Cenozoic Evolution of Larger Benthic Foraminifers: Paleoceanographic Evidence for Changing Habitats

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Abstract. The ever-increasing treasure-trove of paleoceanographic data relating to evolving Cenozoic ocean structure, including geographic and bathymetric gradients, provides novel insights into long-term changes in environmental conditions influencing shelf, ramp and oceanic-platform habitats occupied by carbonate-producing ecosystems. Similarly, recent studies documenting the influence of internal waves on mid- and deep-shelf habitats provides equally exciting insights into previously unrecognized environmental variability experienced by organisms living in those habitats. Paleocene-Eocene photic-dependent carbonates were dominated by calcitic coralline red algae and larger benthic foraminifers (LBF), with aragonitic corals and calcareous green algae more restricted temporally and spatially. Morphologies of LBF are strongly influenced by light availability and water motion, with larger, flatter and more fragile shapes characteristic of lower light, low wave-energy environments. Since substantial LBF habitat is at middle to outer shelf or ramp depths (i.e., ~30 to ~130 m), understanding the influence of internal waves on these habitats as oceanic thermal gradients developed through the Cenozoic can provide crucial insights into evolving environmental conditions where the most diverse and highly specialized LBF biotas occurred.

Key words: Carbonate ramp, reef, internal waves, thermocline gradients, symbiosis

Introduction

Understanding biological and geochemical processes associated with modern carbonate systems is essential to interpreting fossil reefs and carbonate sedimentation. Recognizing the limitations of uniformitarianism is equally crucial (Pomar & Hallock 2008). Cenozoic carbonate-producing ecosystems emerged from the remnants of Cretaceous biotas, evolving in the warm alkaline oceans of a Greenhouse world, then modifying as Icehouse conditions developed. The latter included stronger latitudinal and bathymetric temperature gradients, declining atmospheric CO_2 concentrations and declining calcium concentrations and alkalinity in the oceans.

Paleocene-Eocene photic-dependent carbonates were dominated by calcitic coralline red algae and larger benthic foraminifers (LBF), with aragonitic corals and calcareous green algae more restricted temporally and spatially. In this paper, we compare Hottinger's (1998) synthesis of records of diversifications and extinctions of Cenozoic LBF lineages in the context of published evidence for changes in ocean circulation and thermocline structure as Icehouse conditions developed (e.g., Lear et al. 2000). Moreover, given that much of the diversification was at middle to outer shelf depths (i.e., ~30 to ~130 m), synthesizing emerging records of the

influence of internal waves at those depths (e.g., Wolanski et al. 2004; Leichter et al. 2005) with the records of oceanic thermal gradients through the Cenozoic (e.g., Dutton et al. 2005) can provide crucial insights into how environmental conditions changed for middle and outer shelf benthic habitats.

Larger Benthic Foraminifers (LBF)

The LBF are an informal group of benthic foraminifers characterized by relative large size (e.g., generally > 1mm and up to 6 cm in diameter – Lee 1998) and complex internal morphologies. Modern representatives host a rich variety of algal endosymbionts in a relationship similar to that between corals and their zooxanthellae. By analogy, fossil LBF are interpreted to also have hosted algal symbionts (e.g., Lee 1998; Hallock 1999; and references therein).

Extant LBF worldwide belong to members of six long-ranging families, the Amphisteginidae, Alveolinidae, Nummulitidae, Peneroplidae, Rotaliidae, and Soritidae (e.g., Hallock 1999). One other family, the Calcarinidae, is characteristic of the late Neogene in the Indo-west Pacific, where some species are prolific producers of beach sands (e.g., Hohenegger 2006). Amphisteginidae, Calcarinidae, Nummulitidae and Rotaliidae are all families in the order Rotaliida, and are characterized by relatively transparent (i.e.,

hyaline) calcite shells. Members of these families typically host diatom endosymbionts. In contrast, the other families are Miliolida, whose shells of randomly arranged calcite crystals covered by a veneer of brick-like crystals impart a porcelaneous appearance that is relatively opaque to light (e.g., Debenay et al. 2000). The shells of many of the larger miliolids have thinned outer walls to permit light into the chamberlets. Larger miliolids host a diversity of algal symbionts (e.g., Lee & Anderson 1991). The Alveolinidae host diatoms. One lineage of Peneroplidae hosts rhodophyte symbionts while a second lineage has chlorophyte symbionts. Similarly, one lineage in the Soritidae hosts dinoflagellate symbionts while the second hosts chlorophytes.

Distributions of modern taxa of LBF are strongly influenced by light (Fig.1). Both between species and within species trends in morphology, especially shape and surface-to-volume ratios, reflect light intensity and water motion (e.g., Hohenegger 2005), both of which influence rates of calcification (e.g., Hallock et al. 1986). Thus, both conceptual (Hallock & Glenn 1986; Beavington-Penney & Racey 2004) and numerical (e.g., Hallock 1987; Mateu-Vicens et al. 2008) models have been developed to interpret paleoenvironments of LBF-rich limestones.

Hallock (1988, 1999) also noted that some taxa, notably the porcelaneous Soritidae and the stellate Calcarinidae, have tended to diversify "laterally", specializing to different relatively shallow-water, higher light habitats, while modern Amphisteginidae, and Nummulitidae have diversified vertically, with robust shapes characteristic of shallower dwelling species and flat shapes characteristic of deeper depths.

Historically, the terms photic or euphotic have been used to describe environments where there was sufficient light for an excess of photosynthesis over respiration (e.g., Hallock & Schlager 1986). Pomar (2001) proposed terminology to distinguish among photic habitats. He used "euphotic" only for depths where light is sufficient for high rates of photosynthesis and associated hypercalcification, typically less than 30 m even in very clear water. He used "mesophotic" to characterize depths where light is sufficient for photosynthesis to support substantial calcification rates, but not true hypercalcification, i.e., depths in the 20-70 m range, again dependent upon water transparency. He used the term "oligophotic" to characterize depths where there is limited light penetration sufficient to support calcifiers like coralline red algae, and very thin flat LBF and corals. As Hallock (1987) demonstrated using a modeling approach, well developed biotas adapted to low light for photosynthesis depend upon consistently high water transparency that permits light penetration to depths >70 m. Such consistently high water

transparency only occurs where surface waters are sediment free and have extremely low nutrient and plankton concentrations.

LBF assemblages typically characterize Pomar's (2001) light-defined zones (Fig. 1). Most of the miliolid LBF, as well as most calcarinids, live primarily in euphotic habitats. On the Florida reef tract, Soritidae (especially the Archaiasinae) show depth zonation, but none are common below about 30 m. Worldwide, robust *Amphistegina* also are found abundantly at less than 30 m, with progressively thinner or smaller chambered morphologies dominating below 30 m. Nummulitids can be found at less than 30 m, but most dominate at mesophotic to oligophotic depths (>30m, see Hohenegger 2005). Several extant nummulite species, whose shapes are very thin and flat, have depth distributions that peak at 70 m or deeper.

Water motion is another important environmental parameter influencing LBF distributions. Both wave energy and light decrease exponentially with depth, and both influence shell morphologies similarly, which is one reason LBF are excellent paleodepth indicators. Lenticular shapes, thicker shell walls and, in the case of the calcarinids, stellate morphologies allow such foraminifers to thrive and hypercalcify in high light, high wave-energy environments such as reef flats of the Indo-Pacific.
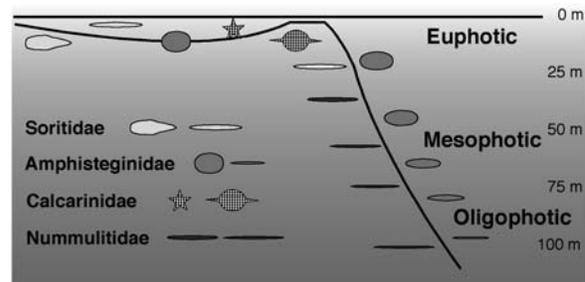

Figure 1: Major families of larger benthic foraminifers illustrating shapes and general depth ranges (Hallock 1999) in the context of euphotic, mesophotic and oligophotic habitats as defined by Pomar (2001).

In contrast, discoid morphologies are best adapted to quieter environments, where they either burrow their apertural face into the surficial sediments at a low angle, leaving most of the dorsal surface exposed to light, or sit flat on the substratum. Either way, they are superbly adapted to harvesting food and dissolved nutrients from the substratum and pore waters, while their algal symbionts capture radiant energy from sunlight. If their habitat is infrequently disturbed, e.g., by storm waves or deposit-feeding animals, these foraminifers can literally spend years accumulating the sparse resources required for reproduction (Hallock 1985). Exceptions to this generalization for discoid morphologies are shallow-dwelling Soritidae

that commonly attach to hard or phytal substrata in reef-flat environments.

Costs and benefits of algal symbiosis
There are energetic costs to establishing and maintaining symbioses between heterotrophic hosts and photoautotrophic symbionts (e.g., Hallock 1981; Stoecker 1998). Unless environmental conditions tip the energy balance in favor of benefits of symbiosis, photoautotrophic and heterotrophic taxa will predominate. The energy from photosynthesis must provide more than half the energy needed by the holobiont to be beneficial (Stoecker 1998).

Hallock (1981) predicted that, under nutrient-poor conditions with sufficient light, algal symbiosis can provide literally orders of magnitude energetic advantage over autotrophic-heterotrophic strategies. She further postulated that the most advantageous conditions for algal symbiosis occur when essential nutrients are extremely scarce and the only concentrated forms available are in particulate organic carbon such as plankton, bacteria or organic detritus.

Hallock (1985) examined life history strategies that would be most advantageous for LBF. She concluded that hydrodynamic environments, which tend to also be high light environments, would favor faster growth, higher fecundity and relatively short life spans. In contrast, Hallock (1985, 1987) predicted that, in mesophotic to oligophotic environments where radiant energy is limited but the probability of disturbance by hydrodynamic events is much reduced, longer life spans and production of fewer, larger embryons are advantageous. Mesophotic conditions appear to be optimal if water transparency is relatively dependable, because the holobionts are still able to get substantial energy from photosynthesis, while the potential for either photo-oxidative stress or physical damage by hydrodynamic events are low. The greatest risk is the potential for insufficient sunlight during turbidity events, although there is the potential for energy supplementation from feeding. Interestingly, the two extant families most prevalent in mesophotic and oligophotic depths are the amphisteginids and nummulitids. The former can become dormant within 24 hours of darkness, while at least some of the latter are bacteriovores (Lee 1998).

Oligophotic environments tend to be low energy, both radiant and hydrodynamic. So the limiting factor must be the tradeoff between the energy required to support the symbiosis versus the energy gain from photosynthesis. The morphological investment in maintaining a symbiosis appears to be extreme in very low light environments – long lives spent producing extremely large, flat shells. The strategies appear similar for zooxanthellate corals in oligophotic environments: significant investment in structures that optimize light capture rather than food capture (e.g., Jarrett et al. 2005). As a consequence, light energy must be relatively predictable for the investment to be beneficial, requiring that water column transparency be consistently very high.
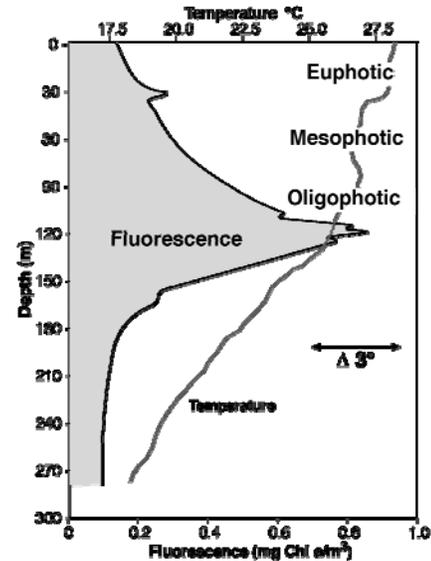

Figure 2: Data from Hallock et al. (1991) showing surface-to-thermocline temperature and fluorescence gradients for the modern northern Caribbean, annotated to indicate changes in light and temperature in the upper 150 m.

Bathymetric gradients and internal waves
In modern subtropical and tropical oceans, outside of upwelling zones, surface waters are warm and generally relatively well mixed by winds down to roughly 100 m. The base of the mixed layer/top of the thermocline also corresponds to the top of the pycnocline and nutricline, as well as the chlorophyll maximum zone (Fig. 2). In addition, O_2 concentration declines and pCO_2 increases relatively rapidly with depth. Above this layer, there is sufficient light for photosynthesis but generally limited nutrients. Below there is minimal light, but more organic carbon and biological activity utilizing oxygen, releasing nutrients and CO_2. This zone is very biologically and chemically dynamic.

The base of the mixed layer and uppermost thermocline corresponds with deeper mesophotic to oligophotic conditions described for outer shelf and ramp biotas. Thus, changes in physical and chemical conditions along that gradient would strongly influence deeper dwelling LBF biotas. The final consideration here is the influence of internal waves on LBF in mesophotic and oligophotic environments.

Leichter and colleagues studied internal waves in Jamaica and the Florida Keys, recording substantial temperature fluctuations on tidal frequencies at depths below about 30 m (e.g., Leichter et al. 2005; Leichter

& Genovese 2006). Wolanski et al. (2004) recorded temperature variations with depth in Palau, where strong internal waves impart as much as five degrees of temperature variability on habitats between 30 and 100 m depth on tidal cycles (Fig.3).
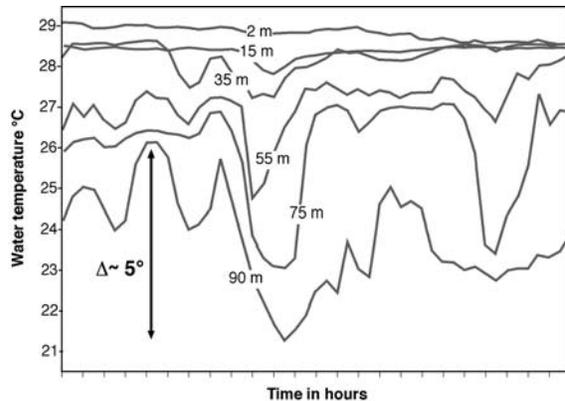

Figure 3: Data from Wolanski et al. (2004) recording internal wave activity on tidal cycles on the shelf of Palau, Western Caroline Islands, annotated to show that benthic communities living at 90 m depth experience substantial temperature fluctuations.

As a consequence, subtropical/tropical mesophotic and oligophotic biotas can experience temperature ranges of several degrees on internal-wave cycles. Those same organisms are experiencing comparable or greater changes in nutrients, organic carbon, and pCO_2. For LBF and other calcifying organisms, the latter may be particularly important as higher pCO_2 in the cooler waters, when pushed into shallower depths, should result in strong saturation gradients.

Cenozoic LBF: A brief summary
The end-Cretaceous extinction event (~65 Ma) was followed by an extended carbonate depositional hiatus (e.g., Newell 1982). Surviving shallow-water benthic foraminifers with established algal symbioses (e.g., miliolids) diversified, producing new lineages. New symbiotic associations developed in other lineages, especially diatom associations with rotalid taxa (Fig. 4). By ~60 Ma, new benthic taxa with complex morphologies were appearing (Hottinger 1998) and by the early Eocene, large, complex nummulitids were prominent carbonate-sediment producers in a variety of shelf and ramp environments (Beavington-Penney & Racey 2004). Extinctions eliminated the largest and most prominent forms of nummulitids and orthophragminids by the end of the Eocene.

New taxa arose in the Oligocene, the most prominently the lepidocyclinids and miogypsinids, though diversities, both horizontal and vertical were somewhat lower than during the Eocene apex (Beavington-Penney & Racey 2004). Lepidocyclinids and other characteristic Oligo-Miocene taxa were gone by the Early Pliocene. The amphisteginids,

which arose in the Paleocene-Eocene, have since been represented through the Cenozoic, as have the Soritidae, Peneroplidae and new lineages of the Nummulitidae. With the Neogene closure of the circumtropical seaway and the isolation of Atlantic biotas, the archaiasine lineage of the Soritidae diversified in the Western Atlantic, while the Calcarinidae diversified in the Indo-west Pacific.
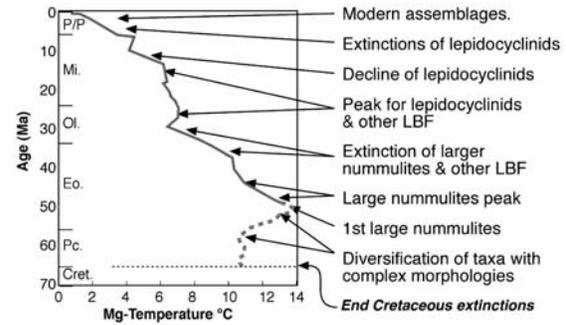

Figure 4: Comparison of the development of deep-sea temperatures (Leer et al. 2000) with diversification and extinction history of larger benthic foraminiferal (LBF) lineages (Hottinger 1998).

Given the prevalence of LBF as carbonate-sediment producers during the Cenozoic, especially during the Paleocene-Eocene, understanding and interpreting the environments in which LBF were living continues to be both scientifically and economically important. Hallock et al. (1991) compared Paleogene evolution and extinction events in LBF and planktic foraminifers, postulating that changing patterns in ocean circulation influenced nutrient regimes that were reflected in changing biotic assemblages. One goal of our paper is to consider how the evolution of oceanic conditions during the transition from the Greenhouse world of the early Paleogene to the Icehouse world of the Neogene influenced mesophotic to oligophotic habitats and biotas.

An interesting comparison can be made between the history of the LBF as interpreted by Hottinger (1998) and history of ocean stratification, as indicated by bathymetric temperature gradients that have been reconstructed for the subtropical north Pacific (Dutton et al. 2005). Note that the diversification of the large nummulites and other Paleogene LBF occurred when the deep sea was warmer (Fig. 4). The apex of these groups occurred when there was minimal temperature gradient between the thermocline and the deep sea, as reflected by minimal differences between $\Delta^{18}O$ in the shells of surface-dwelling planktic foraminifers and the shells of either *Subbotina*, which are thermocline-dwelling foraminifers, or shells of deep-sea benthic foraminifers (Fig. 5). In contrast, times when bottom temperatures were rapidly decreasing were characterized by increasing rates of extinctions of LBF (Fig. 4).

Directions for future studies

We postulate that the history of changes in Cenozoic ocean circulation associated with changes from early Paleogene Greenhouse to Neogene Icehouse conditions are recorded in evolutionary changes in LBF biotas. We recommend that future studies compare details of stratification of the ocean, as recorded by planktic foraminifers, with corresponding changes in LBF assemblages. We postulate that environmental conditions of middle and outer shelves can be more thoroughly interpreted by understanding changes in thermocline structure of impinging oceanic waters. Such progress will require more detailed comparisons of planktic and LBF records, and more research on the role of internal waves on modern outer shelf habitats.
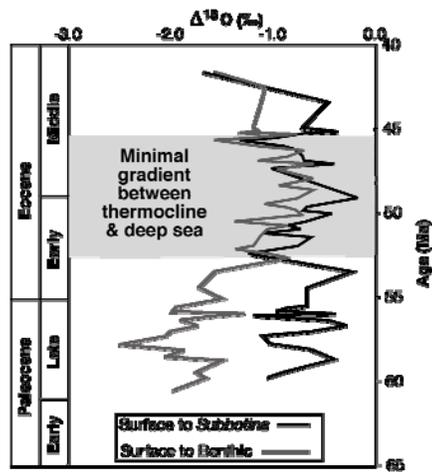

Figure 5: Data from Dutton et al. (2005) showing surface-to-thermocline (*Subbotina*) versus surface-to-bottom $\Delta^{18}O$ gradients, which indicate temperature gradients at the Shatzky Rise, subtropical North Pacific, during the Paleocene and Eocene. The bracketed time when differences between the gradients were minimal corresponds to the apex time for Eocene nummulites and other LBF according to Hottinger (1998).

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