C

CALCITE

Sue J. McLaren
University of Leicester, Leicester, UK

Definition

The minerals calcite, *aragonite*, and vaterite are naturally occurring polymorphic forms of calcium carbonate ($CaCO_3$). At normal Earth surface pressures and temperatures, low magnesian calcites are the only stable $CaCO_3$ phase. Calcite has a trigonal crystal system, perfect cleavage in three directions, conchoidal fracture, and a hardness of three on Moh's scale. Calcite often has a massive habit, although dog-tooth spar (scalenohedrons) and rhombohedral forms are also common. The mineral's color is commonly white or colorless, but may be yellow, pink, pale blue, or even red in hand specimen; in thin section, it is colorless. Most calcite is relatively pure, but impurities include ferrous iron, magnesium, manganese, and strontium. Calcites with less than four mole percent $MgCO_3$ are termed low magnesian calcites, while those containing 4–30 mole percent are known as high magnesian calcites. Calcite is readily soluble and effervesces vigorously in cold dilute hydrochloric acid and it is stained red by the organic dye Alizarin Red S.

Calcite is generally a major constituent of carbonate rocks and is a commonly found earth mineral. Limestones must be made of more than 50% carbonate minerals (Tucker and Wright, 1990). Calcite tends to precipitate from freshwater where Mg:Ca ratios are generally low (<1). Carbonate minerals are highly soluble in waters rich in carbon dioxide, which results in most limestones being susceptible to *diagenesis*. *Diagenesis* leads to the alteration of a carbonate deposit by various geochemical processes that result in changes in mineralogy, texture, and fabric. Over time, skeletal and non-skeletal carbonate grains and carbonate matrix alter to low magnesian calcite and calcite cements are precipitated in primary and secondary pore spaces. In the process, *aragonite* is often partially or totally dissolved. During transformation from high to low magnesian calcite, the initial structure is kept but Mg^{2+} is leached from the crystal. The crystal sizes of calcite cements that form can be grouped into *micrite* (<4 microns), microspar (4–10 microns), and spar (>10 microns).

Typical freshwater low magnesian calcite-rich deposits include *calcretes*, tufa, travertine, cave speleothems, and *eolianites*. High magnesian calcites are common components of *beach rocks*, shallow marine sediments, and the skeletons of marine organisms. According to Mackenzie et al. (1983), there is an increase in the content of magnesium within skeletal high magnesian calcite from polar regions towards the tropics, which is related to changes in temperature and seawater saturation of carbonate ions.

Bibliography

Mackenzie, F. T., Bischoff, W. D., Bishop, F. C., Loijens, M., Schoonmaker, J., and Wollast, R., 1983. Magnesian calcites: low temperature occurrence, solubility and solid solution behaviour. In Reeder, R. J. (ed.), *Carbonates: Mineralogy and Chemistry. Reviews in Mineralogy.* Washington, DC: Mineralogical Society of America, Vol. 11, pp. 97–144.

Tucker, M. E., and Wright, V. P. 1990. *Carbonate Sedimentology.* Oxford: Blackwell, pp. 482.

Cross-references

Aragonite
Beach Rock
Calcrete/Caliche
Diagenesis
Eolianite
Micrite

David Hopley (ed.), *Encyclopedia of Modern Coral Reefs*, DOI 10.1007/978-90-481-2639-2,

CALCRETE/CALICHE

Barbara H. Lidz
U.S. Geological Survey, St. Petersburg, FL, USA

Synonyms

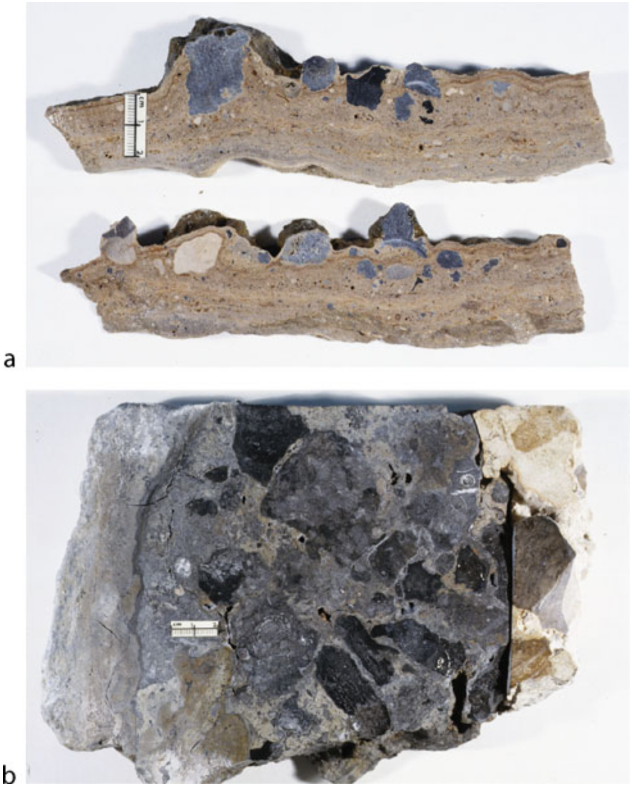
Breccias; Calcium-carbonate cement; Hardpan; Impermeable crust of soluble calcium salts; Laminated crust; Pedogenic calcareous soil; Secondarily deposited calcareous material on native-limestone surface; Soilstone crust; Strongly indurated wafer-thin calcareous layers; Subaerial $CaCO_3$ crust; Subaerial-exposure surface; Unconformity

Definition

Laminated subaerial-soilstone crusts (calcrete/caliche) are found in diverse carbonate environments throughout geological history (e.g., Swett, 1974; Harrison and Steinen, 1978; Kahle, 1978). Florida crusts accrete vertically in a series of wafer-thin layers, through capillary interaction of wet/dry processes on exposed limestone (Multer and Hoffmeister, 1968). The limestone underlies a thin mantle of organic-rich soil that contains cryptocrystalline calcite, derived from periodic dissolution of in situ carbonate particles. Drill cores show Florida crusts cap five Pleistocene chronostratigraphic marine sequences, as unconformities (Enos and Perkins, 1977). Extensive subsurface persistence renders the crusts significant stratigraphic markers for regional sequence correlation. Radiometric dates that correlate with Pleistocene glacial cycles indicate times when subsurface crust-source sites were dry land (Robbin, 1981). In the Florida Keys, crust accretion rates are uniform within, but inconsistent between, northeast (1 cm/2 ka) and southwest (1 cm/4 ka) sites (Robbin and Stipp, 1979). Inconsistency results from different local ambient conditions during crust formation (e.g., variability of limestone porosity, soil, humus, detrital carbonate, and erosion). Inconsistent accretion rates result in different thicknesses of calcrete (see Figure 1a and b in entry entitled, *Porosity Variability in Limestone Sequences*).

Calcrete textures

Calcretes have various textures depending upon the type of material present at the site of formation and/or the processes involved in formation. Rhizoliths or rhizoconcretions are small cylindrical or conical root-cast structures, usually branching or forked, that form in a sedimentary rock. Rhizoliths may consist of calcrete or chert and resemble in shape the plant roots they have replaced. Calcretes that consist of aggregated, clustered, or flocculated grains are said to be clotted. Patches of dark, dense, fine-grained areas ultimately surrounded by sparry calcite can characterize clotted rocks. The squashing of soft micrite pellets usually produces clotting. Calcretes that have different colors, commonly resulting from oxidation of iron components, are said to be mottled, but multicoloration is not the only characteristic. Mottled calcretes also can contain small irregular pieces of material in a sedimentary matrix of a different texture.



Calcrete/Caliche, Figure 1 (**a**) Large, angular, naturally blackened pebbles embedded in brown, layered, fine-grained calcrete form a breccia (compare with calcretes shown in a and b in entry entitled, Porosity Variability in Limestone Sequences). Sample is from Ramrod Key (lower Florida Keys). Ramrod Key limestones also contain charred twigs (charcoal; not shown). Charcoal in 5-ka calcrete indicates natural forest fires occurred before the invasion of modern man. (**b**) A multicolored, well-cemented breccia was collected at a depth of ~6 m below sea level from quarry tailings in a solution pit on Big Pine Key (lower Florida Keys). The sample was cut, and the left part artificially blackened in the laboratory by heating at 400°C for one-half hour to reproduce darkening similar to colors of blackened pebbles widely found in the Florida-Caribbean Pleistocene and Holocene record. Note layered calcrete crust on left side of specimen. Blackened fragments include preexisting calcrete and fossiliferous Key Largo Limestone (coral). Original rock colors are visible in unheated section at right. Rulers in both photos are 2 cm long. See Figure 2a in entry entitled, Florida Keys, for locations of Ramrod Key and Big Pine Key.

Breccias are coarse-grained clastic rocks composed of angular fragments of any kind of preexisting native rock. Mineral cement binds the fragments together in a fine-grained matrix of sand, clay, or calcrete. Breccias may result from talus accumulation (sedimentary breccia), igneous processes (volcanic and explosive breccias), tectonic processes (fault breccia), disturbance during sedimentation (intraclastic breccia), or collapse of rock material (solution and collapse breccias). Solution and collapse breccias are common in karst settings such as Florida where sinkholes and other types of karst features form. Also common in Pleistocene and Holocene limestones throughout the Florida-Caribbean region are multihued blackened limestone pebbles in a calcrete matrix (Figure 1a and b). Simple laboratory (heating) experiments and observations (campfire sites) have shown that pebbles of limestone (coral, mollusc, grainstone, and calcrete) can blacken almost instantaneously when heated to between 400° and 500°C (Shinn and Lidz, 1988). Being the lightning capital of the U.S., Florida has, and has had in the geological past, no shortage of sources of ignition for lighting of natural forest fires.

Bibliography

Enos, P., and Perkins, R. D., 1977. *Quaternary Sedimentation in South Florida*. Tulsa, OK: Geological Society of America Memoir 147.

Harrison, R. S., and Steinen, R. P., 1978. Subaerial crusts, caliche profiles, and breccia horizons: comparison of some Holocene and Mississippian exposure surfaces, Barbados and Kentucky. *Geological Society of America Bulletin*, **89**, 385–396.

Kahle, C. F., 1978. *Subaerial Exposure of Silurian Shelf-Margin Reefs.* Oklahoma City, OK: Northwestern Ohio: AAPG-SEPM Annual Meeting Program (Abs), p. 79.

Multer, H. G., and Hoffmeister, J. E., 1968. Subaerial laminated crusts of the Florida Keys. *Geological Society of America Bulletin*, **79**, 183–192.

Robbin, D. M., 1981. Subaerial $CaCO_3$ crust: a tool for timing reef initiation and defining sea level changes. In *Proceedings International Coral Reef Symposium*, 4th, Manila, Philippines, **1**, 575–579.

Robbin, D. M., and Stipp, J. J., 1979. Depositional rate of laminated soilstone crusts, Florida Keys. *Journal of Sedimentary Petrology*, **49**(1), 175–180.

Shinn, E. A., and Lidz, B. H., 1988. Blackened limestone pebbles: fire at subaerial unconformities. In James, N. P., and Choquette, P. W. (eds.), *Paleokarst*. New York: Springer, pp. 117–131.

Swett, K., 1974. Calcrete crusts in an Arctic permafrost environment: *American Journal of Science*, **274**, 1059–1063.

Cross-references

Florida Keys
Last Glacial Lowstand and Shelf Exposure
Porosity Variability In Limestone Sequences
Reef Drilling

CARBON FLUXES OF CORAL REEFS

Marlin J. Atkinson
Hawaii Institute of Marine Biology, Kaneohe, Hawaii

Synonyms

Carbon dynamics

Definition

The carbon fluxes of coral reefs are the rates of carbon exchange between sea water and reef organisms, communities, and habitats. They characterize key biochemical processes such as photosynthesis, respiration, and calcification, as well as important biogeochemical transformations such as diagenesis and dissolution. Fluxes are reported as rates of exchange per area.

Introduction

A coral reef is a living structure that maintains itself at sea level by the combined biogenic calcification of a variety of taxa. A healthy, sustainable coral reef ecosystem is comprised of diverse communities that capture and utilize energy from sunlight, waves, and organic particles. The motivation for studying carbon fluxes of coral reefs is to delineate and characterize these rates of energy transfer in order to compare reefs with other ecosystems and to compare among reefs, and to predict responses of reefs to natural or anthropogenic perturbations.

Specific communities within a coral reef ecosystem achieve high rates of photosynthesis and, consequently, production of organic carbon. Over the past 80 years, a variety of ideas have been advanced to explain these high rates of carbon production. One prevalent view is that close physical and ecological relationships between autotrophs (organisms such as plants that produce organic carbon from inorganic carbon) and heterotrophs (organisms that consume organic carbon, i.e., most animals) create an ecosystem where plant nutrients (compounds of nitrogen, phosphorus, sulfur, etc.) are either retained within the biota or recycled within the community, maximizing carbon production. A more recent view is that coral reefs produce organic carbon that is low in nutrients and is quickly respired. This article provides an overview of the carbon dynamics or carbon fluxes of coral reefs.

Fluxes of dissolved inorganic carbon

The amount of carbon, in both dissolved and particulate forms, is orders of magnitude lower in the water column above a coral reef than it is in the biota or in the sediments (Table 1). Dissolved inorganic carbon (in the form of dissolved carbon dioxide and carbonate and bi-carbonate ions) is removed from the water column by autotrophs and converted to, or "fixed" into, both organic compounds (tissue and dissolved organic compounds) and inorganic compounds (notably calcium carbonate skeletons of marine algae and corals; Kinsey, 1985; Hatcher, 1997; Gattuso et al., 1998; Atkinson and Falter, 2003). The total amount of carbon fixed into organic matter per day is termed gross primary production. Gross primary production is typically estimated by adding daytime net photosynthesis to the 24-h respiration rate, based on dark respiration. Light respiration can be up to two times greater than dark respiration. Published values of gross primary production that assume light respiration equals dark respiration are therefore of questionable accuracy

(Langdon et al., 2003). In practice, flux of oxygen is used instead of carbon dioxide to estimate net photosynthesis and respiration, assuming photosynthetic and respiratory quotients of 1.0 (range 0.8–1.2). Many such measurements have produced a uniform "metabolic standard" for reefs (Table 2).

Gross primary production varies from 100 to 2,000 mmol C m^{-2} d^{-1}, depending on habitat (Table 2). Sand communities have the lowest production (100–300 mmol C m^{-2} d^{-1}), with reef flats being moderate (350–500 mmol C m^{-2} d^{-1}), and communities with high surface area of coral and algae exhibiting maximal values (1,000–2,000 mmol C m^{-2} d^{-1}). These metabolic rates are consistent between reefs, suggesting that they are independent of species composition. Thus, carbon metabolism on reefs has a tri-modal distribution (Table 2), and estimates of carbon production and calcification (production of calcium carbonate) can be made based on knowledge of bottom type or habitat. These three basic habitats of coral reefs can be easily identified and mapped with airborne and satellite imaging systems (Hochberg et al., 2003). Ecosystem-wide estimates of gross primary production are possible by applying average metabolic rates to the areal extent of those habitats (Andrefouet and Payri, 2000). Gross primary production can also be estimated by measuring the number of photons absorbed into the benthos with remote-sensing image data and multiplying by 0.033 mol oxygen/mol photons (Hochberg and Atkinson, 2008). Thus, the amount of energy converted from tropical sunlight to organic matter on a reef flat represents about 3% efficiency. Sunlight incident on tropical reef flats is typically ~30–40 Einstein m^{-2} d^{-1} or 10,000 kJ m^{-2} d^{-1}, whereas 1 mol organic C m^{-2} is about 400 kJ m^{-2}.

Carbon Fluxes of Coral Reefs, Table 1 Mass of carbon (**C**) in mmol m^{-2} in 1 m of the water column above the benthos, in the living benthos (autotrophic and heterotrophic), and in the top-most 1-m of sediments (solid and dissolved phases)

Pool	C
1-m water column	10–250
Living benthos	
Autotrophic	22,400[a]
Heterotrophic	~5,000[b]
1-m sediments	
Solid phase	300,000[c]
Dissolved phase	5–125[d]

[a] Values for benthic autotrophs calculated from dry weight biomass estimates (Odum and Odum, 1955) and assuming a C:N:P ratio of 550:30:1 (Atkinson and Smith, 1983).
[b] Benthic heterotrophic biomass content calculated assuming nearly all of the biomass is composed of CH_2O
[c] Assuming a porosity of 0.5 (Buddemeier and Oberdorfer, 1988) and a sediment density of 2.7 g cm^{-3}.
[d] This estimate assumes pore water dissolved organic carbon concentrations are equal to ambient water dissolved organic carbon concentrations (Tribble et al., 1990).

Community respiration varies over the same range as gross primary production (Table 2). Benthic communities with high gross primary production tend to exhibit high community respiration, indicating much of the respiration of organic material occurs within the habitat. Most of the respiration probably occurs within the organisms that fix the carbon; some is the result of consumption and/or microbial decomposition of organic detritus. Measurements of production and respiration over periods shorter than 1 week do not adequately reflect longer-term net ecosystem metabolism. This is because in the case of autotrophs, a day's gross primary production depends on cumulative ambient light on that day; the daily gross respiration depends on the amount of stored photosynthate on that day (Falter et al., 2001).

Net production of carbon

Net community production (NCP – Table 2), the excess carbon produced over a 24-h period (gross primary production minus community respiration), varies among habitats. In classic reef zonation, more carbon is produced than is respired on the fore-reef and algal crest, instead being exported to the back-reef area as detritus and dissolved organic carbon. As it is carried across the reef, a proportion of it is utilized by downstream heterotrophic communities (Crossland et al., 1991; Kinsey, 1985). In practice, the delineation between producer and consumer habitats is not always clear. For example, many back reef

Carbon Fluxes of Coral Reefs, Table 2 Gross primary production (**P**), Community respiration (**R**), Net Community Production (**NCP**), and Net Community Calcification (**G**) in mmol C m^{-2} day^{-1} for various habitats as originally tabulated by Kinsey (1985) with additional data from Gattuso et al. (1993), Gattuso et al. (1996), Kraines et al. (1996), Kraines et al. (1997), Boucher et al. (1998), and Andrefouet and Payri (2000). Means are in **bold** followed by the range in parentheses. To convert to grams of carbon, multiply by 12 g mol^{-1} and divide by 1,000 mg g^{-1}. A negative value for NCP indicates that habitat must import organic carbon to match its respiratory demand

Habitat	P	R	NCP	G
Average reef-flat	**640** (330–1,580)	**600** (290–1,250)	−220–310	**130** (20–250)
Algal pavement	**460** (170–580)	**300** (40–560)	0–130	**90** (70–110)
High coverage	**1,180** (660–1,920)	**1,280** (500–2,000)	−830–250	**240** (110–320)
Sandy areas	**130** (80–230)	**130** (90–200)	−40–30	**35** (10–70)
Shallow lagoon	**450** (210–1,080)	**430** (180–790)	−200–280	**40** (20–55)
Entire reef systems	**390** (190–640)	**370** (190–570)	0–70	**45** (3–135)

areas that have significant coral rubble can have high net production. Thus, much of this zonation of production and consumption is dependent on the nature of the substrate. Sand and mud have a tendency to be heterotrophic (negative net production), while areas exposed to high water motion and hard substratum with algae tend be autotrophic (positive net production). Rich coral areas and knolls usually have high gross production, but a net production that is close to zero. Seaward areas with a relatively high net production can be sustained by dissolved nutrients in the incoming ocean waters, and where high water motion can support higher nutrient uptake and photosynthetic rates than calmer areas (Hearn et al., 2001; Carpenter and Williams, 2007). Nutrient uptake is proportional to nutrient concentration and water velocity, with a coefficient of proportionality that is directly related to the friction of the water flowing over the bottom communities (Atkinson and Falter, 2003). The energy dissipated as bottom friction helps drive net photosynthesis and net production of carbon, and is of order 1,000 kJ m^{-2} d^{-1} (Hearn et al., 2001), or about 10% of the energy in sunlight for typical cross-reef currents. Organic carbon production has high ratios of carbon:nitrogen:phosphorus (C:N:P), reflecting dominant production by macrophytes (Atkinson and Grigg, 1984).

Fluxes of planktonic carbon

Coral reef communities take up suspended planktonic organic matter (detritus, phytoplankton, zooplankton) as a source of "new" carbon – i.e., carbon they do not fix themselves via photosynthesis (Ayukai, 1995; Ribes et al., 2003; Yahel et al., 1998). Reported rates of particulate carbon uptake are, however, relatively low (<40 mmol C m^{-2} day^{-1}), compared to rates of gross primary production and community respiration (Table 2). Suspended organic matter is thus relatively unimportant as a source of carbon for many hard and soft coral communities. However, it is an important source of specific essential nutrients for many communities, and food for some (Fabricius et al., 1998; Sebens et al., 1997).

Fluxes of dissolved organic matter

Dissolved organic carbon comes from microbial decomposition of plant and animal detritus and fecal material. It is ubiquitous in water over coral reefs, and it typically occurs at concentrations much greater than those of particulate organic matter (50 mmol m^{-3}). Dissolved organic carbon is taken up and released by a variety of organisms, including corals and sponges (Schlichter and Liebezeit, 1991; Hoegh-Guldberg and Williamson, 1999; Yahel et al., 2003). Rates of dissolved organic matter metabolism can be either significant or insignificant in the context of total metabolism. Much of the metabolism has been attributed to symbiotic bacteria (Ferrier-Pages et al., 1998; Yahel et al., 2003), but the cycling of dissolved organic matter at the community and ecosystem scales remains poorly understood. The metabolism of specific organic compounds occurring in low concentrations, such as steroids, can have substantial impacts on the biology of specific organisms (Tarrant et al., 2004).

Reef waters also contain dissolved organic nitrogen; it is typically exported from reef communities (Wilkinson et al., 1984). The nature of dissolved organic nitrogen and the rate kinetics of its uptake are also unknown, making it difficult to establish their rates of uptake or recycling. Like dissolved organic compounds, generally, dissolved organic nitrogen may be resistant to chemical breakdown in seawater and require bacterial or sponge communities for re-mineralization; its uptake and release by the benthic community will thus strongly depend on the composition and abundance of the benthic biota.

Fluxes of sediment carbon

Sediments in coral reefs typically contain $<1\%$ organic carbon, indicating little sequestration of organic carbon into these systems. By contrast, rates of inorganic carbon deposition (as calcium carbonate skeletons) are large, its production accounting for approximately 10–20% of gross primary production. Communities with high gross primary production tend to have the highest calcification rates (Table 2). Calcification is positively correlated to light and net photosynthesis (Gattuso et al., 1999); the activation energy to produce a typical amount of calcium carbonate represents only 1% of the energy in gross primary production (activation energy for carbonate precipitation is ~4 kjoule m^{-2} d^{-1} for 0.1 mol $CaCO_3$ m^{-2} d^{-1}). The rate of calcification is positively correlated to carbonate ion concentration in the sea water (Atkinson and Cuet, 2009); projected decreases in carbonate over the next 60 years from rising atmospheric carbon dioxide may reduce coral calcification by up to 30% (Smith and Buddemeier, 1992; Kleypas and Langdon, 2006). Dissolution of carbonates occurs naturally inside coral heads (Entsch et al., 1983), in interior pore-spaces of coral reef sediments (Tribble et al., 1990), and from the erosion action of boring organisms (Tribollet, 2008). Historically, rates of dissolution have been much slower than rates of biogenic precipitation ($<10\%$; Tribble et al., 1990), but it is now suggested (Hoegh-Guldberg et al., 2007) that ocean acidification will reverse the relative rates.

Pore-water carbon

Coral reef frameworks are partially lithified carbonate structures on which reef communities grow. Pore-waters of reef frameworks are mostly anoxic and contain elevated levels of dissolved nutrients (Sansone et al., 1990). This combination of low oxygen and high nutrients is a common feature of many coral reefs and a direct result of oxidation of organic matter in the interstitial spaces (Tribble et al., 1990). The subsequent production of carbonic acid from the oxidation of organic matter lowers pore-water pH and reduces the activity of the carbonate ion, thus facilitating *in situ* dissolution of carbonate (primarily aragonite). Reef pore-waters become anoxic at depths of less than 1 m into the framework; however, some reef pore waters become anoxic within centimeters of the framework surface (Falter and Sansone, 2000b).

Hydraulically driven transport of water into, through, and out-of coral reef frameworks has long been hypothesized as the primary driver of framework diagenesis – the transformation of skeletal materials into limestone rock (Haberstroh and Sansone, 1999). It is proposed that the water brings both oxygen and particulate organic matter into the interstitial pore-spaces to sustain carbon metabolism (Huettel and Rusch, 2000). Coral reef frameworks are highly permeable, typically with hydraulic conductivities (K) ranging between 10 and 1,000 m day^{-1}. Consequently, ambient hydraulic pressure gradients across coral reef frameworks do seem large enough to drive the flow of interstitial water (Falter and Sansone, 2000a) and thus drive diagenesis in the manner postulated. Wave-induced mixing is an important process controlling the exchange of shallow pore-water with overlying water (Falter and Sansone, 2000a). Thus, variations in the oxygen and pH structure of pore-waters within the top 2 m of sediment are affected by a habitat hydrodynamics, which is affected by its location on the reef and the direction of waves impinging on the reef. The deep anoxic regions of the reef frameworks, beyond the effects of wave-induced mixing, are high in methane and sulfate (Sansone et al., 1990).

Summary

Ranges, means, and limits of carbon metabolism are summarized for coral reefs worldwide; zones and habitats of carbon production and consumption are also described. The underlying functional processes and parameterizations of those processes are discussed. At this time, however, there are gaps in knowledge, and it is particularly noted that interactions with nutrients are not yet well established.

Dissolved inorganic carbon (i.e., carbon dioxide gas, bicarbonate, and carbonate ion) is removed from the water column by autotrophs and fixed into organic (tissue and photosynthate) and inorganic (calcium carbonate skeletons) compounds. Gross primary production and community respiration rates vary greatly in different habitats of reefs, with much of the respiration of organic material occurring within the organism or the habitat in which it was produced. Net community production varies among habitats. In classic reef zonation, carbon from the fore-reef is exported to the back-reef area as detritus and dissolved organic carbon. Coral reef communities take up suspended planktonic organic matter at rates that are relatively low compared to their own primary production. Sediments in coral reefs typically contain <1% organic carbon, indicating little sequestration of organic carbon into these systems. Dissolution of calcium carbonate occurs naturally inside coral heads, in interior pore-spaces of coral reef sediments, and from the erosion action of boring organisms. Globally, the surface area of coral reefs is small and thus coral reefs have negligible effect on the global carbon cycle.

Bibliography

Andrefouet, S., and Payri, C., 2000. Scaling-up carbon and carbonate metabolism of coral reefs using in-situ data and remote sensing. *Coral Reefs*, **19**, 259–269.

Atkinson, M. J., and Cuet, P., 2009. Possible effects of ocean acidification on coral reef biogeochemistry: topics for research. *Marine Ecology Progress Series*, **373**, 249–256.

Atkinson, M. J., and Falter, J. L., 2003. Coral Reefs. In Black, K. P., and Shimmield, G. D. (eds.), *Biogeochemistry of Marine Systems*. Boca Raton, FL: CRC Press, pp. 40–64.

Atkinson, M. J., and Grigg, R. W., 1984. Model of a coral reef ecosystem: II. Gross and net benthic primary production at French Frigate Shoals, Hawaii. *Coral Reefs*, **3**, 13–22.

Atkinson, M. J., and Smith, S. V., 1983. C:N:P ratios of benthic marine plants. *Limnology and Oceanography*, **28**, 568–574.

Ayukai, T., 1995. Retention of phytoplankton and planktonic microbes on coral reefs within the Great Barrier Reef, Australia. *Coral Reefs*, **14**, 141–147.

Boucher, G., Clavier, J., Hily, C., and Gattuso, J. P., 1998. Contributions of soft-bottoms to the community metabolism (primary production and calcification) of a barrier reef flat (Moorea, French Polynesia). *Journal of Experimental Marine Biology and Ecology*, **225**, 269–283.

Buddemeier, R. W., and Oberdorfer, J. A., 1988. Hydrogeology and hydrodynamics of coral reef pore waters. *6th International Coral Reef Symposium, Brisbane, Australia*, **2**, 485–490.

Carpenter, R. C., and Williams, S. L., 2007. Mass Transfer of photosynthesis on coral reef algal turfs. *Marine Biology*, **151**, 435–450.

Crossland, C. J., Hatcher, B. G., and Smith, S. V., 1991. Role of coral reefs in global ocean production. *Coral Reefs*, **10**, 55–64.

Entsch, B., Boto, K. G., Sim, R. G., and Wellington, J. T., 1983. Phosphorus and nitrogen in coral reef sediments. *Limnology and Oceanography*, **28**, 465–476.

Fabricius, K. E., Yahel, G., and Genin, A., 1998. In-situ depletion of phytoplankton by an axoothanthallae soft coral. *Limnology and Oceanography*, **43**, 354–356.

Falter, J. L., and Sansone, F. J., 2000a. Hydraulic control of pore water geochemistry within the oxic-suboxic zone of a permeable sediment. *Limnology and Oceanography*, **45**, 550–557.

Falter, J. L., and Sansone, F. J., 2000b. Shallow pore water sampling in reef sediments. *Coral Reefs*, **19**, 93–97.

Falter, J. L., Atkinson, M. J., and Langdon, C., 2001. Production-respiration relationships at different time-scales within the Biosphere 2 coral reef biome. *Limnology and Oceanography*, **46**, 1653–1660.

Ferrier-Pages, C., Gattuso, J. P., Cauwet, G., Jaubert, J., and Allemand, D., 1998. Release of dissolved organic carbon and nitrogen by the zooxanthellate coral Galaxea fascicularis. *Marine Ecology Progress Series*, **172**, 265–274.

Gattuso, J.-P., Pinchon, M., Delasalle, B., and Frankignoulle, M., 1993. Community metabolism and air-sea CO2 fluxes in a coral reef ecosystem (Moorea, French Polynesia). *Marine Ecological Progress Series*, **96**, 259–267.

Gattuso, J. P., Pinchon, M., Delesalle, B., Canon, C., and Frankignoulle, M., 1996. Carbon fluxes in coral reefs. I. Lagrangian measurement of community metabolism and resulting air-sea CO_2 disequilibrium. *Marine Ecological Progress Series*, **145**, 109–121.

Gattuso, J. P., Frankignoulle, M., and Wollast, R., 1998. Carbon and carbonate metabolism in coastal aquatic ecosystems. *Annual Review of Ecological Systems*, **29**, 405–434.

Gattuso, J. P., Allemand, D., and Frankignoulle, M., 1999. Photosynthesis and calcification at cellular, organismal, and community levels in coral reefs: a review of interactions and control by carbonate chemistry. *American Zoologist*, **39**, 160–183.

Haberstroh, P. R., and Sansone, F. J., 1999. Reef framework diagenesis across wave-flushed oxic-suboxic-anoxic transition zones. *Coral Reefs*, **18**, 229–240.

Hatcher, B. G., 1997. Organic production and decomposition. In Birkeland, C. (ed.), *Life and Death of Coral Reefs*. New York: Chapman & Hall, pp. 140–174.

Hearn, C. J., Atkinson, M. J., and Falter, J. L., 2001. A physical derivation of nutrient-uptake rates in coral reefs: effects of roughness and waves. *Coral Reefs*, **20**, 347–356.

Hochberg, E. J., and Atkinson, M. J., 2008. Coral reef benthic productivity based on optical absorptance and light-use efficiency. *Coral Reefs*, **27**, 49–59.

Hochberg, E. J., Atkinson, M. J., and Andrefouet, S., 2003. Spectral reflectance of coral reef bottom-types worldwide and implications for coral reef remote sensing. *Remote Sensing of Environment*, **85**, 159–173.

Hoegh-Guldberg, O., and Williamson, J., 1999. Availability of two forms of dissolved nitrogen to the coral *Pocillapora damicornis* and its symbiotic zoooxanthellae. *Coral Reefs*, **133**, 561–570.

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., et al., 2007. Coral reefs under rapid climate change and ocean acidification. *Science*, **318**, 1737–1742.

Huettel, M., and Rusch, A., 2000. Transport and degradation of phytoplankton in permeable sediment. *Limnology and Oceanography*, **45**, 534–549.

Kinsey, D. W., 1985. Metabolism, calcification, and carbon production: I. Systems level studies. *5th International Coral Reef Congress, Tahiti*, **4**, 505–526.

Kleypas, J. A., and Langdon, C., 2006. Coral reefs and changing seawater chemistry. In Phinney, J. T., Hoegh-Guldberg, O., Kleypas, J., Skirving, W., and Strong, A. (eds.), Coral reefs and climate change science: science and management. *American Geophysical Union Monograph Series, Coastal Estuary Studies*, **61**, 73–110.

Kraines, S., Suzuki, Y., Yamada, K., and Komiyama, H., 1996. Separating biological and physical changes in dissolved oxygen concentration in a coral reef. *Limnology and Oceanography*, **41**, 1790–1799.

Kraines, S., Suzuki, Y., Omori, T., Shitashima, K., Kanahara, S., and Komiyama, H., 1997. Carbonate dynamics of the coral reef system at Bora Bay, Miyako Island. *Marine Ecology Progress Series*, **156**, 1–16.

Langdon, C., Broecker, W. S., Hammond, D. E., Glen, E., Fitzsimmons, K., Nelson, S. G., Peng, T. H., Hajdas, I., and Bemani, G., 2003. Effects of elevated CO_2 on the community metabolism of an experimental coral reef. *Global Biogeochemical Cycles*, **17**(1), 1011, doi: 10,1029/2002GB001941.

Odum, H. T., and Odum, E. P., 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecology Monograph*, **25**, 1415–1444.

Ribes, M., Coma, R., Atkinson, M. J., and Kinzie III, R. A., 2003. Particles removal by coral reef communities: a major source of nitrogen. *Marine Ecology Progress Series*, **257**, 13–23.

Sansone, F. J., Tribble, G. W., Andrews, C. A., and Chanton, J. P., 1990. Anaerobic diagenesis within recent, pleistocene, and eocene marine carbonate frameworks. *Sedimentology*, **37**, 997–1009.

Schlichter, D., and Liebezeit, G., 1991. The natural release of amino acids from the symbiotic coral *Heteroxenia fuscescens* (Ehrb.) as a function of photosynthesis. *Journal of Experimental Marine Biology and Ecology*, **150**, 83–90.

Sebens, K. P., Grace, S. P., Helmuth, B., Maney, Jr., E. J., and Miles, J. S., 1997. Water flow and prey capture by three scleractinian corals, *Madracis mirabilis*, *Montastrea cavernosa*, and *Porites porites* in a field enclosure. *Marine Biology*, **131**, 347–360.

Smith, S. V., and Buddemeier, R. W., 1992. Global change in coral reef ecosystems. *Annual Review of Ecological Systems*, **23**, 89–118.

Tarrant, A. M., Atkinson, M. J., and Atkinson, S., 2004. Effects of steroidal estrogens on coral growth and reproduction. *Marine Ecology Progress Series*, **269**, 121–129.

Tribble, G. W., Sansone, F. J., and Smith, S. V., 1990. Stoichiometric modeling of carbon diagenesis within a coral reef framework. *Geochimica Cosmochimica Acta*, **54**, 2439–2449.

Tribollet, A., 2008. The boring microflora in modern coral reef ecosystems: a review of its roles. In Wisshak, M., and Tapanila, L. (eds.), *Current Developments in Bioerosion*. Berlin/Heidelberg: Springer, pp. 67–94.

Wilkinson, C. R., Williams, D., Sammarco, P. W., Hogg, R. W., and Trott, L. A., 1984. Rates of nitrogen fixation on coral reefs across the continental shelf of the central Great Barrier Reef. *Marine Biology*, **80**, 255–262.

Yahel, G., Post, A. F., Fabricius, K., Marie, D., Vaulot, D., and Genin, A., 1998. Phytoplankton distribution and grazing near coral reefs. *Limnology and Oceanography*, **43**, 551–563.

Yahel, G., Sharp, J. H., Marie, D., Hase, C., and Genin, A., 2003. In-situ feeding and element removal in the symbiotic-bearing sponge *Theonella swinhoei*: Bulk DOC is the major source for carbon. *Limnology and Oceanography*, **48**(1),141–149.

Cross-references

Carbonate Budgets and Reef Framework Accumulation
Diagenesis
Dolomitization
Nutrient Pollution/Eutrophication
Ocean Acidification, Effects on Calcification
Platforms (Cemented)
Solution Processes/Reef Erosion

CARBONATE BUDGETS AND REEF FRAMEWORK ACCUMULATION

Chris T. Perry
Manchester Metropolitan University, Manchester, UK

Definition

Carbonate budget: A quantitative measure, typically using census-based data, of the net rate of carbonate production within a given reef or carbonate sedimentary environment. The approach enables rates of reef carbonate production and erosion, associated with different biological, chemical and physical processes, to be quantified.

Introduction

In many tropical reef environments, corals are important primary producers of calcium carbonate ($CaCO_3$) and thus play a key role in reef framework construction. High percentage coral cover is often taken as indicative of a high rate of $CaCO_3$ accumulation and thus of rapid reef growth potential. However, corals represent just one of the carbonate producing groups that contribute to reef construction. Carbonate is also added to a reef's structure by calcareous algae and other calcareous encrusting organisms, through carbonate sedimentation, and by the precipitation of marine cements. Alongside these constructive processes, a range of physical and biological processes also operate to directly erode the accumulating reef structure. This eroded carbonate may subsequently re-accumulate within the reef structure or be exported out of the reef system. Summing the rates at which these different carbonate producing and eroding processes operate, thus allows the net rate of carbonate production on a reef to be quantified. A carbonate budget is thus a summation of the inputs and outputs of carbonate within the active carbonate producing environment and is typically expressed as a measure in kg $CaCO_3$ m^{-2} $year^{-1}$. Carbonate budget assessments, although logistically complex to construct, thus provide a useful estimation of net carbonate production rates on a reef at a given point in time. They also provide a mechanism for quantifying the relative importance of different carbonate producing and eroding processes, and provide an important insight into inter-reef variations in styles and rates of reef framework development. This has relevance to understanding both variability in the composition of accumulating reef framework structures and actual rates of framework accumulation.

Quantifying reef framework production and cycling

Coral reefs and reef sedimentary landforms are unique in that they are composed predominantly of calcium carbonate ($CaCO_3$) that results almost entirely from ecological processes. Corals typically represent the primary constructional components on most reefs and can add significant amounts of carbonate per unit area of reef surface (Vecsei, 2004). However, other carbonate producing processes also add additional $CaCO_3$ to the reef framework, the most important being by calcareous encrusters (especially crustose coralline algae), and the precipitation of syn- and early post-depositional cements (Perry and Hepburn, 2008). Significant amounts of primary carbonate are also produced in the form of sediment by other organisms or plants that induce $CaCO_3$ deposition. These additional sources of carbonate can contribute significant quantities of carbonate to the reef structure and may actually dominate $CaCO_3$ accumulation in specific reef settings (Bosence, 1984; Camoin et al., 2006).

A range of physical and biological erosional processes also influence rates and styles of reef framework accumulation. Bioerosion (the biological erosion of carbonate substrates) is facilitated by a wide range of reef-associated faunas, including species of fish and echinoids, and endolithic forms of sponges, bivalves and worms (see Chapter *Bioerosion*). These biological agents drive the direct degradation of both primary and secondary reef framework constituents and, as a by-product, may produce large amounts of sediment (Scoffin et al., 1980; Bruggemann et al., 1996). Physical disturbance, associated with storms and cyclones, is an important episodic process that influences reef framework development, largely through the generation of coral rubble, the deposition of which is an important reef-building process in its own right (Hubbard, 1997; Blanchon et al., 1997), and through the export of reef-derived sediments (Hubbard et al., 1990).

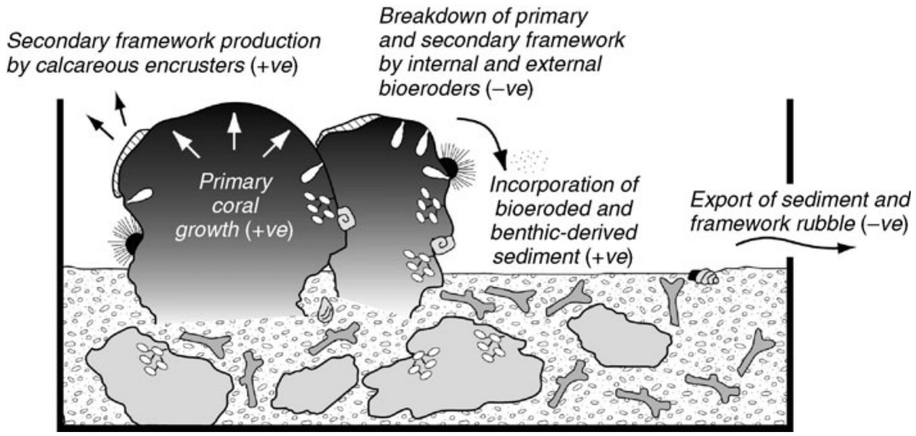
These various carbonate producing and cycling processes may thus exert either a "constructive" or "destructive" (*sensu* Scoffin, 1992) influence on reef-related carbonate accumulation, and the relative importance of each, within a given reef system, controls net rates of carbonate accumulation. This concept is defined by the carbonate budget approach to conceptualizing and quantifying reef geomorphic performance and can be viewed as the sum of gross carbonate production from corals and calcareous encrusters, as well as sediment produced within or imported into the reef, less that lost through biological or physical erosion, dissolution or sediment export (Figure 1). The balance between these different inputs and outputs represents the net production rate of framework $CaCO_3$ and can be expressed as:

$$\text{Net rate of framework CaCO}_3\text{ production} = [(P_{pf} + P_{sf}) - P_e] + Sed_i$$

where

P_{pf} = Primary framework carbonate production.
P_{sf} = Secondary framework carbonate production.
P_e = Primary and secondary framework carbonate lost to erosion.
Sed_i = Sediment incorporated into the reef framework (includes both benthic carbonate sediment and by-products of framework erosion less that exported from the reef).

Several detailed studies have quantified net rates of carbonate production, using carbonate budgets approaches, at the reef system scale, and these including studies on Caribbean reefs in Barbados (4.48 kg $CaCO_3$ m^{-2} yr^{-1}; Scoffin et al., 1980) and St. Croix (0.91 kg $CaCO_3$ m^{-2} yr^{-1}; Hubbard et al., 1990), and in the Indo Pacific in Hawaii (0.89 kg $CaCO_3$ m^{-2} yr^{-1}; Harney and Fletcher, 2003) and Indonesia (ranging from 11.68 to −7.6 kg $CaCO_3$ m^{-2} yr^{-1}; Edinger et al., 2000). Several studies have also utilized census-based budget approaches to quantify rates of sediment production within reef-related sedimentary environments. These include estimates of reef island sediment production (Hart and Kench, 2007), and epiphytic carbonate production in seagrass beds (Nelson and Ginsburg, 1986; Perry and Beavington-Penney, 2005). It is relevant to note that rates of carbonate production on shallow-water reefs have also previously been estimated using measures of alkalinity change in the waters overlying reefs (see Chapter *Density and Porosity: Influence on Reef Accretion Rates*). This approach provides an estimation of total carbonate production and early dissolution (Smith and Kinsey, 1976), and while resultant production estimates are in broad accord with the gross production estimates determined in process or census-based studies, it is not possible to quantify the production and erosion rates associated with individual organisms and/or processes. The approach thus has



Carbonate Budgets and Reef Framework Accumulation, Figure 1 Schematic illustrating the main production (+ve) and erosional (−ve) processes that determine a reefs carbonate budget.

significant merit but provides a different suite of data to census-based studies and does not enable the relative importance of different producer/eroder groups to be quantified.

Variations in carbonate production at the reef system scale

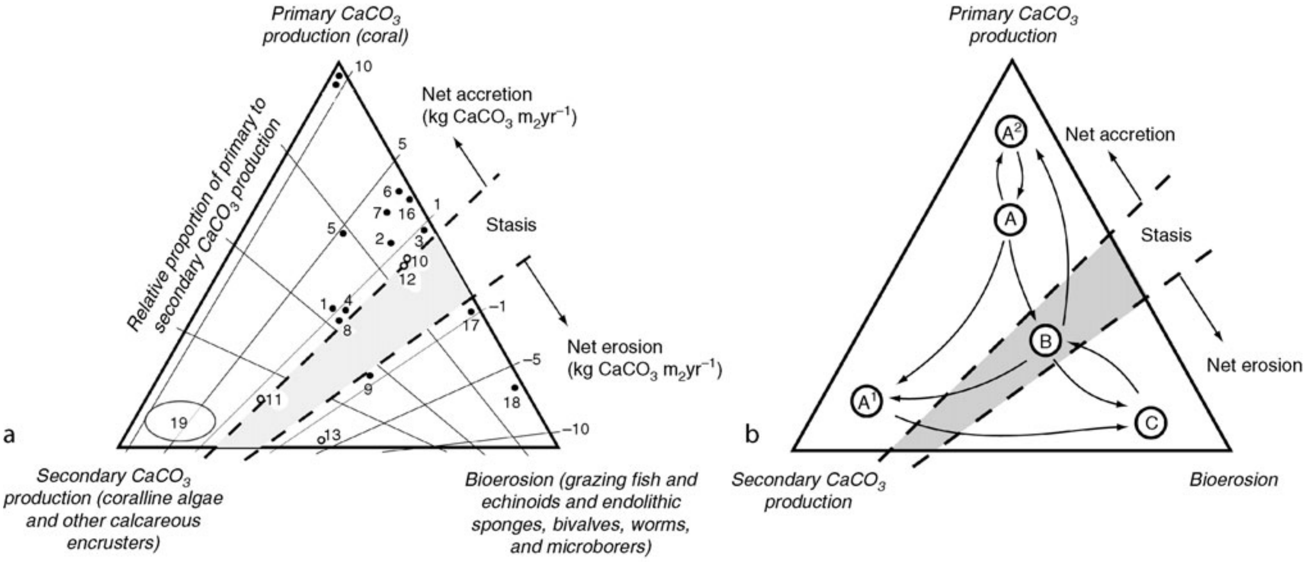
One important aspect of considering reef carbonate production from a carbonate budget perspective is the ability to quantify inter-reef variations in styles of reef framework accumulation. Kleypas et al., (2001), for example, highlighted a range of conceptual reef states that directly relate to variations in relative rates of carbonate production, sediment import and export and framework erosion. These different states demonstrate how shifts in the relative importance of individual processes, associated with different types of reef-building environments or environmental conditions, can result in fundamentally different reef budgetary states and reef framework structures. Production-dominated reefs, for example, exhibit rates of *in situ* biological $CaCO_3$ production far in excess of rates of carbonate degradation and thus the budget is positive. This state is consistent with the rapid vertical growth trajectories exhibited by “keep-up” or “catch-up” reefs during the Holocene sea-level rise. In contrast, import-dominated reefs contain a high proportion of sedimentary material that is often terrigenous in origin. These reefs also have positive budgets, and good examples include the reefs described from the inner-shelf areas of the Great Barrier Reef in Australia (Smithers and Larcombe, 2003), Thailand (Tudhope and Scoffin, 1994) and Mozambique (Perry, 2005). Bioerosion-dominated reefs exhibit negative budgets with primary and secondary carbonate production being exceeded by biological substrate degradation. Examples include areas of high carbonate turnover, such as the non-framebuilding coral communities described from Oman (Benzoni et al., 2003) and the Red Sea (Riegl and Piller, 2000). Similar erosion-dominated states may also arise where non-calcifying groups become dominant and rates of carbonate production are reduced. A good example of this has been described from the reefs around Uva Island, offshore Panama (Eakin, 2001).

Carbonate budgets and long-term rates of reef framework accumulation

The conceptual budgetary states discussed above provide a framework for understanding the influence of carbonate production and erosion processes on reef accretion potential and framework fabric development at the system scale. In reality, however, framework types and their production rates are likely to vary markedly within different reef sub-environments (reef crest, shallow reef front, reef slope, etc.) depending upon the composition and abundance of coral species, species growth rates and, variations in the types and rates at which different productional and erosional processes operate. Perry (1999) illustrated spatial variations in the relative importance of these various processes and the resultant framework fabrics across a fringing reef system in north Jamaica, and these intra-reefal variations are also evident in budget assessments conducted in different areas of individual reef systems (Eakin, 1996). Over longer (millennial) timescales, these variations aggregate to determine net framework accumulation rates that are evident in many reef core records. Data available from many reefs on Australia’s Great Barrier Reef demonstrate a relatively consistent relationship between facies type and net long-term accretion rates; highest rates (> 8 m ka^{-1}) occurring in branched coral facies, intermediate rates (typically < 5 m ka^{-1}) occurring in head coral facies, and the slowest rates (< 2 m ka^{-1}) occurring within algal crust facies (Hopley et al., 2007). These datasets also demonstrate marked changes in framework accretion rates during different phases of reef growth, with slow net accretion immediately following initiation, highest rates occurring as reefs accreted under rapidly rising sea levels, and slow or suppressed rates as reefs reach sea level. These variations reflect the carbonate production states and processes associated with different phases of reef development and can thus be viewed as an interplay between community states (and thus net carbonate production rates) and sea-level position. It follows from this that different sea-level histories in different regions should be reflected in different accretion rate histories. For example, because Caribbean reefs have only recently reached present sea level (e.g., Toscano and Macintyre, 2003), the Late Holocene period has been characterised by vertical framework accretion and positive carbonate budgets. In contrast, sea levels in the Western Indo-Pacific region were attained ~ 6,000 years ago (with some reefs also then subjected to somewhat higher than present levels and subsequent sea-level fall e.g., Smithers et al., 2006). Thus in the Indo-Pacific, the Late Holocene period has been associated with dramatically reduced rates of carbonate production and vertical accretion (Hopley et al., 2007).

Using carbonate budgets to monitor changes in reef "health"

As outlined above, the balance between processes producing $CaCO_3$ and those removing it or converting it to sediment exerts an important influence on net rates of reef carbonate production and accumulation at a range of scales in time and space. Transitions in the rates at which any of the individual, or combined processes (either constructive or destructive) operate consequently have important implications for reef structures and reef-associated sedimentary landforms because they may shift the balance of the carbonate budget. Such changes may be driven either by direct anthropogenic activities (see Done, 1999; Hallock, 2001), or by climate-change induced shifts in sea level, temperature or seawater chemistry. All have the potential to modify the ecological functioning of reefs - changes that are



1. Discovery Bay, Jamaica (Land 1979)
2. Rio Bueno, N. Jamaica (Mallela & Perry 2007)
3. Cane Bay, St. Croix (Hubbard et al. 1990)
4. Kailua Bay, Hawaii (Harney & Fletcher 2003)
5. Bellairs Reef, Barbados (Scoffin et al. 1980)
6. Phuket, Thailand (Scoffin 1997)
7. LaSaline Reef, Reunion (Conand et al. 1997)
8. Uva Island, Panama (Eakin 1996) - Pre 1982/83 El Nino
9. Uva Island, Panama (Eakin 1996) - Post 1982/83 El Nino
10. Back-Reef-Uva Island, Panama (Eakin 1996) - Post 1982/83 El Nino
11. Reef-Flat: Uva Island, Panama (Eakin 1996) - Post 1982/83 El Nino
12. Fore-Reef: Uva Island, Panama (Eakin 1996) - Post 1982/83 El Nino
13. Reef-Base: Uva Island, Panama (Eakin 1996) - Post 1982/83 El Nino
14. Gosong Cemara, Java (Edinger et al. 2000)
15. Palau Kecil, Java (Edinger et al. 2000)
16. Lagun Marican, Java (Edinger et al. 2000)
17. Bondo, Java (Edinger et al. 2000)
18. Palau Panjang, Java (Edinger et al. 2000)
19. Algal ridges

Carbonate Budgets and Reef Framework Accumulation, Figure 2 (**a**) Ternary diagram showing different carbonate production states determined by variations in the relative importance of primary (coral) and secondary (calcareous encruster) carbonate production and carbonate breakdown to sediment/dissolution by bioerosion. Budget state points occupied by different reefs at the reef-wide scale (*closed circles*) and the reef sub-environment scale (*open circles*) where appropriate carbonate budget data exists are shown. (**b**) Conceptual model showing hypothetical transitions and potential pathways in reef carbonate production states driven by ecological or environmental change. Points A and A^1 are analogous to "production-dominated" reef states with production dominated by corals and calcareous encrusters, respectively. Point C is analogous to a "bioerosion-dominated" state. Subtle transitions in production status (e.g., A-A^2 and vice versa) may occur due to intermittent disturbance events where the relative importance of carbonate producers and/or the ratio of production to bioerosion changes, but the system is still one of positive net production. In some cases, reefs may shift from states of net accretion to net erosion (pathway A-B-C). Cessation of disturbance or an adaptation of the coral community (e.g., recruitment of, or replacement by, new, better adapted species) may allow transitions back to conditions of high carbonate production, with either similar (pathway C-B-A) or modified net production rates (C-B-A^2). Adapted from Perry et al. (2008).

consistent with the "phase shift" concept (Done, 1992) – and thus to alter the carbonate depositional system. Such changes clearly demonstrate the potential for reef budget states to shift from positive (accretionary) to negative (erosional), a concept illustrated in recent studies of both anthropogenically impacted reefs in Indonesia (Edinger et al., 2000) and those impacted by El Nino-related sea-surface temperature fluctuations in the Eastern Pacific (Eakin 1996; 2001). In both cases, elevated rates of bioerosion have lead to shifts from positive to negative budgetary states, and emphasize the potential value, to reef health assessments, of quantifying budgetary components on coral reefs.

These concepts were recently developed by Perry et al. (2008) who proposed a framework production states approach that integrates assessments of the three key carbonate budget process groupings; primary production by coral, secondary production by calcareous encrusters, and bioerosion. The approach allows different states of reef production to be plotted within a ternary space (each process defining one corner of the ternary space; Figure 2a) and delineates areas of net accretion, net erosion, or accretionary stasis. One of the potential advantages of this approach is that it allows the relative importance of different process groups to be considered, thus acknowledging that while corals often dominate carbonate production, in some reef settings it is the calcareous encrusters (especially the coralline algae) that make an equal or greater contribution to reef framework production. Similarly, appropriate consideration can be given to the role played by bioeroders in determining net carbonate production rates. This ternary approach also provides a useful mechanism for tracking temporal variations in the budgetary states of individual reefs, especially where ecological shifts (driven by either intrinsic or extrinsic factors) may modify the relative production rates or the abundances of carbonate producers/eroders (Figure 2b). This approach compliments the coral-macroalgal shifts identified within ecological reef phase shift models by encompassing transitions in carbonate production states resulting from different community states and disturbance regimes.

Summary

A carbonate budget is a quantitative measure of the net rate of carbonate production on a reef (or within a carbonate sedimentary environment). The approach relies on census-based measures of the different producer and eroder groups on a reef – the individual measures of production and erosion being summed to determine net production rates per unit area of reef surface (typically expressed as a measure in kg $CaCO_3$ m^{-2} $year^{-1}$). The use of carbonate budgets, although methodological complex, has considerable conceptual merit for understanding spatial and temporal variations in styles of reef framework development. Budgets also have considerable quantitative merit for determining production states at a given point in time and for tracking temporal shifts in carbonate productivity (e.g., production to erosion-dominated states) such as may result from both intrinsically and extrinsically-driven environmental change.

Bibliography

Benzoni, F., Bianchi, C. N., and Morri, C., 2003. Coral communities of the northwestern Gulf of Aden (Yemen): variation in framework building related to environmental factors and biotic conditions. *Coral Reefs*, **22**, 475–484.

Blanchon, P., Jones, B., and Kalbfleisch, W., 1997. Anatomy of a fringing reef around Grand Cayman: storm rubble not coral framework. *Journal of Sedimentary Research*, **67**, 1–16.

Bosence, D. W. J., 1984. Construction and preservation of two modern coralline algal reefs, St. Croix, Caribbean. *Palaeontology*, **27**, 549–574.

Bruggemann, J. H., van Kessel, A. M., van Rooij, J. M., and Breeman, A. M., 1996. Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: Implications of fish size, feeding mode and habitat use. *Marine Ecology Progress Series*, **134**, 59–71.

Camoin, G., Cabioch, G., Eisenhauer, A., Braga, J. C., Hamelin, B., and Lericolais, G., 2006. Environmental significance of microbialites in reef environments during the last deglaciation. *Sedimentary Geology*, **185**, 277–295.

Done, T. J., 1992. Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia*, **247**, 121–132.

Done, T. J., 1999. Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. *American Zoologist*, **39**, 66–79.

Eakin, C., 1996. Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982–1983 El Nino at Uva Island in the eastern Pacific. *Coral Reefs*, **15**, 109–119.

Eakin, C. M., 2001. A tale of two ENSO events: carbonate budgets and the influence of two warming disturbances and intervening variability, Uva Island, Panama. *Bulletin of Marine Sciences*, **69**, 171–186.

Edinger, E. N., Limmon, G. V., Jompa, J., Widjatmoko, W., Heikoop, J. M., and Risk, M. J., 2000. Normal coral growth rates on dying reefs: are coral growth rates good indicators of reef health? *Marine Pollution Bulletin*, **40**, 606–617.

Hallock, P., 2001. Coral reefs, carbonate sediments, nutrients, and global change. In: Stanley, G. D. (ed.), *The history and sedimentology of ancient reef systems*. Kluwer, Topics in Geobiology, Vol. 17, pp. 387–427.

Harney, J. N., and Fletcher, C. H. III, 2003. A budget of carbonate framework and sediment production, Kailua Bay, Oahu, Hawaii. *Journal of Sedimentary Research*, **73**, 856–868.

Hart, D. E., and Kench, P. S., 2007. Carbonate production of an emergent reef platform, Warraber Island, Torres Strait, Australia. *Coral Reefs*, **26**, 53–68.

Hopley, D., Smithers, S. G., and Parnell, K. E., 2007. The geomorphology of the great barrier reef: development, diversity and change. Cambridge: Cambridge University Press, xiii+532.

Hubbard, D., Miller, A., and Scaturo, D., 1990. Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, US Virgin Island): applications to the nature of reef systems in the fossil record. *Journal of Sedimentary Petrology*, **60**, 335–360.

Hubbard, D. K., 1997. Reefs as dynamic systems. In: Birkeland, C. (ed.), *Life and death of coral reefs*. New York: Chapman & Hall, pp. 43–67.

Kleypas, J., Buddemeier, R. W., and Gattuso, J. P., 2001. The future of coral reefs in an age of global change. *International Journal of Earth Sciences*, **90**, 426–437.

Nelson, J. E., and Ginsburg, R. N., 1986. Calcium carbonate production by epibionts on *Thalassia* in Florida Bay. *Journal of Sedimentary Petrology*, **56**, 622–628.

Perry, C. T., 2005. Structure and development of detrital reef deposits in turbid nearshore environments, Inhaca Island, Mozambique. *Marine Geology*, **214**, 143–161.

Perry, C. T., 1999. Reef framework preservation in four contrasting modern reef environments, Discovery Bay, Jamaica. *Journal of Coastal Research*, **15**, 796–812.

Perry, C. T., and Beavington-Penney, S. J., 2005. Epiphytic calcium carbonate production and facies development within subtropical seagrass beds, Inhaca Island, Mozambique. *Sedimentary Geology*, **174**, 161–176.

Perry, C. T., and Hepburn, L. J., 2008. Syn-depositional alteration of coral reef framework through bioerosion, encrustation and cementation: taphonomic signatures of reef accretion and reef depositional events. *Earth Science Reviews*, **86**, 106–144.

Perry, C. T., Spencer, T., and Kench, P., 2008. Carbonate budgets and reef production states: a geomorphic perspective on the ecological phase-shift concept. *Coral Reefs*, **27**, 853–866.

Riegl, B., and Piller, W., 2000. Reefs and coral carpets in the northern Red Sea as models for organism-environment feedback in coral communities and its reflection in growth fabrics. In: Insalaco, E., Skelton, P., and Palmer, T.,(eds.), *Carbonate Platform Systems: components and interactions*. London: Geological Society, Special Publications, Vol. 178, pp. 71–88.

Scoffin, T., 1992. Taphonomy of coral reefs: a review. *Coral Reefs*, **11**, 57–77.

Scoffin, T. P., Stearn, C. W., Boucher, D., Frydl, P., Hawkins, C. M., Hunter, I. G., and MacGeachy, J. K., 1980. Calcium carbonate budget of a fringing reef on the west coast of Barbados. I. erosion, sediments and internal structure. *Bulletin of Marine Science*, **30**, 475–508.

Smith, S. V., and Kinsey, D. W., 1976. Calcium carbonate production, coral reef growth, and sea level change. *Science*, **194**, 937–939.

Smithers, S. G., and Larcombe, P., 2003. Late Holocene initiation and growth of a nearshore turbid-zone coral reef: Paluma Shoals, central Great Barrier Reef. *Australia. Coral Reefs*, **22**, 499–505.

Smithers, S. G., Hopley, D., and Parnell, K. E., 2006. Fringing and nearshore coral reefs of the Great Barrier Reef: episodic Holocene development and future prospects. *Journal of Coastal Research*, **22**, 175–187.

Toscano, M. A., and Macintyre, I. G., 2003. Corrected western Atlantic sea-level curve for the last 11,000 years based on calibrated ^{14}C dates from *Acropora palmata* and mangrove intertidal peat. *Coral Reefs*, **22**, 257–270.

Tudhope, A., and Scoffin, T. P., 1994. Growth and structure of fringing reefs in a muddy environment, South Thailand. *Journal of Sedimentary Research, A*, **64**, 752–764.

Vecsei, A., 2004. A new estimate of global reefal carbonate production including the fore-reefs. *Global and Planetary Change*, **43**, 1–18.

Cross-references

Bioerosion
Corals: Biology, Skeletal Deposition, and Reef-Building
Density and Porosity: Influence on Reef Accretion Rates
Floatstone
Framestone
Packstone
Rudstone
Sea Level Change and Its Effect on Reef Growth
Submarine Lithification
Taphonomy

CARBONIFEROUS REEFS

Markus Aretz
Université de Toulouse (UPS), Toulouse, France

Definition

All reefs, which formed during the Carboniferous period (ca. 359–299 Ma). The Carboniferous is the longest period of the Phanerozoic Eon. It was named after the abundance of Coal-bearing strata in its upper half.

Although the geological perspective has to be considered, the Carboniferous period shows considerable overlap to modern times. Reefs formed during times of profound global changes – greenhouse to icehouse climates, dramatically changed continent configuration during the process of supercontinent formation, and important and frequent sea level changes to name only a few of them. Timing and duration of reef development and their dimensions varied considerably on a regional scale, but on the global scale reefs developed throughout the entire Carboniferous period (Aretz and Vachard, 2007). Overall reef abundance was more common than what has been often postulated, but lower compared to peak times of reef development in the Middle Palaeozoic (Webb, 2002).

Characteristic is the lack of a stable reef community. A broad range of bioconstructors – microbial communities, calcareous and siliceous sponges, rugose and tabulate corals, bryozoans, brachiopods, and calcareous algae – contributed in varying abundances to different stage of reef development (as initiation, formation, stabilization, and domination). However, microbial communities were very abundant and crucial for many Carboniferous reefs.

Reefs occurred along a bathymetric gradient from the intertidal/subtidal interface to several hundred meters of depth. Very different reef types developed from small undifferentiated patch-reefs to atoll reefs on oceanic sea mounts to reef tracts along shelf margins. The scarcity of the latter had an important influence on the geometry of many Carboniferous shelf systems.

Individual reef development reflects the local and/or regional tectono-sedimentary environments, but climate seems to be the most important global driving force. Major re-organisations in the reef environments occurred at the base of the Carboniferous, around the Mid-Carboniferous boundary, and at the base of the latest Carboniferous.

The oldest reefs are shallow water microbial reefs near the base of the Carboniferous in Eastern Australia. Mud-dominated mounds and buildups often labeled as Waulsortian Mounds developed in deeper ramp settings of many tropical and subtropical shelf systems of Early Carboniferous age. Often they rose into the photic zone, which resulted in a marked biodiversity increase in the vertical profile of the individual mound. Contemporaneous reefs in shallow waters formed by the above mentioned organisms in various abundances were wide spread in Gondwana, Laurussia, Armorica, Kazakhstan, China, and in the Panthalassa Ocean.

After climate cooling in the Mid-Carboniferous, corals did not contribute to reef formation any more. In the tropics and subtropics various calcareous algae (tubular algae, phylloid green algae and red algae) and chaetetid sponges contributed to the formation of three basic types. In somewhat more temperate waters pelmatozoans, bryozoans, brachiopods, and microbial communities were the main contributors to the formation of reefal/reef like structures (Wahlman, 2002).

In the latest Carboniferous period, following a short global warming, reefs of the tropical Tethyan realm consisted of calcareous algae and calcareous sponges, whereas in subtropical to temperate waters *Palaeoaplysina* mounds occurred in shallow settings and bryozoan-*Tubiphytes* reefs in deeper settings (Wahlman, 2002).

Bibliography

Aretz, M., and Vachard, D., 2007. Carboniferous: Introduction. In Vennin, E., Aretz, M., Boulvain, F., and Munnecke, A. (eds.), *Facies from Palaeozoic Reefs and Bioaccumulations*. Mémoires du Musée d´histoire Naturelle de Paris, 198, pp. 227–230.

Wahlman, G. P., 2002. Upper Carboniferous – Lower Permian (Bashkirian–Kungarian) mounds and reefs. In Kiessling, W., Flügel, E., and Golonka, J. (eds.), *Phanerozoic Reef Patterns*. SEPM. Special Publications, 72, pp. 271–338.

Webb, G. E., 2002. Latest Devonian and Early Carboniferous reefs: depressed reef building after the middle Paleozoic collapse. In Kiessling, W., Flügel, E., and Golonka, J. (eds.), *Phanerozoic Reef Patterns*. SEPM. Special Publications, 72, pp. 239–269.

Cross-references

Algae-Macro
Atolls
Barrier Reef (Ribbon Reef)
Binding Organisms
Climate Change and Coral Reefs
Corals: Biology, Skeletal Deposition, and Reef-Building
Devonian Reef Complexes of the Canning Basin
Sea Level Change and Its Effect on Reef Growth
Sponges

CAY FORMATION

Peter Flood
University of New England, NSW, Armidale, Australia

Definition

A cay (sometimes spelled key or quay) is a small, low elevation island composed of coral reef detritus of rubble or shingle and/or sand sized materials that have accumulated on the reef top surface.

Formation

Cays are formed when ocean waves and tidal currents transport loose sediment across the reef top surface to a depositional node where concentration occurs and the sedimentary pile rises above the high tide (Hopley, 1981; Gourlay, 1988). Over time soil and vegetation may develop on the cay surface. This process is assisted by the presence of extensive sea bird populations and their associated guano deposition, which acts as a fertilizer for the developing vegetation.

There is a basic division of cays into windward shingle cays and leeward sand cays or mixed shingle/sand cays depending on the surface area and size of the associated reef top.

Stoddart and Steers (1977) seminal study of cays and the subsequent study by Stoddart et al. (1978), showed that cays on reefs of the Great Barrier Reef vary from small ephemeral sand patches emerging only at low tide to variable sizes of vegetated sand and shingle or mixed sand/shingle cays to the complex low wooded islands which are characterized by variable development of mangrove vegetation (McLean and Stoddart, 1978; Stoddart, 1965, 1969). The classification scheme of Stoddart and Steers (1977) is applicable throughout the various reef provinces (Indian Ocean, Maldives, Indonesia, Central Pacific Ocean, Fiji, Samoa, Polynesia, atolls; Atlantic Ocean, Caribbean, etc). One variant of the mixed sand/shingle cay type are called motus. This variety, unlike the sand-shingle cays that are molded by wave refraction, lie on unbroken reefs on atoll rims. They are formed by the deposition of shingle on the windward edge as storm boulder ridges. Such ridges serve as an anchor to further leeward deposition of sand-sized sediment (Nunn, 1994). Dickinson (2001; 2009) suggests that many of the Pacific Ocean motus are in fact “pinned” to the elevated abandoned reef flat which developed during higher-than-present sea levels during the mid-Holocene period.

Hopley et al. (2007, p.364, Fig. 10.16) have provided a summary of the attributes and frequency of reef types and cays on the Great Barrier Reef Province.

The cays are subjected to a range of physical, biological, and chemical variables that influence the morphological development (Flood, 1977, 1980, 1981, 1986; Umbgrove, 1947; Hopley, 1982, 1997; Chivas et al., 1986). Once the cay extends above the limit of high tide the wind action commences and the dry sands of the upper beach are transported inland to form dunes. This wind action produces an asymmetrical cross profile of the cay with a higher elevation on the windward side. Dunes of up to three meters elevation are not uncommon. Once colonized by pioneer vegetation and the presence of nesting colonies of sea birds, the humic and fertility content of the soil increases and larger vegetation such as shrubs and trees commence to grow. In addition, once the cay reaches a critical size, a fresh and/or brackish lens may become established towards the center of the cay.

The groundwater flow is usually radial from the core of the cay outward toward the beach (Vacher and Quinn, 1997). In the intertidal beach zone, interstitial seawater evaporates and calcium carbonate in the form of aragonite is deposited in the interparticulate pores of the beach sediments to form beachrock (Stoddart and Cann, 1965). Also, where large colonies of sea birds are resident over long periods their guano can cement and/or replace the cay sediments to produce phosphate rock or cay rock.

Serial changes in cay vegetation have been reported (Flood and Heatwole, 1986) as well as changes in their shape related to climatic fluctuations (Flood, 1986) and the impact of tropical cyclones (Flood and Jell, 1977; Scoffin, 1993; Verstappen, 1954; Woodroffe, 1993). There is considerable anxiety being expressed by those Indian Ocean and Pacific Island nation people who live on the low lying coral cays. They are concerned about the predicted climate changes and sea level rise (Woodroffe et al., 1990). Any sea level change will impact on the sediment source and the supply of sediment to and from the cay (Kench et al., 2005). Predicting the present and future stability is a challenging task for geomorphologists and engineers (Dickinson, 2001; 2009). Examples have been reported where the residual beach rock outcrops indicate the earlier presence of cays which were destroyed during hurricane/cyclone events.

The dates of Holocene sea level maximum for selected oceanic islands have been summarized by Nunn (1994) and Dickinson (2001) who found that in the millennia since 5,000 BP, no single scenario prevails and the observed patterns of sea level behavior vary depending on just where on the Earth the observations are made. This variability is related to the different properties and behaviors of the lithosphere.

Summary

A cay is a supratidal feature developed on the reef top. It represents a stage in the evolutionary accumulation of reef derived detritus commencing as a subtidal back, developing further as an intertidal bank, and then a supratidal island (unvegetated) to vegetated island (several steps in the complexity of vegetation).

A cay is the product of the interaction of the geological processes of sediment production, erosion, and transportation and the hydrodynamic process related to tidal processes and wave action (and cyclonic/typhoon/hurricane activities). Usually on oval or elongate platform reefs, the nodal point where the current/wave action energy decreases and sediment accumulates is situated on the reef top and not beyond the reef top in the area of the leeward sediment wedge.

The action of oceanic birds is of paramount importance in transporting seeds to colonize the surface of the cay; the dead vegetation adds to the humic deposits thereby enhancing the possibility of vegetation further colonizing the surface of the cay. Guano material also enhances the fertility of the soil profile, and around the beaches of the cays beach rock, may form in the subsurface. On the larger cays, a freshwater/brackish water lens can develop and enhance the vegetative growth from shrubs to extensive forests of *Casuarina* and *Pisonia* trees.

Bibliography

Chivas, A., Chappel, J., Polack, H., Pillans, B., and Flood, P. G., 1986. Radiocarbon evidence for the timing and rate of island development, beach-rock formation and phosphatization at Lady Elliott Island, Queensland, Australia. *Marine Geology*, **69**, 273–287.

Dickinson, W. R., 2001. Paleoshoreline record of relative Holocene sea levels on Pacific Islands. *Earth-Science Reviews*, **55**, 191–234.

Dickinson, W. R., 2009. Pacific atoll living: how long already and until when? *Geological Society of America Today*, **19**(3), 4–10.

Flood, P. G., 1977. Coral cays of the Capricorn and Bunker groups, Great Barrier Reef Province, Australia. *Atoll Research Bulletin*, **195**, 1–24.

Flood, P. G., 1980. Cyclone “Simon” changes cays. *Reflections Newsletter of the Great Barrier Reef Marine Park Authority*, **6**, 4.

Flood, P. G., 1981. Coral cays and cyclones. *Beach Conservation*, **42**, 6.

Flood, P. G., 1986. Sensitivity of coral cays to climate variations, Southern Great Barrier Reef, Australia. *Coral Reefs*, **5**, 13–18.

Flood, P. G., 1988. Shoreline changes on coral cays, Capricorn Section, Great Barrier Reef Marine Park, Australia. *Proceedings Sixth International Coral Reef Symposium*, Australia, Vol. 2, pp. 219–224.

Flood, P. G., and Heatwole, H., 1986. Coral cay instability and species turnover of plants at Swain Reefs, Southern Great Barrier Reef, Australia. *Journal Coastal Research*, **2**, 479–496.

Flood, P. G., and Jell, J. S., 1977. The effect of cyclone “David” (January, 1976) on the sediment distribution patterns on Heron Reef, Great Barrier Reef, Australia. *Proceedings Third International Coral Reef Symposium*, Miami, Vol. 2, pp. 119–125.

Gourlay, M. R., 1988. Coral cays: products of wave action and geological processes in a biogenic environment. *Proceedings Sixth International Coral Reef Symposium*, Townsville, Vol. 2, pp. 491–496.

Hopley, D., 1981. Sediment movement around a coral cay, Great Barrier Reef, Australia. *Pacific Geology*, **15**, 17–36.

Hopley, D., 1982. *The Geomorphology of the Great Barrier Reef: Quaternary Development of Coral Reefs*. New York: Wiley.

Hopley, D., 1997. Geology of reef islands of the Great Barrier Reef, Australia. *Developments in Sedimentology*, **54**, 835–866.

Hopley, D., Smithers, S. G., and Parnell, K., 2007. *The Geomorphology of the Great Barrier Reef Development Diversity and Change*. Cambridge: Cambridge University Press.

Kench, P. S., McLean, R. F., and Nichol, S. L., 2005. A new model of reef island evolution: Maldives, Indian Ocean. *Geology*, **33**, 145–148.

McLean, R. F., and Stoddart, D. R., 1978. Reef island sediments of the northern Great Barrier Reef. *Philosophical Transactions Royal Society of London, A*, **291**, 101–117.

Nunn, P. D., 1994. *Oceanic Islands*. Oxford: Blackwell.

Scoffin, T. P., 1993. The geological effects of hurricanes on coral reefs and the interpretation of storm deposits. *Coral Reefs*, **12**, 203–221.

Stoddart, D. R., 1965. British Honduras cays and the low wooded island problem. *Transactions of the Institute of British Geographers*, **36**, 131–147.

Stoddart, D. R., 1969. Post-hurricane changes on the British Honduras reefs and cays: re-survey of 1965. *Atoll Research Bulletin*, **131**, 1–25.

Stoddart, D. R., and Cann, J. R., 1965. Nature and origin of beach rock. *Journal of Sedimentary Research*, **35**(1), 243–247.

Stoddart, D. R., McLean, R. F., and Hopley, D., 1978. Geomorphology of reef islands, northern Great Barrier Reef. *Philosophical Transactions Royal Society of London, Series B*, **284**, 39–61.
Stoddart, D. R., and Steers, J. A., 1977. The nature and origin of coral reef islands. In Jones, O. A., and Endean, R. (eds.), *Biology and Geology of Coral Reefs*. New York, Academic Press, Vol. 4 (2), pp. 59–105.
Stoddart, D. R., Fosberg, F. R., and Spellman, D. L., 1982. Cays of the Belize Barrier Reef and Lagoon. *Atoll Research Bulletin*, 256.
Umbgrove, J. H. F., 1947. Coral Reefs of the East Indies. *Geological Society of America Bulletin*, **58**, 729–777.
Vacher, H. L. and Quinn, T. M. (eds.), 1997. *Geology and Hydrology of Carbonate Islands. Developments in Sedimentology.* Elselvier, Amsterdam, Vol. 54
Verstappen, H. Th., 1954. The influence of climatic change on the formation of coral islands. *American Journal of Science*, **252**, 428–435.
Woodroffe, C. D., 1993. Morphology and evolution of reef islands in the Maldives. *Proceedings 7th International Coral Reef Symposium*, Guam, **7**, 1217–1226.
Woodroffe, C. D., 2002. Reef island sedimentation on Indo-Pacific atolls and platform reefs. *Proceedings 9th International Coral Reef Symposium*, Bali, **2**, 1187–1192.
Woodroffe, C. D., McLean, R., Polach, H., and Wallensky, E., 1990. Sea level and coral atolls: late Holocene emergence in the Indian Ocean. *Geology*, **18**, 62–66.

Cross-references

Atoll Islands (Motus)
Beach Rock
Coral Cay Classification, and Evolution
Coral Cays Geohydrology
Coral Cays, Vegetational Succession
Low Wooded Islands
Unvegetated Cays

CHAMISSO, ADELBERT VON (1781–1838)

James Bowen
Southern Cross University, Lismore, NSW, Australia

By the end of the eighteenth century, investigation into the major problems of reef formation and the nature of coral "insects" had advanced considerably: the definitive investigations by Peysonnell resulted in general agreement that reefs were created in some way by minuscule polyps. Aboard the cruise of the *Adventure* to Tahiti by Cook was the German naturalist Johann Reinhold Forster (1729–1798) who distinguished a fundamental feature of atolls, namely that the formation of a circular structure enables the coral colonies to resist the rage and power of the ocean.

In the same period, once they gained control of the North Pacific with their ice-free port of Vladivostock, the Russians also became active. Of early significance were the findings of Adelbert von Chamisso, born in France and later settled in Berlin, the naturalist who sailed on the first voyage of the Russian ship *Rurik* in 1815–1818 under the command of Otto von Kotzebue around the Pacific to the Hawaiian, Marshall and Mariana groups. In an account entitled "On the Coral Islands" in an appendix to Kotzebue's narrative of the voyage, Chamisso made two important observations.

Firstly, he pointed out that corals thrive best in windward, turbulent reef fronts, stating that the larger species of corals, which form blocks measuring several fathoms in thickness, seem to prefer the more violent surf on the external edge of the reef a point amplified further on, that the windward side of the reef, exposed to the unremitting fury of the ocean, should first rise above the element that created it. His second observation attempted to explain why atolls appear in wide expanses of turbulent oceans, almost out of nowhere: because, he reasoned out, that the corals have founded their buildings on shoals in the sea; or to speak more correctly, on the tops of mountains lying under the water, and that, even further, variation in magnitude and distribution of atoll clusters probably depends on the size of the sub-marine mountain tops, on which their basis is founded.

Once back in Russia, Kotzebue published his findings in German in 1821 in three volumes under the general title *Reise um die Welt* (Voyage around the World), Chamisso writing much of the third volume, which became available to English geologists in a translation the same year.

Bibliography

Bowen, J., 2002. *The Great Barrier Reef: History, Science, Heritage.* Cambridge: Cambridge University Press.
Chamisso, A. von, 1821. On Coral Islands. In Otto von Kotzebue, *Voyage of Discovery into the South Seas and Bering's Straits.* Trans. H. E. Lloyd, London: Longmans, Hurst, Rees, Orme and Brown.
Chamisso, A. von, c.1986. *A Voyage Around the World with the Romanzov Exploring Expedition in the Years 1815–1818 in the Brig rurik, Captain Otto von Kotzebue*. Translated and edited by Henry Kratz. Honolulu: University of Hawaii Press.

Cross-references

Cook, James (1728–1779)
Peysonnell, Jean-Andre (1694–1759)

CLASSIFICATION OF CARBONATES

Christopher G. St. C. Kendall[1], Peter Flood[2]
[1]University of South Carolina, Columbia, USA
[2]University of New England, Armidale, Australia

Definition and introduction

Rocks are classified in order to communicate information about them. Limestone classifications are often intended to convey information about the composition and so, the depositional setting. All classifications of limestones tend to be rather arbitrary and they frequently overlap or do not fit one's particular needs. Since binocular microscopes or hand lenses are the tools that are commonly available to the professional or academic geologist, a practical classification should be based on descriptions that use these tools. When these instruments are used, it is usually possible to identify the individual grains forming the rock. Thus, most classifications require that the most significant sedimentary particle in the rock be described. For instance, if a rock is composed of ooids, it is termed an oolitic limestone. If the limestone also contains a minor element such as skeletal fragments, then it is called a skeletal-oolitic limestone.

Two of the most widely used classifications are those of Folk (1959, 1962) and Dunham (1962). Both classifications subdivide limestones primarily on the basis of their matrix content and their major component grains.

Most limestones are classified by Folk (1959, 1962) as allochemical rocks if they contain over 10% allochems (transported carbonate grains). Based on the percentage of interstitial material, the rocks may be further subdivided into two groups: sparry allochemical limestones (containing a sparry calcite cement of clear coarsely crystalline mosaic calcite crystals) and microcrystalline allochemical limestone (containing microcrystalline calcite mud, micrite, which is subtranslucent grayish or brownish particles less than about 5 μm in size) (Figure 1). Further subdivision is based on the allochem ratios of Folk (1962) as is illustrated in Scholle and Ulmer-Scholle (2003) (Figure 2).

Thus, Folk's classification (Figures 1 and 2) is most suited for thin section study. Note that he terms rocks with appreciable matrix as micrites while matrix-free rocks that contain sparry calcite cement are termed sparites. Sparites and micrites are further subdivided on the basis of their most common grains.

In contrast, Dunham's classification (Figures 3 and 4) and its modification by Embry and Klovan (1971) and James (1984) update and illustrations deal with depositional texture. For this reason, Dunham's scheme is better suited for rock descriptions that employ a hand lens or binocular microscope. For example, if the grains of a limestone are touching one another and the sediment contains no mud, then the sediment is called a grainstone. If the carbonate is grain supported but contains a small percentage of mud, then it is known as a packstone. If the sediment is mud supported but contains more than 10% grains, then it is known as a wackestone, and if it contains less than 10% grains and is mud supported, it is known as a mudstone.

If one compares the two classifications, a rock rich in carbonate mud is termed a micrite by Folk and a mudstone or wackestone by Dunham. Moreover, a rock containing little matrix is termed a sparite by Folk and a grainstone or packstone by Dunham. The wide range of percentage of mud matrix that a carbonate may have and still be termed a packstone by Dunham sometimes reduces the utility of this classification. Embry has modified the classification of Dunham and Klovan (1971) to include coarse grained carbonates (above figure). In their revised scheme, a wackestone in which the grains are greater than 2 mm in size is termed a floatstone and a coarse grainstone is called a rudstone.

Both terms are extremely useful in the description of limestones. Embry and Klovan modified the boundstone classification of Dunham in order to graphically express the role that organisms performed during accumulation. They introduced terms such as bafflestone, bindstone, and framestone, which are useful in concep, but these can be extremely difficult to apply to ancient limestones where diagenesis and sample size can limit one's ability to determine an organism's function.

Other modifications followed Folk's (1965) recognition that though micrite is more commonly a product of sedimentary accumulation, it can also be cement, and/or a product of diagenesis. To this end, Reid et al. (1990) and Wright (1992) and others are not alone in reemphasizing the need to recognize the role of micrite and other allochems as a product of sedimentary matrix, internal cavity sedimentary fill, diagenesis, and cementation, and that some carbonate grains are the products of later diagenetic modifications. The reader is urged to recognize the multiplicity of origins of carbonates, though their sedimentary origin is commoner.

A short history of limestone classifications

The classification of limestones has been constantly updated as new analytical techniques have been developed and new information has become available. This has resulted in new understandings about the origin and depositional setting of carbonate particles and carbonate sediments.

Limestone classifications underwent a rapid evolution shortly after Wolf (1961) published an excellent summary of the early classification schemes for carbonates. In this, he recognized that many of these classifications unfortunately were inefficient and commonly misleading; in particular, the descriptive terms used to describe carbonates included detrital, clastic, fragmental, granular, fossiliferous, calcarenite, coquina, etc. Each one of these terms conveys one particular aspect of information, but ignored, among other things, the presence or absence of cement or matrix.

Earlier classifications include Twenhoffel's of 1932 which recognized three major limestone groups:

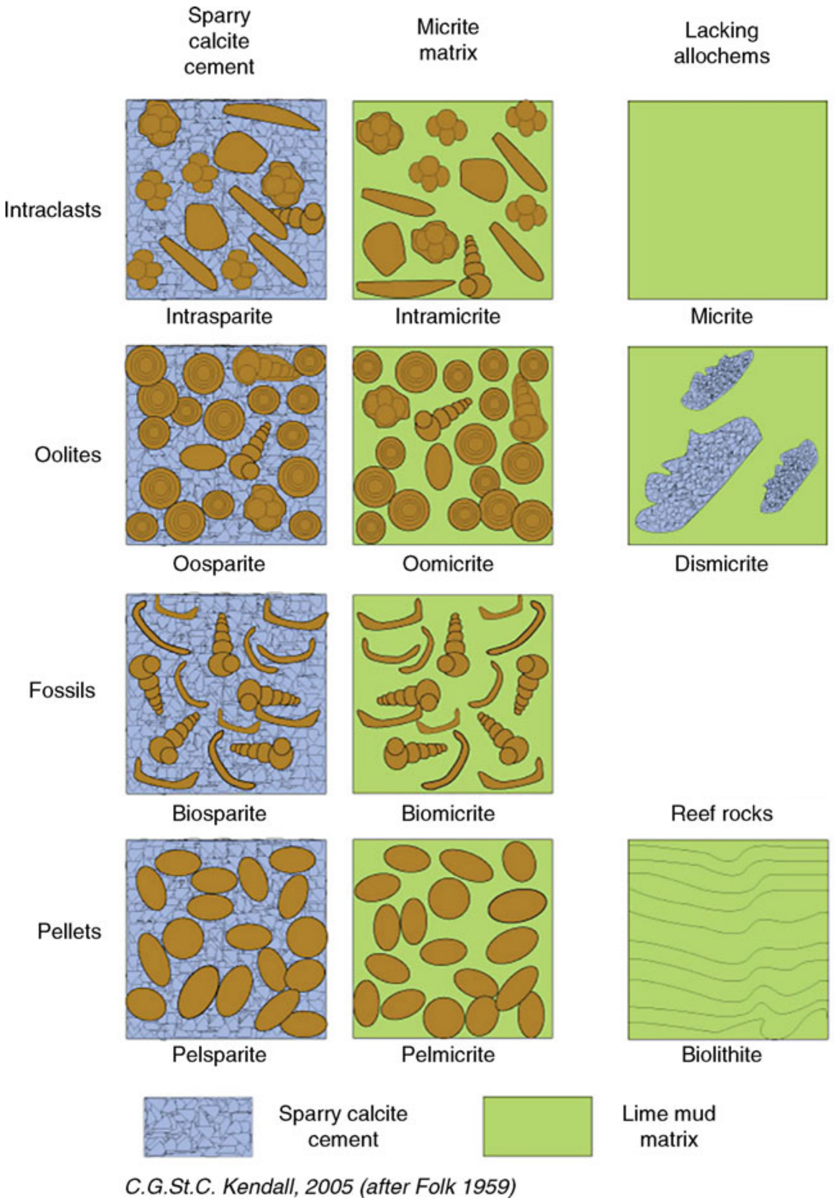
1. Organic origin
2. Chemical origin
3. Mechanical origin

In the 1930s, workers differentiated between the following types of limestones:

1. Hard
2. Mud or soft

In the 1950s, workers recognized:

1. Uncemented
    (a) Calcilutites (mud sized)
    (b) Calcarenites (sand sized)
    (c) Calcirudite (gravel sized)
    (d) Mixture of (a), (b), and (c).
2. Primary hard (chemical or biochemically cemented)
3. Secondary hard (diagenetically modified)

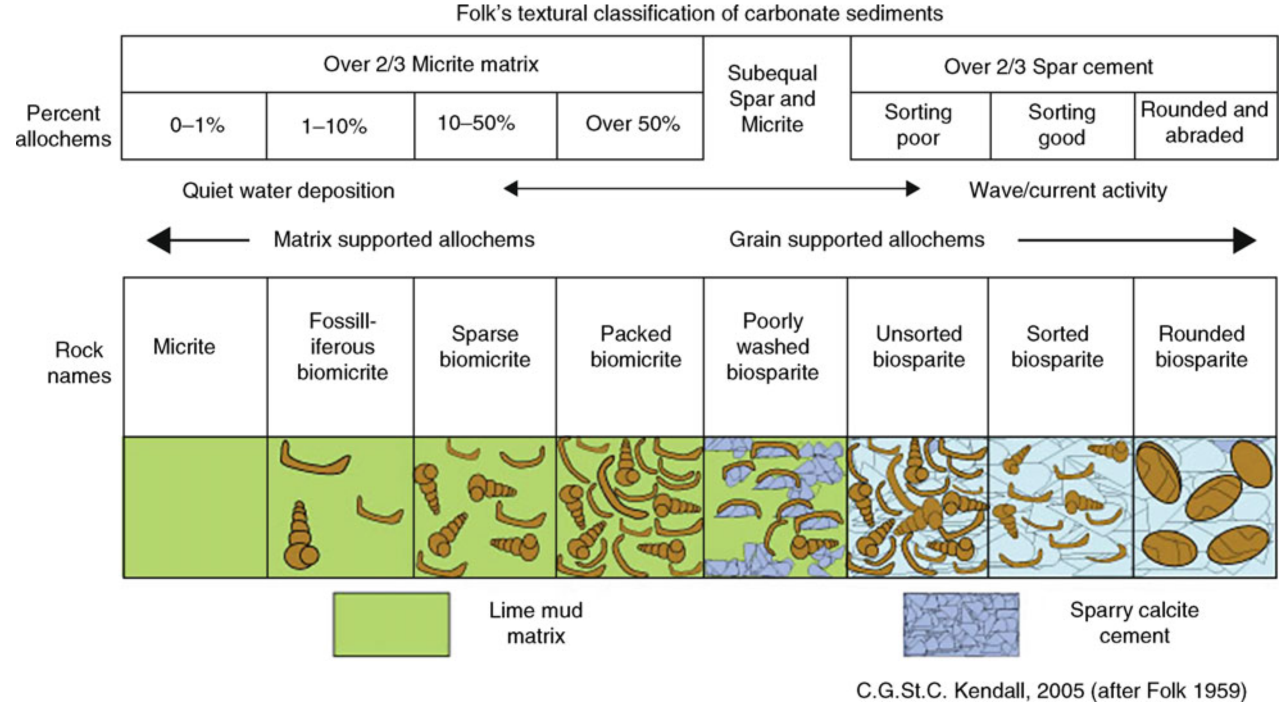


Classification of Carbonates, Figure 1 Folk (1962) limestone classification table identifies the component (or allochemical) particles and whether the matrix is micrite or lime mud or a sparry calcite cement precipitated between the grains. Should intraclasts form >25% of the grains, then the rock is named an intraclastic limestone; if intraclasts are <25% and ooids are >25%, the rock is an oolitic limestone; if intraclasts and ooids are <25% each, then the rock is known as a biogenic, or skeletal, or pelletal limestone, according to the relative percentages of these allochical grains. Limestones with multicomponents are named after these mixtures (e.g., a biopelsparite). A dismicrite is a micrite with spar-filled blebs (generally burrows) and a biolithite is a biologically bound rock.

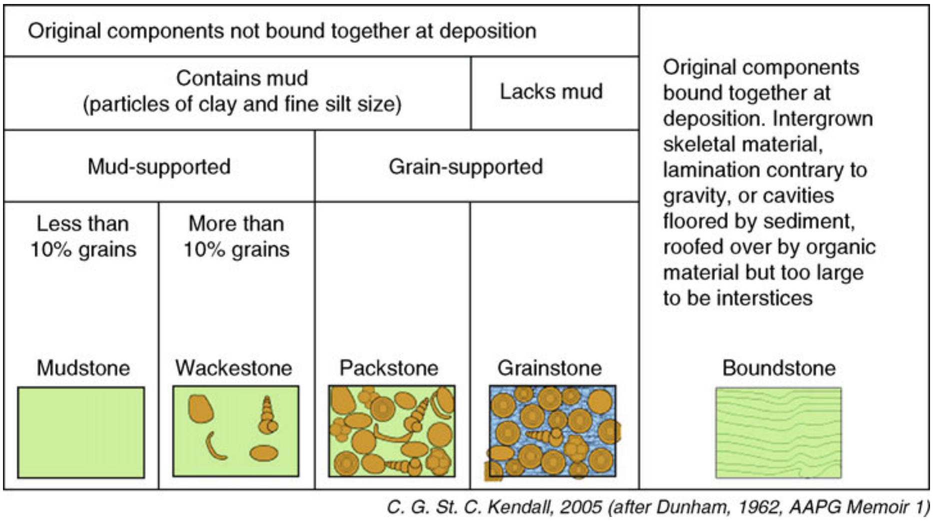
In the late 1950s and early 1960s descriptions were based on size nomenclature, namely, calcilutile, calcarenite, and calcirudite. Others used calculite and calcisiltite for mud and silt sized, respectively. The work of Illing (1954), Folk (1959), Carozzi (1960), Dunham (1962), Embry and Klovan (1972), and James (1984) addressed these shortcomings and the two commonly accepted schemes that evolved from these are used today in industry and academia. As explained above, these are based on the classification schemes of Folk (1962) and Dunham (1962).

Pettijohn (1952) divided limestones into two groups:

1. Autochthonous – formed in situ by biochemical processes
2. Allochthonous – consisting of transported and redeposited material.

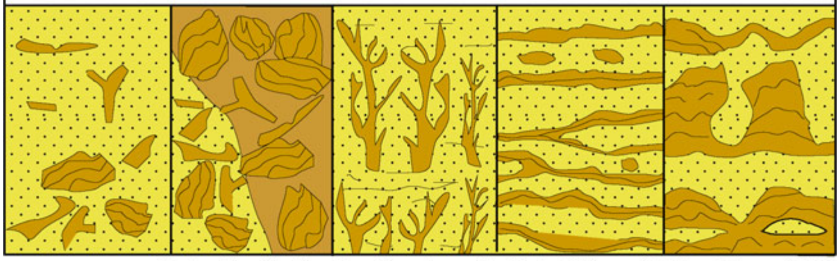


Classification of Carbonates, Figure 2 Folk's (1962) textural spectrum for carbonate sediments records 8 phases of sorting and rounding with the intent of capturing the deposition settings from low energy (*left*) to high energy (*right*). In very low-energy settings, micrites or mud-sized carbonate accumulate; in intermediate-energy settings, micrites with greater concentrations of allochemical particles, winnowed grain, and mud accumulations result; in high-energy settings, sorting and rounding of grains winnow most of the micrite matrix away. Textural inversions are the result of storm events that mix sediments from different settings or introduce short-lived conditions into a normally low-energy setting.



Classification of Carbonates, Figure 3 Dunham's 1962 classification of carbonate rocks is intended to convey information related to their depositional setting. Carbonates that are supported by matrix (mud) or framework (grains) form the basis of this classification. The end members include noncrystalline limestones often characterized by referencing the major component grains.

Allochthonous		Autochthonous		
Original components not bound organically at deposition		Original components bound organically at deposition		
>10% grains >2mm				
Matrix supported	Supported by >2mm component	By organisms that act as baffles	By organisms that encrust and bind	By organisms that build a rigid frame work
Floatstone	Rudstone	Bafflestone	Bindstone	Framestone



Textural classification of reef limestones after Embry & Klovan (1971) and James (1984)

Classification of Carbonates, Figure 4 Embry and Klovan (1971) modification of the Dunham's (1962) biologic classification of organically bound rocks. "Floatstone" replaces Dunham's "packstone"; the term "rudstone" replaces grain-supported biogenic limestones, and other organically bound rock are termed "bafflestone," "bindstone," or "framestone," depending on the character of the organic structures. These latter terms are often used to describe the fabric of reefs, bioherms, and other biogenic carbonates.

The Allochthonous grains are usually sourced intraformational or certainly intrabasinal.

The early researchers appreciated the complicated nature of carbonate rocks. They classified them both on the basis of origin of the components and depositional textures. Carozzi (1960) also offered a classification scheme which recognized several subtypes of Autochthonous and Allochthonous varieties of carbonates.

It was Folk (1959) who first successfully presented a comprehensive carbonate classification. He divided limestones into autochthonous, the so-called biolithites, and allochemical, those composed of various types of grains and matrix or cement. One or more grains can be associated with lime mud (= micrite) or lack micrite and instead are cemented by sparry calcite (= sparite). This classification has genetic implications and hence the conditions of the depositional setting and the formation of the grains are inferred. Interpretations about the depositional setting are of fundamental significance to oil/gas exploration and hence this classification scheme has gained wide acceptance.

Durham (1962) proposed another classification scheme that is used as much as Folk (1959, 1962) by the oil/gas industry. Both classifications distinguish allochems, matrix or micrite, and sparry calcite cement and both schemes emphasize texture (depositional texture and hence depositional setting). Both are widely used today with some modifications (Embry and Klovan, 1971; James, 1984) to the virtual exclusion of all other limestone classification schemes. Many geologists use the two schemes interchangeably. Concurrently, micrite is recognized both as a sedimentary matrix, internal cavity sedimentary fill, and as a diagenetic product and cement, while some carbonate grains are the products of later diagenetic modifications (Reid et al., 1990; Wright,1992).

Application of the recommended carbonate classification schemes

Irrespective of the classification scheme used (Folk or Dunham), the first question one should ask when classifying limestone is "can the deposition texture still be recognized?"

We recommend that a step-by-step approach be used in the Dunham scheme. The order of questions to be asked is:

1. Is the depositional texture recognizable?
   No – called crystalline limestone
   Yes – go to 2.
2. Was the rock bound together during deposition?
   Yes – boundstone
   No – go to 3.
3. Components deposited as distinct grains
   Grain supported – no mud – grainstone
   Grain supported – some mud – packstone
   Mud supported > 10% grains – wackestone
   Mud < 10% grains – mudstone

This classification key can be represented in a diagrammatic way (see Dunham Classification Scheme diagram).

Summary

A variety of classification schemes have been proposed for limestones that provide information relating to their origin, component composition, grain size, presence of matrix or cement, and depositional setting. The first universally accepted scheme was that of Folk, developed in 1959 to integrate the origin, component composition, grain size, and depositional setting. This was elaborated further in 1962. Folk's scheme is most suited for the study of thin sections of limestones.

An alternative classification scheme was proposed by Dunham in 1962. This is more suited for limestone descriptions made when using a hand lens or binocular microscope. It was further modified in 1971 by Embry and Klovan. Dunham's scheme is now commonly used by the oil/gas exploration industry.

A subsequent modification was proposed by James in 1984. It enables these various earlier schemes to be used interchangeably. The classification schemes can be represented in diagrammatic form.

Bibliography

Carrozzi, A. V., 1960. *Microscopic Sedimentary Petrography*. New York/London: Wiley.

Dunham, R. L., 1962. Classification of carbonate rocks according to depositional texture. *Memoir American Association Petroleum Geologists*, **1**, 108–121.

Embry, A. F., and Klovan, J. E., 1971. A late Devonian reef tract on Northeastern Banks Island, NWT. *Canadian Petroleum Geology Bulletin*, **19**, 730–781.

Folk, R. L., 1959. Practical petrographic classification of limestones. *Bulletin American Association Petroleum Geologists*, **43**, 1–38.

Folk, R. L., 1962. Spectral subdivision of limestone types. In Ham, W. E. (ed.), *Classification of Carbonate Rocks*. *American Association of Petroleum Geologists Memoir I*, pp. 62–84.

Folk, R. L., 1965. Some aspects of recrystallization in ancient limestones. *Society of Economic Paleontologists and Mineralogists (spec. pub.)*, **13**, 14–48.

Illing, L. V., 1954. Bahaman calcareous sands. *Bulletin American Association of Petroleum Geologists*, **38**, 1–95.

James, N. P., 1984. Shallowing-upwards sequences in carbonates. In Walker, R. G. (ed.), *Facies Models*. Canada: Geological Association of Canada, Geoscience Canada, (Rpr. Series 1), pp. 213–228.

Pettijohn, F. J., 1952. *Sedimentary Rocks*. New York: Harper & Brothers.

Reid, R. P., Macintyre, I. G., and James, N. P., 1990. Internal precipitation of microcrystalline carbonate: a fundamental problems of sedimentologists. *Sedimentary Geology*, **68**, 163–170.

Scholle, P. A., and Ulmer-Scholle, D. S., 2003. A color guide to the petrography of carbonate rocks. *AAPG Memoir*, **77**, 474.

Twenhoffel, W. H., 1932. *Treatise on Sedimentation*. Baltimore, MD: Williams & Wilkins.

Wolf, K. H., 1961. An introduction to the classification of limestones. *Neues Jahrbuch for Geology and Paleontology – Monatschefte*, **5**, 236–250.

Wright, P. V., 1992. A revised classification of limestones. *Sedimentary Geology*, **76**, 177–185.

Cross-references

Bindstone
Floatstone
Framestone
Micrite
Packstone
Rudstone
Wackestone

CLIMATE CHANGE AND CORAL REEFS

Janice M. Lough
Australian Institute of Marine Science, Townsville, QLD, Australia

Definition

Climate: Weather expected at given location and time of year, based on observations over at least 30 years, including average values and range of variability.

Climate change: Significant and persistent change in average and/or variability of climate.

Greenhouse gas: Constituent of atmosphere that absorbs and emits thermal infrared radiation.

Greenhouse effect: Trapping by atmospheric greenhouse gases of thermal infrared radiation, which otherwise would be lost to space, within climate system. Without the natural greenhouse effect, the earth would be about 30°C cooler and uninhabitable.

A rapidly changing climate

Climate change is not new. Global and regional climate has varied and changed in the past on a range of time scales due to a variety of internal and external causes (IPCC, 2007a, Chap. 1). Organisms and ecosystems, such as coral reefs, have survived, changed their distribution, and adapted to many of these past changes.

We are, however, in a new era of rapidly changing global climate as a consequence of human activities. The evidence for increasing greenhouse gases due to burning of fossil fuels, land-use changes and agriculture activities since the late eighteenth century is unequivocal (IPCC, 2007a, Chap. 2). The atmospheric concentration of the main greenhouse gas, carbon dioxide (CO_2), has risen about 40% from 280 ppm in 1750 to 383 ppm in 2007, the highest concentration of the last 650,000 years and possibly the last 20 million years. Not only are atmospheric concentrations of greenhouse gases rising but also the rate of increase is accelerating (Canadell et al., 2007).

This increase in atmospheric greenhouse gases results in significant positive radiative forcing of the global climate system and global warming attributable to human activities. The most recent Intergovernmental Panel on Climate Change Fourth Assessment (IPCC-AR4) report provides observational and paleoclimatic evidence for significant recent warming of global climate that matches theoretical and modeled consequences of increased greenhouse gas concentrations (IPCC, 2007c). The relatively modest global warming observed to date has already been associated with changes in the global climate system such as more intense rainfall, more frequent droughts, sea-level rise, loss of Arctic sea ice, melting of land-based ice, and a widening of the tropical climate belt (IPCC, 2007a, Chap. 3; Seidal et al., 2007). The rate of warming is about twice as fast for land masses compared to oceans and for high latitudes of the Northern Hemisphere compared with that for low latitude regions. Observed changes in climate are driving changes in the world's biological and physical systems that are all consistent with a rapidly warming climate (IPCC, 2007b; Rosenzweig et al., 2008).

The observational record shows that the average global land and sea temperature climate of the most recent 30 years (1979–2008) is significantly warmer (+0.55°C) than the climate at the end of the nineteenth century (1871–1900; Figure 1a). The tropical oceans, home to the world's coral reefs, have also significantly warmed (at about 70% of the global average value) by +0.40°C between the same periods (Figure 1b). The rate of warming has accelerated from 0.05°C (global) and 0.04°C per decade (tropical oceans), for the period 1871 to 2008, to 0.12°C (global) and 0.08°C per decade (tropical oceans) for the recent period 1950–2008.

Coral reef ecosystems, which occur in the naturally warm tropical oceans and are one of the largest sources of global marine diversity (Sala and Knowlton, 2006), are considered among the "most vulnerable ecosystems" to global climate change (IPCC, 2007b, Chap. 4, p. 214). This global-scale threat is occurring against a backdrop in which many of the world's coral reef ecosystems have already been degraded by direct human pressures. These local and regional stressors include overfishing, destructive fishing, and decline in water quality due to increased sediment, nutrient, and chemical pollution from changes in coastal land use (Hughes et al., 2003; Buddemeier et al., 2004). Fifteen years ago, a group of coral reef experts concluded that such "human pressures pose a far greater immediate threat to coral reefs than climate change, which may only threaten reefs in the distant future." (Wilkinson and Buddemeier, 1994, p. VIII).

Climate factors affecting coral reefs

Physical climatic environment of coral reefs: defining the envelope

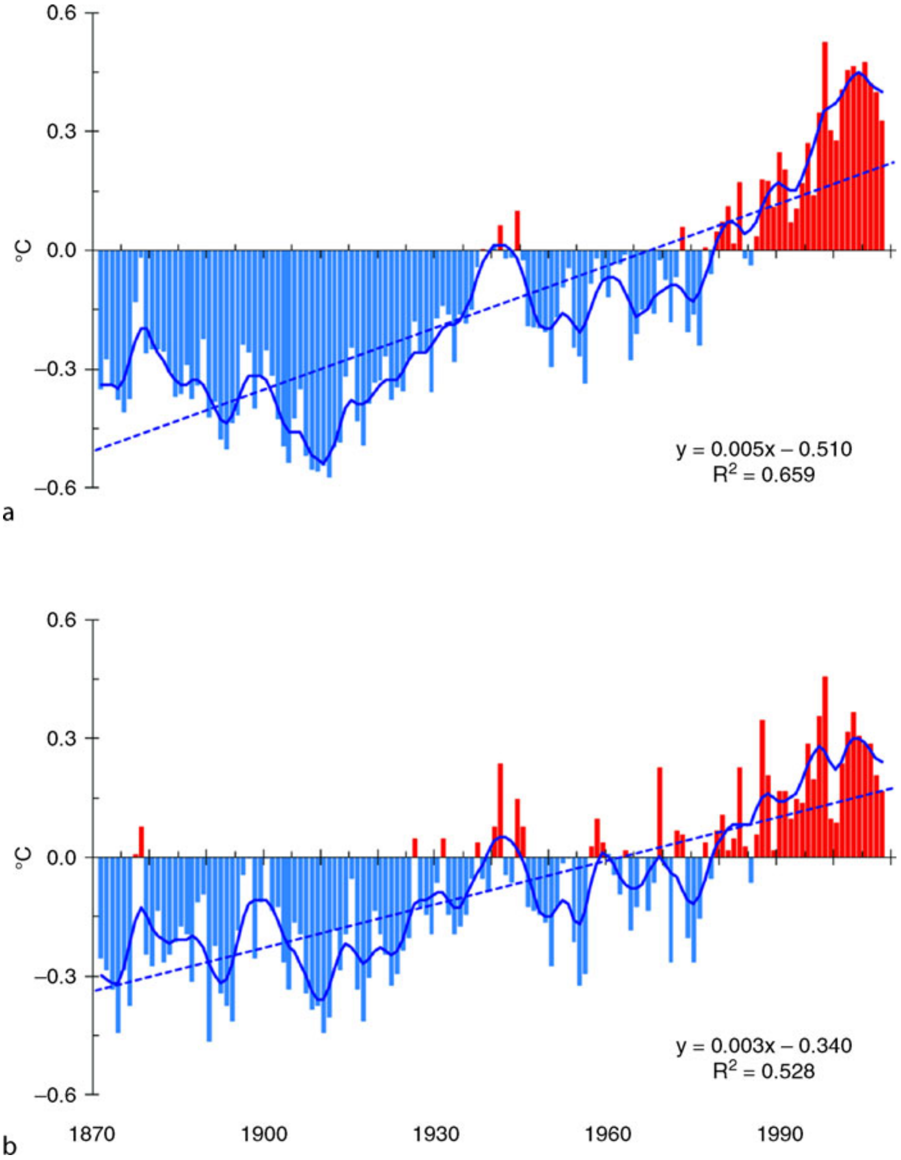
To assess the consequences of change requires the understanding of present-day environmental controls on tropical coral reefs (see also *Corals: Environmental Controls on Growth*). They are largely confined to shallow, warm, clear, and well-lit waters with 18°C identified as the minimum annual sea surface temperature (SST) necessary for reef growth and although upper thermal limits are less clear, nowhere, at present, is considered too warm for coral reef development (Achituv and Dubinsky, 1990). Comparing present-day distribution of nearly 1,000 reefs and a range of environmental variables, Kleypas et al. (1999a) found that the most important factors were warm SSTs (averaging 27.6°C), high aragonite saturation (ranging from 3.28 to 4.06 and 3.83 marking the transition from coral reefs to non-reef-forming coral communities), and high available light. In general, present-day coral reefs live within a relatively narrow range of these three variables (Hoegh-Guldberg, 2005).

Other weather and climatic factors affecting coral reefs

Water temperatures, ocean chemistry, and available light thus broadly define, given suitable bathymetry, where coral reefs occur. Salinity and nutrient supplies are more regionally specific controls which are modulated by the amount of rainfall and freshwater flow into nearshore reef environments. Also regionally important are ocean circulation patterns that control larval supplies between reefs (connectivity) and upwelling of nutrients. Coral reefs span a range of environments from clear oceanic waters to low salinity and turbid waters near land (Fabricius, 2005).

Tropical cyclones (see *Tropical Cyclone*/*Hurricane*), the most destructive of the world's weather systems, are natural sources of disturbance to many coral reefs poleward of ~10° from the equator (Emanuel, 2003). Tropical cyclones, through the large waves they generate, can directly affect and even decimate reef structures and coral assemblages as well as reducing salinity through heavy rainfall and causing coastal destruction associated with storm surges (Dollar, 1982; Massel and Done, 1993). Given time (~10–20 years), and no other sources of environmental stress, coral reefs can recover from such local physical disturbances (Done, 1999; Hughes and Connell, 1999; Coles and Brown, 2007). In addition to the immediate physical impacts of tropical cyclones, their local occurrence has been shown in the Caribbean to have longer term consequences by limiting subsequent coral recruitment, survival, and compounding coral cover declines due to other factors (Gardner et al., 2005; Crabbe et al., 2008).

El Niño-Southern Oscillation (ENSO) events are the principle source of interannual global climate variability. This highly coupled ocean–atmosphere phenomenon is centered in the tropical Pacific producing significant climate and societal impacts throughout the tropics and some extratropical regions (McPhaden et al., 2006). ENSO fluctuates between two phases, El Niño and La Niña, each associated with distinct and different atmospheric and oceanic climate anomalies. From the perspective of coral reefs, the most significant of these anomalies are widespread warming of much of the tropical oceans during



Climate Change and Coral Reefs, Figure 1 Annual anomalies (from 1961 to 1990 mean), 1871–2008 of (**a**) global average land and sea surface temperatures and (**b**) tropical average sea surface temperatures. *Thick line* is 10-year Gaussian filter emphasizing decadal variability. Linear regression line also provided (Data sources: HadCRUTV3, and HadiSST2 http://www.cru.uea.ac.uk; Jones et al., 1999; Brohan et al., 2006; Rayner et al., 2003).

the evolution (typically over 12–18 months) of an El Niño event, as happened in 1982–1983 and 1997–1998. Both phases are also associated with changes in tropical rainfall amount and intensity (in particular floods and consequent increases in freshwater flows to nearshore reefs) and in preferred locations of tropical cyclone activity.

Impacts of climate change on coral reefs

Warmer waters and coral bleaching

At the heart of tropical coral reefs is a mutually beneficial relationship between the coral animal and single-celled photosynthetic plants. In return for protection and essential nutrients, the algae play a role in light-enhanced calcification and provide sufficient cheap energy to the coral host to allow rapid calcification and thus form the massive and complex carbonate structures of coral reefs (Barnes and Chalker, 1990; Veron, 2000). Coral bleaching describes the loss by the coral animal of all or some of these algae and their photosynthetic pigments so that the white calcium carbonate skeleton becomes visible through the translucent coral tissue. Coral bleaching is a response of the coral to an environmental stress such as unusually cold or warm temperatures, low salinity, or pollution.

Coral bleaching is not a new phenomenon due to global warming.

Corals live within 1–2°C of their upper thermal threshold, beyond which bleaching occurs (Coles et al., 1976; Jokiel and Coles, 1977). Currently maximum summer SSTs (the time of year when corals are most at risk from thermal stress) on coral reefs averages 29.5°C and ranges between 28.2 and 34.4°C (Kleypas et al., 1999a). There is not an absolute temperature at which corals bleach, rather (which is evidence of adaptation over the long term) the threshold varies with ambient SSTs (Berkelmans, 2002).

Observations off the Pacific coast of Panama in 1983 presented one of the earliest "most alarming" reports of "large-scale" bleaching of corals which was tentatively linked to the 1982–1983 El Niño (Glynn, 1983). Subsequent studies clearly linked these unusual events to warmer-than-usual SSTs (Brown, 1987; Glynn, 1996; Jokiel and Brown, 2004). What is new and now clearly associated with warming of the tropical oceans are mass coral bleaching events where entire reefs are affected and which can be locally attributed to unusually warm maximum SSTs (Smith and Buddemeier, 1992; Brown, 1997).

The real wake-up call regarding the sensitivity of corals to warmer waters was during the major El Niño event of 1997–1998 (McPhaden 1999) which coincided with the warmest year in global instrumental records (Hansen et al., 2006). Bleaching was reported from nearly every coral reef region and 16% of the world's reefs was estimated to have been damaged (Wilkinson, 1998, 2004). The scale and magnitude of this event, during which impacts could be tracked round the world's coral reefs as each reached its unusually warm seasonal SST maximum, catalyzed efforts both to understand and monitor conditions conducive to coral bleaching.

In an influential paper (Hoegh-Guldberg, 1999), mass coral bleaching events were firmly linked to warming of tropical seas as a result of climate change and, using global climate model (GCM) projections for selected locations, the author suggested that thermal thresholds for coral bleaching could be regularly exceeded within a matter of decades. Various studies have demonstrated that the level of thermal stress on coral reefs is closely linked to coral bleaching (e.g., Berkelmans et al., 2004) and that the level of this stress has been increasing as the tropical oceans warm (Lough, 2000; Barton and Casey, 2005; Sheppard and Rioja-Nieto 2005).

Several of the recent mass coral bleaching events have been associated with El Niño events (Williams and Bunkley-Williams, 1990). These do not cause coral bleaching but they increase the likelihood in many coral reef regions of thermal conditions conducive to coral bleaching (Lough, 2000; Eakin et al., 2009). Some reef locations, e.g., along the South Pacific Convergence Zone in the western tropical Pacific, are more likely to be unusually warm during the La Niña phase of ENSO [bleaching was observed here, e.g., during the 1998–1999 La Niña (Wilkinson, 2004)].

Consequences of coral bleaching

A recent comprehensive review paper (Baker et al., 2008) summarizes much that we have learned and much that we still need to understand about the mass coral bleaching events that have affected many of the world's coral reefs since the 1980s. As a consequence of bleaching, corals may fully recover, partially recover, or die, and there are a range of short- and long-term impacts on coral reef ecosystems. Examples include declines in abundance of coral- and reef-associated species, reduced coral growth rates, increased susceptibility of corals to diseases, enhanced rates of bioerosion, and impaired reproduction and recruitment.

The intensity and occurrence of coral bleaching associated with widespread thermal stress shows considerable variability. Bleaching is frequently more intense at the surface than on the sides of individual colonies, which implicates high light levels as a contributing factor (Salm and Coles, 2001; Brown and Dunne, 2008). Local weather conditions of slack winds, low cloud amount, and little water motion all favor both warming and increased light penetration through the water column. Different coral taxa show different thermal susceptibility, with branching corals often showing greater sensitivity than massive species (Marshall and Baird, 2000; McClanahan et al., 2004, 2005). Large-scale field surveys clearly demonstrate spatial clusters of more or less bleaching (Berkelmans et al., 2004; McClanahan et al., 2007a, b). Experimental studies suggest that high water motion can reduce the incidence of bleaching (Nakamura and Van Woesik, 2001; West and Salm, 2003; Smith and Birkeland, 2007). This is supported by field observations of reduced bleaching in regions of strong water motion due to tides, upwelling, mixing and wave energy (Salm and Coles, 2001; Skirving and Guinotte, 2001; Reigl, 2003), though in some locations high water flow has been suggested to reduce the corals ability to deal with thermal stress (McClanahan et al., 2005). Rapid cooling of SSTs by tropical cyclones can also locally reduce the occurrence and intensity of coral bleaching (Manzello et al., 2007).

Recovery from a bleaching disturbance is also variable across all spatial scales and across different coral reef communities (Golbuu et al., 2007; Baker et al., 2008). Some reefs recovered relatively rapidly from the catastrophic 1997–1998 event (e.g., Indian Ocean reefs), whereas others (e.g., Caribbean/western Atlantic reefs) continue to decline, due to ongoing local stressors. Lack of other local stressors is an important factor in determining how well coral reefs recover from bleaching (Sheppard et al., 2008). However, even with recovery of hard coral cover, there is evidence of differential recovery of various components of the original coral reef ecosystem, which results in a different community structure after the event (Smith et al., 2008). Key effects include loss of structural complexity and habitat, local extinctions, loss of biodiversity and key functional groups (Graham et al., 2006), and both immediate and long-term consequences for corals themselves (McClanahan et al., 2009) and associated reef organisms (Pratchett et al., 2009).

An important question is to what extent corals and their symbionts maybe able to increase their tolerance to thermal stress with continued rapid global warming. Some argue that the potential for such successful adaptation on the time scales of observed and projected warming is limited (Hoegh-Guldberg, 1999, 2005). There is, however, experimental and observational evidence that some corals in some circumstances can and have increased their thermal tolerance by switching to a more thermally tolerant type of algal symbiont (Berkelmans and van Oppen, 2006; Goulet, 2006; Maynard et al., 2008; Oliver and Palumbi, 2009).

Warmer water temperatures and coral diseases

Increased numbers of reports of diseases affecting marine organisms, including corals, have been tentatively linked to warming waters and El Niño events (Harvell et al., 1999). Coral disease outbreaks on the Great Barrier Reef (GBR) have been linked to temperature stress (Jones et al., 2004; Bruno et al., 2007), and experimental and observational studies show that coral black band disease is enhanced in warmer waters and high light conditions (Boyett et al., 2007).

Warmer water temperatures: other effects

Warmer water temperatures can also directly affect physiological processes and distributions of corals and associated organisms. The northward range of two branching coral species has recently expanded in the western tropical Atlantic (Precht and Aronson, 2004). Coral community structure may change as juvenile corals grow more slowly and appear to die faster in warmer waters (Edmunds, 2004, 2007). Warmer temperatures have also been shown experimentally to affect larval supply, settlement, and survival (Negri et al., 2007; Nozawa and Harrison, 2007). Observational evidence of recent slowing in coral growth rates have also been linked to the combined effects of warmer waters and ocean acidification (De'ath et al., 2009; Tanzil et al., 2009).

Changing ocean chemistry

A more insidious consequence, and potentially catastrophic (Veron, 2008), of increasing greenhouse gases for marine calcifying organisms is ocean acidification. About 30% of the extra CO_2 human activities have injected into the atmosphere has been absorbed by the oceans (Feely et al., 2004; Sabine et al., 2004) – if this had not happened, the earth would have warmed more than it has. Absorption of CO_2 lowers the pH, decreases the availability of carbonate ions, and this lowers the saturation state of the major shell and skeleton forming carbonate minerals (Kleypas et al., 2006) Observational and modeling evidence demonstrates ongoing decline in the aragonite saturation state of Caribbean waters over the period 1996–2006 (Gledhill et al., 2008). Lowering ocean pH essentially shifts the balance of the geochemical equations whereby marine organisms, such as corals, calcify. Various modeling and experimental studies also demonstrate the reduced ability of corals to form their skeletal structures in more acidic waters (Kleypas et al., 1999b; Langdon and Atkinson, 2005; Orr et al., 2005; Doney et al., 2009).

Weaker coral reef structures reduce their structural resilience to the natural forces of erosion and a slower growth rate sets back recovery after disturbances. A recent experimental study suggests that ocean acidification can itself, and in combination with higher water temperatures, induce coral bleaching (Anthony et al., 2008). Ocean acidification affects not only corals (Guinotte and Fabry, 2008; Kuffner et al., 2008). Crustose coralline algae are particularly sensitive, and any setback to them may significantly undermine their vital role of cementing reef components together (Littler and Littler 1984; see also Chapter *Algae, Coralline*). The poorly cemented reefs of the eastern tropical Pacific (where aragonite saturation of waters is naturally low) may provide a picture of future coral reefs as the oceans continue to acidify (Manzello et al., 2008).

Sea level

Global average sea level has risen by about 20 cm over the past century, primarily due to thermal expansion of the oceans and, to a lesser extent, melting of land and sea ice (IPCC, 2007a, Chap. 5), and the rate of rise has accelerated in recent decades (Church and White, 2006). Although continued rising sea levels are of significance for many densely populated, low-lying tropical communities adjacent to coral reefs (McGranaham et al., 2007), a steady rise in sea level is not considered a major threat to present day coral reefs. Global sea level has been relatively stable for the past several thousand years and some reefs are limited by today's levels and the rates of rise are considered well within the ability of corals to keep up (Smith and Buddemeier, 1992; Done and Jones, 2006).

Linking the physical environment with biological processes

Determining how coral reefs and associated organisms have and will respond to changing conditions depends upon good observational studies of both the physical environment and biological responses. Ocean climate clearly controls many aspects of coral reef ecosystems but even for the one of the best studied coral reef ecosystems, the Great Barrier Reef, our ability to determine the biotic responses of its many component organisms to climate, climate variation, and climate change is limited. The myriad organisms that make up a tropical coral reef such as microbial assemblages, plankton, macroalgae, seagrass beds, intertidal mangrove, salt marshes and wetlands, benthic invertebrates, sharks and rays, marine mammals, marine reptiles, fishes, and corals are variously sensitive to water characteristics (temperature, chemistry, and nutrient supply), ocean circulation patterns, and extreme events such as tropical cyclones and freshwater flood plumes (see various chapters in Johnson and Marshall, 2007).

Although we have much better knowledge of the global distribution and health of coral reefs (http://www.reefbase.org/main.aspx), it is still difficult to clearly identify a significant increase in coral bleaching events due to confounding factors of greater awareness of the problem and hence more people looking for bleaching events (Oliver et al., 2009). Objective, large-scale methods are necessary for observing, for example, where and when bleaching occurs. These need to be supported by detailed and continuous local-scale observations that track coral reef mortality and recovery from such stress events (Spalding, 2009). It is also important to identify both bleaching-resistant (i.e., reduced impacts despite high thermal stress) and bleaching-resilient (i.e., rapid recovery after stress) coral reefs (McClanahan et al., 2007a). There have been dramatic improvements, through remote sensing, in our capabilities to observe coral reefs across large spatial scales but we still cannot routinely identify bleaching occurrences (Andrefouet and Riegl, 2004; Elvidge et al., 2004; Mumby et al., 2004). Satellite-based observations since the 1980s have also dramatically improved our ability to detect anomalies in surface ocean climate, and a range of products, based on “oceanic hotspots” (Goreau and Hayes, 1994), now routinely identify potential bleaching conditions in near real time (Eakin et al., 2009; http://coralreefwatch.noaa.gov/). Although such monitoring cannot prevent bleaching, it now allows scientists and reef managers to document the intensity, impacts, and recovery of reefs from such disturbances (see various chapters in Phinney et al., 2006; van Oppen and Lough, 2009).

Projected future climates for coral reefs

Predicting future climate

Several factors must be considered to understand and document the potential consequences and impacts of a rapidly changing climate. First, high-quality environmental observations are needed to determine the climatic envelope of particular organisms. Second, we need sufficient understanding of the complex physics of the global climate system, with the various interactions between the atmosphere, ocean, land, cryosphere, and biota, to realistically model current climate. Such GCMs then provide the basis for projecting future changes as a consequence of radiative forcing by greenhouse gases (IPCC, 2007a, Chap. 10). GCMs still, for example, have difficulties in correctly simulating certain components of tropical climate (Neale and Slingo, 2003; Reichler and Kim, 2008). The spatial resolution of GCMs is also relatively coarse which makes projecting to regional scales, most relevant to coral reefs, a challenge (IPCC, 2007a, Chaps. 8 and 11). Third, although based on the same physical laws, different GCMs vary in how they handle (parameterize) key small-scale processes. This can lead to slightly different results both for present and future climate simulations but such parameterizations are necessary to keep computational costs down to manageable levels. There is, therefore, no single “perfect” GCM and the most recent IPCC-4AR uses multimodel averages of a large number of independent climate projections to account for intermodel variability (Pierce et al., 2009).

Finally, projecting future climates depends on predicting future greenhouse gas concentrations. These depend on a variety of socioeconomic factors that determine the global response and level of commitment to reduce and stabilize greenhouse gas emissions in the atmosphere (mitigation) and, hence, the magnitude and timing of future climate changes. The IPCC constructed a number of plausible scenarios to specify the concentrations of greenhouse gases as input to GCMs (Nakicenovic and Swart, 2000). These range from very carbon-intensive futures with high emission rates (750–800 ppm CO_2 by 2100) to scenarios where emissions are reigned in very quickly (450–500 ppm CO_2 by 2100). Many scientists consider that greenhouse gas reductions well below those of the low emissions scenario are necessary to avoid dangerous climate change (Hansen et al., 2008). We are currently tracking above the high emission scenario (Canadell et al., 2007; Raupach et al., 2007) and, without significant mitigation, we are committed to ongoing, rapid, possibly intensifying climate changes for the foreseeable future, and there is the specter of irreversible changes on the scale of thousands of years (Solomon et al., 2009). Reducing greenhouse gas emissions by 70% by 2100 would, however, halve the magnitude of temperature changes compared to the high emissions scenario and would confine warming of the tropical oceans to 0.5–1.0°C (Washington et al., 2009).

Projected global changes

Average global temperatures are projected to be ~2–4°C warmer (1.1–6.4°C maximum range from different scenarios) by 2090–2099 compared to 1980–1999 and tropical SSTs are ~1–3°C warmer. An intensified hydrological cycle will increase rainfall in tropical high rainfall regions, reduce rainfall in the subtropics, and the intensity of rainfall extremes will increase. Ocean pH will decrease by 0.1–0.3 pH units. There may be fewer tropical cyclones, but those that do occur are likely to be more intense. It is unclear from global model projections as towhat will happen to ENSO events but they are likely to continue as a significant source of interannual climate variability affecting coral reefs (IPCC 2007a, Chap. 10). A conservative estimate is that sea level will rise 20–60 cm by the end of this century, but this value underestimates the contribution of accelerated melting of land ice (Howat et al., 2007; Meier et al., 2007).

A changing climate for coral reefs: future impacts

Several aspects of the current and ongoing changing climate are of significance for corals reefs, and the environmental envelope they are used to with warming water temperatures and ocean acidification are likely to be most important (Kleypas et al., 2001; Fabricius et al., 2007; Hoegh-Guldberg et al., 2007; Lough, 2008):

- Warmer waters increasing incidence of coral bleaching and diseases; direct effects on physiological processes of corals and other reef organisms.
- Ocean acidification weakening skeletons and reef structures; direct effects on physiological processes of corals and other reef organisms.
- More intense tropical cyclones increasing incidence of localized reef destruction.
- More intense rainfall and river flow increasing frequency of low salinity waters that extend further offshore, stress corals osmotically, and raise ambient nutrient loadings, producing an environment that favors phytoplankton production, proliferation of macroalgae, increases in filter feeders, and Crown-of-Thorns outbreaks.
- Changed ocean circulation patterns affecting reef connectivity, upwelling, and nutrient supplies.
- Changes to ENSO activity (at present ill-defined) are likely to continue as source of significant interannual climate variability with El Niño events increasing probability of warmer waters throughout most of tropics and, therefore, conditions conducive to coral bleaching and coral diseases superimposed on warmer baseline water temperatures.
- Rising sea level may drown some deeper reefs, increase shallow areas available to others, and wash away low-lying reef islands and cays. Likely to increase destruction associated with more intense tropical cyclones due to higher storm surges and intensified coastal erosion.
- Combined effects of chronic acidification with increased frequency of disturbances to reefs (bleaching, tropical cyclones) and reduced recovery intervals between disturbances.
- Compromising of physical structure of reefs with an overall decline in building of calcium carbonate reef structures, a shift in balance from net calcification to net erosion, and an increased available bare substrate for algae.
- Loss of structural complexity will reduce the range of habitats and shelter available for other reef-associated organisms.

The net effects of this range of increasing chronic and acute stressors associated with a changing climate (combined with, in many locations, already degraded coral ecosystems) are likely to be much simpler and ecologically less complex coral reefs characterized by lower biodiversity. Coral reef "ecosystems" will not respond as a whole (Guinotte et al., 2003) and their regional makeup will change as some species are better able to cope while others become locally extinct (Graham, 2007; Carpenter et al., 2008) and some expand and others contract their current distributions. There will be direct physiological responses by taxa other than corals to warming waters and ocean acidification. For example, experimental evidence suggests that future temperature and acidification scenarios will lead to reduced fitness and biodiversity losses in coral reef fishes (Munday et al., 2008; Przeslawski et al., 2008).

Several studies have considered aspects, singly and in combination, of these projected climate change impacts on coral reefs. Projections of future SSTs and aragonite saturation state of the Pacific Ocean for the late twenty-first century suggest that nearly all present-day coral reef habitats are likely to be marginal for reef development (though the projected changes are not outside the ranges of current marginal reef habitats). The potential for poleward migration of coral reefs (which depends on temperature, ocean chemistry, and suitable substrate) appears limited (Guinotte et al., 2003). The magnitude of future warming is likely to vary spatially with consequent spatial variability in future bleaching impacts and frequency (Sheppard, 2003; Sheppard and Rioja-Nieto, 2005; McClanahan et al., 2007b). Increases of only 1°C in Caribbean SSTs will expand the extent and intensity of bleaching events to 100% of the area (McWilliams et al., 2005). A similar increase on the Great Barrier Reef (GBR) would increase the occurrence of bleaching from the ~50% observed in 1998 and 2002 to ~80%, with increases of 2–3°C increasing the area of the GBR that bleaches to 97–100% (Berkelmans et al., 2004). Avoiding near-annual coral bleaching events within 30–50 years requires corals increase their thermal tolerance levels by 0.2–1.0°C per decade (Donner et al., 2005), and coral recovery may require management actions that reduce expansion of algae between disturbances (Wooldridge et al., 2005). Modeling studies also suggest that improving water quality through improved agricultural practices can significantly raise the thermal threshold for bleaching (Wooldridge, 2009).

Some studies have also attempted to identify the "tipping point" at which coral reefs can no longer sustain themselves as carbonate structures. Cao and Caldeira (2008) estimate that prior to the Industrial Revolution, 98% of coral reefs lived in waters with suitable carbonate chemistry, whereas once atmospheric CO_2 levels reach 450 ppm, only 8% of reefs will be in waters with the necessary aragonite saturation level. Dramatically, Hoegh-Guldberg et al. (2007, p. 1741) suggest that CO_2 levels greater than 500 ppm combined with water temperatures 2°C warmer will "reduce coral reef ecosystems to crumbling frameworks with few calcareous corals" and similarly that once CO_2 reaches 560 ppm "all coral reefs will cease to grow and start to dissolve" (Silverman et al., 2009, p. 1).

Combined disturbances and recovery intervals

Long-term observational studies demonstrate the sensitivity of coral reef communities to repeated disturbances. Tropical cyclones, bleaching events, low salinity waters due to heavy rainfall and river flows, outbreaks of diseases, and coral predators (such as Crown-of-Thorns starfish – see *Acanthaster Planci*) all have direct and flow-on effects to coral reef communities (Wilson et al., 2006; Riegl and Purkis, 2009). Impacts and recovery are variable and repeated disturbances with reduced intervals between them are likely to increasingly compromise the structural integrity and community makeup of these ecosystems (Done et al., 2007; Feary et al., 2007; Wakeford et al., 2008). Because of such multiple climate and local physical stressors on coral reefs, a more holistic modeling approach is required to projecting future status of coral reef ecosystems (Sarmineto et al., 2004).

Potential actions

Drastic and immediate reductions of anthropogenic greenhouse gas emissions to the atmosphere are the first step to stabilizing global climate and the climatic environment of coral reefs. Coral reefs have been described as one of the "world's failing ecosystems and one of the most persuasive examples of the effects of global environmental damage" (Downs et al., 2005, p. 486). What other actions, if any, can assist the maintenance of present-day coral reefs into the future? First, protection of these ecosystems from local direct stresses enhances their resilience and recovery from the additional stresses of climate change. This has led to many calls for greatly expanded networks of marine protected areas (Bellwood et al., 2004; Pandolfi et al., 2005; Mora et al., 2006; Wilson et al., 2006; Hughes et al., 2007). At all levels, it is the addition of humans into the equation of coral reefs that is causing the problems (Downs et al., 2005; Mora and Ginsburg, 2008) and it has been argued that we only lack the commitment to implement appropriate protection strategies (Sale, 2008). Second, it is clear that some coral reefs and parts of coral reefs are more resistant to climatic stresses such as bleaching and some are more resilient as demonstrated by relatively rapid recovery. Such reefs and locations within reefs are clear targets for enhanced protection (West and Salm, 2003; McClanahan et al., 2007a; Graham et al., 2007, 2008; Diaz-Pulido et al., 2009). Third, climate change and increased likelihood of significant disturbances need to be incorporated into selecting, designing, and managing marine protected areas (Baker et al., 2008; Game et al., 2008). Fourth, we need to improve early warning systems, seasonal climatic outlooks, and monitoring of physical and biological conditions on reefs (Weeks et al., 2008; Maynard et al., 2009; Spillman and Alves, 2009). Finally, we need improved GCMs for the tropics (Shukla et al., 2009) including better spatial resolution to allow better and more reliable predictions to be made for specific reef provinces (Donner et al., 2005, 2009).

Summary

Coral reef ecosystems are highly vulnerable to stresses associated with a changing climate. These stresses are superimposed on local stresses in many regions that have already resulted in significant degradation in the goods and services that healthy coral reefs provide (Buddemeier et al., 2004). Coral reefs are unlikely to disappear, but in the future they are likely to calcify less and there will be fewer reefs that are able to sustain the necessary reef framework that supports many thousands of marine organisms with a consequent loss in marine biodiversity (Guinotte et al., 2003). Our understanding of the full consequences of a rapidly changing climate and ocean chemistry for coral reef ecosystems is still limited and, unfortunately, the experiment is occurring in real time in the real world. The consequences of anthropogenic climate change for coral reefs are inequitable. The countries most responsible for anthropogenic climate change produce 6–11 times more CO_2 per person than the more than 400 million people living close to coral reefs (Donner and Potere, 2007). It is, however, these communities that will suffer most from the loss of the goods and services provided by healthy coral reef ecosystems.

Bibliography

Achituv, Y., and Dubinsky, Z., 1990. Evolution and zoogeography of coral reefs. In Dubinsky, Z. (ed.), *Ecosystems of the World, Vol. 25: Coral Reefs*. Amsterdam: Elsevier, pp. 1–9.

Andrefouet, S., and Riegl, B., 2004. Remote sensing: a key tool for interdisciplinary assessment of coral reef processes. *Coral Reefs*, **23**, 1–4.

Anthony, K. R. N., Kline, D. I., Diaz-Pulido, G., Dove, S., and Hoegh-Guldberg, O., 2008. Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 17442–17446.

Baker, A. C., Glynn, P. W., and Riegl, B., 2008. Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science*, **80**, 435–471.

Barnes, D. J., and Chalker, B. E., 1990. Calcification and photosynthesis in reef-building coral and algae. In Dubinsky, Z. (ed.), *Ecosystems of the World, Vol. 25: Coral Reefs*. Amsterdam: Elsevier, pp. 109–131.

Barton, A. D., and Casey, K. S., 2005. Climatological context for large-scale coral bleaching. *Coral Reefs*, **24**, 536–554.

Bellwood, D. R., Hughes, T. P., Folke, C., and Nystrom, M., 2004. Confronting the coral reef crisis. *Nature*, **429**, 827–833.

Berkelmans, R., 2002. Time-integrated thermal bleaching thresholds of reefs and their variation on the Great Barrier Reef. *Marine Ecology Progress Series*, **229**, 73–82.

Berkelmans, R., De'ath, G., Kininmonth, S., and Skirving, W. J., 2004. A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: spatial correlation, patterns, and predictions. *Coral Reefs*, **23**, 74–83.

Berkelmans, R., and van Oppen, M. J. H., 2006. The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope' for coral reefs in an era of climate change. *Proceedings of the Royal Society of London B*, **273**, 2305–2312, doi:10.1098/rspb.2006.3567.

Boyett, H. V., Bourne, D. G., and Willis, B. L., 2007. Elevated temperature and light enhance progression and spread of black band disease on staghorn corals of the Great Barrier Reef. *Marine Biology*, **151**, 1711–1720.

Brohan, P., Kennedy, J. J., Harris, I., Tett, S. F. B., and Jones, P. D., 2006. Uncertainty estimates in regional and global observed temperature changes: a new dataset from 1850. *Journal of Geophysical Research*, **111**, D12106, doi:10.1029/2005JD006548.

Brown, B. E., 1987. Worldwide death of corals – natural cyclical events or man-made pollution? *Marine Pollution Bulletin*, **18**, 9–13.

Brown, B. E., 1997. Coral bleaching: causes and consequences. *Coral Reefs*, **16**, S129–S138.

Brown, B. E., and Dunne, R. P., 2008. Solar radiation modulates bleaching and damage protection in a shallow water coral. *Marine Ecology Progress Series*, **362**, 99–107.

Bruno, J. F., Selig, E. R., Casey, K. S., Page, C. A., Willis, B. L., Harvell, C. D., Sweatman, H., and Melendy, A. M., 2007. Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biology*, **5**, e124, doi:10.1371/journal.pbio.0050124.

Buddemeier, R. W., Kleypas, J. A., and Aronson, R. B., 2004. *Coral Reefs and Global Climate Change*. Arlington, VA: Pew Center on Global Climate Change.

Canadell, J. G., La Quere, C., Raupach, M. R., Field, C. B., Buitenhuis, E. T., Ciais, P., Conway, T. J., Gillett, N. P., Houghton, R. A., and Marland, G., 2007. Contributions to accelerating atmospheric CO_2 growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 18866–18870.

Cao, L., and Caldeira, K., 2008. Atmospheric CO_2 stabilization and ocean acidification. *Geophysical Research Letters*, **35**, L19609, doi:10.1029/2008GL035072.

Carpenter, K. E., Abrar, M., Aeby, G., Aronson, R. B., Banks, S., Bruckner, A., Chiriboga, A., Cortes, J., Delbeek, J. C., DeVantier, L., Edgar, G. J., Edwards, A. J., Fenner, D., Guzman, H. M., Hoeksema, B. W., Hodgson, G., Johan, O., Licuanan, W. Y., Livingstone, S. R., Lovell, E. R., Moore, J. A., Obura, D. O., Ochavillo, D., Polidoro, B. A., Precht, W. F., Quibilan, M. C., Reboton, C., Richards, Z. T., Rogers, A. D., Sanciangco, J., Sheppard, A., Sheppard, C., Smith, J., Stuart, S., Turak, E., Veron, J. E. N., Wallace, C., Weil, E., and Wood, E., 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science*, **321**, 560–563.

Church, J. A., and White, N. J., 2006. A 20th century acceleration in global sea-level rise. *Geophysical Research Letters*, **33**, L01602, doi:10.1029/2005GL024826.

Coles, S. L., and Brown, E. K., 2007. Twenty-five years of change in coral coverage on a hurricane impacted reef in Hawaii: the importance of recruitment. *Coral Reefs*, **26**, 705–717.

Coles, S. L., Jokiel, P. L., and Lewis, C. R., 1976. Thermal tolerance in tropical versus subtropical Pacific reef corals. *Pacific Science*, **30**, 159–166.

Crabbe, M. J. C., Martinez, E., Garcia, C., Chub, J., Castro, L., and Guy, J., 2008. Growth modelling indicates hurricanes and severe storms are linked to low coral recruitment in the Caribbean. *Marine Environmental Research*, **65**, 364–368.

De'ath, G., Lough, J. M., and Fabricius K. E., 2009. Declining coral calcification on the Great Barrier Reef. *Science*, **323**, 116–119.

Diaz-Pulido, G., McCook, L. J., Dove, S., Berkelmans, R., Roff, G., Kline, D. I., Weeks, S., Evans, R. D., Williamson, D. H., and Hoegh-Guldberg, O., 2009. Doom and boom on a resilient reef: climate change, algal overgrowth and coral recovery. *PLoS ONE*, **44**(4), e5239, doi:10.1371/journal.pone.0005239.

Dollar, S. J., 1982. Storm stress and coral community structure in Hawaii. *Coral Reefs*, **1**, 71–81.

Done, T. J., 1999. Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. *American Zoologist*, **39**, 66–79.

Done, T. J., and Jones, R. N., 2006. Tropical coastal ecosystems and climate change prediction: global and local risks. In Phinney, J. T., Hoegh-Guldberg, O., Kleypas, J., Skirving, W., and Strong, A. (eds.), *Coral Reefs and Climate Change. Science and Management*, Coastal and Estuarine Studies. Washington, DC: American Geophysical Union, Vol. 61, pp. 5–31.

Done, T., Turak, E., Wakeford, M., DeVantier, L., McDonald, A., and Fisk, D., 2007. Decadal changes in turbid-water coral communities at Pandora Reef: loss of resilience or too soon to tell? *Coral Reefs*, **26**, 789–805.

Doney, S. C., Fabry, V. J., Feely, R. A., and Kleypas, J. A., 2009. Ocean acidification: the other CO_2 problem. *Annual Review of Marine Science*, **1**, 169–192.

Donner, S. D., Heron, S. F., and Skirving, W. J., 2009. Future scenarios; a review of modelling efforts to predict the future of coral reefs in an era of climate change. In van Oppen, M. J. H., and Lough, J. M. (eds.), *Coral Bleaching. Patterns, Processes, Causes and Consequences*. Berlin: Springer, pp. 159–173.

Donner, S. D., and Potere, D., 2007. The inequity of the global threat to coral reefs. *Bioscience*, **57**, 214–215.

Donner, S. D., Skirving, W. J., Little, C. M., Oppenheimer, M., and Hoegh-Guldberg, O., 2005. Global assessment of coral bleaching and required rates of adaptation under climate change. *Global Change Biology*, **11**, 2251–2265.

Downs, C. A., Woodley, C. M., Richmond, R. H., Lanning, L. L., and Owen, R., 2005. Shifting the paradigm of coral-reef 'health' assessment. *Marine Pollution Bulletin*, **51**, 486–494.

Eakin, C. M., Lough, J. M., and Heron, S. F., 2009. Climate variability and change: monitoring data and evidence for increased coral bleaching stress. In van Oppen, M. J. H., and Lough, J. M. (eds.), *Coral Bleaching. Patterns, Processes, Causes and Consequences*. Berlin: Springer, pp. 41–67.

Edmunds, P. J., 2004. Juvenile coral population dynamics track rising seawater temperature on a Caribbean reef. *Marine Ecology Progress Series*, **269**, 111–119.

Edmunds, P. J., 2007. Evidence for a decadal-scale decline in the growth rates of juvenile scleractinian corals. *Marine Ecology Progress Series*, **341**, 1–13.

Elvidge, C. D., Dietz, J. B., Berkelmans, R., Andrefouet, S., Skirving, W., Strong, A. E., and Tuttle, B. T., 2004. Satellite observation of Keppel Islands (Great Barrier Reef) 2002 coral bleaching using IKONOS data. *Coral Reefs*, **23**, 123–132.

Emanuel, K., 2003. Tropical cyclones *Annual Review of Earth and Planetary Sciences*, **31**, 75–104.

Fabricius, K. E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin*, **50**, 125–146.

Fabricius, K. E., Hoegh-Guldberg, O., Johnson, J., McCook, L., and Lough, J., 2007. The vulnerability of coral reef ecosystems of the Great Barrier Reef to climate change. In Johnson, J., and Marshall, P. (eds.), *Climate Change and the Great Barrier Reef. A Vulnerability Assessment*. Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, pp. 516–554.

Feary, D. A., Almany, G. R., Jones, G. P., and McCormick, M. I., 2007. Coral degradation and the structure of tropical reef fish communities. *Marine Ecology Progress Series*, **333**, 243–248.

Feely, R. A., Sabine, C. L., Lee, K., Berelson, W., Kleypas, J., Fabry, V. J., and Millero, F. J., 2004. Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. *Science*, **305**, 362–366.

Game, E. T., Watts, M. E., Wooldridge, S., and Possingham, H. P., 2008. Planning for persistence in marine reserves; a question of catastrophic importance. *Ecological Applications*, **18**, 670–680.

Gardner, T. A., Cote, I. M., Gill, J. A., Grant, A., and Watkinson, A. R., 2005. Hurricanes and Caribbean coral reefs: impacts, recovery, patterns, and role in long-term decline. *Ecology*, **86**, 174–184.

Gledhill, D. K., Wanninkhof, R., Millero, F. J., and Eakin, C. M., 2008. Ocean acidification of the Greater Caribbean Region 1996–2006. *Journal of Geophysical Research*, **113**, C10031, doi:10.1029/2007JC004629.

Glynn, P. W., 1983. Extensive ‘bleaching’ and death of reef corals on the Pacific coast of Panama. *Environmental Conservation*, **10**, 149–154.

Glynn, P. W., 1996. Coral reef bleaching: facts, hypotheses and implications. *Global Change Biology*, **2**, 495–509.

Golbuu, Y., Victor, S., Penland, L., Idip, D., Emaurois, C., Okaji, K., Yukihira, H., Iwase, A., and van Woesik, R., 2007. Palau’s coral reefs show differential habitat recovery following the 1998-bleaching event. *Coral Reefs*, **26**, 319–332.

Goreau, T. J., and Hayes, R. L., 1994. Coral bleaching and ocean “hot spots”. *Ambio*, **23**, 176–180.

Goulet, T. L., 2006. Most corals may not change their symbionts. *Marine Ecology Progress Series*, **321**, 1–7.

Graham, N. A. J., 2007. Ecological versatility and the decline of coral feeding fishes following climate driven coral mortality. *Marine Biology*, **153**, 119–127.

Graham, N. A. J., McClanahan, T. R., MacNeil, M. A., Wilson, S. K., Plunin, N. V. C., Jennings, S., Chabanet, P., Clark, S., Spalding, M. D., Letourneur, Y., Bigot, L., Galzin, R., Ohman, M. C., Garpe, K. C., Edwards, A. J., and Sheppard, C. R. C., 2008. Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. *PLoS ONE*, **3**(8), e3039, doi:10.1371/journalpone.0003039.

Graham, N. A. J., Wilson, S. K., Jennings, S., Polunin, N. V., Bijoux, J. P., and Robinson, J., 2006. Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 8425–8429.

Graham, N. A. J., Wilson, S. K., Jenning, S., Polunin, N. V. C., Robinson, J., Bijoux, J. P., and Daw, T. M., 2007. Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conservation Biology*, **21**, 1291–1300.

Guinotte, J. M., Buddemeier, R. W., and Kleypas, J. A., 2003. Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin. *Coral Reefs*, **22**, 551–558.

Guinotte, J. M., and Fabry, V. J., 2008. Ocean acidification and its potential effects on marine ecosystems. *Annals New York Academy of Science*, **1134**, 320–342.

Hansen, J., Sato, M., Kharecha, P., Beerling, D., Berner, R., Masson-Delmotte, V., Pagani, M., Raymo, M., Royer, D. L., and Zacjos, J. C., 2008. Target atmospheric CO_2: where should humanity aim? *The Open Atmospheric Science Journal*, **2**, 217–231.

Hansen, J., Sato, M., Ruedy, R., Lo, K., Lea, D. W., and Medina-Elizade, M., 2006. Global temperature change. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 14288–14293.

Harvell, C. D., Kim, K., Burkholder, J. M., Colwell, R. R., Epstein, P. R., Grimes, D. J., Hofmann, E. E., Lipp, E. K., Osterhaus, A. D. M. E., Overstreet, R. M., Porter, J. W., Smith, G. W., and Vasta, G. R., 1999. Emerging marine diseases – climate links and anthropogenic factors. *Science*, **285**, 1505–1510.

Hoegh-Guldberg, O., 1999. Climate change, coral bleaching and the future of the world’s coral reefs. *Marine and Freshwater Research*, **50**, 839–866.

Hoegh-Guldberg, O., 2005. Low coral cover in a high-CO_2 world. *Journal of Geophysical Research*, **110**, C09S06, doi:10.1029/2004JC002528.

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell, C. D., Sale, P. F., Edwards, A. J., Caldeira, K., Knowlton, N., Eakin, C. M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R. H., Dunbi, A., and Hatziolos, M. E., 2007. Coral reefs under rapid climate change and ocean acidification. *Science*, **318**, 1737–1742.

Howat, I. M., Joughin, I., and Scambos, T. A., 2007. Rapid changes in ice discharge from Greenland outlet glaciers. *Science*, **315**, 1559–1561.

Hughes, T. P., Baird, A. H., Bellwood, D. R., Card, M., Connolly, S. E., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J. B. C., Kleypas, J., Lough, J. M., Marshall, P., Nystrom, M., Palumbi, S. R., Pandolfi, J., Rosen, B., and Roughgarden, J., 2003. Climate change, human impacts and the resilience of coral reefs. *Science*, **301**, 929–933.

Hughes, T. P., Bellwood, D. R., Folke, C. S., McCook, L. J., and Pandolfi, J. M., 2007. No-take areas, herbivory and coral reef resilience. *Trends in Ecology and Evolution*, **22**, 1–3.

Hughes, T. P., and Connell, J. H., 1999. Multiple stressors on coral reefs: a long-term perspective. *Limnology and Oceanography*, **44**, 932–940.

IPCC, 2007a. In Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. L. (eds.), *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.

IPCC, 2007b. In Parry, M. L., Canziani, O. F., Palutikof, J. P., van der Linden, P. J., and Hanson, C. E. (eds.), *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.

IPCC, 2007c. Summary for policymakers. In Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. L. (eds.), *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.

Johnson, J. E., and Marshall, P. A. (eds.), 2007. *Climate Change and the Great Barrier Reef. A Vulnerability Assessment*. Australia: Great Barrier Reef Marine Park Authority and Australian Greenhouse Office.

Jokiel, P. L., and Brown, E. K., 2004. Global warming, regional trends and inshore environmental conditions influence coral bleaching in Hawaii. *Global Change Biology*, **10**, 1627–1641.

Jokiel, P. L., and Coles, S. L., 1977. Effects of temperature on the mortality and growth of Hawaiian reef corals. *Marine Biology*, **43**, 201–208.

Jones, R. J., Bowyer, J., Hoegh-Guldberg, O., and Blackall, L. L., 2004. Dynamics of a temperature-related coral disease outbreak. *Marine Ecology Progress Series*, **281**, 63–77.

Jones, P. D., New, M., Parker, D. E., Martin, S., and Rigor, I. J., 1999. Surface air temperature and its variations over the last 150 years. *Reviews of Geophysics*, **37**, 173–199.

Kleypas, J. A., Buddemeier, R. W., Archer, D., Gattuso, J.-P., Langdon, C., and Opdyke, B. N., 1999b. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science*, **284**, 118–120.

Kleypas, J. A., Buddemeier, R. W., and Gattuso, J.-P., 2001. The future of coral reefs in an age of global change. *International Journal of Earth Sciences*, **90**, 426–437.

Kleypas, J. A., Feely, R. A., Fabry, V. J., Langdon, C., Sabine, C. L., and Robbins, L. L., 2006. *Impacts of ocean acidification on coral reefs and other marine calcifiers: A guide for future research*. Report of a Workshop held 18–20 April 2005, St Petersburg, FL, Sponsored by NSF, NOAA and the US Geological Survey.

Kleypas, J. A., McManus, J. W., and Meñez, L. A. B., 1999a. Environmental limits to coral reef development: where do we draw the line? *American Zoologist*, **39**, 146–159.

Kuffner, I. B., Andersson, A. J., Jokiel, P. L., Rodgers, K. S., and Mackenzie, F. T., 2008. Decreased abundance of crustose coralline algae due to ocean acidification. *Nature Geoscience*, **1**, 114–117.

Langdon, C., and Atkinson, M. J., 2005. Effect of elevated ρCO_2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. *Journal of Geophysical Research*, **110**, C09S07, doi:10.1029/2004JC002576.

Littler, M., and Littler, D. S., 1984. Models of tropical reef biogenesis: the contribution of algae. *Progress in Phycological Research*, **3**, 323–364.

Lough, J. M., 2000. 1997–98: Unprecedented thermal stress to coral reefs? *Geophysical Research Letters*, **27**, 3901–3904.

Lough, J. M., 2008. A changing climate for coral reefs. *Journal of Environmental Monitoring*, **10**, 21–29.

Manzello, D. P., Brandt, M., Smith, T. B., Lirman, D., Hendee, J. C., and Nemeth, R. S., 2007. Hurricanes benefit bleached corals. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 12035–12039.

Manzello, D. P., Kleypas, J. A., Budd, D. A., Eakin, C. M., Glynn, P. W., and Langdon, C., 2008. Poorly cemented coral reefs of the eastern tropical Pacific: possible insights into reef development in a high-CO_2 world. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 10450–10455.

Marshall, P. A., and Baird, A. H., 2000. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs*, **19**, 155–163.

Massel, S. R., and Done, T. J., 1993. Effects of cyclone waves on massive coral assemblages on the Great Barrier Reef: meteorology, hydrodynamics and demography. *Coral Reefs*, **12**, 153–166.

Maynard, J. A., Anthony, K. R. N., Marshall, P. A., and Masiri, I., 2008. Major bleaching events can lead to increased thermal tolerance in corals. *Marine Biology*, **155**, 172–182.

Maynard, J. A., Johnson, J. E., Marshall, P. A., Eakin, C. M., Goby, G., Schuttenberg, H., and Spillman, C. M., 2009. A strategic framework for responding to coral bleaching events in a changing climate. *Environmental Management*, **44**, 1–11, doi:10.1007/s00267-009-9295-7.

McClanahan, T. R., Ateweberhan, M., Graham, N. A. J., Wilson, S. K., Ruiz Sebastian, C., Guillaume, M. M. M., and Bruggemann, J. H., 2007a. Western Indian Ocean coral communities: bleaching responses and susceptibility of extinction. *Marine Ecology Progress Series*, **337**, 1–13.

McClanahan, T. R., Ateweberhan, M., Muhando, C. A., Maina, J., and Mohammed, M. S., 2007b. Effects of climate and seawater temperature variation on coral bleaching and mortality. *Ecological Monographs*, **77**, 503–525.

McClanahan, T. R., Baird, A. H., Marshall, P. A., and Toscano, M. A., 2004. Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. *Marine Pollution Bulletin*, **48**, 327–335.

McClanahan, T. R., Maina, J., Moothien-Pillay, R., and Baker, A. C., 2005. Effects of geography, taxa, water flow, and temperature variation on coral bleaching intensity in Mauritius. *Marine Ecology Progress Series*, **298**, 131–142.

McClanahan, T. R., Weil, E., Cortes, J., Baird, A. H., and Ateweberhan, M., 2009. Consequences of coral bleaching for sessile reef organisms. In van Oppen, M. J. H., and Lough, J. M. (eds.), *Coral Bleaching. Patterns, Processes, Causes and Consequences*. Berlin: Springer, pp. 121–138.

McGranaham, G., Balk, D., and Anderson, B., 2007. The rising tide: assessing the risks of climate change and human settlements in low elevation coastal zones. *Environment and Urbanization*, **19**, 17–37.

McPhaden, M. J., 1999. Genesis and evolution of the 1997–98 El Niño. *Science*, **283**, 950–954.

McPhaden, M. J., Zebiak, S. E., and Glantz, M. H., 2006. ENSO as an integrating concept in earth science. *Science*, **314**, 1740–1745.

McWilliams, J. P., Cote, I. M., Gill, J. A., Sutherland, W. J., and Watkinson, A. R., 2005. Accelerating impacts of temperature-induced bleaching in the Caribbean. *Ecology*, **86**, 2055–2060.

Meier, M. F., Dyurgerov, M. B., Rick, U. K., O'Neel, S., Pfeffer, W. T., Anderson, R. S., Anderson, S. P., and Glazovsky, A. F., 2007. Glaciers dominate eustatic sea-level rise in the 21st century. *Science*, **317**, 1064–1067.

Mora, C., Andrefouet, S., Costello, M. J., Kranenburg, C., Rollo, A., Veron, J., Gaston, K. J., and Myers, R. A., 2006. Coral reefs and the global network of marine protected areas. *Science*, **312**, 1750–1751.

Mora, C., and Ginsburg, R., 2008. A clear human footprint on the Caribbean coral reefs. *Proceedings of the Royal Society of London B*, **275**, 767–773.

Mumby, P. J., Skirving, W., Strong, A. E., Hardy, J. T., LeDrew, E. F., Hochberg, E. J., Stumpf, R. P., and David, L. T., 2004. Remote sensing of coral reefs and their physical environment. *Marine Pollution Bulletin*, **48**, 219–228.

Munday, P. L., Jones, G. P., Pratchett, M. S., and Williams, A. J., 2008. Climate change and future for coral reef fishes. *Fish and Fisheries*, **9**, 261–285.

Nakamura, T., and van Woesik, R., 2001. Water-flow rates and passive diffusion partially explain differential survival of corals during 1998 bleaching event. *Marine Ecology Progress Series*, **212**, 301–304.

Nakicenovic, N., and Swart, R. (eds.), 2000. *Special Report on Emissions Scenarios. A Special Report of Working Group III of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.

Neale, R., and Slingo, J., 2003. The Maritime Continent and its role in the global climate: a GCM study. *Journal of Climate*, **16**, 834–848.

Negri, A. P., Marshall, P. A., and Heyward, A. J., 2007. Differing effects of thermal stress on coral fertilization and early embryogenesis in four Indo Pacific species. *Coral Reefs*, **26**, 759–763.

Nozawa, Y., and Harrison, P. L., 2007. Effects of elevated temperature on larval settlement and post-settlement survival in scleractinian corals, *Acropora solitaryensis* and *Favites chinensis*. *Marine Biology*, **152**, 1181–1185.

Oliver, J. K., Berkelmans, R., and Eakin, C. M., 2009. Coral bleaching in space and time. In van Oppen, M. J. H., and Lough, J. M. (eds.), *Coral Bleaching. Patterns, Processes, Causes and Consequences*. Berlin: Springer, pp. 21–39.

Oliver, T. A., and Palumbi, S. R., 2009. Distributions of stress-resistant coral symbionts match environmental patterns at local but not regional scales. *Marine Ecology Progress Series*, **378**, 93–103.

Orr, J. C., Fabry, V. J., Aumont, O., Bopp, L., Doney, S. C., Feely, R. A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F., Key, R. M., Lindsay, K., Maier-Reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R.G., Plattner, G. -K., Rodgers, K. B., Sabine, C. L., Sarmiento, J. L., Schlitzer, R., Slaterm R. D., Totterdell, I. J., Weirig, M. -F., Yamanaka, Y., and Yool, A., 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, **437**, 681–686.

Pandolfi, J. M., Jackson, J. B. C., Baron, N., Bradbury, R. H., Guzman, H. M., Hughes, T. P., Kappel, C. V., Micheli, F., Ogden, J. C., Possingham, H. P., and Sala, E., 2005. Are U.S coral reefs on the slippery slope to slime? *Science*, **307**, 1725–1726.

Phinney, J. T., Hoegh-Guldberg, O., Kleypas, J., Skirving, W., and Strong, A. (eds.), 2006. *Coral Reefs and Climate Change: Science and Management*, Coastal and Estuarine Studies. Washington, DC: American Geophysical Union, Vol. 61.

Pierce, D. W., Barnett, T. P., Santer, B. D., and Gleckler, P. J., 2009. Selecting global climate models for regional climate change studies. *Proceedings National Academy of Science of the United States of America*, **106**, 8441–8446.

Pratchett, M. S., Wilson, S. K., Graham, N. A. J., Munday, P. L., Jones, G. P., and Polunin, N. V. C., 2009. Coral bleaching and consequences for motile reef organisms: past, present and uncertain futures. In van Oppen, M. J. H., and Lough, J. M. (eds.), *Coral Bleaching. Patterns, Processes, Causes and Consequences*. Berlin: Springer, pp. 139–158.

Precht, W. F., and Aronson, R. B., 2004. Climate flickers and range shifts of reef corals. *Frontiers in Ecology and the Environment*, **2**, 307–314.

Przeslawski, R., Ahyong, S., Byrne, M., Worheides, G., and Hutchings, P., 2008. Beyond corals and fish: the effects of climate change on noncoral benthic invertebrates of tropical reefs. *Global Change Biology*, **14**, 2773–2795.

Raupach, M. R., Marland, G., Ciais, O., Le Quere, C., Canadell, J. G., Klepper, G., and Field, C. B., 2007. Global and regional drivers of accelerating CO_2 emissions. *Proceedings National Academy of Science of the United States of America*, **104**, 10288–10293.

Rayner, N. A., Brohan, P., Parker, D. E., Folland, C. K., Kennedy, J. J., Vanicek, M., Ansell, T., and Tett S. F. B., 2006. Improved analyses of changes and uncertainties in marine temperature measured in situ since the mid-nineteenth century: the HadSST2 dataset. *Journal of Climate*, **19**, 446–469.

Rayner, N. A., Parker, D. E., Horton, E. B., Folland, C. K., Alexander, L. V., Rowell, D. P., Kent, E. C., and Kaplan, A., 2003. Globally complete analyses of sea surface temperature, sea ice and night marine air temperature, 1871–2000. *Journal of Geophysical Research*, **108**, 4407, doi:10.1029/2002JD002670.

Reichler, T., and Kim, J., 2008. How well do coupled models simulate today's climate? *Bulletin American Meteorological Society*, **89**, 303–311.

Reigl, B., 2003. Climate change and coral reefs: different effects in two high-latitude areas (Arabian Gulf, South Africa). *Coral Reefs*, **22**, 433–446.

Riegl, B. M., and Purkis, S. J., 2009. Model of coral population response to accelerated bleaching and mass mortality in a changing climate. *Ecological Modelling*, **220**, 192–208.

Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T. L., Estrella, N., Seguin, B., Tryjanowski, P., Liu, C., Rawlins, S., and Imeson, A., 2008. Attributing physical and biological impacts to anthropogenic climate change. *Nature*, **453**, 353–357.

Sabine, C. L., Feely, R. A., Gruber, N., Key, R. M., Lee, K., Bullister, J. L., Wanninkhof, R., Wong, C. S., Wallace, D. W. R., Tilbrook, B., Millero, F. J., Peng, T.- H., Kozyr, A., Ono, T., and Rios, A. F., 2004. The oceanic sink for anthropogenic CO_2. *Science*, **305**, 367–371.

Sala, E., and Knowlton, N., 2006. Global marine biodiversity trends. *Annual Review of Environmental Resources*, **31**, 93–122.

Sale, P. F., 2008. Management of coral reefs: where we have gone wrong and what we can do about it. *Marine Pollution Bulletin*, **56**, 805–809.

Salm, R. V., and Coles, S. L. (eds.), 2001. *Coral Bleaching and Marine Protected Areas*. Proceedings of the Workshop on Mitigating Coral Bleaching Impact through MPA Design. Bishop Museum, Honolulu, Hawaii, 29–31 May 2001. Asia Pacific Coastal Marine Program Report #0102. Honolulu, Hawaii: The Nature Conservancy.

Sarmineto, J. L., Slater, R., Barber, R., Bopp, L., Doney, S. C., Hirst, A. C., Kleypas, J., Matear, R., Mikolajewicz, U., Monfray, P., Soldatov, V., Spall, S. A., and Stouffer, R., 2004. Response of ocean ecosystems to climate warming. *Global Biogeochemical Cycles*, **18**, GB3003, doi:10.1029/2003GB002134.

Seidal, D. J., Fu, Q., Randel, W. J., and Reichler, T. J., 2007. Widening of the tropical belt in a changing climate. *Nature Geoscience*, **1**, 21–24.

Sheppard, C. R. C., 2003. Predicted recurrences of mass coral mortality in the Indian Ocean. *Nature*, **425**, 294–297.

Sheppard, C. R. C., Harris, A., and Sheppard, A. L. S., 2008. Archipelago-wide coral recovery patterns since 1998 in the Chagos Archipelago, central Indian Ocean. *Marine Ecology Progress Series*, **362**, 109–117.

Sheppard, C., and Rioja-Nieto, R., 2005. Sea surface temperature 1871–2099 in 38 cells in the Caribbean region. *Marine Environmental Research*, **60**, 389–396.

Shukla, J., Hagedorn, R., Hoskins, B., Kinter, J., Marotzke, J., Miller, M., Palmer, T. N., and Slingo, J., 2009. Revolution in climate prediction is both necessary and possible. A Declaration at the World Modelling Summit for Climate Prediction. *Bulletin of the American Meteorological Society*, **90**, 175–178.

Silverman, J., Lazar, B., Cao, L., Caldeira, K., and Erez, J., 2009. Coral reefs may start dissolving when atmospheric CO_2 doubles. *Geophysical Research Letters*, **36**, L05606, doi:10.1029/2008GL036282.

Skirving, W., and Guinotte, J., 2001. The sea surface temperature story on the Great Barrier Reef during the Coral Bleaching Event of 1998. In Wolanski, E. (ed.), *Oceanographic Processes of Coral Reefs. Physical and Biological Links in the Great Barrier Reef.* Boca Raton, FL: CRC, pp. 301–313.

Smith, L. W., and Birkeland, C., 2007. Effects of intermittent flow and irradiance level on back reef *Porites* corals at elevated seawater temperature. *Journal of Experimental Marine Biology and Ecology*, **341**, 282–294.

Smith, S. V., and Buddemeier, R. W., 1992. Global change and coral reef ecosystems. *Annual Reviews of Ecological Systems*, **23**, 89–118.

Smith, L. D., Gilmour, J. P., and Heyward, A. J., 2008. Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching. *Coral Reefs*, **27**, 197–205.

Solomon, S., Plattner, G. -K., Knutti, R., and Friedlingstein, P., 2009. Irreversible climate change due to carbon dioxide emissions. *Proceedings National Academy of Science of the United States of America*, **106**, 1704–1708.

Spalding, M., 2009. Detecting and monitoring coral bleaching events. In van Oppen, M. J. H., and Lough, J. M. (eds.), *Coral Bleaching. Patterns, Processes, Causes and Consequences*. Berlin: Springer, pp. 69–82.

Spillman, C. M., and Alves, O., 2009. Dynamical seasonal prediction of summer sea surface temperatures in the Great Barrier Reef. *Coral Reefs*, **28**, 197–206.

Tanzil, J. T. I., Brown, B. E., Tudhope, A. W., and Dunne, R. P., 2009. Decline in skeletal growth of the coral *Porites lutea* from the Andaman Sea, South Thailand between 1984 and 2005. *Coral Reefs*, **28**, 519–528.

van Oppen, M. J. H., Lough, J. M. (eds.), 2009. *Coral Bleaching. Patterns, Processes, Causes and Consequences*. Ecological Studies. Berlin Heidelberg: Springer-Verlag, Vol. 205, 178pp.

Veron, J. E. N., 2000. *Corals of the World*. Townsville: Australian Institute of Marine Science, 1382 pp.

Veron, J. E. N., 2008. Mass extinction and ocean acidification: biological constraints on geological dilemmas. *Coral Reefs*, **27**, 459–472.

Wakeford, M., Done, T. J., and Johnson, C. R., 2008. Decadal trends in a coral community and evidence of changed disturbance regime. *Coral Reefs*, **27**, 1–13.

Washington, W. M., Knutti, R., Meehl, G. A., Teng, H., Tebaldi, C., Mawrence, D., Buja, L., and Strand, W. G., 2009. How much climate change can be avoided by mitigation? *Geophysical Research Letters*, **36**, L08703, doi:10.1029/2008GL037074.

Weeks, S. J., Anthony, K. R. N., Bakun, A., Feldman, G. C., and Hoegh-Guldberg, O., 2008. Improved predictions of coral bleaching using seasonal baselines and higher spatial resolution. *Limnology and Oceanography*, **53**, 1369–1375.

West, J. M., and Salm, R. V. 2003. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Conservation Biology*, **17**, 956–967.

Wilkinson, C. R. (ed.), 1998. *Status of Coral Reefs of the World: 1998*. Townsville: Global Coral Reef Monitoring Network, Australian Institute of Marine Science.

Wilkinson, C. R. (ed.), 2004. *Status of Coral Reefs of the World: 2004*. Townsville: Global Coral Reef Monitoring Network, Australian Institute of Marine Science.

Wilkinson, C. R., and Buddemeier, R. W., 1994. *Global climate change and coral reefs: implications for people and reefs*. Report of the UNEP-IOC-ASPEI-IUCN Global Task Team on the Implications of Climate Change on Coral Reefs. Gland, Switzerland: IUCN.

Williams, E. H., and Bunkley-Williams, L., 1990. The world-wide coral reef bleaching cycle and related sources of coral mortality. *Atoll Research Bulletin*, **335**, 1–71.

Wilson, S. K., Graham, N. A. J., Pratchett, M. S., Jones, G. P., and Polunin, N. V. C., 2006. Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology*, **12**, 2220–2234.

Wooldridge, S. A., 2009. Water quality and coral bleaching thresholds: formalising the linkage for the inshore reefs of the Great Barrier Reef, Australia. *Marine Pollution Bulletin*, **58**, 745–751.

Wooldridge, S., Done, T., Berkelmans, R., Jones, R., and Marshall, P., 2005. Precursors for resilience in coral communities in a warming climate: a belief network approach. *Marine Ecology Progress Series*, **295**, 157–169.

Cross-references

Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity
Climate Change: Increasing Storm Activity
Corals: Environmental Controls on Growth
El Niño, La Niña, and ENSO
Ocean Acidification, Effects on Calcification
Remote Sensing
River Plumes and Coral Reefs
Sea Level Change and Its Effect on Reef Growth
Symbiosis
Temperature Change: Bleaching
Tropical Cyclone/Hurricane
Zooxanthellae

CLIMATE CHANGE: IMPACT OF SEA LEVEL RISE ON REEF FLAT ZONATION AND PRODUCTIVITY

David Hopley
James Cook University, Townsville, QLD, Australia

Definitions

Climate change: projected changes to atmosphere and ocean which may affect coral reefs and their biota in a detrimental way, usually considered over the next 100 years or so.

Sea level rise: one of these projected changes resulting initially from thermal expansion of the oceans and longer term melting of glaciers, projected to be 13–68 cm by 2100.

Reef flat: the intertidal part of the coral reef, exposed at low tide, often sediment covered but with living corals in pools, for example as micro atolls, or around the lower edges of the reef flat where exposure is of shorter duration.

Productivity: the production of calcium carbonate forming the framework and sediments of the reef. Usually expressed as kilograms per square metre per year (kg m^2/year), the figure may be converted into reef accretion rates by taking into account the density and porosity of the contributing organisms and detrital facies.

Introduction

The impact of sea level rise on coral reef flats was one of the first considerations raised in relation to climate change and coral reefs. Most publications in the 1980s considered the impact to be a beneficial one. This was especially so in the Indo-Pacific area, where isostatic adjustments had produced a sea level at or above its present position for over 6,000 years. Many reefs are now adjusted to this level with lagoons infilled, sediments dominating the reef flat and living corals limited to shallow pools (Figure 1). Such reef flats are too shallow for at least half the tidal cycle for the transmission of waves with sufficient energy to entrain and transport all but the finest sediments.

Many general references on Greenhouse effects emphasized the rejuvenation of reef tops (e.g., Henderson-Sellers and Blong, 1989) whilst others went as far as suggesting reefs could be drowned and many ecosystems eliminated (e.g., Falk and Brownlow, 1989). Some scientific assessments suggested that renewed coral growth would make reef flats aesthetically more pleasing (e.g., Hopley and Kinsey, 1988).

Reef flat attributes and sea level rise

Atlantic reefs have experienced a continuous sea level rise throughout the Holocene (for isostatic reasons) with the result that their shallowest points are commonly subtidal and have a living coral cover. They are thus well placed to accelerate their growth as sea level rises. Indo-Pacific reefs, however, already at sea level for over 6,000 years, are very different. Many lagoons have been completely infilled (see *Reef Classification by Hopley (1982)*). Rather than living corals, shingle ridges and cemented platforms are to be found on the windward margins of many reefs and mangroves have colonized the sheltered areas behind them. The result is the typical low wooded island morphology found, for example, on the northern Great Barrier Reef (GBR). Reef flats are sediment covered often stabilized by binding organisms such as seagrass and macro algae. Corals, including micro atolls may be confined to moated parts of the reef flat.

Geomorphologically, these reef flats are inert for much of the time. As demonstrated by Kench and Brander (2006), at Warraber Island in Torres Strait (maximum tidal range ca. 4 m), Lady Elliott Island, in the southern GBR (1.7 m) and Cocos-Keeling atoll in the Indian Ocean, (1.2 m), both the high loss of energy of incident waves at

Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity, Figure 1 Inert reef flat which has been at sea level for >5,000 years. Coconut (Poruma),Torres Strait.

the reef edge and long subaerial isolation at low tides are the reasons for their being insufficient energy for sediment movement. The Warraber reef flat is inactive for long periods, with waves above 0.05 m on the outer reef flat <30% of the time and 0.1 m only 19% of the time on each Spring to Neap cycle. "Energy windows", when waves can perform geomorphic work, are determined by critical water depths which are exceeded between 16.2 and 38% of the time at the GBR sites. However, on Cocos-Keeling because it is open to oceanic swells and has a low tidal range, this time period can be up to 76% of the time, thus accommodating greater sediment movement.

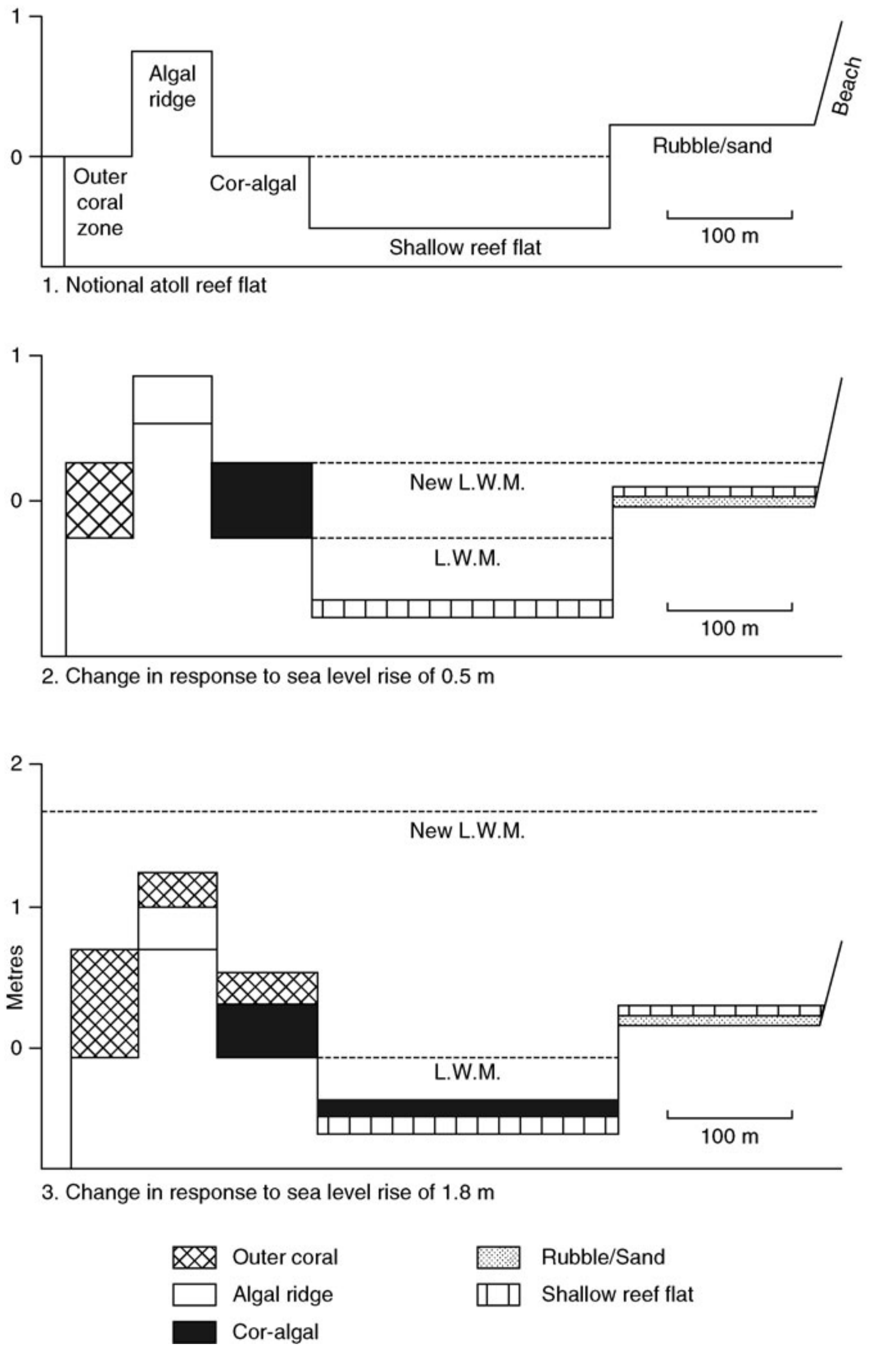
Reef flat response to sea level rise

Analyses of different scenarios of rates of sea level rise on the typical zones of reef flats and reef islands have been made by Hopley and Kinsey (1988); Hopley (1993); Hopley (1997); Hopley et al. (2007). Projections for 2100 by Hopley and Kinsey (1988) were up to 1.8 m, but by 1993, they were a more modest 30 cm to 1.0 m (average 60 cm), by 1997 23–96 cm and currently 13–68 cm (all figures from IPCC reports). Although the rate of annual sea level rise ranges from only 5 to 15 mm/year, this is important for reef flat ecology because it approximates the vertical growth rates of some of the slower growing corals. The realized value of sea-level rise will determine how much and how quickly vertical accommodation space is added, the places and heights that corals may grow, and the wave energy, currents and hence sediment transport on the reef flat (see *Accommodation Space*). Response in the form of vertical accretion can also be calculated. Estimates using alkalinity anomaly measurements (Kinsey, 1985), closely match those from the geological record (Davies and Hopley, 1983). For the major ecological zones these vertical accretion rates are:

- 100% coral on hard substrates – modal rate of 7–8 mm/year but up to 15 mm/year for highly porous branching corals on a hard substrate.
- Algal pavement – 3–4 mm/year
- Reef flat sand and rubble – 0.4 mm/year

Using these figures Hopley and Kinsey (1988) suggested that reef flats would be completely rejuvenated in 100–150 years accreting initially at 4 mm/year then accelerating to 7 mm/year. Reef growth rates from dated cores indicate that all reefs would be drowned by a sea level rise >8–9 mm/year. For many inshore reefs of the GBR, rejuvenation would be aided by inundation of 1–1.5 m raised reef substrate dating from higher sea level stands of the mid-Holocene times.

By the mid-1990s sea level rise projections were more conservative (0.3–1.0 m, average 60 cm). Hopley (1997) modeled the impact of both the earlier rise of 1.8 m and a more modest 0.5 m on a typical atoll reef flat (from Bikini, Emery et al., 1954) (Figure 2). The higher rise resulted in the inundation of the entire reef flat by about 2070, the outer flat becoming entirely coral covered, producing sediment for the deepening lagoon and inner sand/rubble flat as wave transport became more efficient. In contrast the response to the slower rate of rise was a reef flat that more or less retained its original zonation. The inner flat may become shallowly submerged but even here transport of sediment from the windward margin may maintain its level at about LWM. Calculating the calcium carbonate production for a 1 m wide transect across the entire 70 m wide atoll reef flat produced a figure of 2,020 kg/year for the present time, and a similar



Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity, Figure 2 Modeled atoll reef flat and response to a sea level rise of 0.5 and 1.8 m by, 2100 (from Hopley, 1997).

2,220 kg/year for the similar zonation in 2100 after a 0.5 m rise. After a rise of 1.8 m, by contrast (Figure 2), the carbonate production rate across the reef flat was 4,950 kg/year and the reef flat zonation highly modified with much of the active coral growth having moved shorewards.

Hopley et al. (2007) also undertook a similar exercise for a >3 km wide reef top typical of some GBR planar reefs Again, calcium carbonate productivity was increased only marginally by a rise in sea level of 0.5 m. However it was more than doubled by the larger rise as the reef top was rejuvenated. In both instances water levels would rise over the reef flat, laterally transporting much of the new material towards leeward cays, or lagoons. This would be especially so if a large proportion of the new growth was in the form of fragile branching corals, small foraminifera or other easily transportable sediment components.

Some efficiency in sediment movement may be lost as the new reef top becomes rougher with new vertical relief in the form of coral spurs, storm rubble, etc. (Kench and Brander, 2006). Generally shallow lagoons are likely once more to become effective sediment sinks. In some circumstances, there may be a surplus that can contribute to island construction.

Reef island responses

Initial climate change predictions described dire consequences for reef islands, as contours representing extreme high tide level were merely moved upward on island shores. However, researchers working directly on the physical processes on reefs (see Hopley et al., 2007 for discussion) generally agree that rising sea levels of the magnitude projected over the next 100 years will be far less damaging and will produce substantial reworking of surficial sediments enough to at least maintain the island mass. Island stability will be aided by a retaining effect of beach rock and other cemented materials. Additional transported sediments and higher water levels will allow cyclonic storms to more effectively emplace shingle ridges to motus, a very important part of the island building processes (e.g., Bayliss-Smith, 1988; Maragos et al., 1973). Sediment movement will also occur on a more regular basis. Kench and Brander's (2006) research on mesotidal Australian reefs indicated that sediment movement is currently restricted to less than 50% of the time. On Warraber Reef in Torres Strait (and other Indo-Pacific reefs) effective sediment movement ceased about 2,000 years ago but a rise in sea level of only 0.5 m may unlock stored sediments which will be moved towards an adjacent cay or motu.

Similar responses have been modeled on Raine Island (northern GBR) by Gourlay and Hacker (1996). They indicated that the height of the beach berm is determined by the run-up height of the dominant wave action – at highest Spring Tide. A berm elevation of 4 m could be built by small flat waves of 0.5 m height breaking directly onto a beach at a tide level as low as 2.3 m. They showed that a small rise in sea level without any corresponding build up of reef flat level would result in the attainment of greater berm height under most weather conditions, i.e., build-up of the island by an amount which would exceed the amount of increase in water level. On Raine Island they suggest that with a 0.6 m rise in sea level, larger 1.6 m waves would increase berm height by a factor of 0.8 m. Smaller waves of 0.5 m would increase the height by 1.2 m, i.e., berm height would increase from an initial 4.0 m to up to 5.2 m.

Whilst the island mass may remain as a habitat for plants and animals it will be highly disturbed. Deposition on one part of the shore will be matched by erosion elsewhere as both prevailing wind directions and storm frequencies add to the impacts of sea level rise. Reworking of older parts of the island may remove a high proportion of the mature organic soils and vegetation which form the most favorable habitat including as agricultural land for human populations. For migratory species such as seabirds and turtles, the reworked island may for a time, still provide a valuable resource but for permanent residents, coral reef cays may quickly become uninhabitable.

Other factors influencing reef flat change

The start of this entry presented the optimistic view that coral reefs may be one of the few ecosystems to benefit from sea level rise. The discussion that followed suggested the optimism may be well founded in the light of renewed upward growth, changed wave action and increased sediment movement. However, sea level rise is not the only factor in climate change. Whilst increased cyclone activity may help add new ridges to reef islands, other environmental changes such as temperature rise and ocean acidification will have detrimental affects resulting in widespread coral mortality.

Sheppard et al. (2005) have described the results of coral bleaching in reefs of the Seychelles. Prior to the 1998 event fringing reefs had an outer veneer of 0.5 m high thickets of staghorn corals and massive *Porites*. Stripping of this veneer reduced reef roughness and created a pseudo sea level rise that was superimposed over a regional rise of ca. 5 mm/year. Sheppard et al. modeled the reef flat conditions of 1994, 2004 and 2014 concluding that the rate of erosion of Seychelles beaches would double in the next 10 years.

These figures are of great concern for many of the world's reefs subjected to rising sea level. However, reef disintegration as described for the Seychelles may not be nearly as rapid elsewhere, determined largely by the composition of the reef flat corals. Reef flat surfaces subject to a small fall in sea level remain within the energetic wave zone as well as the intertidal zone of highly active bioerosion. Where branching corals dominate the reef flat, stripping and pseudo-sea level rise may impact on the adjacent shore, as in the Seychelles. However, where massive or encrusting corals are dominant even though they may die in response to environmental change, they may not be removed, but stay *in situ* on the reef flat for 5,000 years or more, as illustrated by Hayman Island in the central GBR (Kan et al. 1997). Here a pseudo sea level rise is not superimposed on regional sea level behavior.

Summary

Responses of reef flats to sea level rise in the twenty-first century will likely be many and varied. The response in each case will depend on specific reef characteristics and environmental setting: the existing height of the reef relative to sea level; the local tidal range and rate of sea-level rise; the existing composition and zonation of coral assemblages, and hence susceptibility to the exacerbating effect of pseudo sea-level rise; the changing ecology with changed environmental conditions and disturbance regimes; and propensity for old and new sediments to be transported by wave action.

The only generalization is that the response of coral reefs will not be the same in all locations.

Bibliography

Bayliss-Smith, T. P., 1988. The role of hurricanes in the development of reef islands, Ontong Java Atoll, Solomon Islands. *Geographical Journal*, **154**, 377–391.

Davies, P. J., and Hopley, D., 1983. Growth facies and growth rates of Holocene reefs in the Great Barrier Reef. *Bureau Mineral Resources Journal*, *Australian Geology and Geophysics*, **8**, 237–251.

Emery, K. O., Tracey, J. I., and Ladd, H. S., 1954. Geology of Bikini and nearby atolls. *US Geological Survey Professional Papers 26-A*, 1–265.

Falk, J., and Brownlow, A., 1989. *The Greenhouse Challenge: What's to be Done?* Ringwood, Vic: Penguin Books.

Gourlay, M. R., and Hacker, J. L. F., 1991. *Raine Island Coastal Processes and Sedimentology*. Univ. of Qld. Dept. of Civil Engineering Report CH40/91 + Appendices, 68pp.

Henderson-Sellers, A., and Blong, R., 1989. *The Greenhouse Effect*: *Living in a Warmer Australia*. NSW Univ.

Hopley, D., 1982. *The Geomorphology of the Great Barrier Reef: Quaternary Development of Coral Reefs*. New York: John Wiley Interscience, 453pp.

Hopley, D., and Kinsey, D. W., 1988. The effects of rapid short-term sea rise on the Great Barrier Reef. In Pearman, G. I. (ed.), *Greenhouse: Planning for Climate Change*, CSIRO, pp. 189–201.

Hopley, D., 1993. Coral reef islands in a period of global sea-level rise. In Saxena, N. (ed.), *Recent Advances in Marine Science and Technology '92*, PACON Conference, Honolulu, 1992, pp. 453–462.

Hopley, D., 1997. Coral reef islands – implications of more modest global change predictions. In Saxena, N. (ed.), *Recent Advances in Marine Science and Technology*, *96*, PACON96, pp. 249–258.

Hopley, D., Smithers, S. G., and Parnell, K. E., 2007. *The Geomorphology of the Great Barrier Reef*: *Development*, *Diversity and Change*. Cambridge: Cambridge University Press, 532pp.

Kan, H., Nakashima, Y., and Hopley, D., 1997. Coral communities during structured development of a fringing reef flat, Hayman Island, the Great Barrier Reef. In *Proceedings of the 8th International Coral Reef Symposium*, **1**, 465–470.

Kench, P. S., and Brander, R. W., 2006. Wave processes on coral reef flats: implications for reef geomorphology using Australian case studies. *Journal of Coastal Research*, **22**, 209–223.

Kinsey, D. W., 1985. Metabolism, calcification and carbon production: 1 Systems level studies. *Proceedings of the 5th International Coral Reef Congress*, *Tahiti*, **4**, 505–526.

Maragos, J. F., Baines, G. B. R., and Beveridge, P. J., 1973. Tropical cyclones create a new land formation in Funafuti Atoll. *Science*, **181**, 1161–1164.

Sheppard, C., Dixon, D. J., Gourlay, M. R., Sheppard, A., and Payet, R., 2005. Coral mortality increases wave energy reaching shores protected by reef flats: examples from the Seychelles. *Estuararine Coastal and Shelf Science*, **64**, 223–234.

Cross-references

Accommodation Space
Climate Change: Impact On Coral Reef Coasts
Climate Change and Coral Reefs
Geomorphic Zonation
Hydrodynamics of Coral Reef Systems
Recent Sea Level Trends
Reef Flats
Sediment Dynamics

CLIMATE CHANGE: IMPACT ON CORAL REEF COASTS

Charles Sheppard
University of Warwick, Coventry, UK

Definition

Climate change is impacting directly on coral reef coasts. When warm spikes, superimposed on a long-term gradual warming trend, cause massive mortality of corals, the elevation of the shallow reef relative to the shore is lowered, thereby increasing the wave energy that reaches the shore and the consequent erosion of low lying shores.

Introduction

A primary service supplied by coral reefs to the human communities which live near them is that of shoreline protection. Infrastructure and settlements occur along the shorelines of many hundreds of atolls, as well as along thousands of kilometers of shoreline of high islands. They are all protected to a considerable extent by the breakwater effect provided by coral reefs that fringe those shores. The reef's service in this respect is invaluable, but quantification of the effects and costs caused by their degradation lags well behind many of the better studied biological effects. Much of what we do know derives from engineering models.

The main impacts are caused by increases in the amount of wave energy which strikes the shoreline when the adjacent reef deteriorates, and when its elevation drops relative to sea level. In the recent past, this form of deterioration has come mainly from coral extraction to obtain limestone for building purposes, and from coral mortality caused by diseases. Now, and in the foreseeable future, it will be compounded by effects of global warming.

Traditional extraction of corals for use as building material, both as whole colonies or as excavated blocks of reef, has occurred for centuries. Perhaps the best known example of this has taken place in the Maldives, where the lack until recently of any significant quantity of alternative building material has meant that the reef flats around several settlements, especially the capital Malé, have been severely excavated. There are no good estimates of quantities taken, but it seems likely that around Malé the reef flat appears to have been excavated by local people to such an extent that they have lowered its elevation relative to sea level by at least half a meter.

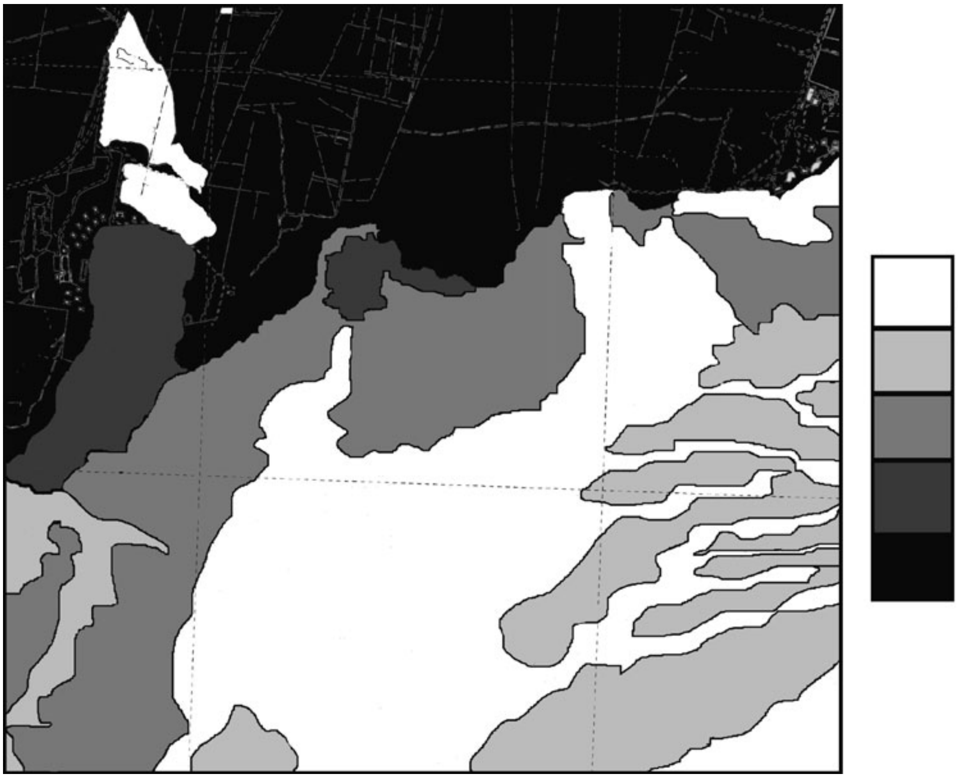
Coral mortality from disease has especially affected the elevation of reef crests in the Caribbean. Until the 1980s the shallowest zone of corals comprised Elkhorn coral, *Acropora palmata* (Geister, 1977). This species grows upward to reach the low water mark in very dense thickets of over 2 m tall, even protruding above the water at low tides. However, over much of the Caribbean, these shallow water reefs have now disintegrated almost completely.

Enormous stands of very solid limestone colonies that packed the zone from the surface to about 4 m depth have been almost totally eliminated by disease (Rosenberg and Loya, 2004). As a result, affected reefs no longer contain a wave break reaching the low water level. Instead, this zone now consists of disintegrating rubble, remnants of the once-living branching coral, with a completely different ecological character. The areas are extensive: Figure 1 is an example from the island of Anguilla, where the extensive shallow, dead reef was previously a healthy *Acropora palmata* zone.

Sea water warming – the third cause of wide-scale erosion of coral reefs – is increasing in importance. Warm spikes, superimposed on a long-term gradual warming trend, have caused massive mortality of corals in many parts of the world. In the context of shoreline protection, the significant mortality is that of the very shallow corals on reef crests and reef flats. It results in a drop in the elevation of the corals, followed by a corresponding drop in the ability of the reef to absorb wave energy, and a consequent increase in the amount of wave energy that reaches the shore.

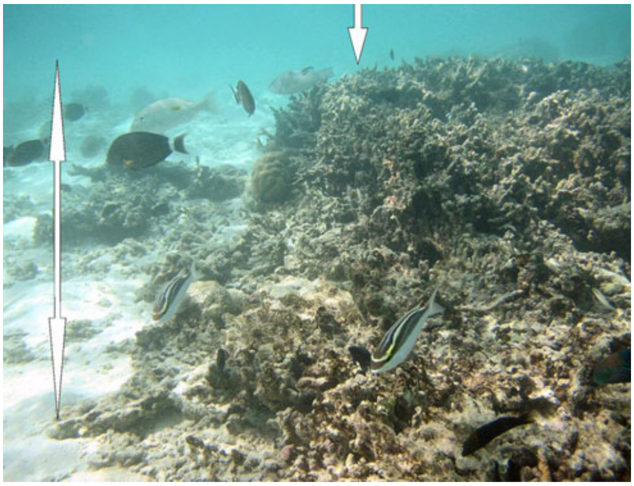
Quantification of the problem: a case study

The effectiveness of the "breakwater" role of reefs is well known in general principle and assumed to be substantial, but has been poorly measured and is difficult to predict. However an example from the Seychelles (Sheppard et al., 2005) has estimated approximate magnitudes. There, concern was expressed about several areas of apparently increased shoreline erosion as well as a smaller number of areas where substantial pulses of sand had been pushed onshore over coastal roads. In 1998, warming in the central granitic islands had caused substantial coral mortality which was not recovering to any significant degree; indeed the reefs appeared to be slowly disintegrating. Prior to the late 1990s, the fringing reefs around the granitic islands had supported a complex ecology, including rich growths of corals. Luxuriant reef flats extended seaward from the sandy coasts of the islands to the reef face, or drop-off. These reef flats supported dense stands of corals (along with patches of seagrass, sand, and rubble) which grew up from the reef flats to the surface of the water at low tide (Figure 2). The horizontal, solid platform of the reef flat on which these corals grew is located



Climate Change: Impact On Coral Reef Coasts, Figure 1 Simplified section of a Geographical Information System map of Anguilla, Eastern Caribbean, showing distribution of dead Elkhorn reef. Map is approximately 500 m^2. The *mid gray color* (see key) was probably all Elkhorn before being killed before the1980s. Further, the darkest gray (bare rock with algae) may also have been Elkhorn but has decayed through erosion sufficiently so as not to be recognisable as such. *Pale gray* is reef dominated by soft corals (Gorgonacea) but with some limited quantities of the reef building *Montastraea* coral. White is various mixtures of seagrass and sandy substrate with some seagrass.

Climate Change: Impact On Coral Reef Coasts, Figure 2 Fringing reef of Praslin Island, Seychelles. Reef flat is 205 m wide, on calm day with small waves breaking at the edge of the reef flat. *Dark patches* underwater are seagrasses to shoreward and dead coral further seaward.



Climate Change: Impact On Coral Reef Coasts, Figure 3 Underwater photograph (2004) of the profile of one of the reefs (off the main island), showing *Acropora* stand which had been dead for about 6 years and which has been progressively disintegrating. *Top arrow* represents distance between low water and the top of the reducing coral stand, *lower arrow* represents the distance between the 2004 upper surface of the coral stand and the plane of the reef flat.

generally 1–2 m below low tide. Typically, perhaps half of any single reef flat was covered by tall branching corals which, by the early 2000s, were dead and slowly disintegrating (Figure 3), with the result that the upper surface of the coral stands was eroding and dropping relative to sea level (Figure 4).

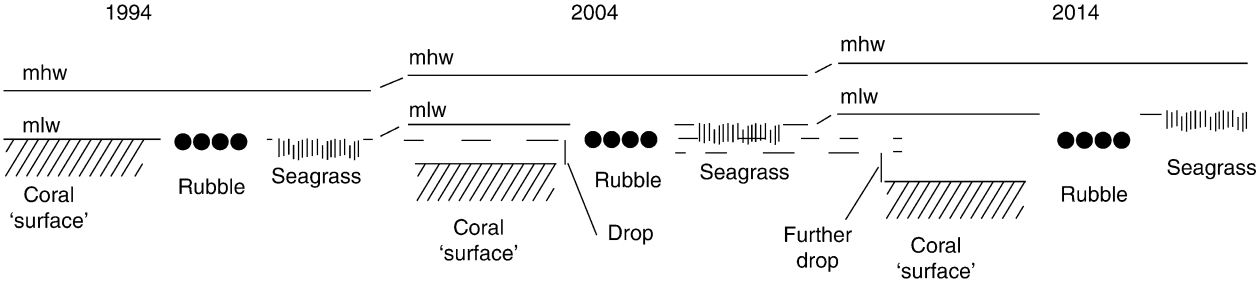
Wave set up, transformation, and propagation to the shore on coral reefs have been researched by Gourlay and colleagues (Gourlay, 1994, 1996a, b, 1997; Gourlay and Colleter, 2005; Massel and Gourlay, 2000), based on both laboratory experiments and field measurements (Hardy et al., 1990; Hardy and Young, 1996). Important factors include the width of the reef flat; the proportion of the reef flat covered by corals; the depth in calm water conditions of both the tops of the coral stands and their base relative to the platform and sea level; and the height of the coral stand (pre- and post-mortality and collapse). Equations can be derived to predict the wave-forced, raised water level on reef flats resulting from wave breaking. This in turn depends on offshore wave height and period, and the decay of energy from reef edge to shoreline. Sea level rise may be factored in, as well as rounding and smoothing of the reef crest and reef flat as corals die and disintegrate.

In the Seychelles study it was found that the main driver of change in wave energy reaching shores was the "pseudo-sea level rise" created by increased depth resulting from disintegration of coral colonies. An additional factor was a reduction in rugosity as irregular and rough coral colonies slowly became converted to a smoother plane. Also taken into account was the proportion of each section of reef flat that was covered by corals (areas covered by seagrass or sand were treated differently by assuming either no change or by assuming that seagrass beds can grow vertically in response to changing water levels). In a before and after comparison (all coral stands reaching the low water surface compared to complete disintegration of the corals) the reduced roughness and greater depth resulted in much greater wave energy reaching the shore (Figure 5). Mitigating against the rising energy reaching the shore to some degree was coral mortality at the reef crest. Disintegration of these corals rounded off the reef in that area, affecting the initial wave set-up, in some cases changing reef morphology so that formerly distinctive reef flat, crest, and slope became blended together over a near-indistinguishable boundary. Reef flats with partial disintegration of previously abundant corals permitted about 20–60% more energy to strike the shoreline, whereas total disintegration permitted an additional 75% energy. An average 7–8% reached the shore before the mass coral mortality, about 11% in 2004, and a predicted 18% will reach the shore when coral attrition is complete. The sequence of events included an initial pulse of sand being created as corals initially died (in 1998), after which it, and the sand on the beach, was removed in an extended erosion phase.

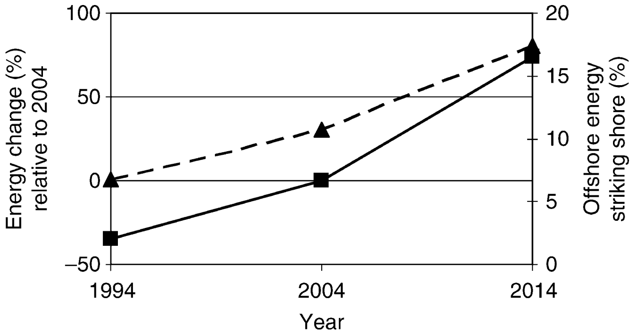
There appear to be no quantitative data for other shoreline areas protected by coral reefs, though the effect is becoming commonplace, with shoreline attrition, especially on many coral atolls, being meters or tens of meters (Figure 6).

Summary

A case study conducted in the Seychelles is described, in which it was estimated that the demise of the shallow



Climate Change: Impact On Coral Reef Coasts, Figure 4 Sketch of measured parameters at the three stages, from left to right: a decade ago, today, and a decade in the future. Note that coral surface drops each decade, while seagrass keeps pace with sea level rise. Bare rock (not shown) remains unchanged in elevation throughout. (From Sheppard et al., 2005.)



Climate Change: Impact On Coral Reef Coasts, Figure 5 Graphs of wave energy reaching shore (average of 14 reefs). *Left*: *Y* axis and *solid line* is change in energy (%) relative to the year of observation. *Right*: *Y* axis and *dashed line* shows percent of offshore energy reaching shore at the three time intervals.

Climate Change: Impact On Coral Reef Coasts, Figure 6 Example of recent shoreline erosion on a coral atoll (Chagos archipelago, Indian Ocean). The dead palm trees are now in the low intertidal zone and show that the land extended considerably to the left of their position - in fact to the exposed ridge on the left of the photo. Horizontal land loss here has been 20–30 m. (Photo Anne Sheppard.)

corals has and will result in an approximate doubling of wave energy striking the previously protected shorelines. This has resulted in substantial erosion with a high cost to the local population.

There are many anecdotal stories of shoreline erosion from around the world, especially around atolls. It is likely that a proportion of them are exaggerated or that the observations made are merely reflecting seasonal changes; it is well known that sandy shorelines behind coral reefs can change by tens of meters or even more on a seasonal basis. However, it is usually not too difficult to distinguish between seasonal changes and unidirectional or progressive changes that have progressed for several years, if only because the latter soon begins to show erosion of previously stable and long-lived shoreline vegetation (Figure 6), and then erosion of built infrastructure. Nevertheless the poor signal-to-noise ratio in matters of shoreline movement is a serious problem, making it difficult, in some cases, to distinguish between the seasonal and storm-driven noise in the system and any underlying, serious progressive trend that may be occurring. What is clear is that all forms of coral damage, whether from local, direct impacts, or from climate change, will reduce the effectiveness of the breakwater effect provided by living coral reefs. Furthermore, in some cases, changes seen to date will be very much less than those predicted for the near future if temperatures continue to rise and if polluting discharges and mechanical extraction continue to reduce the abundance and resilience of coral reefs that fringe shorelines.

Bibliography

Geister, J., 1977. The influence of wave exposure on the ecological zonation of Caribbean coral reefs. In *Proceedings of the 3rd International Coral Reef Symposium*, Vol. 1, pp. 23–29.

Gourlay, M. R., 1994. Wave transformation on a coral reef. *Coastal Engineering*, **23**, 17–42.

Gourlay, M. R., 1996a. Wave set-up on coral reefs. 1. Set-up and wave generated flow on an idealised two dimensional horizontal reef. *Coastal Engineering*, **27**, 161–193.

Gourlay, M. R., 1996b. Wave set-up on coral reefs. 2. Set-up on reefs with various profiles. *Coastal Engineering*, **28**, 17–55.

Gourlay, M. R., 1997. Wave set-up on coral reefs: some practical applications. In *Proceedings of the 13th Australian Coastal and Ocean Engineering Conference*, Christchurch, pp. 959–964.

Gourlay, M. R., and Colleter, G., 2005. Wave-generated flow on coral reefs – an analysis for two dimensional horizontal reef-tops with steep faces. *Coastal Engineering*, **52**, 353–387.

Hardy, T. A., Young, I. R., Nelson, R. C., and Gourlay, M. R., 1990. Wave attenuation on an offshore coral reef. In *Proceedings of the 22nd Coastal Energy Conference, Delft*, Vol. 1, pp. 330–344.

Hardy, T. A., and Young, I. R., 1996. Field study of wave attenuation on an offshore coral reef. *Journal of Geophysical Research*, **101**, 14311–14326.

Massel, S. R., and Gourlay, M. R., 2000. On the modelling of wave breaking and set-up on coral reefs. *Coastal Engineering*, **39**, 1–27.

Rosenberg, E., and Loya, Y. (eds.), 2004. *Coral Diseases*. Springer, p. 500.

Sheppard, C. R. C., Dixon, D. J., Gourlay, M., Sheppard, A. L. S., and Payet, R., 2005. Coral mortality increases wave energy reaching shores protected by reef flats: examples from the Seychelles. *Estuarine, Coastal and Shelf Science*, **64**, 223–234.

Cross-references

Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity
Climate Change: Increasing Storm Activity
Climate Change and Coral Reefs
Engineering On Coral Reefs With Emphasis On Pacific Reefs
Indian Ocean Reefs
Reef Flats
Reef Front Wave Energy
Sea Level Change and Its Effect on Reef Growth

CLIMATE CHANGE: INCREASING STORM ACTIVITY

Joshua Madin
Macquarie University, NSW, Sydney, Australia

Synonyms

Increasing ecological disturbance; Increasing tropical cyclone (hurricane, typhoon) frequency and intensity

Definition

An increase in the intensity and/or frequency of storms relative to a predefined expectation (e.g., historic yearly average or quantile).

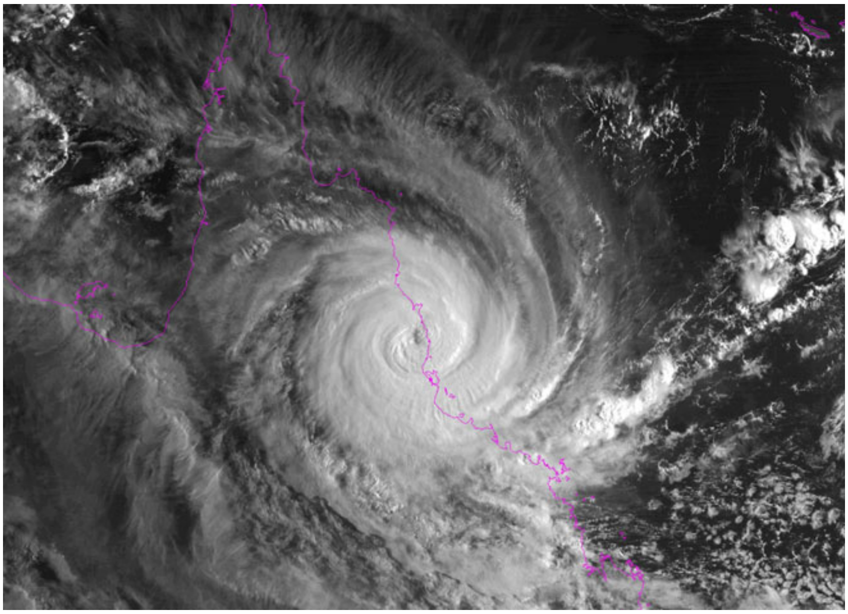
Introduction

Increasing storm activity is a hypothesized consequence of climate change that results predominantly from warming sea surface temperatures (SST). Significant scientific debate revolves around whether or not the storm activity is increasing and, if so, whether any increases are a consequence of global warming. This debate exists primarily because detecting such trends depends on the temporal and spatial scales examined, the duration and quality of available meteorological records, and the kinds of statistical and mathematical approaches used in analyses. Storms temporarily alter the physical state of coral reefs in a number of direct and indirect ways (see *Tropical Cyclone/Hurricane*). Direct examples include changes in salinity (via rainfall) and impinging wave climate (via wind). Indirect examples include increased terrestrial runoff and associated changes in turbidity, chemistry, and human-induced pollution levels. By altering the physical state of ecological communities, storms are an important form of ecological disturbance that significantly shape ecological systems and are hypothesized to be at least partially responsible for the levels of species diversity. Increasing storm activity will drive changes in the biological and physical structure of coral reefs, and in turn the ecology of organisms that rely of on the reef habitat for shelter. Although some studies have forged mechanistic links between storm activity and coral reef vulnerability, the impacts of increasing storm activity on coral reef ecology and physical structure of reefs remain largely unknown (Figure 1).

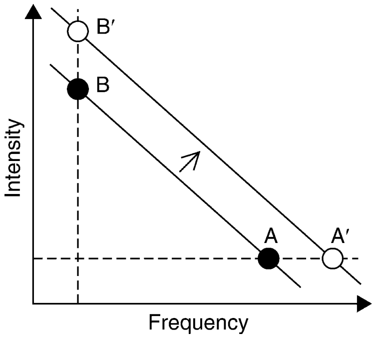
Evidence

Theory suggests that tropical storm activity should increase with global mean temperature as warmer seas fuel tropical storm generation (Emanuel, 1991). While growing evidence strongly suggests that SST is increasing in tropical seas (see *Temperature Change: Bleaching*), evidence for increasing storm activity is less clear cut. Part of the reason for this uncertainty is that storm activity is comprised of two components that must be considered simultaneously: storm intensity and storm frequency (Figure 2). In general, more intense storms are less frequent (e.g., yearly cyclones) and less intense storms are more frequent (e.g., daily to weekly squalls). An increase in storm activity would theoretically shift this relationship upward (illustrated by the arrow in Figure 2). Such a shift can be interpreted in two ways. First, storms of a given intensity would increase in frequency within a given time period (A to A’, Figure 2; e.g., an increase in the number of category 3 cyclones each year). Second, storms of a given frequency would increase in intensity (B to B’, Figure 2; e.g., the largest yearly storm is more intense on average).

Early attempts to detect changes in storm activity focused on frequency and uncovered no clear trends. In fact, a more recent modeling effort suggests that Atlantic tropical storm frequencies might even decrease under future greenhouse-gas-induced warming (Knutson et al., 2008). Despite possible decreases in storm frequencies, studies (including Knutson et al., 2008) have shown that storm intensity is increasing. For instance, Emanuel (2005) looked at storm power dissipation (a measure of the total energy generated by a storm) and found it to be highly correlated with temperature, reflecting global warming. These results appear paradoxical according to Figure 2: how can tropical storm intensity increase but yearly frequency decrease or stay unchanged? The answer becomes apparent when looking at the distributions and extremes of yearly storm intensities rather than averages (Gaines and Denny, 1993). In a study looking at the maximum wind speeds generated by tropical cyclones, Elsner



Climate Change: Increasing Storm Activity, Figure 1 Cyclone Larry crosses the Great Barrier Reef, Australia, in 2006 (MTSAT-1R: Satellite image originally processed by the Bureau of Meteorology from the geostationary satellite MTSAT-1R operated by the Japan Meteorological Agency).



Climate Change: Increasing Storm Activity, Figure 2 A schematic of the general inverse relationship (*bottom solid line*) between storm intensity and frequency, the two components of storm activity. Increasing storm activity would result in the relationship moving outwards (*top solid line*). See text for details.

et al. (2008) show that, while there is no trend in frequency nor the average maximum wind speed of yearly cyclones, the upper quantiles of maximum wind speeds indeed increase from year to year. That is, in each year a similar number of tropical storms reach "cyclonic" status and the maximum wind speeds generated by storms are similar on average; however, the maximum winds speeds of the largest storms are increasing. Simulations by Knutson and Robert (2004) support this idea, finding that warming induced by greenhouse gas entrapment may lead to increasing occurrence of highly destructive category 5 storms. Furthermore, Hoyos et al. (2006) link the increasing trend in number of category 4 and 5 hurricanes for the period 1970–2004 directly to the trend in sea surface temperatures. However, Emanuel et al. (2008) concludes in a reanalysis of data from his 2005 study that the increase in power dissipation in recent decades cannot be completely attributed to global warming.

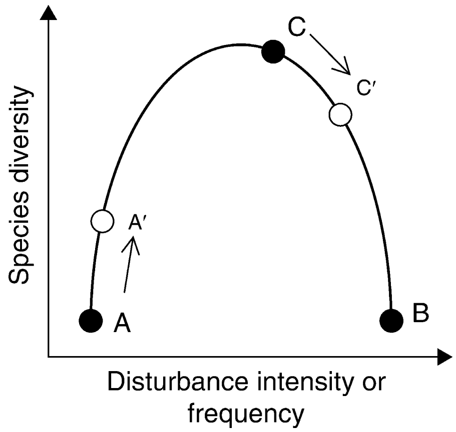
In summary, despite the growing evidence that the distribution of tropical storm intensities per year has stretched upward, the link between increasing storm activity and global warming remains unclear. The World Meteorological Organization (2006) state in a press release that "though there is evidence both for and against the existence of a detectable anthropogenic signal in the tropical cyclone climate record to date, no firm conclusion can be made on this point" and that "no individual tropical cyclone can be directly attributed to climate change."

Conclusions: consequences for coral reefs

Storms have a number of direct and indirect effects on coral reefs. Direct effects include mechanical damage and sedimentation to corals and reef structures by waves, storm surges, and currents, as well as lowered salinity by torrential rainfall (Woodley et al., 1981; Massel and Done, 1993; Madin and Connolly, 2006; Fabricius et al., 2008). Indirect effects include pollution and sedimentation caused by terrestrial runoff (Fabricius, 2005). Storms also have sub-lethal effects on the reef-building corals, such as physiological stresses that can lead to decreased growth, competitive ability, and reproduction as well as increased susceptibility to disease and bleaching.

One way to conceptually illustrate the influence of increasing storm activity on coral reef biodiversity is via the Intermediate Disturbance Hypothesis (IDH; Connell, 1978). According to this hypothesis, a patch of reef that is exposed to mild and/or infrequent disturbances is likely to become dominated by one or a few species (the stronger competitors), resulting in low species diversity (point A in Figure 3) because these low-level storms rarely remove the dominant corals to create an empty space for new species to settle. On the other hand, very few species are able to survive extreme and/or frequent disturbance events, such as unusually high wave forces, bombardment and scouring by waterborne objects, and/or lowered salinity, also resulting in low species diversity (point B, Figure 3). As a result, species diversity tends to be highest on average at some intermediate disturbance level (e.g., near point C, Figure 3).

Assuming that the IDH provides a reasonable approximation for the relationship between the storm-induced disturbances and coral diversity, then increasing storm activity will affect the diversity of different reefs in different ways. For example, diversity might be expected to *increase* in benign reef patches that currently have low levels of diversity due to recent history of low disturbance (A to A’, Figure 3). Conversely, diversity is expected to *decrease* on those portions of reef patches that currently have high diversity due to a recent history of intermediate disturbance (C to C’, Figure 3). In order to make predictions about how reefs might change if storm activity were to increase, Madin et al. (2008) use an engineering model to measure the mechanical vulnerability of different colony shapes to storms. They show that, if storm activity increases and/or ocean acidification weakens carbonate structure (see *Ocean Acidification, Effects on Calcification*), future reefs will have fewer corals and be dominated by small and simple forms, which will in turn support lower levels of whole-reef biodiversity than do present-day reefs.



Climate Change: Increasing Storm Activity, Figure 3 A schematic representation of the Intermediate Disturbance Hypothesis. See text for details.

In summary, even through the use of a simple model (the IDH), it becomes clear that the influence of increasing storm activity on coral reef systems is likely to be complex and dependent on many factors, including history (e.g., past disturbance regimes; see *Historical Ecology of Coral Reefs*), plant and animal biology and biomechanics, dispersal to other reefs, growth plasticity (responsiveness to the environment), and, if changes are sufficiently gradual, adaptation (generational shifts in characteristics that improve survival; see *Adaptation*).

Bibliography

Connell, J. H., 1978. Diversity in tropical rainforests and coral reefs. *Science*, **199**, 1302–1310.

Elsner, J. B., Kossin, J. P., and Jagger, T. H., 2008. The increasing intensity of the strongest tropical storms. *Nature*, **455**, 92–95.

Emanuel, K. A., 1991. The theory of hurricanes. *Annual Review of Fluid Mechanics*, **23**, 179–196.

Emanuel, K., 2005. Increasing destructiveness of tropical cyclones over the past 30 years. *Nature*, **436**, 686–688.

Emanuel, K., Sundararajan, R., and Williams, J., 2008. Hurricanes and global warming: Results from downscaling IPCC AR4 simulations. *Bulletin of the American Meteorological Society*, **89**, 347–367.

Fabricius, K. E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin*, **50**, 125–146.

Fabricius, K. E., De’ath, G., Puotinen, M. L., Done, T., Cooper, T. F., and Burgess, S. C., 2008. Disturbance gradients on inshore and offshore coral reefs caused by a severe tropical cyclone. *Limnology and Oceanography*, **53**, 690–704.

Gaines, S. D., and Denny, M. W., 1993. The largest, smallest, highest, lowest, longest, and shortest: Extremes in ecology. *Ecology*, **74**, 1677–1692.

Hoyos, C. D., Agudelo, P. A., Webster, P. J., and Curry, J. A., 2006. Deconvolution of the factors contributing to the increase in global hurricane intensity. *Science*, **312**, 94–97.

Knutson, T. R., and Robert, E. T., 2004. Impact of CO2-induced warming on simulated hurricane intensity and precipitation: Sensitivity to the choice of climate model and convective parameterization. *Journal of Climate*, **17**, 3477–3495.

Knutson, T. R., Sirutis, J. J., Garner, S. T., Vecchi, G. A., and Held, I. M., 2008. Simulated reduction in Atlantic hurricane frequency under twenty-first-century warming conditions. *Nature Geoscience*, **1**, 359–364.

Madin, J. S., and Connolly, S. R., 2006. Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature*, **444**, 447–480.

Madin, J. S., O’Donnell, M. D., and Connolly, S. R., 2008. Climate-mediated mechanical changes to post-disturbance coral assemblages. *Biology Letters*, **4**, 490–493.

Massel, S. R., and Done, T. J., 1993. Effects of cyclone waves on massive coral assemblages on the Great Barrier Reef: Meteorology, hydrodynamics and demography. *Coral Reefs*, **12**, 153–243.

Woodley, J. D., Chornesky, E. A., Clifford P. A., Jackson, J. B. C., Kaufman, L. S., Knowlton, N., Lang, J. C., Pearson, M. P., Porter, J. W., Rooney, M. C., Rylaarsdam, K. W., Tunnicliffe, V. J., Wahle, C. M., Wulff, J. L., Curtis, A. S. G., Dallmeyer, M. D., Jupp, B. P., Koehl, M. A. R., Neigel, J., and Sides, E. M., 1981. Hurricane Allen’s impact on Jamaican coral reefs. *Science*, **214**, 749–755.

World Meteorological Organization, 2006. Summary Statement on Tropical Cyclones and Climate Change. Press release

Cross-references

Adaptation
Climate Change and Coral Reefs
Ecomorphology
Historical Ecology of Coral Reefs
Ocean Acidification, Effects on Calcification
Temperature Change: Bleaching
Tropical Cyclone/Hurricane
Waves and Wave-Driven Currents

COCOS (KEELING) ISLANDS

Colin D. Woodroffe
University of Wollongong, Wollongong, NSW, Australia

Definition

The Cocos (Keeling) Islands are a remote group of islands, forming a single horseshoe-shaped atoll and an isolated island, North Keeling, in the eastern Indian Ocean. They represent the only atoll that Charles Darwin visited and became central to his theory of coral reef development, and have played a central role in several subsequent debates about reef development in relation to sea level.

Introduction

The Cocos (Keeling) Islands are an Australian Territory in the eastern Indian Ocean, and comprise an atoll that has had a particularly significant place in the development of coral reef studies. This was the only coral atoll that Charles Darwin visited during the voyage of the *Beagle*, and it therefore played a particularly central role in his theory of reef development. It was subsequently visited by several other naturalists. The horseshoe-shaped atoll has a series of sandy reef islands around its rim and a central lagoon that is relatively well flushed during southeast tradewinds, but incompletely flushed during times when winds blow from the northwest.

History

The Cocos (Keeling) Islands were probably first sighted by Captain William Keeling in 1609. Captain James Clunies Ross visited the islands in 1825 and cleared some vegetation for a settlement. Clunies Ross worked for Alexander Hare who settled on the islands in 1826 with a small entourage of workers, and Clunies Ross himself returned in 1827 and commenced an alternative settlement. Relations between Clunies Ross and Hare deteriorated until Hare left the islands in 1831, after which Clunies Ross' family, known as "Kings of the Cocos," ran the islands as a coconut plantation. In 1955, they became a territory of Australia, and in 1978 the Australian government purchased all the land, except Oceania House, Clunies Ross' residence, and the surrounding grounds.

The atoll became particularly associated with coral reefs because it was visited from 1 to 12 April 1836 by Charles Darwin aboard *HMS Beagle*. During the voyage across the Pacific, Darwin had deduced his remarkable "subsidence" theory of coral reef development in which he considered that a mid-ocean volcanic island would first be encircled by a fringing reef, but that through gradual subsidence of the volcanic basement and vertical growth of the surrounding reef, this would progress through a barrier reef stage, ultimately becoming an atoll. Darwin made a number of insightful observations on the Cocos (Keeling) Islands, but he was particularly pleased because he felt that shoreline erosion and undercutting of coconut trees on West Island supported his theory that the atoll was slowly subsiding. Cocos featured prominently in Darwin's book on coral reefs (Darwin, 1842).

The Cocos (Keeling) Islands were subsequently visited by several other naturalists, in some cases advocating support for alternative theories (Woodroffe and Berry, 1994). Particularly, detailed observations of the reef islands and an estimate of the sediment budget were made by Henry Brougham Guppy during 1888 (Guppy, 1889). Guppy's visit was funded by John Murray and several of his observations consequently supported an alternative view advocated by Murray that atolls built out horizontally through progradation of the reef front. A descriptive account of the islands appeared in a book entitled *Coral and atolls* by Wood-Jones, who spent a year there as the medical doctor during 1905–1906 (Wood-Jones, 1912). Extensive collections of the fauna and an analysis of the historical significance of Clunies Ross' writings were undertaken by Gibson-Hill (1953) and an account of Darwin's time on the atoll was compiled by Armstrong (1991).

Atoll morphology and physical characteristics

The Cocos (Keeling) Islands comprise a southern horseshoe-shaped atoll (South Keeling Islands, hereafter referred to as Cocos) with more than 20 sandy reef islands around a shallow lagoon (Figure 1), and a northern reef island with a small remnant lagoonlet, North Keeling. These rise from an ocean floor that is about 5,000-m deep, and are the only seamounts within the discontinuous Vening Meinesz chain to reach sea level, making Cocos one of the more isolated atolls.

Cocos is dominated by the southeast trade winds and has persistent swell from the southeast for most of the year, refracting around the atoll but breaking on the entire perimeter. Tidal range is 1.1 m at springs, and the atoll is influenced by occasional tropical cyclones, although there is little evidence of severe storms on the reef flat which does not have large reef blocks or shingle ridges typical of more storm-prone atolls in the Pacific. During short periods, particularly in El Niño years when there are only light winds from the northwest, lagoonal flushing is reduced and episodes of fish kill and coral death have been recorded.

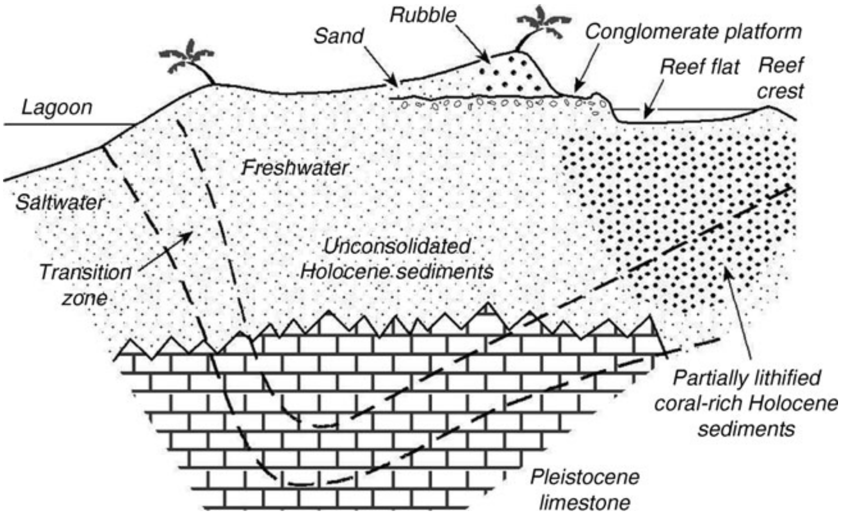
Cocos (Keeling) Islands, Figure 1 A SPOT satellite image of the main atoll of the Cocos (Keeling) Islands, showing the horseshoe-shaped rim on which the reef islands occur. The lagoon is 8–14-m deep in the north, but contains a reticulate pattern of reefs and numerous blueholes in its southern part, with incursion of sand carried across the reef flat and deposited as sand aprons at the lagoonward terminus of interisland passages. The dark, purplish blue areas in the lee of the two elongate islands (West Island and South Island) are seagrass-covered sand flats (Image sourced from the Cocos (Keeling) Islands Geographical Information System, Geoscience Australia).

Atoll rim and Lagoon

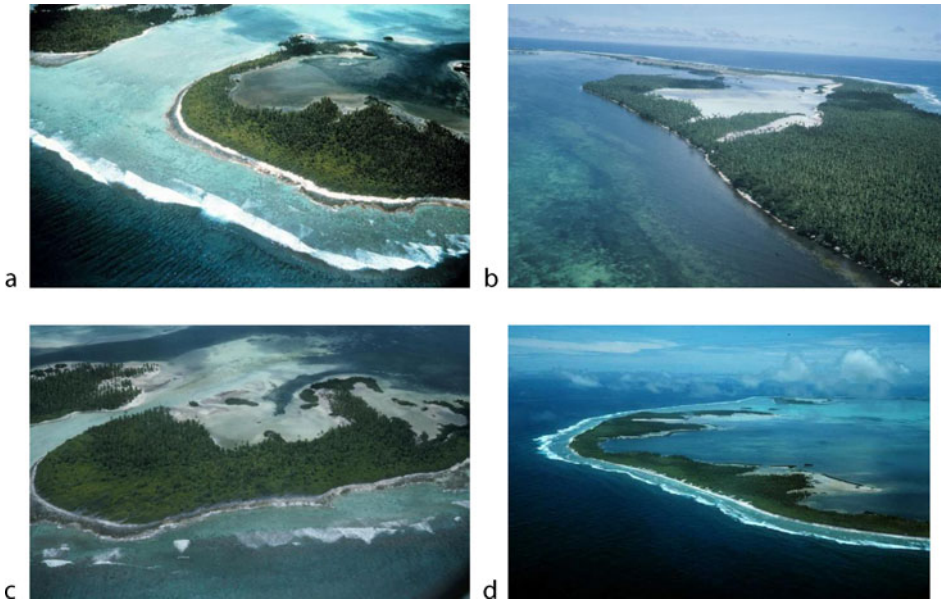
The horseshoe-shaped rim of the atoll is near continuous except in the northern part where there are openings 12–14-m deep, on the western and eastern side of Horsburgh Island. Drilling and radiocarbon dating indicate that the Holocene rim has accumulated over the Last Interglacial reef limestone encountered at depths of 10–14 m below sea level (Woodroffe et al., 1994) (Figure 2). This older limestone, which represents the rim of an atoll that formed the last time the sea was at or close to its present level, is extremely porous and it plays a significant role in the groundwater hydrology of the atoll (Woodroffe and Falkland, 1997).

The lagoon covers about 190 km^2 and comprises a number of distinct areas. There are shallow sand flats that occur in the lee of South Island, which dry at lowest tides, and support a cover of seagrass. Much of the southern part of the lagoon comprises a reticulate pattern of reefs, some of which are 0–3-m deep, others which are exposed at the lowest tide. This network of reefs separates deeper holes, termed blueholes. These reach 20 m or more deep and have a sporadic cover of branching or foliose corals, much of which is dead. They harbor sharks in their murky waters. The northern lagoon is 8–12-m deep and floored largely with sandy sediments.

The lagoon is incompletely flushed because the interisland passages are shallow and many dry at low tide (Figure 3a), limiting their effectiveness for the exchange of water from the ocean (Kench, 1998; Kench and McLean, 2004). Sediment is carried into the lagoon and there are sand sheets that are gradually infilling the southernmost blueholes (Smithers et al., 1993). Minor lagoonlets, termed teloks (Figure 3b), occur on the lagoon side of the larger elongate islands. These are very shallow and muddy areas separated from the ocean by a ridge.



Cocos (Keeling) Islands, Figure 2 Schematic cross-section of the atoll (based on drilling results in Woodroffe et al., 1994). The depth at which the underlying Pleistocene limestone is encountered varies from 8 to 14 m, and reef islands are up to 800-m wide.



Cocos (Keeling) Islands, Figure 3 Aerial oblique views of the rim of Cocos: (**a**) Pulu Pandan and the passage to the south of it, on the eastern rim of the atoll; (**b**) West Island showing the telok (lagoonlet); (**c**) one of the smaller islands on the eastern rim of the atoll; (**d**) South Island (Photos C. Woodroffe).

There are minor ridges developed on the lagoon shore, and the teloks experience restricted exchange of water with the lagoon. A similar sequence of ridges, resembling a crab claw, extend on either side of the southern passage, and the distinct succession of ridges that extend from the southeastern shore of West Island appears to be gradually decreasing water movement over the intertidal flats in their lee.

There are extensive areas of the atoll rim and of the lagoon flats that are intertidal and which shoal, or dry, at the lowest tides (Figure 3c). These have provided an environment in which large colonies of *Porites*, including both a massive species and a branching species, have grown upward to a point at which their upward growth is constrained by exposure during the lowest tides. This microatoll growth form was first described from Cocos by Guppy, and has become a focus for research, because the upper surface provides a low-resolution record of past water level. Extensive survey of these corals around the margin of Cocos has shown the subtle variations that exist in the elevation at which this upper limit to coral growth occurs (Smithers and Woodroffe, 2000). The upper surface morphology across two of the larger specimens has enabled an insight into water-level changes relative to this atoll over the past century, indicating minor oscillations in the limit of coral growth and a slight rise in water level that is generally less than that inferred from tide gauges from around the world (Smithers and Woodroffe, 2001).

Reef islands

Figure 1 shows a SPOT satellite image of the horseshoe-shaped atoll and the islands on its rim (Figures 4a and 4b). There are two major elongate islands, West Island and South Island which occupy about 60% of the southern rim of the main atoll (Figure 3d). The remainder are small crescent-shaped islands, separated by inter-island passages, most of which shoal at low tide. Horsburgh Island on a lone reef at the north of the atoll, is shaped by wave refraction and reaches elevations of 3–4 m. The majority of islands are perched on a conglomerate platform. Guppy (1889) suggested that this represented a former reef flat, a view supported by Woodroffe et al. (1990). Conglomerate platform (termed brecciated coral-rock by Darwin (Figure 4c), reef conglomerate by Guppy and breccia platform by Wood-Jones) generally reaches up to 0.5 m above MSL, although locally reaching 1 m, and is inundated by waves at the highest tides.

Radiocarbon dating of fossil corals from within the conglomerate indicates that it was formed 4,000–3,000 years BP (Woodroffe et al., 1994). Locally, several corals in their growth position have been identified growing at an elevation above that to which they are presently able to grow. Several of these corals are massive *Porites* that adopted a microatoll form, whereas others are branching *Porites*. These corals provide evidence that the former reef flat was formed around 3,000 years ago when the sea was 50–80 cm higher than it is now with respect to Cocos (Woodroffe et al., 1990).

Darwin drew a schematic cross-section of "Keeling atoll" (although Darwin's notes indicate that the cross-section was not actually of Cocos, but of Whitsunday Atoll) showing the prominent algal rim (at the reef crest), a near horizontal reef flat, the conglomerate platform (which he termed ledge of coral rock) (Figure 4c), and

Cocos (Keeling) Islands, Figure 4 Characteristic shorelines of Cocos: (**a**) Trannies beach at the northern end of West island; (**b**) a broad reef flat on the eastern rim; (**c**) extensive conglomerate on the southwestern end of Horsburgh Island; (**d**) beachrock at the southern end of West Island (Photos C. Woodroffe).

the seaward ridge of the island, steeper on the oceanward side and sloping gradually toward the lagoon. Figure 2 shows a typical section of the eastern rim of the atoll. Many of the islands show the typical cross-sectional morphology that was sketched by Darwin, comprising an oceanward ridge crest, a lower-lying central area, and a less prominent lagoonward ridge. Islands are predominantly sandy, although with shingle in some places, and coral boulders along the oceanward shore of those on the eastern rim where the reef flat is narrowest. There are a number of outcrops of beachrock, bedded dipping parallel to the modern beach, along several of the oceanward beaches (Figure 4d), and occasional outcrops of cay sandstone, which is horizontally bedded and less well lithified.

Darwin inferred different formative processes for islands on windward and leeward sides of the atoll. On the windward (eastern) side he considered that islands accreted solely by addition of material on the oceanward shores, whereas on the leeward (western) side he envisaged that island growth resulted from a combination of oceanward accretion, augmented by lagoonward addition of sediment by waves from the lagoon. By this mechanism, Darwin accounted for the wider islands on the leeward of the atoll. Radiocarbon dating has provided some support for this pattern of accretion on West Island which seems to have accumulated primarily by oceanward accretion, but also with some lagoonward growth (Woodroffe et al., 1999). The crescent-shaped islands on the eastern margin of Cocos were described in detail by Guppy (1889) who proposed a model for their growth involving spit elongation driven by unidirectional currents through the inter-island channels. This evolutionary model has not been fully tested by dating.

Islands are highest along their oceanward side. The oceanward beach ridge is generally 3–4 m above MSL; however, in some places the fine sand is winnowed from the beach by wind and the beach ridge is topped by a dune. Such dunes are not typical of atoll reef islands in general. South Island has a dune ridge 6–7-m high, reaching as high as 11 m on the southwestern corner of South Island. West Island, which remains the administrative center, has an oceanward ridge that is characteristically 3–4 m above MSL (much of the southern part of this island has been altered during runway construction), but rises to 7 m above sea level in the area where residential buildings have been constructed on a dune. On Home island, where the Cocos Malay kampong is found, the oceanward ridge generally reaches an elevation of 3 m above MSL, but at one location a dune rises up to 5 m (Woodroffe and McLean, 1994).

Summary

The Cocos (Keeling) Islands consist of the main atoll of Cocos, and the isolated North Keeling (Pulu Keeling) which is Australia's smallest Commonwealth National Park. These rise from deep water, and the southern atoll consists of a near continuous rim with linear islands on the southern margin and a series of crescentic islands on the eastern side. The islands are anchored in their present location by an underlying conglomerate platform that was formed as a reef flat in mid Holocene when the sea level was higher than present. The islands themselves are largely sand, with restricted dune development on the most exposed oceanward shore. Their elevation is generally 3–4 m above modern sea level, and as the latest tide gauge, installed in 1992, shows evidence of sea-level rise, signs of inundation in the lowest-lying areas may be an omen of more frequent flooding in future (Woodroffe, 2008).

Bibliography

Armstrong, P., 1991. Under the Blue Vault of Heaven: A study of Charles Darwin's Sojourn in the Cocos (Keeling) Islands. Indian Ocean Centre for Peace Studies, Western Australia, 120 pp.

Darwin, C., 1842. *The Structure and Distribution of Coral Reefs*. Smith, London: Elder and Co., 214 pp.

Gibson-Hill, C. A. (Editor), 1953. Documents relating to John Clunies Ross, Alexander Hare and the settlement on the Cocos-Keeling Islands. *Journal of the Malayan Branch of the Royal Asiatic Society*, **25**, 306.

Guppy, H. B., 1889. The Cocos-Keeling islands. *Scottish Geographical Magazine*, **5**, 281–297, 457–474, 569–588.

Kench, P. S., 1998. Physical processes in an Indian Ocean atoll. *Coral Reefs*, **17**, 155–168.

Kench, P. S., and McLean, R. F., 2004. Hydrodynamics and sediment flux of hoa in an Indian Ocean atoll. *Earth Surface Processes and Landforms*, **29**, 933–953.

Smithers, S. G., and Woodroffe, C. D., 2000. Microatolls as sea-level indicators on a mid-ocean atoll. *Marine Geology*, **168**, 61–78.

Smithers, S. G., and Woodroffe, C. D., 2001. Coral microatolls and 20th century sea level in the eastern Indian Ocean. *Earth and Planetary Science Letters*, **191**, 173–184.

Smithers, S. G., Woodroffe, C. D., McLean, R. F., and Wallensky, E., 1993. Lagoonal sedimentation in the Cocos (Keeling) Islands, Indian Ocean. In *Proceedings of the 7th International Coral Reef Symposium*, Guam, pp. 273–288.

Wood-Jones, F., 1912. *Coral and Atolls: A History and Description of the Keeling-Cocos Islands, with an Account of Their Fauna and Flora, and a Discussion of the Method of Development and Transformation of Coral Structures in General*. London: Lovell Reeve, 392 pp.

Woodroffe, C. D., 2008. Reef-island topography and the vulnerability of atolls to sea-level rise. *Global and Planetary Change*, **62**, 77–96.

Woodroffe, C. D., and Berry, P. F., 1994. Scientific studies in the Cocos (Keeling) Islands: an introduction. *Atoll Research Bulletin*, **399**, 1–16.

Woodroffe, C. D., and McLean, R. F., 1994. Reef Islands of the Cocos (Keeling) Islands. *Atoll Research Bulletin*, **403**, 1–36.

Woodroffe, C. D., and Falkland, A. C., 1997. Geology and hydrogeology of the Cocos (Keeling) Islands, Indian Ocean. In Vacher, H. L., and Quinn, T. M. (eds.), *Geology and Hydrogeology of Carbonate Islands*. Amsterdam: Elsevier, pp. 885–908.

Woodroffe, C. D., McLean, R. F., Polach, H., and Wallensky, E., 1990. Sea level and coral atolls: Late Holocene emergence in the Indian Ocean. *Geology*, **18**, 62–66.

Woodroffe, C. D., McLean, R. F., and Wallensky, E., 1994. Geomorphology of the Cocos (Keeling) Islands. *Atoll Research Bulletin*, **402**, 1–33.

Woodroffe, C. D., McLean, R. F., Smithers, S. G., and Lawson, E., 1999. Atoll reef-island formation and response to sea-level change: West Island, Cocos (Keeling) Islands. *Marine Geology*, **160**, 85–104.

Cross-references

Atolls
Blue Hole
Conglomerates
Darwin, Charles (1809–1882)
Eastern Indian Ocean – Northern Sector
Indian Ocean Reefs
Microatoll
Subsidence Hypothesis of Reef Development

COLD-WATER CORAL REEFS

André Freiwald
Senckenberg Meeresgeologie, Wilhelmshaven, Germany

Synonyms

Deep-water coral reefs

Definition

Cold-water coral reef. Qualitative term depicting the general contrast to warm-water coral reefs in the tropics and subtropics. The ambient seawater temperature range of known cold-water reefs is 4–14°C. The primary framework is constructed by colonial, azooxanthellate Scleractinia.

Deep-water coral reef. Qualitative term describing the general bathymetric setting of these reef systems, which is deeper than 40 m water depth but with the majority thriving in 200–1500 m depth.

Introduction

Since Linnean times in the eighteenth century, it is known that azooxanthellate corals form substantial aggregations in cold and deep waters and in geographic regions far beyond the shallow-water coral reef belt of the lower latitudes. Until the 1970s, research and sampling of corals in deep waters was restricted to single beam echo soundings and dredge hauls. First visual documentations of this type of ecosystem came from drop cameras and few manned submersible operations, which shed more light in some cold-water reef environments (Squires, 1963; Wilson, 1979). The development of advanced hydro-acoustic sounding systems, such as swath bathymetry and the wider assessment of remotely operated vehicles (ROVs), initiated a worldwide burst to study cold-water coral ecosystems all over the world supported by multinational strategic research programs, which attracted biologists, geologists, and oceanographers to better understand the environmental controls and functionality of this cosmopolitan type of coral ecosystem. Of the 711 known azooxanthellate scleractinian species, 622 live in water depths deeper than 50 m, but only a small group of 6 species is capable to construct reefal framework with *Lophelia pertusa* and *Madrepora oculata* as the most important cosmopolitan representatives (Messing et al., 2008; Roberts et al., 2009a).

Dimensions and time constraints of cold-water coral reefs

Cold-water coral reefs are self-sustained and spatially well-defined coral framework-sediment systems measuring tens of meters to kilometers in lateral extension and up to 40 m in thickness, thus influencing local current regimes (Dorschel et al., 2007; Mienis et al., 2007). Most cold-water coral reefs occur in water depths of 200–1500 m, where light is almost reduced or absent, although some reefs exist in much shallower depths due to specific hydrographic conditions, that is, in some upwelling fjord settings (Freiwald et al., 2004; Försterra et al., 2005; Roberts et al., 2006). Reefs generally occur in groups of hundreds if not thousands in a given area like on many places of the Norwegian continental shelf, or off Apulia, Ionian Sea (Fosså et al., 2005; Savini and Corselli, 2010). A focus on the Norwegian coral systems may underpin the substantial reef-constructing capability of these unexpectedly large coral build-up seabed structures. The last glacial ice shields vanished from the shelf about 13–12 ka ago, and the first appearance of *Lophelia* corals was dated 11 ka, short after the last major cold spell, the Younger Dryas Event, from one of the northernmost coral reef provinces in northern Norway (Lopez Correa, unpublished data). This coral age and the high latitudinal position coincides with the onset of the modern oceanographic regime in the north eastern Atlantic, the full establishment of the poleward flowing Atlantic Current system, which seemingly had carried coral larvae as North as to the Stjernsund, Finnmark District. This allows the following assumption. All the cold-water reefs in Norwegian shelf and fjord settings formed within the past 11 ka. This is a relatively short time span to develop mature biogenic seabed structures with the dimensions given above. Performing a first conservative calculation of the $CaCO_3$ flux and production rates for cold-water corals, Lindberg and Mienert (2005) concluded that Norwegian corals contribute with flux and production rates reaching 4–12% of that of warm-water reefs. Further south, post-glacial onset of cold-water coral growth in the Porcupine Seabight and southeast Rockall Bank recolonized fossil cold-water carbonate mounds at and after 11 ka, contemporaneously with the onset of the Norwegian coral spread towards the North (Frank et al., 2009). Even further south, cold-water corals fade off just after the Younger Dryas period in the Gulf of Cádiz (Wienberg et al., 2009). The least we can conclude from these data of rise and decline ages is that reef-constructing *Lophelia* and *Madrepora* quickly responds to changing climates and productivity regimes along the northeastern Atlantic continental margin.

Colony, thicket, coppice, reef

Another apparent character is the low diversity of the primary coral framework constructing species. In contrast to warm-water coral reef framework, only one to three colonial scleractinian species form the backbone of cold-water reefal framework in a given area (Stanley and Cairns, 1988), thus acting as typical ecosystem engineers. Most significant framework-forming azooxanthellate scleractinians are *L. pertusa*, *M. oculata*, *Solenosmilia variabilis*, *Goniocorella dumosa*, *Enallopsammia profunda*, and *Oculina varicosa*. The latter species lives with endosymbiotic zooxanthellae in the photic zone but without photo-endosymbionts in aphotic depths (Reed, 2002).

The initiation of what will become a reef eventually with time starts with a dense larval spatfall of one or two of the above-mentioned species within a relatively localized area. After metamorphosis of the settled larvae, the corals develop colonies that steadily intermingle with neighboring colonies with time, thus increasingly monopolizing the seabed to form low-relief *thickets* of 10–30 cm height (Squires, 1964). Such thickets provide support and shelter for other organisms that become attracted to the newly created habitat. The corals protect themselves efficiently against competitors with their anti-fouling ability – the skeleton-overcoating tissue or coenosarc. The tissue spread upon those organisms that try to settle onto the coral skeleton, which subsequently becomes encalcified by tissue-controlled precipitation of faint aragonite layers to entomb the epizoans (Harmelin, 1990; Freiwald and Wilson, 1998). With continuing growth of coral colonies within a thicket, a separation of live from dead and tissue-barren framework induces a further important step in the evolution of a complex ecosystem, which is called the *coppice* stage. The tissue-barren framework is now prone to colonization by other sessile organisms, such as foraminifers, hydrozoans, octocorals, serpulids, molluscs, bryozoans, brachiopods, and a diverse array of sponges among others. Therefore, species richness of the coral-associated assemblage of sessile organisms is more diverse in the tissue-barren part of a coral colony than in the upper live part of the colony resulting in a clear faunal zonation pattern (Freiwald, 2002; Mortensen and Fosså, 2006). Of some importance is the infestation of the tissue-barren coral framework by boring and endolithic organisms, which opens a new dimension in micro-habitat colonization but also tend to weaken the framework stability through bioerosion. Most effective bioeroders are boring alectonid, clionaid, and phloeodictyid sponges, which deeply excavate the coral skeleton, thus facilitating the collapse of a colony or even larger parts of thickets (e.g., Beuck and Freiwald, 2005; Beuck et al., 2007, 2010). In the coppice stage, accumulation of coral fragments and remains of the associated skeletal fauna becomes prominent. However, another pre-requisition is needed to transform coppices into a high-relief reef stage – continuous trapping and baffling of suspended particles advected by the bottom-near current regimes. These imported particles entirely consist of the remains of pelagic organisms, such as planktonic foraminifers, coccolithophorids, and pteropods, or they represent a mixture of pelagic and terrigenous silt and clay particles, which are then called hemipelagic sediments. In any case, the matrix infill between the dead coral framework, either pelagic or hemipelagic, largely contributes to the relief-forming growth of a given reef structure. Without this additive, pure coral framework would disintegrate by processes like bioerosion (see above) and would end as a low-relief coral rubble substrate. Sediment trapping is facilitated by the current velocity decelerating effect of the coral framework, by the mucus binding of particles, and is probably enhanced by large quantities of arborescent agglutinated benthic foraminifers, which live attached to coral skeletons, thus enhancing the baffling capacities considerably (Messing et al., 2008). Particle flux in cold-water coral settings shows a pronounced seasonality as a matter of pelagic production cycles in the fertile surface waters (Duineveld et al., 2007). In general, the current regime at depths of the corals keeps sedimentary particles in suspension and therefore, off-reef sedimentation rates are low if any. The intermingling of biological with geological processes, such as new colonization, coral growth, with subsequent trapping and deposition of suspended fine-grained particles within the loci of coral reefs, is regarded as the main driver to enhance the formation of elevated reef structures within fairly short time scales (Roberts et al., 2006, 2009a and see above).

Coral habitats, some key species and trophic webs

Mature reefs provide a variety of macro- and microscale habitats, which enhance biodiversity compared to adjacent off-reef habitats. According to Mortensen and Fosså (2006), macro-habitats in a typical reef consist of the *live coral zone* on top and upper flanks, then the *dead coral zone*, which consists of older in situ or fragmented coral framework underneath, and at the base, a belt of *coral rubble zone* mixed with background sediments that surround the structure. Micro-habitats are the surfaces of tissue covered living corals, the detritus laden surface of dead corals, the cavities inside dead coral skeleton, and the free space between coral branches. The live coral zone shows only few characteristic species that cope with the protective and reactive coenosarc of the corals. The eunicid polychaete *Eunice norvegica* is regarded as a non-obligate mutualist that takes food from the corals, cleans the polyps from sediment particles, and stimulates precipitation of coral skeleton to build a protective tube inhabited by the worm (Mortensen, 2001). Moreover, *E. norvegica* is able to actively aggregate pieces of small coral colonies, thus enhancing coral patch formation (Roberts, 2005). Another polychaete frequently observed on living corals is the polynoid *Harmothoe oculinarum* (Jensen and Frederiksen, 1992). The rosalinid foraminifer *Hyrrokkin sarcophaga* is known as a common parasite of cold-water corals and associated fauna, such as the file clam *Acesta excavata* (Cedhagen, 1994; Freiwald and Schönfeld, 1996; Beuck et al., 2008). Predatory gastropods in the living coral zone, probably grazing coral tissue and mucus are several coralliophilinid species such as *Babelomurex sentix* and *Coralliophila richardi* (Taviani et al., 2009). Other characteristic grazers commonly observed in the living coral zone are starfishes like *Porania pulvillus* (Wienberg et al., 2008). Sponges strongly associated with live corals are *Hexadella detritifera*, *Lissodendoryx diversichela*, *Hymeraphia verticillata*, and *Mycale lingua* (e.g., van Soest et al., 2005, 2007). None of the species mentioned above is obligate to cold-water corals, but seemingly they occur in greater abundances in this habitat. The dead coral zone shows highest diversity of coral associates (Mortensen and Fosså, 2006), which use the complex coral framework in various ways but mostly as hard substrate. Only focusing on bivalves here, some characteristic species are *A. excavata*, *Asperarca nodulosa*, *Bathyarca pectunculoides*, *Chlamys sulcata*, and *Delectopecten vitreus*, among many others. Moreover, the coral skeleton is utilized by a vast array of boring organisms; the ones which have an endolithic lifestyle among them are fungi, sponges, polychaetes, and bryozoans (see Beuck and Freiwald, 2005; Beuck et al., 2007, 2010; Wisshak et al., 2005).

Along with increasing research efforts on cold-water coral reef systems, it became increasingly clear that especially the framework-building *L. pertusa* acts as an ecological engineer by providing a variety of habitats, shelter, substrates, and by provision of particulate and dissolved organic matter, thereby attracting a myriad of species (Roberts et al., 2009a; Wild et al., 2008). Regional species filing useful for estimations of gamma diversity found with *Lophelia* started with 895 species (see the seminal review of Rogers, 1999), and later on with 1,300 coral-associates. A current database for the HERMIONE Project of the European Commission listed nearly 2,900 species sorted out for synonyms and calibrated taxonomy using the World Register of Marine Species database (www.marinespecies.org; Freiwald, in preparation) of which 140 species were described new to science from this reef system during the past 15 years. The most diverse taxa are crustaceans (493 species), mollusks (420 species), sponges (386 species), cnidarians (338 species), and fishes including sharks and rays (278 species). It should be noted that many taxa are yet not sufficiently treated and validated by experts, and that even in well-studied coral sites sampling efforts are yet under-representative to provide a solid base for quantitative biodiversity studies to better understand the entire community and their ecological functioning. Most advanced biodiversity studies from cold-water reefs were provided by Jonsson et al. (2004) from the Swedish Kosterfjord, from Mortensen and Fosså (2006) comparing several reefs from within and off the Norwegian Trondheimsfjord, and from Roberts et al. (2009b) with a study on the Scottish Mingulay reef system.

Unlike warm-water reefs, which also rely on solar radiation as intimate energy resource, cold-water coral reefs are largely dependent on the export of organic matter from primary production in photic surface waters to the seafloor (Duineveld et al., 2007; Davies et al., 2009). In a first comprehensive study of the trophic food web and food supply from coral habitats along the southeastern Rockall Bank slope, Duineveld et al. (2007) noted a remarkable paucity of deposit-feeders compared to abyssal communities and a short trophic length of the food chain dominated by filter-feeders, added by predators and scavengers. The major food source is from suspended particles. However, our present knowledge is limited if not contradictory as to what extent zooplankton forms a significant part of the suspended load (see Duineveld et al., 2007 for discussion).

Summary

In the recent years, knowledge on the general distribution, biology, geology, and hydrography has generated a wealth of information on the subject of cold-water coral reefs and their associated communities through the application of state-of-the-art marine instrumentation (Roberts et al., 2009a). Cold-water coral reefs are formed by a small group of colonial azooxanthellate scleractinians as biological engineers and thereby providing a great variety of habitats attractive for a diverse associated community. These framework-constructing corals trap suspended sedimentary particles to generate a three-dimensional structure within an astonishingly short time and at rates comparable to some tropical shallow-water coral reef systems.

Bibliography

Beuck, L., and Freiwald, A., 2005. Bioerosion patterns in a deep-water *Lophelia pertusa* (Scleractinia) thicket (Propeller Mound, northern Porcupine Seabight). In Freiwald, A., and Roberts, J. M. (eds.) *Cold-water Corals and Ecosystems*. Heidelberg: Springer Verlag, pp. 915–936.

Beuck, L., Freiwald, A., and Taviani, M., 2010. Spatiotemporal bioerosion patterns in deep-water scleractinians from off Santa Maria di Leuca (Apulia, Ionian Sea). *Deep-Sea Research Part II*, **57**, 458–470.

Beuck, L., López Correa, M., and Freiwald, A., 2008. Biogeographical distribution of *Hyrrokkin* (Rosalinidae, Foraminifera) and its host-specific morphological and textural trace variability. In Wisshak, M., and Tapanila, L. (eds.) *Current Developments in Bioerosion*. Heidelberg: Springer, pp. 329–360.

Beuck, L., Vertino, A., Stepina, E., Karolczak, M., and Pfannkuche, O., 2007. Skeletal response of *Lophelia pertusa* (Scleractinia) to bioeroding sponge infestation visualised with micro-computed tomography. *Facies*, **53**, 157–176.

Cedhagen, T., 1994. Taxonomy and biology of *Hyrrokkin sarcophaga* gen. et sp. n., a parasitic foraminiferan (Rosalinidae). *Sarsia*, **79**, 65–82.

Davies, A. J., Duineveld, G. C. A., Lavaleye, M. S. S., Bergman, M. J. N., van Haren, H., and Roberts, J. M., 2009. Downwelling and deep-water bottom currents as food supply mechanisms to the cold-water coral *Lophelia pertusa* (Scleractinia) at the Mingulay Reef complex. *Limnology and Oceanography*, **54**, 620–629.

Dorschel, B., Hebbeln, D., Foubert, A., White, M., and Wheeler, A., 2007. Hydrodynamics and cold-water coral facies distribution related to recent sedimentary processes at Galway Mound west of Ireland. *Marine Geology*, **244**, 184–195.

Duineveld, G. C. A., Lavaleye, M., Bergman, M. J. N., de Stigter, H., and Mienis, F., 2007. Trophic structure of a cold-water coral mound community (Rockall Bank, NE Atlantic) in relation to the near-bottom particle supply and current regime. *Bulletin of Marine Science*, **81**, 449–467.

Försterra, G., Beuck, L., Häusserman, V., and Freiwald, A., 2005. Shallow-water *Desmophyllum dianthus* (Scleractinia) from Chile: characteristics of the biocoenoses, the bioeroding community, heterotrophic interactions and (paleo)-bathymetric implications. In Freiwald, A., and Roberts, J. M. (eds.), *Cold-water Corals and Ecosystems*. Heidelberg: Springer Verlag, pp. 937–977.

Fosså, J. H., Lindberg, B., Christensen, O., Lundälv, T., Svellingen, I., Mortensen, P. B., and Alsvåg, J., 2005. Mapping of *Lophelia* reefs in Norway: experiences and survey methods. In Freiwald, A., and Roberts, J. M. (eds.), *Cold-water Corals and Ecosystems*. Heidelberg: Springer Verlag, pp. 359–391.

Frank, N., Ricard, E., Lutringer-Paquet, A., van der Land, C., Colin, C., Blamart, D., Foubert, A., Van Rooij, D., Henriet, J.-P., de Haas, H., and van Weering, T., 2009. The Holocene occurrence of cold water corals in the NE Atlantic: implications for coral carbonate mound evolution. *Marine Geology*, **266**, 129–142.

Freiwald, A., 2002. Reef-forming cold-water corals. In Wefer, G., Billett, D., Hebbeln, D., Jørgensen, B. B., Schlüter, M., and van Weering, T. C. E. (eds.), *Ocean Margin Systems*. Heidelberg: Springer, pp. 365–385.

Freiwald, A., and Schönfeld, J., 1996. Substrate pitting and boring pattern of *Hyrrokkin sarcophaga* Cedhagen, 1994 (Foraminifera) in a modern deep-water coral reef mound. *Marine Micropaleontology*, **28**, 199–207.

Freiwald, A., and Wilson, J. B., 1998. Taphonomy of modern deep, cold-temperate water coral reefs. *Historical Biology*, **13**, 37–52.

Freiwald, A., Fosså, J. H., Grehan, A., Koslow, T., and Roberts, J. M., 2004. Cold-water coral reefs. *UNEP-WCMC Biodiversity Series*, **22**, 1–85.

Harmelin, J. G., 1990. Interactions between small sciaphilous scleractinians and epizoans in the northern Mediterranean, with particular reference to bryozoans. *P.S.Z.N.I.: Marine Ecology*, **11**, 351–364.

Jensen, A., and Frederiksen, R., 1992. The fauna associated with the bank-forming deepwater coral *Lophelia pertusa* (Scleractinia) on the Faroe shelf. *Sarsia*, **77**, 53–69.

Jonsson, L. G., Nilsson, P. G., Floruta, F., and Lundälv, T., 2004. Distributional patterns of macro- and megafauna associated with a reef of the cold-water coral *Lophelia pertusa* on the Swedish west coast. *Marine Ecology Progress Series*, **284**, 163–171.

Lindberg, B., and Mienert, J., 2005. Post-glacial carbonate production by cold-water corals on the Norwegian Shelf and their role in the global carbonate budget. *Geology*, **33**, 537–540.

Messing, C. G., Brooke, S. D., Reed, J. K., and Richardson, S., 2008. A possible role for agglutinated foraminifers in the growth of deep-water coral bioherms. *Deepsea Coral Symposium 2008*, Wellington, New Zealand, pp. 107.

Messing, C. G., Reed, J. K., Brooke, S. D., and Ross, S. W., 2008. In Riegl, B., and Dodge, R. E. (eds.), *Coral Reefs of the USA*. Springer, pp. 763–787.

Mienis, F., de Stigter, H., White, M., Duineveld, G. C. A., de Haas, H., and van Weering, T., 2007. Hydrodynamic controls on cold-water coral growth and carbonate-mound development at the SW and SE Rockall Trough Margin. *NE Atlantic Ocean. Deep-Sea Research Part I*, **54**, 1655–1674.

Mortensen, P. B., 2001. Aquarium observations on the deep-water coral *Lophelia pertusa* (L., 1758) (Scleractinia) and selected associated invertebrates. *Ophelia*, **54**, 83–104.

Mortensen, P. B., and Fosså, J. H., 2006. Species diversity and spatial distribution of invertebrates on deep-water *Lophelia* reefs in Norway. *Proceedings of the 10th International Coral Reef Symposium, Okinawa*, pp. 1849–1868.

Reed, J. K., 2002. Comparison of deep-water coral reefs and lithoherms off southeastern USA. *Hydrobiologia*, **471**, 57–69.

Roberts, J. M., 2005. Reef-aggregating behaviour by symbiotic eunicid polychaets from cold-water corals: do worms assemble reefs? *Journal of the Marine Biological Association of the United Kingdom*, **85**, 813–819.

Roberts, J. M., Davies, A. J., Henry, L. A., Dodds, L. A., Duineveld, G. C. A., Lavaleye, M. S. S., Maier, C., van Soest, R. W. M., Bergman, M. J. N., Hühnerbach, V., Huvenne, V. A. I., Sinclair, D. J., Watmough, T., Long, D., Green, S. L., and van Haren, H., 2009b. Mingulay reef complex: an interdisciplinary study of cold-water coral habitat, hydrography and biodiversity. *Marine Ecology Progress Series*, **397**, 139–151.

Roberts, J. M., Wheeler, A. J., and Freiwald, A., 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science*, **312**, 543–547.

Roberts, J. M., Wheeler, A., Freiwald, A., and Cairns, S., 2009a. *Cold-water Corals – The Biology and Geology of Deep-Sea Coral Habitats*. Cambridge: Cambridge University Press.

Rogers, A. D., 1999. The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. *International Review of Hydrobiology*, **84**, 315–406.

Savini, A., and Corselli, C., 2010. High-resolution bathymetry and acoustic geophysical data from Santa Maria di Leuca Cold Water Coral province (Northern Ionian Sea—Apulian continental slope). *Deep Sea Research Part II*, **57**, 326–344.

Squires, D. F., 1963. Modern tools probe deep water. *Natural History*, **72**, 22–29.

Squires, D. F., 1964. Fossil coral thickets in Wairarapa, New Zealand. *Journal of Paleontology*, **38**, 904–915.

Stanley, G. D., and Cairns, S. D., 1988. Constructional azooxanthellate coral communities: an overview with implications for the fossil record. *Palaios*, **3**, 233–242.

Taviani, M., Angeletti, L., Dimech, M., Mifsud, C., Freiwald, A., Harasewych, M. G., and Oliverio, M., 2009. Coralliophilinae (Gastropoda: Muricidae) associated with deep-water coral banks in the Mediterranean. *The Nautilus*, **123**, 1–7.

Van Soest, R. W. M., and Lavaleye, M. S. S., 2005. Diversity and abundance of sponges in bathyal coral reefs of Rockall Bank. NE Atlantic, from boxcore samples. *Marine Biology Research*, **1**, 338–349.

Van Soest, R. W. M., Cleary, D. F. R., de Kluijver, M. J., Lavaleye, M. S. S., Maier, C., and van Duyl, F. C., 2007. Sponge diversity and community composition in Irish bathyal coral reefs. *Contributions to Zoology*, **76**, 121–142.

Wienberg, C., Beuck, L., Heldkamp, S., Hebbeln, D., Freiwald, A., Pfannkuche, O., and Monteys, X., 2008. Franken Mound: facies and biocoenoses on a newly-discovered "carbonate mound" on the western Rockall Bank. NE Atlantic. *Facies*, **54**, 1–24.

Wienberg, C., Hebbeln, D., Fink, H. G., Mienis, F., Dorschel, B., Vertino, A., López Correa, M., and Freiwald, A., 2009. Scleractinian cold-water corals in the Gulf of Cádiz—First clues about their spatial and temporal distribution. *Deep-Sea Research Part I*, **56**, 1873–1893.

Wild, C., Mayr, C., Wehrmann, L., Schöttner, S., Naumann, M., Hoffmann, F., and Rapp, H. T., 2008. Organic matter release by cold-water corals and its implication for fauna-microbe interaction. *Marine Ecology Progress Series*, **372**, 67–75.

Wilson, J. B., 1979.'Patch' development of the deep-water coral *Lophelia pertusa* (L.) on Rockall Bank. *Journal of the Marine Biological Association of the United Kingdom*, **59**, 165–177.

Wisshak, M., Gektidis, M., Freiwald, A., and Lundälv, T., 2005. Bioerosion along a bathymetric gradient in a cold-temperate setting (Kosterfjord, SW Sweden): an experimental study. *Facies*, **51**, 93–117.

Cross-references

Aragonite
Bioerosion
Carbonate Budgets and Reef Framework Accumulation
Corals: Biology, Skeletal Deposition, and Reef-Building
Holocene Reefs: Thickness and Characteristics
Molluscs
Nutrient Pollution/Eutrophication
Sediment Dynamics
Sponges
Swathe Mapping
Taphonomy

CONGLOMERATES

Lucien F. Montaggioni
University of Provence, Marseille Cedex 3, France

Synonyms

Conglomerate pavements; Conglomerate platforms; Conglomerate promenades; Exposed limestone coral; Rampart-rocks; Shingle conglomerate

Definition

Conglomerates are defined as exposed, cemented reef-derived detritus, dominantly composed of coral rubble.

Environment: mostly, windward sides of reefs; occasionally, on leeward sides near passes and channels.

Morphology and structure: Conglomerates exhibit either a planar, mainly horizontal surface ("platform") or steeply dipping (>20°) beds to lee ("basett edge"). Each platform usually has a fairly constant elevation relative to the present mean sea level. But the heights can vary between 0.6 and 1.0 m in areas subject to microtidal regimes and about 1.0–3.5 m in areas subject to macrotidal conditions. Their internal structure reveals the superimposition of distinct beds varying in thickness and grain size, thus reflecting changes in sediment supply and water energy. Locally, there are large coral boulders embedded in the rubble.

Lithology and diagenesis: The conglomerate matrices are poorly sorted grainstones, packstones and rudstones. Diagenetic features include typical marine cements (e.g., irregular or isopachous rims of fibrous aragonite, high-magnesian calcite, peloidal micrite) locally showing geotrophic (pendant) habits.

Origin: Conglomerates are interpreted as generated by storms and cyclones. These are probably the counterparts of shingle and gravel sheets and ramparts today, accumulated close to sea level. Accordingly, the horizontal surface is generally believed to be primary in origin.

Age of deposition: radiocarbon dating of coral and molluscan fragments suggests that deposition occurred between less than 1,000 and about 6,000 years BP in the Pacific.

Potential use: indicators of mid-late Holocene sea-level changes.

Parental features

Bassett edges, boulder ramparts, cemented platforms, shingle ridges, beach-rocks.

Bibliography

Montaggioni, L. F. and Pirazzoli, P. A., 1984. The significance of exposed coral conglomerates from French Polynesia (Pacific Ocean) as indicators of recent relative sea-level changes. *Coral Reefs*, **3**, 29–42.

Scoffin, T.P., 1993. The geological effects of hurricanes on coral reefs and the interpretation of storm deposits. *Coral Reefs*, **12**, 203–221.

Scoffin, T.P. and McLean, R.F., 1978. Exposed limestones of the Northern Province of the Great Barrier Reef. *Philosophical Transactions of the Royal Society of London*, A, **291**, 119–138.

Cross-references

Antecedent Platforms
Atoll Islands (Motu)
Bassett Edges
Beach Rock
Boulder Zone/Ramparts
Megablocks
Platforms (Cemented)
Shingle Ridges

CONSERVATION AND MARINE PROTECTION AREAS

Jon C. Day
Great Barrier Reef Marine Park Authority (GBRMPA),
Townsville, QLD, Australia

Definitions

Conservation is an ethic of resource use, allocation, and protection, with a primary focus upon maintaining the health and biological diversity of the natural world.

Cumulative impacts are the change in the environment which results from the incremental impact of two or more individual events which, when added to other closely related past, present, and reasonably foreseeable probable future events, will compound, magnify, or increase each other or their own environmental impacts.

Ecosystem-based management is an integrated approach to management that considers the entire ecosystem, integrating the ecological, social, economic, and institutional perspectives, and emphasizing the protection of ecosystem structure, functioning, and key processes.

Marine management is a continuous, interactive, adaptive, and participatory management process, comprising a set of related tasks, which collectively work towards achieving a desired set of goals and objectives.

Marine protected area (MPA) network is an organized and systematic collection of individual MPAs, connected in some way by ecological or other processes.

Protected area is a clearly defined geographical space, recognized, dedicated, and managed through legal or other effective means to achieve the long-term conservation of nature with associated ecosystem services and cultural values (Dudley, 2008). Hence, an MPA is a protected area within the marine (intertidal or sub-tidal) realm.

Introduction

In many parts of the world, coral reefs have been actively conserved for centuries to ensure continuing access to food sources such as fish and shellfish. In most western countries, however, the need to protect coral reefs, and the importance of conserving marine areas, has only been recognized in the last 50–70 years.

Problems arise when marine and coastal resources, such as coral reefs or their resident species, are considered as “open to everyone” with “free” access to virtually all users. Often referred to as “The Tragedy of the Commons” (Hardin, 1968), this commonly leads to excessive use and habitat degradation. These generalizations, of course, vary between countries according to cultural perceptions of private, public, and common property.

The long-held belief that marine resources were almost unlimited and inexhaustible has now proven to be a myth; many living marine resources may be renewable if harvested sustainably, but there are finite limits to marine exploitation. Today, as never before, there are many more pressures on marine environments and a growing awareness of the *cumulative impacts* of those pressures. There are many striking example around the world of the consequences of poorly managed coral reefs or untimely responses to warning signs.

Marine protected areas (often abridged to the term MPAs) are one of a variety of practices at the international, regional, national, and local level to protect coral reefs. Other conservation strategies are being applied at a range of scales from international agreements to local community-based management areas.

Globally, the rate of coral reef degradation, however, greatly exceeds the rate of effective coral reef conservation; hence, far more needs to be done to effectively protect coral reef systems – arguably the most biologically diverse ecosystems on the planet.

Status of coral reefs globally

Pressures on coral reef systems can be regarded as either human-induced (e.g., mining/quarrying, unsustainable fishing, pollution, heavy-metal impacts, climate change, technological innovations enabling greater use) or natural events (e.g., cyclones, tsunami). The effects of such pressures on coral reefs can range from negligible to catastrophic, and can be episodic or chronic. It is also important to recognize issues such as *cumulative impacts* (both direct and indirect) and the synergistic effects of such pressures, none of which is easily considered. The combined chronic effects of over-fishing, by-catch, habitat degradation, pollution, and food-web changes have had significant impacts, resulting in formerly abundant species now being rare and marked changes in resource utilization.

The 2008 Status Report of the World's Coral Reefs (Wilkinson, 2008) estimates that 19% of the world's original reefs are effectively lost forever; 15% are seriously threatened with loss likely in next 10–20 years; and 20% are under threat of loss in 20–40 years. The latter two estimates are made without considering the looming threats of global climate change or that effective future marine management may conserve more coral reefs. If current pressures continue, some consider that 60% of the world's coral reefs may be severely damaged by 2050.

Key threats to marine conservation and especially coral reefs

1. *Climate change* – Climate change impacts on coral reefs and marine ecosystems are already having marked environmental effects, and the consequent impacts are likely to flow onto the industries that depend on these areas as well as coastal communities. The impacts of climate change on marine biodiversity are being observed throughout the world – carbon dioxide concentrations have increased dramatically in recent decades; the oceans are warming and becoming more acidic, frequently bleaching large areas of coral; and sea-level rise is now flooding some coastal communities.
2. *Land-based water quality* – Coral reefs can be impacted by a variety of land-based pressures including agricultural runoff, inadequate sewage and stormwater treatment, siltation from coastal development, deforestation or beach re-nourishment projects, contamination from petroleum products, etc.

   Agricultural runoff can contain herbicides, pesticides, and nutrient fertilizers. Elevated levels of nitrogen and phosphorus may result in algal blooms that can potentially grow much faster and out – compete corals.

   Human sewage, often untreated, can add nutrients, microorganisms, and other pollutants to coral reefs and can cause eutrophication.
3. *Unsustainable harvesting (fishing or collecting)* – Unsustainable harvesting can cause a variety of negative impacts on coral reefs, including altering *trophic* interactions causing indirect environmental effects. For example, where predators have largely been removed, increases in the population of their prey have resulted in unexpected flow-on effects. Unsustainable fishing or the depletion of fish spawning sites can also reduce genetic variation in a population, making it harder for species to adapt to environmental change.

   Over-fishing can have major impacts on target species and has led to the extinction of species in some areas (e.g., Queen Conch), but can also have major impacts on non-target species (by-catch) as well as cause habitat destruction.

   Discarded fishing gear (e.g., ghost nets) can damage reefs and also have major impacts on marine biodiversity. Marine debris, especially plastics and monofilament fishing line, can abrade corals and prove lethal for birds, fish, and turtles that become entangled in it or mistake it for food and ingest it.
4. *Direct physical damage (e.g., blast fishing, dredging, mining, infilling, etc.)* – Many fishing practices harm coral reefs by physically damaging habitat or by killing non-targeted species. Blast fishing occurs in some parts of the world, whereby underwater explosions are used to injure fish so that they float to the surface where they are easily captured. The blast, however, also destroys coral and flattens the reef structure. In some places, fishermen use cyanide or other poisons to stun fish so that they can be captured alive, but small fish and coral polyps may also be killed.

   Limestone mining or infilling for coastal developments have obvious major impacts, completely destroying coral reefs or severely altering hydrological flow patterns.

   The depletion caused by the harvest of coral and "live rock" for the aquarium/curio trade has damaged many reefs around the world.
5. *Indirect impacts from marine or coastal developments* – Human activities on land such as the building of ports, industrial infrastructure, deforestation, tourism facilities, or other coastal developments can lead to increased rates of sedimentation affecting adjacent reefs. High sediment loads can smother corals or decrease light penetration, thereby reducing the photosynthetic ability of the symbiotic algae in coral.
6. *Unsustainable tourism/recreation* – Anchors, accidental boat groundings, and propeller strike can all crush and scar coral. The fins of divers and snorkelers and even their diving equipment can inadvertently damage coral. Well-meaning tourists may feed reef fish, but this can change feeding behavior with other flow-on effects. Similarly, shell collecting, fossicking, and uncontrolled reef-walking can have detrimental impacts on corals.
7. *Invasive species (pest plants, animals, diseases) or outbreaks of native species* – Invasive marine species may be introduced by a variety of vectors, including ballast water discharge, biofouling on vessel hulls or within internal seawater pipes in commercial and recreational vessels, aquaculture operations (accidentally or intentionally) and aquarium imports, as well as marine debris carried by ocean currents.

   At high densities, outbreaks of species that eat juvenile or adult corals can cause major problems for reefs and their associated species (e.g., the crown-of-thorn starfish, a long-spined species of sea urchin, and a small gastropod snail have all caused major problems in many coral reefs around the world).

   The types and extent of diseases attacking corals have increased markedly in recent years and coral diseases such as Black Band and White Plague are becoming more prevalent, especially following bleaching stress. Bacteria in sewage pollution are a suspected cause of White Band disease in corals.

8. *Shipping and related issues* – Oils and hydrocarbons inadvertently discharged, or deliberately washed overboard, can cause impacts, especially if they occur during coral spawning. Coral reefs and mangroves are more susceptible to the impacts of oil spills compared to sandy beaches or seagrass beds. Other ship-sourced threats include sewage discharge and toxic discharges, as well as the impacts of antifouling paint used on vessels.

Effective reef conservation

An emerging realization is that effective marine conservation requires a lot more than just protecting areas in MPAs alone; in order to provide for the future, including any sustainable use, effective reef conservation requires the following:

1. Understanding, and effective management, of the wider context (i.e., the surrounding waters and the ecological processes that influence the coral reef as well as the nearby catchment areas); this means, in effect, integrated land/sea management;
2. Sustainable resource utilization (especially fishing and collecting) of the coral reef as well as the surrounding marine area;
3. Effective marine protection (which may be by declaring an MPA through a legal or other effective means);
4. Effective stakeholder involvement (industry and community); and
5. Where appropriate, the incorporation of traditional management approaches.

Marine protected areas

In recent decades, considerable efforts have occurred worldwide to establish MPAs to improve marine conservation. A diverse array of MPA types, each with its own label and priorities, has arisen in coastal and marine areas throughout the world.

In this instance, MPA is used as a broad generic or "umbrella" term, reflecting the IUCN definition amended in 2008 of a protected area:

> *A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values.*

IUCN has seven categories of protected area, ranging from highly protected "no-take" areas, intended only for scientific research (IUCN Category IA), through no-take areas that may be accessed by the public but where virtually all types of extraction are prohibited (IUCN Category II), to multiple-use areas in which the sustainable extraction or collection of natural resources may occur (IUCN Category VI).

One of the better known MPAs with coral reefs is the Great Barrier Reef Marine Park (GBRMP), covering 344,400 km^2 on Australia's northeast coast. Because of the iconic status of the Great Barrier Reef, many people believe the entire area is a marine sanctuary or marine reserve, and therefore protected equally throughout. While the entire area is protected by law, many do not understand that the GBRMP is a multiple-use MPA, in which a wide range of activities and uses are allowed, including many extractive industries in certain zones (but not mining nor drilling for oil), while still protecting one of the world's most diverse ecosystems (refer to the GBRMP Activity Matrix, Figure 1).

A major rezoning of the GBRMP occurred from 1999 to 2004, with the primary aim to improve the protection of the range of biodiversity throughout the GBRMP. The final outcome included an increase in "no-take" zones to over 33% of the entire area, with an additional 33% zoned to ensure comprehensive habitat protection (refer to map showing the zoning in the GBRMP, Figure 2).

The comprehensive, multiple-use zoning system in the GBRMP (which comprises IUCN categories IA, II, IV, and VI) is a systematic network that effectively governs all human activities, providing high levels of protection for specific areas, while allowing a variety of other uses, including shipping, dredging, aquaculture, tourism, boating, diving, commercial fishing, and recreational fishing, to occur in certain zones.

The most optimistic estimates indicate that less than 1% of the world's oceans are currently in any type of MPA, and only a small proportion of coral reefs is adequately protected. While there are many effective MPAs, there are also many 'paper parks' that are not achieving what was intended when they were declared.

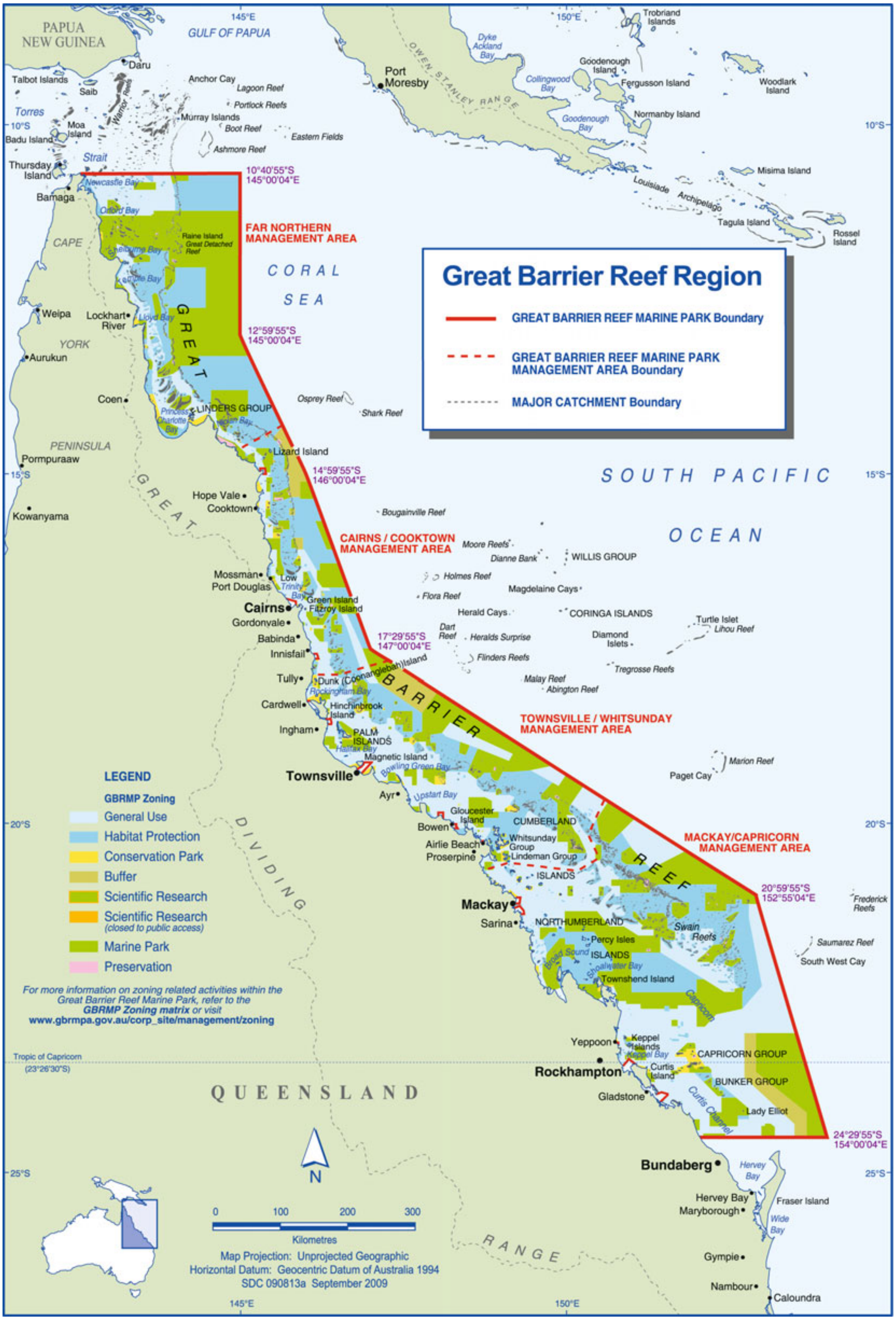
Recent declarations of several large MPAs, which include coral reefs such as Papahanomoukuakea (NW Hawaiian Islands) and the Phoenix Islands in the Republic of Kiribati, are encouraging, but collectively are still not enough to meet global targets set by international conventions such as the Convention on Biological Diversity.

The benefits of MPAs

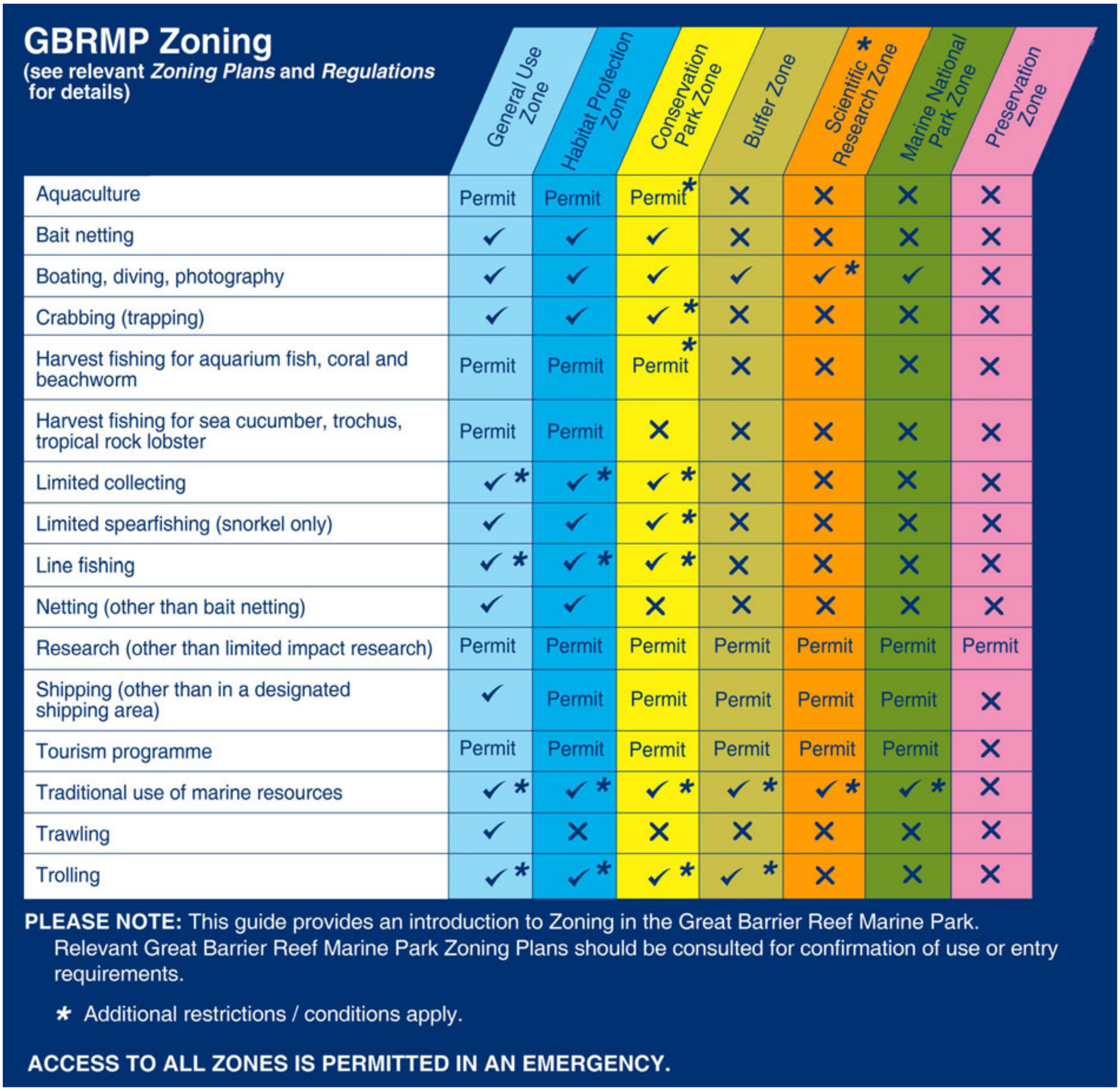
Single MPAs, particularly those containing appropriately chosen "no-take" areas, can provide a range of benefits including helping to maintain biodiversity, enhance nonconsumptive opportunities, and improve stocks that have commercial and recreational value in adjacent areas.

The benefits of MPAs, however, will be greatly increased if they are effectively linked to provide ecologically coherent networks. Any MPA network should be designed to link individual areas and comprehensively represent the region's spectrum of marine life characteristics, not just a subset of habitats or only species of special interest.

The focus on MPA networks recognizes the fact that a broad-area-integrated network that has been systematically developed and managed is often more effective than a series of small, highly protected areas surrounded by "a sea" of unmanaged activities.



Conservation and Marine Protection Areas, Figure 1 Map showing part of the GBRMP zoning plan.



GBRMP Zoning
(see relevant *Zoning Plans* and *Regulations* for details)

	General Use Zone	Habitat Protection Zone	Conservation Park Zone	Buffer Zone	Scientific Research Zone *	Marine National Park Zone	Preservation Zone
Aquaculture	Permit	Permit	Permit *	✗	✗	✗	✗
Bait netting	✓	✓	✓	✗	✗	✗	✗
Boating, diving, photography	✓	✓	✓	✓	✓ *	✓	✗
Crabbing (trapping)	✓	✓	✓ *	✗	✗	✗	✗
Harvest fishing for aquarium fish, coral and beachworm	Permit	Permit	Permit *	✗	✗	✗	✗
Harvest fishing for sea cucumber, trochus, tropical rock lobster	Permit	Permit	✗	✗	✗	✗	✗
Limited collecting	✓ *	✓ *	✓ *	✗	✗	✗	✗
Limited spearfishing (snorkel only)	✓	✓	✓ *	✗	✗	✗	✗
Line fishing	✓ *	✓ *	✓ *	✗	✗	✗	✗
Netting (other than bait netting)	✓	✓	✗	✗	✗	✗	✗
Research (other than limited impact research)	Permit	Permit	Permit	Permit	Permit	Permit	Permit
Shipping (other than in a designated shipping area)	✓	Permit	Permit	Permit	Permit	Permit	✗
Tourism programme	Permit	Permit	Permit	Permit	Permit	Permit	✗
Traditional use of marine resources	✓ *	✓ *	✓ *	✓ *	✓ *	✓ *	✗
Trawling	✓	✗	✗	✗	✗	✗	✗
Trolling	✓ *	✓ *	✓ *	✓ *	✗	✗	✗

PLEASE NOTE: This guide provides an introduction to Zoning in the Great Barrier Reef Marine Park. Relevant Great Barrier Reef Marine Park Zoning Plans should be consulted for confirmation of use or entry requirements.

* Additional restrictions / conditions apply.

ACCESS TO ALL ZONES IS PERMITTED IN AN EMERGENCY.

Conservation and Marine Protection Areas, Figure 2 GBRMP "activities matrix".

Tools for marine management

MPA managers generally do not manage natural systems or specific marine species *per se*; rather they manage the human impacts associated with those resources. Marine management is usually undertaken to achieve a desired set of goals and objectives; it is important that these goals and objectives are clearly established and widely known.

Ecosystem-based management and adaptive management are two key aspects of the effective management of any MPA, and these are particularly important because of the following:

1. The interconnectedness of different habitats of the marine environment and the interdependency upon neighboring biological communities;
2. The impacts from adjacent land or sea areas that may threaten the integrity of even the best managed MPA;
3. The three-dimensional aspects of what needs to be managed (few MPAs are well known, easily viewed, or easily "delineated" for management purposes, which means they are hard to see, hard to manage, and enforce). "Out-of-sight, out-of-mind" is part of the problem;

4. Ownership issues (for most marine areas worldwide, open-access resources are poorly or insufficiently regulated).

When used in the context of the above management and planning approaches, the following management tools are widely used by MPA managers:

Zoning – Spatial allocation using zoning is an accepted practice within many MPAs around the world. Zoning can separate conflicting uses and provide for high levels of protection for specific areas while allowing a variety of uses, including fishing, to continue in other zones.

Permits and licensing – When used in conjunction with a zoning plan and other management tools, permits, and licences can:

(a) further regulate use in high-use or sensitive areas;
(b) encourage responsible behavior in users and assist in monitoring activities; and
(c) require the collection of data for planning and management.

Certain permit applications may also trigger the need for a comprehensive environmental impact assessment to be undertaken.

Enforcement and surveillance – Without an effective compliance and enforcement program, an MPA will not achieve its objectives. In time, its regulations will neither be accepted nor complied with by users or locals. Implementation and enforcement of regulations may include checking locations, size restrictions, bag limits, fishing season, or gear type, and can protect habitats, by-catch species, and spawning stock.

Enforcement and compliance can be very expensive because of the costs of resources, including trained personnel and access to appropriate vessels, aircraft, or specialist equipment. Enforcement should not, however, be considered as the only management approach or the tool of last resort.

Public education and community engagement – These are both integral to effective marine management. Communicators must build awareness of the threats and instil an acceptance for change. Effective public education and enlisting the assistance of key stakeholder groups, combined with enforcement and compliance, can result in valuable outcomes.

Research and monitoring – Research and monitoring can help MPA managers to diagnose problems, prioritize and implement solutions, assess the results and effectiveness of management actions, and forecast future conditions. Having the best available information for decision making helps ensure effective marine management of an MPA.

The above are only some of the main management tools used in coral reef conservation; other spatial tools include plans of management, specific closures, or special management areas. Non–spatial management tools include effective legislation, advisory committees, industry partnerships, best practice guidelines, or user fees such as the "Environmental Management Charge" applied in the GBRMP.

Key lessons learnt

1. In most MPAs worldwide, there are real challenges in maintaining existing levels of marine management, let alone coping with rapidly escalating levels of use or increasingly complex issues, such as climate change. Finding the right balance between protection and sustainable use is essential, and issues like cumulative impacts are becoming increasingly important to address.
2. An integrated management framework is important for effective marine management. Without it, intersectoral conflicts, incompatible activities, and inefficient systems will prevail. Integration across use sectors, levels of government, and the land–sea boundary are all fundamental to effective ocean governance and marine conservation.
3. Manage at the ecosystem level, not for single species. Most fishery management efforts focused on managing a single target species have failed. The more appropriate and effective approach requires managing all components and ecological processes as part of ecosystem-based management.
4. Local communities and indigenous people should be involved in marine management; successful examples of effective conservation have comprised a combination of "top-down" approaches (through government working with appropriate agencies or organizations), combined with effective "bottom-up" input involving community engagement. Widespread public support is essential if marine conservation efforts are to be successful and sustainable.
5. Apply the precautionary principle. We will never know precisely how coral reef ecosystems function or how they will cope with pressures such as climate change. But enough is known to cautiously proceed with management, comprehensively using the best available science and expert opinion (not waiting for perfect information) and adaptively managing as we continually learn.
6. Ensure that all MPA planning is open, transparent, collaborative, and adaptive, using the best available scientific, traditional, and local knowledge. Accommodate the economic, social, and cultural aspirations of communities within the ecological constraints.
7. Better technology can be a "double-edged sword" – while it may assist management (e.g., remote sensing, satellite imagery), it can also mean that users are able to access areas and resources that previously were inaccessible.

What is the future for reef conservation?

As the global population increases markedly, the pressures on coral reefs are increasing significantly as are the difficulties in ensuring reef conservation. Regrettably, many governments are not focused on long-term reef conservation outcomes, focusing more on short-term development issues or resource use; this means that matters such as long-term sustainability, adequate resourcing for relevant agencies, and funding for conservation are often of lower priority.

The conservation of the world's coral reefs is today at "cross-roads"; paraphrasing Kingsford et al. (2009)

1. In most areas, there is sufficient knowledge to implement effective policy, but effective implementation largely depends upon education, political will, community aspirations, and social and economic capacity;
2. As the knowledge of what is required for coral reef conservation has increased, so have the pressures; and
3. Proactive reef conservation measures that aim to build resilience to better cope with the likely pressures are considerably more cost efficient and are often less risky than waiting until the pressures have occurred and then trying to address them through reactive management.

Websites

Great Barrier Reef Marine Park Authority http://www.gbrmpa.gov.au
- Rezoning the Great Barrier Reef http://www.gbrmpa.gov.au/corp_site/management/representative_areas_program
- Vulnerability Assessment to Climate Change http://www.gbrmpa.gov.au/corp_site/info_services/publications/misc_pub/climate_change_vulnerability_assessment/climate_change_vulnerability_assessment

International Maritime Organization http://www.imo.org/home.asp
Locally Managed Marine Areas http://www.lmmanetwork.org
MPA News http://www.depts.washington.edu/mpanews/
ProtectPlanetOcean http://www.protectplanetocean.org/
United Nations Atlas of the Oceans http://www.wri.org/publication/reefs-risk-map-based-indicator-potential-threats-worlds-coral-reefs
United Nations, Oceans and the Law of the Sea, http://www.un.org/depts/los/general_assembly/general_assembly_reports.htm
World Conservation Union (IUCN) Global Marine Programme http://www.iucn.org/about/work/programmes/marine/

Bibliography

Day, J. C., 2006. Marine protected areas. In Lockwood, M., Worboys, G., and Kothari, A. (eds.), *Managing Protected Areas: a Global Guide*. London: Earthscan, pp. 603–634.
Day, J. C., 2008. Planning and managing the Great Barrier Reef Marine Park. In Hutchings, Kingsford, and Hoegh-Gulberg (eds.). *The Great Barrier Reef – Biology, Environment and Management*. CSIRO and Springer, pp. 114–121.
Dudley, N., (ed.), 2008. *Guidelines for Applying Protected Area Management Categories*. Gland, Switzerland: IUCN.
Ecological Applications, 2003. The science of marine reserves. *Ecological Applications*, **13**(supplement), 3–228.
Hardin, G., 1968. The tragedy of the commons. *Science*, **162**(3859), 1243–1248.
Kelleher, G., and Kenchington, R. A., 1992. *Guidelines for Establishing Marine Protected Areas*: *A Marine Conservation and Development Report*. Gland and Cambridge: IUCN.
Kingsford, R. T., Watson J. E. M., Lundquist C. J., Venter O., et al, 2009. Major conservation policy issues for biodiversity in Oceania. *Conservation Biology*, **23**(4), 834–840.
Salm, R. V., Clark, J. R., and Sirila, E., 2000. *Marine and Coastal Protected Areas: A Guide for Planners and Managers*, 3rd edn. Gland and Cambridge: IUCN.
Sobel, J., and Dalgren, C., 2004. *Marine Reserves: A Guide to Science, Design and Use.* Washington, DC: Island Press.
Wilkinson, C., 2008. *Status of Coral Reefs of the World: 2008*. Townsville, Australia: Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, 296p.

Cross-references

Acanthaster planci
Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity
Climate Change: Impact On Coral Reef Coasts
Climate Change: Increasing Storm Activity
Climate Change and Coral Reefs
El Niño, La Niña, and ENSO
Engineering On Coral Reefs With Emphasis On Pacific Reefs
FORAM Index
Heavy Metal Accumulation in Scleractinian Corals
Impacts of Sediment on Coral Reefs
Infrastructure and Reef Islands
Mining/Quarrying of Coral Reefs
Nutrient Pollution/Eutrophication
Ocean Acidification, Effects on Calcification
Reefs at Risk: Map-Based Analyses of Threats to Coral Reefs
Temperature Change: Bleaching
Tsunami

COOK, JAMES (1728–1779)

James Bowen
Southern Cross University, Lismore, NSW, Australia

James Cook was the first of the great explorers of the eighteenth century to present a comprehensive account of the almost invisible reefs in the great open expanses of the Pacific Ocean. Intensified speculation had been mounting on such hazards to navigation when the destructive power of coral reefs was given sensational publicity in Cook's account of his successful discovery of the mysterious and elusive Great South Land, following the British scientific expedition in command of the *Endeavour* to Tahiti in 1769 for scientists to observe the Transit of Venus.

While subsequently exploring the unknown eastern coast of New Holland, on June 11, 1770, his ship crashed into one of the invisible reefs and the eventual discovery of a way out of the bewildering complexity of the "labyrinth" of submerged reefs created a sensation. He published his description of the impact and the beaching of the vessel for repairs. Once safe in the ocean, Cook wrote one of the most powerful coral reef images ever: "A Reef such as is here spoke of is scarcely known in Europe, it is a wall of Coral Rock rising all most perpendicular out of the unfathomable Ocean… the large waves of the vast Ocean meeting with so sudden a resistance make a most terrible surf, breaking mountains high."

In 1770, after his encounter with the Great Barrier Reef, Cook had become aware of a major scientific controversy among European and British naturalists that in some mysterious way coral reefs were built neither by rocks nor by petrified plants as 2,000 years of tradition had supposed, but were the production of microscopically small animals, then part of the extensive range of unknown, unclassified organisms collectively termed "insects".

Barely 4 years later, during his second 1772–1775 exploratory voyage in the Pacific in command of the *Resolution*, as he navigated past continental islands in the central Pacific with elevated relict fringing reefs, he recorded in his *Journal* for June 1774 his puzzlement "If these Coral rockes were first formed in the Sea by animals, how came they thrown up, to such a height? Has this Island been raised by an Earth quake or has the sea receded from it? Some philosophers [scientists] have attempted to account for the formation of low isles such as are in this Sea, but I do not know of any thing has been said of high Islands or such as I have been speaking of," thereby providing speculation for further reef research.

Bibliography

Bowen, J., 2002. *The Great Barrier Reef: History, Science, Heritage*. Cambridge: Cambridge University Press.

Cook, J., 1770–1771. In Beaglehole, J. C. (ed.) 1955. Repr. 1968, *The Voyage of the Endeavour 1768–1771*. Cambridge: Cambridge University Press for the Hakluyt Society.

CORAL CAY CLASSIFICATION AND EVOLUTION

Scott G. Smithers, David Hopley
James Cook University, QLD, Townsville, Australia

Definition

A coral cay is an island formed from sediments derived from the reef on which it sits and swept by refracted waves to a focal point on the reef flat where they are deposited. A cay initially may remain intertidal and lack vegetation, but with time it is likely to build up to be above sea level, acquire a vegetation cover, and become partially lithified.

Introduction

Islands associated with coral reefs have been occupied or used by humans for millennia. They became known to western society as voyages of discovery crossed tropical waters. A distinction has been made between "high" islands composed of continental rocks and "low" islands of biogenic carbonate sediments produced by reef organisms. The variety of morphologies that were observed became a focus of early studies:

> "There are different opinions amongst ingenious theorists, concerning the formation of such low islands".
> (James Cook, 17 April, 1777)

Scientific studies of reef islands were first made in the nineteenth century in south-east Asia and the Australian Great Barrier Reef (GBR) and subsequently in the Pacific and Indian Oceans and in the Caribbean Sea (see Table 1; Stoddart and Steers, 1977) (see *Steers, James Alfred (1899–1987)*; *Stoddart, David Ross (1937–)*).

As the diversity of form became evident, various attempts at classification were undertaken. More recently research has extended to understand processes that form and maintain coral cays and their origin, age, and evolution. Many of these investigations, especially the development of classifications, were based on studies of the GBR (Spender, 1930; Steers, 1929, 1938; Fairbridge, 1950; Stoddart and Steers, 1977; Hopley, 1982, 1997; Hopley et al., 2007). The GBR is the largest reef province in the world, which when combined with the adjacent Torres Strait contains over 1,000 islands including approximately 350 coral cays (Hopley et al., 2007). Stretching over 15° of latitude and with reefs extending from the mainland to the shelf edge, the GBR provides a diversity of environments which are responsible for the great variety of coral cay types found within its waters (see entry: Section 10.1.3 in Hopley et al., 2007).

Cay formation: wave influences

Coral cays generally occur on reef flats at or very close to sea level. The reef flat need not be large (many occur on small reefs <1 km^2), and some sand cays in the Maldives have been shown to develop over lagoonal sediments while the reef flat is still evolving (Kench et al., 2005). A supply of biogenic sediments is fundamental for cay formation, but most reef tops have partial veneers of sand and shingle and there are many with diffuse sediment sheets that remain unconcentrated. The most critical factor for cay formation is the centripetal pattern of sediment movement produced by waves and currents in response to reef shape; centripetal sediment transport delivers sediment to a focal point or depositional node where it may accumulate (see *Hydrodynamics of Coral Reef Systems*; *Wave Shoaling and Refraction*; *Waves and Wave Driven Currents*).

Two related features of wave transformation over a reef control whether or not deposition is spatially concentrated. The first is the convergence of waves. The depth of water just beyond the reef front means that waves do not fully

Coral Cay Classification and Evolution, Table 1 Flora of reef islands

Ocean	Island(s)	No.	Or area	Source	Total No. of sp.	% Indigenous
Atlantic ocean						
	Belize cays			ARB256 (Stoddart et al. 1982) ARB258 (Fosberg et al. 1982)	178	82
	Cayman Island cays			Sauer (1982)	102	67.6
	Glovers Reef[a]	6		ARB257 (Stoddart et al. 1982)	70	n.a
	Jamaican cays	15		ARB351 (Stoddart and Fosberg 1991)	105	79.0
Indian ocean						
	Cocos-Keeling[a]	22		ARB404 (Williams 1984)	130	46.9
	Diego Garcia[a]		30 km^2	ARB313 (Topp 1988)	191	n.a.
	Kavaratti[a] (Lacadives)		3.63 km^2	ARB266 (Sivadas et al. 1983)	117	n.a.
	South Indian cays	6		ARB161 (Stoddart and Fosberg 1972)	84	n.a.
	Winhingili[a]; Addim atoll Maldives		0.97 km^2	ARB231 (Spicer et al. 1989)	72	n.a.
Pacific ocean						
	Bikini[a]	22		ARB315 (Fosberg 1988)	67	52.2
	Kapingamarangi[a]	22	112 ha	ARB362 (Woodroffe and Stoddart 1992)	99	50.5
	Nui[a]		337 ha	ARB362 (Woodroffe and Stoddart 1992)	86	51.2
	Ontong Java[a]		650 ha	ARB362 (Woodroffe and Stoddart 1992)	146	56.2
	Suwarrow[a]		200 ha	ARB362 (Woodroffe and Stoddart 1992)	45	51.1
Great Barrier Reef	Northern cays	80		ARB348 (Fosberg and Stoddart 1991)	380	66.6
	Bushy (Redbill)		4.5 ha	ARB350 (Walker et al. 1991)	34	82.3
	Green		15 ha		114	47.4
	Heron		19 ha	ARB349 (Stoddart and Fosberg 1991) ARB440 (Rogers 1986)	51	49.0
	Lady Musgrave		13 ha	ARB350 (Walker et al. 1991)	51	54.9

ARB atoll research bulletin and volume
[a] Atoll motus

refract and accommodate themselves to the reef front. Instead, around the reef perimeter except at the windward tip, they pass over the reef crest at a slight angle, leading to a zone of wave convergence toward the leeward reef flat. This is indicated clearly by the pattern of the aligned coral zone (see *Geomorphic Zonation*) on many reefs. However, centripetal transport and concentrated deposition are not developed on all reefs. Reef shape is critical, as it controls the pattern of refraction. Convergence of wave trains is most likely on oval reefs. However, interference of wave patterns by upwind reefs may mean that the waves approaching a reef are already refracted. In these circumstances, a clear focal point from further refraction may not be achieved, impeding island formation.

The second important feature of waves is their ability to transport sediment. Much wave energy is dissipated on the reef edge due to breaking and reflection. However, some energy is transmitted and smaller waves reform beyond the break point and move over the reef, where they are attenuated very slowly, unless water depths are exceptionally shallow or the bottom is very rough. The competency of reformed waves to move sediment is markedly diminished, even during major storms. Thus, coarse sediment is likely to be deposited on the windward margin where a shingle cay may form. Where waves tend to break normal to the reef front, this may be a rampart-like linear feature paralleling the reef crest (Figure 1; see *Shingle Ridges*). Alternatively, there may be sufficient refraction at the apex of a reef to concentrate coarser sediments into a compact island.

Coral Cay Classification and Evolution, Figure 1 Windward shingle ridge parallel to reef front, Turtle 2 Reef GBR.

Generally, waves propagating over the reef flat beyond the rim are only competent to transport sands and finer sediments. As these waves slowly attenuate, sediments may be transported a considerable distance leeward.

Deposition occurs where refracted waves converge, either along the center of the reef or in a nodal area toward the lee. However, on very large reefs, waves that are distant from the reef front may become incompetent to transport even fine sediments that remain spread over the reef flat. Leeward sand cays thus form where there is both a centripetal convergence of refracted waves and sufficient wave power to transport sediments to a focal point. On large reef flats, sediment transport by refracted waves may be augmented by locally generated short-period wind waves, with their influence growing as rising tides increase fetch over broad reef platforms (Samosorn and Woodroffe, 2008). In high-energy areas and/or on smaller reef platforms, sediments may be swept entirely off the reef. Because maximum wave height over a reef flat is constrained by water depth (which is tidally modulated) and wave attenuation is a function of friction, a reef energy window index can be calculated from the ratio of the reef flat depth at mean spring high tide and reef width, which indicates potential geomorphic activity over a particular reef platform (Kench and Brander, 2006).

Cay sediments

The textural characteristics of reef sediments play an important role in the bimodal distribution of reef flat sediment deposition observed on many reefs. Because shingle and rubble tend to break down into sands of approximately 2ø (Orme, 1977), a distinctly bimodal distribution of sediments and depositional environments develops under the wave-energy conditions described above (see *Sediments, Properties*; *Sediment Dynamics*; *Reef Flats*). Nonetheless, the basic division of reef islands into windward shingle cays and leeward sand cays is very much oversimplified.

Studies of GBR cays (Maxwell et al., 1961, 1964; McLean and Stoddart, 1978) suggest that for each cay type, either sand or shingle, sediments textures are remarkably uniform. McLean and Stoddart (1978) examined sediments of cays on the northern GBR and found that shingle is relatively homogeneous in composition (mainly *Acropora* clasts) but varies in size and shape, whereas sand cay sediments are mainly well-sorted (<1ø) medium to coarse sands (0–1.5ø) derived from a wider range of biota and are compositionally very similar to reef flat sediments. Where winds blow from one prevailing direction, the beaches on sand cays contain the coarsest sediments, particularly on the windward shore. Winnowing by the wind transports finer sand to the cay interior or berm, though dune structures are rare or poorly developed on most cays. McLean and Stoddart (1978) found that the finest sediments were associated with soils, either as a component of the active soil profile or within buried soil horizons.

The broad patterns established for GBR cay sediments are generally applicable elsewhere. Although sand cay sediments occur within a narrow textural range, small but distinct variations between cays develop due to differences in proportions of constituent components (which may be related to the nature of the reef flat), differences in distances, modes, and rates of transport from source area to cay (dependent on the size of the reef and the location of the cay upon it), and variations in residence time since deposition. Coral cays may include minor amounts of siliciclastic sediment; pumice fragments floated in from volcanic source areas are common and can form distinctive strata up to 30 cm thick on some cays. Pumice fragments up to 0.5 m in diameter have been found, but more commonly they range between 1 and 5 cm in size. Occasionally, continental rocks reach cays in the roots of floating trees.

Criteria used in classification

Several coral cay classification schemes have been proposed to accommodate and in some cases explain the variation in morphological and compositional diversity outlined above. Steers (1929) suggested three classes of reef islands based on his detailed work on the GBR in the 1920s and 1930s: sand cays, shingle cays, and low wooded islands. Spender (1930) proposed a general classification of reefs and low islands that recognized five classes of reef, four of which support reef islands (1) a sand cay; (2) a sand cay and unvegetated rampart; (3) a sand cay and vegetated rampart without extensive mangroves across the reef platform; and (4) a sand cay, vegetated rampart, and mangrove-forested reef flat. Spender referred to this latter class as "island reefs" but they are synonymous with Steers's low wooded islands by which they are better known today (see *Low Wooded Islands*).

Fairbridge (1950) identified five classes of island based on sediment type, vegetation cover, and the occurrence of emergent reef flat – a function generally of late Holocene relative sea-level history that can vary geographically (Hopley et al., 2007). Fairbridge's cay classes were (1) unvegetated sand cays; (2) vegetated sand cays; (3) shingle cay, with or without vegetation; (4) sand cay with shingle ramparts, vegetated or unvegetated islands and with mangrove swamp over reef top; and (5) island with exposed platform of older emergent reef, sometimes fringed by more recently deposited sediments. Hopley (1982, 1997) reviewed the literature on GBR reef islands and their classification and concluded that four criteria can be used to define a reef-island classification equally applicable to coral cays formed in other reef regions. The four key criteria that form the basis of reef-island classification are as follows:

Criterion 1: Sediment type. Sand, shingle, or a mixture of both can dominate reef islands. In areas of moderate energy and a prevailing wind direction, shingle is typically located toward the windward edge of the reef platform, and sand cays generally form near the leeward margin due to hydrodynamic sorting. This distinction may be less clear in areas rarely affected by storms where shingle deposits may be lacking or on reefs affected by frequent high-energy storms where successive ridges of storm-deposited coarse material may form the island core, but are surrounded by a sandy beach (e.g., Lady Musgrave Island, southern GBR). Reef islands developed where wind direction seasonally reverses are also less likely to show the classic bimodal distribution of sediments, especially on smaller reef platforms where mixing is likely.

Criterion 2: Island location on the reef platform. Where sediments are available and the reef platform size and energy regime allow sorting to occur, shingle cays form near the windward reef margin and sand cays to leeward. On some platforms, reef islands may occupy a significant proportion of the reef flat; coral cays on lagoonal reefs within Maldivian atolls can occupy as much as 56% of the reef top (Kench et al., 2008). Where cays are large relative to the reef platforms on which they sit, it is difficult to define whether a cay is windward or leeward, as is also the case where cays are located centrally on the reef due to either seasonal wave climate reversals or a function of reef geometry.

Criterion 3: Island shape. Cay shape broadly falls between elongate and compact (oval to round). This trait is largely controlled by the interaction of reef shape and wave refraction and transformation around and across a reef. Compact islands form where sediment transport to a single focal node is most efficient. Therefore, the directional consistency and energy of the prevailing wave climate and the complicating effects of obstructions such as adjacent reefs on the transfer of this energy to the reef platform also influence island shape. Generally, but not always, compact cays are more stable than elongate cays; the ends of which can be particularly sensitive and move with small changes in wind and wave direction with a seasonal periodicity (e.g., Flood, 1986).

Criterion 4: Vegetation cover. Coral cays are either unvegetated or vegetated, with the extent of vegetation often reflecting island size, age, and stability. Climate, especially rainfall and frequency of storms, can also be important, but larger, older, and more stable islands generally possess better soils and groundwater aquifers best able to sustain vegetation. Reef-island vegetation is discussed further in Section Reef-island vegetation.

The four criteria above can be used to describe and classify reef islands that range from small and unstable unvegetated sandy cays to complex low wooded islands (see Section Classification: island types). It is important to note that two criteria – vegetation cover and island shape – may change abruptly, especially on reefs exposed to extreme events. For example, Pickersgill Cays on the GBR were reported as slightly vegetated by the Australian Pilot early in the twentieth century but unvegetated when Spender (1930) and Steers (1929) visited in 1929 and were again unvegetated in 1973 (Stoddart et al., 1978a). Rapid changes in reef-island morphology can be established by comparing aerial photographs or accurate GPS surveys at event and seasonal time scales, and these methods commonly document significant shifts in shoreline at these short time scales (e.g., Frank and Jell, 2006). Historical maps available for some reef islands can be compared with later versions to show significant change over the past 50–100 years (e.g., Stoddart et al., 1978b; Flood, 1986). Relict beach rock outcrops indicate the position and shape of cay shorelines in the longer term past that can be very different to the present day morphology. Cay dynamics are covered in Section Factors influencing cay stability.

Classification: island types

The main classes of coral cay are described in the following section. The defining features of major reef-island classes are depicted schematically in Figure 2.

Unvegetated cays

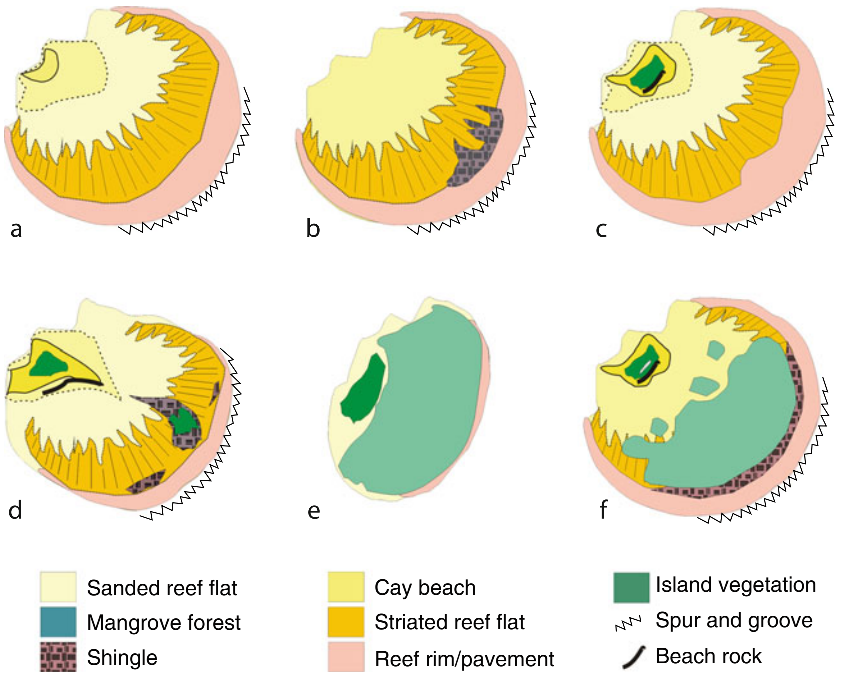
Unvegetated cays clearly lack vegetation. They are generally small and unstable; both conditions constrain the establishment and survival of plant cover. A mean area of just 0.5 ha was determined for 18 unvegetated cays surveyed in the 1973 northern GBR expedition (Stoddart et al., 1978a). They may be composed of sand and/or shingle and can be either elongate or compact. They are the most common cay type (see *Unvegetated Cays*).

Unvegetated sand cays

Linear unvegetated sand cays form on medium to large planar reefs (see Chapter *Reef Classification by Hopley, (1982)*) of elongate shape where wave refraction generates opposing wave trains that meet along a central axis and where sediment accumulation takes place. Linear unvegetated cays may also form where winds seasonally reverse, producing an elongate, spit-like accumulation toward the leeward reef margin. Hopley (1982) considered that the migrating linear sand banks on the large planar reefs of Princess Charlotte Bay, northern GBR resulted from seasonal shifts between dominant south-easterly trade winds and lighter, more northerly monsoonal winds. Bidirectional monsoons have also been linked to the abundance of elongate unvegetated cays in Indonesia (Tomascik et al., 1997). Compact unvegetated cays form where strong centripetal sediment transport focuses deposition within a restricted locus (Figure 3a). Many are highly mobile and unstable (Hopley, 1978; Aston, 1995), especially the smaller (<0.1 ha) “ephemeral” cays that may be submerged at high tide (Figure 3a). Stoddart et al. (1982) concluded that many of these cays in the Caribbean, such as Paunch and Curlew Cay, may be second generation features reformed following the destruction of larger cays during storms. Larger unvegetated cays up to 400-m long and 120-m wide are often flanked by beach rock, suggesting greater stability.

Unvegetated shingle cays

Linear unvegetated shingle cays are very unstable reef islands, vulnerable to reworking and erosion near the reef front (Figures 2b and 3b). They are typically the product of



Coral Cay Classification and Evolution, Figure 2 Schematic plan views of major reef-island classes: (**a**) unvegetated sand cay; (**b**) unvegetated shingle cay; (**c**) vegetated sand cay; (**d**) multiple island (with vegetated shingle island); (**e**) mangrove island (note no spurs and grooves as low-energy setting); (**f**) low wooded island.

high-energy storms and form as shingle ramparts coalesce. Unvegetated shingle cays can remain reasonably intact between storms, and cementation of basal sediments can occur, forming bassett edges (cemented lower parts of shingle ridges), which steeply dip away from the reef front (see *Bassett Edges*). However, bassett edges preserved after ramparts are eroded occur like outcrops of beach rock on many reef flats, suggesting that unvegetated shingle cays have also limited longevity (Hopley, 1982). Compact unvegetated shingle cays are generally restricted to small reefs, but vary from relatively mobile mounds of shingle and rubble through to complex structures with some degree of cementation.

Vegetated cays

Eventually some unvegetated cays achieve sufficient stability for vegetation to successfully establish and this vegetation may confer additional stability (see Section Reef-island vegetation). As for unvegetated cays, vegetated cay sediments range from pure sand to shingle, and shapes range from linear to compact (see *Vegetated Cays*).

Vegetated sand cays

Vegetated cays are usually more stable than unvegetated cays, but can still change morphology and position. For example, in the Caribbean, Hurricane Hattie in 1961 completely removed St. George's East Cay that was 110-m long and 0.3 ha in size (Stoddart et al., 1982). Hopley (1982) argued that compact vegetated cays (Figures 2c and 3c) are more stable than linear cays because (1) they usually have a proportionally larger vegetated area; (2) beach rock outcrops give better protection as they armor the beaches rather than become detached as on unvegetated cays; and (3) colonizing species tend to dominate linear cays for a longer period. Some vegetated cays are barely emergent at high tide, but others support dunes that rise several meters (Figure 3c). Beach rock can occur on the more stable long-axis flanks of compact and even linear vegetated cays, with massive outcrops exposed by subsequent erosion. For example, beach rock was absent from only one (Upolu Cay) of the 17 vegetated cays on the GBR mapped by Stoddart et al. (1978a). Flood (1977) also noted that beach rock was common on the 14 vegetated cays in the Bunker and Capricorn Groups he examined. Moderate though not necessarily extended stability is required for beach rock formation (see *Beach Rock*), and massive outcrops confer additional stability to a cay under erosive conditions. In contrast, spits at the ends of these islands are characteristically mobile and commonly shift from season to season. Mineralization of phosphates derived from guano has cemented sediments beneath the vegetation cover to form phosphate rock on some cays (e.g., Raine Island, GBR; Figure 7), also increasing island stability.

Vegetated mixed sand and shingle cays

Mixed sand and shingle cays may develop where wind direction shifts seasonally and shingle is supplied during

Coral Cay Classification and Evolution, Figure 3 (**a**) Leeward unvegetated sand cay, Wheeler Reef, GBR. (**b**) Shingle cay with extended spit, Pandora Reef, GBR. (**c**) Vegetated sand cay, Bushy Island, Redbill Reef, GBR. *Note*: the zone of shrub vegetation fronting the interior *Pisonia* forest. (**d**) Tupai Atoll motus, French Society Islands. (**e**) Windward vegetated shingle island, showing constructional ridges and leeward vegetated sand cay, Fairfax Reef, southern GBR. (**f**) Low Isles, GBR, the classic low wooded island, site of the 1929 Royal Society Expedition.

one season and sand during the other (e.g., this process accounts for mixed sand and shingle cays in Torres Strait). Alternatively, shingle may be deposited during storms, with sand deposition during regular weather conditions. The latter mode appears to explain the sediment pattern of Lady Musgrave Island on the southern GBR. There, shingle ridges have been episodically deposited by storm waves, with sand accumulating around the margins during normal trade wind weather. Mixed cays also develop where the character of sediments produced on the reef or delivered to the focal point of accumulation change through time, as may occur when reef geometry is modified or changing sea levels modify reef flat hydrodynamics. In the atolls of the Caribbean, these mixed islands typically comprise a windward shingle ridge and leeward sand area. Lime and Hunting Cays are examples (Stoddart et al., 1982).

Reef islands deposited on atoll rims generally fall within this class, although the proportions of sand and shingle vary. On open-ocean atolls (see *Atolls*) in very low energy areas, e.g., close to the equator, islands may be predominantly sand but at latitudes where cyclones are more regularly experienced they tend to be dominated by shingle and boulders (see *Tropical Cyclone/Hurricane*). These linear shingle islands are generally larger than those found for example on barrier reef systems and are thus able to maintain a freshwater lens and diverse vegetation. Many of these islands have been home to Polynesian peoples for centuries or millennia and are commonly referred to as motu [Figure 3d; see *Atoll Islands (Motu)*].

Vegetated shingle cays

Vegetated shingle cays are uncommon. One Tree Island, Lady Elliot Island and East Hoskyn and Fairfax Islands (Figures 2d and 3e), all located at the southern end of the GBR, are among the few cays of this type to have been scientifically analyzed. However, Tomascik et al. (1997) suggest that they are probably common on the exposed parts of the Great Sunda Barrier in Indonesia. These cays typically develop near the windward margins of larger reef flats or centrally on smaller ones exposed to high energy. Most vegetated shingle cays are compact in form as linear shingle cays are usually either too narrow to retain adequate freshwater or too mobile for vegetation to endure. Where vegetation survives, the greater stability of the shingle cay allows vegetation succession to proceed until cyclonic disturbance occurs (Hopley, 1982). Observations from the atoll of Ontong-Java suggest that in areas of episodic high-energy storms and sufficient sediment supply, these cays may go through cycles of destruction, reformation, and revegetation (Bayliss-Smith, 1988). Stoddart et al. (1982) noted the mobility of these cays in the Caribbean, where substantial changes were recorded at North Spot and Rugged Cays between 1960 and 1972.

Hopley (1982) suggested that shingle cays developed from shingle ramparts, with the "tongues" of shingle and rubble that commonly trail leeward from ramparts also possibly involved; One Tree Island in the southern GBR has formed this way. The near concentric shingle ridges at Lady Elliot Island similarly document its formation over several millennia by the progradation of shingle ridges deposited during episodic storms (Chivas et al., 1986). However, as noted above, evidence from various locations suggests that storms may also destroy these features.

Mangrove islands

In low energy areas, mangroves may colonize reef flats (Figure 2e) and encourage sediment accumulation and island formation. Sediments deposited beneath the mangroves vary from peats to carbonate mud. Mangrove islands are rare on the GBR, but are more common in Torres Strait (Hopley, 1997) where despite a relatively high-tide range mangroves more frequently develop in sheltered areas behind shingle ramparts. Similarly, reef top mangrove islands are reported from various locations in Indonesia without rampart protection but where low-energy conditions prevail due to proximity to the equator and associated benign wind regime [e.g., Pulu Panjang in the Berau Islands (Tomascik et al., 1997)]. They are common on reefs lacking windward ramparts in the Caribbean (Stoddart and Steers, 1977), but are generally restricted to high reef tops, areas of low energy, and areas of relatively low tidal range. Mangroves are common on the reefs of Belize and are associated with different types of island (Stoddart et al., 1982). "Mangrove cays" are mud mounds with a simple covering of mangroves: "Mangrove cays with dry sand areas" have featureless low lying sand areas within the mangroves; "Moat Islands resemble the low wooded islands of the GBR; and "Mangrove range" are complex and extensive arrays of mangroves with intermittent sand ridges especially on the windward side (see also Woodroffe, 1995). Mangroves are also common in sheltered locations within the three offshore atolls (e.g., Murray et al., 1999). In Florida Bay, mangrove islands began to accrete as the shallow Miami Limestone was flooded in the late transgression, with various models proposed to explain the location and processes of formation. Recent geochronological and lithological investigations suggest net accumulation punctuated by erosion episodes over the past few thousand years as the rate of relative sea-level rise slowed to its present position (Oches et al., 2009) (see *Mangrove Islands*).

Multiple islands

Multiple vegetated islands on a single reef are rare on the GBR; there are just two long-standing examples – Fairfax (Figure 3e) and Hoskyn Islands in the Bunker Group. Each includes both a vegetated shingle and vegetated sand cay on a single reef platform, shingle cay to windward, and sand cay to leeward (Figure 2d). On large reefs subject to seasonal reversal of winds but only rare storms, sand cays may develop at opposite ends of the platform; this appears to be the case at Masig-Kodall (Yorke Island) in Torres Strait (9°45′S) where seasonally reversed waves interacting with an unusually shaped reef produces two depositional nodes and islands. The same process is probably responsible for the occurrence of multiple islands in the Indonesian Archipelago, where according to Tomascik et al. (1997, p. 819) they are "not a rare occurrence."

Low wooded islands

The basic pattern of a low wooded island comprises a windward shingle cay, a leeward sand cay, and significant mangrove development over the intervening reef top (Hopley, 1997; Figures 2f and 3f; see *Low Wooded Islands*). This combination of features may occupy a great proportion of the reef top, usually between 25 and 50% but up to as much as 75% (Stoddart et al., 1978a). The majority of “classic” low wooded islands on the GBR occur on relatively small planar reefs on the inner shelf (e.g., Low Wooded Island – 87.9 ha), but they can occur on larger reefs (e.g., West Hope Island – 315 ha) (Stoddart et al., 1978a). Shingle ramparts that grade upward from the reef flat and have steep leeward faces are encountered at varying distances from the windward margin. These ramparts frequently parallel the reef edge, but shingle tongues may trail toward the reef interior (see *Shingle Ridges*). Mangrove stands develop in the relatively protected area behind the shingle ramparts and may eventually expand to cover much of the reef flat. The degree of mangrove colonization was considered to reflect the stage of island development by some workers (Steers, 1937; Fairbridge and Teichert, 1947), but others contend the degree of protection afforded by windward structures is responsible (Stoddart et al., 1978c; 1982). Stoddart (1980) suggested that once the protection is provided, the extent and rate of spread of reef top mangroves varies markedly between reefs, and the mangroves are in fact opportunistic colonizers. Organic muds occur beneath the mangroves on some islands but elsewhere the mangroves grow over sandy reef flats. Fields of emergent fossil microatolls document the higher mid-Holocene sea level and later regression experienced by the planar reefs on which low wooded islands on the GBR have formed (McLean et al., 1978; Chappell et al., 1983) (see *Mid-Holocene*).

The leeward sandy cays are morphologically diverse. Some are small, ephemeral, and unvegetated but larger vegetated cays replete with terraced morphology also occur (e.g., Ingram Island). The characteristic complexity of low wooded islands ensures that they are a heterogenous group. Stoddart et al. (1978a) distinguished four low wooded island types, *low wooded island with limited reef top mangroves and a separate sand cay* are most numerous. *Low wooded island with reef top mangroves extending between windward shingle and leeward sand cays* are also common, with Bewick Island on the northern GBR the type-example. “*Turtle-type*” low wooded islands lack the central reef flat, with shingle ramparts and conglomerates extending to the leeward cays (Figure 1). They are generally restricted to small reef platforms (<60 ha) where they occupy a large proportion of the reef flat. The final class described by Stoddart et al. (1978a) includes those that could not be assigned to the groups above. Hannah Island, a sand cay completely encircled by mangroves, provides an example.

A chronology for reef flat formation and low wooded island accretion on the GBR has been established by radiocarbon dating (see Hopley et al., 2007 for summary). The dates suggest that (1) many low wooded islands formed under higher sea-level conditions prior to 3,000 years ago; (2) there is no consistent pattern in the timing and order of shingle and sand cay development on different reefs; and (3) many low wooded islands were in place or substantially developed by the mid-Holocene and exist in similar form today, suggesting stability in the longer term. However, comparison of the detailed maps of Low Isles and Three Isles in 1928–1929 (Spender, 1930) with those produced later show modifications to ramparts, mangroves and cays, indicating that change may be constantly taking place (Stoddart et al., 1978b; Frank and Jell, 2006). Although the most detailed descriptions of these islands come from the inner northern GBR, equivalents occur in other reef provinces and include Salt and Pigeon Cays in Jamaica, and the Snake Cays in Belize, where they are referred to as “moat islands.”

Reef-island vegetation

Vegetation plays an important role in the evolution of coral cays, being integral to all classification schemes, and showing important changes through time (see *Coral Cays, Vegetational Succession*). Progressive accretion is expressed by “rings” of vegetation from low creepers and grasses growing on recently deposited carbonate sands immediately behind the beach, through a zone of shrub vegetation on young soils with minor organic content, to an internal climax vegetation of woodland or forest growing on mature soils (see *Soils of Low Elevation Coral Structures*; Figures 3c and 4). The vegetation itself, together with the developing soils contributes to stability. Erosional episodes with subsequent return to progradation may result in the shrub or woodland vegetation being exposed immediately behind the beach or with a new area of colonizing vegetation fronting the climax vegetation.

The initial establishment of vegetation and subsequent changes has a number of requirements. Colonizing vegetation requires a degree of stability and access to some rainfall or brackish water (Figure 5). Addition of organic matter to the raw carbonate sediments comes not only from the vegetation but also from bird guano as nesting and roosting birds become attracted to the cay. As noted,

Coral Cay Classification and Evolution, Figure 4 Climax forest vegetation dominated by *Ficus benghalensis*, Soneva Fushi, Maldives.

Coral Cay Classification and Evolution, Figure 5 Pioneering creeper vegetation, pantropical *Ipomea pes-caprae*, Rodrigues Island, Indian Ocean.

the presence of phosphatic cay sandstone (Figure 7) is indicative of mature vegetation and is an obvious source of nutrients for the higher plants (see *Phosphatic Cay Sandstone*).

The origin of the vegetation on islands that may be hundreds or even thousands of kilometers from continents or other coral islands and the structured similarity of the cay vegetation worldwide were enigmatic to early explorers and naturalists. However, it soon became apparent that the seeds of many of the plants float and reach remote shores via ocean currents. Other seeds are ingested by birds and excreted on the island, or attached to plumage, sometimes causing the mortality of the bird. In both cases, the seeds are deposited with an organic fertilizer. More recently, exotic plants have been brought to islands by early settlers (e.g., Polynesian voyagers) and in some instances became dominant over the original preexisting vegetation. However, the harsh environment of coral cays with strong environmental influences such as climate, water availability, soil, and nutrient limitations enforces pantropical controls on the success or otherwise of cay plants and is the ultimate reason for the structural similarity of coral cay vegetation worldwide.

Physiognomic similarities conceal what is a very complex flora. For example, atolls thousands of kilometers into the Pacific and Indian Oceans have plant lists ranging up to almost 300 species [Table 1; e.g., Kiribati, 290 species (Thaman, 1987)], even though nearly all coral cays and low reef islands are less than 6,000 years old. Also in spite of the isolation of many reef islands, they have very few endemic plants. The number of plant species is dependent on:

(a) Island size (even for isolated atoll motus, this is an important factor)
(b) Remoteness from other islands or most importantly continental land masses
(c) The period of human occupation (and introduction of exotics)
(d) The frequency of disturbances which can range from natural events such as cyclones or tsunamis to human disruptions for coconut plantations or nuclear weapon testing

Dispersal distance from other land masses may not be based on present geography, but instead could reflect land configuration and the distribution of island "stepping stones" present during glacial low sea levels. For example, on the northern GBR at the maximum of the last glacial the whole continental shelf was dry and mainland carbonate dominated shorelines would have stretched, for example, across the Gulf of Papua allowing the retention of a wide range of plants currently found on the cays. Present day reefs that are further off shore would, at that time, have been high limestone islands and whilst, for a short period, they may have been little or no land in the form of islands on the continental shelf, as reefs were initially drowned by the post glacial sea level (see *Holocene High Energy Window*), the nearby mainland would have been a permanent source of floating seeds carried out to the offshore evolving cays. Today, the islands of this area have 380 species of plants (Fosberg and Stoddart, 1991). In contrast, the reefs and islands of the southern GBR would have remained isolated from continental Australia, even at the maximum low sea-level stage. Today, these islands (the Bunker-Capricorn Group) support only 80 species, between 22 and 40 on individual islands (Stoddart and Fosberg, 1991).

The range of substrate types is also important in determining the number of species present on an island. Sand and shingle substrates have contrasting species lists but these are expanded if different types of cemented substrate such as conglomerate or phosphatic cay sandstone occur. This was one of the conclusions of Sauer (1982) in his comprehensive review of vegetation on the Cayman Islands with a focus on the unconsolidated carbonate sediments, the vegetation of which is equivalent to that of Caribbean cays. His conclusions are applicable across other Atlantic and Indo-Pacific reef islands.

Sauer noted the importance of introduced species that can contribute 50% of cay flora (Table 1). Indigenous cay flora have very poor defensive mechanisms and are easily displaced. For example, on Mopelia atoll in the Society Islands, 50 of 85 species are introductions (Sachet, 1983). However, introduced species, unless cultivated, can also quickly disappear. During World War II, 129 species were introduced to Canton atoll, but by 1973 only 14 persisted. Sauer also examined the distribution of coral island plants, noting that while endemics were few, the flora of Atlantic islands had many commonalities as did that of the Indo-Pacific. There is also a distinctive pantropical element. The best known of these is the coconut tree, *Cocos nucifera,* but away from its source area of Southeast Asia, it is an introduction on most islands. Pantropical species are mostly dispersed as float seeds with the ability to remain viable for at least 6 months. More often than not these pantropical species are part of the initial beachfront colonizing vegetation (Figure 5). Sauer (1982) noted 11 pantropical species on the Caymans, but many more occur in the Pacific. For example, of the 380 species listed for the northern GBR (Fosberg and Stoddart, 1991), 25 also grow on the Cayman Islands though a number may be introductions. Twenty-seven GBR species were also found on Jamaican cays (Stoddart and Fosberg, 1991) and 33 on the cays of Belize (Fosberg et al., 1982).

Many questions remain unanswered about coral cay vegetation. Although apparently simple, with a classic pattern of ecological succession, the highly successful mechanisms of dispersal reinforce at the species level, the global physiognomic similarities. However, even this ability does not answer all questions. As Sauer (1982) noted, the fossil record for this vegetation is very poor, though clearly going back until at least the Tertiary. It has thus become involved in plate tectonics and changes to global land masses, especially the isthmus of Panama, which now closes the link between Caribbean and the Indo-Pacific. While there are possibilities of some flora migrating around the southern tip of Africa, this would entail a long route outside the tropics. Today's pantropical species may be the last vestige of the more open Tertiary geography of meso-America.

Age, evolution, and relationships to Holocene sea level

A foundation, usually a reef flat at or near to sea level, is necessary for reef-island formation, but it may be small and not yet sea level constrained (Hopley, 1997; Kench et al. 2005). The relationship between reef growth, sea level, and reef flat formation on a global scale is complicated by various factors including postglacial isostatic adjustments of the continents and ocean basins, which have produced broad geographic differences in relative sea-level history and especially when reef tops first approached the sea surface (Clark et al., 1978; Lambeck et al., 2002). Pirazzoli (1991) presents detail on these patterns (see *Glacio-Hydro Isostasy*), but the relative sea-level curves for most of the Pacific and the Caribbean and thus the potential onset of cay formation in these two provinces are very different. Modern sea level in the former was reached 6,000–5,000 years ago, in places rose 1–2 m higher and has then fallen to present, whereas in the Caribbean it has been rising throughout the Holocene but, slowing over the past few thousand years. Modern sea level has only recently been reached (Toscano and Macintyre, 2003). Further, at a more regional scale, isostatic influences driven by differential loading by postglacial transgressive seas can produce variable relative sea-level histories as deeper shelf edge areas subside under water load (delaying reef flat formation) and shallower inshore areas possibly upwarp (Hopley, 1983; Lambeck and Nakada, 1990). Other factors that influence when a reef reaches sea level and provides a base for reef-island development include the depth from which the reef has grown and the size of the reef and its lagoon. Typically, reef islands are oldest where current sea level was reached early – in the mid-Holocene, where the reefs grew from shallow substrates and were thus sea level constrained earlier, and where they grew on relatively small reefs with smaller lagoons that were infilled more rapidly than those of larger reefs.

The relationships described above are demonstrated on the GBR, where stable vegetated cays are strongly associated with planar reefs; 41 of 43 are on planar reefs that grow above shallow pre-Holocene foundations (mean: 10.8 m) and are relatively small (mean: 4.1 km^2). Planar reefs also have the oldest mean reef top age (~6,000 years), so that depending on where reef geometry and hydrodynamic conditions initially focus sediment deposition, cay formation could have begun 6,000 years ago (Hopley et al., 2007). In Hopley's (1982) evolutionary classification of reefs [see *Reef Classification, Hopley (1982)*], planar reefs represent a senile stage approaching the end of their growth trajectories. Significantly, most reef islands with any degree of permanence are found on these senile reefs though at the time of their initiation the reef could have been at an earlier state (even reef patches) and persisted through the mid to late Holocene period of lagoon infilling and reef flat extension. Thus, at the geological time scale the factors that promote the advance of reefs through the reef growth sequence are also important drivers of cay formation. Spender's (1930) hypothesis that reef-island formation is strongly influenced by relative sea-level fall and reef platform emergence was dismissed for more than five decades (Steers, 1937; Stoddart, 1965). However, the importance of hydroisostatic upwarping of the inner shelf in accelerating the development of reefs to planar stage and as a consequence improving reef-island accumulation and, possibly, preservation is now generally accepted for the GBR.

Most reef islands on the GBR and all low wooded islands are inside the zero hydroisostatic isobase. Emergent reef occurs beneath reef islands in many other settings (discussed below). Kench et al. (2005) suggested that some Maldivian cays began to develop prior to reef flat formation, and West Indian cays have formed where sea level has risen gradually to present since the mid-Holocene (Woodroffe, 2003). Radiocarbon-dated fossil microatolls underlie many of the reef islands which have been investigated on the GBR, suggesting that most of them developed after the reefs had reached sea level (see Hopley et al., 2007 chapter 10), but the occurrence of ~75 unvegetated cays on platforms close to sea level suggests that emergent reef platforms are not absolutely necessary. Reef islands on the Cocos (Keeling) Islands, Indian Ocean are also deposited over fossil reef flat that are made emergent by the falling late-Holocene sea levels (Woodroffe et al., 1999). Dickinson (2004) revisited the earlier ideas of Schofield (1977) and proposed that wave-resistant emergent palaeoreef flats strongly influenced the development of stable reef islands on many Pacific atolls, but he acknowledged that less stable "unpinned" reef islands are common on reef flats that remain flooded by lower tides. These higher foundations that confer stability to overlying islands are not always composed of Holocene reef. Cays composed of or attached to Pleistocene reefal deposits, or occasionally eolianites (see *Eolianite*), are common in the Bahamas and offshore from British Honduras (Milliman, 1973).

Establishing precise chronologies for reef-island formation is difficult as radiocarbon dates age the death of the contributing organism and not the age of the deposit; in many settings, these two ages can be centuries or even millennia apart. If the radiocarbon chronologies are correct, rapid sand production, delivery, and cay deposition occurred on many planar reefs of the GBR between 4,000 and 3,000 years ago, with only relatively minor modifications since. Similar histories are reported from elsewhere (Kench et al., 2005; see Woodroffe, 2008), including for Warraber in Torres Strait where bulk sand ages suggest a growth chronology very similar to those of the GBR cays described above. However, AMS radiocarbon dating of specific skeletal components suggests that the mid-Holocene age may be an artifact of age determination on bulk sands; ages of molluscs indicate sustained incremental accretion of Warraber over the past 3,000 years (Woodroffe et al., 2007). This pattern of incremental development is observed on many reef islands across the Indo-Pacific, rather than rapid deposition in discrete periods or phases (Woodroffe, 2008). It is important to note that progressive sea-level change and island growth may modify sediment production, transport efficiency over the reef platform, and depositional nodes. For example, where sea level has fallen during the late Holocene, reduced reef flat depths may significantly reduce sediment delivery to leeward cays (Kench and Brander, 2006).

The central, oldest areas of cays may be indicated by the presence of mature vegetation and greater soil development (see previous section), although Woodroffe and Morrison (2001) found no clear relationship between soil development and age at Makin Island, Kiribati. Reef-island formation has not ceased, and new reef islands will form if reef growth and sediment production continues. Hopley et al. (2007) present average estimates of the time required to progress through this sequence on the GBR and emphasize that small shallow lagoonal reefs can transform into planar reefs in as few as 250 years. Thus, where sediment supply is adequate and reefs of suitable elevation, geometry, and energy exposure exist, reef islands may form quite rapidly.

Factors influencing cay stability

There are many records of cays, including those with a mature vegetation cover, disappearing completely, both during storms and over longer periods of time. Lines of beach rock on numerous reef flats attest to the previous presence of a cay even where there may be no historical record. A number of factors are involved which may also require consideration when assessing the future impacts of global climate change. For the 300 reef islands of all types found within the Great Barrier Reef Marine Park, Aston (1995) carried out a statistical analysis of the factors that contributed to stability. They varied with island type but included:

(a) *Location on reef flat and size of reef*. The position of the cay on the reef flat is determined by wave refraction patterns, which on most small to moderate size reefs is toward the lee side. On large reefs and irregularly shaped reefs, the area of sand delivery may be less focused and broad areas of sediment deposition in the central reef flat may result. Any cay that forms will be highly mobile as small weather changes result in contrasting wave refraction patterns.

(b) *Size of cay*. Reef islands may vary from a few tens of meters in diameter, to several kilometers. As it takes a considerable period for large bodies of sediment to accumulate, the larger islands are indicative of stability, requiring major changes in energy conditions to produce significant changes to the cay shoreline.

(c) *Shape of cay*. Cays vary from oval to elongate. Oval cays represent a sediment body that has been constructed by the same energy conditions over a period of time and are the most stable. Linear cays, often with highly mobile spits on both ends, are by far the least stable with location and orientation of the spits often changing seasonally especially in monsoonal climates (Figure 8).

(d) *Vegetation*. A degree of stability is required for a mature vegetation to take hold on sand cays. Very important is the availability of a freshwater lens associated with cays with a minimum width of ~120 m (see *Coral Cays – Geohydrology*). Vegetation is not only indicative of at least some degree of stability but also through the binding action of roots, the addition of organic matter to soils and protection from heavy tropical storms by the canopy, it adds further to the island stabilization process.

(e) *Cementation*. Several cementation processes produce hard rock outcrops which retard erosion. Intertidally beach rock can form very quickly (Figure 6). Similar intertidal cementation can occur on shingle islands forming conglomerate outcrops. On older islands, which have had a mature vegetation for some time and which have been used as nesting or roosting sites for sea birds, the leaching of guano into the soil can result in the formation of phosphatic cay sandstone (Figure 7) at the water table.

(f) *Sediment budgets*. Over time the delivery of sediments to the reef flat, and ultimately to the reef cay, can change. Initially when the reef first reaches sea level, its high proportion of coral cover may be producing calcium carbonate at rates up to 10 $kg/m^2/yr^{-1}$, though much of this goes into the infilling of irregularities in the maturing reef flat. Ultimately, the reef flat may become totally sediment covered with delivery of

Coral Cay Classification and Evolution, Figure 6 Massive beachrock, so important for cay stability, Wilson Island, southern GBR.

Coral Cay Classification and Evolution, Figure 7 Phosphatic cay sandstone formed from the leaching of guano, Raine Island, northern GBR.

sediment to the cay during this period of change declining significantly. This may be due to a reduction in the ability of waves to transport sediment to a focal point (see *Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity*) or to the stabilizing effect of reef flat sea grass or macroalgae (e.g., at Green Island GBR where eutrophication in the 1950s and 1960s caused an expansion of sea grass on the adjacent reef flat which prevented delivery of sand to the cay, see Hopley, 1982, pp. 333–335. Erosion of the cay has taken place subsequently).

(g) *Platform height*. A fall in relative sea level since a cay first formed (due to hydroisostatic or other causes) can leave a cay "perched" on its reef flat. The effect is to greatly reduce the power of waves to deliver sediment which is now limited to only a small part of the tidal cycle. An erosional phase may result though a rise in sea level may have the opposite effect (see *Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity*). Kench and Brander (2006) give some Australian examples.

(h) *Meteorological conditions*. Cay location and morphology are strongly influenced by ambient weather conditions including storms which occur on a regular basis, producing short-term cycles of erosion and aggradation. However, there are many examples of changing wind strengths and direction causing longer term changes to reef islands as wave refraction patterns across the reef flat are modified and the orientation of an island changes or its location is changed so that it now loses sand over the reef edge (see Hopley et al., 2007, Chapter 13.5.3).

Coral cay dynamics

Coral cays, composed of largely unconsolidated sediments, are classic natural systems in a state of dynamic equilibrium. Any change to the cay formation process – weather conditions, sediment budgets, reef morphology, or ecology – will produce an immediate response in the cay. Sediments are easily moved and high-energy events such as storms or tsunami can produce major changes. However, small but significant changes are constantly taking place, over single tidal cycles, seasonally, over periods of years to decades in response to climate fluctuations, or in response to high-energy events. Each of these time scales is examined below with the majority of examples coming from the GBR where many islands of all types have been the subject of monitoring programs and a comparative study of all 300 islands within the Marine Park has been undertaken (Aston, 1995).

(a) Tidal cycle changes

Hopley (1981, 1982) measured beach profiles around islands and sediment movement on the adjacent reef flat using sediment traps (Hopley, 1981) at three contrasting sites on the GBR over periods of high spring tides of up to 5 days. The sites were at Wheeler cay (a small unvegetated sand cay) (Figure 3a), Bushy Island (a maturely vegetated cay with *Pisonia* forest) (Figure 3c), and Three Isles cay (the leeward vegetated sand cay of a major low wooded island). Results were much as expected, with the largest changes to the beach and greatest sediment movement on the adjacent reef at unvegetated Wheeler Reef and smallest at the partially protected low wooded island site of Three Isles cay (Table 2).

(b) Seasonal changes

Monsoonal climates produce significant changes to coral cays. This is illustrated by Coconut (Poruma) Island in Torres Strait, a narrow island of about 40 ha (Figure 8). Bi-monthly surveys at 21 sites in 1996–1997 recorded great mobility in the terminal spits with an annual pattern of erosion during the summer north-westerly monsoon, but with a return of sediment from the reef flat under the influences of the winter south-easterlies. However, this cay is close to the reef edge and a circulatory movement of sediment around the island does produce a small net loss of sand of about 20,000 m^3, equivalent to about 1% of the island volume (Hopley and Rasmussen, 1998).

Cays of the Maldives are also under strong monsoonal influence with large gross changes (31–21% of beach area) in shoreline position between seasons, reflecting significant reversals in sediment flux of 9–23 × 10^3 m^3 biannually (Kench and Brander, 2006). However, annual net change is small (2–15%) indicating the island is in dynamic equilibrium.

Coral Cay Classification and Evolution, Table 2 Contrasting beach changes, reef-flat sediment movement, and cay migration: Wheeler Cay (unvegetated); Bushy Island (mature vegetated); and Three Isles (low wooded island cay)

	Wheeler Cay	Bushy Island	Three Isles
Range of mean wind speeds (ms^{-1})	2.0–7.5	2.5–10.5	7.5–13.0
Mean daily beach change (cm)	17.46	2.74	1.51
Maximum mean daily beach change (cm)	24.95	2.76	1.98
Mean daily sediment trap recovery (g)	531.1	204.2	22.8
Maximum mean daily sediment trap recovery (g)[a]	793.1	344.4	39.7
Recorded long-term migration (m)	110	~40	~35
Period	1975–77	1936–74	1929–73

[a] This is the maximum mean recovery from all traps set. Individual traps have recorded up to 4,063 g on a single day on Wheeler Cay.

(c) Decadal changes

Longer term surveys from aerial photography and ground truthing can determine if there is a long-term trend in cay changes and the dimensions of these changes. On Raine Island (northern GBR), Gourlay and Hacker (1991) reported erosion of up to 20 m and accretion of up to 40 m between 1967 and 1990 at specific points around the shore as the cay became more elongate. Annual sand movement on this small vegetated cay was about 5,000 m^3. On Warraber in Torres Strait, maximum net shoreline movements over a 20-year period were around 60 m and at Green Island near Cairns, about 50 m between 1945 and 1978 (see Hopley, 1982). In the Bunker-Capricorn Islands, Flood (1988) measured average shoreline movements of between 14 and 53 m between 1972 and 1986 with maximum changes of up to 116 m.

These decadal changes include responses to specific cyclonic events, but also reflect long-term variations to weather patterns. In Torres Strait, wind records between 1951 and 1992 show a statistically significant increase in winter winds from the south-east, and an increase in wind speed at about 1975–1977. Realignment and a change in shape has occurred on some cays. Similar changes took place in the Bunker-Capricorn Islands. Here the annual wind energy vector has oscillated within a 45° arc from south-south-east in the early 1960s to east-south-east

Coral Cay Classification and Evolution, Figure 8 Seasonal fluctuations in shoreline position, Poruma Island, Torres Strait.

in the 1970s, sufficient to cause some of the shoreline changes experienced during this period (Flood, 1986).

(d) High-energy, low-frequency events

Cyclonic events can cause erosion or accretion on reef islands depending on the tidal conditions and sediment availability at time of impact. If tides are high, erosion usually results; if low, then accretion may occur (Flood, 1986). Storm surges that exacerbate erosion on mainland sites have far less an impact on cays on offshore reefs, which generally lack the gradual shoaling of mainland bays and the funneling effect of coastal embayments. Many examples have been described from the GBR (Flood, 1980, 1981, 1986; Flood and Jell, 1977; Hopley, 1972). Cyclone Emily (1972) with a central pressure of 985 hPa produced surge levels >2 m on the Queensland mainland near Gladstone, but only 0.8 m as it passed over offshore Heron Island (Hopley, 1972). On nearby One Tree Reef, around 27 m of rubble was added to the ramparts on the southeast side of the island as this cyclone struck at low tide. In contrast, Cyclone Winifred (982 hPa) in 1986 passed over Green Island at high tide producing 70 m of erosion on the unstable spit. At low latitudes where the Coriolis force is insufficient to generate mature cyclones, swell waves from cyclones at slightly higher latitudes can still affect island shores.

Tsunamis can be experienced in many reefal areas. The 2004 Indian Ocean event (see *Tsunami*) caused washovers in several island groups (e.g., Maldives, Chagos) and although leaving erosional scars of up to 2 m and depositional sand sheets extending inland, the overall geomorphological impact was not as great as might have been expected.

All of these natural changes can be exacerbated by anthropogenic activities (see *Infrastructure and Reef Islands*; *Engineering on Coral Reefs with Emphasis on Pacific Reefs*). Groynes, rock walls, boat channels, and changes to reef flat ecology can all result in changes to beach morphology and sediment budgets with erosion being the most common result.

Future for reef cays

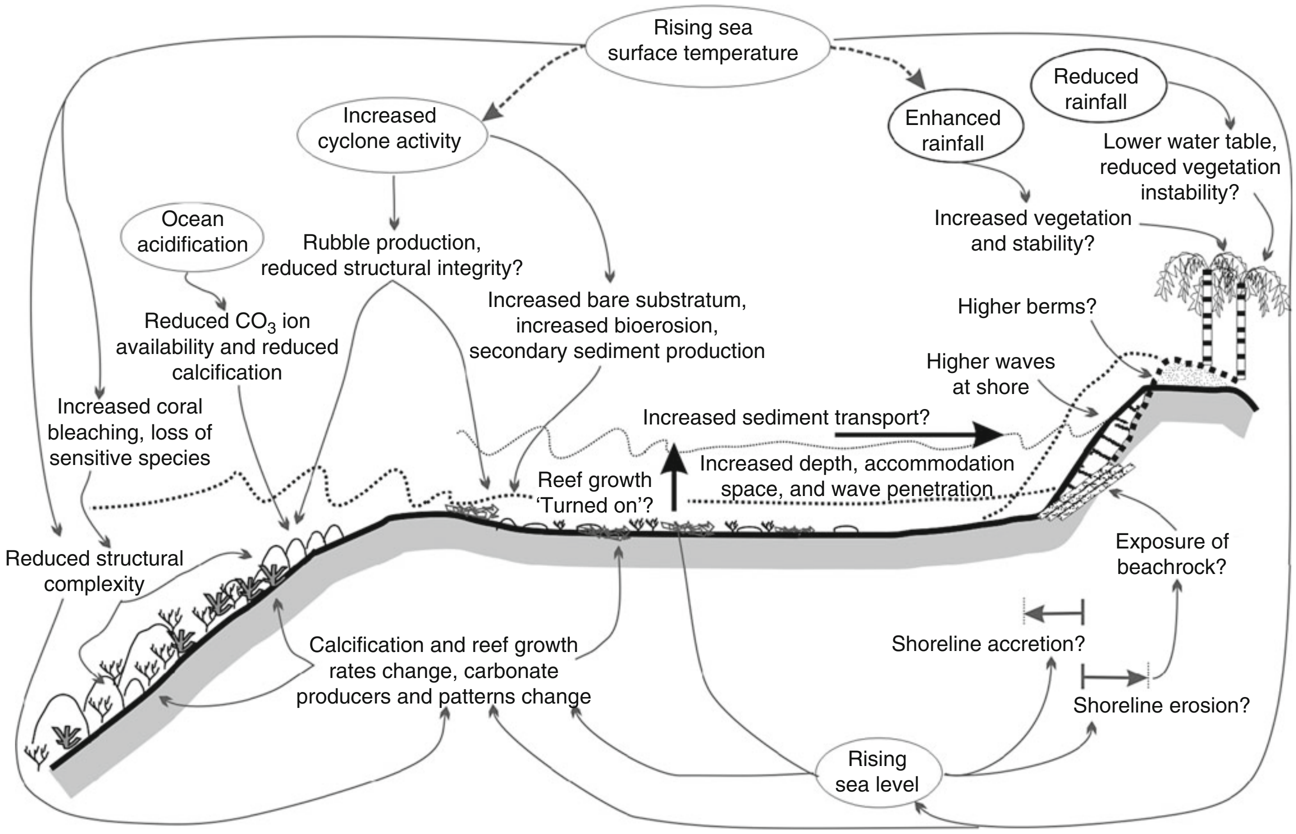
Cays are dynamic landforms that are mostly low and composed of unconsolidated sediments. They are widely perceived as particularly vulnerable to climate and sea-level changes projected as imminent consequences of anthropogenic activities (IPCC, 2007). Some believe that they are more resilient – that their dynamic nature will allow them to adjust. Some of the key potential impacts of sea level and climate changes on reef islands are schematically represented in Figure 9 and discussed further below.

Sea-level rise

Early concerns that sea-level rise will simply drown reef islands are now considered oversimplistic, with island response reflecting the complex interplay of numerous physical, biological, and chemical factors. On some reefs, rising sea levels will allow larger waves to propagate further through more of each tidal cycle, increasing the transport of available sediment to islands. On reef flats affected by falling late Holocene sea levels, sediment deposits have accumulated and these may be mobilized shoreward – Hopley (1996) suggested that a sea-level rise of just 0.5 m would achieve this on many reefs. Hopley (1996) also modeled carbonate budgets for an idealized reef flat affected by a 0.5-m and 1.8-m rise by 2100 and showed that under the lower rate almost the entire reef would vertically accrete and reef morphology would not significantly change (see *Climate Change: Impact of Sea-Level Rise on Reef Flat Zonation and Productivity*). However, at the higher rate the algal zone transformed to coral cover, markedly increasing calcium carbonate production. The enhanced carbonate productivity would yield sediments suitable for reef-island construction, and because greater depth improves shoreward sediment transport, Hopley concluded that faster sea-level rise at first may be more beneficial for reef-island sustainability than a slower rate. Many reef geomorphologists agree that projected sea-level rise will substantially rework unconsolidated sediments and initially maintain reef-island mass (e.g., Kench and Cowell 2002).

The issue is more complicated, however, as elevation is critical on these low islands. Cay buildup is largely controlled by the characteristics of waves reaching the beach, with berm height – the height of the beach above mean high water – dependent on wave run-up. In a detailed study at Raine Island, Gourlay and Hacker (1991) found that the berm height was controlled by the wave run-up during the highest spring tides and calculated that the island may vertically accrete by an amount larger than the sea-level rise if reef flat aggradation lags behind the rate of sea-level rise and larger waves can reach the beach. However, given the diversity of reef-island morphologies, evolutionary histories, geographical settings, and human pressures, the future for reef islands may be diverse.

Late-Holocene emergence which has been demonstrated to be important to the formation and longer term stability of at least some cays has been discussed above. These factors would lose their influence as sea level increases. Uncertainties exist about future changes in storm frequency and intensity, but increases in both are possible. Higher wave energy might increase shoreline erosion, increase the frequency of inundation events, and threaten the quality and maintenance of groundwater aquifers and the long-term habitability of many reef islands. On Pacific Ocean, Indian Ocean, and Caribbean reef islands, settlements and vital infrastructure are almost without exception located close to the beach, where they are vulnerable to inundation, erosion, and other coastal hazards that may compromise the socioeconomic well-being of island communities. Understanding of some aspects of these interactions has advanced remarkably in recent decades. However, significant gaps still exist which limit capacity to confidently predict the long-term future



Coral Cay Classification and Evolution, Figure 9 Schematic summary of potential climate and sea-level change impacts on reef islands.

of many reef islands. For example, simple models developed for linear and siliciclastic shorelines cannot be directly applied to reef islands.

Reduced carbonate production and ocean acidification

There is heightened concern that thermal stress due to global warming (see *Climate Change: Impact on Coral Reef Coasts*) and changes in ocean pH associated with fossil fuel use (see *Ocean Acidification, Effects on Calcification*) is reducing both the amount of calcium carbonate produced on reefs and the durability of the sediments, both of which have the capacity to influence reef sediment budgets and ultimately the availability of sediments to maintain and build reef islands. The intensity and scale of coral bleaching has increased markedly since the 1960s, with entire reef systems affected by major events in 1998 and 2002 (see *Temperature Change: Bleaching*). Bleaching events not only affect corals, but also affect other photosymbiotic organisms such as foraminiferans that are very important contributors to many reef islands (Yamano et al., 2000). Calcification rates for corals on the world's best-managed reef – the GBR – are projected to decline by 14% compared to 1990 (D'eath et al., 2009) and it has been further projected that coral cover will decline on reefs beyond 2050 (Hoegh-Guldberg et al., 2007).

Some reef islands accumulated most of their mass long ago, and these islands – especially if large and partially lithified – may be less sensitive to reduced carbonate production and ocean acidification in the short term. They will, however, be less able to dynamically adjust to projected changes in sea level and inundation. Where reef islands are younger, more mobile, and generally on less emergent reef flats, the future looks even less positive as active carbonate production and reef-island accumulation are more tightly coupled on lower reef flats, with efficient transfer of products to the zone of accumulation. In these circumstances, diminished carbonate productivity and sediment supply will probably have more immediate effects on island sediment budgets, morphologies, and prospects.

Bibliography

Aston, J. P., 1995. *The Relative Mobilities of Coral Cays on the Great Barrier Reef Can be Modeled*. Townsville: James Cook University, 267 p.

Bayliss-Smith, T. P., 1988. The role of hurricanes in the development of reef islands, Ontong Java atoll, Solomon Islands. *Geographical Journal*, **154**, 377–391.

Chappell, J., Chivas, A., Wallensky, E., Polach, H. A., and Aharon, P., 1983. Holocene palaeoenvironmental changes central to north Great Barrier Reef, inner zone. Bureau of Mineral Resources. *Journal of Australian Geology and Geophysics*, **8**, 223–235.

Chivas, A. R., Chappell, J., Polach, H. A., Pillans, B., and Flood, P. G., 1986. Radiocarbon evidence for the timing and rate of island development, beach rock formation, and phosphatization at Lady Elliot Island Queensland Australia. *Marine Geology*, **69**, 273–287.

Clark, J. A., 1980. A numerical model of worldwide sea level changes on a viscoelastic earth. In Morner, N. A. (ed.), *Earth Rheology, Isostasy and Eustasy*. New York: Wiley, pp. 525–534.

Clark, J., Farrell, W., and Peltier, W., 1978. Global changes in postglacial sea level: a numerical calculation. *Quaternary Research*, **9**, 265–287.

De'ath, G., Lough, J. M., and Fabricius, K. E., 2009. Declining coral calcification on the Great Barrier Reef. *Science*, **323**, 116–119.

Dickinson, W. R., 2004. Impacts of eustasy and hydro-isostasy on the evolution and landforms of Pacific atolls. *Palaeogeography Palaeoclimatology Palaeoecology*, **213**, 251–269.

Fairbridge, R. W., 1950. Recent and Pleistocene coral reefs of Australia. *Journal of Geology*, **58**, 330–401.

Fairbridge, R. W., and Teichert, C., 1947. The rampart system at Low Isles, 1928–1945. *Reports of the Great Barrier Reef Committee*, **6**, 1–16.

Flood, P. G., 1977. Coral cays of the Capricorn and Bunker Groups, Great Barrier Reef province, Australia. *Atoll Research Bulletin*, **195**, 7.

Flood, P. G., 1980. Cyclone 'Simon' changes cays. *Reflections*, **6**, 4.

Flood, P. G., 1981. Coral cays and cyclones. *Beach Conservation*, **42**, 6.

Flood, P. G., 1986. Sensitivity of coral cays to climatic variations, Southern Great Barrier Reef, Australia. *Coral Reefs*, **5**, 13–18.

Flood, P. G., 1988. Shoreline changes on coral cays, Capricornia Section, Great Barrier Reef Marine Park, Australia. In *Proceedings of the Sixth Coral Reef Symposium*, pp. 219–224.

Flood, P. G., and Jell, J. S., 1977. The effect of cyclone 'David' (January 1976) on the sediment distribution patterns on Heron Reef, Great Barrier Reef, Australia. In *Proceedings of Third International Coral Reef Symposium, Miami*, pp. 119–125.

Fosberg, F. R., and Stoddart, D. R., 1991. Plants of the reef islands of the northern Great Barrier Reef. *Atoll Research Bulletin*, **348**, 82.

Fosberg, F. R., Stoddart, D. R., Sachet, M. H., and Spellman, D. L., 1982. Plants of the Belize cays. *Atoll Research Bulletin*, **258**, 77.

Frank, T. D., and Jell, J. S., 2006. Recent developments on a nearshore, terrigenous-influenced reef: low isles reef, Australia. *Journal of Coastal Research*, **22**, 474–486.

Gourlay, M. R., and Hacker, J. L. F., 1991. *Raine Island: Coastal Processes and Sedimentology*. Brisbane: Department of Civil Engineering, University of Queensland, 68 pp.

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell, C. D., Sale, P. F., Edwards, A. J., Caldeira, K., Knowlton, N., Eakin, C. M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R. H., Dubi, A., and Hatziolos, M. E., 2007. Coral reefs under rapid climate change and ocean acidification. *Science*, **318**, 1737–1742.

Hopley, D., 1972. The storm surge associated with Cyclones Althea and Emily. In Trollope, D. H. (ed.), *Cyclone Althea Part II: Storm Surges and Coastal Effects*. Townsville: James Cook University, pp. 4.1–4.29.

Hopley, D., 1978. Wheeler reef: cay mobility. In Hopley, D. (ed.), *Geographical Studies of the Townsville Area*. Townsville: James Cook University of North Queensland Monograph Series Occassional Paper, Vol. 2, pp. 55–58.

Hopley, D., 1981. Sediment movement around a coral cay, Great Barrier Reef, Australia. *Pacific Science*, **15**, 17–36.

Hopley, D., 1982. *Geomorphology of the Great Barrier Reef: Quaternary Development of Coral Reefs*. New York: Wiley, 453 p.

Hopley, D., 1983. Deformation of the North Queensland continental shelf in the Late Quaternary. In Smith, D. E., and Dawson, A. G. (eds.), *Shorelines and Isostasy*. London: Academic, pp. 347–366.

Hopley, D., 1996. Coral reefs and small islands – Implications of more modest climate and sea-level change predictions: *recent advances in marine science and technology*. In *Proceedings of PACON 96*, pp. 249–258.

Hopley, D., 1997. Geology of reef islands of the Great Barrier Reef, Australia. In Vacher, H. L., and Quinn, T. (eds.), *Geology and Hydrogeology of Carbonate Islands: Developments in Sedimentology*. London, UK: Elsevier Science, Vol. 54, pp. 835–866.

Hopley, D., and Rasmussen, C., 1998. *Coconut Island Sand Erosion Study*. Coastal and Marine Consultancies Pty. Ltd.

Hopley, D., Smithers, S. G., and Parnell, K. E., 2007. *Geomorphology of the Great Barrier Reef: Development, Diversity and Change*. Cambridge: Cambridge University Press, p. 532.

IPCC, 2007, Climate Change, 2007. *Synthesis report. Contribution of working groups I, II and III to the fourth assessment*. In Pachauri, R. K., and Reisinger, A. (eds.), Report of the Intergovernmental Panel on Climate Change, Geneva, Switzerland, IPCC, p. 104.

Kench, P. S., and Brander, R. W., 2006. Wave processes on coral reef flats: implications for reef geomorphology using Australian case studies. *Journal of Coastal Research*, **22**, 209–223.

Kench, P. S., and Cowell, P. J., 2002. Variations in sediment production and implications for atoll island stability under rising sea level. In *Proceedings of the Ninth International Coral Reef Symposium, Bali*, Vol. 2, pp. 1181–1186.

Kench, P. S., McLean, R. F., and Nichol, S. L., 2005. New model of reef-islands formation: Maldives, Indian Ocean. *Geology*, **33**, 145–148.

Kench, P. S., Nichol, S. L., Smithers, S. G., McLean, R. F., and Brander, R. W., 2008. Tsunami as agents of geomorphic change in mid-ocean reef islands. *Geomorphology*, **95**, 361–383.

Lambeck, K., Esat, T. M., and Potter, E. K., 2002. Links between climate and sea levels for the past three million years. *Nature*, **419**, 199–206.

Lambeck, K., and Nakada, M., 1990. Late Pleistocene and Holocene sea-level change along the Australian coast. *Palaeogeography Palaeoclimatology Palaeoecology*, **89**, 143–176.

Maxwell, W. G. H., Day, R. W., and Fleming, P. J. G., 1961. Carbonate sedimentation on the Heron Island Reef. *Journal of Sedimentary Petrology*, **31**, 215–230.

Maxwell, W. G. H., Jell, J. S., and McKellar, R. G., 1964. Differentiation of carbonate sediments on the Heron Island Reef. *Journal of Sedimentary Petrology*, **34**, 294–308.

McLean, R. F., and Stoddart, D. R., 1978. Reef island sediments of the northern Great Barrier Reef. *Philosophical Transactions of the Royal Society of London Series A*, **291**, 101–117.

McLean, R. F., Stoddart, D. R., Hopley, D., and Polach, H. A., 1978. Sea level change in the Holocene on the northern Great Barrier Reef. *Philosophical Transactions of the Royal Society of London, Series A*, **291**, 167–186.

Milliman, J. D., 1973. Caribbean coral reefs. In Jones O. A., and Endean, R. (eds.), *Biology and Geology of Coral Reefs, v. Geology 1*. New York: Academic, pp. 1–50.

Murray, M. R., Zisman, S. A., and Minty, C. D., 1999. Soil–plant relationships and a revised vegetation classification of Turneffe Atoll, Belize. *Atoll Research Bulletin*, **464**, 1–32.

Oches, E., Little, M., and Harris, P., 2009. Geochronology of late-Holocene mangrove island sedimentation in Florida Bay. In *Geological Society of America Annual Meeting*, p. 639.

Orme, G. R., 1977. Aspects of sedimentation in the reef environment. In Jones, O. A., and Endean, R. (eds.), *The Geology and Biology of Coral Reefs*, Vol. 1 – Geology, pp. 129–182.

Pirazzoli, P. A., 1991. *World Atlas of Holocene Sea-Level Change*. Elsevier Oceanography Series, Vol. 58. Amsterdam: Elsevier, 300 p.

Rogers, R. W., 1986. Flowering and fruiting in the flora of Heron Island, Great Barrier Reef, Australia. *Atoll Research Bulletin*, **440**, 9.

Sachet, M.-H., 1983. Natural history of Mopelia Atoll, Society Islands. *Atoll Research Bulletin*, **274**, p. 37.

Samosorn, B., and Woodroffe, C. D., 2008. Nearshore wave environments around a sandy cay on a platform reef, Torres Strait, Australia. *Continental Shelf Research*, **28**, 2257–2274.

Sauer, J. D., 1982. Cayman island seashore vegetation. *Geography*, **25**, 161.

Schofield, J., 1977. Effect of Late Holocene sea-level fall on atoll development. *New Zealand Journal of Geology and Geophysics*, **20**, 531–536.

Sivadas, P., Narayanan, B., and Sivaprasad, K., 1983. An account of the vegetation of Kavaratti Island, Laccadives. *Atoll Research Bulletin*, **266**, 1–9.

Spender, M. A., 1930. Island reefs of the Queensland coast. *Geographical Journal*, **76**, 194–214, 273–293.

Spicer, R. E., and Newberry, D. H., 1989. The terrestrial vegetation of an Indian Ocean coral island: Wilingili, Addu Atoll, Maldive Islands, 1, Transect analysis of the vegetation. *Atoll Research Bulletin*, **231**, 1–14.

Steers, J., 1929. The Queensland coast and the Great Barrier Reef. *Geographical Journal*, **74**, 232–257, 341–370.

Steers, J. A., 1937. The coral islands and associated features of the Great Barrier Reef. *Geographical Journal*, **89**, 1–28, 119–146.

Steers, J. A., 1938. Detailed notes on the island surveyed and examined by the geographical expedition to the Great Barrier Reef in 1936. *Reports to the Great Barrier Reef Committee*, Vol. 4, pp. 51–96.

Stoddart, D. R., 1965. British Honduras cays and the low wooded island problem. *Transactions of the Institute of British Geographers*, **36**, 131–147.

Stoddart, D. R., 1980. Mangroves as successional stages inner reefs of the northern Great Barrier Reef. *Journal of Biogeography*, **7**, 269–284.

Stoddart, D. R., and Fosberg, F. R., 1972. South Indian sand cays. *Atoll Research Bulletin*, **161**, 1–16.

Stoddart, D. R., and Fosberg, F. R., 1991. Phytogeography and vegetation of the reef islands of the northern Great Barrier Reef. *Atoll Research Bulletin*, **349**, 19.

Stoddart, D. R., Fosberg, F. R., and Spellman, D. L., 1982. Cays of the Belize barrier reef and lagoon. *Atoll Research Bulletin*, **256**, 1–76.

Stoddart, D. R., McLean, R. F., and Hopley, D., 1978a. Geomorphology of reef islands, northern Great Barrier Reef. *Philosophical Transactions of the Royal Society of London Series B*, **284**, 39–61.

Stoddart, D. R., McLean, R. F., Scoffin, T. P., and Gibbs, P. E., 1978b. Forty-five years of change on low wooded islands, Great Barrier Reef. *Philosophical Transactions of the Royal Society of London Series B*, **284**, 63–80.

Stoddart, D. R., McLean, R. F., Scoffin, T. P., Thom, B. G., and Hopley, D., 1978c. Evolution of reefs and islands, northern GreatBarrier Reef: synthesis and interpretation. *Philosophical Transactions of the Royal Society of London Series B*, **284**, 149–159.

Stoddart, D. R., and Steers, J. A., 1977. The nature and origin of coral reef islands. In Jones, O. A., and Endean, R. (eds.), *Biology and Geology of Coral Reefs*, Vol. IV – Geology II, pp. 59–105.

Stoddart, D. R., and Walsh, R. P. D., 1992. Environmental variability and environmental extremes as factors in island ecosystems. *Atoll Research Bulletin*, **356**, 71.

Thaman, R. R., 1987. Plants of Kiribati: a listing and analysis of vernacular names. *Atoll Research Bulletin*, **296**, 42.

Tomascik, T., Mah, A. J., Nontji, A., and Moosa, M. K., 1997. *The Ecology of Indonesian Seas, Part 2*. Singapore: Periplus Editions, 746 p.

Topp, J. M. W., 1988. An annotated check list of the flora of Diego Garcia, British Ocean Territory. *Atoll Research Bulletin*, **313**, 19.

Toscano, M. A., and Macintyre, I. G., 2003. Corrected western Atlantic sea-level curve for the last 11,000 years based on calibrated C-14 dates from *Acropora palmata* framework and intertidal mangrove peat. *Coral Reefs*, **22**, 257–270.

Walker, T. W., Chaloupka, M. Y., and King, B. R., 1991. The vascular floras of Bushy and Redbill Islands. *Atoll Research Bulletin*, **350**(II), 24–30.

Williams, D. G., 1984. Vegetation and flora of the Cocos (Keeling) Islands. *Atoll Research Bulletin*, **404**, 29.

Woodroffe, C. D., 1995. Mangrove vegetation of Tobacco Range and nearby mangrove ranges, central Belize Barrier Reef. *Atoll Research Bulletin*, **427**, 1–35.

Woodroffe, C. D., 2003. *Coasts: Form, Process And Evolution*. Cambridge: Cambridge University Press.

Woodroffe, C. D., 2005. Late Quaternary sea-level highstands in the central and eastern Indian Ocean: a review. *Global and Planetary Change*, **49**, 121–138.

Woodroffe, C. D., 2008. Reef-island topography and the vulnerability of atolls to sea level rise. *Global and Planetary Change*, **62**, 77–96.

Woodroffe, C. D., McLean, R. F., Smithers, S. G., and Lawson, E. M., 1999. Atoll reef-island formation and response to sea-level change: West Island, Cocos (Keeling) Islands. *Marine Geology*, **160**, 85–104.

Woodroffe, C. D., and Morrison, R. J., 2001. Reef-island accretion and soil development on Makin, Kiribati, central Pacific. *Catena*, **44**, 245–261.

Woodroffe, C. D., Samosorn, B., Hua, Q., and Hart, D. E., 2007. Incremental accretion of a sandy reef island over the past 3000 years indicated by component-specific radiocarbon dating. *Geophysical Research Letters*, **34**, L03602.

Woodroffe, C. D., and Stoddart, D. R., 1992. Substrate specificity and episodic catastrophe: constraints on the insular plant geography of Suwarrow Atoll, northern Cook Islands. *Atoll Research Bulletin*, **362**, 19.

Yamano, H., Miyajima, T., and Koike, I., 2000. Importance of foraminifera for the formation and maintenance of a coral sand cay: Green Island, Australia. *Coral Reefs*, **19**, 51–58.

Cross-references

Atoll Islands (Motu)
Bassett Edges
Beach Rock
Cay Formation
Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity
Climate Change: Impact On Coral Reef Coasts
Coral Cays, Vegetational Succession
Engineering On Coral Reefs With Emphasis On Pacific Reefs
Eolianite
Glacio-Hydro Isostasy
Holocene High Energy Window
Hydrodynamics of Coral Reef Systems
Infrastructure and Reef Islands
Low Wooded Islands
Mangrove Islands
Mid Holocene
Ocean Acidification, Effects on Calcification
Phosphatic Cay Sandstone
Reef Classification by Hopley (1982)

Reef Flats
Sediment Dynamics
Sediments, Properties
Shingle Ridges
Soils of Low Elevation Coral Structures
Steers, James Alfred (1899–1987)
Stoddart, David Ross (1937–)
Temperature Change: Bleaching
Tropical Cyclone/Hurricane
Tsunami
Unvegetated Cays
Vegetated Cays
Wave Shoaling and Refraction
Waves and Wave-Driven Currents

CORAL CAYS – GEOHYDROLOGY

Kevin E. Parnell
James Cook University, Townsville, QLD, Australia

Synonyms

Atoll island hydrology; Reef island geohydrology

Definition

The geohydrology of coral cays relates to the movement of water through the island and reef framework under coral cays, particularly with respect to the characteristics of the freshwater resource resulting from density differences of freshwater and saltwater as affected by the composition and permeability of the reef framework in the context of its evolutionary history.

Introduction

The earliest work on geohydrology applicable to coral cays was undertaken separately by Ghyben and Herzberg in the late 1800s and early 1900s, who determined the shape and thickness of a freshwater lens that forms under coral cays once they reach a minimum size. The relationship, which is based on the different densities of freshwater and saltwater, is expressed in the Ghyben–Herzberg equation:

$$z = \frac{\rho_f}{(\rho_s - \rho_f)} h,$$

where h is the distance above sea level to the water table (phreatic surface), z is the distance below sea level to the freshwater–saltwater interface, and ρ_s and ρ_f are the densities of saltwater and freshwater, respectively. Using densities of 1.00 g cm^{-3} for freshwater and 1.025 g cm^{-3} for saltwater gives the often quoted relationship

$$z = 40\,h.$$

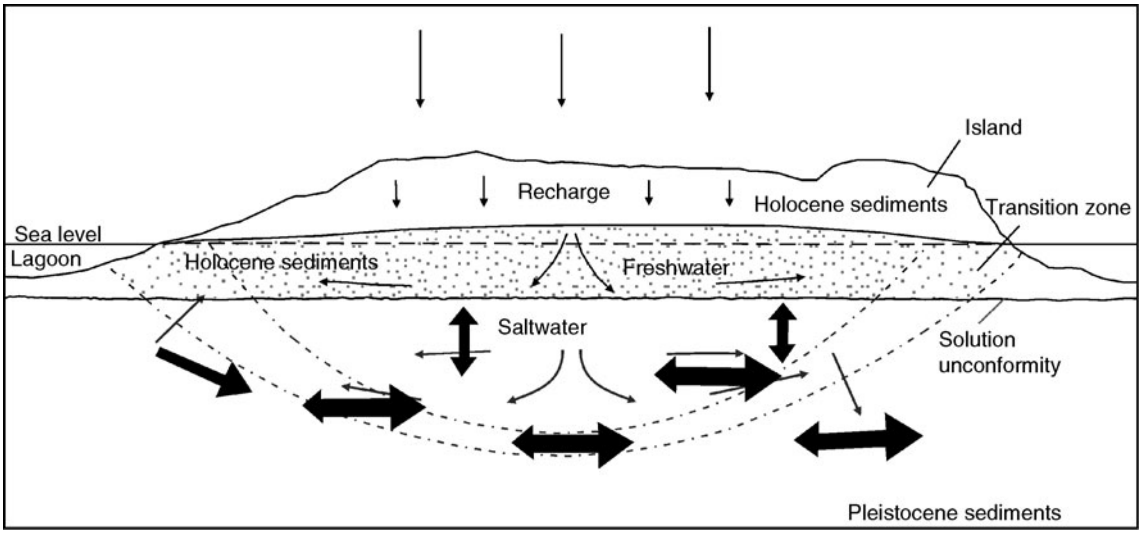
The Ghyben–Herzberg model makes an assumption of a single layer homogeneous medium, and a system in hydrostatic equilibrium, with no mixing of fresh and salt water, giving a sharp transition between the freshwater and saltwater. This model is normally implemented with the Dupuit assumption of horizontal flow (Oberdorfer et al., 1990) and is frequently applied in resource assessments of potable water for human use on inhabited coral cay islands.

In reality, this model makes assumptions that are clearly not valid in most coral reef environments. Tidal fluctuations of the water level are assumed to be negligible, water movement within the lens is assumed to result entirely from recharge-induced changes to the hydraulic head, outflow from the freshwater lens required to maintain mass-balance is assumed to take place at the island margin, and mixing within the framework caused by various water movements and pressure gradients (such as tidal mixing) is not considered. Perhaps most significantly, the assumption of a homogeneous medium rarely holds. In particular, differences in the reef framework above and below the Pleistocene solution unconformity (sometimes called the Thurber discontinuity) typically found 6–25 below the current reef flat level in tectonically stable areas, means that the model is fundamentally flawed. In general, a very broad transition zone between fresh and saltwater can be expected.

The dual aquifer model

The framework below the Pleistocene unconformity is typically highly karstified with high porosity and permeability, due to exposure during much of the period since the last interglacial approximately 120,000 years ago (Vacher, 1997). Seawater can move effectively through the karstified framework, effectively truncating the freshwater lens at the unconformity (Figure 1). The hydraulic conductivity of the Holocene framework is probably 1 or 2 orders of magnitude less than that of the Pleistocene framework (Oberdorfer et al., 1990; Woodroffe and Falkland, 1997).

A two-layer (dual-aquifer) model with a moderately permeable Holocene reef framework overlying a high-permeability Pleistocene aquifer, proposed by Wheatcraft and Buddemeier (1981) has been developed and used by others in modeling and investigations of cay groundwater resources (Ayers and Vacher, 1986; Herman et al., 1986; Oberdorfer et al., 1990; Underwood et al., 1992; Griggs and Petersen, 1993; Bailey et al., 2009; and others). These studies have found a quantitative agreement between model results and physical and chemical field data, giving some confidence in the approach. Tidal flow through the Pleistocene framework has been shown to be particularly significant, overwhelming any density differentials that may limit mixing in the Pleistocene aquifer. Short-term vertical water movements of 1 m or less driven by horizontally directed (in the Pleistocene aquifer) and vertically directed (in the Holocene aquifer; Herman et al., 1986) tidal pulses control the nature of transition zone mixing (Underwood et al., 1992). Other short-term climatic events, such as storms, can also be reflected in water movements that cause mixing in the reef framework. Clearly, the use of the Ghyben–Herzberg–Dupuit model



Coral Cays – Geohydrology, Figure 1 The Ghyben–Herzberg lens of freshwater truncated at the Pleistocene unconformity due to the highly karstified nature of the Pleistocene reef framework (Hopley et al., 2007).

leads to a significant overestimation of freshwater resources on almost all coral cays (Oberdorfer et al., 1990). Bailey et al. (2009) highlight the importance of cemented layers confining the freshwater in the Holecene aquifer. These occur at the reef flat surface, forcing freshwater to discharge in fractures in the cemented layer, or elsewhere on the reef. Hard layers at depth can direct flow, or otherwise confine flow.

Lens thickness and freshwater resources

The thickness of the freshwater lens is typically in the order of 10–20 m on small coral islands (Falkland, 1993), although thinner lenses clearly exist on small islands, and thicknesses of up to 30 m have been measured. The shape of the lens may be asymmetric, typically deeper on the lagoon side of atoll islands (Falkland, 1993), probably due to the preferential accumulation of lower permeability sediments on the lagoon side (Anthony et al., 1989). Anthony (1997) notes that the position of the island on the reef flat, specifically with respect to the prevailing wind is an important determinant of the thickness of the freshwater lens, due to leeward reefs typically having finer subsurface deposits than those on the windward side of the reef platforms. The lower permeability deposits on the leeward island support thicker freshwater lenses than those on windward islands (Bailey et al., 2009). It is suggested by Bailey et al. (2009) that whereas the freshwater lens on leeward islands is truncated at the Pleistocene unconformity, the lens on the (typically smaller) windward islands may not extend to that level. From a number of examples drawn from the literature, windward island lens thickness is in the order of 2–11 m, compared to 12–20 m for leeward islands.

Numerical simulations using the dispersion (as opposed to sharp interface) model SUTRA (Voss and Provost, 2003) presented by Bailey et al. (2009), show clear relationships between recharge, hydraulic conductivity, depth to the Pleistocene inconformity and island width, and the thickness of the freshwater lens.

The lens thickness and consequent water availability (White et al., 2007) can be significantly affected by climatic events, particularly drought. Bailey et al. (2009) simulate El Nino conditions showing that a 6-month drought required a 1.5-year recovery period for the aquifer for islands in the western Pacific.

Modeling presented by Oberdorfer and Buddemeier (1988) show that the dual aquifer may have a significant influence on freshwater resources during times of climate change and rising sea levels. Counter-intuitively, because the depth of the freshwater layer is frequently truncated at the Pleistocene unconformity, a higher sea level may increase total freshwater resources, by opening up more lower permeability sediments for freshwater storage, as long as there is not a coincident loss of island area.

Summary

The Ghyben–Herzberg model is generally inappropriate for the examination of the geohydrology of most coral cays due to the presence of high permeability reef framework below the highly karstified Pleistocene unconformity. A dual layer model, used by numerous authors has provided a good understanding of water flow and of freshwater resources under coral cays, with dominant horizontal saltwater flows through the Pleistocene framework truncating the freshwater lens, with tidally driven vertical movements through the lower-permeability Holocene framework, to which the freshwater lens is confined. The actual thickness of the freshwater lens is dependent on a number of variables, the most important of which is sediment permeability. Dual layer dispersion models are being used to adequately describe water flow and the freshwater resource dynamics of coral cays.

Bibliography

Anthony, S. S., 1997. Hydrogeology of selected islands of the Federated States of Micronesia. In Vacher, H. L., and Quinn, T. (eds.), *Geology and Hydrology of Carbonate Islands*. Amsterdam: Elsevier, pp. 693–706.

Anthony, S. S., Peterson, F. L., Mackenzie, F. T., and Hamlin, S. N., 1989. Geohydrology of the Laura Fresh-Water Lens, Majuro Atoll - a hydrogeochemical approach. *Geological Society of America Bulletin*, **101**, 1066–1075.

Ayers, J. F., and Vacher, H. L., 1986. Hydrogeology of an atoll island - a conceptual-model from detailed study of a Micronesian example. *Ground Water*, **24**, 185–198.

Bailey, R. T., Jenson, J. W., and Olsen, A. E., 2009. Numerical modeling of atoll island hydrogeology. *Ground Water*, **47**, 184–196.

Falkland, A. C., 1993. Hydrology and water management on small tropical islands. In *Proceedings International Symposium on Hydrology of Warm Humid Regions*. International Association of Hydrological Sciences, pp. 263–303.

Griggs, J. E., and Peterson, F. L., 1993. Groundwater-flow dynamics and development strategies at the atoll scale. *Ground Water*, **31**, 209–220.

Herman, M. E., Buddemeier, R. W., and Wheatcraft, S. W., 1986. A layered aquifer model of atoll island hydrology - Validation of a computer-simulation. *Journal of Hydrology*, **84**, 303–322.

Hopley, D., Smithers, S. G., and Parnell, K. E., 2007. *The geomorphology of the Great Barrier Reef: developmemt, diversity and change*. Cambridge: Cambridge University Press.

Oberdorfer, J. A., and Buddemeier, R. W., 1988. Climate change: Effects on reef island resources, In *Proceedings Sixth International Coral Reef Symposium*, **3**, 523–527.

Oberdorfer, J. A., Hogan, P. J., and Buddemeier, R. W., 1990. Atoll island hydrogeology - Flow and fresh-water occurrence in a tidally dominated system. *Journal of Hydrology*, **120**, 327–340.

Underwood, M. R., Peterson, F. L., and Voss, C. I., 1992. Groundwater lens dynamics of Atoll Islands. *Water Resources Research*, **28**, 2889–2902.

Vacher, H. L., 1997. Introducution: Varieties of carbonate islands and a historical perspective. In Vacher, H. L., and Quinn, T. (eds.), *Geology and Hydrology of Carbonate Islands*. Amsterdam: Elsevier, pp. 1–33.

Voss, C. I., and Provost, A. M., 2003. *SUTRA, A Model for Saturated-Unsaturated Variable-Density Ground-Water Flow with Solute or Energy Transport*. Reston: USGS.

Wheatcraft, S. W., and Buddemeier, R. W., 1981. Atoll-Island hydrology. *Ground Water*, **19**, 311–320.

White, I., Falkland, T., Metutera, T., Metai, E., Overmars, M., Perez, P., and Dray, A., 2007. Climatic and human influences on groundwater in low atolls. *Vadose Zone Journal*, **6**, 581–590.

Woodroffe, C. D., and Falkland, A. C., 1997. Geology and hydrogeology of the Cocos (Keeling) Islands. In Vacher, H. L., and Quinn, T. (eds.), *Geology and Hydrology of Carbonate Islands*. Amsterdam: Elsevier, pp. 885–908.

Cross-references

Atoll Islands (Motu)
Cay Formation
Holocene Reefs: Thickness and Characteristics
Internal Circulation
Last Glacial Lowstand and Shelf Exposure
Solution Unconformities

CORAL CAYS, VEGETATIONAL SUCCESSION

Harold Heatwole
North Caroline State University, Raleigh, NC, USA

Definition

Succession: A series of biotic communities replacing each other in an ordered temporal sequence, with each community creating conditions leading to the establishment of its successor.
Aeolian: Having to do with the wind.
Allochthonous: Coming from a source external to an ecosystem, community, or area.
Washover: The sea washing over an island during a storm.

Early colonization

Continental islands have vegetation similar to that of and derived from the adjacent mainland. By contrast, cays have a much more limited subset of mainland floras, filtered by the vagaries of overwater dispersal; however, even for those, vegetation varies from sparse herbs, vines, and grasses to tall, dense forests. The present treatise deals with the causes of that variation and the temporal sequences through which cay vegetation pass.

The course of succession on cays depends on the type of substrate initially present. There are three main types associated with modern coral reefs. Sand cays begin as submerged sand bars that gradually accrete and eventually emerge from the sea. Rubble (or shingle) cays are formed suddenly by material from the reef being broken off and heaped onto the reef flat by a storm. In both cases, bare surfaces of sand or pieces of coral are exposed subaerially (Figure 1) and are available for colonization by terrestrial plants and animals, via some form of over-water dispersal. Mangrove cays differ in that plant succession begins before the cay itself forms. Propagules of mangroves are sea dispersed and take root in shallow water on reefs where they grow into trees. Dead leaves and other organic debris from these trees accumulate around the roots and eventually build up an organically rich mud that may in time become emergent above sea level. Some islands, of course, may be composites of more than one of these types.

Surprisingly, the first successful colonizers of bare cays may be animals, rather than plants. On the Great Barrier Reef of Australia, there are a number of sand cays, completely devoid of vegetation, that nevertheless have a fauna of up to 11 species of terrestrial invertebrates (Heatwole, 1971) such as flies, beetles, earwigs, mites, and isopods that subsist on dead marine organisms washed onto the beach, the carrion of marine intertidal invertebrates, and the excrement or cadavers of seabirds nesting on the island. On some cays, there are, in addition, predators such as centipedes and spiders, that feed on these terrestrial invertebrate scavengers. This assemblage thus depends either directly or indirectly on energy and

Coral Cays, Vegetational Succession, Figure 1 Stages in the succession of vegetation on cays on the Great Barrier Reef of Australia. Top: bare sand cay; dark objects in the foreground are pumice (Bylund Cay, July 1988). Second from top: pioneer vegetation (Lady Elliott Island, 1969). Centre: cay with herb meadow (Bell Cay, July 1982). Second from bottom: savannah zone (Heron Island, January 1971). Bottom: Forest of *Pisonia grandis* (Northwest Island, July 1992). Photographs by Harold Heatwole.

nutrients from allochthonous marine sources, rather than from insular terrestrial ones. The organisms, such as seabirds or crabs that connect the marine and terrestrial ecosystems and relay food from one to the other are known as “transfer” species.

The first plants to become established on bare cays are called “pioneer” species. They are usually transported there as seeds carried by sea currents. Many have special adaptations that improve their chances of dispersal in this way, such as devices that keep them afloat for long periods of time. In addition they need to be either impervious to seawater or resistant to high salinities. Not all species of seeds that are transported by water, however, are capable of becoming established on a bare island. Indeed, the beach wrack of many islands contains abundant seeds of species that have floated ashore but are not otherwise represented in the flora, either because the seeds did not survive the voyage, or because they were unable to germinate under the conditions they encountered upon arrival (Smith et al., 1990).

The successful pioneer species are those that combine the qualities of being able to withstand high salinities and salt spray, scarcity of water, shifting sands, low levels of nutrients in the soil, high temperatures, and bright sunlight. These are the conditions found on bare cays. The earliest pioneer vegetation consists of low herbs, grasses, and vines, often of a creeping habit (Figure 1). Species that put out runners over bare sand with roots descending at intervals are adapted to life on a shifting substrate as they tend to stabilize the sand. In time, pioneers may spread and cover much of the surface of a bare cay.

Peripheral zone of shrubs

A few widespread, tropical shrubs, such as *Scaevola taccada* and *Suriana maritima* constitute a special category of pioneers. Perhaps the best example is Octopus Bush, *Argusia argentea*. a shrub/tree that is widely distributed throughout the Pacific and Indian Oceans. It has a buoyant corky layer around the seed that keeps it afloat for many weeks. It can survive for long periods at sea and in fact the seeds, although not germinating in seawater, germinate better after exposure to seawater. Seeds of this species are dispersed by sea currents over thousands of kilometers to be cast ashore on some remote island where, under the influence of rainwater, they germinate on the upper beach (Lesko and Walker, 1969).

These plants add a new zone of pioneer vegetation by forming a ring of shrubs that encircles the island (Heatwole, 1994). Octopus Bush is mainly on the upper beach as it seldom disperses even a few meters inland because seeds dropping from the parent tree have not been exposed to seawater (Figure 2). Where this shrub is found further inland it often is because the beach has extended since the plant became established. Once a shady, peripheral ring of shrubs has formed, it ameliorates conditions such that other sea-dispersed shrubs and trees find favorable germination sites.

Coral Cays, Vegetational Succession, Figure 2 Zonation of vegetation on a cay on the Great Barrier Reef (Northwest Island, July 1992). There is a band of pioneer vegetation (*foreground*). The shrub "ring" is represented by a single young Octopus Bush (*Argusia argentea*) at high-tide line and a nearly continuous ring of older, tall Octopus bushes on an older level of the upper beach (*middle ground*; *darker green*), bordering the *Pisonia grandis* forest (*background*; *lighter green*). Note the recent erosion of the upper beach. Photograph by Harold Heatwole.

Herb meadows

Pioneer species stabilize shifting sand, shade the surface of the ground, and through adding dead leaves and other organic matter enrich the soil (Wiens, 1962) and begin to form a soil profile. In addition, the shrub ring serves as a windbreak, provides more extensive shade, and screens out salt spray. Providing sufficient fresh water becomes available, these changes facilitate inland conditions that are favorable for species that could not colonize a beach or a bare cay. Very small sand cays have little permanent fresh water but as they grow larger through further accumulation of sand, they surpass the critical size for retaining rain as a lens of freshwater in the soil (Wiens, 1962). The stage is now set for the establishment of species of non-pioneer plants. Most of these new colonists are dispersed by birds, either attaching by hooks or sticky secretions to feathers of a variety of birds, including seabirds, or are carried in the digestive tracts of seed-eating or fruit-eating birds. Once deposited in their new home, they grow and form a meadow of herbs and grasses (Heatwole et al., 1981) (Figure 1). The pioneers either find the new conditions unfavorable to them, or are out competed by the new arrivals and they decline, leaving the center of the island covered by the second wave of colonists. The cay is now zoned, with pioneer species still dominating the upper beach, followed behind by a shrub ring and with a central meadow of herbs and grasses.

Savannah

With increasing bird traffic attracted to the greater plant cover in the interior, the number of species of plants there builds up, including a variety of trees and shrubs that shade the island's central habitat still further and contribute greater amounts of organic matter to the soil. In this way the herb meadow becomes dotted by scattered shrubs and trees to form a savannah (Figure 1), sometimes called parkland. Trees that are common in the savannahs on cays are *Cordia subcordata*, *Calophyllum inophyllum*, *Hernandia peltata*, and *Guettarda speciosa*. Humans have often contributed to this zone by plantations of coconuts (*Cocos nucifera*).

Forests

Over time, the density of arborescent vegetation increases until a forest forms, complete with a ground cover of leaf litter and a more mature soil profile. Species of sea birds, such as the Black Noddy (*Anous minutus*) that require trees for nesting, roost in large numbers in these forests and contribute massive amounts of guano to the soil. Most species of low vegetation of the herb meadow or savannah cannot tolerate the dense shade and high nitrogen levels under the forest and accordingly they disappear, leaving only a sparse cover of nitrophilous plants. Now, the zonation includes a peripheral ring of pioneer species surrounding a shrub ring, with the interior of the island covered by forest or a combination of forest and savannah. All of these stages in the succession of vegetation can be seen on islands on reefs (Figure 2). The forested islands seem to be the end stage in this sequence as no further stages have been witnessed. This does not mean that change ceases, however, or that all islands inevitably reach this final stage. Because of that, some ecologists dispute the validity of the concept of succession. Further changes, however, can be viewed as intervention by forces or agents that halt or reverse what would otherwise be an orderly progression. Some of these retrograde, destructive influences are known (Heatwole, 1984) and are as follow:

Coral Cays, Vegetational Succession, Figure 3 Gannet Cay, Great Barrier Reef (January 1989), a cay that was once much larger and with a well developed herb meadow. It was formerly located farther onto the reef, toward the top of the picture. The automatic weather station seen in the center of the picture was once located in the center of the island. The island has now shifted to the edge of the reef and is losing sand to deeper water as seen by the cascade of sand toward the left end of the island. Photograph by Harold Heatwole.

Erosion

The pattern of zonation of vegetation, described above, can be obliterated by erosion. As direction of prevailing winds shift, or local patterns of sea currents change, beaches on one side of an island may erode and encroach into a herb meadow or even a forest. Often, the beach on the opposite side of an eroding island is prograding and widening the zone available for pioneer vegetation. Thus, instead of concentric vegetation zones, they are off center and lopsided. In extreme cases, cays can move across the reef, eroding on one side and prograding on the other, until eventually, the position of the cay scarcely overlaps that of its former location (Flood and Heatwole, 1986), or a cay may go over the edge of its reef into deep water and disappear altogether (Figure 3).

Marine washover

Severe storms may result in a cay being washed over by waves and the terrestrial vegetation destroyed (Flood and Heatwole, 1986), with succession having to start over again. The history of some islands can be seen in heavily eroded beaches where dark layers of humus (indicating previous times of vegetation cover) are interleaved with layers of light-colored sand (left from times when the island was devoid of vegetation, either because of marine washover or from Aeolian deposition of sand on top of the plants) (Figure 4).

Seabirds

The role of seabirds as transfer organisms, as dispersers of seeds, and as enrichers of the soil, has already been discussed. Birds may also have a destructive effect. Where they nest on a herb meadow in large numbers, their trampling may destroy plants (Heatwole, 1984) and return the island to a previous stage, or even to a bare cay. This is especially likely to occur if the breeding colony is being concentrated into smaller space by continued erosion of an island on one edge of its reef, while the prograding side goes over the edge into deep water.

Coral Cays, Vegetational Succession, Figure 4 A highly eroded beach on Frigate Cay (July 1987) showing alternating layers of dark organic humus and lighter-colored sand, representing successive periods of vegetation cover and bare sand at the surface. Note that encroachment on the herb meadow by erosion has exposed roots of *Boerhavia diffusa* (*upper left*).

Sea turtles

When sea turtles come ashore to nest, the female digs a pit in which she lays her eggs; in the process she may kill plants by uprooting them (Figure 5). Species of the herb meadow are more susceptible because they usually occur as individually rooted plants. By contrast, many pioneer species have runners with multiple root systems, so that even if a large part of the plant is dug up other parts of it

Coral Cays, Vegetational Succession, Figure 5 Nesting sea turtles dig pits in the sand in which they lay their eggs. This activity leaves an uneven terrain of hummocks and pits, as seen in this photograph. The uprooted vegetation dies (*foreground*). Such destruction by turtles can lead to return of herb meadow (without creeping plants) to pioneer vegetation that is anchored over a wide area by runners. Photograph by Harold Heatwole.

still have roots in the soil and the plant can survive. For this reason, where turtles nest in high numbers, succession may be halted or herb meadow even reversed to pioneer vegetation (Heatwole, 1984; Rogers 1989).

Drought

Even in such an equable environment as a tropical island, the weather is not constant. There are year-to-year changes in the amount of rainfall, and these can affect the trajectory of vegetational succession on cays. There has been only one detailed study of this phenomenon and that was on One Tree Island at the southern end of Australia's Great Barrier Reef from 1968 to 1978 (Heatwole, 1981; Heatwole et al., 1981). Rainfall was plentiful for most of the time, but there was a drought of four months, that killed a lot of vegetation. No species of plant went extinct because of the drought, but the most abundant species of the herb meadow (*Melanthera biflora*) declined to less than a quarter of its former biomass. By contrast, a pioneer species (*Ipomoea pes-caprae*) that had been rare in the herb meadow before the drought thrived and increased greatly in biomass to become the dominant species. Thus, the drought caused vegetation in the center of the island to revert to a previous successional stage.

Humans

Humans have a major effect on cays, through direct destruction of vegetation and fauna, construction of buildings, mining guano, altering patterns of erosion, planting gardens and coconut groves, and introduction, intentional or otherwise, of weeds. Lady Elliott Island on the Great Barrier Reef is an example of both good and bad effects of humans. It was first nearly denuded by guano miners who destroyed the vegetation and stripped the soil. Later, it was restored to nearly its former condition by replanting native vegetation as part of the development of an eco-friendly resort.

Summary

As a bare cay forms and increases in size, its vegetation goes through a predictable progression of successional stages: bare cay → pioneer vegetation → pioneer vegetation plus encirclement by shrubs → herb meadow → savannah (parkland) → forest. Plants of the earliest stages tend to be sea-dispersed whereas later the vegetation consists mostly of bird-dispersed species. The vegetation becomes progressively organized into concentric zones with earlier successional stages located peripherally and later ones successively toward the center. This sequence can be altered, or reversed, by various destructive forces, including trampling by seabirds, uprooting of vegetation by sea turtles, drought, erosion of beaches, washover during storms, and human activities.

Bibliography

Flood, P. G., and Heatwole, H., 1986. Coral cay instability and species-turnover of plants at Swain Reefs, southern Great Barrier Reef, Australia. *Journal of Coastal Research*, **2**, 479–496.

Heatwole, H., 1971. Marine-dependent terrestrial biotic communities on some cays in the Coral Sea. *Ecology*, **52**, 363–366.

Heatwole, H., 1981. *A coral island*, Sydney: Collins.

Heatwole, H., 1984. Terrestrial vegetation of the coral cays, Capricornia section, Great Barrier Reef marine park. In Ward, W. T., and Saeger, P., (eds.) (misprint for Saenger), *The Capricornia section of the Great Barrier Reef past, present and future.* St. Lucia: the Royal Society of Queensland and the Australian Coral Reef Society, pp. 87–139.

Heatwole, H., Done, T., and Cameron, E., 1981. *Community ecology of a coral cay, a study of One Tree island, Great Barrier Reef, Australia* (Monographiae Biologicae). The Hague: Dr. W. Junk Publishers, **43**, 1–379.

Heatwole, H., 1994. Colonization of coral islands. In Stevenson, R. E., and Talbot, F. H. (eds.), *Islands*. Surrey Hills (Australia): Reader's Digest, pp. 56–65.

Lesko, G. L., and Walker, R. B., 1969. Effect of sea water on seed germination in two pacific atoll beach species. *Ecology*, **50**, 730–734.

Rogers, R. W., 1989. The influence of sea turtles on the terrestrial vegetation of Heron Island, Great Barrier Reef. *Proceedings of the Royal Society of Queensland*, **100**, 67–70.

Smith, J. M. B., Heatwole, H., Jones, M., and Waterhouse, B. M., 1990. Drift disseminules on cays of the Swain Reefs, Great Barrier Reef, Australia. *Journal of Biogeography*, **17**, 5–17.

Wiens, H. J., 1962. *Atoll environment and ecology*, New Haven: Yale University Press.

Cross-references

Coral Cay Classification and Evolution
Cay Formation
Unvegetated Cays
Vegetated Cays

CORAL REEF, DEFINITION

Terry Done
Australian Institute of Marine Science, Townsville MC, QLD, Australia

Definition

Coral reef: A tract of corals growing on a massive, wave-resistant structure and associated sediments, substantially built by skeletons of successive generations of corals and other calcareous reef-biota.

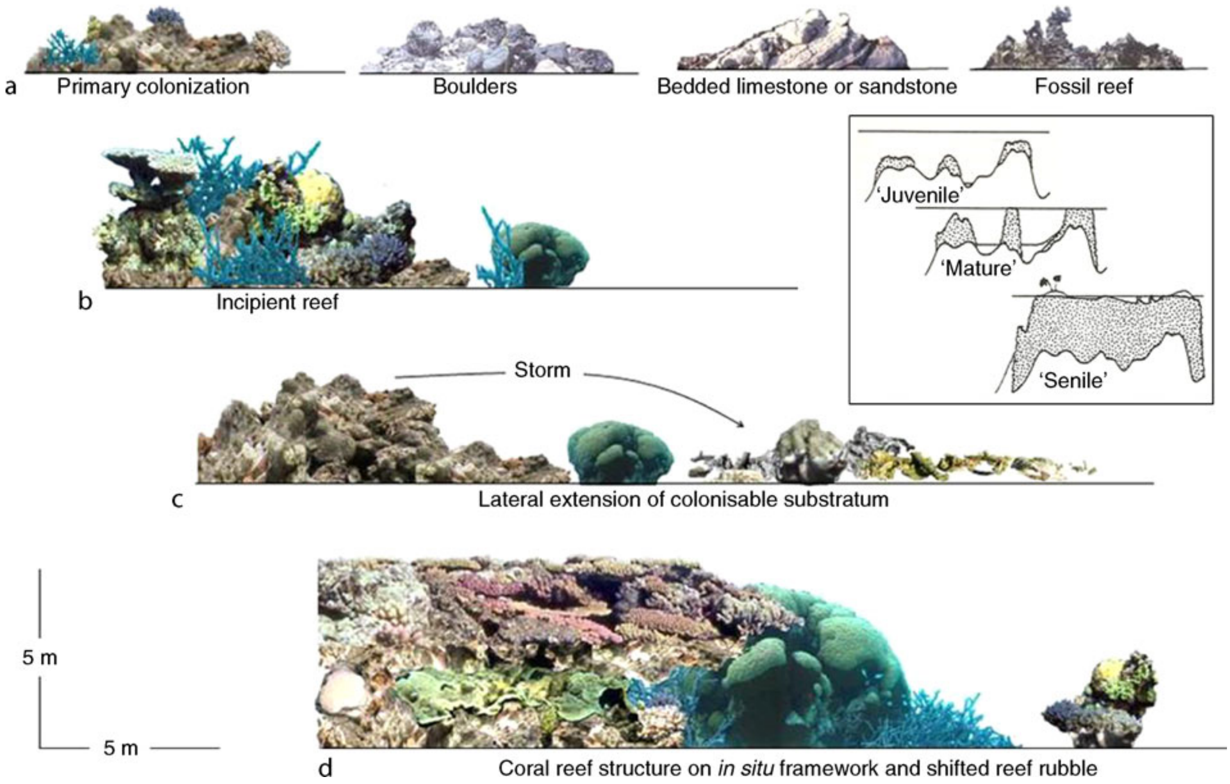
Coral-algal reef: A rigid wave-resistant structure in which scleractinian (stony) corals and crustose coralline algae are the dominant frame-builders. The term "modern" is used to refer to reefs that are forming or have formed in response to late Holocene sea levels (less than 7000 years B.P.) (James and Macintyre 1985).

Introduction

Drawing a parallel with a definition of the coral reef's nearest terrestrial equivalent "forest" as "large tract covered with trees and undergrowth" (Fowler, 1929), "coral reef" could simply be defined as "large tract covered with corals and undergrowth." However, these words fall well short of capturing a coral reef's total character on two major fronts (Stoddart, 1969): first, the notion that the organisms of the reef themselves do not simply cover a tract, but also contribute to its nonliving physical structure (Figure 1) in a way that has no parallel in forests; second, the rich and complex ecological systems of which the corals are part. Documentation of variation in form and process started with Darwin's (1842) recognition of oceanic fringing reefs, barrier reefs, and atolls as a developmental series on subsiding volcanic islands. Such reefs, whose surrounding water depths and thickness exceed 1,000 m, represent the outcome of episodes of reef growth, punctuated by sea-level change, since the Tertiary (Hopley et al., 2007). Other impressive coral reefs are much thinner and much younger, exemplified by reefs on the shallowest parts of continental shelves that were >100 m above sea level as recently as 20,000 y BP and became inundated as recently as 7,000 y BP. There, water depths and reef thickness can be less than a few meters, the entire entity representing reef initiation and growth of the mid to late Holocene epoch (Kennedy and Woodroffe, 2002).

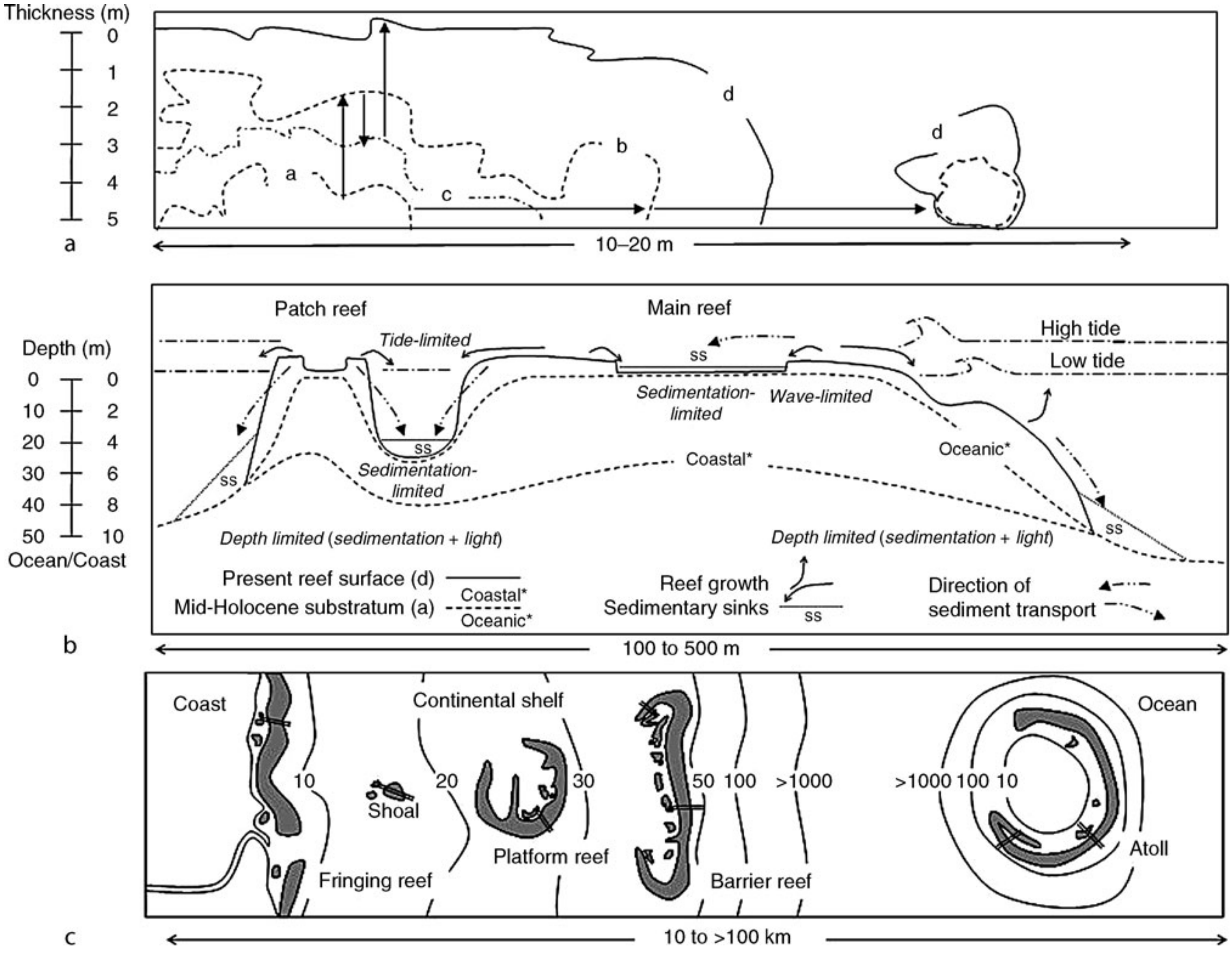
A terminology for coral reefs based on their relationship to land mass and depth of surrounding water (Figure 2c; see also James and Macintyre, 1985; Spalding et al., 2001) includes the following: "fringing reef" (a linear reef with a reef flat some tens of meters across, growing along shelving coastlines and across embayments); "bank barrier reef" (another form of linear coastal reef a little further from the shore than the fringing reef, and sometimes coalescing with one); "barrier reef" (also a linear structure, but fronting deep oceanic waters and broader – usually hundreds of meters across – and separated from the coastline by navigable waters); "atoll" (broadly circular reefs enclosing a wide lagoon); "bank reef" or "platform reef" (a substantial reef fitting none of the above categories, occurring in oceanic and coastal settings). Collectively, these terms account for most of the large scale morphological variability observed in tropical coral reefs. Coral reefs that are substantially built by skeletons of successive generations of corals and other calcareous reef-biota also exist in deep, cold waters (Roberts et al., 2006). However, these "cold-water coral reefs," located at depths well below the impact of breaking waves, are not "wave-resistant" structures in the same sense as shallow tropical reefs.

Smaller scale morphological variability within and among reefs is very strongly determined by the "antecedent topography" on which corals established themselves (Shinn et al., 1977) – i.e., the location, shape and time of Holocene inundation of topographic sea-floor high points of stable substrata (e.g., rocks, fluvial rubble, fossil carbonate reefs or dunes). From the mid-Holocene to the present, primary colonization and the upward and outward accumulation of calcium-carbonate skeletons across that topography has adorned and obscured its shape to varying degrees. This transformation has been represented in whole reefs as a progression through a development series from "initiation" through "juvenile," "mature," and "senile" stages (Figure 1; see also entry *Reef Classification by Hopley (1982)*), a scaled-up manifestation of the series of local scale transitions "a" to "d" in Figure 1 and Figure 2a. In "resorbed" and "remnant" reef structures (see entry *Reef Classification by Maxwell (1968)*), "degenerative" processes have prevailed, as cumulative loss of reef material through storms and erosion (both biological and physical) exceeds accumulation of reef material; the net transitions have been in the reverse direction (e.g., "d" to "c," "b" or "a")



Coral Reef, Definition, Figure 1 Reef growth model. Inset: Hopley's classification of shallow reefs according to their stage of Holocene development (shown as stipple; see also entry *Reef classification* – Hopley 1982). Main section: Local scale processes and events responsible for reef growth. (**a**) Primary coral colonization of newly available substratum and examples of types of substrata made available by last sea-level transgression: boulders (e.g., fluvial; littoral); bedded limestone or sandstone; fossil reef (pitted by subaerial erosion). (**b**) Incipient reef. Coral–algal framework with or without sediment infilling has developed over the substratum in (**a**). (**c**) All the corals and part of the framework have been torn off by storm waves and scattered on the adjacent sea floor, extending the colonisable substratum. One large massive coral remains intact and in place, and another has been thrown clear of the developing reef. (**d**) The surface of the incipient reef has been recolonized and further framework added, filling the space between the developing reef and the first massive coral, now much larger. The massive coral tossed off the reef in (**c**) died and has become substratum for more coral growth. It may in time be moved by another storm, and/or become incorporated into the developing reef. In shallow water, further upward growth of corals and hence the structure will eventually be limited by exposure to the air. In deeper water, further upward growth may occur, or it may be limited by destructive waves (see entry *Corals – Environmental controls on growth*).

The James and Macintyre definition of "coral-algal reef" (above) gives coralline algae equal prominence with stony corals, recognizing their role both in accreting thick algal ridges and in cementing coral skeletons together into a framework. Their definition works extremely well for oceanic reefs worldwide, in which the necessary resistance to powerful ocean waves is inconceivable without the major contribution made by coralline algae. However, the term "coral reef" is also used to describe coral tracts sitting atop accumulations of coral debris with little or no submarine cementation: e.g., cold water reefs (Roberts et al., 2006) and many tropical fringing reefs, shoals, mounds, and banks. This raises the question of whether these latter forms should be excluded and called something else, or included under a more generic definition such as the first one presented above. It would be difficult to apply the James and Macintyre definition – with its emphasis on cementation by coralline algae – to many of the mega-diverse coral reefs in sheltered waters of South-East Asia (Spalding et al., 2001; see *East Indies Triangle of Biodiversity*), the Great Barrier Reef lagoon (Johnson and Risk, 1987; Hopley et al., 2007; Perry et al., 2008), or the rhomboid shoals behind the Belize Barrier Reef. The latter have been described in terms that could be used to describe reefs in sheltered waters in many parts of the world: little submarine cementation; corals stabilized by interlocking of their skeletons; colonies growing to the point of oversteepening and toppling down slope; debris fans at their base; only occasional storm disturbance (Aronson and Ellner, 2007). Lacking major cementation, and lacking exposure to the ocean's strongest waves, their wave-resistance is less in absolute terms than that of oceanic coral–algal reefs. They have, nevertheless, like "coral–algal" reefs, elaborated in the mid- to



Coral Reef, Definition, Figure 2 Coral reef structure at scales of metres to 100s of kilometers. (**a**) Position of reef surface at stages "a" to "d" in Figure 1. Vertical arrows show accumulation (up arrows) and interruption of vertical growth by the storm in Figure 1c (down arrow). Horizontal arrows show the extent of lateral spread of colonisable substrata, providing the potential for the reef to "step out over its own debris" (Blanchon and Jones, 1997). (**b**) Profile of generalized coral reef exposed to waves from the right. The present reef surface has developed over the mid-Holocene substratum (dashed lines) by processes illustrated in Figure 1. (* Note the five times difference between the vertical scales for coastal and oceanic reefs). The major growth directions, sediment movement and dominant environmental factors limiting coral growth and framework development are indicated: viz. light, sedimentation (rate of sediment fall), waves, tide (= exposure to air). (**c**) Diagram of some major reef types and bathymetric settings of coral reefs. Double lines indicate positions of cross-reef transects that could be represented by Fig. 2b. Contours indicate depths in meters. Continental shelf extends from coast to 100 m isobath.

late Holocene as structures widely referred to among scientists as "coral reefs." Their smaller dependence on algal cementation and strong framework is evident in a number of modes of growth in fringing coral reefs (Kennedy and Woodroffe, 2002), in which lateral reef growth over unconsolidated coral debris is prominent. In summary, the first definition (see section 'Definition') is preferred here because it accommodates both the "classic" coral–algal reef style defined by James and Macintyre (1985) and also coral tracts established on less strongly consolidated substrata.

Coral community: geological and ecological definitions

Further differentiation is provided by Buddemeier and Hopley (1988), who distinguish between "coral reef," "coral reef community," and "coral community." They use "coral reef community" to refer to an incipient coral reef (Figure 1b) – not yet a massive wave-resistant structure, but on a developmental trajectory toward that state. Their "coral community" is on no such trajectory: it refers to a local assemblage of corals that are attached directly to nonreef substrata and provide no indication that their predecessors have, or they and their successors will, substantially expand the substratum the way incipient reefs do. The state illustrated in Figure 1a, assuming it was representative of an area of at least hundreds of meters, would be referred to as "just a coral community" so long the corals failed to add to a wave-resistant framework, either in situ or by ending up in a congruent rubble bank.

These terms are useful in placing "coral reef" on a "not-reef" to "reef" continuum, defined in terms of realized or potential "structure." However ecologists use these terms differently: "community ecology" is a rich and long established discipline that focuses on environmental and biological drivers of "structure" in plant and animal communities (May, 1985). "Structure" in a community refers not to physical form, but rather to spatial pattern, species composition, population dynamics and the like. As a simple descriptive term within reef ecology, "a coral community" refers to the corals occupying a local area, irrespective of its substratum (e.g., Done, 1982), and a "coral reef community" refers to the entire ensemble of marine species that occupy a coral reef, and among which the "coral community" is a part. Coral reef communities are extraordinarily rich in species and co-evolved relationships, with important functional roles that facilitate tight recycling of nutrients in nutrient-poor waters (Hallock, 2001), survival in turbid seas (Perry et al., 2008a), and high per unit area productivity of protein, reef building blocks and sediments (Done et al., 1996). The terms "coral community" and "coral reef community" thus have contrasting nuances for earth scientists and biologists. However, their meaning will usually be clear according to the context in which they are used.

The measure of a good definition is the extent to which it eliminates similar entities. In the following sections, the definition is dissected and the terms elaborated using both examples and exceptions. Table 1 describes some of the relevant terms.

A tract of corals

Tracts (viz. "large areas of indefinite extent") of living corals provide food and shelter for much of the abundance and diversity of marine biota for which coral reefs are renowned. In two circumstances, however, living corals are absent – or they are at least too sparse to be reasonably referred to as a "tract" – from what would still be considered legitimate contemporary coral reefs: "dead" and "marginal" coral reefs. In "dead" coral reefs, absence or scarcity of corals is a consequence of a recent (within a human life span) catastrophic impact (e.g., predation, disease, coral bleaching, cyclone). Regardless of whether the corals recover expeditiously (years to decades), this structure would still be considered a "coral reef," albeit "dead," or in an alternate or phase shifted state (Done, 1992; McClanahan et al., 2002). In "marginal" coral reefs, corals are sparse or absent from reef substrata because the supply of coral larvae or viable fragments no longer exists, and/or on-site environmental conditions have become inimical for corals. There are, for example, "drowned reefs" that supported flourishing coral communities before the sea-level transgression but where light is now limiting and sedimentation is excessive for good coral growth and survival. And there are back-reef areas for which the reef's own growth has so greatly changed water circulation that

Coral Reef, Definition, Table 1 Brief glossary of useful terms for describing generic characteristics of corals and coral reefs at spatial scales from <1 mm to hundreds of kilometers. An example of specific reef types is provided in Figure 2c

Term/alternative	Description
Larva/planula larva	Free living soft-bodied embryo that settles on a solid substratum and forms a primary polyp
Primary polyp	The polyp into which the larva metamorphoses
Zooid	A polyp and its corallite
Corallite	The limestone cup that is secreted by each polyp and provides it with structural support
Corallum	The limestone skeleton of a coral colony
Colony	The limestone skeleton plus the living polyp tissue, produced by replication of the primary zooid and all its descendants.
Population	All members of one species living in a defined area, such as a single coral reef. In a regional context, the single reef's population is a "sub-population" of a regional "metapopulation."
Community/assemblage	All colonies of all species occupying a defined area, such as a reef or a specific part of a reef
"Bommie" (Australian vernacular, widely used internationally)	1. A "head" coral two to several meters high and across 2. A patch reef
Patch reef	A number of corals of one to many species growing on a discrete patch of reef substratum associated with a larger structure referred to as the "main reef" in Figure 2b
Coral reef/coral reef complex	See "Definition" (above) and "*Coral Reef – classification*." Its basal footprint (delimited by consolidated reef and adjacent sedimentary deposits) is usually measured in hectares or square kilometers. A coral reef always includes a discrete main section and often includes bommies and patch reefs in the footprint (Figure 2c)
Reef tract	All contiguous and adjacent coral reefs within a particular region. Depending on commonality of the environment and the strength or weakness of material exchanges among them, the reefs in a tract may be considered to constitute a "system," in which the state of one may influence the state of another

regimes of temperature, oxygenation, salinity, and turbidity have become inimical for coral growth (Macintyre, 2007).

Massive structure

A coral reef is "massive" (relative to the size of a human observer) in terms of both its basal area (usually hectares and upward) and its thickness (a nonliving basement usually meters to tens of meters thick and the living corals and diverse other sessile biota attached to it – usually <1 m to a few meters tall). Coral covered substrata of smaller dimensions than these could still legitimately be referred to as "coral reefs," but so long as they were in close vicinity to a larger structure, they would generally be referred to as "patch reefs," and considered to be a physically discrete part of the larger unit: e.g., the patch reefs at the back of such and such a reef.

A generalized picture of the "classic" reef-building processes based on James and Macintyre (1985) and Kan et al. (1997) is as follows: large corals of diverse and irregular shapes remain in place after their death, forming roofed-over cavities (robust branching forms such as *Acropora palmata* – James and Macintyre, 1985) or stacks of head and branching corals (Kan et al., 1997) – the whole becoming a "framework" that becomes inhabited by smaller attached calcareous benthos. Encrusting organisms (calcareous algae) grow over dead surfaces, aid in stabilizing the structure, and provide environmental cues that promote settlement of new corals (Harrington et al., 2004). Assuming there is sufficient water above (Figure 1; see entry *Accommodation Space*), another layer of corals can thereby settle, grow, die, become incorporated into the reef framework, and thus incrementally thicken the reef structure (Pichon, 1974; Kan et al., 1997). In stormy weather (Figure 1c), weakly attached or branching corals are broken, dislodged, and deposited in reef cavities and skeletal conglomerations on the reef slope or adjacent sea floor, allowing the reef to extend laterally by "stepping out over its own debris" (Blanchon and Jones, 1997). The latter process may be a result of settlement of coral larvae on the debris, or regeneration of still viable coral fragments among the rubble.

Another equally important process is infilling. The developing framework can be buried by or partially filled with sediment, with grain sizes from fine silts to coarse rubble, either before or after significant cementation has taken place. The types of corals, types of sediments, stage of cementation, and time and rate of burial produce distinctive layers in the sedimentary profiles of the reef (Shinn et al., 1977) that are reflected in distinctive limestone rocks in fossilized reefs (James and Macintyre, 1985; e.g., see entries *Rudstone, Bafflestone, Framestone, Floatstone*).

Wave resistant structure

All coral reef definitions specify a structure that is highly resistant to wave impacts. Strong swells and waves do sometimes damage framework and cause catastrophic losses to reef biota (see entry *Tropical Cyclone/Hurricane*). However, the change (in terms of tonnes of reef debris created and moved) is generally insignificant compared to mass and volume of reef framework that remain intact and in place. Moreover, the dissipation of wave energy across reef flats, the refraction of waves around reefs, and the flushing of sand through canyons by return flows are highly instrumental in determining the shape of reefs (Blanchon and Jones, 1997). Such a wave on reef interaction promotes the retention of reef-derived blocks, rubble, and finer sediments within the existing reef footprint, and thus the reef's propensity to "step out."

Associated sediments

Coral reefs generate massive amounts of carbonate sediments. Fine sediments (sands and silts) are derived from both bioerosion of large metazoans such as corals, and the post-mortem disintegration other calcifiers, notably foraminifera, small molluscs, and diverse segmented calcareous organisms including coralline algae and crinoids (James and Macintyre, 1985). Coarse sediments (boulders, blocks, rubble, shingle) are moved by storms, currents and gravity (see above and entries *Tropical Cyclone/Hurricane, Hydrodynamics of Coral Reef Systems*). They fall into lower energy deposition sites, including crevices within the reef, talus beds at the base of reef slopes, reef-flat boulder ramparts, sheltered back-reef lagoons and aprons, and gutters. In reefs far from land, most if not all sediments are generated by the reef. However, on some coastal reefs, sediments of terrestrial origin can dominate infilling sediments and the near-reef sedimentary apron (Kleypas et al., 2001; Larcombe and Carter, 2004). These imported sediments may include (1) sediments from the present-day land mass (via surface runoff, dust or ash) and/or (2) sediments from now-submerged mid-Holocene coastal low lands, re-suspended and swept into and around reefs by currents and waves (Larcombe and Carter, 2004).

Substantially built by successive generations of corals and other reef builders

Over scales of decades to millennia, reef growth is dependent on ecological resilience in the resident stony coral populations and other reef builders – their capacity to recover dense populations following those necessary physical disturbances that transform some of them into debris. In a well functioning reef, "other reef builders" perform a number of direct and indirect "bioconstructional roles" in addition to the primary framework building role of stony corals and encrusting coralline algae (Done et al., 1996): "secondary framework builders" such as byrozoans and bivalve molluscs and tube worms add small scale topographic complexity to the framework; microbes condition substrata for coral settlement and contribute to wave-resistance through submarine lithification; "non-framework reef builders" such as foraminifera, erect coralline algae (especially the genus *Halimeda*) and molluscs contribute greatly to reef sediments; "sediment operators," such as holothurians and burrowing worms and molluscs, aerate sediments and contribute to the productivity of sandy lagoons; "facilitators" such as herbivorous fishes and invertebrates keep algal biomass in check that might otherwise limit coral settlement and survival.

Resilience in biota and functional roles is as much dependent on the existence of the wave-resistant structure as it is a contributor to it. A critical third pre-requisite is a hydrodynamic setting that acts to retain the reef debris within the existing reef footprint. Reefs with this combination of resilient populations of corals, other reef builders and facilitators, high carbonate production, and strong retention have been termed "production-dominated" (Kleypas et al., 2001). These authors note that a reef's potential for this strongly autonomous growth may be limited in three ways: by a location and hydrodynamic setting that favors import and incorporation of exogenous sediments – marine or terrigenous ("import-dominated" reefs); export of reef-generated sediments ("export-dominated"); or such a poor larval supply and/or conditions for coral growth that it cannot keep up with losses caused by bioerosion ("bioerosion dominated"). This latter style is classically represented in back reef areas that become isolated from the ocean by the coral reef's own profligate growth (Macintyre, 2007).

"Coral communities" (*sensu* Buddemeier and Hopley, 1988; i.e., those that do not advance beyond stage "a" in Figure 1) are extreme examples of an "export-dominated" setting. These corals settle directly on "non-reefal" substratum, and on their death, are physically and biologically eroded down to silt, or fall off (precluding framework accretion and sedimentary infilling), and are carried by currents and gravity into places too deep, too turbulent or too sandy for additional coral settlement or survival.

"Incipient reefs" (a term preferable to "coral reef communities"; Figure 2b) are coral reefs in the making. They have had insufficient time to complete sufficient incremental vertical growth and "stepping out" to be considered a "coral reef."

Summary

Two similar definitions ("coral reef" and coral-algal reef) are provided, one strictly geological and one that specifies *living* corals as a fundamental defining characteristic of "coral reef." The definition is then dissected, and allied terms such as "coral community" and "coral reef community" discussed, noting the completely different meaning of these terms in geology and ecology. The importance of ecological processes in keeping up the supply of building blocks (corals and reef debris) is discussed. Differences in local environment and in particular, hydrodynamic setting, lead to different intergenerational performance of coral populations, and also the propensity for reefs to act as sediment importers, producers or exporters, or to be in a state of net loss due to bio-erosion. A place's environmental regime considered over decadal time scales and up (including "normal" conditions and extreme events) will determine the likelihood of a coral community making the transition (Figure 1) to an "incipient coral reef" (early stages of development of a wave resistant structure) and a "coral reef" proper. Key determinants are first, whether there is a sufficient density of corals in a sufficiently large area that grow long enough and get large enough to create a wave-resistant structure; and second, whether that structure gets large enough to attenuate and refract waves and currents in a manner that promotes the retention and compaction of its own biogenic sediments within and around itself.

Just as the terms "juvenile," "mature," and "senescent" are applied to the coral reefs as geological structures, so are they applied to the tracts of corals for which the structure is simply "substratum." However, the links between coral dynamics and reef development are poorly understood (Perry et al., 2008b). Improved understanding is important, especially in light of serious, persistent, and widespread declines in coral cover and resilience (e.g., Bellwood et al., 2004) and some very bleak projections for the future of coral reefs under global climate change (Veron, 2008).

Bibliography

Aronson, R. B., and Ellner, S. P., 2007. Biotic turnover on coral reefs: a probabilistic approach. In Aronson, R. B. (ed.). *Geological Approaches to Coral Reef Ecology.* New York: Springer, pp. 61–84.

Bellwood, D. R., Hughes, T. P., Folke, C., and Nyström, M., 2004. Confronting the coral reef crisis. *Nature*, **429**, 827–833.

Blanchon, P., Jones, B., 1997. Hurricane control on shelf-edge-reef architecture around Grand Cayman. *Sedimentology*, **44**, 479.

Buddemeier, R. W., and Hopley, D., 1988. Turn-ons and turn-offs: causes and mechanisms of the initiation and termination of coral reef growth. *Proceedings of the Sixth International Coral Reef Symposium*, **1**, 253–261.

Darwin, C. R., 1842. *The Structure and Distribution of Coral Reefs*. London: Smith, Elder, 214 pp.

Done, T. J., 1982. Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs*, **1**, 95–107.

Done, T. J., 1992. Phase shifts in coral reefs and their ecological significance. *Hydrobiologia*, **247**, 121–132.

Done, T. J., Ogden, J. C., Wiebe, W. J., and Rosen, B. R., 1996. Biodiversity and ecosystem function of coral reefs. In Mooney, H. A., Cushman, J. H., Medina, E., Sala, O. E., Schultze, E. D. (eds.), *Functional Roles of Biodiversity: A Global Perspective*. Chichester: Wiley, pp. 393–429.

Fowler, H. W., 1929. *The Concise Oxford Dictionary of Current English*, 2nd edn. Oxford, UK: Clarendon Press.

Hallock, P., 2001. Coral reefs, carbonate sediments, nutrients and global change. In Stanley, G. D. Jr. (ed.). *The History and Sedimentology of Ancient Reef Systems.* New York: Kluwer/Plenum pp. 387–427.

Harrington, L., Fabricius, K., De'ath, G., and Negri, A., 2004. Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology*, **85**, 3428–3437.

Hopley, D., Smithers, S. G., and Parnell, K. E., 2007. *The Geomorphology of the Great Barrier Reef: Development, Diversity and Change*. Cambridge: Cambridge University Press, 532 pp.

James, N. P., and Macintyre, I. G., 1985. Carbonate depositional environments: modern and ancient. Part 1; Reefs: zonation, depositional facies, diagenesis. *Colorado School of Mines Quarterly*, **80**(3), 70.

Johnson, D. P., and Risk, M. J., 1987. Fringing reef growth on a terrigenous mud foundation, Fantome Island, central Great Barrier Reef, Australia. *Sedimentology*, **34**, 275–287.

Kan, H., Nakashima, Y., Hopley, D., 1997. Coral communities during structural development of a fringing reef flat, Hayman Island, the Great Barrier Reef. *Proceedings of the Eighth International Coral Reef Symposium*, Vol. 1, pp. 465–470.

Kennedy, D. M., and Woodroffe, C. D., 2002. Fringing reef growth and morphology: a review. *Earth Science Reviews*, **57**, 255–277.

Kleypas, J. A., Buddemeier, R. W., and Gattuso, J.-P., 2001. The future of coral reefs in an age of global change. *International Journal of Earth Sciences*, **90**, 426–437.

Larcombe, P., and Carter, R. M., 2004. Cyclone pumping, sediment partitioning and the development of the Great Barrier Reef shelf system: a review. *Quaternary Science Reviews*, **23**, 107–135.

Macintyre, I. G., 2007. Demise, regeneration and survival of some Western Atlantic reefs during the Holocene Transgression. In Aronson, R. B. (ed.). *Geological Approaches to Coral Reef Ecology*. New York: Springer, pp. 181–200.

May, R. M., 1985. An overview: real and apparent patterns in community structure. In Srong, D. R. Jr., Simberloff, D., Abele, L. G., and Thistle, A. B. (eds.), *Ecological Communities. Conceptual Issues and the Evidence*. Princeton, NJ: Princeton University Press, pp. 3–16.

McClanahan, T., Polunin, N., and Done, T., 2002. Ecological states and the resilience of coral reefs. Conservation Ecology 6(2): 18. [online] URL: http:/www.consecol.org/vol6/iss2/art18

Perry, C. T., Smithers, S. G., Palmer, S. E., Larcombe, P., and Johnson, K. G., 2008a. 1200 year paleoecological record of coral community development from the terrigenous inner shelf of the Great Barrier Reef. *Geology*, **36**, 691–694.

Perry, C. T., Spencer, T., Kench, P. S., 2008b. Carbonate budgets and reef production states: a geomorphic perspective on the ecological phase-shift concept. *Coral Reefs*, **27**, 853–866.

Pichon, M., 1974. Dynamics of benthic communities in the coral reefs of Tulear (Madagascar): succession and transformation of the biotopes through reef tract evolution. *Proceedings of the Second International Coral Reef Symposium*, **2**, 55–68.

Roberts, J. M., Wheeler, A. J., Freiwald, A., 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science*, **312**, 543–547.

Shinn, E. A., Hudson, J. H., Halley, R. B., and Lidz, B., 1977. Topographic control and accumulation rate of some Holocene coral reefs: South Florida and Dry Tortugas. In *Proceedings of the Third International Coral Reef Symposium*, Vol. 2, pp. 1–7.

Spalding, M. D., Ravilious, C., and Green, E. P., 2001. *World Atlas of Coral Reefs*. Berkeley, U.S.A: University of California Press.

Stoddart, D. R., 1969. Ecology and morphology of recent coral reefs. *Biological Reviews*, **44**, 433–498.

Veron, J. E. N., 2008. Mass extinctions and ocean acidification: biological constraints on geological dilemmas. *Coral Reefs*, **27**, 459–472.

Cross-references

Accommodation Space
Bafflestone
Barrier Reef (Ribbon Reef)
Climate Change and Coral Reefs
Corals: Environmental Controls on Growth
Cold-Water Coral Reefs
Darwin, Charles (1809–1882)
East Indies Triangle of Biodiversity
Ecomorphology
Eco-Morphodynamics
Floatstone
Framestone
Fringing Reefs
Geomorphic Zonation
Hydrodynamics of Coral Reef Systems
Mid Holocene
Patch Reefs: Lidar Morphometric Analysis
Reef Classification by Fairbridge (1950)
Reef Classification by Hopley (1982)
Reef Classification by Maxwell (1968)
Reef Flats
Reef Typology
Reticulated Reefs
Rudstone
Sedimentation Stress
Tropical Cyclone/Hurricane
Turbid-Zone and Terrigenous Sediment-Influenced Reefs

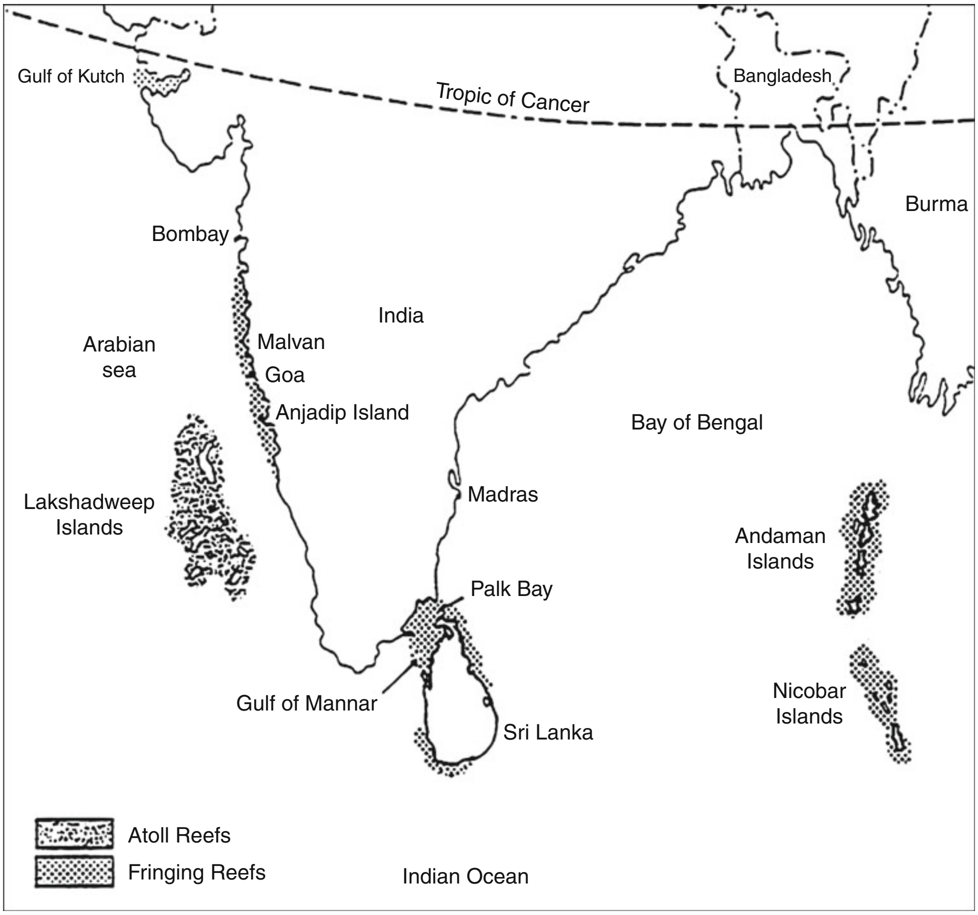
CORAL REEFS OF INDIA

Krishnamoorthy Venkataraman
Marine Biology Regional Centre, Chennai, India

Definition and introduction

Coral reefs are one of the most ancient and dynamic ecosystems of India. Coral reefs not only provide a sanctuary to a myriad of marine life but also play a key role in protecting the coastline from erosion. In addition, people living along the 8,000 km long coastal stretch of India depend on coral reefs for their livelihood (Venkataraman and Alfred, 1998, Venkataraman, 2003). India is centrally placed within the warm tropical region of the Indian Ocean and exhibits extensive coral reefs in its marine territories. In India, major coral reef ecosystems are seen in Gulf of Mannar, Gulf of Kachchh, Andaman & Nicobar, and Lakshadweep Islands, which embrace all the three major reef types (atoll, fringing, and barrier) and include diverse and extensive reef areas of the Indian Ocean (Figure 1). Fringing reefs are found in the Gulf of Mannar and Palk Bay. Platform reefs are present along the Gulf of Kachchh. Patch reefs are present near Ratnagiri, Malvan, and Kerala coasts. Fringing and barrier reefs are found in Andaman and Nicobar Islands. Atoll reefs are found in Lakshadweep. Absence of reefs in the Bay of Bengal along the northeast coast is attributed to the immense quantity of freshwater and silt brought by the rivers such as Ganga, Krishna, and Godavari. The total area of coral reefs in India is estimated to be 2,375 sq km.

The studies on the taxonomy of Indian coral reef started as early as 1847 by Rink in Nicobar Islands, and later in 1898, Thurston worked on coral reefs in Gulf of Mannar region. During the whole of twentieth century, many foreigners contributed to coral reef studies in India. Pillai (1983, 1986), the first Indian worker, published many papers on the coral diversity from all the four major coral reefs of India followed by Venkataraman (2003, 2006), Venkataraman and Alfred (1998), and Venkataraman et al. (2003).



Coral Reefs of India, Figure 1 Major coral reef areas in India.

Coral reefs: East Coast of India

Gulf of Mannar

The Gulf of Mannar reefs are found around a chain of 21 islands that lie along the 140 km stretch between Tuticorin and Rameswaram. These islands are located between latitude 8° 47’N and 9° 15’N and longitude 78° 12’E and 79° 14’E. The islands lie at an average distance of 8 km from the main-land. They are part of the Mannar Barrier reef, which is 140 km long and 25 km wide between Pamban and Tuticorin. Different types of reef forms such as shore, platform, patch, and fringing type are observed in the Gulf of Mannar (Venkataraman et al., 2003). The islands have fringing coral reefs and patch reefs around them. Narrow fringing reefs are located mostly at a distance of 50–100 m from the islands. On the other hand, patch reefs rise from depths of 2–9 m and extend to 1–2 km in length with width of as much as 50 m. Reef flat is extensive in almost all the reefs in the Gulf of Mannar. Reef vegetation is richly distributed on these reefs. Reef flat and reef vegetation including algae occupies 65 and 14 sq km, respectively (D.O.D and S.A.C., 1997). Pillai (1986) had provided a comprehensive account of the coral fauna of this region. There are about 94 species of corals belonging to 32 genera in the Gulf of Mannar. The most commonly occurring genera of corals are *Acropora, Montipora,* and *Porites*. Extensive sea grass beds are present; green turtles, olive ridley turtles, and dugongs are dependent on these sea grasses as their feeding ground.

Andaman and Nicobar Islands

The Andaman and Nicobar group of Islands is located in the South East of the Bay of Bengal, between 6°–14°N latitude and 91°–94°E longitude. They are the emerged part of a plate edge mountain chain and lie on a ridge that extends southward from the Irrawaddy delta area of Burma, continuing the trend of the Arakan Yoma range.

The Andaman and Nicobar group of islands consist of 530 islands, of which only 38 are inhabited, along with a number of exposed islets and rocks. The principal of these is the North Andaman, Middle Andaman with Ritchies archipelago in the east, South Andaman, little Andaman, Baratang, and Rutland Island. The coral reefs are of fringing type and except for a few investigation reports, the reefs of the area still largely remain unknown.

A deep oceanic ridge along 10°N separates the Andaman Group and the Nicobar group of islands. The orientation of the chain of islands is north-south. In these island groups, there are two Marine National Parks viz., Mahatma Gandhi and Rani Jhansi Marine National Parks. The coral fauna is diverse when compared to other parts of India (Turner et al., 2001).

West Coast of India

The West Coast of India between Mumbai and Goa is reported to have submerged banks with isolated coral formations (Nair and Qasim, 1978). Coral patches have been recorded in the intertidal regions of Ratnagiri, Malvan and Rede, south of Mumbai (Qasim and Wafer, 1979), and the Gaveshani bank, 100 km west to Mangalore (Nair and Qasim, 1978).

Malvan

The Malvan coast forms part of the Western Ghats where the Sahyadri ranges gradually meet the Arabian Sea. From Vengurla point, the coast tends towards the north for about 22 km. From Malvan bay, a chain of submerged and exposed rocky islands extends directly south to 15°53’N and 73°27’E. In this chain, several islands exist including Vengurla Rocks at the Southern tip and Sindhudurg Fort at the northern tip. Other small islets around Sindhudurg Fort are Mandel Rock, Malvan Rock, etc. Most of the marine flora and fauna in the intertidal area are exposed during low tide. However, during lowest low tides (particularly negative tides), the coral reefs get exposed. *Porites, Coscinaraea, Turbinaria, Favia,* and *Pseudosiderastrea* are some of the genera reported from this coast (Venkataraman et al., 2003). Siltation is high and salinity may drop to 20 ppt during the monsoons in some habitats, which may restrict the growth of ecologically sensitive forms of ramose corals.

Lakshadweep Islands

The Lakshadweep Islands lie scattered in the Arabian Sea at about 225 – 450 km from the Kerala coast. Geographically, the islands lie between 8°N–12°3’N latitude and 71°E – 74°E longitude. The islands consist of coral formations built up on the Laccadive-Chagos submarine ridge rising steeply from a depth of about 1,500 to 4,000 m off the west coast of India. The Union Territory of Lakshadweep along with the Maldives and the Chagos Archipelagoes form an interrupted chain of coral atolls and reefs on a continuous submarine bank covering a distance of over 2,000 km. This ridge is supposed to be a continuation of the Aravali Mountain, and the islands are believed to be remnants of the submerged mountain cliffs. There are six tiny islands, 12 atolls, 3 reefs and 5 submerged banks, covering an area of 32 km^2 with lagoons occupying about 4,200 km^2. Only 11 of the 36 islands are inhabited. Minicoy Island is separated from the rest of the islands by a 180 km wide stretch of sea known as the Nine-degree Channel.

The coral fauna of Lakshadweep is known to harbor 105 species belonging to 37 genera (Pillai, 1996). *Acropora* spp., *Pocillopora* spp., *Porites* spp., and massive and encrusting favids dominate the lagoon and reef flat faunal elements. *Psammocora* spp. are common in the northern islands. There is an abundance of blue coral *Heliopora coerulea. Millepora* spp. is dominant in the lagoon. Minicoy has species such as *Lobophyllia* and *Diploastrea* that are common to the Maldives but rarely found in the northern islands. Similarly, the genera *Montipora* and *Echinopora* recorded from the northern group of atolls are not recorded in Minicoy.

Gulf of Kachchh

Gujarat State has a 600 km long coastline, which is very rich in various edible fishes and various types of algae. The Gulf of Kachchh is the richest source of floral, faunal and marine wealth of India, as it provides favorable conditions for breeding and shelter to all marine life in the 42 islands. The corals in the Gulf of Kachchh survive through extreme environmental conditions such as high temperature, salinity changes, and high-suspended particulate loads. Gulf of Kachchh Marine National Park and Sanctuary is the first National Park in the country (457.92 sq km). The Gulf of Kachchh has the best developed coral reefs along the western coast. Out of the 42 islands in the Gulf, 34 islands are surrounded by fringing or platform reefs. Out of 37 hard coral species reported earlier, only 36 are currently found.

Geology and geomorphology of Indian coral reefs

Coral reefs characterize an ecosystem of high biological diversity, having the greatest number of species of any marine ecosystem. Coral reefs act as a barrier against wave action along coastal areas thus preventing coastal erosion as well as protecting mangroves and seagrass beds in certain areas, which are the breeding and nursing grounds of various economically important fauna (Venkataraman and Alfred, 1998). However, the processes of erosion, sedimentation, periodic storms, flooding, and sea level change, continually modify the ecosystem. The Holocene transgression, the latest episode of sea-level fluctuations, has left behind many signatures which provide insight into the nature of these changes. Direct and indirect palaeo sea-level indicators (see: *Sea Level Indicators*) have been identified with transgressive, regressive or still-stand conditions. These include specific biological indices of corals, molluscs, foraminifers, etc., and certain geomorphological features such as submarine terraces, reefs, notches, raised marine deposits, beach rocks, buried channels, etc (Vora et al., 1996). Glacio-eustatic sea-level fluctuations, along with relief, lithology, sedimentation, tectonic movements, etc., produce depositional and erosional patterns which govern the topography of the continental shelf of the Andaman and Nicobar Islands and other coral reef areas of India (Bruckner, 1988). The topography of the continental shelves where major coral reefs of India are found

(Gulf of Kachchh, Gulf of Mannar, Lakshadweep, and Andaman and Nicobar Islands) is mainly governed by depositional and erosional processes, which occur during glacioeustatic sea level fluctuations. Other factors involved, directly or indirectly, are structure, lithology, sedimentation, tectonic movements, and climatic changes.

Seismic data from the west coast of India revealed the occurrence of buried reefs off Saurashtra and Ratnagiri, indicating pinnacles and protuberances of different heights. The cliffy coast of southern Saurashtra has preserved a record of the sea level changes during the late Quaternary (Rao and Wagle, 1997). Based on the geomorphic positions of the notches, the older sea strand lies at an elevation ranging from 12 to 15 m above the present BMSL and has been attributed to the last interglacial (MIS-5). Following this, a major tectonic uplift of about 6–9 m was experienced by the southern cliffed coast. The Holocene sea level was recorded at 4–5 m which is about 2 m higher than the general MIS-1 sea level. Thus, the submarine terraces on the shelf must have also been formed during the late Pleistocene to mid-Holocene still stands of the sea level. Radiocarbon dates of surficial samples of algal, oolitic, and coralline limestone (Nair and Hashimi, 1980) collected from the terraces and/or in their vicinity suggest that the innermost terrace along the shelf (55–60 m) is ca 7,845 yrs B.P., and the outermost terrace on the shelf is ca 11,150 yrs B.P.

The distribution of reefs on the west coast shelf is random which perhaps may imply that conditions for reef growth have not been uniform. It is interesting to note that between Mumbai and Mormugao, where the shelf is relatively broader, reefs occur abundantly on the middle and outer shelf. On the other hand, south of Mormugao, where the shelf is narrow, they are sparsely present and only on the outer shelf. Submerged coral reefs may be defined as reefs that were established in relation to a pre-existing sea-level lower than present and occur at depths greater than that commonly associated with vigorous growth of reef building, hermatypic corals. Further, the radiocarbon dating of coral and associated fauna indicates that they are of early Holocene age.

The Lakshadweep Islands rise from a submarine platform with coral reefs in the form of an atoll. It is crescent-shaped having a north-south orientation. The western margin of the lagoon is a submarine bank with a narrow reef below. The lithology is composed of an upper 1–2 m-thick layer of coral rubble, below which is a compact porous crust of conglomerate and soil composed mostly of coral sand. Topography is a flat 1–2 m above sea level. Erosion occurs mostly along the shore towards the northeast and northwest (Anon, 1990).

The Gulf of Mannar extends from Tuticorin to Rameswaram Island in a SW-NE direction and lies between 78°5’ & 79°30’E longitudes and 8°47’ & 9°15’N latitudes, a distance of about 140 km. There are 21 islands between Tuticorin and Rameswaram. All islands are composed of a calcareous framework of dead reef and sand and have a low and narrow sandy coast. Around all offshore islands, well-developed coral reefs occur. Geomorphologically, coral reefs in this area are of fringing type, though some patchy corals are also observed in between Appa Island and Pilliyarmuni Island, and in some areas such as the Bharathinagar coast and the southeast coast of Kariya Shuli Island (Loveson, 1993). Wave cut platforms are common on the coast of Mandapam, Ramaswami Madam, Pudumatam, Valinokkam, etc. Along the coast of the Gulf of Mannar, cliffs occur though at some places these features have been destroyed due to slumping. In the Gulf of Mannar, the slope and width of the continental shelf is approximately the same as the average for the eastern coast of India (Ahmed, 1972). The total width of the shelf is around 30 km having a slope of about 21’. The slope near the shore is about 4’. Recent depth contour maps indicate that the seafloor level decreases along the coast and around the islands due to emergence of the land or lowering of sea level (due to tectonism) and sediment deposition. The beach is gently sloping and marked with altered crests and troughs that are formed due to wave action. As the Gulf of Mannar is on the lee side of the northeast monsoon, there is no long-shore drift from the northeast that might affect the morphology of the spit, (Ahmed, 1972). The southwestern shore of Rameswaram has a tongue shaped spit.

The Andaman and Nicobar Islands are parallel to the arcuate plate boundary separating the Indian and Sunda Plates east of the 9°E ridge (Dasgupta and Mukhopadhyaya, 1993; Rajendran and Gupta, 1989). The ridge is believed to have been formed from sediments scraped off the descending Indian Plate interleaved with ophiolites from the ocean floor beneath the Bengal Fan. In that, the islands are bounded to the east by strike-slip faults and spreading centers, and to the west by a subduction zone, the Andaman and Nicobar ridge acts as a small tectonic plate that has been referred to as the Burma Plate by Curray et al. (1982) and as the Andaman Plate by Dasgupta (1993). The geology of the Andamans is described by Oldham (1884) and Tipper (1911).

A series of earthquakes ranging up to a magnitude of 7.5 under the Andaman and Nicobar Islands on 26 December 2004 shook the entire Andaman Sea region. The end result was that the Burma Plate, which contains the Islands, tilted during an earthquake “swarm” lasting for about 8 min after the major quake off Sumatra. Thus, these islands were a source of the tsunamis that spread out across the Indian Ocean and themselves impacted by tsunamis from the whole series of plate movements on that morning. The effects were very different on the mainland of India to the offshore Andaman and Nicobar Islands.

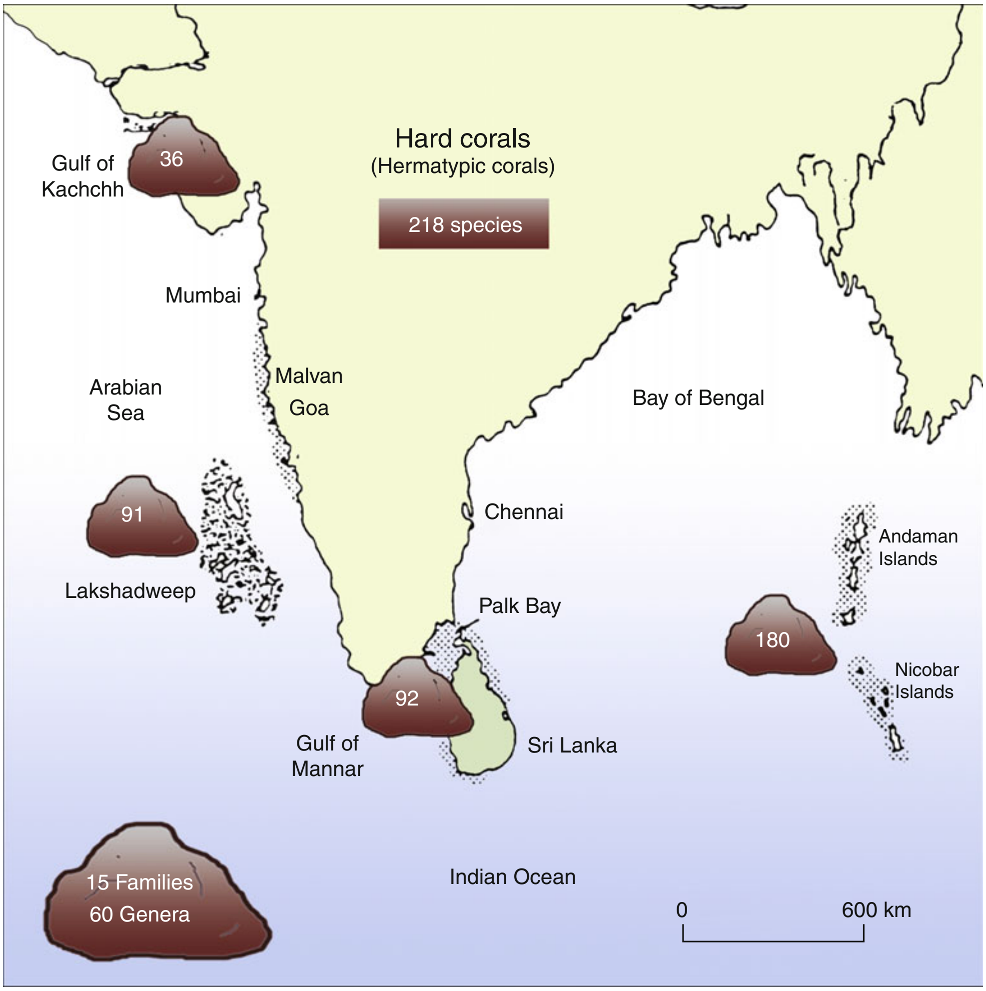
The primary slip offshore of Sumatra was followed by two other slips towards the north. Though some of these findings need to be further substantiated, the fact remains that the Sumatra earthquake caused significant changes to the earth’s tectonic processes (Ortiz and Bilham, 2003). The Andaman and Nicobar area, including Car Nicobar, Katchel, and Campbell Islands were not only affected by the earthquake but also by the tsunami surge. A subsidence of 1–2 m affected the Nicobar Islands with the maximum down-throw at Indira Point near Great Nicobar. Out of the total area of the Nancowry group of islands, 15.64% of the area has undergone major changes. Nearly 6.8% of the area is submerged and 8.9% of area damaged. Maximum change (more than 42%) has been observed in Trinket Island. More than 23% of Katchall and 9% of Camorta and Nancowri and Tarasa groups have undergone major changes. This resulted in a rise in sea-level, inundating the coastal settlements and narrowing the beaches of the islands. Measurements made at Aerial Bay (Diglipur) and Rangat revealed retreat of sea level to the extent of 1.3 m at Campbell Bay, 1.0 m at Chattam Island, 0.8–1.0 m in Aerial Bay and 0.4–0.6 m at Rangat. Land surveys at Diglipur and Mayabunder jetties (North Andaman) confirm a vertical uplift of the land up to 1.2 m from the pre-earthquake levels; exposed piles of the jetties, coral reefs and the receded waterline at these jetties stand as testimony to this change (Figure 3).

The coral reefs of Andaman and Nicobar Islands have been damaged by the impact of the recent tsunami and physical removal of other coral reef associated flora and fauna. The tsunami waves increased the sediment load which has smothered and killed sediment sensitive corals and sea grasses. There is significant contamination of coral reefs and coastal waters by run-off from the land, with large quantities of waste and pollutants, debris, soil, and organic matter. Nesting beaches for the five species of globally threatened marine turtles in the Andaman and Nicobar Islands and on the east coast of India have also been damaged.

Coral reef associated biodiversity

Scleractinian corals

Pillai (1983) recorded a total of 199 species divided among 37 genera, from India, which includes Lakshadweep (78 species), the Gulf of Kachchh (37 species), Palk Bay and the Gulf of Mannar (94 species) and Andaman and Nicobar Islands (135 species) (Figure 2). This account



Coral Reefs of India, Figure 2 Diversity Scleractinia in the major coral reef areas in India.

Coral Reefs of India, Figure 3 The exposed coral reef in the Landfall Island, North Andaman.

includes both hermatypic and ahermatypic corals from the four major coral reefs of India. Venkataraman et al. (2003) identified 15 families, 60 genera and 208 species of Scleractinia (reef building and hermatypic corals) from the four major reefal areas of India such as Gulf of Kachchh (36 species), Lakshadweep (91 species), Gulf of Mannar and Palk Bay (82 species), and Andaman and Nicobar Islands (177 species).

The diversity of scleractinian corals in Gulf of Kachchh is very poor when compared to all the other three major regions of India. Families such as Asterocoeniidae, Pocilloporidae, Euphyllidae, Oculinidae, Agariciidae, Fungiidae, and Trachyphylliidae are totally absent. Species such as *Siderastrea savignayana* and *Acanthastrea hillae* are reported only from Gulf of Kachchh. Twelve families, 34 genera and 91 species are reported from the Lakshadweep Islands. Families such as Astrocoeniidae, Pectiniidae, and Trachyphylliidae are absent. Among the 60 genera recorded in India, only 34 are reported so far from Lakshadweep. Thirteen families, 27 genera and 82 species are reported from the Gulf of Mannar and Palk Bay. From the Andaman and Nicobar Islands, 15 families, 57 genera, 177 species are reported. All the fifteen families reported from India are represented in these islands.

Algae

Marine algae or seaweeds form an important reef resource in India. A recent publication on the compilation of all the new records of marine algae of India shows that benthic marine algal flora of Indian coasts comprises 844 species under 217 genera including forms and varieties (Oza and Zaidi, 2000). Out of these, the maximum number have been recorded from the Gulf of Mannar (302), followed by 202 species from the Gulf of Kachchh, 159 species from the Malvan coast, 89 species from the Lakshadweep group of Islands and 82 from Goa. In India, seaweeds are exploited and used as raw materials for the production of agar, alginates and seaweed liquid fertilizer. Data on seaweed landings in Tamil Nadu from 1978 to 2000 reveal that the quantity (dry wt) extracted in a year during this period varied from 102 to 541 t for *Gelidiella acerosa*, 108–982 t for *Gracilaria edulis,* 2–96 t from *G. crassa,* 3–110 t for *G. foliifera,* and 129–830 t for *G. verrucosa* (Ramalingam, 2000).

Sea grass

Indian coral reefs embrace only 6 genera and 14 species of sea grasses. Distribution of sea grasses along the Indian coast varies with varying species diversity *viz.* Gulf of Mannar 13 species, Gulf of Kachchh and Lakshadweep 7 species and Andaman and Nicobar reefs 9 species (Kannan et al., 1999). All the 6 genera of sea grasses with 11 species are recorded from the Palk bay region. Of the 11 species, *C. serrulata, H. ovalis ovalis, K. pinifolia,* and *S. isoetifolium* are the most widely distributed. Out of the 14 species of sea grasses, nine species occur in the Andaman and Nicobar Islands.

Other marine fauna

Other marine fauna illustrate the great diversity of India's coral reef biota. Some 451 species of sponges from 169 genera have been recorded (Pattanayak and Buddhadeb, 2001). Dominated by Desmospongia, greatest diversity is found in the Gulf of Mannar and Palk Bay. Four turtle species (leather back, Hawksbill, green and Olive ridley) have been observed nesting in the Andaman and Nicobar Islands, (Basker, 1984). Dolphins are common in many areas and dugong in areas of sea grass. More than 1,000 coral reef fish species are found with greatest diversity in the Andaman and Nicobar Islands. There are 3,570 species of marine molluscs (Subba Rao, 1998), almost 3,000 species of Crustacea (Venkataraman and Krishnamoorthy, 1998) and 765 species of echinoderms, 257 in the Andaman and Nicobar Islands alone (James, 1987).

Threats to coral reefs

Coral reef resources have traditionally been a major source of food for local inhabitants and of major economic value in terms of commercial exploitation. The human exploitation of marine resources has increased dramatically over the last few decades for both reasons of commercial and subsistence living. Coral reef ecosystems of India have been exploited for a very long time, but it is only in the last century that the rate of exploitation has increased dramatically due to the increase in the human population. Except for some of the Andaman-Nicobar Islands, no pristine area exists today.

Varied human activities which are a cause for concern over and above the natural disturbances include, runoff and sedimentation from developmental activities (projects), eutrophication from sewage and agriculture, physical impact of maritime activities, dredging, collecting, and destructive fishing practices, pollution from industrial sources and oil refineries and the synergistic impacts of anthropogenic disturbance.

Fishing is a major activity, and at present in the 3,651 fishing villages situated along the 8,129 km coastline of India, about one million are occupied in full time marine capture fisheries. The value of the annual marine fish production of 4.6 m t during the year 2002–2003 and the value of marine products export were US $152.92 m. This is mainly due to the introduction of bottom trawlers, into Indian waters in the early 1960s. Several types of net fishing have also been responsible for the over-exploitation of marine resource. Along with increase in the targeted catch, a number of untargeted fish and other biota are removed from their habitat and discarded as waste (trash fish). Shrimp trawlers probably have the highest rate of by catch bringing in up to 90% more of "trash fish". A total of 1,006 purse seines in India employed for fishing may have the same effect on the seabed as that of the trawl netting. Random capture techniques employed in India destroy immature fish and other non-targeted marine species. Gill nets used to catch fish bring in a host of other animals such as dolphins, turtles, *etc*. Because of the large size of the areas concerned (Gulf of Mannar and Andaman and Nicobar Islands or other areas in India), and the general lack of resources for enforcement, awareness education appears to be more successful than legislation in controlling these activities.

Although now illegal, blast fishing has been a widespread fishing technique in India. Schooling reef fishes are located visually, after which the capture boat moves within close range and a lighted bomb is thrown into the middle of the school. Due to blasting, branching, tabulate and foliose hard corals are shattered while massive and columnar corals are often fractured. Bombs made of chemical fertilizers such as ammonium/potassium nitrate were confiscated from the foreign poachers apprehended in Andaman and Nicobar Islands. Gelatin sticks were observed to be used to blast fish by the fishermen around Gulf of Mannar reefs (Venkataraman et al., 2003).

Sedimentation throughout the coast of India physically interferes with the recruitment of coral larvae, which require a solid substratum upon which to settle and metamorphose. Illegal sand mining in Andaman Islands and illegal coral quarrying in Gulf of Mannar (Tuticorin group of Islands) and some islands of Gulf of Kachchh have caused a lot of sedimentation and siltation on coral reefs.

There has been unprecedented bleaching of hard and soft corals throughout the coral reefs of the world from mid 1997 to late 1998 (Wilkinson, 1998, 2000). Most of the corals in the coral reefs of India have been adversely affected during the bleaching in 1998, which destroyed most shallow water corals. This event has greatly reduced live coral cover in the reef (Venkataraman, 2000). Study conducted after or during the bleaching event reported a reduction in live cover of corals in Gulf of Kachchh (20–40%), Gulf of Mannar (20–40%), Lakshadweep (20–30%) and Andaman and Nicobar Islands (<10%). The live coral cover in Andaman and Nicobar Islands was between 50–75%, which is very high when compared to other reefs in the Indo-Pacific region (Muley et al., 2000, Rajasurya et al., 2002).

In addition to natural and human induced coral degradation, coral diseases are considered to be one of the major problems faced by the coral reefs in recent years. Necrotic lesions, fleshy algal over-growth, black band disease, and white band disease have been reported from the Andaman and Nicobar and Lakshadweep Islands. In addition, a new disease called pink line disease has also been reported recently from Lakshadweep (Ravindran and Raghukumar, 2006).

The coral eating starfish, *Acanthaster planci* was the focus in the late 1980's and early 1990's in the Andaman and Nicobar Islands as well as in other coral reef areas of India (Venkataraman and Rajan, 1995). Although sediment core data have indicated *Acanthaster* outbreaks 10,000 years ago, recent studies have shown a relationship between nutrient input and recruitment success of the larvae. Studies on echinoderm reproduction have demonstrated that the success of the recruitment of their planktonic larvae depends on phytoplankton availability following spawning.

Coral damage from the Tsunami of 26th December, 2004

The major damage to reefs is caused by storms, particularly tropical cyclones and by tsunami. These cause major intermittent damage to reefs, particularly to those reefs that rarely experience these storms. Due to a 1969 cyclone, a large area of coral was buried under sand in the Rameswaram area of the Gulf of Mannar. Likewise, the cyclone of December 1987 in the Bay of Bengal devastated the coral reefs of the Mahatma Gandhi Marine National Park of Port Blair, Andaman that resulted in piles of broken coral colonies scattered near the shore.

A very severe earthquake with a magnitude of 9.0 on Richter scale struck northern Sumatra, Indonesia on 26th December, 2004, and it was widely felt along the east coast of India. In Tamil Nadu, people felt distinct tremors in many parts of Chennai. The quake was also felt along the Coromandel Coast up to some areas in Vizakapatinam. The devastating tidal waves consequent to the earthquake lashed several coastal districts of Tamil Nadu and Puducherry as well as the archipelagos of the Andaman and Nicobar Islands. The Nicobar Islands were most severely hit given their proximity to the island of Sumatra and the epicenter of the earthquake. It is reported that shallow water coral reefs in the Andaman Islands have been exposed 2 m above the water mark (Figure 3) whereas the Nicobar group are submerged 2.0 m below the water mark (Venkataraman, 2006).

Conservation

India has 36 marine protected areas of which 20 are entirely located in intertidal/subtidal or seawater-mangroves, coral reefs, lagoons, estuaries, beaches, etc., and 13 having major parts in marine ecosystem and some part in terrestrial ecosystem (Singh, 2002). The Wildlife Protection Act, 1972 provides protection for these areas and certain marine species. Corals are protected under this act. India's Coastal Regulation Zone Notification (1991) regulates onshore development activities, which affect coastal environments. Coral reef conservation is also included in the Environmental Protection Act (1986), the National Conservation Strategy and Policy Statement on Environmental Development (1992) and the Action Plan of the Ministry of Environment and Forests.

Conclusion

Coral reefs in India have drawn great attention from the eighteenth century onwards. This was achieved from many surveys and expeditions conducted by foreigners, in particular by the British. The introduction of Surgeon Naturalists in the expedition ships helped marine research to flourish in varied fields of fauna and flora. However, in India, major studies have been conducted only on the commercially important organisms such as crustaceans, molluscs, holothurians, and higher vertebrates. Many minor phyla which are not commercially important have not been studied so far. For example, species of different minor phyla that live as the interstitial fauna of coral reef areas have not been studied till date, due to a lack of expertise in this field. Though taxonomy is being taught as a subject in the curricula of schools and colleges, there is no committed institution for the learning of taxonomy except survey departments under the placard of the Government of India. Probably, more than 75% of the biodiversity of coral reefs of the Andaman and Nicobar and Lakshadweep is not yet studied. This is mainly attributed not only to the decline in the number of taxonomists but also due to the lack of facilities. Geological and geomorphological studies are probably even less advanced which is unfortunate given the wide geographical distribution of coral reefs in India.

Bibliography

Ahmed, E., 1972. *Coastal geomorphology of India*. New Delhi: Orient Longman, p. 222.

Anon, 1990. *Coastal area classification and development regulations*. Gazette Notification, Part 11, Section 3 (ii), Govt. of India, No S. C. 595 (FE Desk -1/97), pp. 1–7.

Baskar, S., 1984. The distribution and status of sea turtles in India. In *Proceedings of Workshop on Sea turtle conservation*, Madras, Central Marine Fisheries Research Institute Special Publication, Vol. 18, pp. 21–35.

Bruckner, H., 1988. Indicators for formerly higher sea levels along the east coast of India and on the Andaman Islands. *Hamburger Geographische studien, Heft*, **44**, 47–72.

Curray, J. R., Emmel, F. J., Moore, D. G., and Raitt, R. W., 1982. Structure, tectonics and geological history of the NE Indian Ocean. In Nairn, A. E. M., and Sehli, F. G. (eds.), *The Ocean Basins and Margins, The Indian Ocean*, New York: Plenum, Vol.6, pp. 399–450.

Dasgupta, S., 1993. Seismotectonics and stress distribution in the Andaman Plate. *Memoirs of Geological Society of India*, **23**, 319–334.

Dasgupta, S., and Mukhopadhyaya, M., 1993. Seismicity and plate deformation below the Andaman Arc, northeastern Indian Ocean. *Tectonophysics*, **225**, 529–542.

D. O. D., and S. A. C., 1997. *Coral reef maps of India*. Ahmedabad, India: Department of Ocean Development and Space Application Centre.

James, D. B., 1987. Research on Indian echinoderms a review. *Journal of marine biological Association India*, **25**, 91–109.

Kannan, L., Thangaradjou, T., and Anantharaman, P., 1999. Status of seagrass of India. *Seaweed Research Utilization*, **21**(1&2), 25–33.

Loveson, V. J., 1993. *Geological and geomorphological investigation related to sea-level variation and heavy mineral accumulation along the southern Tamilnadu beaches, India*. Ph.D. thesis, Madurai Kamaraj University, pp. 223.

Muley, E. V., Venkataraman, K., Alfred, J. R. B., and Wafar, M., 2000. Status of coral reefs of India. In *Proceedings of 9th International Coral Reef Symposium*, Bali, Indonesia, 23–27 October, 2000, Vol. 2, pp. 847–854.

Nair, R. R., and Qasim, S. Z., 1978. Occurrence of banks with living corals off the southwest coast of India. *Indian Journal of Marine Science*, **7**, 55–58.

Nair, R. R., and Hashimi, N. H., 1980. Holocene climatic inferences from the sediments of the western Indian continental shelf. *Proceedings of Indian Academy of Sciences*, **B 89**, 229–315.

Oldham, R. D., 1884. Note on the earthquake of 31 December 1881. *Records of Geological Survey of India*, **17**(2), 47–53.

Ortiz, M., and Bilham, R., 2003. Source area and rupture parameters of the 31 December, 1881Mw = 7.9 Car Nicobar earthquake estimated from tsunamis recorded in the Bay of Bengal. *Journal of Geophysical Research*, **108**(B4), 2215. doi:10.1029/2002JB001941, 2003.

Oza, R. M. and Zaidi, S. H. B., 2000. *A revised checklist of Indian marine algae*. India: Central Salt and Marine Chemicals Research Institute, p. 296.

Pattanayak, J. G., and Buddhadeb, M., 2001. Distribution of Marine Sponges (Porifera) in India. In *Proceedings of Zoological Society, Calcutta*, **54**(1), 73–101.

Pillai, C. S. G., 1983. Structure and generic diversity of recent Scleractinia of India. *Journal of Marine Biological Association of India*, **25**(1&2), 78–90.

Pillai, C. S. G., 1986. Recent corals from the southeast coast of India. In *Recent Advances in marine Biology*, New Delhi: Today and Tommorow Publishers, pp. 107–201.

Pillai, C. S. G., 1996. Coral reefs of India, their conservation and management, In Menon, N. G., and Pillai, C. S. G. (eds.), *Marine Biodiversity, Conservation and Management*, Cochin: Central Marine Fisheries Research Institute, pp. 16–31.

Qasim, S. Z., and Wafar, M. V. M., 1979. Occurrence of living corals at several places along the west coast of India. *Mahasagar*, **12**, 53–58.

Rajasurya, A., Zahir, H., Muley, E. V., Subramanian, B. R., Venkataraman, K., Wafar, M. V. M., Khan, S. M. M. H., and Whittingham, E., 2002. Status of coral reefs in South Asia: Bangladesh, India, Maldives, Sri Lanka. In *Proceedings 9th International Coral Ref Symposium*, Bali, Indonesia 23–27 October 2000, Vol. 2, pp. 841–846.

Rajendran, K., and Gupta, H. K., 1989. Seismicity and tectonic stress-field of a part of the Burma-Andaman-Nicobar Arc. *Bulletin of Seismology Society of America*, **79**, 989–1005.

Ramalingam, J. R., 2000. Production of export quality of agar. *Goldern Jubilee Celebrations Souvenir 2000*, Mandapam R. C. of CMFRI, Mandapam Camp., pp. 81–83.

Rao, V. P., and Wagle, B. G., 1997 Geomorphology and surficial geology of the western continental shelf and upper slope of India: A review. *Current Science*, **73**, 330–350.

Ravindran, J., and Raghukumar, C., 2006. Pink-line syndrome, a physiological crisis in the scleractinian coral *Porites lutea*. *Marine Biology*, **149**(2), 347–356.

Singh, H. S., 2002. *Marine protected areas in India Status of coastal wetlands and their conservation*. Gandhihagar, Gujarart: GEER Foundation, pp. 62.

Subba Rao, N. V., 1998. Mollusca. In Director, (ed.), *Faunal Diversity in India.* Kolkata: Zoological Survey of India, pp. 104–117.

Tipper, G. H., 1911. The geology of the Andaman Islands. *Memoirs of Geological Survey of India*, **35**, 4.

Turner, J. R., Vousden, D., Klaus, R., Satyanarayana, C., Fenner, D., Venkataraman, K., Rajan, P. T., and Subba Rao, N. V., 2001. Report of Phase I: Remote sensing and Rapid Site Assessment Survey, April 2001. In *Report on Coral Reef ecosystems of the Andaman Islands, Government of India and United National Development Programme, Global Environment Facility*, pp. 76, with 8 Appendices and 55 Figures and Plates.

Venkataraman, K., 2000. Status survey of the Gulf of Mannar coral reefs following the 1998 bleaching event, with implications for reserve management. In *Proceedings 9th International Coral Ref Symposium*, Bali, Indonesia, 23–27 October 2000, Vol. 2, pp. 841–846.

Venkataraman, K., 2003. *Natural Aquatic Ecosystems of India, National Biodiversity Strategy Action Plan, Thematic Biodiversity Strategy and Action Plan*. Zoological Survey of India, Kolkata, pp. 1–272.

Venkataraman, K., 2006. Impact of the recent tsunami on the marine biodiversity of India. *ENVIS News Letter Zoological Survey of India, Kolkata*, **12**(1&2), 5–11.

Venkataraman, K., and Alfred, J. R. B., 1998. Coral reefs. In Alfred J. R. B., Sanyal, A. K., and Das, A. K. (eds.), *Faunal Diversity in India*. Kolkata: Zoological Survey of India, pp. 391–395.

Venkataraman, K., and Krishnamoorthy, P., 1998. Crustacea. In Alfred, J. R. B., Sanyal, A. K. and Das, A. K. (eds.), *Faunal Diversity in India*. Kolkata: Zoological Survey of India, pp. 133–144.

Venkataraman, K., and Rajan, P. T., 1995. Coral reefs of Mahatma Gandhi Marine National Park and crown-of-thorn starfish phenomenon. In Gangwar, B., and Chandra, K. (eds.), *Proceedings of Island Ecosystem and Sustainable development*, Port Blair: Andaman Science Association and Department of Science & Technology, pp. 124–132.

Venkataraman, K., Satyanarayana, C. H., Alfred, J. R. B., and Wolstenholme, J., 2003. *Handbook on Hard Corals of India*. Kolkata: Zoological Survey of India, pp. 1–266.

Vora, K. H., Wagle, B. G., Veerayya, M., Almeida, F., and Karisiddaiah, S. M., 1996. 1300 km long late Pleistocene-Holocene shelf edge barrier reef system along the western continental shelf of India: Occurrence and significance. *Marine Geology*, **134**(1–2), 145–162.

Wilkinson, C. (ed.), 1998. *Status of Coral Reefs of the World: 1998*. Townsville, Australia: Australian Institute of Marine Science, Web version: http://www.aims.gov.au/scr1998.

Wilkinson, C. (ed.), 2000. *Status of Coral Reefs of the World: 2000*. Townsville, Australia: Australian Institute of Marine Science.

Cross-references

Eastern Indian Ocean – Northern Sector
Indian Ocean Reefs
Maldives
Tropical Cyclone/Hurricane
Tsunami
Western Indian Ocean

CORALS: BIOLOGY, SKELETAL DEPOSITION, AND REEF-BUILDING

John E. N. Veron
Oak Valley, Australia

Definition

Scleractinian corals (Phylum Coelenterata, Class Anthozoa, Order Scleractinia – the true stony corals alive today) have been building coral reefs for 250 million years, reefs that are the biggest structures ever made by living organisms.

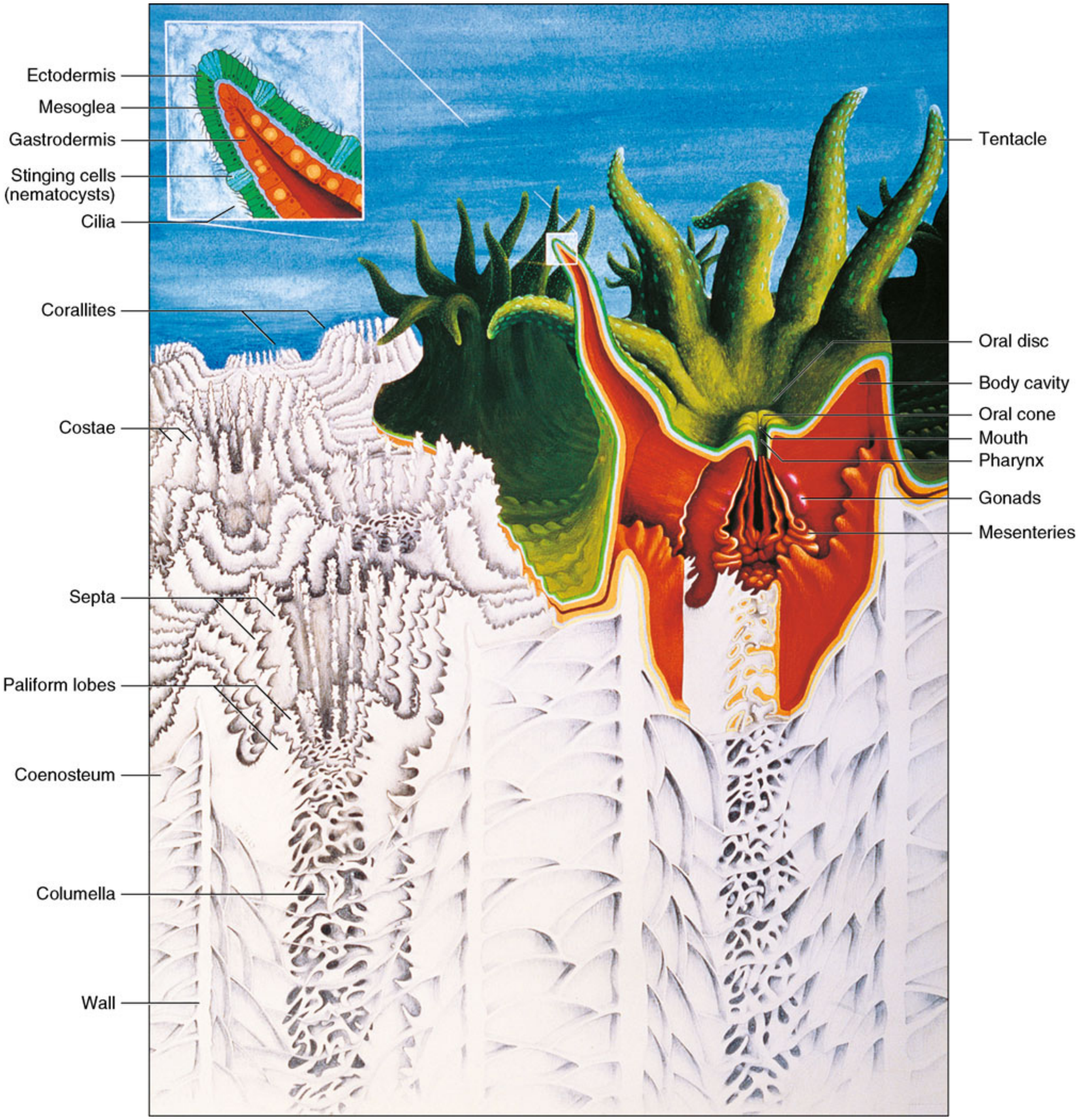
Introduction

Scleractinian corals have a simple structure. Their bodies are sac-like polyps that usually grow together to form colonies. They have a body wall with only two cell layers and a skeleton made of calcium carbonate which is actually outside their body so that the living polyp grows on its skeleton (Figure 1). This simple structure allows most corals to form complex colonies that are readily modified to suit a wide range of environments. Modern coral reefs are principally made of calcium carbonate that has been derived from coral skeletons and cemented into a wave-resistant structure by coralline algae (see *Coral Reef, Definition*). Whereas coralline algae generally have a wider distribution range than corals, both flourish in shallow, turbulent, well-lit environments, which is where highly consolidated reefs best grow. Growth rates of coral colonies and of reefs are very different and are discussed below: coral growth rate is a result of each colony's individual physiological performance within its particular environmental setting and reef growth is a net outcome of history, hydrodynamics, ecosystem processes, and the functional roles of various guilds of species – both constructive and destructive. Moreover, there is wide diversity of entities referred to as "reef," with the contribution of corals likewise varying in importance: these are reviewed briefly here.

Reefs and coral reefs

The term "reef" can mean different things to different people. To most geologists and palaeontologists, reefs are rock formations. To most biologists, reefs are a veneer of living organisms forming an ecosystem, which is both complex and fragile. These two concepts of reefs can seem as remote from each other as forests are from coal deposits, yet they share a common past. Reefs, the geological structures, are the direct products of living ecosystems and as such their formation has always been controlled by the sorts of events that control other ecosystems, both marine and terrestrial.

When considering ancient reefs, it is important to distinguish these "reefs" from the "coral reefs" of today. Corals are not the main builders of all reefs: many ancient reefs, especially those of the Palaeozoic, were not built just by corals but by a wide array of other taxa including



Corals: Biology, Skeletal Deposition, and Reef-Building, Figure 1 The general structure of a coral polyp and underlying coral skeleton (After Veron, 2000).

algae, sponges, and molluscs. In many Palaeozoic reefs, sponges rather than corals were the dominant builders and in some late Mesozoic reefs, the same role was played by molluscs (rudist bivalves).

Even modern reefs are not necessarily coral dominated. Some, forming intertidal structures in the Caribbean and Bermuda, are made by vermetid "worms" (molluscs). There are also widespread subtidal structures dominated by serpulid worms (annelids) and odd reefs everywhere owe their existence to other organisms, especially oysters. However, in terms of quantity, the reefs dominated by organisms other than scleractinian corals and their allies (including a few small taxa such as the blue coral Heliopora and the fire coral Millepora) are insignificant and have little in common with coral reefs other than in the material of which they are made. Such structures excluded, the term "coral reef" still needs constraining, for some deep ocean corals form extensive structures, built by one type of coral (Lophelia). These are commonly called reefs, but they have none of the characteristics of coral reefs as geological structures (they do not form solid limestone) or as biological structures (they do not depend on photosynthesis nor are they biologically diverse).

There is one further distinguishing characteristic of coral reefs: although they are principally made of calcium carbonate derived from coral, coral skeletons need to be cemented into solid rock by coralline algae. Coralline algae generally have a wider distribution range than corals, but those that cement coral debris into reefs flourish in shallow, turbulent, well-lit environments and thus it is they as much as corals that determine where highly consolidated reefs best grow. They may also have a dominant influence on how fast they grow or if they grow at all in deeper water.

Reef carbonates

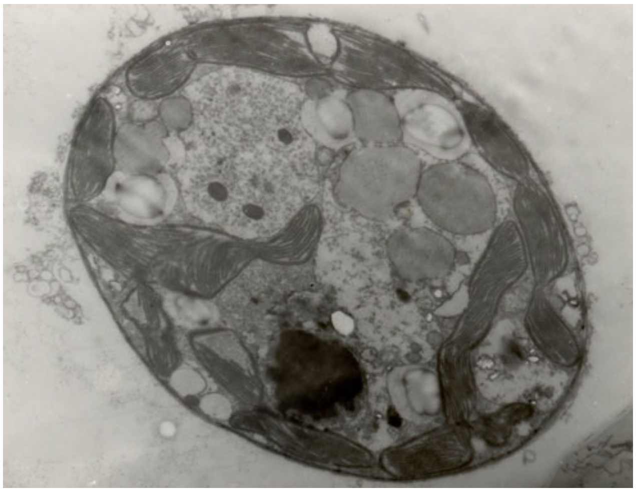
Although most (90–95%) of terrestrial limestone is derived from reefs built by a variety of animals in shallow marine environments, this by no means reflects the principal source of carbonates on Earth. Around 90% of all today's marine carbonates are deep-sea sediments derived primarily from plankton (mostly foraminifera and coccolithophores). Due to their deep water location, these are rarely uplifted to form geological rock formations on land; rather they are either dissolved in the ocean or subducted into the Earth's mantle. Another 5% of carbonates are of mixed composition and are found on continental slopes. In a few regions, these carbonates have been consolidated and uplifted or otherwise exposed on land.

Perhaps surprisingly, only 5% of all carbonates today are of coral reef origin although this small proportion includes vast tracts of mountain slopes like the calcareous reefs of Austria. The proportion of total carbonates which are represented by living reefs is much less than 1%. Nevertheless, this small proportion is all important.

Reef building

If corals grow in sufficient quantity, and the rate of both skeleton production (calcification) and algal cementation exceeds that of erosion, the resulting accumulation of calcium carbonate can form limestone reefs. The success of the process depends on speed, which is why reef-building corals enlist symbiotic algae (zooxanthellae, Figure 2) to harness the energy of the sun to power the process. This begs the question, why do these organisms put so much metabolic effort into reef-building? After all, no other ecosystem in all Earth's history puts anything like as much energy, or such evolutionary focus, into building anything that is dead.

One answer lies in the purpose of skeleton building. Only corals that build reefs have large, three-dimensional, wave-resistant skeletons. This capacity has been achieved by removing the limitations of individuals and replacing them with a wider range of options offered by the formation of colonies (groups of individuals formed asexually and which grow in unison). The implication is that skeletons are needed to form colonies and that colonies are needed to build large wave-resistant structures.



Corals: Biology, Skeletal Deposition, and Reef-Building, Figure 2 An electron microscope image of a zooxanthella. This tiny cell, 10 μm in diameter, has all the structural components of a typical algal cell (Electron microscope image: Ove Hoegh-Guldberg).

The two evolutionary innovations of colony formation and algal symbiosis clearly go together and have very likely evolved together. The importance of this is demonstrated by the fact that most Cnidaria involved in reef-building are both colonial and symbiotic. The two major groups of extinct reef-building corals (rugose and tabulate corals) are also colonial; however, it is not known if they were also symbiotic.

Coral reefs are ecosystems, which mean that they are not just aggregations of individual species competing with each other for survival, but rather groups of species living cooperatively for joint survival. Certainly individual species compete; however, a level of selection takes place which is higher than the selection of species. From a Darwinian perspective, this might be called "selection for survival of the fittest ecosystem" as opposed to selection for the fittest species. Where there is a close symbiosis between two species, the evolutionary success of one species is dependent on that of the other: natural selection acts on the partnership, not the species. A coral reef has hundreds of such interdependencies, resulting in a complex coevolution of subcomponents and entire ecosystems.

This introduces the concept of guilds (Bellwood et al., 2004), where each guild is a functional unit whose task is undertaken by a group of species or individuals. All coral reefs have many guilds including corals (to produce building blocks), coralline algae (to cement the blocks together), herbivores (to prevent macroalgae from taking over), and photosynthetic algae (to provide food). There are also less prominent guilds, forming a hierarchy down to less conspicuous tasks such as parasite control, sediment mixing, and nutrient cycling. The essential point about guilds is that they are functional units selected for because they perform functions efficiently. It matters little what species perform the function, only that they do it with the necessary speed.

Corals are the most prominent reef-builders today because, with their zooxanthellae, they can harness the energy of sunlight to make building blocks sufficiently quickly to outstrip erosion. This is not to say that all zooxanthellate corals contribute to reef-building; perhaps half of all species make no significant contribution to reefs at all for they do not grow in environments suitable for reef growth, especially where the water is too turbid or too cold or where there is limited hard substrate, or because their skeletons are fragile and are easily removed by wave action.

The reason why corals build reefs has as much to do with the physical environment as with organisms: it is a matter of ecology.

Light

Reef-building corals depend on photosynthesis for they use the unlimited resources of solar energy and air to produce food. However, about half of all Scleractinia (the azooxanthellate species) do not have symbiotic algae. Some azooxanthellate corals live on coral reefs, especially under overhangs or in caves, but with the exception of a few species that are both symbiotic and nonsymbiotic, all zooxanthellate corals need light, and it is only these taxa that build reefs. As a result, reefs are restricted to shallow sunlit waters. Azooxanthellate corals are not limited by light or by temperature, nor are they confined to shallow sunlit water; they live in the ocean depths where there is less competition for space. Therefore, they cannot build reefs and must live without food from photosynthesis: food can only come from detritus and the chance of capturing passing plankton.

Algal symbiosis

Symbiosis, the interdependence of different organisms for the benefit of one or both participants, is much more prevalent in the oceans than on land. Within the spectrum of symbioses, zooxanthellae clearly have a special place. They are not just found in Scleractinia; they occur in other cnidarians (soft corals, anemones and their allies) as well as in an assortment of other animals including single-celled ciliated protists, sponges, flatworms, and molluscs (including giant clams). Once thought to be a single species, zooxanthellae have been found to be genetically diverse (consisting of many genetic types or “clades”) (Trench, 1979; Rowan and Powers, 1992), even though under a microscope they all look much the same (Figure 2). They can all live independently, although not in such concentrated numbers nor with such long-term security as they can live in the tissues of hosts. In the case of corals (but not clams), they live inside the cells of the host organisms – in the innermost (gastrodermal) layer of the two cell layer body wall (illustrated above). All zooxanthellae are tiny, around one hundredth of a millimeter in diameter. Seldom does more than one occur in a single gastrodermal cell.

Zooxanthellae photosynthesize as do other green plants, releasing up to 95% of the nutrients they produce to the host organism (Muscatine, 1990). This is a curious arrangement because most corals are voracious feeders on zooplankton and therefore have two very different food sources. Nevertheless, many if not most corals that are kept in darkness (so that their zooxanthellae cannot photosynthesise) will start to die after a few months no matter how much food they have. Somehow, the zooxanthellae have made themselves indispensable. Just how or why remains unresolved.

In brief, important points about algal symbiosis are as follows (Hoegh-Guldberg, 1999 and many subsequent articles). Corals acquire their zooxanthellae either directly from the parent colony or through infection of free-swimming or newly settled larvae. Uptake of nonparental zooxanthellae in early life may be by random chance, giving different advantages to different colonies: some colonies might be infected with temperature-tolerant symbionts, others with more productive ones (this hypothesis has yet to be confirmed). Zooxanthellae readily change in abundance depending on conditions such as season, position on the coral, and light level. More than one genetic type of zooxanthellae can occupy a single colony. The abundance of genetic types varies geographically on any scale (Ulstrup and Van Oppen, 2003) and some genetic types facilitate a faster growth rate than others (Little et al., 2004).

Water depth, turbidity, and latitude

Any factors which alter light in the marine environment will have a significant effect on calcification rates and reef development. Depth is a primary constraint as only a few zooxanthellate corals live below 100 m, even where the water is very clear and the substrate does not slope so steeply that it is shaded. Leptoseris commonly forms extensive beds to at least 160 m in the Red Sea and Hawaii, and there are several records of moderately diverse coral communities at depths of over 100 m elsewhere, including the outermost reef faces of the GBR.

Turbidity has a dominant role to play in controlling light levels in all except clear-water habitats. Where the water is not very clear, as is the case with most reefs near major land masses, coral diversity drops off sharply at depths below about 50 m. Where the water is particularly muddy, the depth limit for any coral can be as little as 5 m. Turbidity, especially that caused by fine clay particles which are easily resuspended by wave action, has other effects on corals besides reducing light.

Latitude also has an effect on light availability, much more in the ocean than on land due to the refraction of sunlight as it enters water. The higher the latitude the shallower coral communities must be in order to have adequate light. This is of less consequence today than in past geological intervals when waters were warm enough for reef-building to occur at high latitudes, even as far as the Arctic and Antarctic circles.

Temperature

Temperature, in synergy to some extent with light, sets limits on the latitudinal spread of corals throughout the world. A different temperature constrains the spread of reefs. The difference between these two – constraints on corals and on reefs – has created havoc in palaeoclimatic reconstructions of past reef environments as well as studies of reef growth because it is so widely misinterpreted.

Low-temperature limits to reef growth

It has been known for decades that reefs do not form where the ocean temperature regularly goes below 18°C for intervals of weeks to months. Reef geologists concerned with the history of reefs refer to this well-established fact, yet in so-doing they often assume that lower temperatures kill corals. This is seldom the case.

As noted above, reef-building allows entire ecosystems to exist, a process that can only happen if rampant growth of macroalgae is held in check (Crossland, 1988). This requires a great deal of uninterrupted energy, which is why reef-building corals are so dependent on symbiotic algae. We have also seen that this symbiosis requires exposure to sunlight, which means living in shallow water. Around 18°C corals are able to produce calcium carbonate fast enough to fulfil their guild role as producers of building materials. They are able to do this not by growing faster than algae, but by creating three-dimensional habitats where herbivores, especially fish, can control algae for them. At lower temperatures, algae usually get the upper hand; however, the corals themselves are not affected by temperatures lower than 18°C. This is best seen along the Ryukyu Islands of Japan where the southern islands have extensive reefs, yet further north the sea temperature progressively decreases until it reaches the critical 18°C point. It is here that reef development fails. The corals, however, do not: nearly half of all coral species regularly tolerate prolonged exposure to 14°C (Veron and Minchin, 1992). A few tolerate 12°C although seldom less (azooxanthellate corals excepted).

High-temperature limits to reef and coral growth

Low- and high-temperature limits do not mirror each other. Oceans can cool until they freeze, yet they cannot warm much beyond the peak temperatures we see today (around 31°C). This is because evaporation holds the upper limit in check, at least it does for extensive areas of ocean. Smaller bodies of water are less constrained, thus, reef lagoons can get at least 5°C warmer than this. Nevertheless, high temperature per se has little direct negative effect on corals. The warmer the water the faster most metabolic processes become and the faster calcification could become if it were not for its effect on zooxanthellae. Faster metabolic rates for zooxanthellae mean faster photosynthesis, which in turn can result in oxygen being produced at rates where it becomes toxic. Corals are forced to expel their increasingly poisonous zooxanthellae and "bleach" in response to temperature and light acting in concert.

High-temperature limits of coral growth and reef growth are approximately the same as they are both linked to the upper limit of the ocean. This link is an evolutionary one and appears to have always existed for there is no interval in geological time where high temperature has excluded reefs from equatorial regions.

Substrate, turbulence, and mechanical effects

Substrate type and water clarity are always closely linked, especially when depth and turbulence are factored in. White calcareous sand, although typically coarse-grained, is light and therefore readily moved around by wave action, in which case it is capable of burying corals if suspended in sufficient quantity. However, it is clay from rivers that adversely affects corals, for not only does it attenuate light, but it also requires cleaning, a costly activity in terms of metabolic energy.

Substrate is also of paramount importance to settling larvae, for these will not settle on sand of any sort, or on substrates that are coated with bacterial slime, as it commonly develops on reefs that have been degraded.

One very obvious effect of turbulence on coral skeleton formation is that wave action produces dense skeletons. Corals in a high-energy environment grow dense skeletons, whereas those in protected areas have light, brittle skeletons. This is partly because of the differences in species that occupy these habitats, yet even within the same species this effect is pronounced.

Water quality

The term "water quality" is commonly used in connection with the health of the marine environment. Water quality that is good for particular coral reefs or coral communities is assumed to have tolerable levels of sediments and nutrients and environmental contaminants.

Salinity is an aspect of water quality that has not been adequately studied. Corals appear to be sufficiently tolerant of high salinity that lethal levels seldom, if ever, occur naturally. The opposite commonly applies to low salinities, for these play a large role in creating areas where there is little or no coral or reef growth.

There are other environmental controls on reef-building hidden in water chemistry that may not overtly limit reef distribution today but which may have been important in the geological past and are destined to become so in the near future. Oceans are normally so well buffered that chemical changes are infinitesimally slow, providing plenty of time for organisms to evolve adaptations to any alteration. However, sometimes the rate of change exceeds physical or biological thresholds and cannot be tolerated by any except the most specialised organisms. This can happen when large tracts of ocean become anoxic, hydrogen sulphide concentrations become toxic, pH alters beyond tolerable limits for calcification, or other contaminants make the water uninhabitable.

Rates of growth and erosion

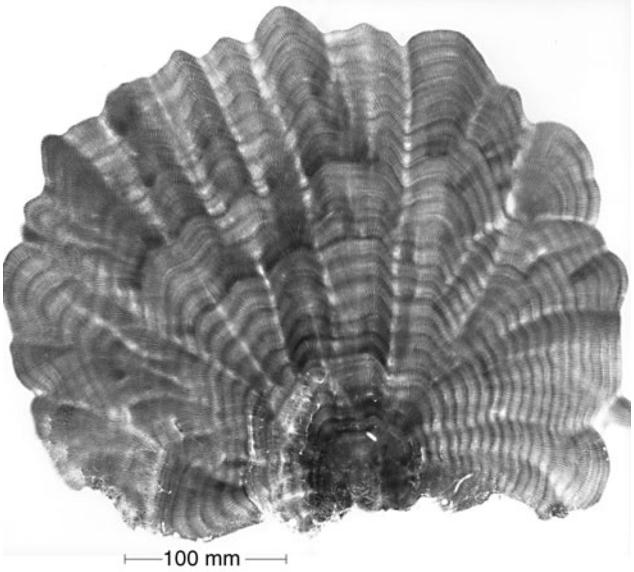
Growth rates of coral colonies and of reefs are very different subjects because (1) reefs are made of a much denser material than are coral skeletons, (2) there are gaps between coral colonies that must be in-filled to make solid limestone and (3) reef accretion is the rate of growth minus the rate of erosion – the latter is commonly greater, especially in marginal habitats. This is the main reason why reefs do not form wherever coral grows.

Coral growth rates

The much-studied coral *Porites* forms large hemispherical colonies which typically grow (radially) at a rate of around 1 cm per year as determined by X-rays of thin slices (Figure 3). Some more heavily calcified colonies of other corals grow at slower rates than this, although most are faster. Staghorn *Acropora* readily grows (linearly) up to about 30 cm per year. Plate-forming Acropora also grows (in diameter) up to about 30 cm per year.

Reef growth rates

Rates of growth of reefs (accretion) can be measured directly from cores taken from reefs or by a wide range of indirect measures of carbonate production (Vecsei, 2004). Normally, the maximum rate of reef growth is about 0.6 m per century (Smith, 1983), although rates in optimal conditions may reach three times this (Montaggioni, 2005; Hopley et al., 2007). These optimal conditions only occur where the water is shallow and clear and currents are strong, the probable reason why continuous areas of reefs (where there is more reef than open ocean) occur only where the tidal range is great and the ocean floor is shallow. These environments provide high light levels combined with continuous flushing and nutrient transport.



Corals: Biology, Skeletal Deposition, and Reef-Building, Figure 3 Growth bands in corals such as seen in this X-ray of a slice of Porites are the marine equivalent of growth rings in trees. They not only allow detailed measurements of growth rates, but can also reveal much about the environment in which the coral grew, including temperature and salinity (X-ray image: Janice Lough).

Rates of reef erosion

There are no reliable estimates of rates of reef erosion because they are too slow to be directly measurable. Best estimates suggest that around 90% of all calcium carbonate produced by coral calcification is removed by erosion. There are four main mechanisms of reef erosion: physical erosion, enhanced chemical erosion, bioerosion, and rainwater dissolution.

1. Physical erosion leads to the formation of channels seen in most reefs due to the action of waves moving rubble back and forth. These channels typically develop into "spur and groove" structures common along most reef fronts exposed to strong wave action. On a bigger scale, erosion caused by tidal currents may produce "deltaic patterns," so named because they resemble river deltas.
2. Changes in ocean chemistry which affect the stability of skeletal material can have a significant effect on the balance of reef accretion and erosion. Ocean acidification, predicted to occur during the present century, will bring this subject to the forefront.
3. Bioerosion is a greatly underrecognized process, yet can be very active in shallow water where it not only erodes the limestone surface but also prevents the growth of newly recruited corals and coralline algae on available substrates. Over thousands of years, the actions of many types of bioeroders, such as the urchins, would probably be capable of keeping pace with slow sea-level falls, or successions of slow falls, and therefore would leave no reef exposed above high tide level. There are many studies of the rate at which different organisms (such as sponges, urchins, limpets, chitons, and parrot fish) ingest limestone (typically up to 18 cm^3 per animal per year for intertidal invertebrates such as sea urchins); however, these cannot be reliably translated into rates at which these animals might plane-off whole reef surfaces.
4. Rainwater dissolution commonly results in "rill weathering," a process that creates interlocking knife-like edges on the surface of limestone outcrops. Depending on the chemical composition of the limestone, some aerially exposed reefs last much longer than others, as evidenced by the ancient reefs that remain intact today.

An important point about these forms of erosion are that the first three occur only when reefs are submerged, while the fourth occurs only when reefs are exposed to the air, either by uplift of the land or by falls in sea level.

Summary

The subject of coral skeleton formation has two separate aspects, reef building and coral growth. Reefs are both geological structures and living ecosystems. Corals are often not the primary builders of Palaeozoic reefs, thus the terms "reefs" and "coral reefs" are not necessarily interchangeable terms in geological contexts. However, scleractinian corals are the builders of most Mesozoic and Cenozoic reefs. The environmental controls on both are similar, not necessarily the same.

The two great scleractinian innovations of colony formation and algal symbiosis allow corals to build reefs. These are closely linked, both functionally and in evolutionary terms. Light and temperature are the dominant parameters.

Light availability is critical for reef-building because of the dependence of corals on algal symbiosis. In turn, light availability is regulated by water depth, turbidity and (in geological time) latitude.

Temperature limits the latitudinal distribution of reefs and constrains the rate of skeleton formation. For ecological reasons, reef formations are limited to oceans that do not cool below 18°C for extended periods of time. However, most corals can grow where temperature commonly falls to 14°C. High-temperature limits to both reef growth and corals are similar, approximately 31°C.

Rates of coral and reef growth are very different. Rates of coral growth vary enormously according to the type of colony formation. Rates of reef growth are dependent on rates of erosion. This occurs by four processes, physical erosion, changes in water chemistry, bioerosion and rainwater dissolution.

Bibliography

Bellwood, D. R., Hughes, T. P., Folke, C., and Nyström, M., 2004. Confronting the coral reef crisis. *Nature*, **429**, 827–833.

Crossland, C. J., 1988. Latitudinal comparisons of coral reef structure and function. In *Proceedings of the Sixth International Coral Reef Symposium*, Vol. 1, pp. 221–226.

Hoegh-Guldberg, O., 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research*, **50**, 839–866.

Hopley, D., Smithers, S. G., and Parnell, K. E., 2007. *The Geomorphology of the Great Barrier Reef: Development, Diversity and Change*. Cambridge, UK: Cambridge University Press.

Little, A. F., van Oppen, M. J. H., and Willis, B. L., 2004. Flexibility in algal endosymbioses shapes growth in reef corals. *Science*, **304**, 1492–1494.

Montaggioni, L. F., 2005. History of Indo-Pacific coral reef systems since the last glaciation: development patterns and controlling factors. *Earth-Science Reviews*, **71**, 1–75.

Muscatine, L., 1990. The role of symbiotic algae in carbon and energy flux in reef corals. In Dubinsky, Z. (ed.), *Ecosystems of the World*. Amsterdam: Elsevier, pp. 75–87.

Rowan, R., and Powers, D. A., 1992. Ribosomal RNA sequences and the diversity of symbiotic dinoflagellates (zooxanthellae). *Proceedings of the National Academy of Science USA*, **89**, 3639–3643.

Smith, S. V., 1983. Coral reef calcification. In Barnes, D. J. (ed.), *Perspectives in Coral Reefs*. Townsville: Australian Institute of Marine Science, pp. 240–247.

Trench, R. K., 1979. The cell biology of plant–animal symbosis. *Annual Reviews of Plant Physiology*, **30**, 485–531.

Ulstrup, K. E., and Van Oppen, M. J. H., 2003. Geographic and habitat partitioning of genetically distinct zooxanthellae (Symbiodinium) in Acropora corals on the Great Barrier Reef. *Molecular Ecology*, **12**, 3477–3484.

Vecsei, A., 2004. A new estimate of global reefal carbonate production including the fore-reefs. *Global and Planetary Change*, **43**, 1–18.

Veron, J. E. N., 2000. *Corals of the World*. Australia: Australian Institute of Marine Science, Vol. 1.

Veron, J. E. N., and Minchin, P. R., 1992. Correlations between sea surface temperature, circulation patterns and the distribution of hermatypic corals of Japan. *Continental Shelf Research*, **12**, 835–857.

Cross-references

Acropora
Algae, Coralline
Algae-Macro
Aragonite
Coral Reef, Definition
Corals: Environmental Controls on Growth
Ecomorphology
General Evolution of Carbonate Reefs
Ocean Acidification, Effects on Calcification
Sediment Durability

CORALS: ENVIRONMENTAL CONTROLS ON GROWTH

Terry Done
Australian Institute of Marine Science, Townsville, QLD, Australia

Definitions

Coral growth: The establishment, survival, and increase in size of living zooxanthellate corals as individuals, populations, and communities.

Coral calcification: The biological process of the synthesis of calcium carbonate by corals. Its rate is reported in gm cm^{-2} year^{-1}. A given rate of calcification is manifest in a coral skeleton as its rate of linear extension (cm year^{-1}) of a particular density (gm cm^{-3}).

Environment: The physical, chemical, nutritional, and ecological milieu in which corals grow.

Microenvironment: "Environment" impinging upon an individual coral in situ.

Introduction

Corals grow vigorously and build reefs in shallow tropical seas, due to the favorable environment, both "latitude-correlated environmental factors" (Veron, 1995) and factors that are not related to latitude. The latitude-correlated environmental factors are solar radiation, temperature, and water chemistry (Kleypas et al., 1999), and those not related to latitude include nature and depth of the substratum, wave climate, salinity, water clarity, nutritional properties of that water, and sedimentation regime. Collectively, they affect growth rate, growth form, reproduction and longevity of individual corals, the trajectories of abundance, size and age-frequency distribution and turnover rates of populations, and the composition and diversity of coral communities. These population and community attributes in turn influence the frequency and amounts of calcium carbonate skeletons that can be delivered to, and accumulate in, reef-building units (framework, boulders, blocks, rubble, and sand) – i.e., contribute to the growth of maintenance of a coral reef and adjacent sedimentary deposits against disaggregating forces of waves, currents, and gravity in shallow tropical seas.

Just as important as the normal fair-weather environment in determining a coral community's extent and structure are the legacies of their history of development, disturbance, and recovery. Coral communities (see *Coral Reef, Definition*) are all works in progress – outcomes of the timing and makeup of successive settling cohorts of coral propagules (larvae and fragments) and a long list of species-specific differences among corals: their performance in competition with other benthic organisms trying to occupy the same piece of substratum (corals, other sessile invertebrates, and algae); attractiveness or resistance to predators and diseases; susceptibility to breakage or dislodgement by storms; propensity to collapse under their own top-heavy weight and fall off the reef into inhospitable depths; propensity to be dislodged, swept, rolled, or pushed from the area by waves and currents.

Coral: the animal–plant symbiosis

Underpinning the coral vigor that builds reefs in tropical seas is the presence of hundreds of thousands of "zooxanthellae" (single-celled dinoflagellate algae in the genus *Symbiodinium*) within every square centimeter of the coral's tissues (Fagoonee et al., 1999; Fitt et al., 2000). Corals that host zooxanthellae are referred to as "zooxanthellate" corals. Within its diurnally and seasonally variable external environment, the coral needs to provide an internal environment that nurtures the zooxanthellae. Whereas corals generally live for decades to centuries, the zooxanthellae populations and coral tissue in which they reside turn over on time scales of weeks to months (Fitt et al., 2000). Under extreme environmental stress, the coral's internal environment can become inhospitable and zooxanthellae populations may crash and the coral tissue get damaged, leading to injury or death of entire coral colonies across vast areas (see *Climate Change and Coral Reefs*).

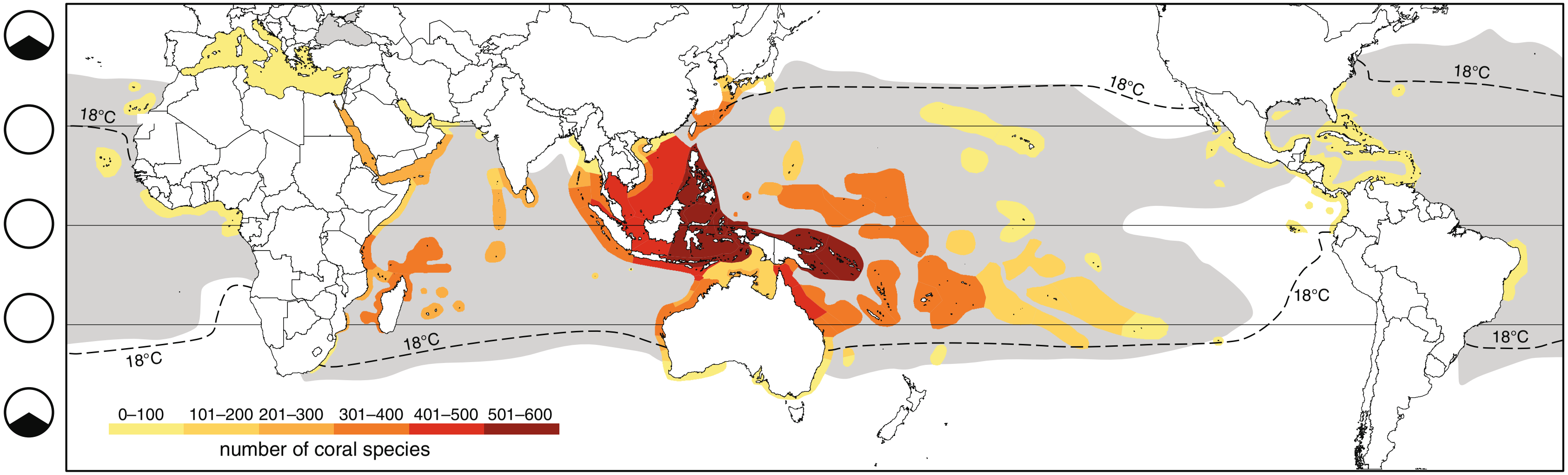
Within coral's favored environment, the symbiotic arrangement between the coral "host" and its zooxanthella "symbiont" provides such a hospitable intracellular environment for the symbionts that their photosynthesis produces a massive surplus of energy-rich compounds (Gattuso et al., 1999). These are used by the coral polyps to fuel their replication and to deposit their shared skeleton. The rate of calcification (see Definition above) in zooxanthellate corals far exceeds that which is possible in cnidarians that lack zooxanthellae: their presence drives "light-enhanced" calcification (Goreau and Goreau, 1959). However, one decade into the twenty-first century, the coral–zooxanthellae symbiosis, in existence since the Tertiary and critical for the development of coral reefs (Stanley and Swart, 1995), faces increasing incidence and severity of both sublethal stresses and lethal extreme events. Recent reviews of implications of global climate change for corals and reefs include Done (1999); Buddemeier et al. (2004); Chadwick-Furman (2006); Kleypas and Langdon (2006); Guinotte and Fabry (2008); and Veron (2008). See also below in this article and the Chapter on *Climate Change*.

Environmental controls on global distribution of corals

Today's global coral distribution (Figure 1) is in part, a legacy of earlier dispersal and establishment processes (Veron, 1995) and in part, a reflection of habitability constraints imposed by the present day environment, notably, those affecting coral's capacity to calcify. Light-enhanced calcification requires a particular regime of water chemistry, temperature, and solar radiation. Globally, the coral regions of the world have been ranked along a spectrum of environmental suitability for coral calcification – from "optimal" to "marginal" (Kleypas et al., 1999; Guinotte et al., 2003). Seas with an aragonite saturation ($\Omega_{\text{aragonite}}$) of >4.0 are "optimal" and >3.5 are "adequate," whereas <3.5 is only "marginal"; sea temperatures >18°C are warm enough to facilitate polyp replication, gametogenesis, and skeletogenesis; solar radiation needs to be sufficient to sustain a dense population of zooxanthellae with a high production of photosynthate. For these reasons, corals are rare and reefs are absent at latitudes >35° north or south of the equator (Veron, 1995): these latitude's low sun angles, short winter day lengths, low temperatures, and low aragonite saturation (Figure 1) all militate against vigorous coral growth. The geographic or depth limit beyond which coral growth is vigorous enough for reef growth has been termed the "Darwin Point" (Grigg, 1982).

Chemistry

A location's position on the "optimal to marginal" spectrum of Guinotte et al. (2003) reflects the ease or difficulty



Corals: Environmental Controls on Growth, Figure 1 Global patterns of latitude-correlated environmental controls on coral growth: light, temperature, and carbonate chemistry. Coral reefs are mostly confined to between 35°N and 35°S of the equator and corals between 40°N and 40°S. *Pie diagrams* indicate (in *white*) the proportion of each year that daily insolation at the sea surface exceeds 200 Einstein per square metre per day (Source: from Figure 2a, after Beer, 1997). The *broken line* indicates position of 18°C sea-surface temperature isotherm in mid-winter (i.e., January average in northern hemisphere; July average in southern hemisphere. Source: Reynolds and Smith, 1995). *Gray shading* indicates northern and southern limits of "adequate" aragonite saturation of seawater for coral calcification (source Kleypas et al., 2001).

with which calcium carbonate is deposited by reef plants and animals. It depends in large part on $\Omega_{\text{aragonite}}$, the degree to which the sea water is saturated with the ionic precursors of aragonite calcium carbonate – the form comprising the skeletons of reef-building corals:

$$Ca^{2+} + CO_3{}^{2-} \leftrightarrow CaCO_3 \tag{1}$$

There is ample Ca^{2+} for calcification in all the world's sea waters (Gattuso et al., 1999). (Indeed, excess Ca^{2+} is toxic to cellular processes, and biogenic calcification, now the keystone process for coral reef existence, is believed to have initially evolved in the Cambrian as a Ca^{2+} detoxification mechanism; Brennan et al., 2004; Kleypas and Langdon, 2006). But the amount of carbonate ($CO_3{}^{2-}$) available can become limiting, because it is very easily converted to the unusable bicarbonate ($HCO_3{}^{-}$) in the presence of H^+ ions: (the lower the pH, the less the $CO_3{}^{2-}$). H^+ ions are evolved when CO_2 dissolves in water, forming carbonic acid (H_2CO_3), which then dissociates:

$$CO_2 + H_2O \leftrightarrow H_2CO_3 \leftrightarrow H^+ + HCO_3{}^- \leftrightarrow CO_3{}^{2-} + H^+ \tag{2}$$

More CO_2 in solution (Equation 2) means more H^+ is evolved and more $CO_3{}^{2-}$ is robbed from the feedstock (Equation 1) that could otherwise have been joined with Ca^{2+} in the skeleton of a reef-building organism. Temperature also affects the solubility of CO_2 (and all other gases) in seawater: the warm waters of the tropics absorb less CO_2 than cool temperate waters, and therefore, less $CO_3{}^{2-}$ is robbed from calcification in the tropics, historically to the great advantage of corals.

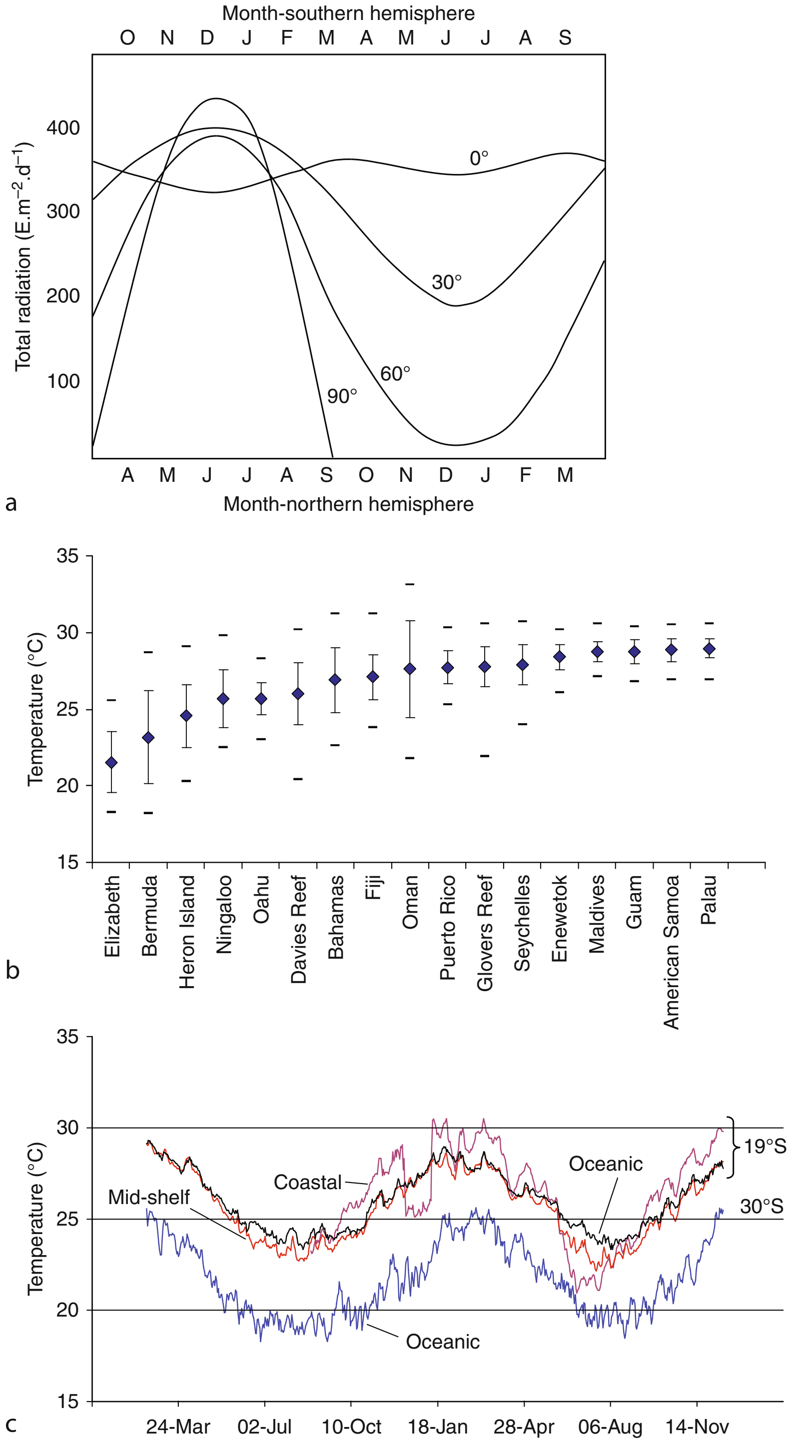
Solar radiation

Solar radiation is a primary environmental driver of production on coral reefs, both organic matter (tissues of plants and animals) and inorganic matter (skeletons), the latter at rates of up to tens of tonnes of calcium carbonate per hectare per year (Kinsey, 1983). The part of the solar radiation spectrum that drives this production is referred to as photosynthetically active radiation (PAR – wave lengths 400–700 nm). Quanta in this range are absorbed by the photosynthetic systems of the zooxanthellae, driving their production of the energy-rich "photosynthate" (glycerol and glucose). Around 95% of the photosynthate is translocated from the zooxanthellae to the cells of the coral host and used throughout the coral colony to build coral tissues, gametes, and aragonite. Calcification occurs at its maximum rate for 4 h around local solar noon (Chalker, 1983), during which time the irradiance of shallow corals with PAR is "saturating" with respect to the ability of the photo systems within the zooxanthellae to use it. The excess irradiance elicits "photoinhibition" in the coral, viz, a reduced photosynthetic efficiency, capacity, or both, compared to the performance at optimal levels of irradiance (Winters et al., 2003). At the high latitude limits of coral distribution, vigorous growth of "phototrophic" corals (those for which photosynthesis is the primary energy source) is precluded by the meager annual quota of PAR both at the water surface (due to short winter day lengths and low sun angles – Figures 1 and 2a) and at depth (due to reflection and absorption – Baker and Smith, 1982).

Temperature

Corals are "poikilothermic" organisms (they cannot regulate their temperature and must operate at the ambient temperature). Diverse coral communities and reefs occur in waters with sea temperatures in the range 18–28°C (Figure 2b). Throughout this range, there are suites of corals for which local temperatures are conducive to tissue growth, skeleton growth, and reproduction: the same coral species can host different types (Clades) of zooxanthellae to suit its particular environmental setting. For example, in the tropics, the world's most widely distributed zooxanthellate coral species *Plesiastrea versipora* (Veron, 2000) hosts zooxanthellae that are predominantly of the ubiquitous Clade C (Rodriguez-Lanetty et al., 2001), a highly efficient photosynthesizer (Cantin et al., 2009) that confers a fast growth rate on the many coral species in which it occurs. However, to survive in temperate waters, *P. versipora* hosts predominantly zooxanthellae of Clade B, which can function and survive at lower temperatures than Clade C (Howe and Marshall, 2002). Likewise, some coral species occupy warmer habitats by hosting warm-adapted zooxanthellae, in this case, predominantly Clade D (Berkelmans and van Oppen, 2006; Cantin et al., 2009). Compared to Clade C, however, the tolerance to marginal temperatures in both cases comes at the cost of a reduced growth rate (Howe and Marshall, 2002; Little et al., 2004). This trade-off has permitted corals to spread widely along the latitude-correlated attenuation of the parameters that govern coral growth: viz, temperature, aragonite saturation, and light. Whereas the zooxanthella complement of adult corals is typically dominated by a single clade, juveniles in some coral species host a mixture of clades (Gómez-Cabrera et al., 2008). The extent to which the identity of the clade dominant in the adult represents a form of selection to the type most suited to the individual coral's micro-environment has yet to be established (Gómez-Cabrera et al., 2008).

With normal local seasonal changes in temperature (~5–7°C – Figure 2c), the coral's metabolism is channeled variously into growth and replication of polyps, gametogenesis, skeletogenesis, and manufacture of stored energy reserves (Harriott, 1993). However, a few days of temperatures outside a particular reef's normal variability can be stressful and sometimes lethal for corals, be they abnormally high temperatures or abnormally low. Temperatures only 1–2°C above its normal summer maximum or below its normal winter minimum can cause coral bleaching (Brown, 1997): hot water bleaching (Goreau and Hayes, 1994) or cold water bleaching (Muscatine et al., 1991). In both cases, the anomalous



Corals: Environmental Controls on Growth, Figure 2 Global and regional variability in reef environments. (**a**) Seasonal variability in daily irradiance at the sea surface at latitudes indicated (modified from an original figure by Beer, 1997). (**b**) Annual temperature variation in sea-surface temperatures at a global selection of coral reefs. Source: Elizabeth Reef – Data Centre, Australian Institute of Marine Science, http://www.aims.gov.au/docs/data-centre/seatemperatures.html. Remainder: NOAA "Coral ReefWatch" http://coralreefwatch.noaa.gov/satellite/current/sst_series_24reefs.html. (**c**) Seasonal variability in sea-surface temperature at reefs at two latitudes on the east coast of Australia. Coastal temperatures are most volatile, and oceanic temperatures are the least.

temperatures can cause expulsion of zoothanthellae, loss of photosynthetic pigments, and subsequent decline of physiological performance, including calcification (Porter et al., 1989), and in severe cases, it can cause death of the coral (Loya et al., 2001). Beyond the latitudinal margins of coral and reef distribution, cold water events, superimposed on low light and aragonite saturation, are sufficiently frequent to cease to be anomalies and to be considered part of a normal seasonal variability that excludes phototrophic corals from establishing and growing, even on suitable substrata. For that reason, the corals on deep cold water reefs lack zooxanthellae, rely entirely on particulate food, and grow very slowly (Roberts et al., 2006).

Environmental variability within regions

Within the broad bounds set by water chemistry, temperature, and solar radiation (see above), environmental factors affecting coral growth also vary greatly over scales of kilometers to tens of kilometers: nature and depth of the substratum, temperature (Figure 2c), wave climate, salinity, water clarity, nutritional properties of that water, and sedimentation regime. Clear waters have traditionally been considered “optimal” for coral growth, and naturally turbid water reefs “marginal,” but for the purposes of the present account, they are viewed as “just different” (Perry and Larcombe, 2003).

Hydrodynamics, light, and sediments

Either too little or too much water motion can limit coral growth and survival. Whereas in moderation, water motion facilitates gas and nutrient exchange through the coral’s surface tissues (Atkinson and Bilger, 1992), strong waves and currents cause physical destruction (see *Hydrodynamics in Coral Reef Systems*; *Tropical Cyclone/Hurricane*), and insufficient flow limits gas and nutrient exchange to the detriment of coral health and survival. Too little flow, which exposes corals to potentially fatal physiological stress, can occur over large areas of the ocean in doldrum conditions. Corals in enclosed reef flats and lagoons are particularly vulnerable to high temperatures, flat glassy waters, and prolonged periods of calm weather. Low- or no-flow conditions thicken the diffusive boundary layer around corals, reduce gas exchange, and make it hypoxic, inducing anaerobiosis in the coral. Moreover, intense light beams condensed by surface ripples can exacerbate the stress caused by high temperatures and low flow, causing corals to bleach at such times (Nakamura and van Woesik, 2001).

Within those habitats where water is in motion, hydrodynamic variables (wave climate, currents, and residence time – see *Hydrodynamics in Coral Reef Systems*) are important determinants of where corals can grow and what morphological form they adopt. In oceanic settings, reefs and islands offer a broad range of environments for corals. Shallow reefs that are exposed to the full force of ocean swells and breaking waves do not necessarily support significant coral growth. On the outer Great Barrier Reef, for example, corals do build physically robust, wave-resistant structures in the surf break area (Done, 1982). But adjacent areas of the reef are often occupied by coral assemblages consisting of mainly small, short-lived corals, whose longevity is severely limited by recurrent breakage, scour, and abrasion. The latter structure and ephemeral dynamics are comparable to those described for some shallow reef slopes on Oahu, Hawaii, where the turnover of corals is so great that the coral veneer is rarely thicker than a single living colony (Grigg, 1998). The contrast of wave-beaten reefs with those of highly enclosed, shallow reef lagoons and embayments is striking. These latter habitats are often occupied by dense and extensive populations of corals whose shapes, sizes (often large), and longevity (often very great) are extremely variable from place to place, their specific composition dictated by the composition of the regional species pool, founder events, and environmental factors other than waves, such as light, sediments, and currents.

On continental shelves, there are greater complexities of environmental pattern and process, as exemplified in the Great Barrier Reef (GBR), whose 2,900 reefs are distributed across a seafloor that slopes from coastal beaches and headlands to a depth of ∼80m at the shelf edge 50–100 km offshore. On most days of the year, big, long period waves generated by distant meteorological drivers surge through interreef passages and break on the outermost reefs. They dissipate strong hydrodynamic forces in the reef’s surf zones and across their tops (Hearn, 1999), and, in conjunction with tidal flows, set up powerful turbulent jets and eddies around their flanks (Wolanski and Hamner, 1988). Depending on reef size, shape, orientation, weather, and state of the tide, different places along the leeward sides of these outer reefs may be completely calm, or they may be impacted by waves from the opposite direction, generated by local winds. These wind waves, which are of smaller wave height and shorter period than the ocean swells, intersect and combine with those oceanic swells that penetrate to behind the outer reefs and then lose height, velocity, and power as they are intercepted by mid-shelf reefs. As they travel into shallow coastal waters, further energy is lost to bottom friction, coarse sediments are rolled along the bottom, and fine sediments are resuspended and mixed through the water column, making it turbid (suspended sediment concentrations of 10–100 mg l^{-1} – Larcombe and Carter, 2004). When the winds subside and tides slacken, the coastal waters clear, as suspended sediments fall to the bottom.

Nutrients

Corals need fixed nitrogen (NH^{4+}, NO^{2-}, NO^{3-}) and phosphate (PO_4^{3-}) to synthesize proteins and nuclear material for cell maintenance, growth, and reproduction, and they are well adapted to exploit them in the low concentrations of oligotrophic surface waters in the oceans. However, excess nutrients are detrimental to coral growth for a number of reasons (Hallock, 2001; Fabricius, 2005): they can limit PAR reaching corals by promoting phytoplankton blooms that reduce water transparency; they can promote the growth of the algal competitors of corals (especially when grazing organisms are scarce); they can promote bioerosion and excessive phosphate can inhibit formation of $CaCO_3$ crystals. Excessive N also promotes the proliferation of zooxanthellae within corals (Dubinsky and Jokiel, 1994), which appears to detrimentally affect growth (Lesser et al., 1994) and to increase the coral's sensitivity to elevated temperatures, and thus the likelihood of lethal bleaching (Wooldridge, 2009).

There are four sources of nutrients to coastal waters: rivers, terrestrial dust, rainfall, and upwelled ocean waters. Dissolved concentrations of key nutrient elements required by corals and their zooxanthellae are usually extremely low on coral reefs due to low input rates, huge dilutions, and uptake by phytoplankton and pelagic bacteria (Furnas et al., 2004). Much of the terrigenous nutrient that flows into coastal waters is rapidly incorporated in phytoplankton–zooplankton-fish food webs (Furnas et al., 2004), to the potential benefit of coastal shrimp and fin-fish fisheries. However, the food web itself can deliver excess nutrients into the waters bathing corals: the feeding detritus and fecal pellets generated by this food web are fed on by microbes, which in turn release dissolved nutrients, with the potential to affect corals detrimentally as described above.

Microenvironment controls on coral growth

A coral's microenvironment consists of (1) *resources* (that it must receive at adequate rates and continuity of supply); (2) *sublethal stresses* (sometimes called "press disturbances" – Connell, 1997), which reduce its capacity to use resources efficiently (e.g., suboptimal temperatures or salinities; low-level pollutants); and (3) *extreme events* (sometimes called "pulse disturbances" – Connell op. cit.), which may kill, injure, or dislodge it during events of short duration (hours to weeks). Extreme natural events, which have characteristic return intervals generally measured in years to decades, include anomalies (high or low) of temperature or salinity, exposure to air (Figure 3), predators (see *Acanthaster planci*), disease, and destructive waves (see *Tsunami*; *Tropical Cyclone/Hurricane*).

On any given reef, corals distribute themselves across ambient environments that are extremely wide ranging, from bright wave-beaten surf zones, across shallow reef tops, and down reef slopes to deep placid twilight zones. Two levels of diversity in the assemblage allow it to occupy such a broad range of environments: the number of available coral species and the plasticity within each species (capacity to adopt a modified form of their basic growth plan). In highly plastic species (the majority), a larva or a fragment will adopt a particular adult growth form that is suited to the precise location in which it happens to settle (e.g., *Acropora humilis*, which adopts a robust form in the surf zone and a lighter structure in deeper waters: *Acropora palmata*, which orients its branches with the waves in the strongest waves, across them in moderate waves, and indifferently to them in calm areas). In species with only one growth form option, the larva or fragment will likely survive only in a single narrowly confined habitat [e.g., *Acropora pyramidalis*, *A. nana* (robust and delicate corals, respectively, found only in surf zones); *Pachyseris robusta*; *Pachyseris speciosa* – encrusting plates, found only in calm waters].

Corals: Environmental Controls on Growth, Figure 3 Exposure to air – the ultimate environmental limit to the upper limit of coral growth. Corals (several species in the genus *Acropora*) exposed to the air during an extreme low tide event. Wheeler Reef, Great Barrier Reef, July 1986.

Corals most often attain their highest abundance, percentage cover, and diversity on reef margins (Kinsey, 1983; Macintyre, 2007), i.e., in horizontal zones usually not more than 30-m wide along the edges of intertidal reef flats; on reef slopes, particularly in the upper 20 m and on the margins of lagoonal patch reefs. One reason that corals are abundant in such areas is because these are the habitats that are first encountered by coral larvae carried to the reef by currents. Once established, these corals have first use of waters that flow or break onto the reef. Most aspects of the environment of shallow margins are optimal for coral growth: influx of solar-radiation is nonlimiting; onflowing water is most saturated in the precursors of coral growth (see Section Chemistry) and richest in the particulate matter on which corals feed (especially zooplankton); and temperature is the same as the adjacent sea (Figure 2c).

As water crosses the shallow reef, key properties are changed by its interaction with the shallow reef and its biota (see *Hydrodynamics in Coral Reef Systems*). For example, the margin-inhabiting corals (and other calcifying organisms) extract calcium carbonate precursors and nutrients from the water, reducing the levels available to corals "down-stream" (i.e., toward the middle of the reef flat). Calcification by a community reduces the water column's total carbon and alkalinity, resulting in a decrease of CO_3^{2-} (reviewed in Nakamura and Nakamori, 2007). When different reef communities are aligned across a reef from their wave-exposed to their sheltered side, their exchanges with the passing water set up seaward to leeward gradients in pH, total carbon and total alkalinity. In effect, the upstream communities strip CO_3^{2-} from the water, limiting its supply to sheltered backwaters, making calcification there impossible. Where corals do grow in such back reef areas, it indicates that seawater with the correct pH, total carbon, total alkalinity, and composition of carbonate species is reaching that place via routes other than a transit across a productive reef flat (e.g., refraction around reef flanks or through broad channels).

Shallow water on reef flats can be easily heated beyond the range preferred or tolerated by corals. This greater temperature volatility is amplified by low-tide ponding and other restrictions on its rate of flushing caused by prior growth of the reef itself (Macintyre, 2007). Where back-reef waters are highly impounded, they can become sinks for rainfall and land-runoff, and for inorganic and organic detritus from the reef upstream, with regimes of temperature, oxygenation, salinity, and turbidity that are inimical for coral growth. Where, by contrast, back-reef habitats are well flushed with ocean waters, corals can grow profusely on sandy lagoon floors and on the margins of back-reef pinnacles and walls.

Solar radiation reaching a coral varies in both space and time, and the key drivers of variability have been reviewed by Anthony et al. (2004): (1) seasonal pattern of daily surface irradiance; (2) variations in clouds; (3) transmittance through the water column, which depends on the optical properties of the water (Baker and Smith, 1982), most notably turbidity; and (4) tides, whose daily and seasonal cycles always affect the depth of the water column and in some circumstances influence turbidity. In a clear oceanic setting, a gradual depth-attenuation of PAR allows corals that are primarily phototrophic to grow to depths as much as 100 m. By contrast, in turbid coastal waters, dissolved and suspended matter attenuates PAR to below useful levels at <20 m. However, corals that gain most of their food by feeding (i.e., heterotrophic corals) can thrive in low light settings, be it deep on a clear water reef or much shallower on turbid water reefs. In both cases, something else may set the lower depth limit to coral distribution; a steep unstable talus in the oceanic reef; a flat muddy sea floor in the coastal reef.

Coral growth

From primary polyp to coral colony

There are approximately 700 species of Scleractinian corals globally (Veron, 2000). Based on their adult shapes, they can be divided into six broad "growth-form" categories (Veron, 1996): *massive* (similar in all dimensions); *columnar* (forming columns); *encrusting* (adhering to the substrate); *branching* (arborescent or tree-like to digitate or finger-like); *foliaceous* (leaf-like); and *laminar* (plate-like). There is considerable variability in the detailed morphology among and within species: for example, massive corals may be taller or squatter; columns may be thick or thin, long or club-like; encrustations may be thick or thin; and branches may have different shapes, thicknesses, densities, taper and departure angles of secondary and tertiary branches, which may or may not fuse. A major contributor to this growth form variability is the local environmental setting, which has a comparable effect to that of the coral's genetic makeup (Veron, 1996) in transformation of the microscopic primary polyp into a flat, fingernail-sized spat, and thence up and out into a particular locally adapted variant of the basic growth form.

The primary polyp develops from a soft-bodied planula larva (see below) that transforms itself into a single soft-bodied polyp within hours of settlement (Hirose et al., 2008), when it glues itself onto something solid (e.g., mollusc shell, dead coral in situ, rubble, rock, or reef framework). The "glue" becomes a perforated shallow calcium carbonate saucer with radial costae (spiky ridges) on top that support the polyp's tissues. This single act of transformation from soft-bodied larva to skeleton-secreting "zooid" (polyp + skeleton) marks the commencement of a period occupancy that may continue for centuries and produce a colony meters high and meters across.

The adult coral colony that eventually develops has one of the basic growth forms listed above. All except "solitary" corals (in which the original zooid just continues to grow, reaching the size of a desert plate or hefty fruit bowl in a matter of a few years) undergo a process of modular growth. Modular growth occurs through vegetative replication (e.g., budding or expansion, and subdivision) of the original zooid and all of its descendants – Rosen, 1986; Kim and Lasker, 1998). While the basic growth forms are constrained genetically, actual colony morphologies adopted by a particular colony of a particular species in a particular place will in large measure be a phenotypic response to its microenvironment: viz, the regimes of chemistry, nutrition, temperature, and light and wave energy that are incident upon it.

Some large coral colonies originate from an unattached fragment, essentially a small version of the adult colonies, for which the environmental milieu is qualitatively similar to that of the adult. However, being unattached means it can be dislodged, projected, or rolled by strong currents (Fox et al., 2003). In wave-swept reef habitats, where oscillating flows make such motion a daily occurrence, it usually kills the remaining polyps and the fragment becomes rubble. In habitats where a fragment is immobilized by lodgment in a crevice or falling into a sheltered place, or is inverted only at intervals of weeks to months at most, the living veneer of polyps survives and deposits an increasing mass and volume of skeleton. In shallow flat habitats with reversing currents, a ball-like *corallith* with live polyps on all sides may develop (Glynn, 1974). But in most viable habitats, the fragment will produce skeletal processes that attach it to adjacent stable substratum and prevent further rolling. Once attached, the environmental needs and vulnerabilities are the same as for other attached corals of comparable size.

Modes of nutrition and coral growth forms

Corals need both large supplies of energy-rich compounds and small amounts of nutrients (N, P) for their growth (tissue and skeleton) and reproduction. Modes of nutrition of corals can be arranged along a spectrum of relative reliance on ingested food as a primary source of energy-rich compounds (Hallock, 2001). In "phototrophic" corals, it is small (but necessary for intake of N and P), and the corals primarily use "photosynthate" (the product of photosynthesis by their symbiotic zooxanthellae). In "heterotrophic" corals, at the other end of the spectrum, there is major reliance on ingested food (zooplankton, organic detritus, and dissolved organic matter). In the middle are "mixotrophic" corals, which use both sources more equally.

Corals build exoskeletons in shapes that facilitate their particular mode of resource use, i.e., adequate interception of solar radiation and particulate food and the water-borne precursors for calcification; use of the moving water to remove the waste products of metabolism. In calm, clear, shallow waters, there is so much light that virtually any shape will be effective in harvesting sufficient PAR. Indeed, these phototrophic corals have to expend energy producing compounds to protect themselves against damaging excess irradiation. However, in wave breaking and surging zones, the range of coral shapes is more limited. These include encrusting forms and/or small colonies of species that adopt a top-heavy form in calmer waters and streamlined and elongated variants of growth forms that are more radially symmetrical in calm waters: e.g., *Acropora palmata* in the Atlantic and several *Acropora* groups in the Indo-Pacific: "*robusta*," "*humilis*," "*nasuta*," and "*palifera*." Only those shapes that can resist dislodgement by normal fair-weather waves can survive for long, and even they will eventually reach a size where their dislodgement is likely (Massel and Done, 1993; Madin and Connelly, 2006; see also *Tropical Cyclone/ Hurricane*).

Depth and light

In deep or turbid water, phototrophic corals often adopt horizontal growth forms to maximize the interception of PAR. However, in places where this exposes them to a rain of sediments falling out of the water column, corals survive by adopting shapes that shed sediments passively or with minimal energy expenditure by the polyps: low convex profiles from which gentle water motion can easily entrain sediment particles; dense networks of flattened branches, perforated with gaps through which sediments can drop and vases whose interaction with the currents sets up a vortex that lifts accumulated sediments clear (Reigl et al., 1996). In some species, notably in the genera *Pocillopora* and *Acropora*, colonies in very sheltered habitats have thinner and more open branches than shallower colonies (Veron, 1995; Wallace, 1999), thereby maximizing extension without investing unnecessarily in a strong skeleton.

The PAR dose reaching corals down a reef slope has been attenuated by absorption and scattering as it passes down through the water column (Baker and Smith, 1982). Deeper phototrophic corals compensate for reduced PAR by elevating zooxanthellae densities, chlorophyll content per zooxanthella, or both. These changes cause them to appear more darkly colored than shallow water corals. In clear waters, corals as deep as several tens of meters can remain saturated and function normally (Chalker, 1983).

In turbid waters, this depth may be only a few meters. There, the day-to-day and week-to-week variation in irradiation a few meters down the slope can, due to frequent resuspension of mud from the adjacent shallow sea floor, be more than an order of magnitude greater than it is at the surface and at equivalent depths in offshore, clear-water benthic habitats (Anthony, 2000; Anthony et al., 2004). Corals on slopes of turbid-water reefs may thus alternate between periods of light deficiency and light excess. Phototrophic corals are therefore confined to the relatively well-lit shallower parts of such reefs, whereas deeper, darker, and muddier parts of these reefs are populated by corals with specific adaptations for those conditions. In very dark (deep or very turbid) waters, only mixotrophic or heterotrophic corals can survive (Anthony, 2000). These corals largely replace the now minimal zooxanthellae-derived photosynthate as the primary food source with dissolved organic matter (saprophagy) or particulate organic matter (detritus and/or zooplankton) (Anthony et al., 2004). In deep (50–4,000 m), dark cold-water coral reefs (4–12°C), approximately ten species of scleractinian corals have been discovered, all completely lacking zooxanthellae (Roberts et al., 2006). They rely entirely on food transported from surface waters to the sea floor, frequently in sites with food supply enhanced by locally accelerated currents.

Ultraviolet radiation (UVR – 390–400 nm) is potentially damaging to corals. However, a number of things protect corals from UVR damage. First, is depth itself: shorter wavelengths are scattered by particles and absorbed by water molecules and dissolved organic compounds more readily than PAR wavelengths (Baker and Smith, 1982). As a result, UVR attenuates to near zero within a few meters at most, and because of the extreme scattering, they irradiate the corals only weakly. Second, shallow corals manufacture sunscreens [mycosporine-like amino acids (MAAs) – Dunlap and Shick, 1998] that shield their tissues from any ambient UV that does reach them. These compounds are especially important for those corals that are periodically left emerged at extreme low tides (Figure 3) and thereby exposed to direct sunlight. Some of the MAAs produced by the corals occurs in mucus that is secreted by emergent corals and protects them from dehydration.

Environmental controls on coral's presettlement stage

The environmental milieu of the coral's presettlement stage is quite different to that of adult corals. Corals develop by two main methods (Harrison and Wallace, 1994; see also *Corals: Biology, Skeletal Deposition, and Reef-Building*): asexually (from the fragments of an existing colony that become separated by budding or breakage from a parent colony – see Section Coral growth) and sexually (from fertilized eggs that grow into pelagic larvae that swim or are carried by currents to their place of settlement). Pelagic coral larvae are released into the water by sexually mature corals (usually >3–5 years old) that produce sperm and eggs. Depending on species, the production of the larvae follows one of the two pathways (1) broadcast spawning or (2) brooding. In broadcast spawning, gravid polyps expel eggs and sperm into the water column during a mass spawning event whose timing is synchronized to lunar cycles. Fertilization takes place in the water column, and the drifting fertilized egg transforms itself into a planula larva over a period of several days (Hirose et al., 2008). During its days in the currents, the metamorphosis from egg to larva is fueled by lipids originating from the egg. Once it has developed its simple gut (~4 days), it can feed on phytoplankton and detritus and presumably does so if it is nowhere near a suitable place to settle (Richmond, 1987). However, at this stage it is competent to settle (Hirose et al., 2008), and it tends to do so quickly when deprived of food in the laboratory (Hirose et al., 2008). When food is supplied, individuals of some species can settle within 2–3 days (Miller and Mundy, 2003). For those that do not settle so quickly, there can be major mortality within the first few days, but survival of others in the water column upwards of 100 days (Graham et al., 2008). During this time they are potentially exposed to environmental hazards such as hyposaline areas, excessively muddy areas, or very clear areas where they may become exposed to damaging doses of UVB radiation (Gleason and Wellington, 1995). In open waters between reefs, they will likely be aggregated into fronts generated by the current's interaction with headlands, islands, and reefs; this aggregation on one hand attract predatory fishes or shrimps, but on the other, take cohorts of competent larvae to potential settlement sites (Wolanski and Hamner, 1988). The broadcast-spawning strategy described above favors colonization of widely dispersed reef substrata and hence the maintenance and/or restoration of those area's reef-building potential (see *Coral Reef, Definition*).

The brooding strategy, by contrast, leads to localized settlement that favors persistence of the local population and local reef-building. In brooding coral species, fertilization takes place within the polyps of the parent colony and so does metamorphosis into the planula larva (Harrison and Wallace, 1994). When expelled several days after fertilization, they are strong swimmers, zooxanthellae bearing, and competent to attach to the reef within minutes to hours of release: they avoid the hazards of days to weeks in the water column that are faced by broadcast pelagic larvae. Brooded larvae have much higher likelihood of finding a suitable settlement place, in this case, close to one that has been tried and tested by the parent colony.

When broadcast larvae are swept over a reef from the sea on a flooding tide, they face the environmental hazard of "the wall of mouths" (Hamner et al., 1988) belonging to coral polyps (Fabricius and Metzner, 2004) and schools of planktivorous fishes that ride the surge along reef edges (Hamner et al., 2007). Those that survive will then receive environmental cues to a potential place for settlement. A hydrodynamic cue alone (Abelson and Denny, 1997) may attract them to within centimeters of solid substrata. Their choice of specific microcrevices may then be guided by chemical cues emitted by coralline algae and microbial films coating the substratum (Harrington et al., 2004). Abelson and Denny (1997) suggest that when hydrodynamic forces are higher than the larva's swimming capacity (as may often be the case in wave-swept reef environments), final site selection may be due to desertion of unfavorable sites rather than exploration and active selection of an appropriate site. For many species it is only after the coral larvae has settled and transformed itself into a rudimentary polyp that it acquires zooxanthellae that multiply within its tissues (Hirose et al., 2008) and contribute to the nutrition of their host.

Reef environments present a wide range of colonizable substrata for the establishment of corals that could occupy that place for decades or even centuries. In wave-swept parts of the reef, the substratum to which a coral attaches is usually big and heavy enough to stay in place against normal hydraulic forces generated by waves (e.g., solid framework and heavy rubble). In sheltered parts of the reef, smaller rubble sizes (coral shingle and mollusc shells) can be colonized by coral larvae, and even sand and mud can be colonized by coral fragments of some species.

Global climate change: implications for coral growth

The net effect of global warming and increases in atmospheric CO_2 per se are detrimental to the biological calcification process (Feely et al., 2004; Hoegh-Guldberg et al., 2007; Guinotte and Fabry, 2008). There is so much more atmospheric CO_2 at the ocean–atmosphere interface today (385 ppm in 2010) compared to preindustrial times (280 ppm) that much more goes into solution, despite the marginal solubility loss caused by increased sea temperature (Sabine et al., 2004). These authors report that if CO_2 reaches double preindustrial levels (560 ppm), there will be a 30% decrease in carbonate ion concentration and a 60% increase in hydrogen ion concentration. There are likely to be differences among calcifiers in their responses to decreasing carbonate ion concentrations, reflecting differences in their carbonate mineralogy and local environmental parameters such as temperature, light, and available nutrients and in the mechanism of biomineralization (Feely et al., 2004). A review by Guinotte and Fabry (2008) suggests that this would cause a 20–60% reduction of calcification rates in tropical reef-building corals, manifest in the skeleton in its two measurable parameters: rate of linear extension (cm day^{-1}) and density (g cm^{-3}) (Barnes and Chalker, 1990; Lough and Barnes, 2000). Any loss of density would cause a decrease in strength and greater vulnerability to storms in corals on the reef (Massel, 1999). A reduction in linear extension rate would mean that individual colonies would take longer to reach size-related thresholds, such as sexual maturity (Albright et al., 2008), escape from overgrowth by other benthos, or vulnerability to dislodgment by storm waves (Massel and Done, 1993; Madin and Connelly, 2006). Most recent field studies have shown a reduction in linear extension and density coincident with rising temperature and atmospheric pCO_2 over recent decades (Cooper et al., 2008; De'ath et al., 2009; Tanzil et al., 2009). A number of studies (noted in Albright et al., 2008) have reported that reduced calcium carbonate saturation has no negative effect on physiological processes other than calcification (viz, tissue growth and photosynthesis) and indeed may even augment them. Paradoxically, any decline in reef-wide calcification caused by atmospheric CO_2 will reduce aqueous CO_2 emanating from the reef itself. Reefs as a whole, including their reef flats and lagoons, tend to be sources of CO_2, due both to calcification by reef communities and the decomposition of plant matter produced on the reef (Suzuki and Kawahata, 1999).

Anthropogenic climate change may be precipitating the sixth great coral reef extinction in 430 million years (Veron, 2008). Reefs are confined to warm shallow waters that are becoming too hot too often, bleaching and killing coral populations on reefs scattered over vast areas of ocean. As a result, recolonization of damaged areas will be weakened, and even in those places where by chance there is good recolonization, the next heatwave, hurricane, flood, pest outbreak, or disease will cut off recovery of high coral cover before it can be completed. Refuge populations themselves are threatened. For shallow ones, it may simply be a matter of time before they are killed by a heatwave, and for deeper and cooler ones, before they become victims of shallowing of the aragonite saturation zone caused by ocean acidification (Feely et al., 2004). This view of the future – predicated on the assumption that environmental changes will be too great and are occurring too fast for there to be any effective adaptation in reef organisms (see Chapter *Adaptation*) – raises some key questions about the viability of the processes and circumstances responsible for maintaining modern coral reefs, i.e., environmental controls on coral growth.

Summary

Coral growth (individuals, populations, and communities) responds to variations in their external environment that are manifest over spatial scales spanning centimeters to degrees of latitude. The specific microenvironment in which a coral settles and in which it may spend anything from years to centuries is determined by vagaries of currents and early survival. Corals and coral reefs exist within a range of local settings within a region (e.g., oceanic vs. continental shelf) and benthic communities and reefs further modify their own environments – dissipation and refraction of waves; ponding of reef-top waters; removal of aragonite precursors and addition of organic and inorganic detritus. As a result, there may be as much variability in the range of microenvironments existing within regions and on individual reefs as there is across much broader geographic areas. This existing variability in microenvironments and the concomitant diversity in species and coral–zooxanthellae partnerships are extremely important for the survival of reefs in a future with global climate change, in which they are faced with rapid changes in environment over all spatial scales.

Bibliography

Abelson, A., and Denny, M., 1997. Settlement of marine organisms in flow. *Annual Review of Ecology and Systematics*, **28**, 317–339.

Albright, R., Mason, B., and Langdon, C., 2008. Effect of aragonite saturation state on settlement and post-settlement growth of *Porites astreoides* larvae. *Coral Reefs*, **27**, 485–490.

Anthony, K. R. N., 2000. Enhanced particle-feeding capacity of corals on turbid reefs (Great Barrier Reef, Australia). *Coral Reefs*, **19**, 59–67.

Anthony, K. R. N., Ridd, P. V., Orpin, A. R., Larcombe, P., and Lough, J., 2004. Temporal variation of light availability in coastal benthic habitats: effects of clouds, turbidity, and tides. *Limnology and Oceanography*, **49**, 2201–2211.

Atkinson, M. J., and Bilger, R. W., 1992. Effects of water velocity on phosphate uptake in coral reef-flat communities. *Limnology and Oceanography*, **37**, 273–279.

Baker, K. S., and Smith, R. C., 1982. Bio-optical classification and model of natural waters. 2. *Limnology and Oceanography*, **27**, 500–509.

Barnes, D. J., and Chalker, B. E., 1990. Calcification and photosynthesis in reef-building coral and algae. In Dubinsky, Z. (ed.), *Ecosystems of the World, Vol. 25: Coral Reefs*. Amsterdam: Elsevier, pp. 109–131.

Beer, T., 1997. *Environmental Oceanography*, 2nd edn. Boca Raton, FL: CRC.

Berkelmans, R., and van Oppen, M. J. H., 2006. The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope' for coral reefs in an era of climate change. *Proceedings of the Royal Society of London Series B*, **273**, 2305–2312, doi:10.1098/rspb.2006.

Brennan, S. T., Lowenstein, T. K., and Horita, J., 2004. Seawater chemistry and the advent of biocalcification. *Geology*, **32**, 473–476.

Brown, B. E., 1997. Coral bleaching; causes and consequences. *Coral Reefs*, **16**, S129–S138.

Buddemeier, R. W., Kleypas, J. A., and Aronson, R. B., 2004. *Coral Reefs and Global Climate Change*. Arlington, VA: Pew Center on Global Climate Change.

Cantin, N. E., van Oppen, M. J. H., Willis, B. L., Meiog, J. C., and Negri, A. P., 2009. Juvenile corals can acquire more carbon from high-performance algal symbionts. *Coral Reefs*, **28**, 405–414.

Chadwick-Furman, N. E., 2006. Reef coral diversity and global change. *Global Change Biology*, **2**, 559–568.

Chalker, B. E., 1983. Calcification by corals and other animals on the reef. In Barnes, D. J. (ed.), *Perspectives on Coral Reefs*. Manuka: Brian Clouston Publisher, pp. 29–45.

Connell, J. H., 1997. Disturbance and recovery of coral assemblages. *Coral Reefs*, **16**, 101–113.

Cooper, T. F., De'ath, G., Fabricius, K. E., and Lough, J. M., 2008. Declining coral calcification in massive *Porites* in two nearshore regions of the northern Great Barrier Reef. *Global Change Biology*, **14**, 529–538.

De'ath, G., Lough, J. M., and Fabricius, K. E., 2009. Declining coral calcification on the Great Barrier Reef. *Science*, **323**, 116–119.

Done, T. J., 1982. Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs*, **1**, 95–107.

Done, T. J., 1999. Coral community adaptability to environmental changes at scales of regions, reefs and reef zones. *American Zoologist*, **39**, 66–79.

Dubinsky, Z., and Jokiel, P. L., 1994. Ratio of energy and nutrient fluxes regulates symbiosis between zooxanthellae and corals. *Pacific Science*, **48**, 313–324.

Dunlap, W. C., and Shick, J. M., 1988. Ultraviolet radiation absorbing mycosporine-like amino acids in coral reef organisms: a biochemical and environmental perspective. *Journal of Phycology*, **34**, 418–430.

Fabricius, K. E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin*, **50**, 125–146.

Fabricius, K. E., and Metzner, J., 2004. Scleractinian walls of mouths: predation on coral larvae by corals. *Coral Reefs*, **23**, 245–248.

Fagoonee, I., Wilson, H. B., Hassell, M. P., and Turner, J. R., 1999. The dynamics of zooxanthellae populations: a long-term study in the field. *Science*, **283**, 843–845.

Feely, R. A., Sabine, C. L., Lee, K., Berelson, W., Kleypas, J., Fabry, V. J., and Millero, F. J., 2004. Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. *Science*, **305**, 362–366.

Fitt, W. K., McFarland, K., Warner, M. E., and Chilcoat, G. C., 2000. Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. *Limnology and Oceanography*, **45**, 677–685.

Fox, H. E., Pet, J. S., Dahuri, R., and Caldwell, R. L., 2003. Recovery in rubble fields: long-term impacts of blast fishing. *Marine Pollution Bulletin*, **46**, 1024–1031.

Furnas, M., Mitchell, A., Skuza, M., and Brodie, J., 2004. In the other 90%: phytoplankton responses to enhanced nutrient availability in the Great Barrier Reef lagoon. *Marine Pollution Bulletin*, **51**, 253–264.

Gattuso, J.-P., Allemand, D., and Frankignoulle, M., 1999. Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: a review on interactions and control by carbonate chemistry. *American Zoologist*, **39**, 160–183.

Gleason, D. F., and Wellington, G. M., 1995. Variation in UVB sensitivity of planula larvae of the coral *Agaricia agaricites* along a depth gradient. *Marine Biology*, **123**, 693–703.

Glynn, P. W., 1974. Rolling stones amongst the Scleractinia: mobile coralliths in the Gulf of Panama. In *Proceedings of the Second International Coral Reef Symposium*, Vol. 2, pp. 183–198.

Gómez-Cabrera, M., del, C., Ortiz, J. C., Loh, W. K. W., Ward, S., and Hoegh-Guldberg, O., 2008. Acquisition of symbiotic dinoflagellates (*Symbiodinium*) by juveniles of the coral *Acropora longicyathus*. *Coral Reefs*, **27**, 219–226.

Goreau, T. F., and Goreau, N. I., 1959. The physiology of skeleton formation in corals II: calcium deposition by hermatypic corals under various conditions in the reef. *Biological Bulletin*, **116**, 59–75.

Goreau, T. J., and Hayes, R. L., 1994. Coral bleaching and ocean "hot spots". *Ambio*, **23**, 176–180.

Graham, E. M., Baird, A. H., and Connolly, S. R., 2008. Survival dynamics of scleractinian coral larvae and implications for dispersal. *Coral Reefs*, **27**, 529–539.

Grigg, R. W., 1982. Darwin Point: a threshold for atoll formation. *Coral Reefs*, **1**, 29–34.

Grigg, R. W., 1998. Holocene coral reef accretion in Hawaii: a function of wave exposure and sea level history. *Coral Reefs*, **17**, 263–272.

Guinotte, J. M., Buddemeier, R. W., and Kleypas, J. A., 2003. Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin. *Coral Reefs*, **22**, 551–558.

Guinotte, J. M., and Fabry, V. J., 2008. Ocean acidification and its potential effects on marine ecosystems. *Annals New York Academy of Science*, **1134**, 320–342.

Hallock, P., 2001. Coral reefs, carbonate sediments, nutrients and global change. In Stanley, G. D. Jr. (ed.), *The History and Sedimentology of Ancient Reef Systems*. New York: Kluwer/Plenum, pp. 387–427.

Hamner, W. M., Colin, P., and Hamner, P. P., 2007. Export-import dynamics of zooplankton on a coral reef in Palau. *Marine Ecology Progress Series*, **334**, 83–92.

Hamner, W. M., Jones, M. S., Carleton, J. H., Hauri, I. R., and Williams, D. McB., 1988. Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. *Bulletin of Marine Science*, **42**, 459–479.

Harrington, L., Fabricius, K., De'ath, G., and Negri, A., 2004. Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology*, **85**, 3428–3437.

Harriott, V. J., 1993. Coral lipids and environmental stress. *Environmental Monitoring and Assessment*, **25**, 131–139.

Harrison, P. L., and Wallace, C. C., 1994. Reproduction, dispersal and recruitment of scleractinian corals. In Dubinsky, Z. (ed.), *Ecosystems of the World, Vol. 25: Coral Reefs*. New York: Elsevier Science, pp. 133–207.

Hearn, C. J., 1999. Wave-breaking hydrodynamics within coral reef systems and the effect of changing relative sea level. *Journal of Geophysical Research*, **104**, 30.007–30.019.

Hirose, M., Yamamoto, H., and Nonaka, M., 2008. Metamorphosis and acquisition of symbiotic algae in planula larvae and primary polyps of *Acropora* spp. *Coral Reefs*, **27**, 247–254.

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell, C. D., Sale, P. F., Edwards, A. J., Caldeira, K., Knowlton, N., Eakin, C. M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R. H., Dunbi, A., and Hatziolos, M. E., 2007. Coral reefs under rapid climate change and ocean acidification. *Science*, **318**, 1737–1742.

Howe, S. A., and Marshall, A. T., 2002. Temperature effects on calcification rate and skeletal deposition in the temperate coral, *Plesiastrea versipora* (Lamarck). *Journal of Experimental Marine Biology and Ecology*, **275**, 63–81.

Kim, K., and Lasker, H. R., 1998. Allometry of resource capture in colonial cnidarians and constraints on modular growth. *Functional Ecology*, **12**, 646–654.

Kinsey, D. W., 1983. Standards of performance in coral reef primary production and carbon turnover. In Barnes, D. J. (ed.), *Perspectives on Coral Reefs*. Manuka: Brian Clouston Publisher, pp. 209–220.

Kleypas, J. A., Buddemeier, R. W., and Gattuso, J.-P., 2001. The future of coral reefs in an age of global change. *International Journal of Earth Sciences*, **90**, 426–437.

Kleypas, J. A., and Langdon, C., 2006. Coral reefs and changing seawater chemistry. In Phinney, J. T., Hoegh-Guldberg, O., Kleypas, J., Skirving, W., and Strong, A. (eds.), *Coral Reefs and Climate Change: Science and Management*. Washington, DC: American Geophysical Union, pp. 73–110.

Kleypas, J. A., McManus, J. W., and Meñez, L. A. B., 1999. Environmental limits to coral reef development: where do we draw the line? *American Zoologist*, **39**, 146–159.

Larcombe, P., and Carter, R. M., 2004. Cyclone pumping, sediment partitioning and the development of the Great Barrier Reef shelf system: a review. *Quaternary Science Reviews*, **23**, 107–135.

Lesser, M. P., Weis, V. M., Patterson, M. R., and Jokiel, P. L., 1994. Effects of morphology and water motion on carbon delivery and productivity in the reef coral, *Pocillopora damicornis* (Linnaeus): diffusion barriers, inorganic carbon limitation, and biochemical plasticity. *Journal of Experimental Marine Biology and Ecology*, **178**, 153–179.

Little, A. F., van Oppen, M. J. H., and Willis, B. L., 2004. Flexibility in algal endosymbioses shapes growth in reef corals. *Science*, **304**, 1492–1494.

Lough, J. M., and Barnes, D. J., 2000. Environmental controls on growth of the massive coral *Porites*. *Journal of Experimental Marine Biology and Ecology*, **245**, 225–243.

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., and Van Woesik, R., 2001. Coral bleaching: the winners and the losers. *Ecology Letters*, **4**, 122–131.

Macintyre, I. G., 2007. Demise, regeneration and survival of some Western Atlantic reefs during the Holocene transgression. In Aronson, R. B. (ed.), *Geological Approaches to Coral Reef Ecology*. New York: Springer, pp. 181–200.

Madin, J. S., and Connelly, S. R., 2006. Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature*, **444**, 477–480.

Massel, S. R., 1999. *Fluid Mechanics for Marine Ecologists*. Berlin: Springer.

Massel, S. R., and Done, T. J., 1993. Effects of cyclone waves on massive coral assemblages on the Great Barrier Reef: meteorology, hydrodynamics and demography. *Coral Reefs*, **12**, 153–166.

Miller, K., and Mundy, C., 2003. Rapid settlement in broadcast spawning corals: implications for larval dispersal. *Coral Reefs*, **22**, 99–106.

Muscatine, L., Grossman, D., and Doino, J., 1991. Release of symbiotic algae by tropical sea anemones and corals after cold shock. *Marine Ecology Progress Series*, **77**, 233–243.

Nakamura, T., and Nakamori, T., 2007. A geochemical model for coral reef formation. *Coral Reefs*, **26**, 741–755.

Nakamura, T., and van Woesik, R., 2001. Water-flow rates and passive diffusion partially explain differential survival of corals during, 1998 bleaching event. *Marine Ecology Progress Series*, **212**, 301–304.

Negri, A. P., Marshall, P. A., and Heyward, A. J., 2007. Differing effects of thermal stress on coral fertilization and early embryogenesis in four Indo Pacific species. *Coral Reefs*, **27**, 759–763.

Perry, C. T., and Larcombe, P., 2003. Marginal and non-reef-building coral environments. *Coral Reefs*, **22**, 427–432.

Porter, J. W., Fitt, W. K., Spero, H. J., Rogers, C. S., and White, M. W., 1989. Bleaching in reef corals: physiological and stable isotopic responses. *Proceedings of the National Academy of Science of the United States of America*, **86**, 9342–9346.

Reigl, B., Heine, C., and Branch, G. M., 1996. Function of funnel-shaped coral growth in a high-sedimentation environment. *Marine Ecology Progress Series*, **145**, 87–93.

Reynolds, R. W., and Smith, T. M., 1995. A high resolution global sea surface temperature climatology. *Journal of Climate*, **8**, 1571–1583.

Richmond, R. H., 1987. Energetics, competency, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. *Marine Biology*, **93**, 1432–1793.

Roberts, J. M., Wheeler, A. J., and Freiwald, A., 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science*, **312**, 543–547.

Rodriguez-Lanetty, M., Loh, W., Carter, D., and Hoegh-Guldberg, O., 2001. Latitudinal variability in symbiont specificity within the widespread scleractinian coral *Plesiastrea versipora. Marine Biology*, **138**, 1175–1181.

Rosen, B. R., 1986. Modular growth and form of corals: a matter of metamers. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **313**, 115–142.

Sabine, C. L., Feely, R. A., Gruber, N., Key, R. M., Lee, K., Bullister, J. L., Wanninkhof, R., Wong, C. S., Wallace, D. W. R., Tilbrook, B., Millero, F. J., Peng, T.- H., Kozyr, A., Ono, T., and Rios, A. F., 2004. The oceanic sink for anthropogenic CO_2. *Science*, **305**, 367–371.

Stanley, G. D., and Swart, P. W., 1995. Evolution of the coral-zooxanthellae symbiosis during the Triassic: a geochemical approach. *Paleobiology*, **21**, 179–199.

Suzuki, A., and Kawahata, H., 1999. Partial pressure of carbon dioxide in coral reef lagoon waters: comparative study of atolls and barrier reefs in the Indo-Pacific Oceans. *Journal of Oceanography*, **55**, 731–745.

Tanzil, J. T. I., Brown, B. E., Tudhope, A. W., and Dunne, R. P., 2009. Decline in skeletal growth of the coral *Porites lutea* from the Andaman Sea, South Thailand between, 1984 and, 2005. *Coral Reefs*, **28**, 519–528.

Veron, J. E. N., 1995. *Corals in Space and Time*. Sydney: UNSW Press, 321 pp.

Veron, J. E. N., 1996. *Corals of Australia and the Indo-Pacific*. North Ryde: Angus and Robertson Publishers, 644 pp.

Veron, J. E. N., 2000. *Corals of the World*. Townsville: Australian Institute of Marine Science.

Veron, J. E. N., 2008. Mass extinctions and ocean acidification: biological constraints on geological dilemmas. *Coral Reefs*, **27**, 459–472.

Wallace, C. C., 1999. *Staghorn Corals of the World*. Collingwood: CSIRO Publishing.

Winters, G., Loya, Y., Rőttgers, R., and Beer, S., 2003. Photoinhibition in shallow-water colonies of the coral *Stylophora pistillata* as measured in situ. *Limnology and Oceanography*, **48**, 1388–1393.

Wolanski, E., and Hamner, W., 1988. Topographically controlled fronts in the ocean and their biological influence. *Science*, **241**, 177–181.

Wooldridge, S. A., 2009. Water quality and coral bleaching thresholds: formalising the linkage for the inshore reefs of the Great Barrier Reef, Australia. *Marine Pollution Bulletin*, **58**, 745–751.

Cross-references

Acanthaster planci
Adaptation
Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity
Cold-Water Coral Reefs
Corals: Biology, Skeletal Deposition, and Reef-Building
Hydrodynamics of Coral Reef Systems
Tropical Cyclone/Hurricane
Tsunami
Waves and Wave-Driven Currents

CORE PLUGS

Eric G. Matson
Australian Institute of Marine Science, Townsville, QLD, Australia

Definition

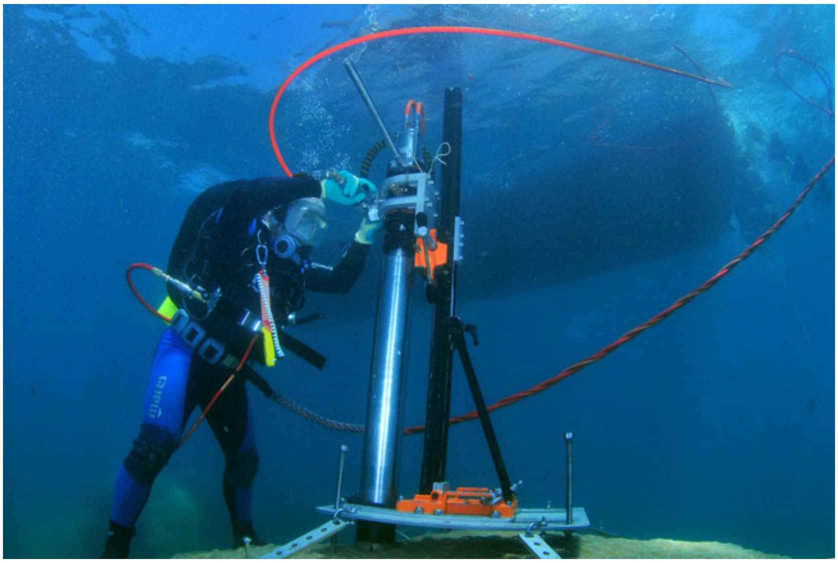
Many massive corals contain annual density bands in their calcium carbonate skeletons, similar to tree rings. Growing at ~1–2 cm/year coral bommies[1] several meters in height can contain several hundred years of continuous coral growth. The annual density bands (visible when slices from coral are X-rayed) provide the chronological control for the extraction of a wealth of high-resolution coral growth and coral paleoclimatic records. These make a substantial contribution to understanding the nature and causes of climate variability and change, in the shallow-water tropical ocean regions, prior to the advent of extensive observational records and complement similar records obtained from tree rings, ice cores, and documentary sources.

Accessing this information requires a sample from the coral and bigger, older corals will provide data over a longer time span (Figure 1). The preferred sampling technique requires the extraction of a core from the coral colony with a tubular drill rig (Figure 2) The corer cuts through the concentric layers of colony growth and when the core is removed, a hole through the colony is created from the living surface to the base. The living tissue of the coral only occupies the outer 0.5–1.0 cm of the colony (the layers below are dead but retain their physical structure), so taking a core 90 mm in diameter removes ~ 63 cm^2 of live coral.

Holes left by coring activities create opportunities for boring organisms to invade a colony and provide a place for sediment to collect and both of these possibilities may cause long term damage to the colony. Many workers seal the core holes with a solid plug to prevent borer access and eliminate sediment collection. Concrete is mostly used to make tapered, cylindrical plugs, slightly larger than the core hole at the big end and slightly smaller at the other end. This taper allows the plug to fit tightly into the hole and remain firmly in place as the coral continues to grow. The plugs are made well before use and soaked in sea water for a month to eliminate soluble components that could damage the coral (Figure 3).

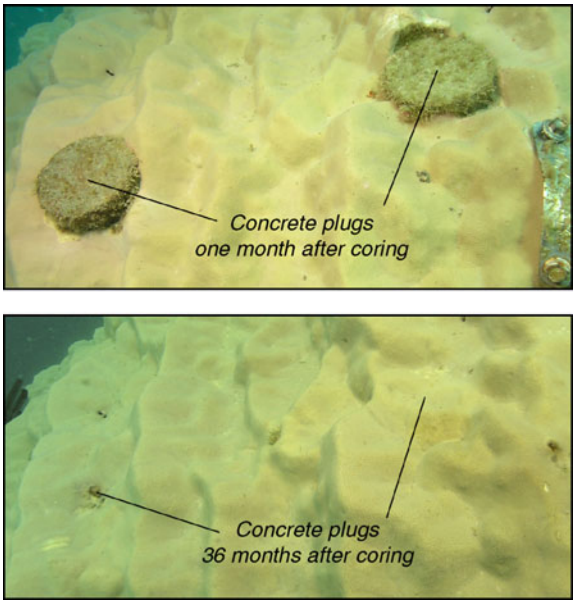
Studies on the Great Barrier Reef (Australia) over a 3 year period have shown that colonies of Porites (sp) are not damaged by the plugs and are able to grow over the concrete plugs completely. The rate of regrowth is dependent on the coral species and prevailing environmental conditions. The relief of the plugs is also important; plugs that sit flush with the colony surface are more likely to be grown over, than those that are higher than the surrounding coral structure (Figure 4). In the GBR study which looked at Porites regrowth after 50 mm diameter cores were taken, the shortest time taken to completely grow over the concrete plug was ~ 30 months, whilst others were still less than half covered after 36 months. A small

Core Plugs, Figure 1 Cores taken form massive, long lived corals like this Porites sp. can provide data about climatic conditions that pre-date instrumental records.



Core Plugs, Figure 2 Cores are extracted from the colony using a variety of methods, shown here is a powerful hydraulic drill rig clamped in place with the operator about to commence cutting.

Core Plugs, Figure 3 When the core has been removed, a hole is left in the colony and this is plugged with a tapered, conical, concrete plug. These plugs are pre-washed in sea water to eliminate soluble toxins and are hammered home in level with the natural surface.



Core Plugs, Figure 4 The *upper portion* of this image shows part of a colony cored and plugged a month before the photo was taken. The *lower portion* of the image shows the same colony 36 months later. The healthy coral has continued growing normally and covered both plugs completely.

number of the colonies showed no growth on the concrete plugs at all.

One of the cored colonies had no plug and acted as a control. This colony not only had apparent damage which could be attributed to the coring activity, but also showed very little of the horizontal growth evident, where plugs were used.

Cores taken from massive long lived corals can provide valuable paleoclimatic information and coral growth histories. The value of these cores must be weighed against the potential risk to the colonies from which the cores are extracted. Sealing the core holes with tapered concrete plugs that have been conditioned by long pre-immersion in sea water reduces the likelihood of long-term damage to cored colonies and in many cases assists the colony to overgrow the damaged area in a relatively short time.

[1] The term “coral bommie” is used in Australia to describe large outcrops of coral often visible from the surface, usually separated from the main reef. In this article, it refers specifically to individual, living colonies of the Porites genus as seen in Figure 1.

Cross-references

Reef Drilling