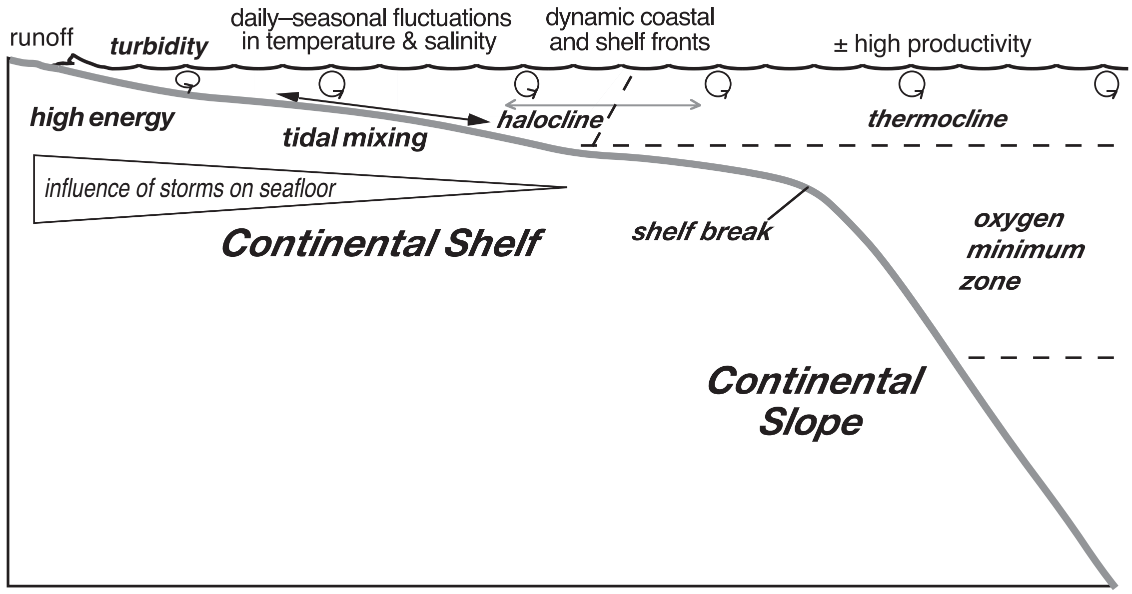
MICROPALEONTOLOGIC PROXIES FOR SEA-LEVEL CHANGE AND STRATIGRAPHIC DISCONTINUITIES



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FORAMINIFERA AS PROXIES FOR SEA-LEVEL CHANGE ON SILICICLASTIC MARGINS

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ABSTRACT: Foraminifera of siliciclastic and mixed siliciclastic–carbonate continental margins are sensitive to changes in sea level because of the complex biological, chemical, and physical oceanographic variables that help to shape foraminiferal niche space. Data on foraminiferal distribution and abundance provide useful proxies for paleoenvironment. Here we emphasize the importance of salinity, temperature, seasonality, food supply (productivity), and dissolved oxygen in controlling the nature of marginal marine, neritic, and upper bathyal foraminiferal biofacies. We also elaborate on the paleoecologic significance and utility of using planktic:benthic ratios, diversity indices, and similarity coefficients for interpreting changes in relative sea level. The recognition and correlation of the systems tracts that define sequence stratigraphic architecture reliably hinge on multi-proxy micropaleontologic evidence, particularly that provided by benthic and planktic foraminifera, coupled with sedimentology and geochemistry.

INTRODUCTION

Micropaleontology and biostratigraphy play vital roles for deciphering the stratigraphic record produced by changes in relative sea level, interpreting the history of global sea-level change, and testing models for the causes of sea-level fluctuations due to the variable influences of tectonics, glacio-eustasy, and climate. The stratigraphic architecture developed in response to changing eustasy, accommodation space, and sediment supply along continental margins (e.g., Haq et al., 1988; Abreu and Haddad, 1998; Hardenbol et al., 1998; Miller et al., 1998) can be interpreted using the tools of marine micropaleontology. Planktic and benthic foraminifera provide chronostratigraphic control and a wealth of paleoenvironmental information for the recognition of depositional systems tracts that develop in response to changes in relative sea level.

Neritic benthic foraminifera have long been used to interpret paleobathymetry, and hence changes in sea level, because recurrent onshore–offshore trends in assemblage composition and diversity characterize many terrigenous continental margins (e.g., Parker, 1948, 1954; Said, 1950; Ellison, 1951; Phleger, 1951, 1956; 1960, 1964; Phleger and Parker, 1951; Bandy, 1953, 1956; Bandy and Arnal, 1957, 1960; Upshaw and Stehli, 1962; Walton, 1964; Murray, 1973, 1991; Boltovskoy and Wright, 1976; Buzas and Culver, 1980; Ingle, 1980; Poag, 1981; Culver and Buzas, 1981, 1983a, 1983b, 1999; Lutze and Coulbourn, 1983/1984; Culver, 1988; Olson, 1990; Sen Gupta, 1999). Q-mode cluster analysis based on percentage data of samples is a common tool to distinguish groups of samples, or biotopes (e.g., inner, middle, and outer neritic and upper bathyal). R-mode cluster analysis based on percentage frequency of species in the samples can be used to distinguish assemblages of species, or biofacies, each characterized by one or more dominant species (e.g., Gevirtz et al., 1971; Lutze and Coulbourn, 1983/1984; Lagoe et al., 1997; Buck et al., 1999). See Parker and Arnold (1999) for a review of quantitative methods of data analysis in foraminiferal ecology.

Here we briefly review some of the salient oceanographic features of terrigenous shelves in terms of the complex and dynamic environmental variables responsible for producing depth-related assemblages of benthic and planktic foraminifera. We emphasize studies of modern benthic and planktic foraminiferal ecology that provide valuable insights into the original biocoenoses (life assemblages) of the upper reaches of the continental margin, those most sensitive to sea-level change, while acknowledging the significant role that taphonomic and postdepositional processes play in modifying these life assemblages. Our goal is to present an overview of how foraminiferal sediment assemblages can be used to track changes in relative sea level. This review includes a discussion of marginal marine, neritic, and upper bathyal foraminiferal biofacies, benthic and planktic foraminiferal ecology with a special emphasis on the importance of seasonality, water masses, and productivity in influencing biocoenoses, as well as paleoecological tools that can be used to decipher temporal and spatial changes in foraminiferal assemblages including planktic:benthic ratios, diversity indices, and similarity coefficients. We also present a generalized model of microfossil response to changing sea level as applied to a sequence stratigraphic (or genetic stratigraphic) framework. The sea-level proxies discussed here focus on siliciclastic systems, but many of the basic paleoecologic and biostratigraphic principles have broader utility in studies of mixed siliciclastic–carbonate depositional systems.

FORAMINIFERAL BIOFACIES AND THEIR RELATIONSHIP TO SEA-LEVEL CHANGE

Marginal Marine Biofacies

Agglutinated (foraminifera, thecamoebians) and calcareous (foraminifera, ostracodes) microfossils occur abundantly in marginal marine depositional systems including salt marshes, estuaries, and lagoons. The pioneering work of Scott and colleagues (Scott and Medioli, 1980; Scott et al., 1980; Scott et al., 1990; Scott et al., 1991; Scott et al.; Scott et al., 1996; Medioli and Scott, 1983) delineated the distributional patterns of modern temperate-salt-marsh agglutinated foraminifera and established their utility in identifying paleo–sea level based on the recognition of high-marsh assemblages. For example, the association of *Trochammina, Jadammina,* and *Miliammina* is diagnostic of salt marshes around the world. Additional research by other workers has focused on environmental and taphonomic controls on marsh foraminiferal distribution, as well as the implications of foraminiferal distributions in sea-level reconstruction (e.g., Goldstein, 1988; Williams, 1989, 1994; Scott and Leckie, 1990; DeRijk, 1995; Goldstein et al., 1995; Ozarko et al., 1997; Saffert and Thomas, 1998; Goldstein and Watkins, 1999; Horton et al., 1999a, 1999b; Patterson et al., 1999;

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Hippensteel et al., 2000; Lloyd, 2000; Horton and Edwards, this volume; Martin et al., this volume; Nikitina et al., this volume).

Modern foraminifera of lagoons, bays, estuaries, and fjords often show distributions related to the influence of salinity, temperature, dissolved oxygen, substrate, and seasonality (e.g., Phleger, 1960; Buzas, 1965, 1969, 1974; Murray, 1968; Ellison, 1972; Jones and Ross, 1979; Poag, 1981; Alve, 1990; Patterson, 1990; Green et al., 1993; Culver et al., 1996). For example, the agglutinated genera *Ammobaculites*, *Miliammina*, and *Ammotium* are common and, in places, constitute nearly monogeneric foraminiferal assemblages in the muddy substrates of the upper reaches of estuaries, river mouths, and brackish lagoons and bays (e.g., Ellison, 1972; Buzas, 1974; Poag, 1981; Alve, 1990; Lloyd, 2000). The agglutinated genera *Eggerella* and *Eggerelloides* occur in the lower reaches of estuaries and in some brackish bays (Murray, 1968, 1991). Calcareous taxa such as *Ammonia* and *Elphidium* frequently dominate modern foraminiferal assemblages in the lower reaches of estuaries, and in normal marine lagoons and bays (e.g., Murray, 1968, 1991; Poag, 1981). Like the *Trochammina–Jadammina–Miliammina* association of salt marshes, the diagnostic agglutinated genera of modern estuaries, lagoons, and bays have been shown to characterize these same marginal marine depositional systems at least as far back as the Cenomanian–Turonian (Late Cretaceous; Tibert et al., this volume). Ostracodes are also useful for distinguishing marginal marine facies because of their sensitivity to temperature and salinity, and because of their ubiquitous and often abundant distribution in these environments (e.g., De Deckker, 1981; Horne, 1983; Forester and Brouwers, 1985; Cronin, 1988; Neale, 1988; Whatley, 1988; Tibert et al., this volume).

Neritic Biofacies

Studies of the modern distributions of benthic foraminifera along terrigenous margins have demonstrated the usefulness of distinguishing biofacies on the basis of predominant genera rather than species (e.g., Walton, 1964; Murray, 1973, 1991; Poag, 1981; Culver, 1988). Benthic foraminiferal biofacies generally trend parallel to the shore and slope, and reflect the influence of changing substrate, water clarity, turbulence, sedimentation rate, seasonality, temperature, food availability, and dissolved oxygen with increasing depth and distance from the shoreline (Fig. 1). The same physical processes and environmental variability responsible for the distribution of modern assemblages were likewise responsible for controlling ancient depth-dependent and distance-from-shore-dependent assemblages.

For example, at a coarse level, four major paralic–upper bathyal biofacies can be recognized in data on benthic foraminiferal distribution from the northern Gulf of Mexico margin (Poag, 1981; Culver, 1988). These biofacies are distinguished on the basis of the greatest genus-level differences between the original seven biofacies of Culver (1988) and include: (1) marginal marine (marsh–estuarine–lagoon), (2) inner to middle neritic (marginal marine to ~ 100 m water depth), (3) outer neritic (~ 100 m to 150–200 m), and (4) upper bathyal (> 150–200 m) (Fig. 2). Such broad generic biofacies analogues, or "predominance facies" of Poag (1981), are applicable to ancient terrigenous assemblages back to at least the Late Cretaceous (e.g., Sliter and Baker, 1972; Nyong and Olsson, 1983/1984; Olsson and Nyong, 1984; Sikora and Olsson, 1991; Kominz and Pekar, 2001; Pekar and Kominz, 2001; Li et al., this volume; Tibert et al., this volume).

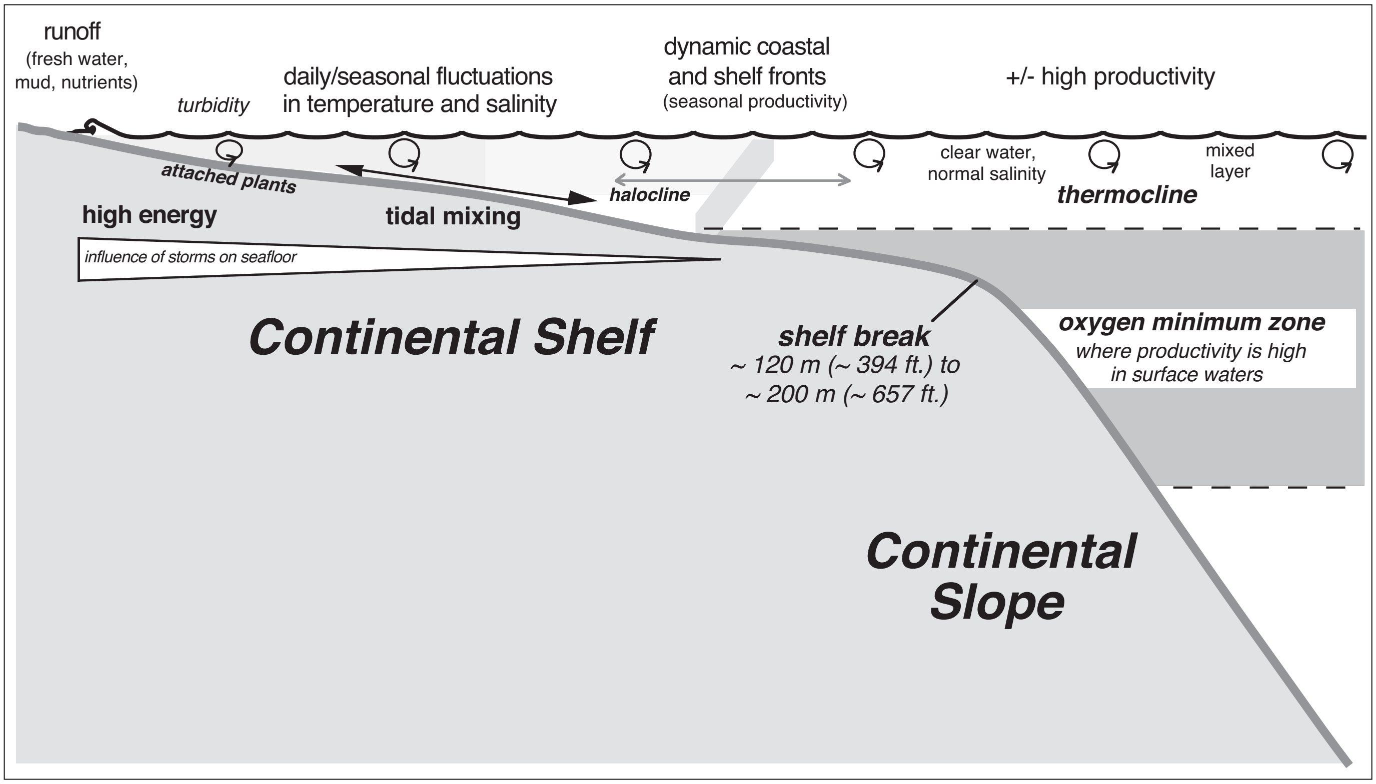


FIG. 1.—Schematic representation of the dynamic physical and biological characteristics of a siliciclastic shelf and upper slope. These characteristics help to shape the composition of foraminiferal communities.

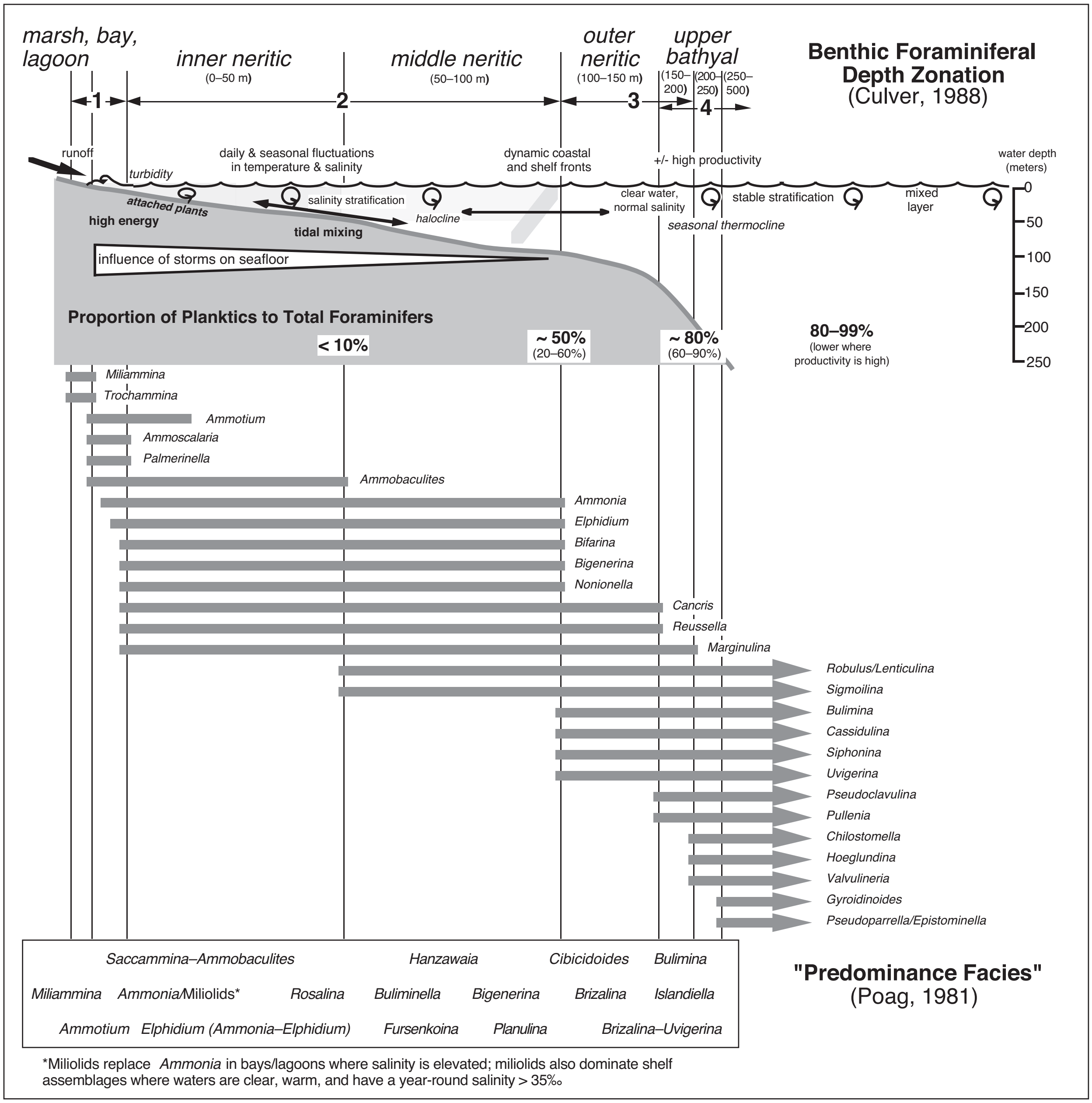


FIG. 2.—Summary of general benthic foraminiferal biofacies trends observed across the northern Gulf of Mexico. Benthic foraminiferal depth zonations are based on Culver (1988). General depth distributions of selected benthic foraminiferal genera are based on persistence within each depth zone (i.e., genera are not necessarily restricted to these zones). Predominance facies of the Gulf of Mexico are based on Poag (1981). In addition to these widespread biofacies, there are several restricted predominance facies off the Mississippi River delta, including *Epistominella, Nonionella, Nouria,* and *Goesella*. *Amphistegina* is concentrated on submerged carbonate banks, and the Miliolid–*Archaias-Homotrema* predominance facies characterizes reefs (Poag, 1981). Values of percent planktic foraminifera (relative to total foraminifera) are based on the data presented by Gibson (1989).

Cushman (1948) and Boltovskoy and Wright (1976), among others, recognized the importance of temperature in explaining the distinctly zonal biogeographic pattern of neritic benthic foraminiferal communities (see also Parker, 1948; Gevirtz et al., 1971; Culver and Buzas, 1999, 2000). The boundaries between these latitudinally delineated foraminiferal provinces, as well as many of the major benthic macrofaunal province boundaries, are located at coastal headlands and are associated with boundaries between surface water masses (e.g., Boltovskoy, 1976; Culver and Buzas, 1999). Planktic foraminifera, like other plankton, also display roughly zonal biogeographic distribution patterns reflecting the major surface ocean currents, as well as latitudinal changes in temperature, seasonality, and productivity (e.g., Bé and Tolderlund, 1971; Bé, 1977; Vincent and Berger, 1981; Hemleben et al., 1989; Leckie, 1989; Rutherford et al., 1999).

In reconstructing the biogeography of modern benthic foraminifera of the continental margins of North America and Central America, Culver and Buzas (1999) emphasized the fact that the compositional differences between shallow-water (< 200 m) and deep-water (> 200 m) communities of the same latitude were greater than those of adjacent neritic communities. The boundary separating neritic and bathyal foraminiferal provinces approximates the position of the modern shelf break, and is itself an important transition in the physical, chemical, and biological character of the water column (Fig. 1). Oceanographic variability across the outer shelf and upper slope includes salinity and temperature structure, tidal currents and mixing, wind-driven upwelling and productivity, seasonal flux of organic matter, as well as dissolved oxygen content in the water column and at the seafloor (e.g., Mann and Lazier, 1991). Therefore, the boundaries between stratified water masses may represent one of a number of important variables in delineating depth-related biogeographic provinces such as the boundary that typically occurs at the shelf–slope transition (e.g., Streeter, 1973; Culver and Buzas, 1981, 1983a, 1983b; Poag, 1981; Denne and Sen Gupta, 1991, 1993, this volume).

Development of Modern Biofacies Distributions

During Jurassic and Early Cretaceous time, assemblages above the CCD were often characterized by diverse representatives of the Nodosariacea, Spirillinacea, Epistominidae, Opthalmidiidae, Buliminidae, or assemblages dominated by simple agglutinated taxa (e.g., Bartenstein and Brand, 1937; Loeblich and Tappan, 1950; Bartenstein et al., 1957; Lutze, 1960; Seibold and Seibold, 1960; Gordon, 1970; Luterbacher, 1972; Kuznetsova, 1974; Gradstein, 1978; Kuznetsova and Seibold, 1978; Sliter, 1980; Copestake and Johnson, 1981; Shipp and Murray, 1981; Exton and Gradstein, 1984; Riegraf et al., 1984). The mid-Cretaceous (Aptian–Cenomanian) was a time of rapid evolution of benthic foraminifera, particularly calcareous trochospirally coiled taxa, and the differentiation of "depth" assemblages bearing an ever-increasing resemblance to the modern (e.g., Sliter, 1980; Loeblich and Tappan, 1988; Sikora and Olsson, 1991; Kaiho, 1998). The observed radiation of calcareous benthic foraminifera was likely due to a number of factors: (1) rising global sea level and the creation of broad shelves and epicontinental seas, (2) episodes of increased productivity and expansion of oxygen minima along continental margins, particularly during oceanic anoxic events, (3) changes in paleogeography, water-mass sources, and ocean circulation, and (4) increased water-column stratification and vertical differentiation of water masses (Sikora and Olsson, 1991; Kaiho, 1998, 1999b; Leckie et al., 2002). As a result, vast new neritic and bathyal niche space was created.

Cooling of the high latitudes and the growth of ice sheets during the Cenozoic caused the shallow seas to withdraw from the continents, but it also increased meridional temperature gradients and further accentuated the vertical gradients of the water column (Cifelli, 1969; Lipps, 1970). As zones of productivity became more focused and water-mass contrasts along the continental margins became sharper, the biofacies that became established during the Cretaceous were likewise constricted by the narrowing neritic ecospace. The well-defined biofacies of terrigenous margins today are in part the product of often sharp, but seasonally dynamic, vertical and horizontal oceanographic gradients (Fig. 1). As sea level changed in the past, benthic foraminiferal assemblages migrated laterally across the shelf and upper slope with the shifting water-mass fronts and depositional environments.

Relationship of Sea-Level Change to Biofacies Continuity and Taxonomic Extinction

Buzas and Culver (1994) studied shelf foraminifera from a succession of six Cenozoic formations deposited in a large embayment of the U.S. Atlantic Coastal Plain (Delaware to North Carolina) in order to determine where the species originate and where they migrate with rising and falling sea level, and to determine if neritic communities behave as a coherent unit over geologic time. An important result of their research is that there is very little community unity from one transgressive–regressive sequence to the next; only a small proportion of species returned to this sizeable embayment with each ensuing transgression. Despite the ephemeral nature of neritic benthic foraminiferal communities, the associations of genera, in particular, define distinctive biofacies (Buzas and Culver, 1994). They concluded that this East Coast depositional embayment contained a subset of a much larger shallow-water community and that "immigrants and emigrants shuffled back and forth to the species pool while extinctions and originations continually altered its species composition" (Buzas and Culver, 1994, p. 1441). Similar trends have been shown to characterize the upper Oligocene (Li et al., this volume) and Miocene (McGowran and Li, 1996; Li and McGowran, 1997) of southern Australia. Here, too, neritic biofacies assemblages are strongly sequential (ongoing change) rather than recurrent at the third order (10^6 yr).

Environmental changes, often associated with fluctuating sea level, including changes in temperature, dissolved oxygen, and/or productivity, have been shown to result in extinctions and/or changes in community structure. For example, neritic and bathyal foraminiferal communities responded to major global perturbations such as the mid-Cretaceous oceanic anoxic events (Eicher and Worstell, 1970; Jarvis et al., 1988; Koutsoukos et al., 1990; Kaiho, 1994b; Culver and Buzas, 2000; Holbourn and Kuhnt, 2001; Holbourn et al., 2001), the Cretaceous–Tertiary boundary event (Keller, 1988, 1992; Kaiho, 1992; Coccioni and Galeotti, 1994; Speijer and Van der Zwaan, 1996; Kaiho et al., 1999; Alegret et al., 2001), and the Paleocene–Eocene Thermal Maximum [the Late Paleocene Thermal Maximum is now called the Paleocene–Eocene Thermal Maximum] (Kennett and Stott, 1991; Speijer et al., 1996, 1997; Thomas and Shackleton, 1996; Kaiho, 1999b). With regard to the mid-Cretaceous oceanic anoxic events, rising sea level may have triggered or amplified global environmental changes by flooding continental areas, creating new deep or intermediate water masses, altering ocean circulation and productivity, and modulating planetary albedo and climatic feedbacks (e.g., Erbacher et al., 1996; Erbacher et al., 1998; Erbacher et al., 1999; Hilbrecht et al., 1996; Leckie et al., 1998; Leckie et al., 2002; West et al., 1998; Gale et al., 2000; Tibert et al., this volume). Two studies in this volume demonstrate that Pennsylvanian–Permian shallow-water fusulinacean evolution (extinction and speciation) was closely related to eustatic sea-level change (Davydov et al., this volume; Ross and Ross, this volume).

PLANKTIC FORAMINIFERAL ECOLOGY AND PLANKTIC:BENTHIC RATIO SIGNALS

Sediment assemblages of fossil planktic foraminifera provide useful information about the nature of the ancient uppermost water column, including temperature, stratification, and productivity. Like many other oceanic organisms, most species of modern planktic foraminifera are adapted to relatively narrow ranges of temperature and salinity (Bé, 1977; Hemleben et al., 1989). Planktic foraminiferal simple diversity is greatest in well-preserved sediment assemblages deposited under normal-salinity waters of the low to mid-latitudes where seasonal or year-round temperature gradients in the upper water column provide a variety of trophic and density-specific niches (Lipps, 1979; Leckie, 1989; Hallock et al., 1991; Leckie et al., 2002). Sediment assemblages that accumulate under ecotones, areas of the ocean where two surface water masses meet or where water-mass fronts shift seasonally, may actually have slightly higher simple diversity due to mixing of biocoenoses (Cifelli and Benier, 1976; Hallock et al., 1991). Seasonal changes in the strength or position of the thermocline are known to be fundamentally important in maintaining marine plankton communities. For example, water-mass stratification affects nutrient availability and recycling, productivity, seasonal succession, reproduction, and predation (Mann and Lazier, 1991).

Most planktic foraminiferal species live vertically stratified in the photic zone (mixed layer and upper thermocline), where their primary food supplies are located (Bé, 1977; Fairbanks and Wiebe, 1980; Hemleben et al., 1989; Arnold and Parker, 1999). Modern planktic foraminifera exhibit diverse feeding strategies, and they play important roles as both prey and predator within the trophic pathways of plankton food webs. Some taxa contain photosymbionts (microscopic algae, typically dinoflagellates or chrysophytes), which confer a competitive advantage in low-nutrient waters, where food supplies may be limited. Most of the symbiont-bearing taxa are spinose, although not all spinose taxa possess symbionts. Many of the modern spinose species are known to entrap and digest metazoan zooplankton such as copepod or larval stages of other plankton, as well as other protozoans such as ciliates or flagellates (Hemleben et al., 1989; Spero, 1998). Non-spinose species snare particulate organic matter (POM) with their pseudopodia. POM may consist of "marine snow," "phytodetritus," or other flocs of organic detritus. In addition to consuming POM, some of the non-spinose taxa may actively prey on the heterotrophic bacteria that colonize and decompose organic detritus (Lee, 1980; Lipps, 1982).

In addition to occupying diverse trophic niches, planktic foraminifera occupy different parts of the upper water column, and a number of species change depth habitats during ontogeny (Bé, 1977; Hemleben et al., 1989; Arnold and Parker, 1999). Ontogeny refers to the growth and development as recorded by increasing number of chambers, increasing test size, and other characteristics such as spine shedding and / or secondary calcification prior to reproduction. For example, some taxa, particularly the symbiont-bearing species, live in the sunlit waters of the mixed layer for much of their brief lives before adding a secondary calcite crust and sinking to greater depths in preparation for gametogenesis (release of gametes). Gametogenesis and early growth of the young foraminifera may occur in the vicinity of the chlorophyll maximum (Spero, 1998), a zone near the base of the mixed layer or upper thermocline where conditions are optimal for phytoplankton productivity (adequate mix of light from above and advective nutrient supply from below). Other taxa may spend their entire lives in the mixed layer or along some part of the thermocline, while others live predominantly at subthermocline depths. These latter deep-dwellers may have yearly life cycles, while many species of planktic foraminifera have monthly reproduction tied into the lunar cycle (Hemleben et al., 1989; Spero, 1998). Periodic reproductive cycles coupled with gamete release near the chlorophyll maximum provide an effective temporal and spatial concentration mechanism to enhance reproductive success (Hemleben and Bijma, 1994; Spero, 1998).

While some species may be perennially abundant in the near-surface waters, many species display distinct seasonal preferences (Bé et al., 1971; Tolderlund and Bé, 1971; Deuser and Ross, 1989). Sediment-trap studies have demonstrated the seasonal nature of planktic foraminiferal assemblages and the variable seasonal flux of planktic foraminiferal shells to the seafloor (Deuser et al., 1981; Thunell and Honjo, 1987; Deuser and Ross, 1989). Therefore, sediment assemblages of planktic foraminifera on the seafloor reflect the time-averaged seasonal succession of species and hence differing hydrographic conditions in the surface waters. The seasonal succession of taxa reflects changing water temperature, water-column density structure, and trophic resources including seasonal changes in primary productivity. Successions may even occur on a geologic timescale of alternating glacial and interglacial cycles as documented by the *Globorotalia menardii* index, which reaches a maximum during interglacial periods over the last 100,000 yr in piston cores from the Gulf of Mexico intraslope basins (Olson et al., 2000; Olson and Thompson, in prep.).

Planktic foraminifera are typically absent or very rare across much of the inner and middle shelf before rapidly increasing in abundance (relative to total foraminifera) across the outer shelf and upper slope (e.g., Phleger, 1951; Grimsdale and van Morkhoven, 1955; Bandy, 1956; Stehli and Creath, 1964; Murray, 1976; Gibson, 1989; Van der Zwaan et al., 1990). For example, Gevirtz et al. (1971) report only 1–5% planktics in ~ 210–240 ft (64–73 m) water depth, steadily rising to > 50% by ~ 360–390 ft (110–119 m) on the continental shelf off Long Island, New York (along this part of the margin, the shelf break occurs at ~ 300–330 ft or ~ 91–100 m water depth). Gibson's (1989) analysis of planktic: benthic ratios from multiple depth transects around the United States reveals that the middle to outer neritic transition at ~ 100 m is characterized by 20–60% planktics and rises to 60–90% planktics by ~ 200 m. Phleger (1960, p. 271) cautions that because planktic foraminifera are characteristic of "undiluted oceanic water", planktic populations "may be as abundant inshore as offshore" along coasts with little significant runoff.

In the modern ocean, planktics typically constitute 80–95% of outer neritic to mid-bathyal foraminiferal sediment assemblages (Fig. 2). However, elevated surface-water productivity can significantly reduce the relative abundance of planktics. The enhanced flux of organic matter from the surface waters to the seafloor stimulates benthic productivity. Although the flux of planktic foraminiferal shells is likely to be higher, there is a greater increase in the relative abundance of benthic foraminifera and other benthic organisms, including ostracodes, echinoderms, and sponges, thereby reducing the planktic:benthic (p:b) ratio of the sediment assemblages (Diester-Haass, 1978; Leckie, 1987; Berger and Diester-Haass, 1988; Herguera and Berger, 1991; Leckie et al., 1998). Therefore, the relationship between percent planktics and water depth across the shelf and upper slope is not always linear and straightforward. Variability in the p:b ratio of sediment assemblages in both slope-parallel and onshore–offshore depth transects is often closely related to productivity and the flux of organic carbon to the seafloor (Van der Zwaan et al., 1990). For example, Berger and Diester-Haass (1988) suggested that where foraminiferal populations have not been significantly altered by differential dissolution, the ratio of benthic-to-planktic foraminifera is a useful proxy for productivity. However, intense upwelling and high productivity along a continental margin can also create an oxygen-minimum zone that may result in decreased benthic foraminiferal abundances and hence higher p:b ratios, as shown by the work of Naidu and Malmgren (1995).

CHANGES IN AGGLUTINATE: CALCAREOUS BENTHIC RATIOS

In marginal marine and neritic habitats of terrigenous margins, the salinity, alkalinity, and carbonate saturation of the waters can greatly affect the taxonomic composition of the living benthic foraminiferal assemblages (biocoenoses), while redox conditions in organic-rich sediments may alter the composition of the death assemblages (thanatocoenoses). In addition to the loss of calcareous taxa due to post-mortem dissolution, weakly constructed agglutinated tests contribute to the taphonomic transformation of the living assemblage into a fossil assemblage (Murray, 1973, 1991; Green et al., 1993; Martin et al., 1996; Martin, 1999; Murray and Alve, 1999). While a number of modern calcareous taxa are tolerant of widely variable salinity fluctuations found in marsh, estuarine, and lagoonal environments, such as *Ammonia* and *Elphidium* (Murray, 1991; Sen Gupta, 1999), their preservation potential is adversely affected by the acidic conditions associated with the organic-rich substrates of these coastal environments. Therefore, agglutinated taxa are among the best proxies for marginal marine depositional systems, because of the taphonomic loss of calcareous species (see Martin, 1999; Horton and Edwards, this volume; Martin et al., this volume; Tibert et al., this volume).

Diverse assemblages of mixed calcareous and agglutinated benthic foraminifera characterize the normal marine waters of terrigenous continental shelves. Typically the transition from brackish marginal marine habitats to open neritic conditions is delimited by a marked increase in the abundance and diversity of calcareous taxa (Fig. 2; Murray, 1991; Sen Gupta, 1999). This is a very useful proxy for ancient neritic assemblages. The nearly monogeneric estuarine agglutinated assemblages are replaced by agglutinated genera such as *Textularia, Eggerella*, and *Saccammina* on the inner shelf, together with diverse species of calcareous benthics (e.g., Parker, 1948; Murray, 1968; Poag, 1981). Modern clastic inner shelves (< 30–50 m) from cold temperate to tropical regions are typically dominated by *Elphidium* (e.g., *E. excavatum*) and *Ammonia* (e.g., *A. beccarii*) (e.g., Parker, 1948; Murray, 1968; Poag, 1981; Sen Gupta, 1999; Buck et al., 1999). However, there are exceptions. For example, along the continental shelf off Long Island, Gevirtz et al. (1971) found that agglutinated taxa dominate benthic foraminiferal assemblages in water depths of ~ 84–240 ft (~ 25–73 m).

Miliolids, calcareous benthic foraminifera with a porcellaneous wall structure (e.g., *Quinqueloculina, Triloculina*), are variable across the inner shelves of terrigenous margins because their distribution is influenced by salinity (e.g., Bandy and Arnal, 1960; Phleger, 1960; Gevirtz et al., 1971; Poag, 1981; Murray, 1991). For example, biofacies with abundant *Ammobaculites* and few *Quinqueloculina* are diagnostic of strong brackish influence such as estuarine or deltaic environments, whereas few *Ammobaculites* and abundant *Quinqueloculina* may characterize inner-neritic conditions away from the direct influence of a river (Fang, this volume). Li et al. (this volume) found miliolids to be abundant and diverse in the ancient cool-water carbonate, inner-neritic environments of southern Australia. Miliolids may also dominate foraminiferal assemblages in warm, normal marine to hypersaline lagoons (e.g., Murray, 1968; Poag, 1981).

FORAMINIFERAL ABUNDANCE, DIVERSITY AND SIMILARITY CALCULATIONS: PROXIES FOR SEA-LEVEL CHANGE

The total number of foraminiferal tests per gram of dried sediment is the foraminiferal number. The benthic foraminiferal number generally increases with increasing depth across the shelf, with peak abundance typically at, or just seaward of, the shelf break in outermost neritic or upper bathyal waters (Parker, 1948, 1954; Bandy and Arnal, 1960; Buzas and Gibson, 1969; Gibson and Buzas, 1973). For example, Gevirtz et al. (1971) report 1–50 benthic specimens per gram at water depths shallower than ~ 210 ft (~ 64 m) and rapidly increasing to typically > 1000 specimens per gram by ~ 360 ft (~ 110 m). At this particular location off Long Island, New York, the shelf break occurs at ~ 300–330 ft, or ~ 91–100 m water depth (Gevirtz et al., 1971). These trends could be due to several factors, including sediment dilution nearer to shore and/or increased primary productivity, and therefore, increased flux of organic matter out of the photic zone near the shelf break and upper slope. The outer-shelf assemblages may also be enriched in reworked Pleistocene specimens because of condensation associated with sea-level rise since the last glacial maximum.

Benthic foraminiferal biomass, and benthic biomass in general, responds rapidly to increased availability of food (e.g., Diester-Haass, 1978; Leckie, 1987; Berger and Diester-Haass, 1988; Herguera and Berger, 1991; Loubere, 1991, 1997; Gooday, 1993; Jorissen et al., 1995; Thomas and Gooday, 1996; Leckie et al., 1998; West et al., 1998; Loubere and Fariduddin, 1999). However, excessive turbidity and high sedimentation rates off major river systems may inhibit the development of benthic foraminiferal communities on the inner shelf (Sen Gupta, 1999). Postdepositional processes can also modify the original sediment assemblages on the shelf and slope. Potential problems include: (1) downslope displacement of shallow-water assemblages by slumping or turbidity currents (recognized by bimodal distribution of taxa, and smeared distribution), and (2) reworking of older assemblages into younger, such as relict shelf assemblages mixed with modern assemblages because of winnowing and condensation with rising sea level (recognized by differences in preservation or presence of older age-diagnostic taxa) (e.g., Bandy, 1953; Bandy and Arnal, 1960; Phleger, 1960; Gevirtz et al., 1971; Murray, 1991). Murray (1991) presents a detailed discussion of the processes of postmortem changes to living assemblages.

Diversity of benthic foraminiferal species on terrigenous continental shelves is related to a number of variables, including water temperature and water depth. As outlined above, however, water depth is really the product of multiple variables as dictated by distance from shore and proximity to “blue water.” The variables of “depth” include water clarity, benthic turbulence, substrate character, water-column stratification, as well as seasonal changes in water-mass character, organic matter flux, and dissolved oxygen content. Benthic foraminiferal diversity typically follows a trend similar to that of benthic foraminiferal number.

Diversity can be described in a number of different ways. Two common indices are simple diversity or species richness (S), which relates to the total number of taxa present, and the Shannon–Wiener diversity index [$H(S)$]. The use of a diversity index compensates for the patchy distribution of individual species, particularly the rare ones (Murray, 1973, 1991). Another measure of diversity is the Fisher alpha index (Murray, 1973, 1991). Along terrigenous continental margins, benthic foraminiferal diversity, both S and $H(S)$, increase across the shelf and then remain constant or decline in bathyal depths (Buzas and Gibson, 1969; Gibson and Buzas, 1973). For many years, diversity described by S has been used in a sequence stratigraphic context (Armentrout and Clement, 1990; Armentrout, 1996) to distinguish sequence boundaries (low S values) from flooding surfaces (high S values). Recently, more robust diversity measurements, such as the SHE index and the Shannon–Wiener diversity index, have been employed to relate changes in diversity to sea-level variations derived from sequence stratigraphy (Buzas and Hayek, 1996, 1998; Wakefield, this volume; Fang, this volume). For example, Wakefield (this volume) found that evenness [ln(E)] is at a minimum at the sequence boundary and increases with ln(S) and $H(S)$ associated with flooding surfaces; ln(E) reaches a maximum at the maximum flooding surface within a depositional cycle (see discussion below related to sequence stratigraphy).

Olson et al. (this volume) explored a new application of the similarity coefficient in a stratigraphic context. In this technique, coefficients are calculated to compare stratigraphically adjacent samples on the basis of the number of foraminiferal species in common to both samples and/or the relative proportions of those species. These values are then plotted against depth in the section to form a biostratigraphic similarity curve based on taxonomic assemblages. A significant change in foraminiferal assemblages (faunal break) is marked by a low degree of similarity on the curve. Curves calculated for specific groups, such as planktic and benthic foraminifera, assist in interpreting the breaks in faunal similarity. For example, similarity breaks in the benthic foraminiferal record are often indicative of detailed bathymetric changes, even within the same biofacies group (see Olson et al., this volume, for specific examples).

BENTHIC FORAMINIFERAL MICROHABITATS: RESPONSE TO ORGANIC CARBON FLUX AND DISSOLVED OXYGEN

Corliss and colleagues (Corliss, 1985, 1991; Corliss and Chen, 1988; Corliss and Emerson, 1990; Corliss and Fois, 1991) demonstrated a relationship between test morphology and microhabitat preference within sediments. They distinguished epifaunal taxa characterized by plano-convex, biconvex, or rounded trochospiral tests, and infaunal taxa characterized by rounded planispiral, flattened ovoid, tapered and cylindrical triserial, or flattened and tapered biserial tests. These authors noted that the relative abundance of infaunal taxa is greater with increasing flux of organic carbon. This relationship has also been observed in other studies (e.g., Kaiho, 1994a, 1999a; Jorissen et al., 1995). In addition, numerous studies of living benthic foraminifera have demonstrated that most trochospirally coiled species inhabit the upper few centimeters of the sediment and would be classified as epifaunal or shallow infaunal (Corliss, 1985, 1991; Kaiho, 1994a). However, Linke and Lutze (1993) stress that the actual microhabitats of benthic foraminifera are much more dynamic than suggested by Corliss' original models.

Organic-carbon flux and dissolved oxygen are important controls on the distribution and abundance of benthic foraminifera (e.g., Phleger and Soutar, 1973; Douglas, 1981; Sen Gupta et al., 1981; Lutze and Coulbourn, 1983/1984; Corliss, 1985; Corliss and Chen, 1988; Loubere, 1991, 1994, 1996, 1997; Sjoerdsma and Van der Zwaan, 1992; Linke and Lutze, 1993; Kaiho, 1994a, 1999a; Jorissen et al., 1995; Bernhard, 1996; Bernhard and Sen Gupta, 1999; Jorissen, 1999; Loubere and Fariduddin, 1999). The microhabitat model of Jorissen et al. (1995) emphasizes the importance of availability of oxygen and food in controlling the distribution of benthic foraminifera in the sediment. For example, a high flux of particulate organic matter (POM) stimulates benthic biomass while at the same time creating increased oxygen stress at the sediment–water interface or within interstitial pore waters. In this way, taxa that live infaunally under oligotrophic to mesotrophic conditions may thrive at the sediment–water interface under eutrophic conditions (Jorissen, 1999).

The movement of water masses across the shelf may vary significantly from one season to the next, and it is these different water masses, their particular physical and chemical characteristics, and seasonal changes in productivity along water-mass fronts that are important variables in controlling the distribution and composition of benthic foraminiferal communities (e.g., Schnitker, 1994; Loubere and Fariduddin, 1999). POM is a major food source for benthic foraminifera, and the flux of POM and dissolved organic carbon (DOC) can greatly affect redox conditions at the seafloor. The flux of POM from terrestrial and marine sources is related to sediment input and the seasonal dynamics of primary productivity in the overlying water column, respectively. DOC is a staple for heterotrophic bacteria, which in turn are an important food source for many species of benthic foraminifera (Lee, 1980; Lipps, 1983; Murray, 1991; Langer and Gehring, 1993; Goldstein and Corliss, 1994; Goldstein, 1999). Lipps (1983) suggested that DOC is utilized by benthic foraminifera, especially in environments where the flux of terrestrial and/or marine POM is limited, such as coral reefs and vast stretches of the deep sea.

Taxa that live in epifaunal or shallow infaunal microhabitats can be considered to be opportunists, because of their dependence on the often intermittent flux of labile, easily metabolized organic matter to the seafloor, whereas deeper infaunal organisms could be considered specialist feeders because of their dependence on the stable supply of more refractory, bacterially mediated organic matter within the sediments (Jorissen, 1999). Some deep-sea trochospirally coiled, calcareous benthic taxa display a rapid response to the flux of organic matter associated with the annual spring bloom (Gooday, 1988, 1993; Loubere and Fariduddin, 1999). These opportunistic phytodetritus feeders have also been recognized in Cenozoic deep-sea sediments (Thomas and Gooday, 1996) and may be associated with lowstand deposits of the mid-Cretaceous (Erbacher et al., 1998; Leckie et al., 1998; West et al., 1998).

Phleger and Soutar (1973) found large standing stocks of benthic foraminifera associated with shallow (75–400 m) oxygen minima along the Pacific margin of California and Central America. The assemblages are characterized by low diversity and high dominance of relatively small, thin-shelled calcareous taxa (see also Bernhard, 1986; Perez-Cruz and Machain-Castillo, 1990; Kaiho, 1994a, 1999a). The rate of oxygen consumption by benthic foraminifera increases markedly with increasing size above ~ 250 μm maximum diameter (Bradshaw, 1961). Phleger and Soutar (1973), however, estimated that the yearly consumption of oxygen by benthic foraminifera in the Santa Barbara Basin was a small fraction (~ 3.5%) of the total flux of oxygen into the basin. Therefore, they concluded that the large standing stocks of benthic foraminifera were not limited by the availability of oxygen. In addition, these authors suggested that high abundances of relatively small specimens may be the consequence of early reproduction under optimal conditions of abundant food supply due to high productivity in the surface waters (Phleger and Soutar, 1973). Large living benthic populations are primarily the result of an abundant food supply from the photic zone (Phleger and Soutar, 1973; Diester-Haass, 1978; Berger and Diester-Haass, 1988; Herguera and Berger, 1991; Loubere, 1994, 1996; Loubere and Fariduddin, 1999).

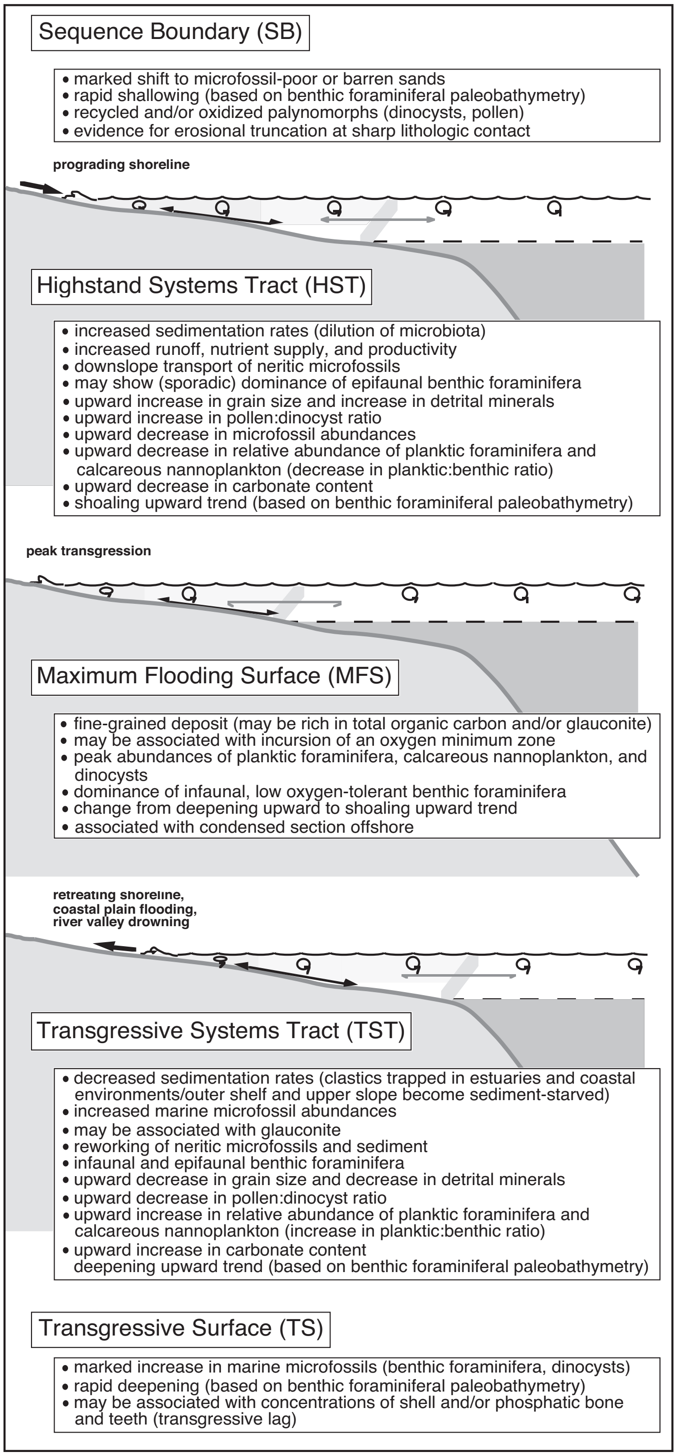
Taxa that live infaunally under oxic to weakly dysoxic conditions tend to live epifaunally and dominate assemblages under dysoxic to anoxic conditions (e.g., Corliss, 1985, 1991; Corliss and Chen, 1988; Corliss and Emerson, 1990; Kaiho, 1994a, b, 1999a; Jorissen et al, 1995; Bernhard and Sen Gupta, 1999; Jorissen, 1999). Taxa indicative of low oxygen indices include elongate–flattened, tapered, and cylindrical morphotypes with small, thin-walled tests and weak ornamentation (Kaiho, 1994a, 1999b). Taxa with similar characteristics are also associated with ancient dysoxic to anoxic sediments (e.g., Berhard, 1986; Koutsoukos and Hart, 1990; Koutsoukos et al., 1990; Kaiho, 1994b; Erbacher et al., 1998; Ehrbacher et al., 1999; Leckie et al., 1998; West et al., 1998; Holbourn et al., 2001).

Differentiation of microhabitats can be used to interpret sea-level changes, climate variations, and associated trends. For example, in the Pleistocene of the Gulf of Mexico large numbers of traditionally infaunal morphotypes, such as uvigerinids and bolivinids, may indicate bottom-water dysoxia and suggest a mechanism for increased water-column stratification via an intensified salinity gradient resulting from increased input of glacial meltwater (low $\delta^{18}O$ values in planktic foraminiferal tests; Moss and Olson, in prep.). By examining microhabitat trends, Kaiho (1999a, 1999b) found a strong correlation between test size of the largest trochospirally coiled calcareous benthic foraminiferal taxa (presumed epifaunal morphotypes), and both deep-water temperature and dissolved oxygen; minimum sizes correlate with warm ($\delta^{18}O$ minima), oxygen-poor, deep waters.

MICROFOSSILS AND SEQUENCE STRATIGRAPHY

In the late 1970s, studies in sequence stratigraphy began to suggest that seismic profiles of subsurface rock units had the potential to image genetically related stratal units bounded by unconformities or their correlative conformities (Vail et al., 1977). Subsequently, these various stratigraphic discontinuities, whether defined using seismic data, well logs, or core and outcrops, have been related to sea-level changes, in part, on the microfossil assemblages retrieved from the stratigraphic record (e.g., Armentrout and Clement 1990; Zellers, 1995; Armentrout, 1996; Thompson and Abbott, this volume; Olson and Thompson, in prep.). Because the sequence boundary is commonly accompanied by subaerial exposure and downcutting, the magnitude of the hiatus may be large near the continental shelf; as the hiatus is traced into the basin, however, less section is missing, and where the duration of a hiatus is minimal, the missing section eventually falls within a single biozone and is extremely difficult to identify (Powell, 1992). In such cases, other techniques (e.g., diversity values, Wakefield, this volume; stratigraphic similarity curves, Olson et al., this volume), rather than missing biozones, may be important in identifying candidate sequence boundaries.

A sequence stratigraphic model of predicted microfossil trends is presented in Fig. 3. These are general trends that apply primarily to siliciclastic shelves, although a number of features are likely to be developed in mixed siliciclastic–carbonate and carbonate-dominated depositional systems as well. It is likely that only a subset of these characteristics is preserved in any given neritic stratigraphic sequence, thereby illustrating the importance of integrating a variety of biostratigraphic data (e.g., foraminifera, calcareous nannofossils, pollen, spores, dinoflagellates) with sedimentology, geochemistry, well-log data, seismic stratigraphy, and stratal architecture (e.g., Van Wagoner et al., 1988; Emery and Myers, 1996). Microfossil patterns often associated with sequence boundaries include (Olson and Thompson, in prep.): (1) the abrupt truncation or diminution of marine microfossil abundance and/or diversity at the horizon (e.g., foraminifera, nannofossils, dinoflagellates; McCarthy et al., this volume, Wakefield, this volume), (2) an overlying increase in terrestrial pollen and spores (e.g., McCarthy et al., this volume), (3) overlying microfossils indicating cooler climate and/or shallower bathymetry (e.g., Li et al., this volume), (4) an overlying decrease in the p:b ratio, and (5) an overlying increase in reworked microfossils (e.g., McCarthy et al., this volume)



Sequence Boundary (SB)

- marked shift to microfossil-poor or barren sands
- rapid shallowing (based on benthic foraminiferal paleobathymetry)
- recycled and/or oxidized palynomorphs (dinocysts, pollen)
- evidence for erosional truncation at sharp lithologic contact

Highstand Systems Tract (HST)

- increased sedimentation rates (dilution of microbiota)
- increased runoff, nutrient supply, and productivity
- downslope transport of neritic microfossils
- may show (sporadic) dominance of epifaunal benthic foraminifera
- upward increase in grain size and increase in detrital minerals
- upward increase in pollen:dinocyst ratio
- upward decrease in microfossil abundances
- upward decrease in relative abundance of planktic foraminifera and calcareous nannoplankton (decrease in planktic:benthic ratio)
- upward decrease in carbonate content
- shoaling upward trend (based on benthic foraminiferal paleobathymetry)

Maximum Flooding Surface (MFS)

- fine-grained deposit (may be rich in total organic carbon and/or glauconite)
- may be associated with incursion of an oxygen minimum zone
- peak abundances of planktic foraminifera, calcareous nannoplankton, and dinocysts
- dominance of infaunal, low oxygen-tolerant benthic foraminifera
- change from deepening upward to shoaling upward trend
- associated with condensed section offshore

Transgressive Systems Tract (TST)

- decreased sedimentation rates (clastics trapped in estuaries and coastal environments/outer shelf and upper slope become sediment-starved)
- increased marine microfossil abundances
- may be associated with glauconite
- reworking of neritic microfossils and sediment
- infaunal and epifaunal benthic foraminifera
- upward decrease in grain size and decrease in detrital minerals
- upward decrease in pollen:dinocyst ratio
- upward increase in relative abundance of planktic foraminifera and calcareous nannoplankton (increase in planktic:benthic ratio)
- upward increase in carbonate content
deepening upward trend (based on benthic foraminiferal paleobathymetry)

Transgressive Surface (TS)

- marked increase in marine microfossils (benthic foraminifera, dinocysts)
- rapid deepening (based on benthic foraminiferal paleobathymetry)
- may be associated with concentrations of shell and/or phosphatic bone and teeth (transgressive lag)

FIG. 3.—Summary of microfossil and sediment assemblage characteristics of key stratigraphic surfaces and systems tracts. Only a subset of these characteristics is likely to be preserved in any given neritic stratigraphic sequence, thereby illustrating the importance of integrating biostratigraphic data with sedimentology, geochemistry, well-log data, seismic stratigraphy, and stratal architecture analysis. See Figure 1 for explanation of symbols.

derived from older strata sourced either from the hinterland (by rivers) or the slope (by slumping).

These unconformity-bounded sequences consist of systems tracts "defined by their position within the sequence and by the stacking patterns of parasequence sets" (Van Wagoner et al., 1988, p. 39). The transgressive systems tract (TST) is bounded by the transgressive surface (TS) or sequence boundary (SB) below and by the maximum flooding surface (MFS) above. The MFS is frequently associated with condensed section deposited during peak transgression (Loutit et al., 1988; Posamentier et al., 1988; Mancini and Tew, 1997). The highstand systems tract (HST) is bounded above by the lowstand systems tract or the SB. Parasequences and parasequence sets are the building blocks of the systems tracts that make up a sequence (Van Wagoner et al., 1988). Parasequences are bounded by marine flooding surfaces. The TST typically consists of a retrogradational parasequence set, whereas the HST consists of an aggradational to progradational parasequence set.

An alternate approach is to utilize maximum flooding surfaces to delineate genetic sequence boundaries (Galloway, 1989a, 1989b). Genetic sequence stratigraphy is a very useful tool when utilizing biostratigraphic data because flooding events are often more easily recognized in fossiliferous mud-dominated lithofacies, whereas erosional (unconformable) sequence boundaries are more easily recognized in poorly fossiliferous, sand-dominated lithofacies (Mancini and Tew, 1995, 1997; Armentrout, 1996; Fang, this volume; Tibert et al., this volume). Microfossil patterns often associated with flooding surfaces include (Olson and Thompson, in prep.): (1) a pulse of deep-water benthic microfossils and maximum paleobathymetry (Armentrout, 1996), (2) maximum incursion into shelf regions of planktic foraminifera, nannofossils, and dinoflagellates (e.g. McCarthy et al., this volume; Tibert et al., this volume), (3) tops of various rare taxa because shallow-water ecology following the flooding surface excludes taxa from the area or because increased clastic detritus dilutes the abundance too much to find specimens, (4) sharp decrease in terrestrial pollen and spores compared to marine palynomorphs (McCarthy et al., this volume), (5) minimum in reworked microfossils, and (6) sharp increase in p:b ratio (Fig. 3). Foraminiferal number is typically greatest at the maximum flooding surface and lowest at the sequence boundary (e.g., Gräfe, 1999; Gräfe and Wendler, this volume). Planktic:benthic ratios may display a similar trend unless (cyclic) change in productivity of calcareous plankton is a dominant component of the sediment supply, in which case the p:b ratio is largely independent of the systems tract (Leary and Hart, 1992; Gräfe, 1999).

SUMMARY

1. Mesozoic–Cenozoic siliciclastic and mixed siliciclastic–carbonate continental margins, as well as epicontinental seas, typically yield diagnostic biofacies because of the dynamic interplay of seasonal changes in temperature and salinity, sedimentation and turbidity, and water-mass structure and productivity with increasing water depth and distance from the shore. Data on foraminiferal distribution and abundance are used to establish a diverse suite of paleoenvironmental proxies, many of which yield qualitative or quantitative information about water depth or changes in relative sea level. Modern foraminiferal distributions across a siliciclastic margin (e.g., Poag, 1981; Culver, 1988) suggest that four biofacies (or "depth zones") may be particularly useful in tracking ancient sea level based on major changes in genus-level dominance with increasing depth and distance from the shoreline. These biofacies are (1) marginal marine (marsh–estuarine–lagoon–bay), (2) inner to middle neritic (to ~ 100 m water depth), (3) outer neritic (~ 100 m to 150–200 m), and (4) upper bathyal biofacies (> 150–200 m).

2. Foraminiferal biofacies and biotopes can be delineated using R-mode and Q-mode cluster analysis, respectively. Planktic:benthic (p:b) ratios provide reliable inferences about paleodepth. Infaunal:epifaunal ratios of benthic foraminifera are useful proxies for oxygen content and food supply, both of which may vary with rising and falling sea level. Abrupt changes in diversity indices [S, $H(S)$, SHE] and/or similarity coefficient mark changes in relative sea level.

3. Sediment assemblages of foraminifera, attendant biogenic and mineral grains, and other sedimentological and geochemical characteristics collectively provide powerful proxies for the delineation and interpretation of sequence stratigraphic architecture. Diagnostic features of transgressive systems tracts (TST) and highstand systems tracts (HST) include changing p:b ratios, benthic foraminiferal biofacies, grain size, carbonate content, sedimentation rate, and microfossil reworking. Flooding surfaces, useful in the delineation of parasequences, are recognized by the rapid influx of marine taxa or abrupt increase in deeper-water benthic and/or planktic foraminifera, whereas maximum flooding surfaces, indicative of peak transgression, are characterized by a peak p:b ratio, peak in foraminiferal number, and concentrations of glauconite, total organic carbon, and/or pyrite.

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