

Geologic and Biologic Controls on the Evolution of Reefs

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Key Words

climate change, corals, habitat area, macroevolutionary resilience, mass extinctions, nutrients, photosymbiosis

Abstract

The shallow, tropical reef environment differs from other marine environments in its more intense competition for space, more limited nutrient concentrations, proliferation of clonal animals, and greater habitat complexity. The evolutionary consequences of these ecologic peculiarities are still poorly understood, but they seem to cause greater turnover rates of reef taxa than nonreef taxa and an especially volatile record of reefs on geologic timescales. The boom and bust pattern of Phanerozoic reef construction is impossible to explain by linear responses to physicochemical changes. Threshold effects appear to be involved not only in reef crises but also in reef expansions. Long-term climate change seems to influence the biotic composition of reefs, but neither climate nor sea-level nor chemical changes in the oceans can elucidate the waxing and waning of reefs. Biological factors affecting spatial competition are thus probably more important than geologic controls on reef evolution.

INTRODUCTION

Tropical coral reefs have long been used by both biologists and geologists as tracers of environmental change. Their preference for warm, nutrient-depleted, well-lit waters and their apparent sensitivity to global change led to the notion of reef development and even reef evolution being largely driven by physicochemical factors (De'ath et al. 2009, Hoegh-Guldberg et al. 2007, Kleypas et al. 1999, Knowlton 2001). Yet the stunning complexity of tropical reef systems in terms of biodiversity, habitat structure, and symbiotic and trophic interactions calls for biologic factors as well, especially for explaining reef evolution in the long run (Wood 1998, 1999). Evolutionary adaptation must have occurred to grant survival of these ecosystems on geologic timescales (Buddemeier & Smith 1999). Indeed, the fossil record suggests that ecologically complex reef systems have been around for hundreds of millions if not billions of years. However, as I will argue below, the interplay of physicochemical (geologic) and biologic factors and evolutionary adaptations did not help much to stabilize reefs on geologic timescales.

Reefs must be broadly characterized to allow for a comparative approach through Earth history: They are here defined as laterally confined structures built by the growth or metabolic activity of sessile benthic aquatic organisms (Kiessling 2003). As such, reefs are primarily seen as dense aggregations of sessile calcifying organisms with a three-dimensional structure. More narrow concepts are often used for modern coral reefs, where terms such as rigid, wave-resistant, tropical, and shallow water are added (Twenhofel 1950, Wood 1998). These restrictions are partly due to the nautical origin of the word reef (from the Middle Dutch word *rif*). They are also due to the strong influence of modern tropical coral reefs on our perception of reefs in general. Several terms have been introduced to circumvent the multitude of reef definitions. The most commonly used are organic buildup, bioherm, carbonate mound, and bioconstruction. The definitions of these terms are basically identical to the broader definition for reefs above. Given that even modern cold- and deep-water coral banks are now described as reefs (Roberts et al. 2006), we are safe to apply this broad definition to the entire geologic past. However, different kinds of reefs may have different geologic or biologic controls. For the purpose of this paper it is thus convenient to separate three basic types of reefs: (a) shallow marine reefs in which sessile hypercalcifying animals (animals with a large skeletal to biomass ratio) and/or algae played a major role in reef construction, (b) microbial reefs in which animals and calcareous algae are absent or only minor constituents, and (c) cold- and deep-water reefs.

This review focuses on shallow-water reefs with tropical affinity and highlights the processes that may have shaped the ups and downs of reef construction and the changes of internal composition and structure on geologic timescales. The controls on microbial reef development appear to be closely linked to the controls on shallow-water reefs and are thus discussed in combination. I often refer to the PaleoReefs Database (PARED), which compiles the geographic, geologic, and biologic information of known Phanerozoic reef structures and holds all the references that cannot be cited herein (Kiessling & Flügel 2002, Kiessling et al. 1999).

EVOLUTION OF REEFS AND WITHIN REEFS

Do Reefs Evolve?

As reefs are formed by highly integrated communities of calcifying organisms, the possibility of community evolution is raised. Reef communities should certainly not be considered superorganisms but nevertheless may evolve to a limited extent. It has been questioned in the past whether communities evolve in a Darwinian fashion, because community-related entities could not be identified as unified individuals with heritability such that selection would directly act upon them (Bambach & Bennington 1996). The notion that reef communities are just chance associations

of species with similar ecologic requirements (Hubbell 1997, Wood 1999) underscores this view. However, theoretical work has now established that selection can indeed occur at the community level (Johnson & Boerlijst 2002, Wright 2008), and empirical work has shown that predictions of neutrality are not met in reef coral communities (Dornelas et al. 2006). So the issue of community evolution cannot be rejected outright as impossible.

One important prerequisite for community evolution is that community configurations can maintain their integrity in the face of disruption (Johnson & Boerlijst 2002). This is evident, for example, in the Pleistocene, when reef coral communities show a surprising stability of community structure in the aftermath of glacially induced sea-level drops (Pandolfi 1996, 1999). However, this pattern might also be explained by the assembly of species with narrow niche breadths (Jackson & Overpeck 2000). Another prerequisite for community evolution is differential robustness and resilience of communities, such that particular communities have a tendency to last longer in evolutionary time. The deep time record of reefs offers two interesting, albeit indirect observations indicating that this condition is fulfilled.

First, it could be shown that the diversity of reef-building communities is connected to their ecological stability on evolutionary timescales, so that some community types seem to persist longer than others (Kiessling 2005a). Second, the 96 reef community types that can be separated in PARED (associations of reef builders at the ordinal and class levels) at the Phanerozoic scale are distributed unevenly through time. Times like today, when only a few community types dominate the global reef systems, alternate with times of many and more evenly distributed compositional types (Kiessling & Flügel 2002). When plotting the number of reef sites recorded within intervals against the evenness (J) of the comprising community types, a significant inverse correlation is evident (**Figure 1**). This implies that reef expansions are associated with a particular community type and suggest that community evolution may largely take place by differential expansion of community types (C. Simpson, personal communication 2009). I emphasize again that the natural selection of communities is not expected to produce complex community-level adaptations or

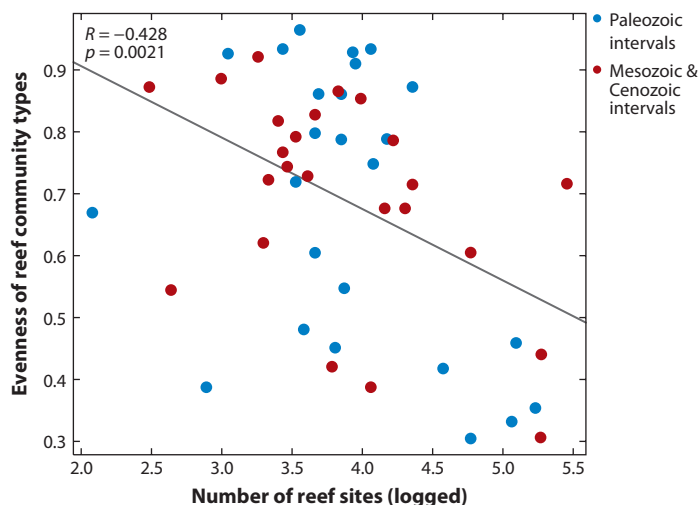


Figure 1

Number of reef sites in pre-Holocene time bins of approximately 10-million-years (Myr) duration plotted against the evenness of reef community types in the PaleoReef Database (PARED). Raw patterns are reported because reef numbers are not serially correlated. The inverse correlation suggests that only a few community types take part in reef booms, whereas community types are more varied during times of low reef numbers. Blue, Paleozoic bins; red, Mesozoic and Cenozoic bins.

lead to the emergence of a superorganism-like community. All reef community evolution means is that the waxing and waning of reef community types is due to the differential survivorship and expansion caused by intrinsic attributes of those community types.

Evolutionary Consequences of Living in Reefs

Competition for space, nutrient depletion, clonality, and habitat complexity are especially pronounced in reefs and apparently were so during most of the Phanerozoic history of reef building. The consequences of clonality are twofold: Mortality due to short catastrophic events is reduced, but clonal taxa are more susceptible to long-term physiologic stress and disease than asexual taxa because asexual propagation in clonal taxa reduces genetic variability (Lasker & Coffroth 1999). Otherwise, the evolutionary consequences of these peculiarities are still poorly understood. The net outcome seems to be greater evolutionary rates within reefs than outside reefs. Stanley (1973) compared the evolutionary turnover of reef taxa and nonreef taxa of bivalves and corals and came to the conclusion that evolutionary turnover is substantially greater in reefs owing to intense competition for space. A more detailed analysis was performed for Triassic-Jurassic times, for which there is evidence of greater origination and extinction rates in genera with a significant affinity for reefs (that is, a greater probability of finding a genus in a reef than in nonreef communities) than for those with an affinity for level-bottom communities (Kiessling & Aberhan 2007). Origination rates were almost constantly higher, whereas extinction rates tend to differ especially during mass extinction episodes. Extinction rates are tightly cross-correlated between reef and nonreef taxa, but origination rates are not. The especially strong impact of some mass extinctions on reefs has long been known, but there are also several misconceptions, which I will discuss separately (see Mass Extinctions).

The tropics are often considered cradles of evolution (Jablonski et al. 2006), and within the tropics reefs seem to be especially prolific at producing new species. Evidence comes from the large number of sibling species in reefs (Knowlton & Jackson 1994), the parallel increase of reef deposits and molluscan diversity in the Late Neogene of the Caribbean (Johnson et al. 2007), and greater diversification rates of reef-associated fishes than others (Alfaro et al. 2007). Therefore, an evolutionary component clearly has to be added to the numerous ecologic explanations of reef diversity.

Surprisingly, the evolutionary origin of reef builders themselves is more enigmatic. Do reef-building taxa preferentially originate outside the reefs to later contribute to reef construction, or is reef-builder diversity generated within reefs? This question is directly relevant to biotic controls on reef evolution, because reef-builder diversity and reef proliferation seem to be tightly coupled at the global Phanerozoic scale (Kiessling 2002, 2005a), although there are exceptions at smaller regional and temporal scales (Johnson et al. 2008). It has been suggested, based on a clustering of stratigraphically young genera in the diversity hot spot of the Indo-West Pacific, that reef corals largely originated there (Stehli & Wells 1971), but the underlying data could also be explained by biodiversity being generated elsewhere and reefs acting as diversity refuges (Pandolfi 1992, Rosen 1984), where diversity is largely driven by habitat area and overlapping geographic ranges (Bellwood & Hughes 2001, Bellwood et al. 2005). A potential solution could be to look at the environments of the stratigraphically oldest occurrences of hypercalcifying taxa and their later fate in terms of reef affinity.

GEOLOGIC HISTORY OF REEF BUILDING

Qualitative Survey

The earliest reefs, dating back to the Early Archaean (~3.4 billion years), were purely microbial, presumably built by the metabolic activity of cyanophytes and other bacteria (Allwood et al.

2006). In the absence of metazoan grazers, microbial reef structures attained impressive complexity and size in the Proterozoic (Turner et al. 1993).

The Ediacaran (the last period of the Precambrian, 630–542 Mya) saw the first reefs in which metazoan organisms are associated with microbes (Grotzinger et al. 2000), but it was not before the rise of archaeocyaths, a group of hypercalcifying sponges, in the Early Cambrian (~520 Mya) that invertebrate metazoans achieved a reef-building potential (Kruse et al. 1995). The dominant reef constructors, however, were still the microbes. Abundant cryptic communities, often involving the same species as on the open surface, provide evidence for intense competition for space in these early reefs (Zhuravlev & Wood 1995). With the extinction of archaeocyaths, the world experienced a return to microbially mediated reef growth with only occasional contributions of metazoans in the form of siliceous sponges (Rowland & Shapiro 2002). As for all invertebrate taxa, reef builders became more diverse and reefs more widespread during the Ordovician (Webby 2002), briefly disrupted by the end-Ordovician mass extinction (~444 Mya). The Silurian and Devonian were times when reefs changed little in large-scale taxonomic composition, internal structure, and biodiversity. Stromatoporoids, a group of hypercalcified sponges probably related to modern cave-dwelling *Astrosclera*, corals, and calcimicrobes were the most conspicuous components in reefs of these periods (Copper 2002).

After a major collapse of metazoan reef building toward the end of the Devonian (375 Mya), reef composition changed considerably during the Carboniferous and Permian. The extinction of Paleozoic stromatoporoids and a great proportion of tabulate corals led to a long-lasting decline in reef building, with microbes, rugose corals, some chaetetid sponges (related to modern cave-dwelling *Acanthochaetetes*), and bryozoans as major reef builders in the Early Carboniferous. In the later part of the Carboniferous until the Early Permian, calcareous algae became prominent reef builders, not by forming a rigid framework but rather by trapping mud between branches (Wahlman 2002). In the later Permian, a suite of hypercalcifying sponges gained importance in reef building, usually accompanied by microbial associations (Weidlich 2002). This composition was essentially maintained until the Late Triassic, when scleractinian corals became prolific reef builders (Flügel 2002).

Calcifying red algae were already conspicuous in Paleozoic reefs, but it was not until the Late Cretaceous (~80 Mya) that modern-type coral-coralline algal reefs emerged. Late Jurassic reefs (~155 Mya) already had a quite modern look except that they were often rich in microbial carbonates and hypercalcified sponges and lacked a strong biogenic binding (Leinfelder et al. 2002). During the Cretaceous, coral reefs gradually declined relative to rudist reefs. However, the reef-building capacity of rudists was low, with the result that the Late Cretaceous was an epoch of reduced reef growth. After a geologically brief recovery interval from the end-Cretaceous mass extinction (65 Mya), the Cenozoic started with a substantial rise in coral-algal reefs, only to be followed by a substantial decline at the end of the Paleocene (56 Mya; Flügel & Kiessling 2002) that lasted for the entire Eocene. Modern-type coral-algal reefs expanded globally during the Oligocene and Miocene, and modern day reef distribution was achieved in the Pliocene (Perrin 2002), just 5 million years ago.

Rudists: a group of aberrant hypercalcifying bivalves with coral-like growth forms that proliferated during the Cretaceous period

Phanerozoic Patterns and Trends

The number of reef sites recorded from each interval of time (bin) can serve as a rough proxy for assessing the fluctuations in Phanerozoic reef proliferation (**Figure 2**). Reef sites rather than individual reef structures were counted, whereby a reef site often lumps several reef structures of the same age and environment within 20 km (Kiessling et al. 1999). This PARED-derived pattern suggests an extreme variability in reef proliferation, with short-lived booms and without serial

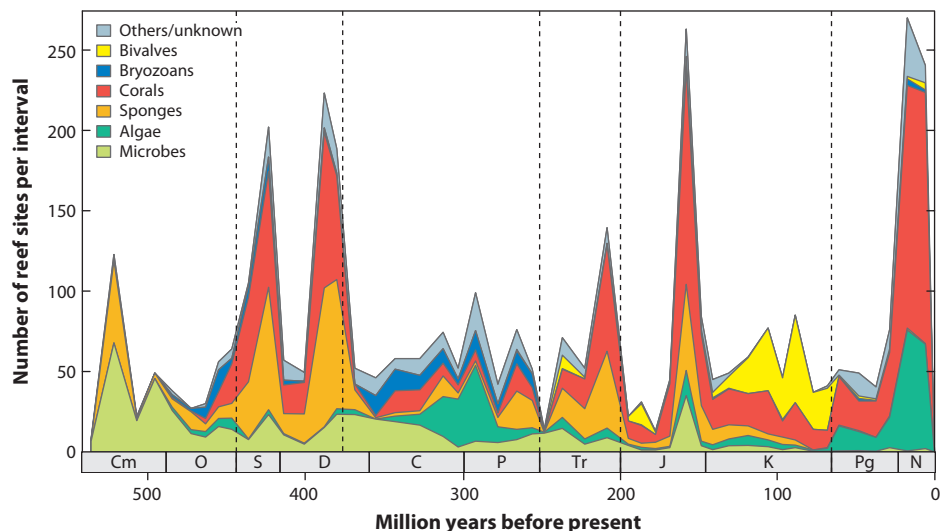


Figure 2

Number of reef sites and their biotic composition plotted by 10-Myr bin. A reef site often lumps several reef structures of the same age and environment within 20 km. The peaks persist if reef abundance is standardized for sampling, albeit with slightly different magnitudes. Vertical dashed lines indicate mass extinction episodes. Abbreviation of geological periods: Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; N, Neogene.

correlation. When taking the measured dimensions of reef sites into account, the fluctuations become even more dramatic (Kiessling et al. 2000). This is in stark contrast to more anecdotal assessments, which depict a gradual increase of reef productivity until a reef crisis leads to a collapse of reef building (Copper 1988, Hallock 1997). There are, of course, a number of preservational and economic biases that may greatly alter the biologic signal in this pattern (Kiessling 2005b). However, even when taking these biases into account (Kiessling 2006, 2008), the basic pattern persists: (a) Reefs seem to be quite rare for most of the Phanerozoic. (b) Reef booms are massive and geologically short-lived, rarely lasting longer than 20 Myr. (c) There is no distinct trend in reef proliferation through the Phanerozoic.

Reef diversity, measured as the average species richness of reef builders within individual reef sites, also lacks a distinct Phanerozoic trend (Kauffman & Fagerstrom 1993, Kiessling 2005a), although the pattern of increase and decline is more asymmetric (**Figure 3**): Reef diversity builds up over tens of millions of years and then drops rapidly, usually at mass extinction events (Kiessling 2005a). The lack of a distinct trend in reef diversity suggests that thresholds might exist for the biologic complexity of reefs, at least when complexity is equated with the number of species and its scaling with ecologic interactions.

There are also distinct trends in Phanerozoic reef building. The most important trends are a decline of microbial participation (**Figure 2**) and inorganic cementation in reef growth and an increase in bioerosion intensity and debris production (Kiessling 2002). None of these trends is monotonic. For example, a notable increase in reef bioerosion is first noted in the middle Mesozoic approximately at the same time as in other environments (Vermeij 1987).

Several researchers have attempted to subdivide the Phanerozoic history of reef building into discrete units. Because the subdivisions give different weight to different reef attributes, they vary widely among researchers (Kiessling 2001b). The seven reef evolutionary units of

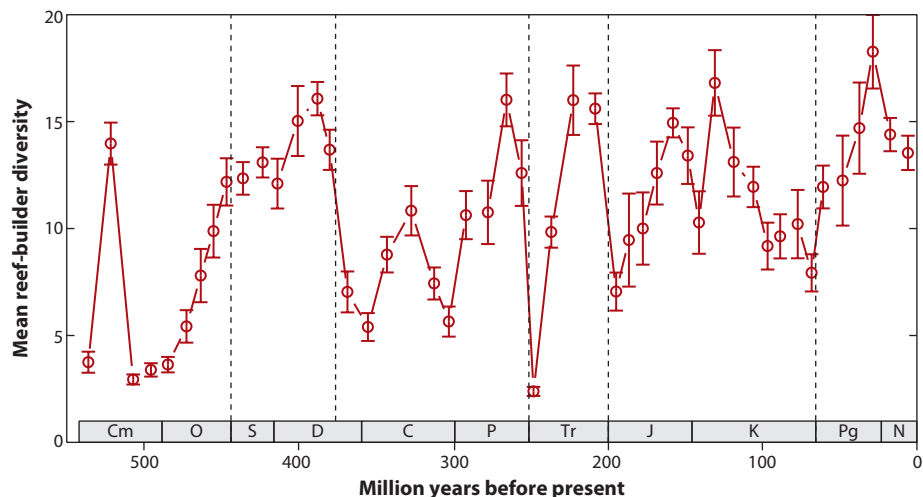


Figure 3

Trajectory of the mean species richness of reef builders in Phanerozoic reefs in 10-Myr bins. The pattern is mostly driven by the relative abundance of low-diversity reefs. For example, the decline in the Neogene is due to abundant low-diversity coral reefs in the Mediterranean region. The trajectory differs slightly from the one reported previously (Kiessling 2005a), because the definition of bins is different. Error bars represent standard errors.

Kiessling (2001b) are based on cluster analysis of a blend of biotic, architectural, and petrographic data and are thus not strictly equivalent to the ecologic evolutionary units recognized in level-bottom communities (Sheehan 1996). An intriguing aspect of the reef evolutionary units is that only two of their boundaries are clearly linked to mass extinctions (the Late Devonian and the end-Cretaceous mass extinctions). This might indicate that the role of mass extinctions in large-scale reef evolution is not very pronounced. However, more work is clearly needed on objective criteria for quantifying evolutionary and ecologic change at the ecosystem level.

GEOLOGIC CONTROLS

Among the important factors controlling modern reef development, temperature and nutrient regimes have long been discussed as the dominant controls on ancient reef development. In addition, sea-level change is a major theme in the geologic literature. Ocean chemistry is a recently recognized factor in modern reefs and not yet explored in ancient reefs, although Veron (2008a,b) has suggested that it may be a common explanation of reef crises. The importance of any of these geologic factors critically depends on the rate of change and frequency of extreme events relative to the rate of evolutionary adaptation. A straightforward approach to estimate the evolutionary impact of individual geologic factors is testing for cross-correlations between changes of these factors and changes in reefs (Kiessling 2002). Of course, this approach has its limitations given the uncertainties in ancient physicochemical parameters, the coarse timescale at which such tests can be performed, and the regional variability of geologic factors.

Climate Change

The role of climate, and especially the temperature component of climate, deserves considerable attention, given current concerns (De'ath et al. 2009, Hoegh-Guldberg et al. 2007). On geologic

Hypercalcification:
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timescales, there is little evidence for climate change affecting reefs in a linear fashion. Changes in mean global temperature as reconstructed from stable oxygen isotopes and the distribution of nonreef climate-sensitive sediments do not correspond to changes in reef abundance or latitudinal distribution (Kiessling 2001a, 2002). Reports linking reef expansions and declines to climate change (e.g., Cecca et al. 2005, Copper 2002, Johnson et al. 1996) fail to explain why other changes in temperature did not lead to a similar response of reefs and why the reported (fairly modest) temperature changes would have such a dramatic effect.

At the coarsest level of greenhouse-icehouse phases, the reef-building ensemble tends to be enriched in calcareous algae during icehouse episodes. The best documented example is the Late Carboniferous–Early Permian Gondwana glaciation during which phylloid and other calcareous algae became prolific reef builders. The notion that ice proceeded toward equatorial latitudes (Soreghan et al. 2008) may explain the profound change in reef composition at global scales. Although the increase of calcareous algae in reefs is also evident in the Cenozoic icehouse phase, it is unlikely that temperature per se caused the algal takeover. Rather, excess nutrients provided by a more intense ocean circulation and dust from poorly vegetated lands seem to be a plausible mechanism (Soreghan & Soreghan 2002).

It is also conceivable that the spread of rudist reefs and the decline of coral reefs in the Late Cretaceous was partly due to global warming (Scott 1995). Traditional models linking this change to competitive displacement (Kauffman & Johnson 1988) are not supported by distributional patterns, which show little overlap (Skelton et al. 1997). That the rudists had a greater tolerance for elevated temperatures than corals can be inferred from their more tropical provenance (Kiessling 2001a). Alternatively, the changing chemistry of the oceans might be a reason for the success of rudists and decline of corals (Stanley & Hardie 1998).

Chemistry of the Oceans

A good correspondence is evident between the relative abundance of hypercalcifying taxa on carbonate substrates (**Figure 4**) and times of prolific reef growth (**Figure 2**). Hypercalcification is obviously tightly coupled to reef growth. The reasons for the proliferation of hypercalcifiers might be sought in chemical changes such as the saturation state of the surface oceans with respect to calcium carbonate or the Mg-Ca ratios in seawater.

Just like temperature, ocean acidification is currently receiving much attention as a control of reef development, because the saturation state of the ocean with respect to calcium carbonate is just as critical for coral growth as is temperature (De'ath et al. 2009, Silverman et al. 2009). However, the boom and bust pattern of reefs and hypercalcifiers is difficult to explain with inferred long-term changes in the saturation state of ocean water, at least if the major trigger is atmospheric $p\text{CO}_2$. Previous analyses failed to find any significant cross-correlation between changes in $p\text{CO}_2$ and changes in reef attributes (Kiessling 2001b, 2002). The impact of $p\text{CO}_2$ on oceanic pH critically depends on the timescale in question. Geologic models of CO_2 concentrations in the atmosphere suggest that these were much greater during most of Earth's history than today (Berner & Kothavala 2001). Yet, at these long timescales, elevated $p\text{CO}_2$ should not necessarily correspond to low calcium carbonate saturation owing to the buffering by increased silicate weathering and corresponding calcium flux to the oceans. The recently proposed curves of oceanic pH and calcium carbonate saturation for the Phanerozoic (Caldeira 2007, Locklair & Lerman 2005) are only valid under particular assumptions such as constant alkalinity and salinity.

The boron isotope composition has been suggested as an independent proxy for pH variations (Honisch et al. 2004, Pearson & Palmer 2000), but its use in deep time is hampered by changes in the isotopic composition of seawater on long timescales (Joachimski et al. 2005). There are thus

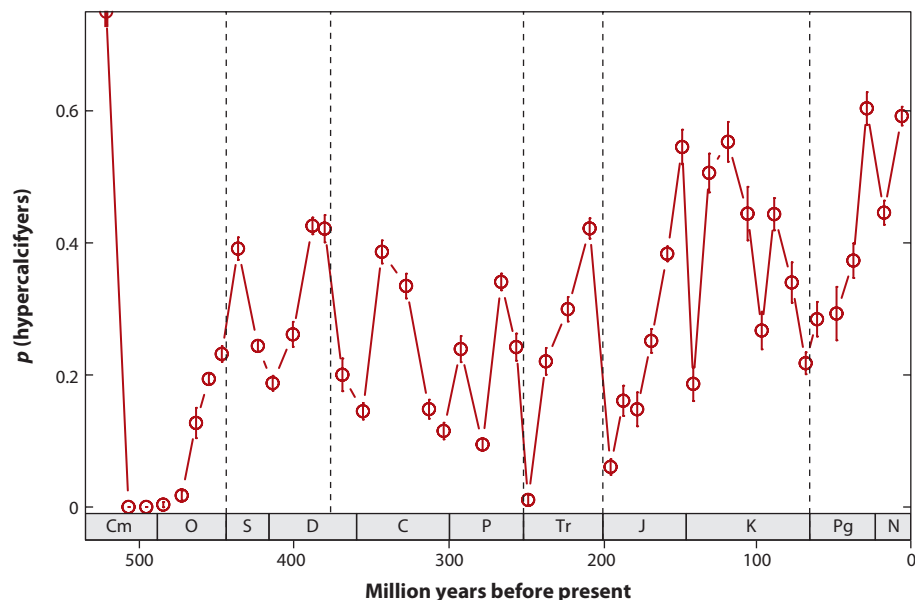


Figure 4

Number of hypercalcifying taxonomic occurrences (calcareous algae, corals, sponges, rudists, bryozoans) relative to all epifaunal macrobenthic occurrences on calcium carbonate substrates recorded in the Paleobiology Database. Error bars represent standard errors.

almost no independent constraints on ancient variations in ocean pH, and using proportions of hypercalcifying taxa or calcium carbonate sediment distributions to infer pH is circular reasoning. Even if weathering and Ca^{2+} fluxes are taken into account, models suggest (*a*) a much lower saturation value for most of the Phanerozoic than today and (*b*) a rather smooth curve (Locklair & Lerman 2005). Neither observation agrees with the patterns of reef development and hypercalcification. The possibility that acidification events caused ancient reef crises will be explored in Mass Extinctions.

A different link between ocean chemistry and reef evolution was proposed by Stanley & Hardie (1998), who observed an agreement between inferred aragonite and calcite seas and the prevailing skeletal mineralogy of reef builders. These researchers supposed that plate tectonic activity controls Mg-Ca ratios in seawater, which in turn are responsible for the evolutionary success of reef builders. This hypothesis is based on experimental data showing that calcite is precipitated from aqueous solution with low Mg^{2+} concentrations, whereas aragonite is precipitated when the Mg-Ca ratio is greater than two. In transferring these results to the organic world, Stanley & Hardie (1998) suggested that aragonitic reef builders such as scleractinian corals would prevail during times of high Mg-Ca, that is, aragonite seas, whereas calcitic reef builders are more common during times of low Mg-Ca. Although the correspondence between modeled Mg-Ca ratios and the original mineralogy of reef builders is much less perfect than assumed (Kiessling et al. 2008), these discrepancies might be explained by insufficient knowledge of ancient Mg-Ca ratios. However, neither the waxing and waning of reefs nor reef diversity can be explained by ancient Mg-Ca variations. For example, the great expansion of coral reefs in the late Cenozoic coincides with a substantial rise in Mg-Ca, but a similarly strong expansion of scleractinian coral reefs in the Late Jurassic occurred during falling Mg-Ca ratios (Kiessling et al. 2008). Thus, the success

Aragonite–calcite seas: large-scale cycles in the dominant mineralogy of inorganic calcium carbonate precipitates, probably linked to secular variations of oceanic Mg-Ca ratios

and failure of reef building per se does not seem to be controlled by changes in Mg-Ca, nor can we predict which higher group of organisms will be successful in reef construction.

Sea Level

The role of sea-level change is multifaceted, but its effect on the availability of shallow water habitat area is an outstanding issue. Large-scale eustatic sea-level changes are the only accessible geologic factor that exhibits a significant cross-correlation with preserved reef numbers and volume at million-year timescales (Kiessling 2002). The correlations are not very strong, perhaps owing to confounding factors such as postdepositional erosion and siliciclastic shedding after orogenies. Glacio-eustatic sea-level changes must have had a profound impact on the global reef area during the Pleistocene, although these changes can currently only be estimated by modeling (Kleypas 1997). Apart from effects of reef productivity, little evidence exists for evolutionary consequences of sea-level changes in reefs, although sea-level changes have been attributed by some as major triggers of mass extinctions (Hallam 1989, Peters 2006).

An underexplored effect of sea-level changes is with speciation due to the separation of oceanic areas during low stands of sea level. Glacial sea-level changes are known to have a significant and lasting effect on the genetic structure of tropical marine species (Benzie 1999), which could lead to an increase in evolutionary rates. Sea-level-driven vicariance events have been suggested to explain the evolutionary pattern of some reef corals (Pandolfi 1992), although there is little evidence for evolutionary effects of these glacial variations on reef community composition in the late Pleistocene of Papua New Guinea and the Southern Caribbean (Pandolfi 1999).

Nutrients

Although climatic changes appear to covary with changes in nutrient regimes, the variability of nutrient input to the oceans is not well quantified. Qualitatively, nutrient availability is thought to have increased through the Phanerozoic. This was inferred from increases in the biomass of skeletal invertebrates (Bambach 1993), metabolic activity (Bambach 1993, Bambach et al. 2002), phytoplankton abundance (Martin 1996), and patterns of strontium, carbon, and sulfur stable isotopes (Martin 1996). All else being equal, a shift of the average ocean from superoligotrophic conditions in the Early Paleozoic to eutrophic conditions in the Neogene (Martin 1996) would mean that nutrient-depleted settings were more widespread in the Paleozoic than later on. The consequences of Paleozoic superoligotrophy would be favorable for reefs in terms of habitat availability, if they were photosymbiotic, but unfavorable if they were not.

A rough proxy for nutrient input could be the isotopic ratio of $^{87}\text{Sr}/^{86}\text{Sr}$ in carbonates, which presents a mixed signal of weathering of continental crust (delivering nutrients) and hydrothermal input from oceanic crust production. The good inverse cross-correlation between changes in reef diversity and changes in the strontium-isotope ratio might indeed suggest reef diversity benefits from low nutrient input (Kiessling 2002), although the hydrothermal component clearly needs to be better constrained.

BIOTIC CONTROLS

Predation, Herbivory, and Competition

Wood (1998, 1999) has strongly emphasized the increase of what she called biological disturbance during the history of reef building. Wood observed that the increase of specialized herbivores

and predators in the Cretaceous and Cenozoic profoundly influenced the community structure of reefs. Examples are the rise of coralline algae and the boost of branching corals with their potential for rapid asexual propagation through colony breakage. The evolutionary trends toward more predators, bioeroders, and herbivores are probably real. However, whereas the increase of biological disturbance may explain several trends in reef attributes, it fails to shed light on the nontrending attributes such as reef productivity and biodiversity.

Competition for space is dictated by the severely limited extent of suitable habitats for the growth of sessile benthic organisms. Sessile organisms require a stable substrate that is not regularly disturbed by sedimentation events or reworking. Substrate stability is available in a variety of settings, but firm substrates in regions of low sedimentation accumulation are clearly the first choice for epibenthic sessile organisms that lack specific adaptations to live on soft substrates. These constraints may explain much of the evolutionary peculiarities in reefs, because reef builders have to invest strongly in growth at the expense of successful reproduction. Hints supporting this assumption come from observations of a faster growth of spawning than of brooding corals of the same species (Ward 1995). Competition between potential reef builders and taxa without the capability to build reefs such as fleshy (that is, noncalcifying) algae must have always existed. All else being equal, competition with noncalcifying sessile taxa should determine the success of reef building in absolute terms. This competition can be relaxed when antifouling grazers are abundant or when nutrients are limited (Sammarco 1996, Wood 1993). The acquisition of photosymbiosis would thus be an important step toward escaping competition not only with noncalcifying but also with calcifying organisms that have higher nutrient requirements.

Photosymbiosis and Nutrient Requirements

The ability of reef corals to thrive in oligotrophic settings is clearly linked to photosymbiosis (Muscatine & Porter 1977). The occupation of nutrient-depleted habitats relaxes competition with more nutrient-opportunistic sessile organisms and reduces bioerosion by endolithic filter feeders. Therefore, the acquisition of photosymbiosis could be an evolutionary response to competition for space. Corals with symbionts are also likely to show different adaptability than corals without symbionts. This is inferred from the hologenome theory of evolution, which predicts a greater adaptive potential for the holobiont than for host and symbiont separately (Rosenberg et al. 2007). The role of photosymbiosis for calcification may have been overestimated in the past, because calcification can be enhanced by photosymbionts, but not necessarily so (Stanley 2003), and hypercalcification can occur without symbionts, for example, in oysters.

Unfortunately, little progress has been made in recent years on the role of photosymbiosis in extinct reef builders. Wood (1993) argued that most Paleozoic reef builders lacked photosymbionts and grew preferentially in mesotrophic settings. If this was the case, the ecologic controls on these ancient reefs were substantially different from those limiting Mesozoic and Cenozoic reefs. Several studies used morphologic criteria to separate zooxanthellate from azooxanthellate corals (Coates & Jackson 1987, Cowen 1983, Rosen 2000). These criteria can safely be applied to late Mesozoic and Cenozoic corals, but they remain equivocal in older periods. Isotopic analyses are suggestive of photosymbiosis in early scleractinians from the Triassic period (Muscatine et al. 2005, Stanley & Swart 1995) and some Cretaceous rudists (Steuber 1996), but not in Early Cambrian archaeocyaths (Surge et al. 1997). Solid data for other reef builders are lacking.

However, the great evolutionary benefit of mutual symbiosis (adaptive potential, escape from spatial competition) would represent a strong macroevolutionary pressure toward mutualistic symbioses, and the flexibility of symbiont acquisition today (Baird et al. 2007) might suggest that this is a smaller evolutionary step than sometimes assumed. Although dinoflagellates, to which

zooxanthellae belong, have a good fossil record only since the Late Triassic (Falkowski et al. 2004), zooxanthellae are not the only symbionts found in modern reef corals. Just like most animals, corals harbor a large suite of microorganisms, which contribute to their nutrition or increase disease resistance (Reshef et al. 2006, Rosenberg et al. 2007).

An indirect test of the likelihood of mutual symbiosis allowing reefs to thrive in nutrient-depleted settings can be provided by ancient reef distribution patterns. Global distributions in relation to continental configurations and inferred surface currents can indicate if reefs grew within or close to nutrient-rich upwelling zones (Kiessling et al. 1999). More details on nutrient requirements can be gained from regional paleogeography and sedimentary context (Kershaw 1993). Taken together, the patterns suggest that reefs were predominantly nutrient-opportunistic during only two episodes (Kiessling 2002): a prolonged interval from the Carboniferous to Early Permian when the reef factory was dominated by microbes and algae (**Figure 2**) and a geologically brief interval in the Early Jurassic when a suite of semi-infaunal bivalves were important reef builders (Fraser et al. 2004).

Although the distributional evidence is not conclusive about the symbiotic status of reef builders, a preference for relatively nutrient-depleted settings can thus be inferred for the great majority of Phanerozoic reefs, achieved by either photosymbiosis or other mechanisms. The above-mentioned cross-correlation between strontium isotopes and reef diversity is stronger for Paleozoic reefs than for Mesozoic and Cenozoic reefs, implying that Paleozoic reefs were more sensitive to variations in nutrient input. Finally, the increasing proportion of reefs growing in settings influenced by siliciclastic sedimentation (Kiessling 2002) supports the view that Paleozoic reefs were even more strongly adapted to nutrient-depleted settings than younger reefs.

Biodiversity

I observed (Kiessling 2005a) that the mean species richness of reef builders at a given time (**Figure 3**) contributes to the stabilization of globally averaged reef attributes such as community composition, reef architecture, and the growth density of reef builders. Major changes in reef attributes usually only occurred when reef diversity was low. As already mentioned, reefal carbonate production was also found to be cross-correlated with reef-builder diversity, but only without temporal lag. This means that over long timescales biodiversity may help create large volumes of reefs (or diversity and productivity are controlled by similar factors) but does not stabilize productivity. More work at finer temporal and spatial scales and modeling approaches is clearly needed to fully understand this diversity-stability relationship at evolutionary timescales. Mass extinctions may break the diversity-stability relationship (Kiessling 2005a), so they require special attention.

MASS EXTINCTIONS

Patterns and Causes

Irrespective of their causes, mass extinctions form an evolutionary control on reefs in their own right. Mass extinctions led to profound declines of reef diversity and reefal carbonate production, but at the level of geologic stages, only four of the Big Five extinction episodes (Raup & Sepkoski 1982) also qualify as reef crises, at least when taking reefal calcium carbonate production as a proxy of reef health: the end-Ordovician (444 Mya), the Late Devonian (Frasnian-Famennian, 375 Mya), the end-Permian (251 Mya), and the end-Triassic (200 Mya). The end-Cretaceous extinction, although certainly catastrophic from a genealogical perspective, cannot qualify as a reef

crisis. Neither carbonate production nor reef diversity were affected at the resolution of geological stages (Flügel & Kiessling 2002). At the 10-Myr sample resolution (**Figures 2, 3**), just three mass extinctions also qualify as reef crises. At this resolution, the buildup of reefal productivity continued across the Ordovician-Silurian boundary. On the other hand, there are tremendous reductions in reefal productivity that are not associated with global biodiversity crises, for example, at the end of the Silurian and Jurassic periods.

The metric of carbonate production is, of course, especially sensitive to biases of the geologic record and strongly dependent on the temporal resolution. However, the basic pattern holds when sampling biases are taken into account (Kiessling 2008), and the metric is closest to what is understood when the current reef crisis is discussed: Reefs and population sizes of reef-building species are in decline, but confirmed global extinctions of reef taxa are still modest (Bellwood et al. 2004, Pandolfi et al. 2003). The modern example demonstrates that reef productivity can degrade prior to reef diversity collapse. This may explain why reef production is more volatile than reef diversity in the geologic record.

Veron has recently suggested that ocean acidification may be the singular factor responsible for major reef crises (Veron 2008a,b). Veron forwarded two major arguments in support of his hypothesis: (a) the prevalence of million-year reef gaps after mass extinctions and (b) the non-selectivity in extinctions between zooxanthellate and azooxanthellate corals. These observations are not universally true. They fail especially at the end-Cretaceous mass extinction, the last and best explored of the Big Five. First, the postextinction reef gap was geologically very brief (less than a million years for tropical reefs and zero for deeper-water reefs), and the earliest Paleogene reefs were even more widespread than the latest Cretaceous reefs (Flügel & Kiessling 2002). The relatively large extinction of zooxanthellate corals is not mirrored by a decline of coral reef production at the stage level (Kiessling & Baron-Szabo 2004), because surviving coral genera were more prolific reef builders than in the latest Cretaceous. The expansion of coralline algae after the K/T boundary (Aguirre et al. 2000) may also have contributed to the success of reef building. Second, there is good evidence that zooxanthellate corals experienced significantly greater extinctions than azooxanthellate corals (Kiessling & Baron-Szabo 2004, Rosen & Turnšek 1989).

The concept of reef gaps is generally problematic. Reef gaps are often used in geology to describe the complete absence of or extremely reduced reef growth in the aftermath of mass extinctions. However, reduced reef growth seems to be the norm rather than an exception (**Figure 2**), and true reef gaps are virtually absent if microbial reefs are included in the reef definition. Reef gaps are also rare when we focus on reefs constructed by hypercalcifying metazoans. So defined, the Middle and Late Cambrian epochs would represent the longest Phanerozoic reef gap (Rowland & Shapiro 2002). Among the Big Five, only the earliest Carboniferous and the Early Triassic qualify as metazoan reef gaps for a prolonged interval of time (Flügel & Kiessling 2002, Webb 2002). The presence of calcimicrobial reefs in both these reef gaps (Lehrmann 1999, Webb 1998) testifies that a long-lasting episode of ocean acidification is unlikely. Ocean acidification has been invoked to explain the end-Triassic mass extinction (Hautmann 2004), but the evidence is circumstantial, and extreme boundary conditions for volcanic activity must be assumed to achieve the required undersaturation of the oceans with respect to calcium carbonate (Berner & Beerling 2007).

Ocean acidification as a single cause for the extinction-related reef crises is therefore unlikely. The possibility that ocean acidification played a role in some reef crises is certainly worth pursuing, but rapid climate change (Late Devonian, end-Triassic), excess nutrification (Late Devonian), as well as oxygen shortage and H₂S poisoning (end-Permian) must also be considered as proximate causes. A major challenge will be to explain reef crises in the absence of global perturbations and elevated extinction rates.

Evolutionary Consequences

Although fundamental changes in reef systems occurred independent of mass extinctions (see Geologic History of Reef Building), several reef attributes were affected for prolonged times by those mass extinctions that also qualify as reef crises. These consequences include the high-ranked taxonomic composition of reef-building communities, numeric abundance, and calcium carbonate production (Flügel & Kiessling 2002), latitudinal extent (Kiessling 2001a), and skeletal mineralogy (Kiessling et al. 2008). Not all these attributes are affected simultaneously or at similar magnitude. The term macroevolutionary resilience may be appropriate to evaluate the ability of reefs to return to a preextinction composition after a severe global perturbation. Evidence for macroevolutionary resilience could be established if the reef-building consortium reverted to preextinction composition at the class level and if other attributes are also similar.

Evolutionary and ecologic consequences of mass extinctions appear to have been especially severe when important reef-building groups suffered extreme extinctions. For example, the great change in reefs across the Late Devonian extinctions is largely due to the massive extinction of stromatoporoids and tabulate corals (Copper 1994). Macroevolutionary resilience was extremely low. In contrast, the end-Ordovician mass extinction has long been known to be associated with major extinction rates but only limited ecologic consequences (McGhee et al. 2004), such that macroevolutionary resilience was high. This is also true for the end-Permian mass extinction, which remains a mystery in several respects. The extreme magnitude of the extinctions is mirrored by profound taxonomic changes, but ecologic changes in reefs appear to be modest after metazoan reef recovery. Paleozoic stony corals completely vanished, but several genera of calcareous sponges survived the mass extinction (Weidlich et al. 2003) and were important reef builders in the Permian and Triassic. Although the similarities are only conspicuous for particular reef types (Flügel 2002), the preferential survival of coralline sponges caused macroevolutionary resilience for these types of reefs. The consequences of the end-Triassic and end-Cretaceous mass extinctions were more profound. Again, preferential extinction of important hypercalcifying taxa (calcifying sponges and rudists, respectively) led to low macroevolutionary resilience.

INTERPLAY OF CONTROLS

Whereas biologic controls such as biodiversity may help stabilize intrinsic reef attributes, geologic and biologic controls do not interact in a way to make reefs a stable ecosystem when global reef abundance or volume is taken as a metric. Reef proliferation is partly governed by eustatic sea level, but this, as any other known geologic factor, does not fluctuate nearly as strongly as reef production. Threshold effects, possibly caused by emergent properties in reef systems, must therefore be important in reef evolution. This is not to say that reef evolution is completely self-organized. Geologic changes can enhance evolutionary changes that lead to enormous effects. An example for reef evolution might be sought in the Triassic period. Although currently untested, the earliest scleractinians known from the Middle Triassic may already have possessed photosymbionts (Stanley & Swart 1995). However, the major expansion of reef corals and reefs in general occurred much later during the Late Triassic. Recent climatic modeling suggests that the Late Triassic experienced a substantial drawdown in $p\text{CO}_2$ (Goddéris et al. 2008), approximately at the same time that morphological data suggest a substantial expansion of zooxanthellate corals occurred (Kiessling 2009). From the dinoflagellate perspective, a symbiotic relationship with corals would be a reasonable strategy to overcome the shortage of CO_2 by benefiting from (in addition to supporting) the calcification of the host (Goddéris et al. 2008). This scenario would explain why reefs managed to expand in abundance and even latitudinally in a cooling world.

Paleobiology database: the most comprehensive online resource on the taxonomy and distribution of fossils and their environmental setting (<http://paleodb.org>)

SUMMARY POINTS

1. At large temporal (Phanerozoic) and spatial (global) scales, reefs might evolve in a more Darwinian fashion than previously acknowledged, that is, by selection acting on reef communities with variability.
2. Reef taxa seem to exhibit higher evolutionary turnover, that is, higher origination and extinction rates than nonreef taxa.
3. The boom and bust pattern of ancient reef building suggests that positive feedbacks and threshold effects are important in both reef expansion and reef destruction.
4. Long-term climatic change tends to be associated with changes in the biotic composition of reef builders but not with reef proliferation and geographic distribution.
5. Hypercalcification is a prerequisite for prolific reef building, but neither variation of carbon dioxide concentrations in the atmosphere nor Mg-Ca ratios in seawater can explain the ups and downs in reef production.
6. Competition for space is key to understanding reef evolution. One way of relaxing spatial competition is by the acquisition of photosymbiosis, which allows growth in nutrient-depleted settings. Shallow-water tropical reefs have probably been adapted to nutrient-depleted settings since the Early Paleozoic. Although it cannot currently be determined if photosymbiosis was as widespread in Paleozoic reefs as in Mesozoic and Cenozoic reefs, nutrients and sedimentation thus seem to have had a similar control on reef development through their entire Phanerozoic history.
7. Some but not all mass extinctions had long-lasting or permanent consequences for reef evolution. I propose the term macroevolutionary resilience to assess the ability of reef systems to return to preextinction compositions at geologic timescales.

FUTURE ISSUES

1. Quantitative data on ancient reef composition and distribution should be utilized more strongly for assessing evolutionary patterns of reefs.
2. Novel approaches are needed to assess the likelihood that variations in calcium carbonate saturation state directly affected ancient reefs, causing reef crises.
3. The development of mathematical models on reef evolution is an urgent need as a complementary approach to empirical analyses. So far, models have largely been dedicated to reef development without considering evolution. Evolutionary models should incorporate the evolutionary cost of investment on growth rather than reproduction.
4. The Pleistocene offers outstanding opportunities to bridge the gap between ecological and evolutionary factors. Although a number of studies on Pleistocene reefs are available, these should be expanded to achieve a better global coverage.
5. More details on morphology, growth rates, and inferred ecological attributes need to be incorporated into global databases such as the Paleobiology Database to refine our assessment of controls on reef evolution.

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