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Marginal and non-reef-building coral environments

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Introduction

This special issue of *Coral Reefs* stems from a thematic session held at the European Meeting of the International Society for Reef Studies held in Cambridge in September 2002. A wide range of papers were presented, covering aspects of oceanography, sediment transport and accumulation, sedimentary settings, species assemblages, coral physiology, and geological evolution. These presentations emphasized the diversity and potential significance of the coral communities that occur in a wide range of what might be described as “marginal” settings, and demonstrated the geological and ecological significance of marginal and non-reef-building coral environments. Most papers published in this issue were submitted from researchers who presented work at the Cambridge meeting; however, some additional contributions were also accepted.

When we were organizing the thematic session on “marginal” and non-reef-building coral environments at Cambridge, and then in editing this Special Issue, we wondered whether the title of this Special Issue, and specifically the word “marginal,” could be a little misleading (we expand a little on this thought in sections below). In this introductory paper, the term “marginal” marine is used in a broad sense, to describe settings where coral communities or framework reefs occur either close to well-understood (or strongly perceived) environmental thresholds for coral survival (*sensu* Kleypas et al. 1999) or in areas characterized by “sub-optimal” or fluctuating environmental conditions. These

include settings characterized by high or low temperatures, salinities, or nutrient levels, or by low light penetration or low aragonite saturation states. We are aware that much of this issue generally considers only one component of an ecological biota, so the use of the term “coral communities” here and in many of the papers in this issue might equally be read as “coral biotopes,” “coral assemblages,” or “ecological assemblages of corals.” Further, we use “framework reefs” here to explicitly denote those coral assemblages that have produced accretion through the production of reef framework, and we do not intend this as a contribution to any debate on what does or does not constitute a reef.

The settings under consideration in this issue include settings where external factors act to change parameters such as temperature, salinity, nutrient load, and suspended sediment concentrations over a variety of magnitudes and timescales (e.g. “permanently,” seasonally, over lunar and other cycles, and episodically). Such settings may be considered by some as “marginal” in terms of reef-building potential, for example, the production of reef framework, but they are clearly important for maintaining a rich diversity of coral community and reef types, and as localized sites of coral and carbonate sediment production and, in some cases, accumulation.

Coral communities

Tropical coral reef communities are most commonly associated with shallow, clear, warm-water settings within low-latitude regions. The environmental parameters that occur in these settings are widely regarded as being “optimal” and, by association, are often taken as the “norm” for coral growth and reef-building (Fig. 1). There are also broadly held views that traditional concepts of reef building are at least related to, if not require, high community productivity. These views are supported by reference to the numerous studies that have reported high rates of coral growth, rapid rates of

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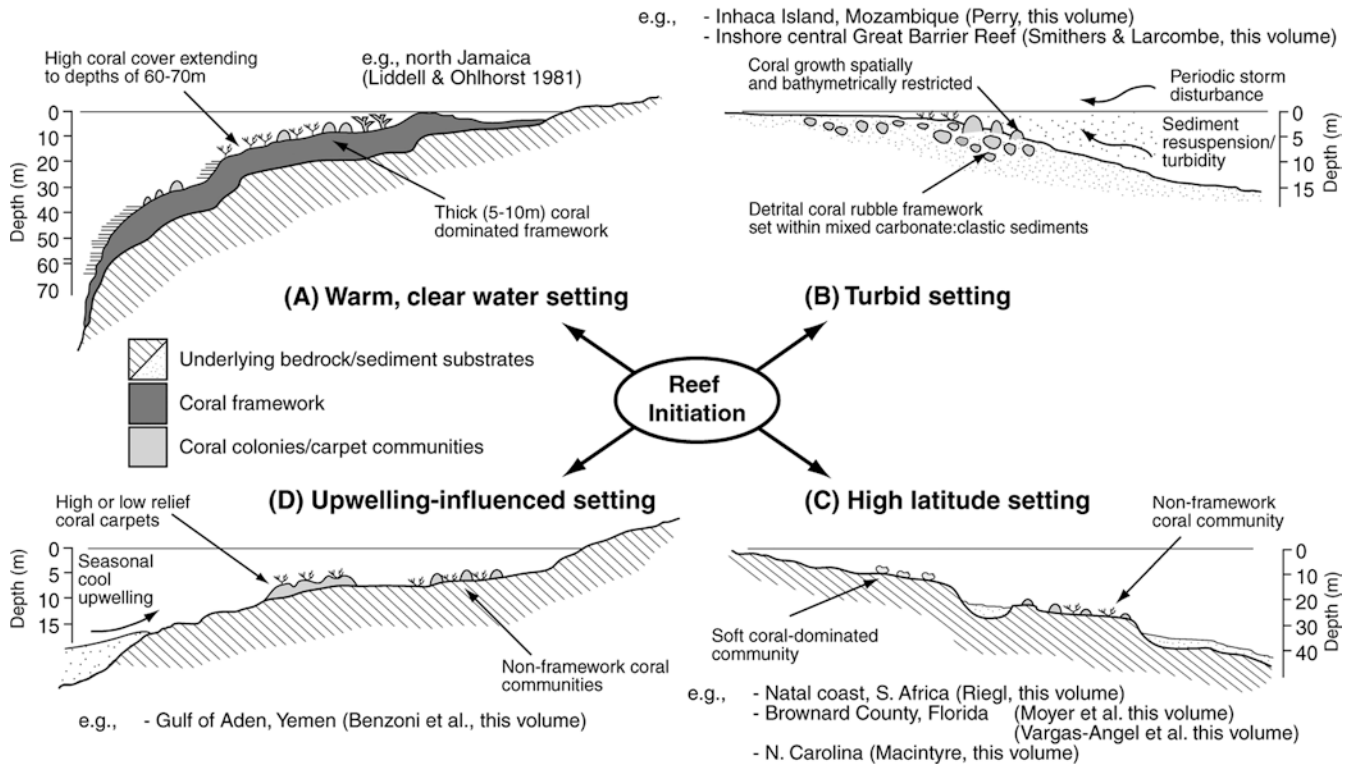


Fig. 1 Schematic diagram illustrating the character of the coral communities that develop under **A** perceived “optimal” environmental conditions, and **B, C, D** those associated with a range of “marginal” reef settings described in this issue

production of carbonate framework and sediment, and, as a result, extensive reef construction and accretion in these settings. Associated with these views is an understanding that if environmental conditions shift away from those regarded as optimal, then so too might the productivity and complexity of the coral reef communities. Demonstrated latitudinal differences in coral community structure and the physical extent of coral reefs (e.g. Harriott and Banks 2002) appear to support this perception. In higher-latitude settings, environmental parameters such as low mean annual and seasonal temperatures and low aragonite saturation state frame the limits of hermatypic coral growth (Budde-meier 1997; Kleypas et al. 1999). Such changes reduce, in some cases, coral species diversity and the extent of reef framework development, as emphasized in the examples of high-latitude coral communities described by Riegl (10.1007/s00338-003-0335-0) from the Arabian Gulf and South Africa. Towards the very limits of coral survival, corals may occur only as isolated colonies growing on exposed bedrock (Macintyre, 10.1007/s00338-003-0329-y; Moses et al., 10.1007/s00338-003-0346-x) and therefore, like corals in a range of environments, do not form reef structures. These latitudinal differences are usually associated with shifts in the composition of carbonate sediment assemblages, with different skeletal components varying in abundance with

latitude (see Halfar et al. 2000). Although a variable relationship, to some extent these different sediment compositions reflect changes in temperature (Lees 1975) and aragonite saturation state (Kleypas et al. 1999).

It is reasonable to assume that the fluctuating nature of environmental parameters that characterize these higher-latitude settings will in some circumstances cross between states of “no coral growth” and “coral growth.” Environmental variation in these settings may also result in fluctuating coral community structures and, depending upon the nature of the community change undergone and the amount of time involved, temporal change in the potential for framework-building. Variation in community structure is addressed by Ferreira et al. (10.1007/s00338-003-0328-z), who describe species flux in high-latitude settings off southeast Brazil. Temporal change in the potential for framework construction is indicated by Moyer et al. (10.1007/s00338-003-0334-1) in relation to the coral communities in another high-latitude setting (off Fort Lauderdale, Florida). Here, coral communities are developed on submerged, relict reef ridges which are orientated parallel to the present shoreline, at depths of 7–13 and 15–30 m. Despite significant past framework-building potential in these areas, and the presence of many common Caribbean reef species which contribute to framework building elsewhere in the region, there is no active framework accretion (Fig. 1). The present lack of reef development may reflect recent constraints exerted by fresh- and groundwater inputs, rather than temperature. Vargas-Angel et al. (10.1007/s00338-003-0336-z) also report on coral communities from near Fort

Lauderdale, but provide a description of flourishing *Acropora cervicornis* communities. These communities occur in areas that are reportedly beyond the previously reported temperature limits of this coral and, in contrast to other Caribbean sites, do not appear to have suffered the widespread effects of white band disease.

Environmental constraints on reef-building potential are not, however, solely confined to higher-latitude areas. Similar constraints on coral reef communities also occur within lower-latitude settings, particularly in areas influenced by cool, nutrient-rich upwelling waters. Within these areas, framework development may be restricted in extent, or else coral communities occur which do not form framework reefs but rather coral carpets (*sensu* Riegl and Piller 2000; Fig. 1). Monotypic and oligotypic coral-carpet communities of this type occur along upwelling-influenced sections of the southern Yemen coast (Benzoni et al., 10.1007/s00338-003-0342-1). The occurrence of different such communities is discussed in the context of exposure to upwelling-influence and wave energy. These coral communities occur in settings where environmental conditions broadly mimic those that occur in higher-latitude settings and, as a result, have previously been referred to as environments characterized by a “pseudo high-latitude effect” (Sheppard and Salm 1988) or as forming “thermally marginal areas” (Glynn 1977). Similarly restricted coral reef development has previously been reported from Panama (Glynn 1977) and Oman (Glynn 1993).

Constraints on reef growth also occur in areas subjected to either ongoing or periodic (seasonal) sediment influx or resuspension. These environmental factors can produce turbid water, which is often sufficient to significantly restrict light penetration through the water column. Under these conditions, coral communities may still flourish, but reef framework development may be restricted (or even absent), and coral communities may only occur down to depths of a few meters (Fig. 1). The paper by Perry (10.1007/s00338-003-0339-9) describes the coral communities around Inhaca Island, southern Mozambique, in settings characterized by high turbidity and high sediment mobility. At these sites, coral communities fringe the seaward margins of wide intertidal sandflats. High turbidity restricts coral communities to depths of < 6 m, and the reef structure comprises coral rubble within a mixed carbonate-siliciclastic sediment matrix. Historical evidence indicates that these reefs are ephemeral in character, being subject to periodic mortality driven by sediment mobilization (*cf.* Scoffin 1997). Despite this, the coral communities are characterized by high species diversity, with ~160 coral species having been reported from these reefs. Similar high-turbidity nearshore coral settings at Paluma Shoals, on the inner-shelf of the central Great Barrier Reef, are described by Smithers and Larcombe (10.1007/s00338-003-0344-z), who report on the results of a coring study of these muddy reefs. The corals form structures similar to those reported by Perry (10.1007/s00338-003-0339-9), and the coral communities are similarly bathymetrically

restricted, yet have a highly diverse coral assemblage. The internal structure of the Paluma Shoals “reef” comprises detrital coral rubble within a mud-dominated matrix. Radiocarbon dates indicate that these coral communities have been forming for at least 1,000 years, possibly initiated by exposure of suitable substrates along an eroding shoreline.

One important point to raise here relates to the issue of coral diversity and reef development. There is often a perception that high-diversity coral assemblages are indicative of sites characterized by extensive framework accumulation and that, by inference, areas of restricted (non-reefal) coral community occurrence are likely to be faunally impoverished. The previous two examples, which describe sites characterized by high coral diversity (around 160 coral species) but which both lack framework development, highlight the fallacy of such a view (see also Rosen 2002). Indeed, one only has to look at the extensive reef systems that developed around the margins of the Mediterranean during the Miocene (*e.g.*, Dabrio et al. 1981; Pomar 1991) which were constructed of primarily one coral species, or the modern reef development that occurs in sites of relatively low coral diversity in areas such as Lord Howe Island or Bermuda, to realize that there is no credence in the view that high coral diversity should be equated to reef “health” or to the potential for carbonate accumulation.

While coral communities clearly survive and form localized coral buildups even under conditions of high turbidity, these environments are far from what has generally been considered as “optimal” in terms of coral growth and survival (*c.f.* Potts and Jacobs 2003). In a study from St. Lucia, Nugues and Roberts (10.1007/s00338-003-0338-x) examine the extent to which sediment stress may impact corals over short timescales by facilitating algal overgrowth. The study indicates that sediment may impact corals initially through smothering, but that it is subsequent sediment trapping within algal mats that restricts coral recruitment or colony regeneration. Such sediment–community interactions have significance beyond immediate mortality events of coral species, especially in sites subject to longer-term sediment stress. It is likely that at such sites, coral communities will shift towards those that are, by virtue of their life-history traits, more sediment tolerant. This has not only ecological but also geological implications, by potentially modifying rates and patterns of carbonate accumulation.

An important additional influence on carbonate accumulation and cycling derives from the taphonomic alteration processes such as bioerosion, encrustation, and cementation, which are widely acknowledged as important controls on coral framework accumulation in clear-water reef settings. The effects of these processes in high-latitude, upwelling-influenced or turbid reef sites remain very poorly understood. Macdonald and Perry (10.1007/s00338-003-0340-3) examine bioerosion of coral framework within the turbid lagoon environment at Discovery Bay, north Jamaica. Their study sites are

naturally turbid, but turbidity levels are exacerbated by human input of fine bauxite sediment. Fine-grained mud accumulates in many areas of the lagoon and reef framework development is extremely restricted. In contrast to previous suggestions that high turbidity and high sedimentation rates may inhibit internal bioerosion of coral heads, rates of internal bioerosion are comparable with those occurring within adjacent clear-water settings, and appear to reflect a borer community dominated by bivalves rather than sponges. Thus, while high turbidity may inhibit the extent of active coral cover and growth, high rates of substrate bioerosion may be maintained.

Disturbed or just different?

The papers presented in this volume dealing with specific “marginal” reef environments provide an overview of the nature of coral community development under a range of environmentally constrained settings. It is clear from these studies that thriving and often diverse coral communities do occur in such environments, and that these coral communities have the potential to persist for, and develop over, long periods of time (>1,000 years; see Smithers and Larcombe, 10.1007/s00338-003-0344-z). Given this, it is perhaps important to think about these more marginal reef settings as alternative states of development rather than as disturbed or restricted versions of the coral reefs that develop in low-latitude, warm, clear-water settings. The environments of these reefs are far from unusual or unique, clearly being common in the late Holocene phase of high sea level, and their study provides an opportunity to assess the broad diversity of coral reef communities that develop under a range of natural conditions.

Coral reefs are often referred to as the “rainforests of the ocean,” and, to develop our argument, it is useful to consider forests as an analogue, albeit an imperfect one, for coral reef systems. At the global scale, there are many different types of forests or woodlands, ranging from stunted forests on exposed high ground, through boreal coniferous forests, temperate summer-green forests, to the rainforests of the tropics (Olson et al. 1983). These are well recognized as being different, each with its own range of community assemblages, characteristics, and environmental constraints—one type is not necessarily considered a “poor cousin” of another (see also Rosen 2000). The BIOME models of global vegetation identify 11 distinct forest types, i.e., those with a closed canopy, 7 parkland and savannah vegetation types, which are open with scattered trees, and several other vegetation types without trees (Prentice et al. 1992; Haxeltine and Prentice 1996; Kaplan 2001). Within each type, the forest of a particular area is likely to possess a multitude of differences in species composition and abundance. At the regional scale, there are contrasts in the detailed composition of forests, with the dominant taxa dependent on local conditions (Ozenda and Borel

2000). Further, the evolution through time of one forest type and its gradual replacement by another is also well understood and documented (Iversen 1958; Overpeck et al. 2003) and examples abound in mainland Europe of forest changes during the most recent postglacial phase of ice-retreat and general climatic warming (e.g., Godwin and Tallantire 1951; Huntley 1988, 1998; Velichko et al. 1997). It is even apparent that the sequence of forest changes, and the component taxa, has been different for different interglacials (West 1980; Watts 1988). Overall, then, one form of forest is recognized as distinct from another, in terms of their species assemblage and their controlling factors—although the latter are imperfectly understood, and it is also clear that they have different developmental histories through time.

As for forests, we consider that it is inappropriate to consider one type of coral reef a poor example of another. Partly because of the obvious practical difficulties in the detailed documentation of coral reef systems, even in relatively modern times with modern technology, and despite the notable efforts of some researchers in documenting regional spatial differences between coral communities (e.g., Done 1982), reef science lags behind some other branches of natural science in documenting and acknowledging the different make-up, dynamics, and driving factors behind the variety of communities we find. Not every coral reef can be or “should be” the reefal equivalent of a pristine rainforest deep in the Amazon Basin, and, in many instances, our understanding of the history and environmental variability of the reef is inadequate. Much of this is apparent to increasing numbers of reef researchers and managers, and we will not labor the point further.

The study of these “marginal” reefs has two significant additional applications. First, it may provide useful analogues for studies of ancient reef environments. From a geological perspective, many of the large Holocene reef structures associated with warm, clear-water settings do not fit with the “reef” structures that are preserved in the fossil record and are, indeed, far more analogous to the restricted coral communities of marginal settings. Of course, this should not be surprising, because settings characterized by upwelling and sediment input will have been similarly common at many times in the past. Eustatic changes in sea level influence the nature of Holocene reefs, not only directly through their impacts on accommodation space, and hence their internal structure, but also through their impacts on oceanographic and sedimentary processes (see also Larcombe and Carter, 2003). Second, study of these reefs may provide an insight into the future status and character of reefs that become exposed to more “marginal” conditions by changing environmental parameters (see Kleypas et al. 1999). These may, for example, be related to increased sediment input, or to changing global climatic and oceanographic conditions. In essence, reefs that currently occur under more “optimal” conditions may become more marginal in character through either local or regional shifts in

temperature, salinity, light penetration, or aragonite saturation state. The final four papers of this issue address aspects relevant to this point.

One way of assessing the impacts of environmental change and of species tolerance to environmental parameters is through exposure experiments. Manzello and Lirman (10.1007/s00338-003-0327-0) examine the occurrence of colonies of *Siderastrea radians* and *Porites furcata* in areas of fluctuating temperature and salinity in Biscayne Bay, Florida, and indicate that the occurrence of these colonies may reflect adaptive tolerance to high salinity fluctuations. Similar adaptations to environmental stress are discussed by Kelmo et al. (10.1007/s00338-003-0335-0) concerning the effects of the 1997–98 El Niño on coral communities within turbid environments in northern Brazil. The authors report variable impacts on different components of the reef system and suggest that those that survived relatively unscathed may represent groups that have become pre-adapted to stresses imposed by the high turbidity conditions. Comparable adaptive tolerances to stress are also discussed by Riegl (10.1007/s00338-003-0335-0), who suggests that a temporal change in the susceptibility of *Acropora* corals to the bleaching episodes in 2002 may reflect phenotypic adaptation following earlier bleaching episodes. These studies raise some interesting points in relation to our understanding of how coral reef systems may respond and adapt to future climatic and environmental change.

The paper by Guinotte et al. (10.1007/s00338-003-0331-4) addresses aspects of habitat marginality on a much larger spatial scale. The authors model the effects of changing sea-surface temperature and aragonite saturation state across the Pacific basin, through to 2069. The models indicate potentially serious consequences for many shallow reef communities across the Pacific. In particular, many presently thriving, high-diversity, low-latitude areas may become marginal with respect to sea-surface temperature and much of the Pacific may become marginal in terms of aragonite saturation state. Such changes, if realized, have the potential to significantly modify rates and patterns of reef carbonate production and accumulation in affected areas.

Concluding thoughts

The papers presented in this issue provide an insight into both the diversity of coral communities that occur in “marginal” marine settings and some of the variables that may influence the susceptibility of these systems to future environmental change. These contributions emphasize a growing recognition of the diverse range of environmental settings in which coral communities occur, many of which are clearly outside normally acknowledged regimes of temperature, salinity, or light penetration. While these coral communities may not produce extensive framework structures and, in some cases, show little evidence of net carbonate accumulation, they represent important sites of coral colonization and carbonate sediment production.

We suggest that it is more appropriate that these be considered not as restricted or disturbed communities, but as alternative states of coral community development. Much more research is needed, however, to understand the dynamics of these marginal communities (perhaps especially in terms of coral “turnover rates” and of the processes of carbonate production and cycling) and, where appropriate, their accretion histories. It would also be of interest to determine the contribution of these reef systems to global estimates of coral community development. These coral communities are probably far more common than previously thought, and as such should be considered part of the environmental norm.

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