Post Pleistocene Urban Renewal in Coral Reefs

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Introduction

In this paper are examined some aspects of coral reef problems that have not been dealt with adequately before. The biological and ecological diversity of modern reefs is probably greater than any comparable association in earlier geological history. This is related to a very high order of trophic integration and organisation which is perhaps more complex than that of any other major ecosystem, terrestrial or marine. The evolution of such associations is not yet understood, especially as it seems to have taken place in one of the most stable of environments—the tropical sea shore. Although the geological record indicates that reefs are among the oldest continuously existing communities on earth, there is considerable evidence also that the modern reefs are not stable and mature communities but are undergoing successional changes typical of youthful assemblages.

The Maximum Age of Modern Reefs

With the onset of the continental glaciations of the Pleistocene period, there began a time of stress unusual in the long previous history of coral reefs. At least five major glaciations waxed and waned during the last million years, cold glacial climatic stages alternating with warm interglacial ones. Immense continental glaciers, concentrated in Antarctica and on the land masses surrounding the North Atlantic, grew by capturing water from the oceans and thereby caused large, rapid changes in the world wide sea level. These marine oscillations were eustatic in origin and are to be distinguished from more localised, relative, changes due to tectonic or isotatic factors. The amplitude of the glacially controlled sea level changes during the Pleistocene is estimated to have been between 250 and 300 meters. The present datum is only about two thirds of the maximum sea level recorded during earlier interglacial periods, some of which were certainly warmer and longer than the present warm stage. The existence of eustatic shorelines of Pleistocene age between 10 and 50 meters above modern sea level suggests that during one or more of the previous interglacial periods the Antarctic ice sheet must have been much thinner and Greenland perhaps deglaciated.

Despite the oscillations of the sea level occasioned by the growth and decay of the continental ice caps, the mean surface temperature of the tropical seas ap-

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pears to have remained relatively stable throughout with maximum variations of only ± 4°C. However, it is likely that the tropical belt became narrower during the glacial maxima and wider during the minima. No significant faunal or floral changes seem to have occurred in the marine tropics during this time.

Reefs are very sensitive to changes in sea level. Their well-known dependence on sunlight and high ambient temperatures restricts these communities to the upper 80 meters, and reef frame-building to the upper 20 meters of the euphotic zone in tropical latitudes. This is related to photosynthetic activity of the zooxanthellae present in all reef-building corals, which increases the calcification rate in direct proportion to the ambient light intensity; i.e., coral skeleton growth is much faster in the well illuminated shallow zones of the reef than in the deeper more shaded parts.

In the subsequent discussion it is important to keep in mind the differences between coral communities *per se* and coral reefs. The former are more or less "open" populations of individuals scattered on the bottom and lacking any built up foundation of their own, whereas the latter have as core a wave-resistant framework of large massive corals cemented and buried in place and forming discrete topographic structures which are maintained and expanded into the teeth of the prevailing seas. Whereas colonisation of new surfaces, *e.g.* wrecks, by simple coral communities takes only a few years, the establishment of a true framework community takes much longer, probably between 700 to 1500 years. Thus, the existence of framework reefs, modern or fossil, indicates shallow tropical conditions and a relatively stable sea level. Any fall, or regression, of the sea level will leave reefs "stranded", whereas a rapid rise will "drown" existing reefs.

We will now examine the effect of the sea level changes that took place at the end of the Pleistocene period with the melting of the last great continental ice sheets of North America and Europe, starting about 18,000 years ago. At that time the world wide sea level stood some 130 meters below the modern datum. The melting of the glaciers was so fast that the sea rose at an average rate of 1.1 cm yr., and a maximum rate of 2.3 cm yr., until approximately 5000 years ago when the sea stabilised at its present level. Because of the uneven melting rate of the glaciers, the rise of the sea occurred with a series of starts and stops. There were at least three intervals, each between 800 and 2000 years long, when the transgression of the sea slowed, stopped or even reversed for a short time. Apparently no reefs grew during the times of maximum rise, but during each of the temporary halts, approximately 14,000; 11,000; and 8,500 years ago, reefs started to grow, and characteristic bench marks such as tidal nips and wave-cut platforms were left at the −60 m, −40 m and −25 m levels respectively, only to be "drowned" when the sea rose again.

The stabilisation of the post glacial sea level at its modern datum only 5,000 years ago marks the beginning of the Recent period, and is a point in time before which the shallow water reefs of the present day could not have become established. Thus, even the oldest of the living reefs must have developed within historic times;

therefore, postdating the emergence of the Near Eastern, Indic, and Oriental civilisations by several millenia.

Chance and Variation in the Development of Modern Reefs

Several enigmatic features of coral reefs can be re-examined in the light of the supposition that the modern reefs are only just beginning to recover from their latest eustatic shock, and that processes akin to "urban renewal" are still occurring in these relatively young marine communities.

The first problem concerns the uneven, almost haphazard development of the outer reefs along any given coral coast. The seaward slope is in some places formed of extremely rich and diverse framebuilding communities, whereas in nearby localities the framework is missing and there are only scattered coral patches on bare rock. In many cases, there are no obvious environmental factors to which such uneven development can be related and no signs of past catastrophes such as hurricanes, earthquakes, tsunamis, and fresh water floods. All other things considered, the most likely explanation is that the development of frame-building reef communities, as contrasted to that of simple coral populations, is a matter of chance—in some localities the hermatypic populations reach the "critical mass" required for framework formation, whereas in other sites it may in varying degrees be slower or it may never start at all. The four or five millenia that have passed since the establishment of the modern reefs has not been long enough for random effects to be damped out.

A similar variability, probably also due to chance as it is not obviously related to environmental factors, is seen in the patchy distribution of the more abundant coral species on large reefs. For example, over considerable parts of the 150 km long north coast of Jamaica, the dominant framebuilding coral of the buttress zone is *Montastrea annularis*. However, scattered in an apparently random way, there are also extensive areas where the dominant buttress framebuilder is *Agaricia tenuifolia*.

The size, shape, and orientation of the buttresses, or spurs, are not dependent upon the particular species of framebuilder involved, but are a community adjustment to the force and direction of the prevailing seas. All other things being equal, the factor that seems to determine which corals become dominant in any part of a given reef zone is probably no different from that which governs the distribution of the reef communities themselves: chance. It seems possible that the observed variations in the species rank of corals in a mature reef community may have been established long before through perpetuation of what were initially local random nonuniformities of the pioneer coral populations which colonised the newly submerged sea bottom about 5000 years ago.

Diversity and Evolution of Reef Communities

There is considerable ecological and genetic polymorphism within populations of reef corals, and it may be supposed that the sudden and repeated sea level changes during the Pleistocene led to a certain degree of fragmentation of reef populations, resulting in isolation of gene pools and possibly to speciation. A classic example of this type of evolution is the Brazilian reef coral fauna which developed in isolation after being cut off from the main Caribbean root stock by the Amazon and Orinoco Rivers in the late Cenozoic.

Of the several types of variation found in corals, the best known is the form diversity related to environmental factors such as intensity and direction of light, turbulence, sedimentation, and so forth. These eco-variants are continuously intergrading and are not genetically controlled. A second type of variation among reef corals, less well understood although very widespread, is characterised by differences of color, thickness of coenosarc, and shape of calices and appears to be relatively independent of the environment. Such variants often grow side by side in the reef and more rarely are combined within single physiologically continuous colonies as chimaeras. There are no intergrades, and the forms appear to be genetically determined. A third source of variation in reef building coelenterates may be the zooxanthellae. Recent data from zoanthidea suggests that the zooxanthellae can influence the phenotype of the animal host. In some species of reef corals with a wide vertical range, the zooxanthellae in the deep water variants, growing under reduced light intensity, appear to be physiologically distinct from those of shallow water variants living in bright light.

In this context it may be significant that ahermatypic corals, which lack zooxanthellae, show very little eco-form diversity in comparison to the hermatypic, or reef building corals, even though they often occur together and are therefore exposed to similar environmental conditions.

The existence of various types of polymorphism among the reef corals must have adaptive significance. The repeated world-wide destruction of reef biotopes by the sudden sea level changes that accompanied the five major Pleistocene glaciations must have severely stressed the delicately adjusted reef eco-systems. Yet the well-preserved fossil reefs of the Pleistocene show that there has been no significant reduction of the coral fauna as a result, indeed, the number of reef corals seems slightly higher now than it was at any time during the Tertiary and Quaternary periods. It is possible that the stability of reef populations during the Pleistocene may be due to the inherent polymorphism which is really a kind of built-in redundancy. Unfortunately, such mechanisms fail to explain why the evolution of modern reef associations seems mostly to have occurred during a period of stable warm climate several million years before the start of the ice age. It is almost as though equable and optimum environmental conditions induce evolutionary instability in reef corals, whereas stabilisation of species occurs during periods of stress.