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Reef coral diversity and global change

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Abstract

Regional anthropogenic processes such as pollution, dredging, and overfishing on coral reefs currently threaten the biodiversity of stony corals and other reef-associated organisms. Global climate change may interact with anthropogenic processes to create additional impacts on coral diversity in the near future. In order to predict these changes, it is necessary to understand the magnitude and causes of variation in scleractinian coral diversity throughout their 240 million year history. The fossil record documents long periods of speciation in corals, interrupted repeatedly by events of mass extinction. Some of these events relate clearly to changes in global climate. Diversity in reef corals has increased since their last period of extinction at the end of the Cretaceous (65 My BP), and is still rising. During the last 8 million years, the fragmentation of the once pantropical Tethys Sea separated corals into two major biogeographical provinces. Periods of glaciation also have caused major changes in sea level and temperature. Accumulated evidence supports the theory that relative habitat area and changing patterns of oceanic circulation are mainly responsible for the two observed centres of recent coral diversity at the western tropical margins of the Atlantic and Pacific oceans. At predicted rates of climate change in the near future, coral reefs are likely to survive as an ecosystem. Increases in sea level may actually benefit corals and lead to regional increases in diversity if new habitat area on back reefs is opened to increased water circulation and thus coral dispersal. Rising temperature may cause higher rates of coral mortality and even local extinction in isolated, small populations such as those on oceanic islands. The effects of increases in ultraviolet radiation (UV) are largely unknown, but likely to be negative. UV may damage planktonic coral propagules in oceanic surface waters and thus decrease rates of gene flow between coral populations. This may result in increased local extinctions, again with the strongest impact on widely separated reefs with small coral populations. The largest threats to coral diversity are regional anthropogenic impacts, which may interact with global climate change to exacerbate rates of local species extinctions. Centres of high reef coral diversity coincide with human population centres in south-east Asia and the Caribbean, and thus the greatest potential for species loss lies in these geographical areas.

Keywords: biogeography, climate change, coral reef, diversity, evolution, human disturbance, Scleractinia

Introduction

Tropical coral reefs and rain forests are two of the most diverse natural communities on earth, and are similar in their high level of biologically generated physical complexity and co-evolved associations between species. The diversity of living organisms (= total number of species) on coral reefs is probably several orders of magnitude higher than presently known, in part because many reef organisms are small and cryptic, and thus difficult to find and collect (Reaka-Kudla 1996). Rates of species extinction on coral reefs likely are also much higher than realized, and are rising (Reaka-Kudla 1996). Coral reefs currently are undergoing a process of degradation, due to anthropogenic stresses such as dredging, pollution and overfishing, especially on reefs situated near human population centres in south-east Asia and the Caribbean (Wilkinson 1992, 1996; Roberts 1993; Hughes 1994). Global processes of climate change predicted for

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the near future also may impact the diversity of reef organisms. Aspects of global climate change with the largest potential effect on the species diversity of reef organisms include predicted increases in sea level, temperature, and levels of ultraviolet radiation (Glynn 1991, 1996; Smith & Buddemeier 1992; Shick *et al.* 1996; Wilkinson 1996). In order to assess the potential mechanisms and magnitude of change in species diversity that may occur on reefs in the future, it is important to examine the patterns and causes of such change during the long geological history of reef-building corals.

I review here the evolution of reef-building scleractinian corals since their appearance 240 million years before the present (My BP). I focus on climate and plate tectonic changes over time, and concurrent patterns of coral radiation and extinction during major geological periods. Then I discuss existing patterns of coral diversity and the theories proposed to explain them. Finally, I examine rates of global climate change predicted to occur in the near future, and their potential impacts on reef coral diversity worldwide. I rely heavily on the extensive review by Veron (1995), to which the reader is referred for a more in-depth analysis of coral evolution and biogeography.

Patterns of reef coral diversity during geological history

Scleractinian corals are the major builders of recent coral reefs (Achituv & Dubinsky 1990). They have a long and well-documented geological history, due to their aragonite skeletons which easily fossilize and are abundant in fossil deposits at sites around the world. The geological history of patterns of reef coral diversity is based on these fossil deposits, and reconstruction of palaeoclimates and tectonic plate movements (Newell 1971).

The earliest coral reefs appeared in the Palaeozoic Era, more than 450 My BP (Hill 1956). They were built by rugose and tabulate corals, both of which became extinct at least 5 million years before the first appearance of scleractinians during the mid-Triassic, ≈ 240 My BP (Wells 1956). Rugose corals had a different pattern of septal arrangement and skeletal secretion than do scleractinians, and thus are unlikely to be the direct ancestors of the Scleractinia (Veron 1995). When the Scleractinia first appeared in the Triassic, the earth's climate was warmer than today, and there was a wide tropical zone. The continents were unified as a super-continent, Pangaea, with one large world ocean, Panthalassa (Fig. 1a). Oceanic circulation in Panthalassa likely was very wide latitudinally due to the great size of the ocean. Thus, warm water currents probably reached farther from the equator than they do today (Veron 1995 and references therein).

The Scleractinia probably evolved from a non-calcareous anthozoan ancestor (Veron *et al.* 1996). Analysis of fossils shows that seven suborders of Scleractinia appeared in the mid-Triassic (Fig. 2). New molecular evidence indicates that the Scleractinia as a group are monophyletic, although some lines within the group may have diverged at or before the evolution of skeletogenesis (Romano & Palumbi 1996; Veron *et al.* 1996). The ancestors of lightweight corals with complex architecture (including the families Acroporidae, Agariciidae, and Poritidae) may have separated very early from those with more massive, heavily calcified skeletons (including the families Fungiidae, Faviidae, and Siderastreidae) (Romano & Palumbi 1996).

The earliest Scleractinia were widely scattered, solitary, and did not build reefs (Wells 1956). By the late Triassic, they had become more widespread and colonial. They built scattered reefs throughout the Tethys Sea and tropical rim of the Panthalassa Ocean (Wells 1956; Newell 1971) (Fig. 1a). The Tethys Sea was a tropical seaway which slowly opened between the northern and southern continents as they separated, and which was a major habitat occupied by reef corals during most of their long history (Newell 1971). During the Triassic, the Tethys Sea was still closed at its western end, and thus oceanic circulation was not yet circumglobal (Fig. 1a). Sixty-seven genera of corals evolved in 17 families during this period (Fig. 2), but by the end of the Triassic, a major extinction of marine life occurred, which only 18 genera (= 29%) of scleractinian corals survived (Veron 1995).

Reef-building ceased for 4–10 million years following the end-Triassic extinctions (Wells 1956; Veron 1995). At the start of the Jurassic, the proto-Atlantic Ocean opened as the western and eastern continents separated, and the Tethys became much more extensive, reaching all the way to eastern Panthalassa, and resulting in circumglobal circulation along the equator (Fig. 1b). This change, with its great increase in shallow tropical seas, probably was responsible for the great radiation of the Scleractinia during the Jurassic (Veron 1995). At this time the Scleractinia reached their all-time high diversity of 150 genera in the Tethys Sea and 51 in Panthalassa Ocean, compared with a total of only 117 extant genera today (Veron 1995). Scleractinians became the major reef builders and constructed extensive reefs throughout the expanded Tethys Sea, including the future Mediterranean and Caribbean (Wells 1956) (Fig. 1b). The Panthalassa Ocean probably acted as a barrier to dispersal, much as the Eastern Pacific Barrier does today (Veron 1995). Several distinct biogeographical provinces of corals developed during the Jurassic (Newell 1971).

Corals continued to exhibit high diversity throughout the Cretaceous (Fig. 2). Due possibly to changing geochemical conditions for carbonate deposition in the sea,

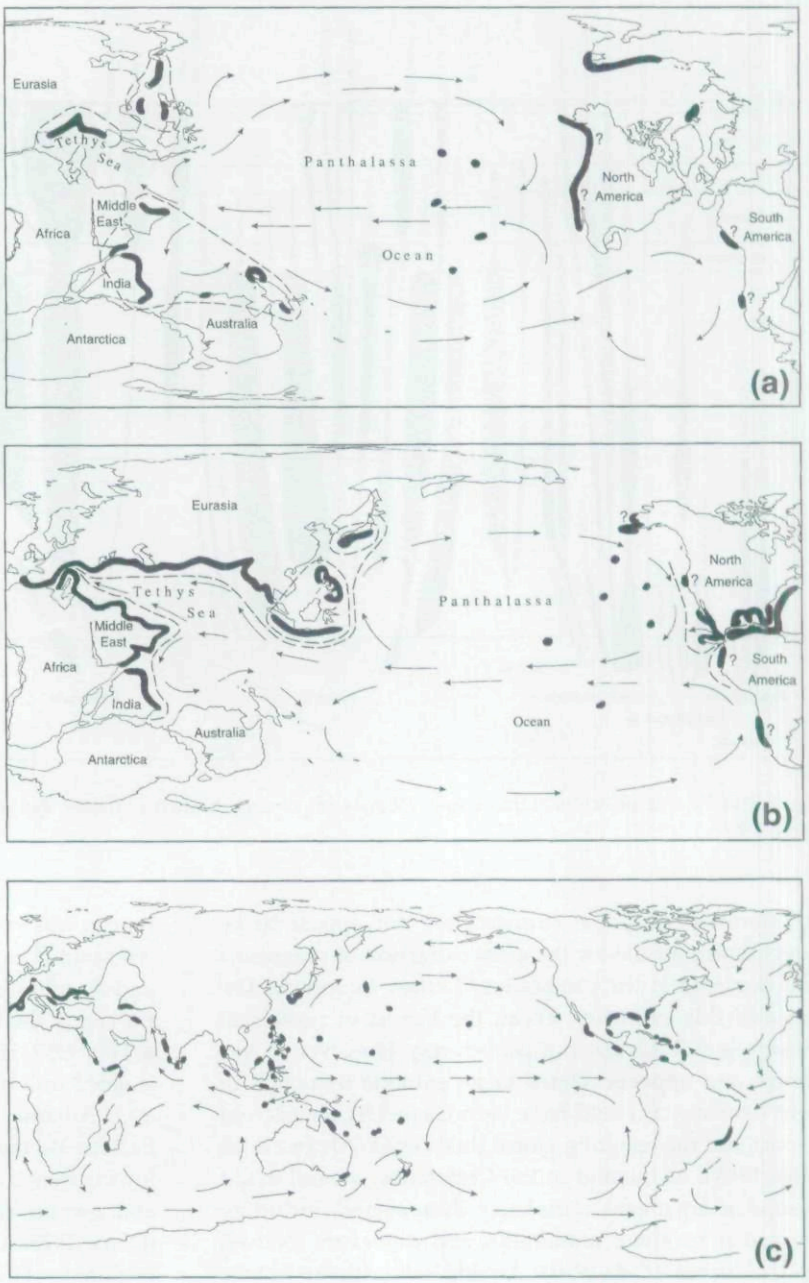

Fig. 1 The ancient world during selected geological intervals, showing distribution maxima of coral reefs and/or reef corals. Broken lines enclose principal coral provinces (after Veron 1995). (a) Late Triassic, (b) late Jurassic, (c) Miocene.

rudist bivalves replaced scleractinians as the main reef builders during the early Cretaceous, and remained dominant for 30 million years (Veron 1995). Corals co-existed with rudists during this time, but occurred in deeper habitats along the seaward margins of reefs (Newell 1971). The continents continued to spread, and the earth entered a warming period, in which temperatures reached 10–15°C higher than at present, the poles were devoid of ice, and a wide band of warm water may have extended from 45°N to 70°S (Veron 1995). These conditions allowed coral reefs to extend further latitudinally than they do today, with approximately equal extension to the north and south of the equator (Newell 1971). Major changes in sea level accompanied these climate changes, in which almost 40% of continental area became submerged. This great increase in the surface area of shallow warm seas also had a positive effect on coral reef development (Veron 1995). By the end of the Cretaceous, all major extant families of reef corals had evolved (Fig. 2), and most genera were distributed througout the tropics due to circumglobal water circulation in the open Tethys seaway (Veron 1995).

At the end of the Cretaceous, sea level receded as the earth cooled and entered a glacial mode. However, this

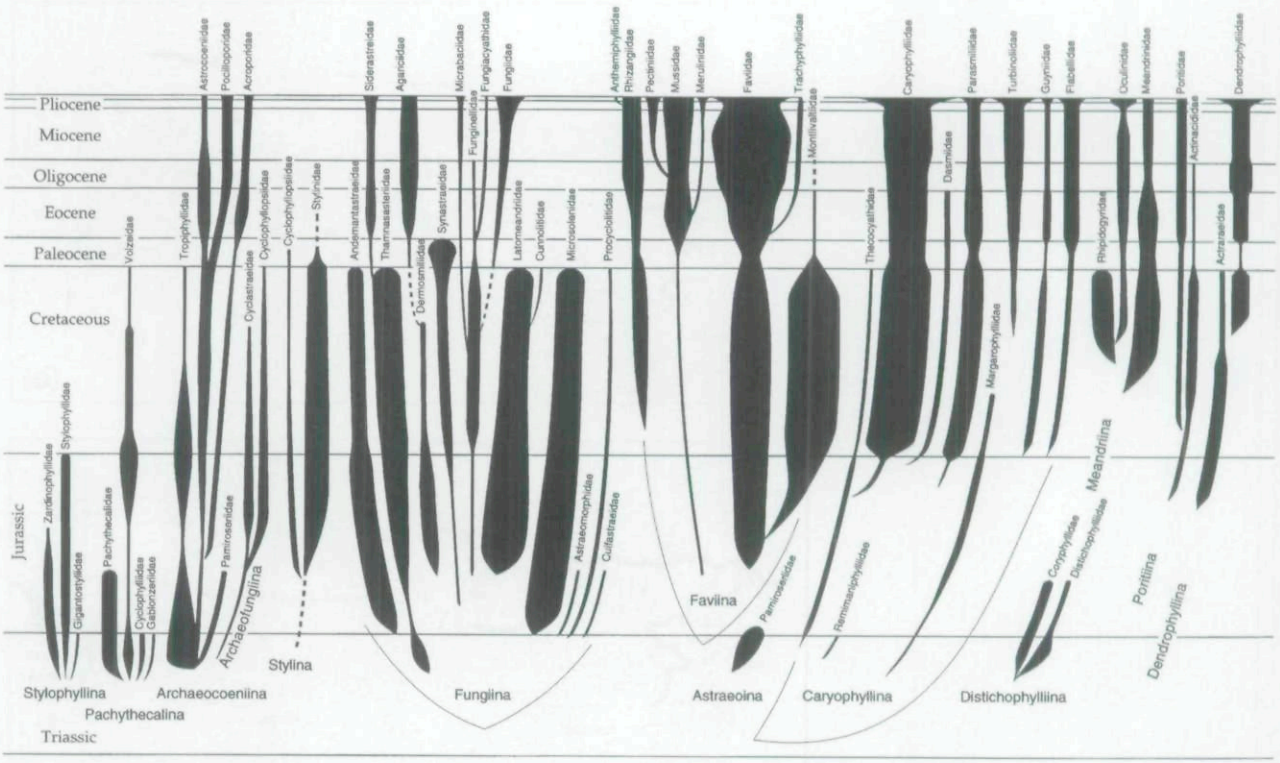

Fig. 2 Family tree of scleractinian corals. The width of each branch indicates the relative number of genera in each family (after Veron 1995).

deterioration of global climate does not appear to be directly responsible for the mass extinction of organisms that occurred at the Cretaceous/Tertiary boundary. The cause of this extinction event, the largest in geological history, is still a subject of controversy. However, it was abrupt and appears related to an extreme reduction in light intensity, as could have been caused by an asteroid impact and the resulting global dust cloud (Alvarez *et al.* 1980, 1984). At the end of the Cretaceous, several major groups of organisms completely disappeared, including the rudist bivalves, ammonites and dinosaurs (Newell 1971; Alvarez *et al.* 1980). Among scleractinian corals, 70% of genera and 1/3 of families became extinct (Veron 1995). This event marks the end of the era of highest diversity in reef corals, which spanned more than 170 million years during most of the Mesozoic (Fig. 2).

During the relatively short period of the Cenozoic (65 My BP to the present), coral diversity slowly increased from the small number of species that survived the Cretaceous. By the end of the Oligocene (24 My BP), scleractinians had radiated into more than 100 genera, and during the Miocene most extant species of corals evolved (Veron 1995). The Tethys Sea closed due to land movement in the Middle East area, creating a final barrier to circumglobal circulation (Wells 1956; Newell 1971) (Fig. 1c). The once diverse reef coral fauna of the Mediterranean was exterminated as this sea became an evaporative basin (Veron 1995). During the Pliocene, the Atlantic and Pacific Oceans became completely separated with the rise of the Isthmus of Panama at 3.5–3.2 My BP (Grigg & Hey 1992) (Fig. 1c). With these events, reef corals were isolated into the two major provinces of the Indo-Pacific and Atlantic that define recent coral biogeography. Eastern Pacific corals underwent a major extinction following their separation from the Caribbean faunal region, and remain an isolated and depauperate fauna today (Dana 1975; Glynn & Colgan 1992) (Fig. 3). At the beginning of the Pleistocene (2.5 My BP), the world entered full glacial mode, with accompanying extremes of sea level and climate change. Sea level has undergone at least 17 cycles of rise and fall during the Pleistocene, ending in the most recent low sea-level stand of 120–135 m below present level, at 18 000 years ago (Grigg & Epp 1989). This resulted in emergence of an almost continuous land mass between Australia and Asia, and temporarily separated the reef corals of the Pacific and Indian Oceans (Potts 1983; Pandolfi 1992b). The high-diversity coral fauna of south-east Asia was displaced to an eastern Indonesian refuge, and the area was repopulated entirely from its eastern margin when sea level rose again (Veron 1995).

The impact of recurrent and rapid Pleistocene sea-level

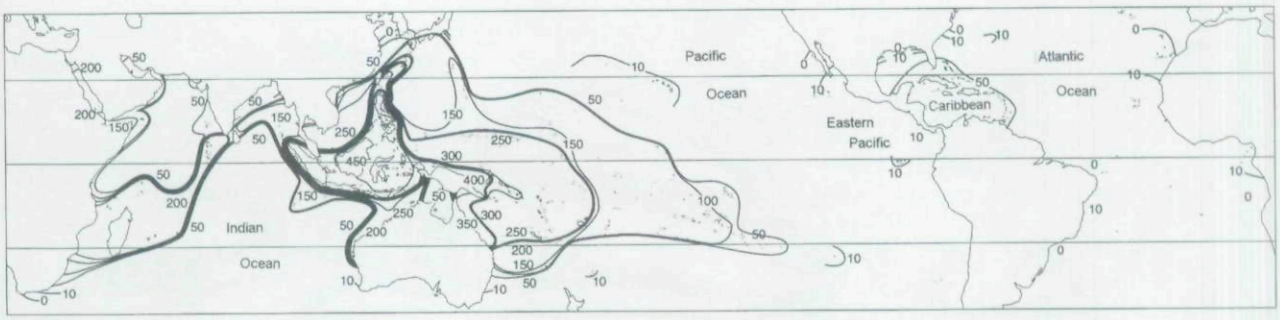

Fig. 3 Recent patterns of species diversity in scleractinian reef corals. Contour lines were derived from the distribution ranges of genera and species, and show the estimated total number of species in each area. The Indo-Pacific region includes both the Indian and Pacific Oceans (after Veron 1995).

changes on coral evolution in south-east Asia is a subject of debate. Some authors claim that the changing habitats available to reef corals during this time may have induced high rates of speciation, as populations of scleractinian corals became isolated during periods of low sea level (McManus 1985; Rosen 1988 and references therein). Others support the view that Pleistocene sea level changes retarded speciation in reef corals (Potts 1983, 1985; Veron 1995). In South-east Asia, coral communities were in an almost constant process of retreat from the Coral Sea as sea level fell, followed by recolonization of the area as sea level rose again. Rates of sea-level change were rapid (mean = 20 m per 3200 years) relative to the timespan needed for speciation via genetic isolation between populations, due to the relatively long lifespans of hundreds of years in some corals (Potts 1983, 1985). If the latter theory of lack of speciation during the Pleistocene is correct, it may explain in part the homogeneity of south-east Asian coral fauna. Due to the close proximity of islands in the region relative to the dispersal capacity of some corals, separate populations likely resumed gene flow frequently between glaciations. The lack of differentiation among corals in this area may have been enhanced further by the process of hybridization between closely related coral species, creating a pattern of reticulate evolution in which coral taxa may have diverged and then reunited later, much as is known for some terrestrial plant species (Veron 1995).

After the close of the Pleistocene (10 ka), scleractinians began to build present-day coral reefs at ≈ 9–6 ka (Veron 1995; Kayanne 1996). Reef corals became locally extinct from some marginal areas such as Hawaii (Grigg 1981) and possibly the tropical eastern Pacific (Dana 1975) during climate changes in the Pleistocene, and are in the process of recolonization.

Recent patterns of reef coral diversity

The biogeography and diversity of recent reef corals is the product of separation of a once pantropical fauna into two distinct regions, recovery from the last ice ages, and recolonization of depopulated areas (see above). The two major provinces of the Indo-Pacific and Atlantic have almost no species overlap, and share only 7 out of 117 total recent coral genera (= 6%) (Veron 1985).

A large proportion of coral genera became extinct in the Atlantic following the rise of the Isthmus of Panama and subsequent climate changes (Veron 1985; Achituv & Dubinsky 1990). The centre of Atlantic coral diversity, the Caribbean Sea, is small and under strong continental influence (Fig. 3), and thus easily affected by climate changes as well as anthropogenic stress (Wilkinson 1992; Roberts 1993). Only 65+ recent coral species in 27 genera occur in the Atlantic; one of these (*Siderastrea radians*) also is found in the Indo-Pacific (Veron 1995). The Gulf Stream carries warm water and coral propagules from the tropical Atlantic to sites along the eastern coast of North America, thus extending the latitudinal range of Atlantic corals (Figs 3 and 4). Reef corals are absent from much of tropical eastern South America (Fig. 3), likely due to the large amounts of fresh water and sediment released by the Amazon and Orinoco rivers. In the eastern tropical Atlantic, the westerly direction of equatorial currents (Fig. 4) may prevent the immigration of coral propagules from Caribbean populations, resulting in low reef coral diversity (Fig. 3). The diversity of reef corals in the Atlantic Ocean is much lower than that of the Indo-Pacific region. This may be due to the geographical isolation in the Atlantic of a relatively small area of coral habitat, and climate changes during the Pleistocene which resulted in mass extinctions (Veron 1985).

The Indo-Pacific region harbours the highest diversity of recent scleractinians, with > 500 species in 97 genera (Veron 1995). The region is relatively homogenous faunistically, and some coral species span the entire region. There is a clear centre of diversity in the west Pacific, where > 450 coral species co-occur, although relatively high diversity of > 200 species extends across the Indian Ocean to the Red Sea (Fig. 3).

Latitudinal patterns of reef coral diversity are thought

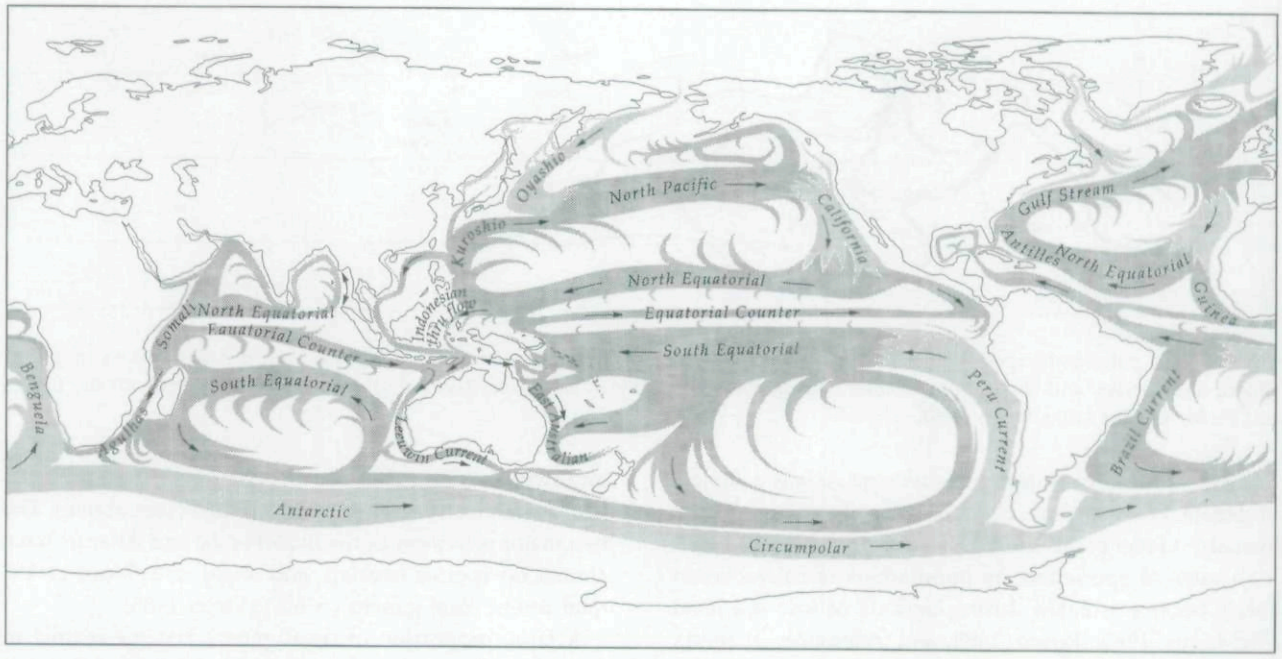

Fig. 4 Oceanic surface circulation patterns. Only the major patterns are shown, without seasonal variations or regional detail (after Veron 1995).

to be governed primarily by ocean circulation that carries warm water away from the tropics along the western margins of the oceans (Veron 1988; Veron & Minchin 1992). The effect is seen in the latitudinal extension of reef corals along the coasts of Japan, eastern Australia, and south-east Africa (Fig. 3). The complete absence of reef corals from large expanses of deep water in the Indian and Pacific Oceans is due to lack of the shallow hard substratum required for coral growth. Low diversity in some tropical continental shelf areas which do contain suitable shallow habitats for reef corals, appears to be related to adverse environmental conditions, such as high salinity and extreme temperatures in the Persian (Arabian) Gulf (Coles 1988) and low salinities around much of India (Rosen 1971; Achituv & Dubinsky 1990).

Reef coral diversity decreases eastward in the Pacific Ocean, and corresponds to a decrease in shallow habitat area and the increasingly upstream position of islands in predominantly westward-flowing tropical surface currents (Fig. 4). A large expanse of deep water with no islands, termed the East Pacific Barrier, separates the depauperate eastern Pacific coral fauna from the rest of the Indo-Pacific (Fig. 3). As well as being geographically isolated, the corals of the eastern Pacific exist under extreme environmental conditions, on a narrow continental shelf subjected to cool upwelled waters, low salinity and high turbidity (Glynn & Stewart 1973; Dana 1975; Glynn & Colgan 1992). Reef corals may have become largely extinct in the eastern Pacific following the rise of the Isthmus of Panama (Dana 1975). Since then, reefs in this area have undergone repeated cycles of damage and recovery (Glynn & Colgan 1992). Present rates of extinction among eastern Pacific corals probably are high due to the marginal and changing physical conditions, and their small population sizes. During the 1982–83 El Niño–Southern Oscillation (ENSO) event, which resulted in local climate anomalies, the reef coral fauna of the Galapagos Islands experienced 97% mortality, a near extinction (Glynn 1991; Glynn & Colgan 1992). Eastern Pacific reefs presently are in a process of recolonization from the west, retarded by the westward direction of most surface currents in the tropical Pacific, and the great size of the East Pacific Barrier (Dana 1975; Glynn & Colgan 1992).

Centres of high coral diversity occur at the western margins of the Atlantic and Pacific Oceans, and to a lesser extent at the western edge of the Indian Ocean (Fig. 3). The causes of this pattern have been the subject of speculation and conflicting theories (reviewed by Rosen 1988 and Veron 1995). Stehli & Wells (1971) proposed that centres of reef coral diversity along the western margins of the oceans (Fig. 3) are centres of species origin. According to their theory, these areas have high local rates of speciation, and newly evolved species spread out to more peripheral areas. McManus (1985) and Pandolfi (1992a) have further claimed that the Indo-Pacific diversity centre, south-east Asia, has high rates of speciation because marine populations in the area were successively isolated during glaciations, and then rejoined after divergence of species was complete, resulting in

overlap between separated faunas in the Pacific and Indian Oceans. This view has been challenged by Potts (1985) who claims that low rates of coral speciation occurred during the Pleistocene glaciations (see discussion above). Pandolfi (1992b) also has proposed that marginal areas in the Indo-Pacific have high speciation rates, as evidenced by their high proportion of endemic coral species, and that these newly evolved species then migrate into centres of diversity.

A problem with all of the above theories is that there is no clear evidence that sites of present occurrence of coral species correspond to their sites of origin. Thus, patterns of endemism or faunal overlap cannot be related conclusively to sites of coral speciation, and cannot serve as comprehensive explanations for centres of diversity (reviewed in Rosen 1988 and Veron 1995). Sites of coral species origin in most cases are probably obliterated by the effects of changing oceanic circulation patterns, which repeatedly connect and reseparate coral populations (Veron 1995). The control of genetic connectivity between corals by a changing physical factor (water currents) results in a process of reticulate evolution, in which coral taxa may successively speciate and hybridize depending the strength of water circulation patterns between populations on different reefs (Veron 1995). According to Veron, three major factors may be important to the maintenance of western foci of diversity in reef corals: (i) the large surface area of shallow habitat for corals in the western tropical Pacific and Atlantic Oceans; (ii) The capacity for long-distance dispersal via currents in some corals; and (iii) the predominantly westward direction of tropical oceanic currents.

The first factor is important because, due to their large surface area of shallow substratum, the western tropical Pacific and Atlantic may support large populations of corals in many types of habitats. This factor alone may lead to low rates of extinction and greater chances for successful establishment of coral species, relative to smaller areas with less diverse coral habitats (i.e. small oceanic islands) (Rosen 1971; Veron 1995).

The second factor of potentially long lifespan in coral propagules means that some coral species may be able to colonize habitats far from their places of origin. A long larval lifespan of up to several months (100 days) has been demonstrated for only one coral species (Richmond 1987). Other examined corals have shorter-lived larval phases of 20–30 days, and thus their larvae may disperse relatively short distances (Harrison *et al.* 1984). However, some corals also have a second mechanism of dispersal, in that they may attach attach to pieces of floating material such as pumice, wood, or even human debris (Jokiel 1989, 1990). Rafted coral colonies have potential dispersal phases of years, and may release sexually produced larvae along the way (Jokiel 1989). The capacity for long planktonic life (as larvae or rafted colonies) in at least some corals probably allows enough gene flow between closely space islands in the western Pacific and Atlantic (Fig. 3) to maintain large, interbreeding populations within these areas (Veron 1995). Between more widely separated coral populations, oceanic circulation serves as the main mechanism of long-distance dispersal and thus genetic continuity. Changing circulation patterns during palaeoclimate cycles have thus controlled the evolution of new coral species (Veron1995).

The impact of the third factor, the predominantly westward direction of tropical currents (Fig. 4), is that surface waters carry coral propagules toward the western edges of oceans, and provide one-way gene flow to latitudinally marginal coral faunas, such as those in Japan and southeastern Australia (Veron 1995). These currents also progressively isolate central and eastern Pacific coral populations. Jokiel & Martinelli (1992) designed a computer simulation in which they showed that the western Pacific focus of diversity in corals could be generated by the sole mechanism of coral dispersal via oceanic circulation patterns. Thus, centres of coral diversity may represent sites of accumulation of species rather than of species origin.

The above factors of habitat area and current patterns may largely explain the high-diversity centres of reef corals in the western Pacific and Atlantic oceans. In contrast, relatively high diversity extends across the Indian Ocean, with lack of a clear western focus. This pattern also may be explained largely by physical factors. The Indian Ocean is the only one with an eastern source of high diversity coral propagules, via an open connection with the tropical western Pacific (Fig. 4). It is also the only ocean with a continuous continental margin within the tropics to further facilitate coral dispersal (Fig. 3). Finally, only the Indian Ocean lacks a large surface area of shallow habitat along its western margin, and thus this area cannot support large coral populations relative to those in the western Atlantic and Pacific oceans. The control of coral diversity by physical factors would also account for the regional phenomenon of high diversity in the Red Sea (Fig. 3), which benefits from circulation patterns in the Indian Ocean (Fig. 4) that carry diverse coral propagules to this otherwise geographically marginal area.

There is a great deal that cannot be known about the causes of coral diversity patterns. For most geographical areas, coral diversity has been determined reliably only to the level of genus (Veron 1995). This fact has distorted previous analyses of coral evolution, because genera with many species are given equal weight to those with only one or a few species. Even so, estimated patterns of coral species diversity (Fig. 3) do not substantially differ from those of genera (reviewed in Veron 1995). Despite the

many unsolved problems in recent coral biogeography, the impacts of near-future global change on patterns of coral diversity can be predicted to some extent.

Effects of global change

Substantial global climate change is expected to occur in the near future, caused mainly by increasing concentrations of radiatively active gases in the atmosphere from anthropogenic sources. This alteration in the earth's atmosphere will result in a net global warming, and increase in certain wavelengths of irradiance (reviewed by Smith & Buddemeier 1992; Shick *et al.* 1996). I will focus here on three specific aspects of predicted climate change and their impact on reef coral diversity: increases in (i) sea level, (ii) sea temperature, and (iii) levels of ultraviolet radiation.

Sea level is expected to rise ≈ 50 cm during the next 100 years (range = 15–95 cm) (IPCC 1995; see also similar figures in Smith & Buddemeier 1992). This rate compares with known rates of vertical coral reef growth of 1–10 mm y^{-1} (= 10–100 cm/100 years) (reviewed by Smith & Buddemeier 1992). Thus, many reefs will be able to keep up with the predicted sea-level rise. Even if not, they will be submerged by less than one metre during the next century. Many coral reefs have already reached their upward limit of growth at present sea level (Buddemeier 1992), and may be released from this vertical constraint by a rise in sea level. Rising sea level also may allow more water circulation between segregated lagoons and outer reef slopes. This could increase the exchange of coral propagules between reef habitats and lead to higher coral diversity in inner reef areas. A recent international conference concluded that reef corals would probably benefit from some sea level change (Roberts 1993). In the past, reef corals have survived sea level rises of > 200 cm per 100 years, lasting for periods of > 1000 years, which is more than twice the rate predicted for the near future (Smith & Buddemeier 1992).

Tropical sea surface temperatures are expected to increase by 1–3 °C during the next century (Wilkinson 1996). This rate compares with changes of 2–4 °C since the last glacial period (Smith & Buddemeier 1992). Recent reef corals appear to be locally adapted to sea temperatures. Thus, corals from Enewetak where the local average maximum temperature is 31 °C exhibit the same metabolic stress responses to elevations of 1–2 °C as do corals from Hawaii where the local maximum is only 27 °C (Jokiel & Coles 1990). Given the close association between coral metabolism and local sea temperatures, global warming may result in increased rates of damage and mortality to reef corals at sites around the world. Corals react to thermal stress by bleaching, in which they lose their symbiotic zooxathellae. Prolonged bleaching leads to decreased rates of growth and reproduction, and if corals do not recover their zooxanthellae, eventually to the death of entire colonies (Glynn 1996). High-temperature stress may thus result in increased rates of local extinction, especially of small coral populations at isolated sites. At the geographically isolated Galapagos Islands, thermal stress associated with an ENSO event has been documented to cause 97% mortality in reef corals (Glynn 1991; Glynn & Colgan 1992). Small and otherwise non-lethal increases in global temperature may interact with climate anomalies such as ENSO events to further elevate sea temperatures during short periods. One positive effect of temperature increase on coral diversity is that it may extend high diversity to some reefs in latitudinally marginal areas, which presently are temperature-limited (Johannes *et al.* 1983; Veron & Minchin 1992). However, some marginal reefs which experience wide variation in temperature (both extreme lows *and* highs), as in the Arabian Gulf (Coles 1988), may be negatively impacted by increased temperatures.

Levels of tropical irradiation at ultraviolet (UV-B) wavelengths are expected to increase by 1–10% in the near future (Smith & Buddemeier 1992). This is a small increase, but the potential impacts are poorly understood. UV-B is known to damage planktonic organisms floating in oceanic surface waters (reviewed in Smith & Buddemeier 1992; Shick *et al.* 1996). Since corals disperse mainly via planktonic larvae, increases in UV-B could have potentially far-reaching effects on coral biogeography. Reduced viability of planulae larvae would cause coral populations to become more genetically isolated, and depress the recruitment rates of young corals to benthic habitats. UV-B radiation also may combine with elevated temperature to accelerate coral bleaching (Drollet *et al.* 1995; Glynn 1996; Shick *et al.* 1996). Although largely unknown, the effects of elevated UV on coral diversity are likely to be negative.

As an ecosystem, coral reefs are likely to survive predicted rates of global change. However, as documented in the geological record, substantial reduction in coral diversity may occur if global change extends over a long period, or becomes too rapid for corals to respond evolutionarily. A more immediate threat to the biodiversity of reef corals is regional anthropogenic stress, in the form of dredging, mining and overfishing. These pressures are most intense near human population centres, some of which coincide with centres of coral diversity (Wilkinson 1992, 1996; Roberts 1993). Thus, the highly diverse coral communities of south-east Asia and the Caribbean are the most threatened, and the potential for species loss is high. These regional stresses

may interact with global climate change to accelerate rates of biodiversity loss on coral reefs.

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