

CONTROLS OF MODERN AND FOSSIL REEF DEVELOPMENT
COMMON GROUND FOR BIOLOGICAL AND GEOLOGICAL RESEARCH

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INTRODUCTION

At the time of Dana and Darwin, the list of reef controls was limited to physical factors within the scope of oceanographic measurement at the time. From the discrepancy between thick ancient-reef sequences and the limited depth range of corals, subsidence emerged as the focal point for discussions of the day. Examination of the organisms inhabiting the reef was considered:

"an entertaining experience but, as might have been expected, entirely fruitless as far as the origin of the reef is concerned". (W. M. Davis, 1928, in Hopley, 1982)

Since then, the scientific community has gradually come to appreciate the value of a multidisciplinary approach in coral-reef studies. Useful geologic models cannot simply look for physical similarities between modern and ancient reefs, but must also focus on the processes that have produced them. Conversely, an understanding of biological process is incomplete without the integration of physical factors that set the stage for reef development and continue to exert important controls over spatial and temporal variability.

With this in mind, this paper provides a broad overview of the factors controlling the character of reefs, modern and ancient. It attempts to present the information within a framework useful to both physical and biological researchers, although the geologic bias of the author will surely surface. Lengthy discussion of each factor is precluded by space limitations, and the discussion will, therefore, focus on interactions of physical and biological processes as well as their variability in space and time. In general, more recent articles are cited as it is easier for the reader to work backward through the literature. To those geologically inclined readers used to starting at the base of the stratigraphic record, and to those who played important roles in earlier investigations, I apologize.

GENERAL CONTROLS

Figure 1 reviews the major controls of reef development and scales over which they operate. Larger-scale, physical factors (tectonics, sea-level history and temperature) set the stage for reef development. In one sense, they determine where reefs can form in the first place. In conjunction with antecedent topography, these macro-scale factors are responsible for initially determining the gross morphology of the reef. Meso-scale factors (e.g. light, wave energy, nutrients, sediment level and predation) are more responsible for molding both the surficial character of the reef as well as the depositional fabric of the reef interior. Unlike macro-scale

controls, which are more of an all-or-nothing proposition, meso-scale controls operate more along gradients serving to fine-tune the physical and biological character of the reef along its surface. These controls are effective over the widest range of scale, and are generally the most likely to draw interdisciplinary interest.

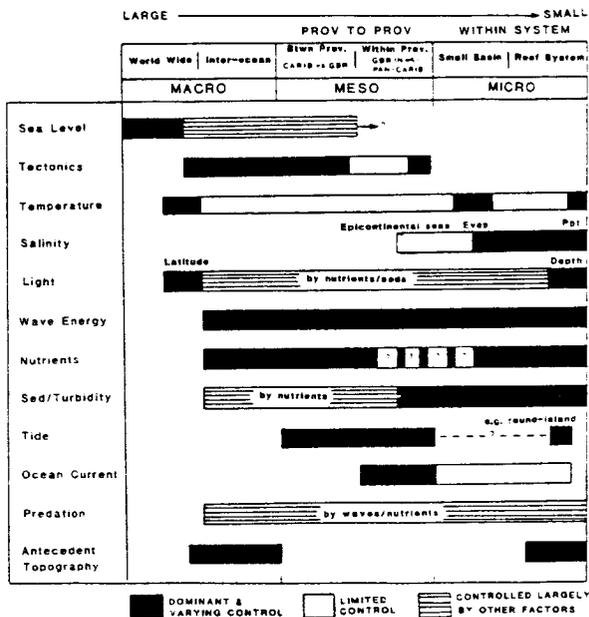


Figure 1. Summary of factors affecting development of modern and fossil reefs. The horizontal bars show the approximate range of scale over which the various controls operate.

Environmental Factors Favoring Reef Development

As has been noted many times, coral reefs fare best in areas characterized by clear, warm waters which are well-agitated and free of sediment. Clear water promotes the photosynthetic activity of zooxanthellae hosted by most shallow-water corals. Active water movement circulates nutrients produced within the reef, removes wastes (including sediment), maintains high oxygen levels and discourages predation by herbivores and coralivores. Sediment reduces water clarity and damages reef biota by smothering or abrasion.

As early as the 1800's, the general confinement of reef corals to waters between 25 and 30 degrees C was recognized. While subsequent studies have refined these early concepts, the latitudinal restraints (ca. 28 degrees north and south of the Equator) cited by Dana (1853) remain largely unmodified. At the organism level, coral growth typically increases with temperature (Shinn, 1956; Glynn and Stewart, 1973; Weber and White, 1974).

Hopley (1982) inferred a thermal control over the southward decrease in coral diversity along the Great Barrier Reef, citing reduced coral-growth rates, lower levels of feeding and compromised reproduction as likely causes. While most studies have concentrated on the adverse effects of lower temperature (e.g. Walker, *et al.*, 1982), recent coral bleaching described by Glynn (1984) has drawn attention to effects of elevated temperature as well.

While having little effect in open-ocean environments, salinity can be important at the local level or in extreme situations where it falls outside the range of 25-40 o/oo (Buddemeier and Kinsey, 1976). Darwin (1874) cited reduced salinity as the cause for reef breaks opposite major river systems. More recently, Hopley (1982) cited examples of widespread damage to inshore reefs off Queensland during episodes of heavy fresh-water runoff. On numerous occasions in the geologic record salinity variations have triggered shifts between coral and algal-dominated communities in restricted epicontinental seas. In the Michigan Basin, the "smoking gun" can be seen in the form of extensive evaporite deposits overlying abandoned reefs.

Larger-Scale Morphological Controls

Larger, primarily geological controls exert an important influence on the location and morphology of reefs. In conjunction with meso-scale factors, they determine the character of the depositional package preserved by reef accretion.

Tectonics - Gross-morphological differences between the reefs of the Caribbean and eastern Australia are in large part a response to differences in the tectonic settings of the two areas. The Great Barrier Reef occurs along a passive (i.e. tectonically "quiet") continental margin. The broad, uninterrupted shelf provides the necessary foundation for a long, continuous reef system. In contrast, the Caribbean is a more complex and tectonically active region characterized by continual vertical and lateral movement over the past 65 million years. The result is a fragmented crust with individual islands and small banks often moving independently of one another. The segmented chain of steep-sided islands and the corresponding lack of broad, shallow shelves has favored smaller-scale reefs located closer to shore. The broader platforms of the northern Bahamas and the more-continuous reefs in the Eastern Caribbean (e.g. Belize) share tectonic settings more similar to that of eastern Australia.

From an evolutionary standpoint, tectonics has played an equally important role. The opening and closing of the Tethys Sea controlled circumtropical dispersal of coral larvae by east-to-west oceanographic currents through most of Miocene time. Formation of the isthmus of Panama further segmented Atlantic and Pacific provinces. In northern Australia, movement of the continent toward the equator has expanded the range of reef corals gradually southward since the Miocene (Davies, *et al.*, 1987). In this context, subsurface reefs in the southern GBR are much younger (i.e. Pleistocene) than their northern counterparts.

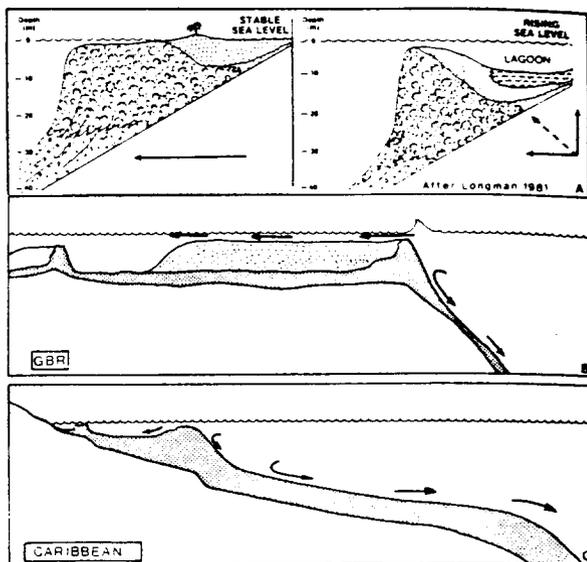


Figure 2. A. Diagrams illustrating the shape of the depositional package resulting from accretion during stable sea level (left) and rising sea level (right). After Longman (1981). B. Internal character of many reefs along the GBR. The initial Holocene reefs (stippled) formed primarily during rising sea level. Once sea level stabilized and the reefs "caught up", accretion shifted to lateral progradation. C. "Typical" Caribbean reef profile. Note the greater importance of the fore-reef area compared to the GBR example. Note the greater importance of offshore sediment transport (arrows). The lighter gray approximates the underlying Pleistocene surface in both B and C.

Antecedent topography - Smaller-scale topographic controls are exerted by antecedent features upon which early reefs colonize. The origins of these features include previous reefs (Halley, *et al.*, 1977), karst (Purdy, 1974), structural features, terraces cut during stillstands of sea level, or siliciclastic coastal and shelf features (Searle, 1983).

Along the northeast shore of St. Croix, in the Caribbean, the history of reef development is closely tied to slope breaks encountered by rising sea level (Adey, *et al.*, 1977; see Fig. 2b). The relief provided by these features facilitated sediment removal during the early stages of reef development. Reefs colonizing the antecedent slope break at the shelf edge were further encouraged by vigorous water movement characterizing this zone (Roberts, *et al.*, 1975). In both the Caribbean (Adey and Burke, 1977) and the Great Barrier Reef (Hopley, *et al.*, 1978) the elevation of the antecedent substrate colonized during the Holocene transgression has determined the likelihood and timing of those reefs reaching sea level. In the Hawaiian Islands, Grigg (1982) proposed that atoll formation is confined to those seamounts that have not subsided below the level of coral growth over the past 20-70 million years.

Along the 2,000 km of the Great Barrier Reef, the gross morphology of individual reefs varies from

elongate, shore-parallel barriers in the microtidal to mesotidal (tide range = 1-2.5 m), north-central region (i.e. the Ribbons) to large, deltaic features and shore-normal ridges in areas of higher tidal range to the north and south (tide range = 6 m in the Pompeys at the southern end; see Fig. 3). This pattern is very similar to that observed in barrier islands and tidal deltas along siliciclastic shorelines (Hubbard, 1977). Whether this pattern is related to colonization of an antecedent, tidally controlled substrate, to present-day accretionary patterns controlled by contemporary tidal variations as proposed by Maxwell (1970), or to some other factor(s) must await detailed coring.

Sea level - Sea-level changes are important over a variety of scales (for a recent review, see Davies and Montaggioni, 1985). The relationship between the rate of sea-level rise and the amount of carbonate incorporated within the reef controls the shape of the depositional sequence as viewed in outcrop (Fig. 2a).

Global changes in sea level (i.e. those related to glaciation), when superimposed on regional differences in tectonic movement, can result in very different relative sea-level histories from one reef system to another. In the Caribbean, the rate of sea-level rise decreased 3-5,000 years ago, but continued slowly until present. Many of the shelf-edge reefs are still in the process of "catching up" with rising sea level. This has resulted in reef systems in which sloping forereef environments dominate (Fig. 2b). Along the Great Barrier Reef, relative sea level stabilized 6,200 years ago (Thom and Chappell, 1975), affording the reefs a greater opportunity to reach sea level. Once the reefs reached sea level, vertical accretion shifted to lateral progradation of reef-derived detritus preserved in extensive reef flats behind the reef crest (Davies and Hopley, 1983; see also Fig. 2c).

The differing morphological character of these reefs is translated into different sets of restraints on the organisms inhabiting them. In the Caribbean, vertical gradients along the sloping reef front control zonation of present-day biota and processes. Along the Great Barrier Reef, lateral gradients across extensive reef flats provide very different sets of problems for the organisms inhabiting them. For example, it is possible that differing strategies of herbivory and coral recruitment in the two areas (Sammarco, 1982) are, at least in part, in part a function of these factors.

Kinsey (1982) pointed out the relevance of this to carbonate production in the two areas. The greater importance of more-productive forereef zones should result in higher average rates of carbonate production in Caribbean reefs. Of equal importance are the effects of morphological differences on the fate of sediment produced by bioerosion in the two areas. In the Great Barrier Reef, most of this material is retained in actively prograding reef flats (i.e. moved landward; Fig. 2c); in the Caribbean, a significant portion (up to half) of this material is moved downslope (i.e. seaward) and exported over the steep shelf margin (Fig. 2b). Thus, differences in

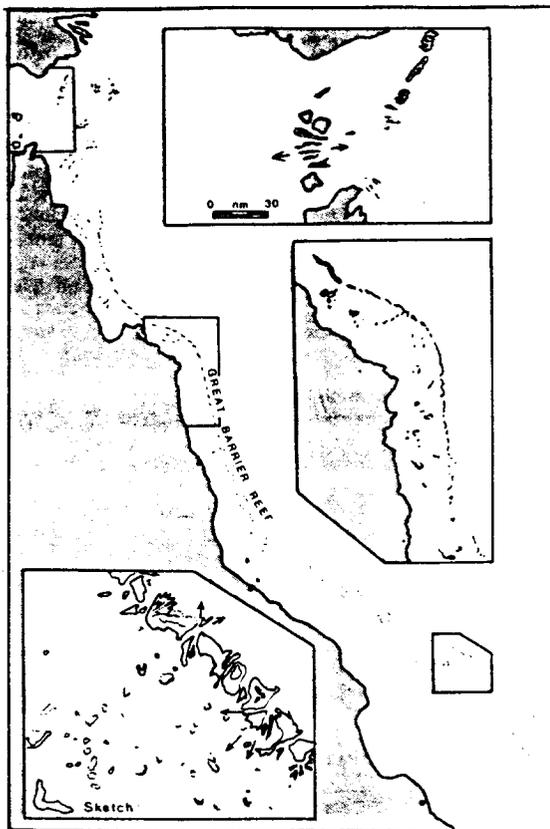


Figure 3. Changes in reef character along the Great Barrier Reef. The central portion of the reef is characterized by linear barriers near the shelf edge (center inset). Tidal range is low in this region. To the north and south, the reefs are more massive, and take on either a deltaic character or a pattern of east-west linear ridges. This is similar to patterns seen in siliciclastic systems under similarly varying tidal regimes.

rates of carbonate production and preservation in the two regions are not solely an artifact of methodological differences used in studying the two areas (Kinsey, 1982), but also a reflection of real differences in the two areas caused by differing tectonic and sea-level histories.

Controls of Surface Cover

On a smaller, more-variable scale, light, wave energy, sedimentation, nutrients and levels of herbivory exert influences over the organisms inhabiting the reef surface. The smaller scale over which these factors generally operate, combined with their inherent temporal and spatial variability, makes them common ground for physical and biological study. To the biologist, the relevance of these controls is obvious. Unfortunately, many geologists attempting to make or use "reef models" adopt an approach of simply comparing the physical attributes of modern and ancient reefs rather than trying to understand the processes occurring on modern reefs in the context of the depositional signatures that they produce.

Only by understanding the effect that these have on modern reefs, and then considering how these processes have changed through geological time can we hope to make realistic comparisons between modern reefs and their ancient counterparts.

Light - The most widely cited control of reefs and the corals that dominate them today is light. The earliest discussions date back to the work of Quoy and Gaimard (1825; cited in Dana, 1853). The importance of photosynthesis is reflected in the measurements of Land, et al. (1975) which showed that $^{13}C/^{12}C$ ratios in three important Caribbean corals more closely matched those of their zooxanthellae than those of the plankton in surrounding waters. The role of light in enhancing calcification was initially suggested by experiments of Goreau (1961). One of the major unresolved questions relates to the specific mechanism by which this light enhancement takes place (for a review, see Gladfelter, 1985). In very shallow water, the growth of some corals may be inhibited by overexposure to light. Near the lower extent of coral growth, certain corals (e.g. Leptoseris) have developed mechanisms to concentrate or change the character of low-level light to enhance photosynthesis (Schlichter and Fricke, 1986).

Light varies with a number of other factors and, therefore, cannot be considered by itself. Increased levels of suspended sediment and plankton both result in light scattering and absorption, thereby lowering light intensity. Differences in the maximum depth of corals in the western Atlantic, the open Pacific and the Great Barrier Reef are likely the result of these factors. Turbidity can significantly alter the vertical zonation of reefs only short distances apart.

The dominant reef-building corals today are members of the genera Montastrea, Porites and Acropora. Their widespread occurrence is, at least in part, due to their morphologic plasticity. The demonstration by Grauss and Macintyre (1982) that transplanted colonies of M. annularis will adapt their growth form to that of the surrounding corals infers a response to light, as opposed to genetic differences in deep vs shallow-water corals or zooxanthellae. In the Acropora's, morphology appears more related to wave energy (Shinn, 1966; Done, 1983).

Because of the dependence on photosynthesis, coral growth generally decreases with water depth although the relationship is variable among species and environments. As discussed by Hubbard (1985), rates of reef accretion occurring along a depth gradient need not mimic the patterns of calcification exhibited by organisms inhabiting the reef surface. Therefore, great care must be exercised in extrapolating from coral-growth rates to reef accretion.

Growth rates of M. annularis in the Caribbean and P. lutea in the Pacific decrease markedly with depth. Other corals typically decrease their growth rates with depth, but not always in a regular pattern. Isdale (1981, 1984) reported a seaward and southward decrease in the growth rate of Porites sp. along the Great Barrier Reef,

citing depth, rainfall and latitude as important, light-related factors. The southward decrease is likely a response to the lower sun angle and shorter day as documented by Bak (1974) in the Caribbean. The landward increase in coral-growth rate, however, is contrary to expected trends in light, sedimentation or nutrient levels, leaving unanswered questions about the controls in this case.

Wave energy - Agitation of waters along the reef crest performs several important functions, including nutrient cycling, sediment removal and inhibition of predators. Differences in wave energy exert a control over variability of reefs both between oceans and along gradients within individual systems. The high-energy, swell-dominated climate of the open Pacific has favored the formation of massive, algal ridges armoring upper reef surfaces. In the Caribbean, similar features occur along the highest-energy margins, but the reef structure of this region is more dominated by coral assemblages. In the Great Barrier Reef, coralline algae play an important role in binding reef corals together into a more rigid mass (e.g. the encrusted coral facies of Davies and Hopley, 1983), but, their occurrence on the reef crest is limited to thin (20-50 cm) crusts along the upper reef surface (Hopley, 1982). One has to wonder why algal ridges have not been described from the Great Barrier Reef, which lies intermediate between the energy regimes of algal ridges in the Caribbean and the Pacific. Possible explanations include the high tidal range along portions of the GBR, or the dominance of locally generated seas (John Marshall, pers. comm.) compared to the swell-dominated regime of the eastern Caribbean or open Pacific. Another possibility relates to the greater coral diversity of the GBR compared to either the Caribbean or along mid-Pacific atolls. While the reasons for lower diversity differ between the Caribbean and the mid-Pacific regions, their lower coral diversities may translate into an environment more favorable for competition by coralline algae. Also, the more rapid recolonization by Acropora following storm damage along the GBR may further discourage algal colonization in the wake of even frequent disturbance.

Several zonation schemes have focused on prevailing wave energy as a primary control of reef development (Adey and Burke, 1977; Geister, 1977; Pichon, 1978; Done, 1983; see Fig. 4). While the importance of storms has been mentioned, it has usually been within the context of reef destruction. Figure 5 illustrates that in the Caribbean, an adequate explanation of the reef distribution described by Adey and Burke (1976) involves both prevailing wave energy and storm frequency. The general decrease in day-to-day wave climate (wave-energy roses) from the Windward Islands through the northern Bahamas is similar to that proposed by Adey and Burke (1976). In addition, however, major storms follow two distinct paths, contrary to the earlier findings of Gentry (1971), who concluded that no regular pattern existed in the region.

In the Leeward Islands, the vigorous wave climate favors Acropora palmata, which can rapidly grow above the zone of constantly moving sediment on the active reef crest. The geometry of this coral

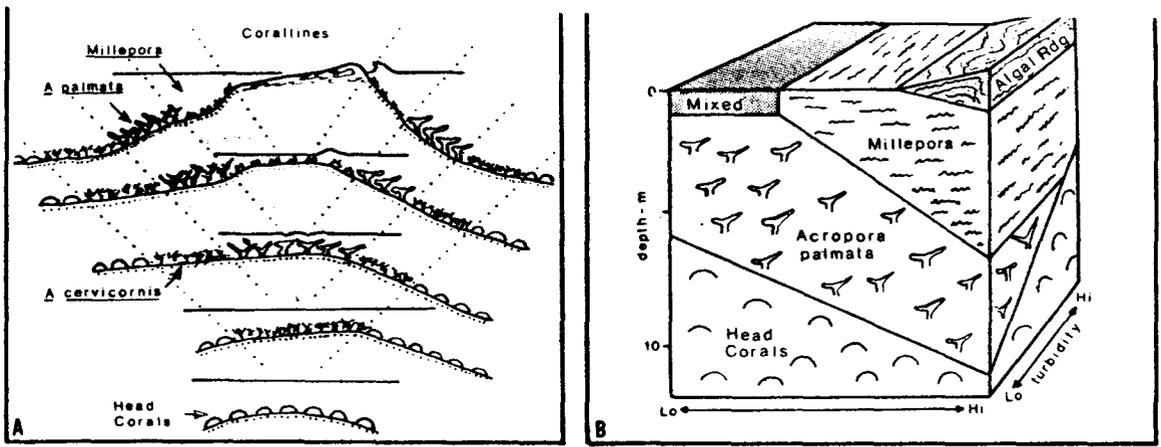


Figure 4. A. Reef zonation associated with varying wave energy in the Caribbean. This simplified scheme is modified after Geister (1977). With decreasing wave energy, the reef-crest zone is removed and the subjacent one takes its place. B. Reef zonation as a function of wave energy and water clarity. After Adey and Burke (1977).

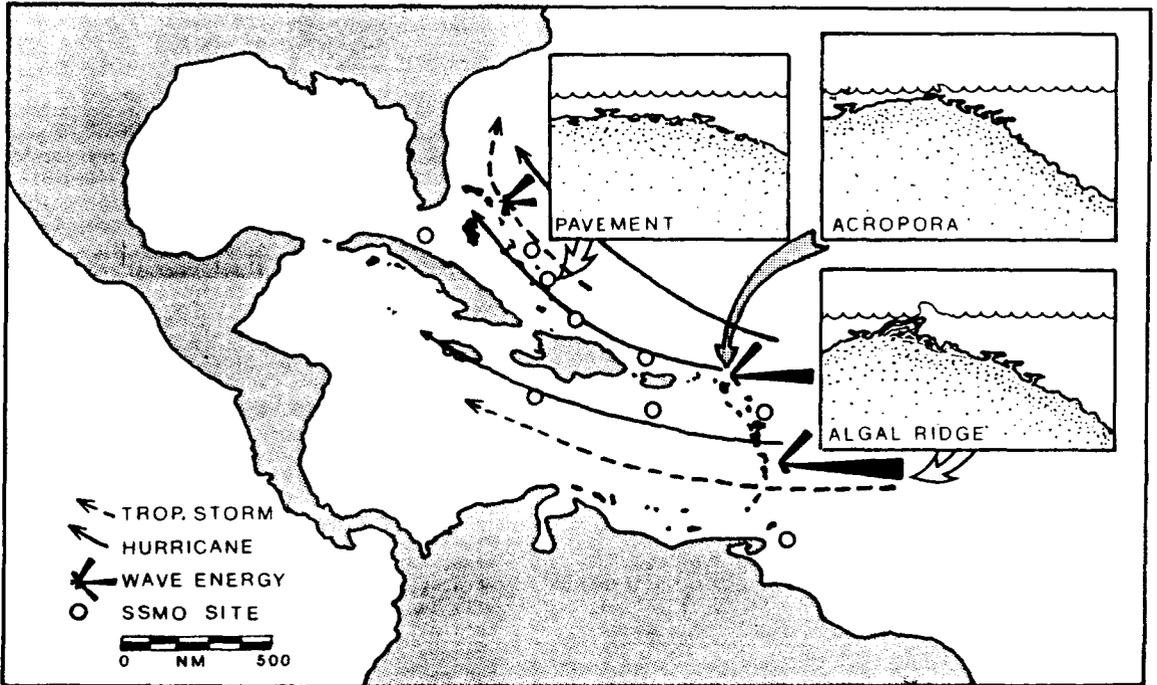


Figure 5. Wave energy as a control of reef character in the Caribbean. Wave energy is derived from U.S. Naval data collected over a 30+ year period (survey sites shown by open circles). The wave-energy roses are representative of regional trends, and show the relative importance of wave energy coming from different directions. Note the general importance of easterly flow and the increase in total wave energy toward the eastern sites. Hurricane and tropical-storm paths are also shown. In the northern Bahamas, reef crests dominated by poor coral development and wave-swept pavements dominate under conditions of high storm frequency but low prevailing wave energy. In the eastern Caribbean, *Acropora palmata* reefs occur in areas characterized by moderate storm frequency and high prevailing wave energy. Areas of frequent storm passage and high prevailing seas are characterized by algal ridges.

is uniquely adapted to the hydrodynamic forces exerted by the prevailing seas (Graus, et al., 1977). In the Windward Islands, prevailing wave energy is likewise high, but the greater frequency of hurricanes precludes the maintenance of a reef crest dominated by corals easily broken by storm waves. Broken Acropora fragments are overgrown by corallines, which eventually form thick ridges. The energetic conditions that prevail between storms discourage grazers and borers, and apparently inhibit the colonization of epiphytes that can be harmful to the corallines forming the algal ridges. In the northern Bahamas, the regular passage of storms again precludes the persistence of A. palmata, except in limited areas of refuge. The slowing of hurricanes in this region as they encounter high pressure from the adjacent continent, added to the impact of open-ocean swell, further increases the level of destruction on the reef crest. The quiet intervening conditions between storms favor intense grazing and the settlement of fine-grained sediment, both of which interfere with coral recruitment in the brief intervals between storms.

Sedimentation - An extensive body of literature exists on the effects of sedimentation on reefs and reef biota. The brief treatment of this subject here does not reflect a secondary level of importance, but rather an inability to adequately address this complex control within the limited space of this article. For a more complete review, the reader is referred to Hubbard (1987). Sediment impacts include light attenuation, burial, abrasion and disruption of reproduction and recruitment. On a larger scale, sedimentation levels exert important controls over reef morphology (Hubbard, 1985a), with the removal of sediment produced by bioerosion looming as one of the major problems with which the reef must deal (Hubbard, et al., in press).

Much recent attention has focused on environmental impacts of development. Unfortunately, most of these fall in the category of "post-mortem autopsies" of reefs killed by very high levels of stress. To date, little quantitative information exists on sub-lethal effects of longer-term, lower levels of sediment stress. Detailed study of the effects of varying sediment size and composition should be a focus of future interests.

Nutrients and herbivory - The recent recognition that only sparse nutrients reach reefs in open-ocean settings (Marshall, 1965; Weibe, et al., 1975) has changed earlier models stressing the importance of a steady supply of nutrients to the reef. Even in more continental settings (e.g. Crossland and Barnes, 1983), the reef largely functions as a self-sufficient nutrient system with blue-green algae responsible for much or most of the primary production.

The emphasis on nutrients has gradually shifted to understanding the role of nutrients in limiting the biota that occur on tropical shelves (Kinsey and Davies, 1977). Effects on corals can range from direct limitations of important metabolic processes (e.g. phosphates inhibiting calcification: Simskiss, 1964) to encouragement

of other biota that compete with corals. In general, elevated nutrient levels discourage corals in favor of fleshy algae and other organisms which are either dependant on nutrients or else are outcompeted by corals in lower-nutrient settings. Steneck (1986) has stated that, in the absence of herbivores, corallines "become fouled by fleshy algae in zones of intensive wave action". Coralline-algal ridges appear to be an exception to this generalization.

Along the Great Barrier Reef, the distribution of sponge communities is related to cross-shelf variations in light and nutrients (Wilkinson and Trott, 1984; Wilkinson, 1985). In the Caribbean, where nutrient levels are much higher, a more prolific sponge community occurs and is comprised almost totally of non-photosynthetic species, possibly paralleling evolutionary patterns in corals in the two areas (Wilkinson, 1987). Upwelled nutrients from below the thermocline are likely related to the present and past distributions of large Halimeda bioherms that occur behind the outer reef in many areas of the GBR (Davies and Marshall, 1985).

Herbivory plays an important role in maintaining a balance between coral and fleshy algae under normal nutrient conditions. The survivorship of coral recruits is enhanced by intermediate levels of predation which maintain open substrate for settlement of coral larvae (Sammarco, 1982). Disruption of this balance leads to inhibition of coral settlement by algal overgrowth at one extreme and excessive damage to juvenile corals by grazing at the other. On the Great Barrier Reef, grazing (and therefore, bioerosion) is dominated by several fish species (Kiene, 1985), while urchins are (were?) the principal bioeroders in the Caribbean (Ogden, 1977).

From a standpoint of reef evolution, it is important to determine cause vs effect. Have reefs responded to changes in grazing pressure or has the grazing community changed in response to an evolving food resource (i.e. the reef)? An understanding of the evolution of grazing strategies and mechanisms (e.g. the pharyngeal mill in parrot fish; Aristotle's lantern in urchins) is crucial to explaining the accompanying changes in reefs and reef communities throughout the geological past or from ocean to ocean (e.g. Steneck, 1983; see also, Fig. 6).

A recent paper by Hallock and Schlager (1986) has emphasized the role of nutrients in widespread reef mortality in the past. They proposed that many fossil reefs buried by sediment were already killed by nutrient excess before sediment ever reached the reef. Without careful study of smaller-scale responses of individual organisms, and larger-scale coring studies along demonstrated process gradients, such relationships can only be inferred. The numerous examples of abandoned Holocene reefs in the Caribbean (e.g. St. Croix: Adey, et al., 1977; Belize: Macintyre, et al., 1982; Puerto Rico: Hubbard and Morelock, unpubl. data) and drowned reefs in the rock record (e.g. Caning Basin of western Australia: Playford, 1980; Devonian reefs of Canada: Viau, 1983; Muir, et al., 1985)

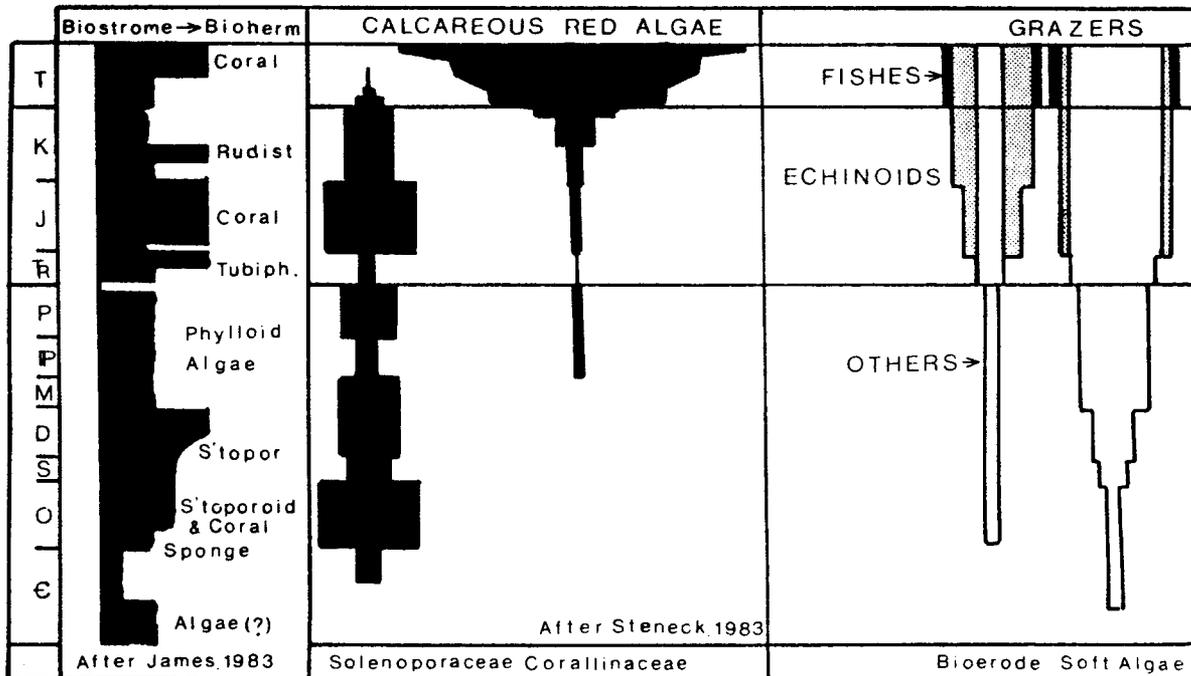


Figure 6. Summary of the evolution of some important reef biota. The column on the left summarizes the character of the "reef" deposits (i.e. biostrome vs bioherm) and the major organisms constructing the reefs through time (after James, 1983). In the center, evolutionary trends in coralline algae are summarized and compared to the evolution of reef grazers, on the right. Steneck (1983) proposed that the shift from the Solenoporaceae to the more durable Corallinaceae was a response to developing grazing pressure and a shift from grazers that only removed soft algae to those that also removed carbonate substrate in the course of feeding. What relationships might be at work in controlling evolutionary changes in other reef biotas? How has this affected the character of reefs through time?

highlight the need to quantify the role of nutrients, as well as sedimentation and the other factors discussed above in "turning reefs on and off".

AN INTEGRATED APPROACH

This paper has provided a brief overview of processes important in controlling modern reefs, and presumably their ancient counterparts. Hopefully the interplay between physical and biological factors has been illustrated. Those attempting to focus on one aspect of the reef by ignoring other related factors will emerge with a biased, narrow, and probably incorrect view of how reefs function.

A geological perspective - Comparisons between modern and ancient reefs have typically centered around the physical attributes of ancient reefs and those perceived to be characteristic of modern reef interiors. Longman (1981) proposed that reefs could be understood largely on the basis of their depositional sequences, thus emphasizing the approach of comparing fabrics and textures between modern and ancient systems. This has led to repeated frustration to the point of questioning the validity of using a uniformitarian approach to reef modeling.

These problems are, in part, related to a likely overemphasis on framework in our modern models. A

critical re-examination of our modern reef cores should show that "framework" represents a much smaller portion of the interiors of modern reefs than the available literature or a swim over the coral-dominated reef surface would suggest. The patterns observed on the reef surface at any one instant are different from those integrated into the reef record over time. Any model which attempts to represent modern reefs must quantitatively integrate constructional process with those that reduce solid carbonate to sediment (Zankl and Multer, 1977; Hubbard, *et al.*, in prep), and must embrace the tremendous variability that has occurred through time or that exists in the present (Hubbard, 1986). Useful models will be derived only from studies that link process and product in modern reefs and then consider how evolutionary changes in those processes can be used to explain ancient sequences that appear very different at a first glance. Certainly it is time to shift our emphases from "who's reefs are bigger, better, thicker, or whatever than who's".

A biological perspective - As discussed above, an appreciation of the importance of geologic factors (e.g. tectonics, sea-level history) in setting the stage for reef development and physical factors (e.g. sedimentation, wave energy) in influencing the organisms that inhabit the reef is a necessary prerequisite for the biologist trying to understand the reef as a system. Compared to geological investigations,

the smaller scale upon which most biological studies are conducted generally results in a better understanding of the link between process and response at the organism level. However, biologists generally tend to relegate large-scale physical factors to roles of secondary importance. While exceptions exist, most of these more detailed studies do not address either temporal or spatial variability within the larger system.

Recent stress events documented on reefs from all oceans have demonstrated the magnitude of this problem. Outbreaks of Acanthaster planci along the Great Barrier Reef and the recent die-off of Diadema antillarum in the Caribbean have raised important questions concerning the periodicity of such events. Are they isolated phenomena related to anthropogenic factors or are they part of a cycle whose scale lies outside the temporal range of our direct measurements? From a standpoint of understanding the relationship between reef construction and bioerosion, the choice of conditions before or after the Diadema die-off as "normal" is of paramount importance. The answers to these types of questions are locked in the recent geologic record (e.g. the recent studies of paleoclimate using fluorescence in corals by Peter Isdale at AIMS). Problems of cyclicity and spatial variability in modern reefs likely represent the greatest potential for drawing together the geological and biological communities and providing important answers to questions of reef development that those groups could not address individually.

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This is contribution number 176 of West Indies Laboratory, Fairleigh Dickinson University.