1.3°C, less variable wet seasons, fewer droughts, floods, and weaker ENSO events produced higher growth rates of individual corals (Gagan et al., 1998) and of coral reefs (see Hopley et al, 2007, ch. 11) within the period 8–7 ka which saw the most rapid reef growth on the GBR. Similar warmer, wetter conditions (from stronger monsoons) have been recorded elsewhere in the tropics in the mid Holocene (e.g. Gagan et al., 2000).

Case study: the Great Barrier Reef

The GBR provides an example of how different types of reef morphology are dependent on different RSL conditions. The GBR shelf is wide (c. 230 km at its widest point) and has undergone differential movement through the Holocene. The offshore part of the shelf has subsided over time compared to the inner shelf due to hydro-isostatic loading, resulting in continuous RSL rise at the outer edge and a mid-late Holocene RSL fall on the inner part of the shelf (Nakada and Lambeck, 1989; Woodroffe, 2009). The reefs at the outer edge of the shelf are primarily made up of framework coral, most often found in keep-up situations, like those of the Caribbean. Inner shelf reefs, on the other hand, are described as 'detrital piles with coral caps' (Hopley et al., 2007, p. 390), with unconsolidated sediment increasing significantly across the shelf. Inner shelf reefs have also undergone emergence and erosion through the mid-late Holocene under slowly falling RSL.

Another factor affecting reef growth and morphology was the "mid *Holocene High Energy Window*" (see entry).

On the GBR, this existed between about 8 and 5.5 ka when outer reefs lagged behind those of the inner shelf (including fringing reefs) and did not protect the inner shelf reefs. Much of the carbonate productivity went into building coral shingle ridges on the shores of adjacent high islands. Subsequently, there has been a decline in both the rate of reef growth (including fringing reef progradation) and shingle ridge accumulation (Smithers et al., 2006).

Summary/conclusions

Broadly speaking, reef accretion in both the Indo-Pacific and Caribbean regions is dominated by ice-sheet-melt-driven sea-level changes through the Holocene. Differences in reef morphology between the two regions, including the amount of framework coral and the extent of reef flats, reflect relatively small-scale variations in regional RSL, which occurred since the mid Holocene. These differences are due to long-lived global-scale isostatic processes which cause sea-floor subsidence (RSL rise) in some regions and RSL fall in others since the mid Holocene.

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Cross-references

Glacio-Hydro Isostasy
Holocene High Energy Window
Holocene Reefs: Thickness and Characteristics
Paleoclimate from Corals
Postglacial Trangression
Reef Classification, Response to Sea Level Rise
Reef Structure
Sea Level Change and Its Effect on Reef Growth
Volcanic Loading and Isostasy

MIDWAY ATOLL (HAWAIIAN ARCHIPELAGO)

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Introduction

Midway Atoll is a subtropical reef near the northwestern end of the Hawaiian Archipelago at 28° 12′ N and 177° 22′ W, approximately 2,000 km from Honolulu and 259 km east of the International Date Line. Midway is an unincorporated U.S. territory and the only island in the archipelago not a part of the State of Hawai‘i. It is second only to neighboring Kure Atoll, 60 km to the northeast, as the Pacific's most northerly atoll. Midway is roughly 9 km in diameter; 40 km^2 in total area; contains two main islands, Sand (1,200 ha) and Eastern (135 ha);

Midway Atoll (Hawaiian Archipelago), Figure 1 Satellite view of Midway Atoll, showing Eastern and Sand Islands (southeast and south), the dredged channel through the perimeter reef (south), and the lagoon and pinnacle reefs (center). Source: Courtesy of Quickbird satellite imagery, 2007.

and one smaller islet, Spit Island (2 ha), (Figure 1). The atoll includes a large, shallow, triangular perimeter reef that encircles a mostly shallow lagoon (6,000 ha) with a maximum depth of 20 m. The perimeter has emergent reef along its northern sector. A similar emergent reef is also found along the northern rim of Kure Atoll suggesting a common origin.

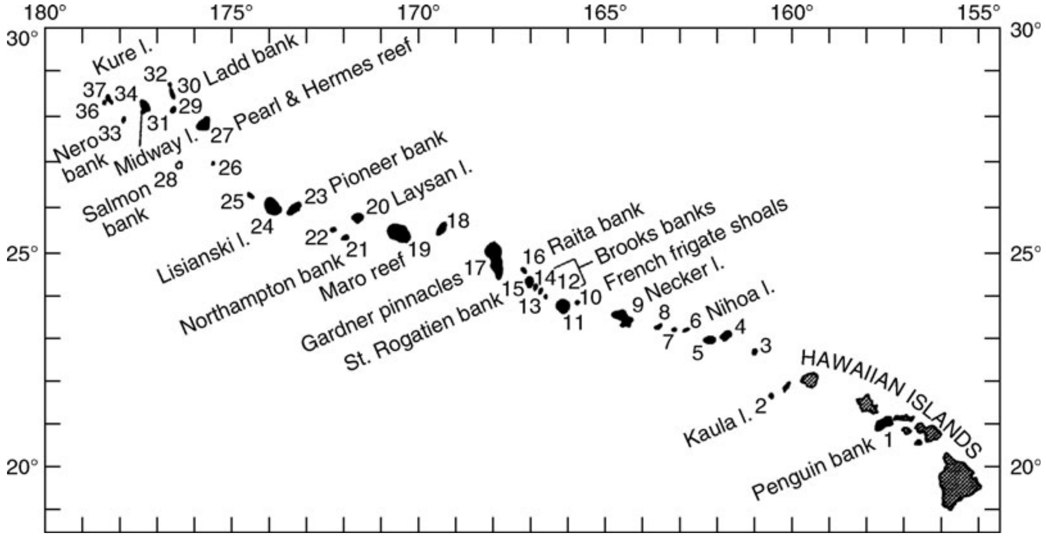
Geology

Midway was formed approximately 28 million years ago over the same volcanic hotspot that is now forming Hawai‘i Island, the largest and south-easternmost island in the chain, 2,500 km southeast of Midway. Midway and Kure Atolls are at the northwest end of the Hawaiian Islands, and are among the six atolls, one low reef island, three high volcanic islands, and 30 submerged banks comprising the Northwestern Hawaiian Islands (Figure 2). Further to the northwest of Kure and Midway, the chain continues as a series of older drowned atolls and islands, called the Emperor Seamounts that extends to the Bering and Kamchatka Trenches off northern Siberia.

In 1965, the U.S. Geological Survey took vertical core samples at Midway and hit the solid basaltic rock formed by ancient volcanic eruptions at 55 m beneath Sand Island and 378 m beneath the reef at the northern edge of the lagoon (Figure 3). Core analyses of foraminifera and limestone revealed a very complex evolution of reef and sediment deposits dating back to the Miocene that formed in shallow waters and providing evidence that the coral reefs have maintained upward growth as the atoll’s volcanic base subsided. At least two Pleistocene unconformities were noted in upper layers, providing evidence of multiple episodes of sea level rise and fall. The thickness of the atoll’s Holocene reef is approximately 160 m, and sediments in the lagoon are 384 m thick consisting of post Miocene deposits. Analysis of fossil corals in the core reveals that previous climatic conditions at Midway were more favorable for growth and abundance of corals. As with contemporary reefs at Midway, coralline algae were also dominant calcifying organisms.

Human history

The first recorded landing at Midway Atoll was made in 1859 by Captain N.C. Brooks aboard the ship *Gambia*. In 1867, the Secretary of the Navy sent Captain Reynolds to take possession of the atoll for the United States. Efforts in 1871 to establish a settlement and open a channel through the perimeter reef failed, and for the next 30 years visits to the atoll were limited to shipwrecked survivors and bird hunters. Midway’s role as an important communication link was established in 1903 when the Commercial Pacific Cable Company chose Sand Island for one of



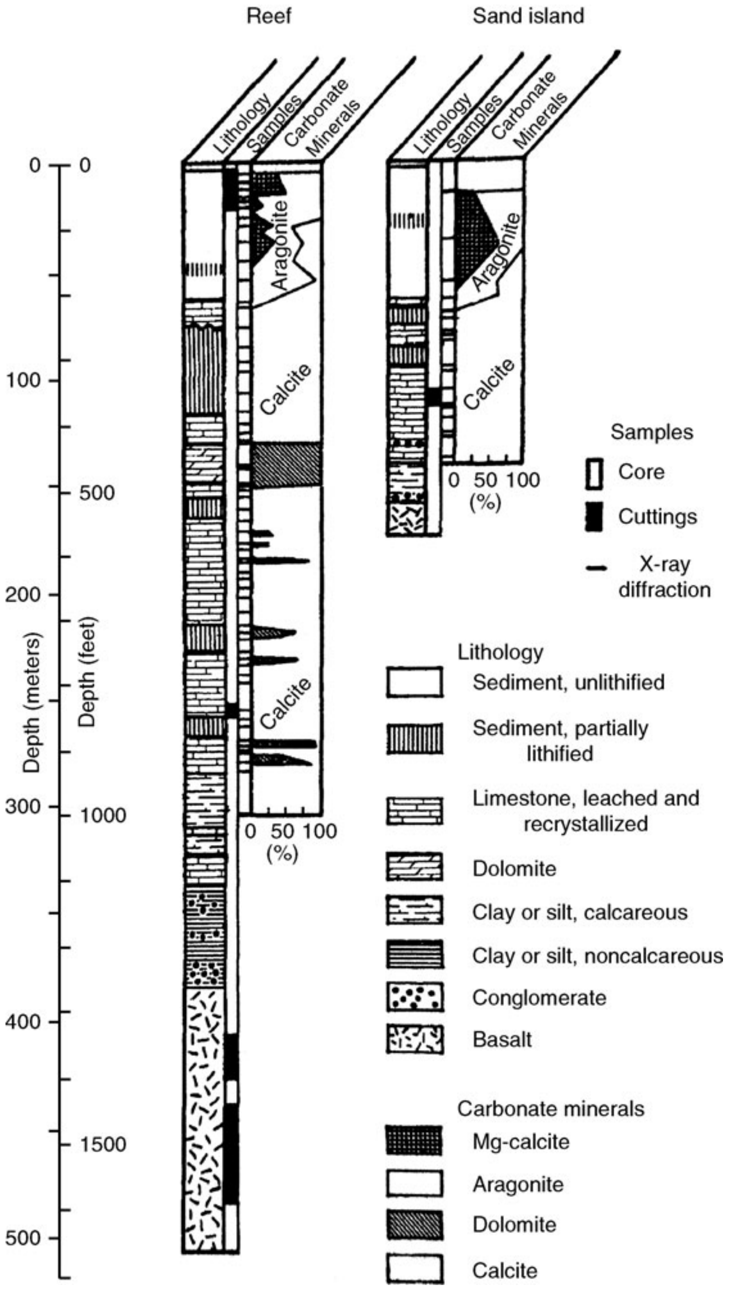
Midway Atoll (Hawaiian Archipelago), Figure 2 Map of the Hawaiian Islands archipelago with Midway near the northwest end and including all of the 37 submerged banks which are numbered. Source: Grigg and Epp (1989).

its relay stations. Cable Company employees reported foreigners landing at Midway, and especially disturbing were Japanese feather hunters who since the 1880s had decimated nesting seabird colonies. In January 1903, President Theodore Roosevelt placed the Midway Islands under the jurisdiction and control of the Navy Department to stop the "wanton destruction of birds that breed on Midway" and to establish a coaling station for Navy warships. In 1935, Pan American World Airways established a seaplane base in the harbor, including the clearing of some coral heads from the lagoon, and constructed a small luxury hotel on Sand Island. Midway became a regular refueling stop on a trans-Pacific route that also included Honolulu, Wake Island, Guam, and Manila. The short-lived era of the "flying clipper" seaplanes ended with the onset of World War II, and in early 1941, a U.S. Naval Air Station was commissioned on Midway. In the summer of 1941, 1,500 workers and a dozen dredges began excavation of the deep ship channel through the southern perimeter reef. "The big lagoon impounded incalculable tons of water coming in over the reefs, and poured it all out through the new channel in a current that often reached six miles per hour", Woodbury (1946) reported. The dredging lowered lagoon water levels and exposed some of the perimeter back reefs. Likely changes in lagoon circulation included suspension of fine colloidal sediments accumulating on the lagoon floor caused by changes in deep water circulation patterns attributed to the new channel. On December 7, 1941, Japanese war planes bombed both Midway and Pearl Harbor.

Midway is well known for its role in the Battle of Midway. On June 3, 1942, a Japanese occupation fleet was spotted by a Midway patrol plane, and early on June 4, Japanese carriers launched three waves of planes to destroy the air base at Midway and clear the way for occupation. Airplanes on both sides of the battle were lost, and extensive physical damage and casualties occurred on Sand and Eastern islands. From June 4–6, most of the battle was fought in open seas northwest of Midway. The Japanese Navy never fully recovered from the loss of all four of its carriers, 256 aircraft, and more than 400 of its best aircrew, and the battle terminated Japanese eastward expansion in the Pacific. The WWII facilities at Sand and Eastern Islands were listed on the National Register of Historic Places on May 28, 1987.

Midway continued to serve as a strategic location for the military after the war. During the Korean conflict, Midway served as a refueling station, and in the late 1950s "Cold War", Midway was substantially upgraded and became a central location for the Distant Early Warning Line's Pacific Barrier, extending from Midway to Adak, Alaska. During the Vietnam War, Midway was a main aircraft and ship refueling station and served as a listening post for foreign submarine activity. Midway was the site of the June 1969 meeting of President Thieu of the Republic of Vietnam and President Richard Nixon. In the waning years of the Cold War, Midway's strategic importance as a military base diminished, but its unique historic associations and superb wildlife habitat quickly gained recognition.

An overlay refuge at Midway Atoll was established in 1988 when the U.S. Navy invited the U.S. Fish and Wildlife Service (FWS) to manage the atoll's extensive wildlife resources. In 1992, the Department of Defense announced plans to close the Midway Naval Air Facility, and in 1996, the FWS assumed expanded jurisdiction over Midway after President Bill Clinton signed an Executive Order that transferred the atoll to the Service. Despite the efforts of Navy to clean up the atoll before transfer to the FWS, there are residual contaminated areas on the main islands where



Midway Atoll (Hawaiian Archipelago), Figure 3 Preliminary logs of two 1965 Midway Atoll drill holes showing lithography, core recovery, and carbonate mineral composition of the cores. Source: Ladd et al. (1967).

soldiers defended the atoll during WWII, and where up to several thousand dependents, contractors, and soldiers lived and worked for more than half a century. Also, metallic debris remains in near shore waters as well as evidence of seeping contaminants and petroleum residues from the main islands.

The National Wildlife Refuge boundaries encompass “1,472 acres” of emergent land and “580,392 acres” of submerged lands and waters, out to “12 nautical miles” (nmi). On June 15, 2006, President Bush added the Midway NWR in his Proclamation designating the NWHI Marine National Monument (MNM), and in 2007, its name was changed to the Papahānaumokuākea MNM. The Monument is managed by the NOAA, FWS, and the State of Hawai‘i, and it protects all 10 of the NWHI out to a distance of 50 nmi, including 30 submerged reefs inside the MNM boundaries. Midway is presently the only destination in the Monument open to public visitation.

Marine species and habitats

Midway Atoll location in subtropical waters offers unique opportunities to study the effect of colder waters on the growth, development, and ecology of coral reefs. The atoll drops off steeply outside the perimeter reef, making it possible to observe within a relatively small area the different organisms and communities associated with pelagic, reef crest, ocean reef slope, deep reef, and lagoon habitats. The lagoon contains circular patch reefs in the deep central lagoon (Figure 1) and shallow back reefs near the lagoon perimeter. Both impede water circulation and trap sand washed over the reefs. These sediments limit coral development in much of the lagoon, except in the deeper central lagoon where stands of the endemic finger coral (*Porites compressa*) flourish. Corals are more abundant on some leeward ocean facing reefs and shallow back-reefs and lagoon pinnacles, but overall, corals are scarce on reefs exposed to ocean waves. A total of 33 species of stony corals and two non-stony corals (*Palythoa* and *Sinularia*) have been recorded at Midway, based on surveys from 2000–2006 and are dominated by *Pocillopora*, *Porites*, and *Montipora* species. These totals are slightly less than the 34–46 species found at the four nearest NWHI atolls and much less than the 66 species at the furthest atoll, French Frigate Shoals (FFS), 1,300 km to the southeast within the MNM. The close proximity of FFS to Johnston Atoll may facilitate dispersal of coral species between the Hawaiian and Line archipelagos and help explain the much higher species totals at FFS. The dominant blue encrusting coral at Midway is now tentatively identified as *Montipora dilatata,* an endemic species that displays spectacular formations in the lagoon and back reef habitats at Midway and several neighboring atolls, but which is rare in the larger MHI. Approximately 12 of the Midway coral species are endemic (~40%), an above-average level for the NWHI but comparable to the remaining NWHI.

In September 2002, marine biologists were surprised to find extensive bleaching of corals at Midway and two neighboring atolls (Kure and Pearl and Hermes) in these subtropical waters. Less severe bleaching occurred again at the same atolls during the late summer of 2004. Corals at Midway, where the 2002 bleaching was especially severe, must adapt to colder winter water temperatures of 18°C, as well as adapting to summer temperatures, normally 8–10 degrees higher. During the bleaching event of 2002, temperatures reached 29°C, 11° higher than the winter lows, and the corals responded by bleaching. Corals have recovered well during the past several years although there has been a net loss of lobe coral (*Porites*) compared to levels at permanent transects in the lagoon prior to the bleaching events at Midway.

Patches of the seagrass (*Halophila*) are reported in the lagoon, and calcareous green algae, brown turban algae, and crustose coralline algae are common on the outer reef crests. Large numbers of rock boring sea urchins (*Echinometra, Heterocentrotus,* and *Echinostrephus)* predominate, hollowing out the dead skeletal portions of live lobe corals (*Porites*) and riddling the coralline algal covered reef crest with numerous holes and burrows. Scientists of the University of California at Santa Cruz are now determining whether reef erosion primarily from the boring urchins is outstripping reef growth, and whether selective removal of urchins would prevent serious erosion of the perimeter reef crests, the main natural barrier protecting the lagoon and islands. Beyond the reef massive spurs and grooves high in coralline algal cover face the open ocean along the northwest to southwest perimeter reefs, providing clear evidence of the importance of coralline algae as a major reef builder and bulwark in the far end of the NWHI. More than 100 species of algae are now known from Midway, including 35 new records for Midway and one species new to science, *Dudresnaya babbittiana*. A thorough 1997 survey reported no alien algal species at Midway. Quantitative surveys in 2006 revealed that *Lobophora, Laurencia, Microdictyon, Padina,* crustose coralline algae, and *Halimeda* in descending order were the most abundant algae at Midway.

The first systematic marine invertebrate survey was done at Midway in 1997. It documented 316 invertebrate species, 250 of which had not been previously recorded at Midway. Crustaceans dominated the larger invertebrate species, composing 46% of the total species. Other conspicuous marine invertebrates included sea urchins, with the burrowing sea urchin *Echinostrephus* responsible for the highest densities in the NWHI reported at Midway and Kure (>12 individuals/m^2). The most common sea cucumber was *Actinopyga* and the most common sea star was *Linckia multifora.* The crown-of-thorns sea star, *Acanthaster plancii,* has been reported at Midway at low levels. The black-lipped pearl oyster, *Pinctada margaritifera,* has also been recently reported at Midway.

A total of 258 species of fish, including 7 pelagic species, have been recorded on Midway reefs by 1993. Despite its low species diversity, Midway's reef fish biomass is higher than in the MHI, largely due to reduced fishing pressures attributed to the protective mandate of the NWR. Midway ranked fifth in terms of species richness, but ranked first in numerical density (2.7 individuals/m^2, and ranked second in fish biomass, (2.5 t/ha) among all locations in the NWHI. Many Midway species grow to larger than average size, and all trophic levels are well represented, including jacks and four species of sharks. Some of these species are either not found on shallow reef habitats in the MHI or are very rare there. Several of these are limited to deep waters in the MHI, but are found at shallow diving depths (15–50 m) at Midway, including the only endemic Hawaiian grouper, the hapu'upu'u, (*Epinephelus quernus*) a species commercially harvested at greater depths (150–200 m) in the MHI, but fully protected within Midway NWR. This disparity in depth distribution is explained by the fish staying in the same isotherms extending upward to shallower depths at Midway compared to their greater depth regimes in the MHI.

Threatened green sea turtles are frequently seen inside the lagoon and basking on beaches, and 2007–2008 marked the first turtle nesting in many years. Endangered hawksbill sea turtles (*Eretmochelys imbricata*) are infrequently seen in the lagoon. About 65 endangered Hawaiian monk seals (*Monachus shauinlandsi*) are usually present at Midway at any time, and pup levels have increased significantly since the establishment of the NWR in 1996. Approximately 150–200 Hawaiian spinner dolphins use Midway's lagoon; bottlenose dolphins are commonly seen outside the reef; and striped dolphins, spotted dolphins, and rough-toothed dolphins have also been reported. Endangered humpback whales and other whales are also occasionally seen off Midway.

Terrestrial wildlife and habitats

Humans have greatly changed Midway Atoll from its original form. The combined effects of dredging and filling, seawall construction, and importation of herbs and many plant species has greatly expanded the original acreage and made Midway a different place, but one that is still a wildlife habitat of worldwide importance. The earliest botanical descriptions of Midway were made in 1902, and since then more than 265 different terrestrial taxa have been identified. Nine of these are endemic to the NWHI and another 17 are indigenous to the HI. One endemic plant species, *Cenchrus agriminoides* var. *laysanensis*, is listed as endangered. Ecological restoration efforts are underway to eradicate invasive and noxious weeds, control others, and restore some habitats with native species. Since the first insect (a moth) was described from Midway in 1894, more than 300 species of arthropods and land snails have been found on Midway, mostly introduced aliens.

Almost two million breeding seabirds of 15 species make Midway one of the most important breeding areas of seabird conservation in the Pacific. Midway hosts the world's largest populations of both the Laysan albatross (396,936 nesting pairs) and black-footed albatross (23,963 nesting pairs) in 2009, accounting for 67 and 39% of the world's totals, respectively. One or two endangered short-tailed albatross generally visit Midway each year, but none have nested yet. Midway's breeding populations of white terns, black noddies, and red-tailed tropicbirds constitute the largest colonies in the Hawaiian archipelago. After eradication of rats in the mid-1990s, the Bonin petrel colony at Midway had rebounded to more than 32,000 pairs by 2005.

In 2004, 20 endangered Laysan Ducks, were transported to Midway from their only home at the time, Laysan Island, within the Hawaiian Islands National Wildlife Refuge (now also within the Papahānaumokuākea MNM). Biologists wanted to establish a second "insurance" population of this endemic duck once found throughout the Hawaiian Islands whose distribution had declined during the past two centuries to the single hyper-saline lake at Laysan Island. The ducks have adapted well to Sand Island, surprising biologists by breeding during their first year on Midway, with at least 10 ducklings surviving. An additional 22 ducks were transported to Midway in 2005, most of which were introduced to Eastern Island. Over the last several years there were declines due to disease, but duck populations have now rebounded to their highest levels at Midway. The atoll also serves as an over-wintering area for several arctic migrant shorebirds, including the globally rare Bristle-thighed curlew. Predator-free islands are required for this large but vulnerable shorebird because they become flightless during their winter molt. Many other migratory birds also visit Midway, some regularly and some rarely.

Current investigations

The provisions of the MNM include the total ban of commercial fishing by 2011, control of access and introduction of alien species, and monitoring, safeguarding, and restoring the many endemic, threatened and endangered species that depend upon Midway and the other atolls and reefs within the MNM for their survival. A management plan for the Monument has been coordinated and approved, and a research plan will soon be completed.

Some research will be devoted to tracking and promoting recovery of depleted, endangered or threatened species as well as fish targeted by commercial fishers that will become fully protected in 2011. Because general visitation will be allowed only at Midway within the Monument, there will be considerable monitoring and controlling of visitors to prevent harm to fish and wildlife, collecting of fish and wildlife, preventing the introduction of invasive and alien species, and minimizing the effects of trash and pollution. Much of the Monument marine habitats including offshore habitats at Midway still remain relatively unexplored, and so some effort will be devoted to exploration for new species and habitats to determine which need to be afforded special status and additional protection. Research will also be conducted to learn more about how relatively pristine reefs function and what lessons can be learned from comparisons with the status of stressed reefs outside the Monument. In addition, research efforts will continue to determine whether reef growth at Midway is keeping pace with erosion and subsidence, and whether additional measures will help to reduce adverse effects, such as selective removal of the large populations of sea urchins that are now eroding key shallow reefs that serve as natural breakwaters for protecting the entire atoll.

Floating marine debris discarded or lost by distant fishing fleets in East Asia continues to accumulate regularly at Midway. Since 1996 when cleanup efforts were initiated, 42,821 kg has been removed from Midway which ranks fifth in total quantity removed. Evidence of increased accumulation rates on the shores and reefs of the NWHI may be attributed to the southward movement of the Subtropical Convergence Zone in the north central Pacific.

Controversies and gaps in current knowledge

A review of the field methods supporting the Darwin Point hypothesis (Grigg, 1982) revealed it relied primarily on limited sampling of one coral species, with little attention directed at crustose coralline algae that dominate shallow reefs at Kure, Midway, and neighboring islands and atolls. The hypothesis also relied on annual mean seawater temperatures and ignored seasonal fluctuations, especially at Kure, Midway, and Pearl and Hermes Atolls. Cooler winter temperatures are thought to reduce coral growth rates, but the summer temperatures are similar along the entire NWHI and high enough not to reduce coral growth rates. Moreover, the warmest summer temperatures that resulted in the coral bleaching events of 2002 and 2004 at the northernmost atolls may be caused by reduced mixing from weaker winds situated closer to the center of the North Pacific high pressure ridge and by decreased circulation within large shallow lagoons (Brainard et al., 2004). Regardless, the atolls have fully recovered from the earlier bleaching as documented by coral re-growth and re-colonization of earlier bleached habitats.

Siciliano (2005) reexamined the Darwin Point hypothesis and reported that, although coral growth rates generally decline as a function of increasing latitude in the NWHI, as first suggested by Grigg (1982), this decrease is habitat-specific. Coral colonies found in protected habitats throughout the NWHI chain (back reef and lagoon habitats on the atolls; bays sheltered from wave action at the islands lacking lagoons) show comparable growth rates of corals regardless of latitude. This may be explained by the microclimatic conditions experienced by corals growing in the shallower, and often warmer lagoon and back reef habitats, where they are not closely related to offshore SST. Conversely, corals growing in exposed habitats throughout the NWHI (fore reef of atolls and reef islands), experience temperatures more akin to offshore SST conditions, and therefore may be more likely to correlate to regional SST gradients, such as decreasing SST with increasing latitude corresponding to decreasing growth rates.

However, the growth rates measured by Grigg (1982) may also be underestimated at Kure Atoll because of selective sampling. In his assessment of coral growth rate throughout the NWHI, Grigg (1982) sampled *Porites lobata* exclusively at 10 m depths at exposed southwest facing fore reefs. Inspection of *Porites*' growth rates in three habitats at Kure Atoll (Table 1, from Siciliano, 2005) reveals that the fore reef has the lowest growth rate for this genus, among all sites sampled. There is strong evidence of local upwelling off the southwest sides of the islands and atolls of the NWHI resulting in cooler waters. Therefore, exclusive sampling from this area is likely to underestimate average growth rates for the atoll as a whole. Even so, the Siciliano (2005) growth rates of *Porites* from the fore reef habitat (4.5 mm/yr) were still higher than those reported by Grigg for *Porites lobata* (3 mm/yr), even if the data comparisons excluded the faster growing, branching species such as *Porites compressa* which is present but not common on Kure's fore reef. However, additional encrusting and massive growth forms of *P. lobata* and *P. evermanni* were included in the 2005 study because they are important reef builders at Kure. Inspection of Table 4.6 also indicates that, if *Porites* growth rates were adjusted to reflect those of other reef-building corals in the fore reef habitat using Grigg's approach (i.e., by averaging the *Porites* growth rates with those of other reef-building genera), the corals' growth rate would increase to 0.8 mm/yr, rather than decrease as suggested by Grigg (1982) who reported an adjusted growth rate of 0.2 mm/yr for Kure Atoll, the basis for proposing the atoll as the Darwin Point. As a result, the latter data sets do not support the early findings of Grigg (1982).

Midway Atoll (Hawaiian Archipelago), Table 1 Mean linear growth rates (mm/yr) of the five main reef-building coral genera in three habitats at Kure Atoll. Source: (Siciliano, 2005)

Genus	Fore reef	Back reef	Lagoon
Porites	4.5	7.4	10.1
Pocillopora	16.9	17.2	16.9
Montipora	1.0	1.0	1.22
Pavona	16.3	7.6	6.3
Leptastrea	2.0	2.2	2.4

Summary and conclusions

Midway Atoll has experienced numerous changes over the past century but is now fully protected indefinitely. Adequate funding for management and restoration measures will contribute to the resilience and survival of the atoll, its habitats, vegetation, fish, and other wildlife. More importantly, Midway is now open again for public visitation that will serve to educate many people about the beauty and value of the Refuge and in turn, promote support and continued protection by future generations.

Factors not necessarily limited to latitude or mean annual SST may be responsible for determining the ultimate fate of Kure and Midway atolls and their coral reefs over geological time. These include anthropogenic impacts, excessive bio-erosion, bleaching events, size of the reef caps, duration of geological time in shallow water, geological instability leading to slumping and collapse of reefs, storms, ocean acidification, sea level rise, weather anomalies, and more rapid rates of subsidence as the atoll moves further away from the Hawaiian Rise into the deeper sea floor. More likely the Darwin Point, including its location, size, and validity will likely be further examined and perhaps revised. Alternatively, the Darwin Point theory may be better characterized as a dynamic concept or axiom rather than a defined point on earth, such as being at Kure or neighboring Midway. A spatially explicit alternative might be to restate it as a zone or gradient of approximately 2,000 km in length stretching from Kure and Midway atolls toward the southeast through the more than 30 drowning banks in the MNM to the islands of Kaua‘i, O‘ahu and Moloka‘i where there are several neighboring submerged coral reefs and banks not presently keeping pace with sea level.

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Cross-references

Algae, Coralline
Atolls
Banks Island: Frasnian (Late Devonian) Reefs In Northwestern Arctic Canada
Bioerosion
Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity
Corals: Environmental Controls on Growth
Darwin Point
Hawaiian Emperor Volcanic Chain and Coral Reef History
Sea Level Change and Its Effect on Reef Growth

MINING/QUARRYING OF CORAL REEFS

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Definition

The extraction of coral, either in the fossil or living form, for use generally in the construction trade. This is a widespread activity in the Indian Ocean in particular, which results in extensive damage to the three-dimensional structure of the reef and its inhabitants.

Recovery of damaged reefs may be very limited, particularly when surfaces are reduced to mobile rubble which inhibits successful coral colonization and growth.

Background

Coral mining has caused extensive degradation of reefs in a number of countries, which include India, Maldives, Sri Lanka, Tanzania, and the Philippines (Brown, 1997a). The use of coral rock as a construction material in many countries in the central Indian Ocean has had a long history, particularly in the building of mosques, temples, and shrines. Early photographs taken by Agassiz in Malé in the Maldives in 1903 show houses constructed of coconut leaves and available timber, but by the mid-late tewntieth century construction of houses, boundary walls, groynes, and breakwaters with coral blocks was commonplace (Brown, 1997b). At Mafia Island, in Tanzania two forms of coral were extracted in the early to late twentieth century for both local and commercial construction (Dulvy et al., 1995); these were fossilized limestone and living reef coral. In Sri Lanka, corals are primarily used in the construction industry for production of mortar and plaster with subsidiary uses as lime in soil improvement and in the ceramic and cement industry. In India, corals (coral fragments or 'challi' rather than coral 'stones') are also used for the production of lime with lime kilns in the Tuticorin area of southern India, exporting lime all over the country to meet the demands of paper and sugar industries, leather tanning and bleaching, mortar production, and white wash paint. Coral 'stones' extracted from areas such as the Gulf of Mannar, India, are used as building blocks or in road construction and as source material for house decorations. Similarly, in West Sumatra branching and massive corals are extracted to sell as decorative materials for house walls. In the offshore islands, it is estimated that over 10–24 tons of shells and corals are collected from the reefs per year in an activity that involves ten people collecting once or twice a week (Tomascik et al., 1997).

While the construction industry is a major user of corals in the above-mentioned countries, it is clear that there is wide variation in the exploitation of specific coral products by different countries. These differences are reflected in the total harvest of coral products and also in the site and method of exploitation. In the mid-1990s, in Sri Lanka the greatest proportion of coral rock (42%) was derived from fossil reefs inshore, whereas live coral collection represented 12% and coral rubble (collected from the beach and reef flats) 30% of the total harvest. In India, the collection of coral fragments greatly exceeded the collection of coral 'stones' mainly because of its ease of collection and the reduced demand for the latter. Conversely, in the Maldives coral rock was much more important in the construction industry in the mid-1990s (Figure 1) than coral fragments, while in Tanzania both fossilized limestone and live coral were used in building work.

Methods of coral extraction

Generally, all living coral is extracted from shallow waters on leeward reef flats and reef edges and in the Maldives from the coral rims of faroes or ring reefs in depths of approximately 2 m of water. The actual choice of sites is dependent on several factors, which include the prevailing weather conditions dictated by the monsoon in the Indian Ocean and the proximity of the final destination of the coral. Throughout South Asia, the manner of harvesting coral rock is very similar, involving manual collection with iron bars (Figure 2). Favored corals include the massive genera *Porites*, *Platygyra, Goniastrea, Favia*, and

Mining/Quarrying of Coral Reefs, Figure 1 Example of the use of coral rock in construction in the Maldives.

Mining/Quarrying of Coral Reefs, Figure 2 Mining coral from shallow reef flats in the Maldives.

Favites as well as the branching genera *Acropora* and *Pocillopora* (Brown and Dunne, 1988). In the Maldives, the mining of coral rock is carried out by a specific group of islanders from Maamigili in Alifu Atoll working from local fishing craft or dhonis. Corals are broken up and transported to the destination and left for a period in the open for the action of sun and rain to clean the rock of its living inhabitants and leach out the salts (Figure 3). The coral is then broken up into irregularly shaped coral nodules which are the directly incorporated into the building trade. It is estimated that in the Maldives, up until 1988, at least 200 m^3 of coral rock had been removed from reefs in North Male Atoll for use in the construction industry (Brown and Dunne, 1988).

Biological effects of coral mining

Very similar biological effects of mining were found in two studies, one in the Maldives (Brown and Dunne, 1988; Dawson-Shepherd et al., 1992) and another in Tanzania (Dulvy et al., 1995). The effects included a marked decrease in coral cover and a lack of coral recovery on mined areas several years after coral extraction had ceased and also a reduction in overall abundance and diversity of fish communities across planktivorous, benthic herbivorous, and omnivorous trophic groupings (Brown and Dunne, 1988; Dawson-Shepherd et al., 1992; Dulvy et al., 1995). A loss of rugosity was also noted on mined reefs in the Maldives (Dawson-Shepherd et al., 1992). Butterfly fish or Chaetodontidae, which rely on corals as a source of food, showed marked reductions on mined sites in Tanzania, while in the Maldives, species such as the damselfish *Chromis* spp. were conspicuously absent from mined areas, probably because they depend on the three-dimensional structure of the reef for shelter and also on a pelagic supply of food. One reason for the poor recovery of these mined reefs lies in the unstable nature of the resulting substrate, which by its mobile nature prevents successful colonization and growth of juvenile corals (Brown and Dunne, 1988; Clark and Edwards, 1994).

Alternative management options and restoration of mined reefs

A number of alternative management options have been put forward to reduce demand for coral rock in the Maldives, which range from the use of concrete blocks (Figure 4) instead of coral rock to the commercial mining of a single faro reef (Brown and Dunne, 1988, 1995). In Mafia Island, Tanzania, the use of sun-dried mud blocks has been suggested as a replacement for coral products (Dulvy et al., 1995; McClanahan et al., 2000). Stricter legislation has also restricted the amount of coral mined in countries such as the Maldives (Brown, 1977b; Sluka and Miller, 1998), while participatory, collaborative management processes have had some success in Sri Lanka (Brown, 1997b) and Tanzania (McClanahan et al., 2000).

The use of artificial reef structures (concrete blocks and mats or chain link fencing and paving slabs) to promote reef growth on mined reefs is extremely costly but effective (Clark and Edwards, 1994) and while transplantation of corals from elsewhere to such structures has had some success, it is suggested that transplantation should only be undertaken if natural recruitment does not occur (Clark and Edwards, 1995; Edwards and Clark, 1998). The latter authors conclude that where suitable surfaces for settlement are available and water quality is conducive to coral growth, natural recruitment can provide significant restoration within 3–4 years. In the Maldives, stabilizing the substrate with concrete mats has encouraged successful coral recruitment on mined substrates.

Mining/Quarrying of Coral Reefs, Figure 3 Weathering of coral rock prior to its use in construction in the Maldives.

Mining/Quarrying of Coral Reefs, Figure 4 The use of concrete blocks in construction in the Maldives.

Summary

There is no doubt that coral mining is still carried out within the Indian Ocean but because of legislation and the adoption of more sustainable alternatives, the quantities of corals mined today are much more limited than they were 20 years ago.

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Cross-references

Coral Reefs of India
Maldives
Reef Restoration

MOATING

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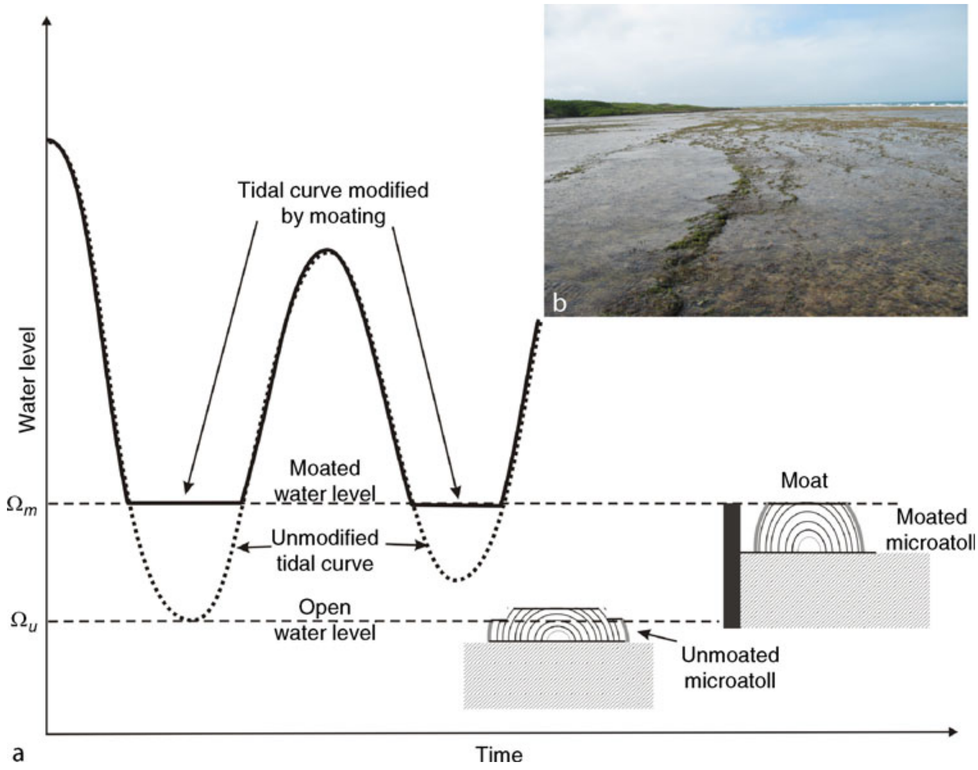
Definition

Moating is the process of constraining the ebbing tide over the reef to produce moats in which low tide water levels remain perched above open water levels (see *Moats*).

Moating truncates the lower part of each tidal cycle at an elevation determined by the height (in the tidal frame) and permeability of the moating structure (Figure 1a). Moating can occur at any intertidal elevation and may only be active during the lowest spring tides.

Where moating occurs behind stable and impervious features, like algal rims (see *Algal rims*) the water level is consistent on every (lower) low tide. In contrast, at mesotidal locations like the central Great Barrier Reef (GBR) open water spring and neap low tides can differ by > 2 m.

Moating allows some reef biota to survive above their open water limits, and must be considered when



Moating, Figure 1 (**a**) shows how moating above the low tide level, modifies the tidal curve and allows intertidal biota to survive above their open water limits. Moating occurs behind structures like these algal terracettes on the reef flat at Bewick Island, northern GBR (**b**).

interpreting intertidal sea-level indicators, especially coral microatolls (see *Microatoll*) (Figure 1a). Moating also has important implications for sedimentation on reefs. It controls the tidal windows when tidal currents are active, and modifies reef flat depths and thus where reef top waves may entrain and transport sediments.

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Cross-references

Algal Rims
Great Barrier Reef Committee
Microatoll
Moats
Reef Flats

MOATS

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Synonyms

Ponds; Reef top pools

Definition

Moats are areas of water held over intertidal reef surfaces above the open ocean level during lower tides. Moats form when ebb-tide drainage is impeded behind biologically constructed or sedimentary structures. The former includes reef crest algal rims and algal terracettes. Sedimentary structures include storm ridges or ramparts (commonly of coral shingle) and minor ridges of sand and gravel. Shallow moats may also pool in subtle reef flat depressions.

Moats behind algal rims can be impressive, impounding water well above the ocean tide, especially in areas of high tidal range. For example, a high algal rim extending > 2 m above the MLWS tide level encircles Redbill Reef on the central Great Barrier Reef, and holds water just 8 cm below MSL during low tides (Hopley, 1982). Moats of this type may cover several km^2. Smaller algal terracettes are common on the seaward slopes of algal rims and form shallower (< 20 cm) moated ponds typically 1–100 m^2 in size.

Moats confined by sedimentary structures may be less permanent in their construction and effect. For example, unconsolidated rubble and shingle ramparts tend to leak initially and are vulnerable to reworking. Although water remains moated above open water, small breaches can episodically lower water levels. Over time compaction, infill of voids with finer sediments, and basal cementation may improve the damming efficiency of these structures, but usually at a lower height than immediately post-emplacement.

Moats occur on most reef flats but are best developed where the tidal range is large, algal rims thrive, and coral growth and storm frequency provide enough rubble and depositional events. Emergent back reef, as produced by late Holocene relative sea level fall, is also excellent substrate for moat development.

Moats are important habitats that may support a diverse reef flora and fauna above the ocean low tide level. Moderately sized and cemented/encrusted moats are more physically stable and typically harbour the most diverse communities, especially where moat water is well flushed daily. Small shallow moats tend to be less permanent, and are vulnerable to biologically limiting thermal and salinity extremes.

Several other features are referred to as moats with varying degrees of correctness. Moated boat channels – containing water of navigable depth – occur on some reef flats, either immediately behind algal rims where surging waves and sediment flux limit reef growth or, on fringing reefs, nearer to the shore where terrestrial runoff achieves the same effect. Although in each case water may moat behind the algal rim, the deeper water is chiefly a function of locally restricted vertical accretion rather than ponding over the reef flat. Maldivian cay shorelines oscillate with monsoonal reversals and similarly constrain upward reef growth near the cay below that of the reef edge. The deeper zone separating the reef rim and cay formed by this process has also been called a moat.

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Algal Rims
Boat Channel
Fringing Reefs
Maldives
Moating
Reef Flats
Shingle Ridges

MOLLUSCS

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The Bailey-Matthews Shell Museum, Sanibel, FL, USA

Definition

The Mollusca are soft-bodied animals that usually have a hard, protective shell. They constitute the most diverse marine phylum and the most diverse group of coral-reef organisms (Paulay, 1997). Coral reefs provide substrata, protection, and food for molluscs (Caterall, 1998; Morton, 1983). In turn, molluscs influence reef growth and internal biological processes. Some gastropods prey directly on live coral tissue, causing, in some cases, a significant impact in structuring of reef communities. Bioerosion of live coral skeletons and coral rock alters and destroys, ultimately reducing them to fine, unconsolidated sediments. Bioeroders may be divided into the epilithic and the endolithic (Glynn, 1997). Using their reinforced radular teeth, epilithic bioeroders abrade limestone in the process of grazing on algae or other organisms. These include chitons, patellids, trochids, littorinids, and neritids (Glynn, 1997). Endolithic bioeroders bore into coral skeletons using chemical and/or mechanical processes. Bivalves in the genera *Lithophaga*, *Gastrochaena*, *Fungiacava,* and *Choristodon* are active borers, whereas *Tridacna* and *Hippopus* show a limited degree of downward penetration (Glynn, 1997; Morton, 1983). Reef-building vermetid gastropods in the genera *Vermetus* and *Dendropoma* can be important contributors to the structure of coral reefs.

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Cross-references

Bioerosion
Sediment Dynamics
Sediments, Properties

MURUROA ATOLL

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Definition

The atoll of Mururoa, also known as Moruroa or Aopuni, lies in the south-eastern end of the Tuamotu Island Group (21°50′S, 138°53′W) in the central Pacific. Politically speaking, this island is part of the French Polynesia.

Geological setting

Mururoa is 28 km long and 11 km wide with a reef rim not exceeding 15 km^2 in surface area. It falls into the open-atoll type with a large natural pass (4,500 km wide, 1–9 m deep) on its leeward side. Its volcanic basement has originated from the Pitcairn hotspot at present operating about 70 km to the south-east of Pitcairn Island (Gillot et al., 1992). The cessation of volcanic activity from about 11 to 10.5 million years favored prominent reef building. Subsidence of the volcanic shield at an average rate of 7–8 mm per millennium has been accompanied by deposition of a sedimentary pile varying between 130 and 570 m thickness (Buigues, 1997). From the end of the 1960s, in relation to nuclear testing, intensive biological, geological, and geophysical surveys were carried out on the modern reef and its carbonate foundations.

Modern reef morphology and zonation

The reef zonation, the composition and distribution of major reef-building biological assemblages have been described by Chevalier et al. (1969), Bablet et al. (1995) and Camoin et al. (2001). Up to 50 coral species have been described from the fore-reef to lagoonal areas.

The outer reef rim

The reef rim, 3 m in maximum elevation, consists of successive islets (« motus ») that form a continuous 400-m wide line along the windward side, and a discontinuous line, 1,100 m wide on the leeward side. The rim is made up of coral rubble mixed with skeletal sand, locally resting on the modern reef flat or overlying emergent, firmly cemented coral conglomerates of mid-to late Holocene age. The reef-flat zone is subdivided into three subzones. The outermost subzone is a typical algal ridge, up to 0.50 m high, 20–50 m wide, mostly made up of coralline algal crusts (*Hydrolithon onkodes*, *Chevaliericrusta polynesiae*) associated with encrusting foraminifera (*Homotrema*, *Acervulina*) and scarce robust branching corals (*Acropora humilis, Pocillopora verrucosa*). Behind the algal ridge, there is a coral-dominated subzone inhabited by stunted branching, massive, and encrusting colonies (*A. humilis* group, *Pocillopora brevicornis*, *Favia stelligera*, *Montipora caliculata*, *Porites lichen*). Behind the islets to the lagoon, there is an inner reef-flat subzone mainly covered by loose detritus and a few corals (*Acropora muricata*, *A. corymbosa*, *A. microphthalma, A. tenuis, and Alveopora allingi*).

The fore-reef zone can be delineated into three subzones. The upper subzone (to about 10 m deep) is gently dipping (less than 15°) and dominantly colonized by robust branching and massive corals (*Acropora robusta* group, *A. humilis* group, *P. verrucosa*, *P. eydouxi*, *F. stelligera*, *Platygyra daedalea*). Between the depth of 10 and 40–50 m, the intermediate fore-reef subzone becomes increasingly steeper (30–45°). The coral cover rate decreases; the dominating coral species include *Acropora nasuta*, *Astreopora myriophthalma*, *Leptastrea transversa*, *Echinopora gemmacea*, *Leptoria phrygia*, *Pocillopora elegans*, together with *Montipora* and *Cyphastrea.* The lower fore-reef subzone below 40–50 m forms a sub-vertical drop-off, locally covered by encrusting, tabular, and foliaceous corals (agariciids mainly) associated with coralline algae and encrusting foraminifera (acervulinids). In addition, the fore-reef zone exhibits terraces at 10, 20, 40, 55, and 65 m and cave-like features at 80, 90, 100, and 150 m deep (Buigues, 1997). The terraces were interpreted as former tops of successive reef units deposited during the late Pliocene and the Pleistocene, while the caves may have been the result of dissolution controlled by colder, interstitial reef waters or by meteoric waters during former low sea stands.

Locally, brackish ponds form in shallow reef-rim depressions (Trichet, 1969) and contain cyanobacterial communities. These develop as mats (matolites or « kopara » according to Défarge et al., 1994) in which calcareous microbialites and phosphorites are deposited (see Richert et al., 2006 for review). These processes are thought to be promoted by nutrient-rich, thermally driven convective currents within the carbonate pile (i.e., the endo-upwelling concept of Rougerie and Wauthy, 1993).

The lagoon

It averages 30–40 m depth and contains numerous reef patches. Coral communities on both lagoonal floor and patches consist chiefly of arborescent *A. muricata* group, *A. pulchra*, massive *Porites lobata*, *Leptastrea purpurea*, *Favia speciosa,* and branching *P. verrucosa*.

Lithology and structure of the sedimentary pile

During the building of the volcanic shield, submarine eruptive events close to the sea surface have alternated with episodes of coral settlement, resulting in coral-rich layers embedded into the volcanic rocks. The deepest occurrence of carbonate deposits is about 950 m beneath the modern rim surface. The volcanic rocks are overlain by a sedimentary pile that comprises two distinct series: a basal volcaniclastic series and a carbonate cap. The entire pile display a number of seismic reflectors identified in cores as unconformity surfaces at the top of different diagenetic units (Buigues, 1997).

The volcaniclastic series

It ranges between 100 and 0 m in thickness from the periphery to the center of the atoll. The series is typified by the superimposition of transgressive (retrograding) depositional sequences. At base the sequences are usually composed of volcanic conglomerates. Progressively upwards, the volcaniclastics decrease in grain size and thickness to thin sand beds. Correlatively, coral-derived material increases in volume, locally forming massive buildups trapped into the volcaniclastics. The younger volcanoclastics are found at around 300 m below the modern reef rim.

The carbonate cap

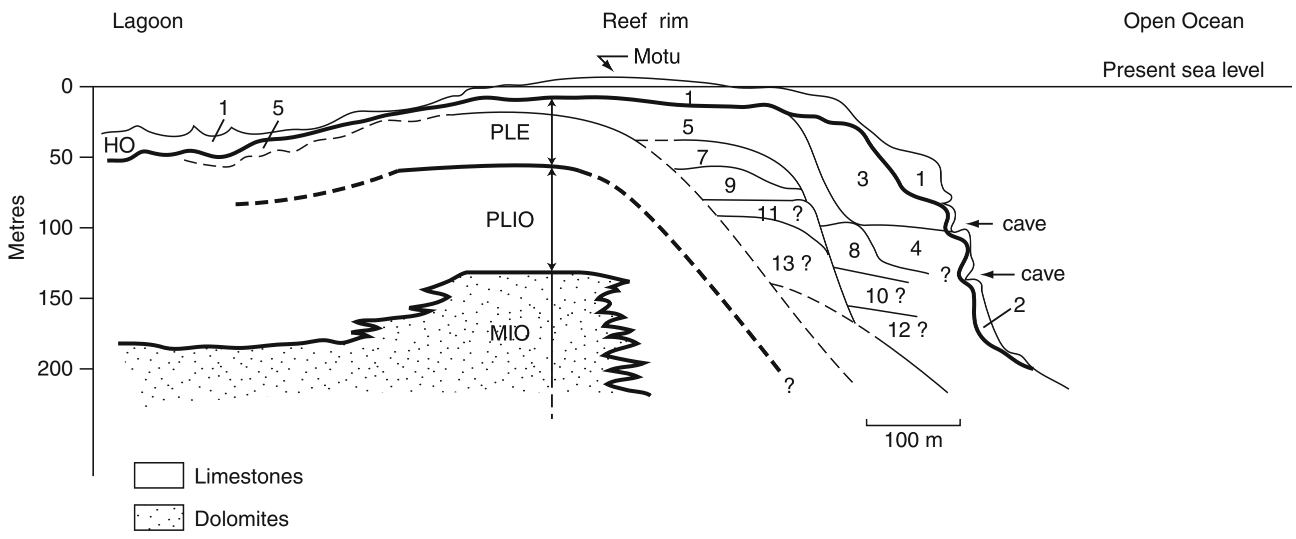
It occurs between 300–500 and 120–220 m beneath the reef rim and the center of the atoll respectively. An array of reef-related facies has been identified and includes coralgal framestones and bindstones, with skeletal rudstones to grainstones typical of high-energy, outer rim environments; coral bafflestones associated with skeletal floatstones to wackestones, characteristic of low-energy environments; coral platestones to sheetstones embedded into wackestones to mudstones, typical of sheltered, lagoon-like environments. The spatial distribution of these facies reveals that the carbonate system has evolved in terms of morphology and architecture over time. The development history of the carbonate cap has been reconstructed on the basis of age determinations, i.e., radiocarbon, uranium-series, and magnetostratigraphy (Buigues, 1997). The settlement of fringing and barrier reefs is likely to have been discontinuous throughout the Miocene, primarily controlled by volcanic activity and, from about 10.5 million years by residual volcanic topography, tectonics, and sea-level changes. The entire volcanic basement has been capped by an extensive flat-topped carbonate platform probably not prior to the Pliocene. The classical atoll morphology is thought to have been acquired during the late Pliocene to Pleistocene. This results from both dissolution in the central platform areas and lateral reef accretion at the periphery in response to changes in sea level (Perrin, 1990; Buigues, 1997; Camoin et al., 2001). From top to base, the carbonate cap is composed of four stratigraphical units. The Holocene reef unit ranges between about 4 and 20 m in thickness. The Pleistocene reef unit is about 50–150 m thick. It displays major unconformity surfaces at 10, 30, 65, 80, and 90 m below present reef surface, separating successive reef generations. The Pliocene reef unit ranges from about 70 to up to 150 m in thickness. The oldest unit (Late Miocene) locally exceeds 150 m in thickness (Figure 1).

Carbonate diagenesis

The carbonate rocks from both the volcaniclastic series and carbonate cap have suffered severe diagenetic alteration (replacement by low-magnesium calcite and dolomite, dissolution, karstification) probably controlled by freshwater aquifers in relation to changes in sea level (Aissaoui et al., 1986). There is a significant increase especially, both in calcite and dolomite diagenesis towards the periphery of the carbonate cap. Apart from the upper 20 m (Holocene) composed of metastable minerals (aragonite, high-magnesium calcite), the cap contains low-magnesium calcite or dolomite. The dolomite unit probably of late Miocene Age, occupies the lower two-thirds of the carbonate cap (Figure 1). Dissolution is one of the most prominent diagenetic features in the carbonate cap. The whole series appears to be severely karstified. Karst starts at 90–100 m and extends down to 150 m within the Pleistocene carbonates, both beneath the rim and the lagoon. Large-scale karstic surfaces also occur 180–200 m deep at the Pliocene–Miocene transition and 220–280 m and 300–350 m deep at the base of the Miocene carbonates.

Pleistocene reef growth and sea-level changes

Uranium-series age determinations of the successive reefs units drilled through the outer rim at Mururoa provide new



Mururoa Atoll, Figure 1 Lithology and structure of the carbonate cap with special reference to the outer reef rim over the last 300 ka, Mururoa Atoll, French Polynesia. *HO* Holocene unit, *PLE* Pleistocene unit, *PLIO* Pliocene unit, *MIO* Miocene unit. Numbers 1–12 refer to Marine Isotope Stages (MIS). Modified from Buigues (1997) and Camoin et al. (2001).

constraints on reef physiography and variations in sea level during the past 300 ka (1 ka = 1,000 years) (Perrin, 1990; Camoin et al., 2001). The outer rim has developed seawards in the form of a series of overlapping fringing reefs (Figure 1). Estimates of former sea-levels are based on the age-depth relationship of selected corals with correction of the present depth for both thermal subsidence of the atoll and habitat-depth range of the corals. Prominent reef units primarily made up of coralgal boundstones have developed during four episodes of high sea stands (MIS stages 1, 5, 7, and 9). The data indicate that sea level was between 17 and 23 m below present sea level (bpsl) at 9 ka. During MIS stage 5 e (around 125 ka), sea level is estimated to have been 6–10 m above present reef surface. The paleo-sea levels at 212 ka (stage 7 c) and 332 ka (stage 9 c) were 11–17 m 26–33 m bpsl respectively. Low sea stands are typified by limited reef growth and large skeletal deposition and include MIS stages 2, 4, and 8. During stage 2 (Last Glacial Maximum), sea level was around 135–140 m bpsl within the 23–17 ka interval. The paleo-sea level during stage 4 at around 60 ka is assumed to have been between 76 and 91 m bpsl, while it was at 79–94 m bpsl during stage 8 d at about 270 ka.

Summary

Mururoa is an open atoll and exhibits low coral diversity (about 50 species). Drilling investigations revealed that the maximal thickness of the carbonate pile ranges between 500 and 220 m. The lowermost part of the pile is late Miocene in age. The typical atoll morphology is likely to have been acquired not before the late Pliocene. During the Pleistocene, and especially the last 300 ka, the outer rim has accreted seawards through a series of stacked fringing-like reef bodies. The carbonate deposits have experienced intense diagenetic alteration by fresh water during successive low sea stands.

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Cross-references

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