NUTRIENT MODELS FOR THE DEVELOPMENT AND LOCATION OF ANCIENT REEFS

Robert J. Stanton Jr.

With 5 figures and 1 table

Department of Invertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles CA 90007, USA

Abstract

The primary function of reef builders, from a geological perspective, is the in situ production of carbonate sediment at a relatively high rate to create a biogenic carbonate body with relief above the sea floor. Reef-building metazoans fall into two broad categories based on the mechanism by which they produce skeletal carbonate — those with primary (autotrophic or photosymbiotic) production through the aid of photosynthetic algae or bacteria, and those with secondary (heterotrophic) production. In modern reefs, carbonate production by photosymbiotic organisms is strongly correlated with low-nutrient, oligotrophic settings and efficient metabolism, whereas carbonate production by heterotrophic reef builders depends on high concentrations of organic nutrients.

Photosymbiotic reef builders are largely responsible for the construction of modern tropical shallow-water reefs, and this appears to have been the case back into the Mesozoic. This conclusion is based on the geologic range of scleractinian corals, the dominant constructors of modern shallow–water reefs. However, the existence of photosymbiotic reef builders in the geologic record cannot otherwise be definitively established. Heterotrophs are responsible for modern deep- and cold-water reefs as well as contributing to the growth of shallow-water reefs. In the absence of firm evidence for photosymbiotic carbonate producers in the geologic record, they are postulated to have been the dominant carbonate-producing metazoans responsible for ancient reefs as well.

In addition to metazoans, photoautotrophs (algae and bacteria growing independently of a metazoan host) were also major carbonate contributors to ancient reefs and mounds. Because carbonate production by both photoautotrophs and heterotrophs depends on nutrient supply rather than the oligotrophic conditions optimal for modern photosymbionts, explanations for the sites and characteristics of ancient reefs must focus on the phenomena and settings that result in sources of abundant nutrients at the geographic scale of reef growth. These nutrient sources consist of localized terrestrial influx, cold seeps, endo-upwelling, and the oceanographic phenomena of upwelling, oxygen minimum zones, and internal waves. Analysis of ancient reefs in terms of nutrient source provides the opportunity, through an alternative paradigm than that provided by modern shallow-water reefs, to understand fundamental controls on growth and distribution of reefs in the geologic record.

Introduction

Modern shallow-water reefs have historically provided the paradigm for the study of ancient reefs. Recognition of ancient reefs was initially through comparison of their external geometry with that of modern reefs; subsequent analysis included comparisons of lithofacies and biofacies. The explication of the ecologic reef by Lowenstam (1950) strongly incorporated in reef study the role of the organisms as members of a distinctive reef community producing in situ carbonate sediment and forming a rigid wave-resistant skeletal framework. Although the incorporation of ecologic fac-

tors was an important step forward in reef analysis, it introduced the problem that modern deep- and cool-water reefs, as well as many ancient reefs (including mud mounds) appeared to lack a skeletal framework and wave-resistance, and thus did not fit the ecologic-reef definition that had been derived from modern reefs. This limiting effect of a strict uniformitarian application of the ecologic reef definition has been circumvented by emphasizing in situ biogenic carbonate production and de-emphasizing skeletal frame and wave resistance, as for the example in the definition of reefs "...as laterally confined biogenic structures, developed by the growth or activity of sessile benthic organisms and exhibiting topographic relief and (inferred) rigidity." (Flügel and Kiessling 2002, p. 3). This shifts the focus to the environmental conditions conducive for inordinately high, localized carbonate production, and to the physical processes of its accumulation, destruction and transportation that created a reef's distinctive external form and internal facies pattern (Stanton, 1967).

Numerous factors have been discussed as being important in determining the geologic history of reefs; these include seafloor topography (Wright, 1994), nutrients and productivity (Allmon and Ross, 2001; Bambach, 1993; Hüneke, et al., 2001; Wood, 1993; Wright, 1994), and the biota (Fagerstrom, 1987). These are well summarized by Kiessling (2002). Settings typical of abundant carbonate production and accumulation – 'carbonate factories' – have been described by Schlager (2003). The objective of this paper, in contrast, is to focus on the environmental factors important to heterotrophs and photoautotrophs because of their postulated dominant role in the formation of ancient reefs. Because reefs are sites of high rates of carbonate production, the most important factors are those that controlled nutrient supply.

Major carbonate producers in modern low-latitude shallow-water reefs are photoautotrophs (algae and bacteria) and photosymbiotic metazoans, most important of which are corals containing zooxanthellae, but also including sponges, mollusks and other organisms. For the host organism, photosymbiosis typically results in rapid growth, large size, and a high rate of skeletal calcification. It is most effective in oligotrophic settings because if nutrients are abundant, phytoplankton production reduces water clarity and thus photosynthesis for the zooxanthellae, organisms of the destroyer guild are more effective in removing carbonate skeletal sediment, and filamentous cyanophytes and macrophytes out-compete the photosymbiont macro-invertebrates for space (Hallock, 2001).

Historically, the photosymbiont paradigm has been the model used in the interpretation of ancient reefs. The alternative, heterotroph paradigm, that carbonate production depends on abundant nutrients to nourish heterotrophic and photoautotrophic organisms, has been applied increasingly to ancient reefs because unequivocal evidence of photosymbiotic organisms is lacking for much of the Phanerozoic. Recognition of the appropriate paradigm is important in the study of ancient reefs because the different paradigms lead to divergent explanations for the setting and pattern of reef growth.

The Phanerozoic record of photosymbiosis

The appropriate paradigm for the study of ancient reefs depends on the ability to determine whether photosymbiosis was present in the geologic record and was an important factor in reef growth. This question of photosymbiosis in earth history has received considerable attention (e.g. Wood, 1993, 1999; Kiessling, 2002). Because the photosynthesizing guest lived within the soft tissue of the host organism, photosymbiosis can not be directly observed in fossils. Consequently, criteria based on secondary attributes of modern photosymbionts have been proposed. These include:

1 Rapid growth is typical of modern photosymbionts. This is generally true, but growth rate is generally unknown for fossils. Consequently, large size is commonly used as a surrogate criterion. This, also is generally true, but is also of limited value because size is correlated with age, which, again, is generally unknown for fossils. Furthermore, because not all modern photosymbionts are large, as exemplified by numerous scleractinian corals and by the mollusk *Fragum*, assumption of photosymbiosis from growth rate or size yields a possible rather than definitive answer for fossils.

2 In general, photosymbionts have life habits by which they maximize the solar-energy uptake for the benefit of the symbiotic algae or bacteria. This is reflected in their habitat preference and morphology, but these characteristics provide only probable interpretations for fossils. Modern zoox-

anthellate corals, for example, all live within the photic zone, but not all corals within the photic zone are zooxanthellate. Among bivalves, the zooxanthellate *Tridacna* fits the photosymbiotic model by being large, living in very shallow water, and having a distinctive epifaunal, gaping posture so the zooxanthellae within the mantle will obtain the maximum sunlight. In contrast, however, the zooxanthellate *Fragum*, is small and infaunal (Ohno et al., 1995). Size and life habit are poor criteria for recognizing zooxanthellate fossil corals or clams. Wood (2000) has reached a similar conclusion with regard to Devonian stromatoporoids.

3 Growth forms and corallite structures present in modern corals are correlated with photosymbiosis (Coates and Jackson, 1987). In the faunas they analyzed, the full range of growth forms is present in both zooxanthellate and azooxanthellate corals, but zooxanthellate corals tend to be multiserial whereas azooxanthellate corals are predominantly solitary or pseudo-colonial. Although the range of corallite diameter in each group is comparable, corallites in zooxanthellate corals tend to be much smaller than in azooxanthellate corals. Corallite integration ranges from high to low in both groups, but tends to be much higher in zooxanthellate corals. These group tendencies can be used to infer whether an assemblage might have included photosymbiotic species, but not to infer beyond a probability as to whether a particular fossil species in the assemblage was a photosymbiont. Further, because these tendencies are also correlated with type and rate of sediment input (Sanders and Baron-Szabo, 2005), they can not be interpreted uniquely in terms of photosymbiosis.

4 Skeletal geochemistry, particularly isotope composition, may provide valuable criteria to distinguish zooxanthellate and azooxanthellate corals. The most thorough evaluation of the use of carbon and oxygen isotopes for this purpose has been that of Stanley and Swart (1995). In their study, modern azooxanthellate corals ..."always show a strong positive correlation between the $\delta^{13}C$ and $\delta^{18}O$ isotopes in their skeletons". This is the case, however, for only 4 of the 7 species they document. They also conclude that "In contrast, within individual zooxanthellate corals there is usually no strong correlation between these isotopes". However, they use only a small part of the total isotopic range for zooxanthellate corals in arriving at this conclusion. With these criteria, they conclud-

ed that the 13 Late Triassic coral species they studied were zooxanthellate (they questioned whether the correlation between the isotopes in two of the species was weak, but if uniform scales are used for their isotope plots this uncertainty is not visually apparent).

An essential requirement in such a study is that diagenesis had not altered the isotopic composition of the fossils. Although their careful analytical procedures and thorough discussion of the effects that diagenesis might have had support their conclusions and the potential value of isotopes in recognizing photosymbiosis in fossil corals, diagenetic alteration of their samples is nevertheless probable for a number of reasons, even though they could not detect it: 1) Seasonal isotopic variations are absent in the specimens. These should have been present if the corals had lived within the photic zone and were dependent for sunlight on their growth. Thus it appears that diagenesis had obliterated the original seasonally variable, isotopic signal. 2) The species analyzed cover the full morphologic range from solitary to multi-serial. That all would be zooxanthellate is contrary to the guidelines of Coates and Jackson (1987) that relate morphologic characteristics of a coral to the probability of its being zooxanthellate. 3) The species that Stanley and Swart (1995) postulated to be zooxanthellate are from very early in the history of scleractinian corals and are from diverse scleractinian taxa. In contrast, it is estimated that the percentage that were photosymbiotic increased during the evolutionary history of scleractinians, but was only about 25% in the Late Triassic (Kiessling, 2002). The high percentage for the samples of Stanley and Swart (1995) again suggests a ubiquitous diagenetic alteration. The existence of zooxanthellate corals in the Late Triassic is possible, but it is not established by isotopic criteria in this study, nor is it by the criteria of size and life habit that Stanley (1981) had postulated earlier (Wood, 1999).

Lacking definitive skeletal criteria by which to recognize photosymbiont fossils, a strictly uniformitarian argument has been that because high carbonate production in modern reefs is due to photosymbiosis in a wide range of organisms, and high carbonate production was responsible for fossil reefs, photosymbiosis therefore must also have been present in ancient as in modern reefs (Cowen, 1988; Talent, 1988). The present consensus, howev-
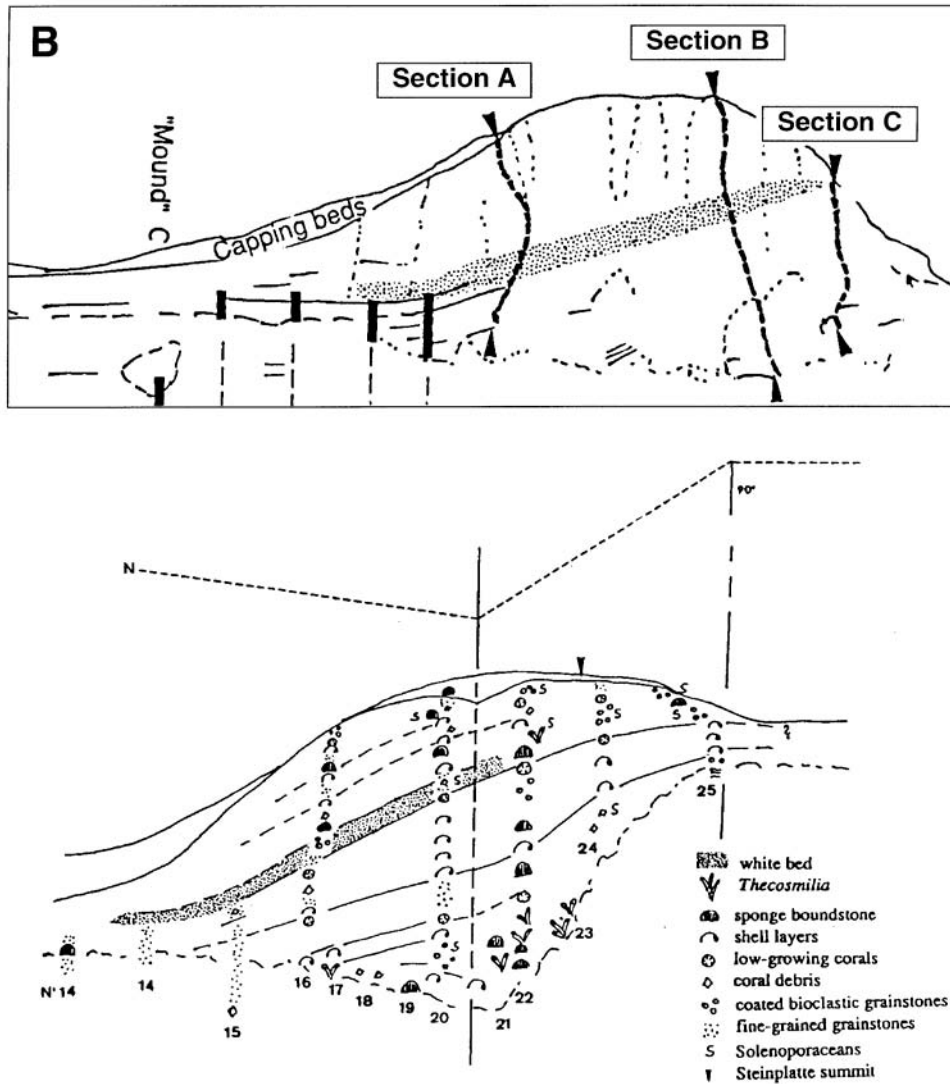
Fig. 1: Biotic content of. A. Profile at the Steinplatte as exposed on outcrop showing the platform-edge transitions: 1) from ramp (right) at about Section B to the distal steepened ramp slope, and 2) from the distal steepened ramp slope to basin floor (left) at about location of Mound C. B. Dominant biota in this platform edge: Note prevalence of shell layers. Dashed line indicates changes in orientation of the outcrop. From Flügel and Koch, 1995.

er, is that although photosymbiosis may reasonably be inferred for scleractinian corals back into the Jurassic (Leinfelder, 2001), it was not an important factor in reef growth until the Cenozoic (Kiessling, 2002). For much of the Phanerozoic, the photo-symbiotic paradigm can not be proven, and appears to be unlikely. Consequently, the alternative het-erotrophic paradigm focussing on localized nutrient supply should be utilized to explain and predict reefs in the geologic record.

Triassic examples of the heterotrophic paradigm

The validity of the heterotrophic paradigm for ancient reefs has been increasingly recognized (e.g. Dupraz and Strasser, 2002). Two Triassic examples from the Alps are presented here. One is the distally steepened ramp that formed the platform-margin at the Steinplatte (Fig. 1A; Piller, 1981; Stanton and Flügel, 1989, 1995; Flügel and Koch, 1995). Here, the colonial scleractinian coral *Retiophyllia* would

appear to be the dominant reef constructor (Piller, 1981). It forms patches in four settings: a) on the outer ramp surface, b) at the slope break from ramp to distally steepened ramp, at an estimated depth of 70-140 m, c) on the distal ramp slope, and d) at the base of the pro-grading carbonate ramp in what must have been a water depth approximately 100 m deeper than at the slope break, e.g., 170 to 240 m (Stanton and Flügel, 1995). Although some

Fig. 2: Upper Norian platform edge, Julian Alps. From Schlaf et al., 1999.

Retiophyllia colonies grew to a height of at least 3 m, it is unlikely that they were zooxanthellate: 1) because their depth range extended to below the base of the photic zone, and 2) because morphologic differences that would be expected across this depth range if they had been zooxanthellate (e.g. Chappell, 1980) are absent. In any case, corals were minor contributors to the Steinplatte carbonate mass both as colonies and as sediment grains. Instead, bivalves, microfossils and sponges the were major sediment contributors (Fig. 1B; Stanton and Flügel, 1989; Flügel and Koch, 1995). Thus, carbonate production depended primarily on heterotrophic organisms, and by inference on abundant nutrients. Coral colonies are minor contributors to other Triassic reefs, as well, as has been described, for example, at Hohe Göll by Zankl (1969) and at Rötelwand by Schäfer (1979). In these examples, coral patches make up perhaps 10% of the mass of reef. It has commonly been assumed that these coral thickets or Riffknospen were point sources of skeletal sediment for the adjacent sea floor, and thus corals were probably much more abundant than is apparent from the abundance of intact colonies in the scattered patches (Zankl, 1969). This was not the case at the Steinplatte, as noted above, and was probably not the case in general because of the relative resistance of the coral skeleton to attrition (Ginsburg, 1956).

Coquinas consisting predominantly of shells of pteriid bivalves form the upper Norian platform-edge in the Julian Alps (Fig. 2; Schlaf et al., 1999). The platform edge was the primary site of mollusk production, with bivalve-rich packstone lower on the slope derived in large part by down-slope transport. Although the coral *Retiophyllia* is a major
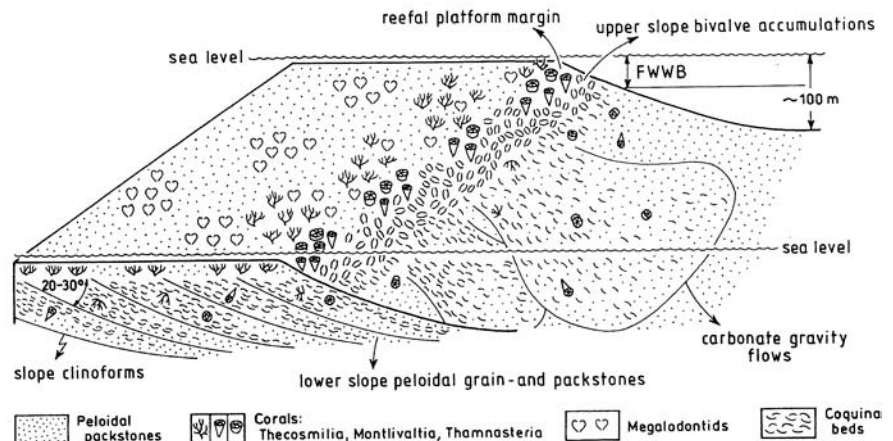
component of framestone patches scattered on the upper surface of the platform margin, pteriid bivalves are also abundant in these patches. Recognizing that the platform edge is primarily the result of carbonate production by heterotrophs, Schlaf et al. (1999) invokes the heterotrophic paradigm and attributes the dominance of the bivalves and the resultant carbonate production to high nutrient supply. This platform margin, as well as other similar Triassic platform margins, including that at the Steinplatte, border intraplatform basins. Black shale in all these basins is indicative of basin-floor anoxia and high rates of organic-carbon accumulation, suggesting high nutrient concentrations as a general feature associated with the growth of all these reefs.

Nutrient sources

Four types of localized nutrient sources are most useful as a framework for analyzing ancient reefs in terms of the heterotrophic paradigm (Table 1).

Table 1. Nutrient sources for heterotrophic reef growth

    Terrestrial input

    Cold seeps

    Endo-upwelling

    Oceanographic phenomena

        Upwelling

        Oxygen minimum zones

        Internal waves

1. Terrestrial input. Organic matter in the oceans is ultimately derived from land. Indicative of this is: 1) some 80% of organic carbon buried in marine sediments is of terrestrial origin (Hay, 1995); and 2) carbon influx from oceanic islands in the southwest Pacific, which contribute perhaps as much as one-third of the particulate organic carbon entering the world oceans, is directly correlated with river runoff (Lyons et al. 2002).

It is difficult to link, however, the input of terrestrial particulate and dissolved organic nutrients to carbonate production because of their riverine origin. One reason is that the oceans off river mouths are characterized by low carbonate accumulation because the associated low salinity and high turbidity are generally inimical to carbonate-producing organisms. Another reason is that because of the high fluvial sediment influx, what skeletal carbonate is produced makes up a minor part of the total sediment budget. On the other hand, scleractinian corals and coral buildups are common within terrigenous to marl sediments in the geologic record and the environmental range of scleractinian corals terms of sediment parameters has expanded during the Mesozoic and Cenozoic (Sanders and Baron-Szabo, 2005). Corals adapted to higher levels of turbidity, sediment influx, and nutrient supply than are characteristic of the stereotypical shallow, clear-water and oligotrophic settings of modern reefs. Terrestrial nutrient supply and associated sediment influs are more important factors for scleractinian corals than the photosymbiotic/oligotrophic paradigm would suggest. The example of Jurassic corals flourishing in areas of terrigenous sedimentation also indicates that potential deleterious clastic sedimentation is counterbalanced by increased nutrient availability (Leinfelder, 2001).

Control of reef growth by terrestrial nutrient supply has been used to explain biotic changes in Devonian reefs in the Western Canada Sedimentary Basin (Eliuk, 1988). Tabulate corals and stromatoporoids were the dominant reef-building skeletal macro-organisms whereas megalodont bivalves, of lesser abundance, were important components of younger, reef-capping and fore-reef-slope strata. Eliuk (1988) proposed that as a terrestrial flora developed during the Devonian on the shelf, soil formation increased and both sediment and organic matter were washed from the shelf into the basin. He explained the decrease in abundance of corals and stromatoporoids by both the increasing turbidity and by nutrient poisoning (this assumes that they were photosymbiotic, and does not take into account the adaptability of both tabulate corals and stromatoporoids to sediment influx as described by Sanders and Baron-Szabo (2005) for scleractinian corals). The contemporaneous increase in heterotrophic megalodonts is explained by the increasing nutrients. It is noteworthy that the Devonian reefs, like the previously described Triassic reefs, bordered on an intra-platform basin containing abundant black shale indicative of high nutrient input.

2. Cold seeps. Venting of hydrocarbons occurs at numerous localities on the modern sea floor and may result in carbonate masses that fall within the size range of reefs. On convergent plate margins, compaction of unconsolidated sediment and migration of interstitial water and hydrocarbons along faults or mud diapirs (Orange et al., 1999) is due to tectonic deformation and compactional loading. On passive plate margins, venting occurs along faults above salt domes. Hydrocarbons may also seep along permeable strata from underlying petroleum reservoirs, as in the North Sea (Hovland et al., 1998).

Both methane and hydrogen sulfide are used for carbonate production at modern seeps and to support a wide diversity of chemoautotrophic organisms (Sibuet and Olu-Le Roy, 2002). In the Gulf of Mexico, for example, symbiotic bacteria in chemoautotrophic lucinid and mytilid bivalves use exclusively either methane or hydrogen sulfide. In addition to skeletal carbonate, bacterially precipitated interstitial carbonate cement is a significant component of the carbonate accumulation at cold seeps. These carbonate bodies have discrete distribution patterns that are determined by the conduits along which the hydrocarbons flow. In the northern Gulf of Mexico, they occur in linear belts along fault traces overlying salt domes. Although seepage has been active since at least the Late Pleistocene (Aharon et al., 1997), the duration of an individual seep is generally less than a few hundred years because movement on the faults appears to turn the hydrocarbon flow on and off (Callender and Powell, 2000).

Carbonate mounds formed by the azooxanthellate coral *Lophelia* occur in the North Sea and north-east Atlantic and have lateral dimensions of up to 1 by 5 km and relief above the sea floor of as much as 100m (Freiwald, 2002). Upward growth of the mounds is as much as 2 cm/yr. (Freiwald et al.,
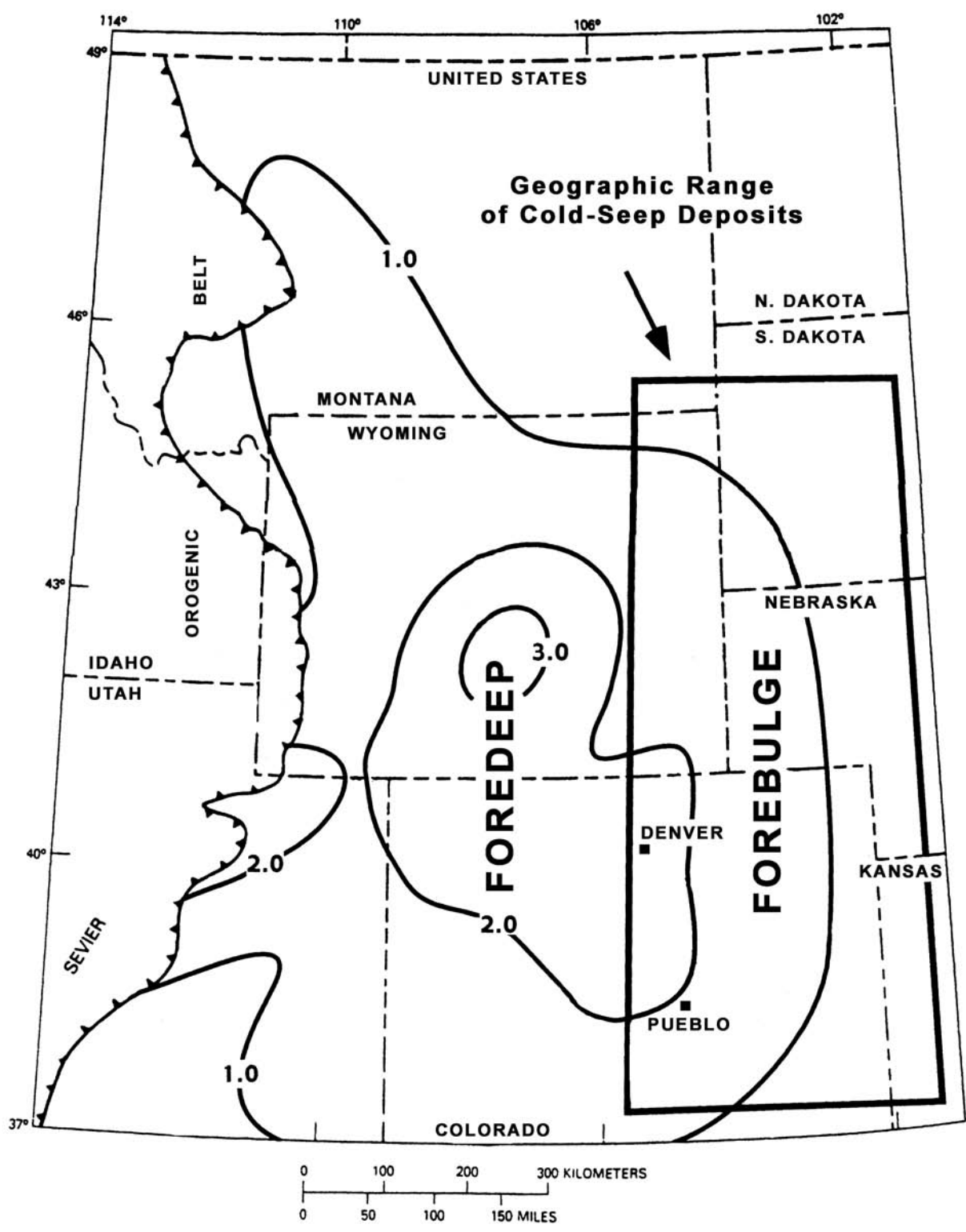
Fig. 3: Sedimentary-tectonic setting of the Tepee Buttes cold-seep deposits in the western interior of the United States. Contours are isopachs in kilometers. From Metz, 2000.

1997). Some of these mounds occur at sites of seepage of light hydrocarbons from the sea floor, leading to the hypothesis that the growth of *Lophelia* and location of the mounds are determined by the hydrocarbon seeps as nutrient sources (Hovland, 1990; Hovland and Risk, 2003). A strong presumptive argument may be made for this connection of seep and mound, but control of nutrient supply and location by ocean currents is probable for many of the mounds, and may be the general explanation in the absence of direct evidence of how *Lophelia* is nourished by the hydrocarbon seepage (Freiwald et al., 2002).

The Tepee Buttes in the United States have a cold-seep origin (Kauffman, et al., 1996) and have served as a model for other cold-seep carbonate buildups (e.g., Gaillard et al. 1992). They are irregular columnar carbonate masses consisting of dense aggregations of mollusk shells, primarily lucinid bivalves, in authigenic bacterial carbonate cement. Their biota and lithology are similar to modern seep deposits in the Gulf of Mexico (Callender and Powell 1997).

The Buttes occur within the Western Interior Cretaceous Basin; they range in age from early Campanian to early Maastrichtian but are restricted within this time span to periods during which thick accumulations of sediment were derived from an orogenic belt to the west, as indicated by major regressive pulses of sedimentation. The distribution of the Buttes was controlled by both regional and local factors. Regionally, the mounds are situated on the forebulge of the Cretaceous fore-arc basin because tensional arching on the outer margin of the foredeep during intervals of rapid sedimentation created avenues for upward migration of fluids (Fig. 3; Metz, 2000). Locally, they occur in linear trends determined by faults and flexures. Thus, their age and location were determined by sediment loading and by tectonic deformation; the distribution patterns of both modern seep deposits and the Tepee Buttes provide a predictive model for the discovery of other seep mounds.

3. Endo-upwelling. The paradox of prolific coral growth and carbonate production on coral reefs in low-nutrient, oligotrophic settings in the tropical oceans has been explained by efficient nutrient recycling and by the photosymbiotic enhancement of skeletal carbonate production. Endo-upwelling may provide an additional nutrient source for reef growth: As a result of geothermal gradients in volcanic islands of the Pacific Ocean, heat flow and upward convection of fluids from deep water adjacent to and within the islands may bring nutrients to the shallow-water reefs to increase productivity there (Rougerie and Wauthy, 1993). Thus, endo-upwelling may help to explain reef growth in this oligotrophic setting by adding nutrients and essential minerals to replace the inevitable loss from the nutrient-poor shallow-water environment. The concept has not been widely accepted by other students of modern reefs, however, for two reasons (Tribble et al., 1994): 1) nutrient recycling is considered adequate to maintain the coral-reef system without a large external source of nutrients, and 2) endo-upwelling at a rate great enough to create a significant nutrient source has yet to be documented.

Endo-upwelling may have been a more important factor in the growth of ancient than in modern reefs because it provided a nutrient source in the absence of photosymbiosis. Devonian reefs in Morocco provide one possible example of endo-upwelling. These reefs grew on topographic highs formed by a ridge of volcanic rocks of earlier Devonian age. The influence of the ridge on currents and storms was emphasized in an early study of these reefs (Brachert et al.,1992). The ridge topography also may have focussed ocean currents to raise the levels of nutrients and oxygen at the reef sites, and may have increased water flux through the accumulating carbonate sediment, which would have promoted early cementation (Hüssner, 1994). More recently, Belka (1998) and Mounji et al. (1998) proposed that the underlying volcanic rock was a source of hydrothermal fluids that could have both provided nutrients for organisms on the mound and promoted early cementation, inorganic precipitation of carbonate micrite, and formation of hardgrounds for epifaunal organisms (Fig. 4). The explanation for these reefs has evolved from the physical effects of sea-floor topography to local sources of nutrients, including the effects of an underlying geothermal gradient and heat flow. The nutrient source may have been a hydrocarbon cold seep, as documented for the Hollard Mound (Peckmann et al., 1999). In any case, endo-upwelling driven by the underlying heat source appears to have been a probable and fundamental cause.

Devonian reefs in the Harz Mountains of northern central Germany formed as atolls on volcanic highs within a clastic-filled basin (Fig. 5; Fuchs,

1990; Gischler et al., 1991; Gischler, 1995). On the basis of isotopic data, Peckmann et al., (2001) concluded that methane provided the nutrients for a chemoautotrophic biota. The methane could have been thermogenic as a result of the volcanic heat source, or could have been derived from the organic-rich basin sediments. In either case, the underlying volcanic rock played a more active role in reef location and growth than merely providing an elevated site for reef growth — fluid migration due to a thermal gradient above the volcanic basement is a clear indication of endo-upwelling of methane from the adjacent marine sediments and probably from nutrient-rich basinal seawater as well.

4. Oceanographic phenomena. Upwelling, oxygen minimum zones, and internal waves may concentrate or localize nutrients and thus strongly affect site-specific carbonate production and reef growth.

Upwelling — The food chain in the oceans is driven by organic material created within the photic zone. Through gravitational settling, however, the organic material is depleted in shallow water; upwelling is important in recycling it and inorganic nutrients back into the photic zone where they are essential for continuing primary production.

Upwelling is strongly controlled by geography: At the regional scale, it is concentrated along the eastern sides of the world's oceans (Flügel and Kiessling, 2002); at a finer scale, it is created through the interaction of ocean currents with seafloor or coastal topography. In coastal upwelling, in which surface water moves ocean-ward and is replaced by deeper and nutrient-rich water, the depth from which the upwelling water is derived, at the base of the mixed layer, is 100 to 200 m in most areas, but may be considerably shallower. For example, off Peru north of 15° S, it is only 25 to 75 m (Hutchings et al., 1995), and off the coast of Oregon and northern California, the surface layer extends to a depth of only 20 m (Smith, 1995). High organic productivity in the present ocean is strongly concentrated in areas of coastal upwelling (Jahnke and Shimmield, 1995; Hay, 1995); distribution of heterotrophic carbonate production and reefs may also have been similarly controlled during much of the Phanerozoic.

Oxygen minimum zone –Dissolved oxygen is low in the oxygen minimum zone (OMZ) as a result of decomposition of organic material that has settled
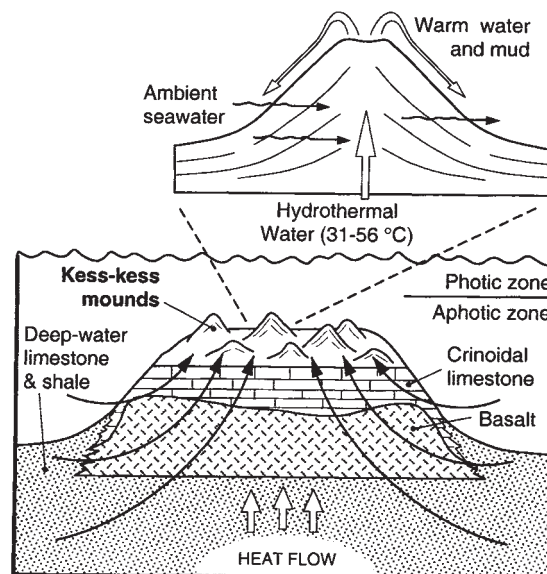

Fig. 4: Postulated geothermally-driven fluid flow, Kess-kess mounds, Morocco. From Mounji et al., 1998.
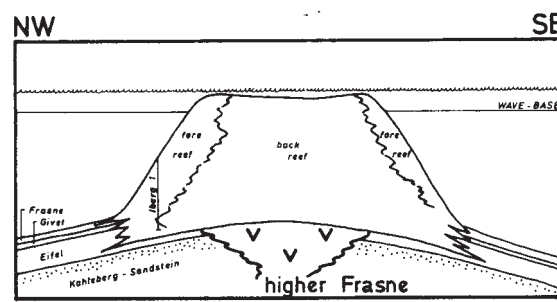

Fig. 5: Cross section of Upper Devonian reef, Harz, Mountains, Germany. Heat flow from the underlying earlier Devonian volcanic rock is postulated to have driven fluid flow from underlying basinal organic-rich sediments. From Gischler et al., 1991.

from the overlying water. The development and persistence of an OMZ requires a stratified water mass because vertical mixing by turbulence or upwelling would both disperse the organic matter and introduce oxygenated water. The depth at which an OMZ might occur in the geologic past is difficult to predict, given that the strength and bounding surfaces of present-day OMZs fluctuate seasonally and with oceanographic conditions (Pickard and Emery, 1992; Cannariato and Kennet, 1999), and over longer time spans as well, as for example during glacial and inter-glacial intervals of the Pleistocene (Dean and Gardner, 1998).

In the modern ocean, the top of the OMZ is commonly the thermocline, at the base of the photic zone, which corresponds to the boundary between warmer water above and cooler water below, and thus to the resultant pycnocline, dividing less dense water of the mixed layer above from denser and more stable water below (Pickard and Emery, 1992). The thermocline at low and middle latitudes in modern oceans is generally between 100 and 200 m (Defant, 1961).

The OMZ is a nutrient maximum in the ocean (Hay, 1995) because organic matter, both residual and that formed by in situ bacterial production, accumulates there (Kepkay et al., 1979). Bacteria are particularly abundant in the OMZ (Mullins et al., 1985; Thompson et al., 1985) and reduce biologically useful nitrate to nitrite, which then diffuses to the boundaries of the OMZ where it is re-oxidized to useable nitrate. The combination of more abundant dissolved oxygen, useable nitrate, and an optimal habitat for sulfate-reducing bacteria results in heightened biologic productivity at the upper OMZ boundary in contrast to either inside or outside the OMZ (Vercoutere et al., 1986). One result is that mats of non-photosynthetic bacteria that grow on the substrate are more common at the edges of modern OMZs than within them (Williams and Reimers, 1983). The fact that microbialite carbonate production is enhanced in OMZs due to the increased abundance of bacteria, but skeletal production is lower than in more oxygenated shallower water, provides an obvious explanation for deep-water mud mounds in the geologic record. In the northeastern Atlantic, *Lophelia* distribution is strongly concentrated at the top of the OMZ just below the thermocline (Freiwald et al., 1997; Freiwald, 2002).

Internal waves — Internal waves at density interfaces such as at the base and top of an OMZ are common and well-studied features in the ocean (Roberts, 1975; Apel, 1987). They have a significant effect on sediment reworking and movement and on vertical mixing within the water column (Ivey and Nokes, 1989; Cacchione and Pratson, 2004); they also significantly enhance organic production (Pingree and Mardell, 1981; Sandstrom and Elliot, 1984; Holligan and Groom, 1986; Rice et al., 1990), and provide nutrients to modern reefs (Andrews, 1983). These effects are accentuated if the slope of the sea floor is such that the internal waves will break where the pycnocline impinges against it.

Through resulting wave agitation of the sea floor, organic matter from the substrate is re-suspended into nepheloid layers in the water column, to be distributed within the area of agitation and into adjacent shallower and deeper areas (Cacchione and Drake, 1986; McCave, 2002). This benthic-pelagic coupling (Graf, 1992) of organic material that is of pelagic origin but is inaccessible to suspension-feeding benthic organism once it has settled on the sea floor unless there is some mechanism of re-suspension was probably extremely important for the growth of deep-water reefs.

The interaction of internal waves with the local sea-floor topography and the re-suspension of organic material where the waves impinge on the sea floor has been correlated with the distribution of *Lophelia* banks around the Faroe Islands (Frederiksen et al., 1992). Internal waves have also been invoked to explain biotic and lithologic features on the ancient sea floor. Thompson and Newton (1987), for example, proposed that the Devonian sea in New York was stratified and that a distinctive brachiopod fauna inhabited the sea floor at the upper boundary of an OMZ. Internal waves on the pycnocline were inferred from current-oriented brachiopods and from winnowed sediment containing small-scale cross-laminations and ripples. Baird and Brett (1991), in another study of Devonian black shales, also concluded that the depositional setting was a dysoxic to anoxic OMZ and they inferred that erosional features and disconformities were the consequence of sub-tidal turbulence and erosion caused by internal waves where the pycnocline impinged on the sea floor.

Upwelling, an OMZ, and internal waves have been integrated to explain the distribution and developmental history of Tournaisian Waulsortian mounds in the Sacramento Mountains of New Mexico (Stanton et al., 2000). The mounds grew on a southward-dipping homoclinal ramp at water depths ranging from approximately 110 to 250 m (Jeffery and Stanton, 1996a). They are situated on and around positive topographic features on the ramp that have been attributed to tectonism and to local erosion and deposition (Ahr, 1989; Jeffery and Stanton, 1996b; Jeffery, 1997).

Mound growth was within an OMZ as indicated by color, total organic content (TOC), and Fe and Mn content of inter-mound ramp strata. Organic carbon accumulation on this part of the ramp corresponds to modern examples of shelf or slope anoxia

resulting from organic carbon input exceeding the available oxygen for its decomposition (Tyson and Pearson, 1991). Upwelling as a control on the growth of Waulsortian mounds has been discussed by Wright (1994), Bridges et al. (1995), Pickard (1996), and Lasemi et al. (1998). It is a likely explanation for the combination of abundance of organic material, the resulting OMZ, and the location of the mounds within this nutrient maximum, but upwelling is a broad, facies-scale explanation. It does not explain carbonate production at the local scale of individual mounds.

Specific locations of mounds may be explained, however, if internal waves on the pycnocline at the top of the OMZ are incorporated into the analysis. Inter-mound strata on the ramp are characterized by fine and homogeneous texture and the absence of scour surfaces or fossil lags. Evidence of local current / wave action is present, however, in several mounds (Wanless and Tedesco, 1991). Considering that the mounds formed well below wave base, these sedimentary features indicate that internal waves impinged against the mounds but not against the adjacent gently sloping inter-mound sea floor.

The explanation of mound growth integrating all the available data is that initial ramp topography accentuated and localized the effects of internal waves at the pycnocline, causing local turbulence on the sea floor, vertical mixing, and enhanced upwelling and phytoplankton productivity. Resuspension of organic matter from the substrate was important for the predominantly suspension-feeding macrofauna, and particularly for the abundant siliceous sponges, which require dissolved nutrients or thoroughly degraded colloidal material for subsistence rather than cellular organic matter that would have been derived from a primary, phytoplankton source (Krautter, 1997; Pisera, 1997). These effects were at a more site-specific scale than that of upwelling alone induced by wind stress and Ekman transport of surface water. With mound growth, topographic disparity on the ramp increased so that the effects of internal waves were increasingly accentuated at the scale of individual mounds in a positive feedback loop (Hüssner, 1994). Enhanced local productivity as a result of benthic-pelagic coupling at the mound sites benefited the suspension-feeding macrofauna, and particularly the heterotrophic carbonate-producing bacteria re-

sponsible for the bulk of the lime mud, of which the mounds are largely constructed.

Conclusions

Study of reefs in the Alps, and elsewhere, has had two significant components. The first has been reef description and comparison in terms of lithology, paleontology, external shape and internal facies geometry, and the external factors of paleogeography and paleobathymetry, but with relatively little attention paid to what determined the specific site at which a reef grew. This, however, is precisely the question necessary to understand their origin and development and to explore for them in the subsurface as petroleum reservoirs or sites of mineral deposits.

The second component has been the historical use of modern shallow-water reefs as models for ancient reefs even though the significant characteristic of these modern reefs – the photosymbiotic nature of the major carbonate producers – generally can not be demonstrated and probably did not exist in ancient reefs, at least prior to the Jurassic or perhaps Late Triassic. Morphologic criteria for photosymbiosis in fossils yield conclusions that are only probabilistic and commonly apply only to assemblages but not individual taxa. Isotopic criteria are potentially more useful, but their validity has not been established.

Uniformitarian arguments for the existence of photosymbiosis are also of limited value. The assumption that abundant carbonate production throughout the Phanerozoic required photosymbiosis as in modern shallow-water reefs is countered by carbonate production in modern deeper- and cooler-water reefs. Another uniformitarian argument is that ancient reefs occur in the same setting as modern shallow-water reefs, and therefore the carbonate producers were also photosymbionts. This hypothesis is countered first by observing that modern and ancient reefs are distinctly different in the relatively greater abundance of microbial mud and cement in ancient reefs (Webb, 1996); the microbial contribution to the reefs is of photoautotrophic origin in shallow-water reefs, but must have been of heterotrophic origin in deep-water mud mounds. It is also countered by the fact that many ancient reefs do not occur in settings similar to those of modern reefs. Sub-photic mud mounds

are one example of ancient reefs not replicated in the present seas. Jurassic reefs in Bavaria grew in a complex pattern of mounds and inter-mound basins on a shallow shelf. Many ancient platform-margin carbonate reef systems occurred in intra-platform settings rather than facing the open ocean. Examples are the Triassic and Devonian reefs discussed above and the Permian reef of West Texas.

Thus, modern tropical reefs provide a limited model for fossil reefs. The photosymbiotic paradigm is based on reef growth in shallow-water oligotrophic settings. The alternative, heterotrophic paradigm, that abundant nutrients were required for carbonate production and reef growth, is proposed as the more robust model for the study of reefs during much of the Phanerozoic. Its application requires quite different environmental characteristics to explain the location and nature of nutrient sources and resulting reef growth.

The most significant of these are terrestrial nutrient sources, endo-upwelling, cold-seep hydrocarbon venting, and oceanographic factors of upwelling, oxygen minimum zones, and internal waves. Analyzing ancient reefs in terms of nutrient supply as controlled by these environmental features should promote better understanding of their origin and development.

Acknowledgements

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