Cenomanian/Turonian Bioevents and Ecostratigraphy in the Western Interior Basin: Contrasting Scales of Local, Regional, and Global Events

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ABSTRACT

Cenomanian/Turonian strata of the Western Interior Basin contain a hierarchy of paleontological event horizons/intervals. These features, which range from millimeters-thick bedding plane surfaces (bioevents) to meters-thick intervals (ecozones), can be defined taxonomically as well as in terms of relative increase or decrease in diversity, abundance, and trophic complexity of benthic faunas. Diversification and diversity reduction represent the direct response of biotas to changes in the marine environment, and reflect changes in the physical, chemical, and/or biological factors that controlled development of benthic communities. Basinwide, high-resolution chronostratigraphy in the Western Interior has allowed testing of the local, regional, or global extent of bioevents and ecozones, and provides an opportunity to compare and contrast paleobiological phenomena of wide-ranging spatial and temporal scales. The results suggest that there was a consistent biological response at all levels of the spatial and temporal hierarchy, resulting in widely correlative ecostratigraphic markers. Western Interior palaeocommunities were dominantly controlled by changes in bottom-water oxygen content and substrate characteristics which, in turn, were strongly influenced by changes in relative sea level and the prevailing climatic regime. The opportunistic nature of low-oxygen-adapted Cenomanian/Turonian community elements was most likely responsible for their sensitivity to palaeoenvironmental changes.
Event-driven paleobiological phenomena (bioevents) comprise an important part of the preserved fossil record. Such bioevents include geologically short-term changes in the evolutionary, ecological, and/or biogeographic character of biotas, as well as their extinction, and are commonly expressed as distinct paleontological surfaces or intervals. Bioevents are recognized at the population, species, and community level, and can be classified as diversification events (e.g., short-term colonization, population expansion and/or immigration events, and rapid speciation), which may produce horizons or thin stratigraphic intervals of increased species richness and/or faunal abundance, or as reduction events (e.g., mass mortality, rapid restriction of community or biogeographic range, and extinction), which can result in intervals that are relatively depauperate or barren of fossils. Both types of bioevents provide distinct stratigraphic markers that are commonly correlative over considerable distances within and between sedimentary basins (Kauffman 1986, 1988a; Kauffman et al. 1991). As such, they provide important chronostratigraphic surfaces/intervals for regional and, in special cases, global correlation.

Ecostratigraphy, as described by Boucot (1986), Kauffman (1986, 1988a), and others, represents the integration of paleobiological data in stratigraphic studies. Its twofold application includes (1) the use of unique paleoecological event horizons or thin stratigraphic intervals as regional chronostratigraphic tools, with resolution surpassing that of many traditional biostratigraphic methods, and (2) the opportunity to study the spatial and temporal evolution of ecological interactions, communities, and ecosystems within successive, narrowly constrained time slices. In this study, paleobiological data (e.g., taxa sets and their relative abundance and diversity characteristics) are used to define widespread bioevent horizons and ecostratigraphic intervals. Different types of ecostratigraphic units representing variable temporal (short- vs. long-term) and spatial (local, regional, and global) scales are recognized. By comparing events of different temporal and spatial scale we seek an improved understanding of the forcing mechanisms that control the evolution of populations, species, and paleocommunities.

Cretaceous strata of the Western Interior Basin, which have been studied intensively, provide an ideal opportunity to examine different scales of events within a high-resolution integrated chronostratigraphic and biostratigraphic framework. Numerous examples of short-term pioneer colonization events, local to regional population blooms, and rapid immigration of new species and biotas, as well as intervals of mass mortality, species loss, and mass extinction are preserved in the Cenomanian/Turonian (C/T) sequence of the Greenhorn Limestone. Bioevent surfaces/intervals dominate most of the C/T stratigraphic section in basinal sites. These biotic events represent a dynamic history of paleoenvironmental changes within the basin, but they also reflect phenomena recognized outside the Western Interior, such as the Cenomanian/Turonian “Oceanic Anoxic Event” (OAE) of Schlanger and Jenkyns (1976), and a global mass extinction (i.e., Raup and Sepkoski 1982; Kauffman 1984a, 1988).
The purpose of this report is to present a preliminary synthesis of the ecostratigraphy of the C/T interval in order to interpret better the primary agents of paleobiological change. Analysis of ecostratigraphic trends within a framework of detailed and integrated stratigraphic, sedimentologic, and geochemical data for the Western Interior Basin, and comparison to the published record of biotic change at C/T sections outside the Western Interior, makes possible evaluation of the ecological/environmental forces that control paleocommunities on short and long time frames, and on local, regional, and global scales. The results suggest that relative changes in climate, sea level, and related oceanographic factors played a major role in controlling the development of mid-Cretaceous paleocommunities and paleobiological event horizons.

*Ecological Units in Stratigraphy*

A great diversity of names and concepts for paleoecological units exists in the stratigraphic literature. Many are poorly defined, contradictory among different definitions, or in some cases not logically defensible as originally defined and/or currently utilized. Because this study deals with several levels of ecological units, we first provide a set of definitions for the terms used herein, and a classification of ecostratigraphic events.

**Paleocommunity** We follow the definition of Kauffman and Scott (1976) in that a paleocommunity, or fossil association, is the preserved subset of an implicitly more diverse original biological community that is preserved at or very near its original habitat. A paleocommunity reflects a relatively tightly defined set of ancient environmental conditions and is characterized throughout its spatial and temporal range by a specific taxa (species) set that may be fully to partially developed or preserved at different times or localities. Paleocommunities are repetitive in space and time but have more limited ranges than biofacies (see later) because of the greater taxonomic restrictions placed on their definition.

**Biofacies** From the time of its introduction (Lowman 1945), the term biofacies has been much debated (e.g., Kay 1947; Moore 1949; Sloss et al. 1949; Weller 1958). Most authors have defined a biofacies as a distinct assemblage or association (*sensu* Kauffman and Scott 1976) of fossils within a stratigraphic unit(s) that reflects, in its biological and ecological characteristics alone, an explicit set of paleoenvironmental conditions, independent of associated physical or chemical characteristics of the containing strata. Many definitions limit a single biofacies to an explicitly defined stratigraphic unit or interval and are therefore mainly concerned with the spatial expression of a biofacies. Some authors (e.g., Bates and Jackson 1987) suggest that a biofacies represents the fossil record of a biocoenosis, or life assemblage, in which case the term equates with a paleo-
community or fossil association. We find this composite of definitions vague and temporally too limiting when one considers that a lithofacies (e.g., a lower shoreface sand) or chemofacies (e.g., C<sub>org</sub>-rich black laminated shale) is repetitive in both time and space.

In this paper a biofacies is defined as collectively comprising all fossil associations (e.g., derived from resident paleocommunities) that are closely similar with regard to species composition and/or details of adaptive morphology among component taxa, and that represent a specifically defined set of environmental parameters. Biofacies may be repetitive in both space (e.g., within a laterally persistent stratigraphic unit) and time (e.g., repeated one or more times within a stratigraphic column), whenever the favorable environmental niche is established. Biofacies may have the same basic taxa set throughout their occurrence, but more commonly they are composed of different, commonly related species with similar or nearly identical adaptive form and environmental niche requirements. Thus different species of byssate epibenthic Inoceramidae (Bivalvia) with morphologically similar but taxonomically distinct species of epibiont oysters and pterid bivalves comprise a single biofacies in the Cenomanian of the Western Interior Basin, even though some of the component species of the biofacies change by immigration or lineage evolution through time. Similarly, a stratigraphically discrete set of forereef communities through time dominated by massive scleractinian head corals with similar colony form comprise a single biofacies, even though species and even genera may change through time.

**Ecostratigraphic Zone (Ecozone)** Vella (1964) and others defined an ecozone as corresponding to a body of rock characterized by a specific taxonomic/ecologic assemblage, with discrete upper and lower boundaries that mark reversible biotic changes. Vella (1964) believed that the biological reversals from one ecozone to another marked secular lateral shifts of facies belts and that their boundaries were therefore diachronous. In the Western Interior Basin, many regionally correlative stratigraphic intervals are characterized by strong dominance of a single paleocommunity, or a closely related set of paleocommunities. Typically, such intervals are marked by relatively sharp boundaries at which community characteristics (species composition and richness, faunal abundance) show marked shifts, in many cases reflecting relative diversification or diversity reduction events. Within these intervals, community characteristics may change very little, reflecting periods of relative stability in the benthic community, or they may vary on scales that are similar within an interval but different between intervals. Although these ecologically defined intervals reflect secular environmental changes, they are typically forced by allocyclic climatic and/or eustatic events. In fine-grained basinal facies of the Western Interior Basin, these events produce widely correlative ecostratigraphic zones that cross Waltherian facies boundaries and whose boundaries are chronostratigraphically significant (essentially isochronous). We designate these time-based ecological
event packages herein as ecozones (fig. 20.1). Their duration is typically less than the biostratigraphic ranges of component taxa, and similarly constructed ecozones may occur at several stratigraphic levels, separated by dissimilar ecozones or nonfossiliferous intervals. Because global climatic/eustatic cycles are hierarchical, ecozones are hierarchical: In the Western Interior we recognize at least two levels, which we designate short-term (climate cycle or shorter scale) and long-term (sea-level cycle scale) (fig. 20.1).

**Biological Event (Bioevent)** Bioevents are short-term (hours or days to kyr) locally, regionally, or interregionally pervasive changes in the ecological, biogeographic, and/or evolutionary character of biotas that are isochronous or nearly so throughout their range. They result from various diversification processes (rapid colonization, short-term population and biomass increase, rapid immigration, punctuated evolution, etc.) or diversity reduction events (population mass mortality, species-level extinction, or major community/ecosystem collapse and mass extinction). Each bioevent is an individual surface or very thin stratigraphic interval potentially useful as a chronostratigraphic horizon. The highest-resolution ecostratigraphic unit, they commonly comprise the boundaries of ecozones (fig. 20.1).

**A Classification of Ecostratigraphic Units**

Bioevents and ecozones fall into two broad categories: (1) diversification bioevents/ecozones (cf. “Constructional Bioevents,” Kauffman 1986, 1988a), which reflect expansion of ancient ecosystems through increase in population size and addition of new taxa through immigration and/or evolution; and (2) reduction bioevents/ecozones (cf. “Destructional Bioevents,” Kauffman 1986, 1988a), which reflect such changes in the ecosystem as lowering of population size and decrease in community diversity through ecological restriction, diminished biogeographic ranges, and/or extinction. Diversification and reduction events are driven by a wide range of physical, chemical, and biological causes, examples of which are discussed later.

Bioevents are related to several different types of stratigraphic units cited in the North American and International Codes of Stratigraphic Nomenclature (ISSC 1976; NACSN 1983). In practice, they are employed as data-based chronostratigraphic units in the development of an integrated event stratigraphic framework for a basin. For example, global to regional origination/extinction bioevents are used to construct composite assemblage biostratigraphic zonations. Other types of bioevents (ecological, biogeographic) provide additional regional to local ecostratigraphic data. In some cases certain physical stratigraphic units at the marker bed or lentil level may also reflect bioevents (e.g., widespread mass mortality, colonization, or productivity events that produce regionally correlative, physically distinct shell/bone/plant beds), providing further chronostratigraphic data. Overall, bioevents are characterized by thin inter-
Figure 20.1. The system used in this study for recognition of ecostratigraphic units is illustrated for an idealized Western Interior Cretaceous stratigraphic sequence. Diversification (D) and reduction (R) bioevents and ecozones are defined based on relative change in quantitative faunal data (species richness and faunal abundance) and biofacies (following the model of Kauffman and Sageman 1990; Sageman et al. 1991). Biofacies levels A–H represent a gradation of increasing community complexity, as would be observed in a transition from highly dysoxic to fully oxygenated paleoenvironments. Resident biofacies represent continuously colonizing background communities; event biofacies reflect short-term colonization or mortality episodes. Bioevents are defined as the short-term shifts in biofacies (single horizons/bedding planes or cm’s—thick units representing hours to days to thousands of years) represented by event communities and/or shifts in resident communities; ecozones correspond to thicker intervals through which resident communities are stable (e.g., short-term ecozones corresponding to limestone/shale hemicycles) or shifting in a consistent direction (long-term ecozones spanning several-meters-thick packages that represent more than 100 kyr).
vals, sharp boundaries, and a geologically short time span (hours/days up to <100 kyr). In mud-dominated depositional systems such as the Western Interior Basin, rock accumulation rates for offshore facies are typically quite low (<1-5 cm/kyr), and condensation is a common phenomenon. Thus many Western Interior bioevents are preserved as discrete bedding plane horizons.

Ecozones may also correspond to biostratigraphic units. In cases where species richness and faunal abundance data reveal diversification ecozones on the scale of one to several meters in Western Interior strata and where such intervals reflect the widespread and short-term population expansion of key “index species,” the abundance zone, or “epibole,” of traditional usage would be represented. Brett and Baird (paper 10 in this volume) have suggested a redefinition of the epibole concept as a paleoecological rather than as a biostratigraphic unit and have expanded the term to include many features similar to the bioevents and ecozones described herein. Because we developed an independent classification system during analysis of Western Interior paleobiological data (described later), and because the term epibole is still primarily thought of as a biostratigraphic unit, we have not applied the new usage suggested by Brett and Baird (paper 10 in this volume), but note instead similarities and differences to their terms where appropriate.

Figure 20.1 illustrates the system used herein for recognition and definition of ecostratigraphic units based on quantitative and interpretative paleoecological data (species richness, faunal abundance, and biofacies). Biofacies are depicted following a model suggested by Kauffman and Sageman (1990) and Sageman et al. (1991) in which each sample interval is assigned resident (taxa persist through sample) and event (taxa confined to single horizons) community or biofacies values based on combined taxonomic, trophic, life habit, abundance, and taphonomic characteristics. When plotted against physical stratigraphy and quantitative faunal data (species richness and faunal abundance), diversification and reduction bioevents and ecozones (short term or long term) can be identified (fig. 20.1).

**Diversification Bioevents**

Diversification bioevents can be classified into three main categories:

1. *Ecological diversification bioevents* include rapid changes in preexisting biotas within a basin that produce greater biomass and larger, more widely dispersed species populations, or rapid addition of taxa resulting in more complex, more diverse, and/or more highly structured ecological relationships within communities. Rapid population and biomass expansion reflect abrupt changes in environmental parameters that tend to favor a given taxon or group of taxa. These parameters include habitat change or expansion, rapid changes in nutrient and food supply, or abrupt reduction of predator and competitor populations. Examples include colonization
events related to abrupt physical changes in current energy and substrates (e.g., deposition of storm beds or turbidites), rapid chemical changes within the substrate and/or water column (e.g., oxygenation during large storms or advection events), or development of favorable biosubstrates (colonization of shell islands by epibionts). Brett and Baird (paper 10 in this volume) have described similar features as ecological epiboles.

2. **Biogeographic diversification bioevents** mainly involve rapid shifts in paleobiogeographic boundaries that lead to immigration of new taxa and biotas into a basin. Identification of biogeographic diversification bioevents depends on documentation that the immigrant taxa preexist outside the region being studied. On entering a basin, new immigrant taxa commonly integrate with resident communities (e.g., through niche partitioning), which leads to increased diversity and ecological complexity. In some cases, however, they may outcompete and eventually replace portions of preexisting biotas, leading potentially to community disruption (and an ecological reduction bioevent). Biogeographic diversification bioevents take place within geologically short time periods and are regional in scale. They may be related to abrupt changes in water mass characteristics (temperature, salinity, etc.) or oceanic/atmospheric circulation patterns, or to the development of new migratory pathways, which result from plate or regional tectonic modification of continental positions and ocean basins, and/or changes in sea level. Brett and Baird (paper 10 in this volume) have referred to similar features as *incursion epiboles*.

3. **Evolutionary diversification bioevents** are rapid origination events that produce new taxa, new anatomical/morphological structures, and/or new behavior/habitat patterns (as in trace fossils), coupled with rapid dispersal of these new traits or taxa. Mechanisms for such rapid change include punctuated evolution (Eldredge and Gould 1972), allopatric evolution (Mayr 1965), macromutation and other macroevolutionary processes (see Stanley 1979 and references therein). Cited authors present many modern and fossil examples. Rapid spread of these new traits or taxa is normally accomplished by passive dispersal processes (transport of germ cells or larvae by wind and currents) or active juvenile and adult mobility. Identification of evolutionary bioevents within a basin is based on analysis of composite taxonomic range data (first and last occurrences plotted against a standardized section) and documentation that new taxa were not preexisting within or outside the region under study.

**Reduction Bioevents**

Reduction bioevents can also be classified into three main categories:

1. *Ecological reduction bioevents* include abrupt reductions in population size, community size, structure and diversity, and larger-scale decline in
ecosystem complexity without evidence of species-level extinction (i.e., affected species are through-ranging or show Lazarus distribution). The most common ecological reduction bioevents are catastrophic mass mortalities of species resulting in abrupt decline in population size and biomass. They range from local demise of subpopulations (but not entire species populations) to rapid declination of regional communities and ecosystems. These diversity reduction events are due to (a) shock from environmental perturbations, such as advection of chemically deleterious water masses, decline in oxygen levels, or abrupt temperature changes at or above the sediment/water interface (SWI), in surface waters or on land; (b) abrupt habitat change or restriction; (c) introduction of disease, unusually high levels of predation, cropping, and competition from new or associated species; or (d) introduction and replacement by lower-diversity communities.

2. Biogeographic reduction bioevents result from abrupt restriction in the biogeographic distribution of through-ranging taxa, caused by rapid local to regional climatic and/or oceanographic changes. Such events result from the erection of biogeographic barriers, most commonly due to plate or regional tectonic regulation, changes of sea level, and/or changes in water mass characteristics between different basins. Like immigration events, these may occur within very short time frames, reflecting dynamic shifts in paleobiogeographic provinces and subprovinces during the Phanerozoic (e.g., the Cretaceous; Kauffman 1984a). In addition, the immigration of one or more devastating species into a complex ecosystem (e.g., a virus, parasitic insect, or general predator) may lead to short-term, local to regional depletion of paleobiogeographic units. Recognition of these events requires an interbasinal high-resolution chronostratigraphic framework against which taxonomic range data and biogeographic distributions can be calibrated. In cases where ecological or biogeographic reduction bioevents produce intervals that are highly depleted or devoid of fossils, they are similar to the outages described by Brett and Baird (paper 10 in this volume).

3. Extinction bioevents involve the regional to global disappearance of individual taxa during background extinction, or of ecologically and genetically diverse taxa during mass extinction. These may occur within thin stratigraphic intervals and thus comprise important reduction bioevents (Alvarez et al. 1984; Kauffman 1988a). Abrupt, widespread loss of individual species may reflect a variety of causes, including competitive displacement by newly evolved taxa, overcropping by predators that causes severe reduction in population size to nonviable levels, the rapid spread of a new disease (as in the American Chestnut), abrupt loss or change of preferred habitat resulting from internal or external forces, and many other factors (e.g., Hallam 1984; Kauffman 1984b). Mass extinctions reflect larger-scale, more global forcing mechanisms, usually a composite of dramatic changes
in the ocean/climate system that exceed the adaptive ranges of ecologically
and genetically diverse taxa. The recognition of extinction bioevents at the
species level requires highly refined biostratigraphic and chronostratigra-
phic frameworks within a basin, knowledge of taxonomic range data in
time equivalent strata of other regions, and a set of independent chrono-
stratigraphic surfaces against which ranges can be compared.

The Consistency of Paleobiological Response

Despite differences in scales, there are many inherent similarities between
short-term bioevents and longer-term patterns in Cretaceous paleocommunities
(e.g., ecozones), and between Cretaceous paleobiological phenomena of local,
regional, and global extent. This suggests to us that there was a consistent
biotic response in populations, communities, and even ecosystems to similar
environmental forcing mechanisms at a wide range of spatial and temporal
scales (in the same way that community evolution might be viewed as a more
complex and longer-term extension of lineage evolution). This consistent re-
response is recorded as a correlative increase or decrease in community diversity
and robustness. It crosses the boundaries between different (time equivalent)
populations and communities and may be geologically instantaneous (bio-
events) or relatively prolonged (ecozones). This hypothesis has significant im-
lications for understanding paleocommunity dynamics and their relationship
to environmental forcing, and will be discussed subsequently in light of the
data presented herein.

Cenomanian/Turonian Bioevents and Ecostratigraphy,
Western Interior, United States

Geological Setting

The Western Interior Basin of North America (fig. 20.2) developed during Late
Jurassic and Cretaceous time as an Andean-style foreland in response to crustal
loading in the tectonically active Sevier Orogenic Belt (Price 1973; Jordan 1981;
Kauffman 1984a). There are five principal tectonic zones in the basin, including
the rapidly subsiding western foredeep basin; an incipient, discontinuous zone
of forebulge uplifts; the broad, moderately subsiding central axial basin; an east-
central hinge zone; and the stable to slowly subsiding eastern cratonic platform
(Kauffman 1984a). As a result of both subsidence and large-scale tectono-
eustatic sea-level fluctuations, the basin was repeatedly flooded by marine
waters from Albian to Maastrichtian time (Williams and Stelck 1975; Kauffman
1977, 1984a). During the Late Cenomanian to Early Turonian portion of the
Greenhorn Marine Cycle, sea level reached peak highstand for the Cretaceous
(Kauffman 1977; 1984a; Hancock and Kauffman 1979; Haq et al. 1987). At this
time the basin reached its greatest size and extended some 4,800 km in a north/south direction, connecting the circumpolar "Boreal" Ocean (present-day Arctic Canada and Alaska) with western Tethys (present-day Gulf of Mexico and Caribbean). East to west the seaway had a maximum width of about 1,600 km, with Early Turonian shorelines from New Mexico through Montana on the west and through Minnesota and Iowa on the east (fig. 20.2).

The Sevier Fold and Thrust Belt was the upland source for the bulk of siliciclastic sediments entering the basin, with only minor contributions from the cratonic lowlands to the east (Kauffman 1984a). As a result, the basin has a
characteristic distribution pattern of marine sediments at maximum flooding of the Greenhorn Cyclothem that generally corresponds to the principal tectonic zones: (1) The western foredeep and forebulge zones (e.g., New Mexico, Arizona, Utah) are characterized by packages of coarse-grained marginal marine and shoreface marine siliciclastics interfingering with finer-grained proximal offshore non- to moderately calcareous mudrocks; (2) the central axial basin and hinge zones (Colorado) are dominated by distal offshore calcareous clay shales
and marls with thinner interbedded pelagic limestones; and (3) the eastern stable cratonic shelf (Kansas) is dominated by sequences of proximal to distal offshore carbonate-rich shales, marlstones, chalky limestones, and (shoreward) clay shales with thin interbedded siltstones/sandstones that reflect high carbonate productivity and/or the diminished influence of siliciclastic sediments derived from western source areas and relatively low sediment input from the east.

The distribution of lithofacies and biotas in the basin suggests that the deepest water lay near its central and east-central portions, and extended southward into the Chihuahua Trough of northern Mexico (Frush and Eicher 1975; Kauffman 1984a). Maximum water depth probably did not exceed 200–300 m in the central part of the basin during the Early Turonian second-order highstand (Kauffman 1977, 1984a, 1985), and evidence suggests that smaller-scale relative sea-level fluctuations (10–50 m) may have been common throughout the Greenhorn Cycle. The basin had a favorable configuration for the development of stratified water masses and benthic oxygen deficiency during sea-level rise and around eustatic highstand, as indicated by the prevalence of organic carbon-rich strata and depauperate benthic faunas in offshore areas; various hypotheses have been offered to explain Western Interior oceanographic conditions (e.g., Frush and Eicher 1975; Kauffman 1977, 1986, 1988a; Eicher and Diner 1985; Hay et al. 1993; Kauffman and Caldwell 1993). Biogeographic data, summarized by Kauffman (1984a), indicate that the part of the basin considered herein was dominated by moist warm temperate to subtropical marine climates during the Cenomanian/Turonian interval.

Because of overall net subsidence of the axial basin throughout deposition of the Greenhorn Cyclothem, some of the most complete sequences of marine strata are preserved in the Colorado region. Accordingly, a reference section for the Cretaceous was established by Cobban and Scott (1972) near Pueblo, Colorado (central axial basin). At this locality (PRS in fig. 20.2) the study interval includes most of the Hartland Shale Member and the lower to middle Bridge Creek Limestone Member of the Greenhorn Limestone. Lateral facies changes in the Western Interior Basin result in changes in lithostratigraphic nomenclature. Thus the study interval corresponds to the Lincoln Limestone and Hartland Shale Members of the Greenhorn Limestone in central Kansas (Hattin 1975; Sageman and Johnson 1985) and to the Dakota Formation and Tropic Shale in southern Utah (Peterson and Kirk 1977) (see fig. 20.2). These units have been the subject of considerable study over the years (e.g., Cobban and Scott 1972; Hattin 1975; Kauffman 1977; Pratt et al. 1985), and were recently the focus of detailed basin-wide investigations by the authors (Elder 1985, 1987, 1988, 1989; Elder and Kirkland 1985; Sageman 1985, 1989, 1991; Harries and Kauffman 1990; Harries 1993).
Study Interval and Methodology

The interval chosen for study spans the middle late Cenomanian through the Early Turonian and contains a mass extinction-recovery interval (Raup and Sepkoski 1982; Kauffman 1984b; Elder 1989; Harries and Kauffman 1990), and several intervals of organic carbon-rich strata, including Oceanic Anoxic Event II of Schlanger and Jenkyns (1976) and Arthur et al. (1990). A detailed west/east transect of the study interval, spanning the major sedimentologic regimes of the Western Interior Basin (described earlier), has been established based on high-resolution event stratigraphic (HIRES) analysis of numerous sections (Elder 1985, 1987, 1989, 1991; Sageman 1985, 1989, 1991; Harries and Kauffman 1990; Harries 1993). This paper presents data from three sections representative of this cross-basin transect (fig. 20.2) to illustrate the history of Cenomanian/Turonian bioevents and ecostratigraphy. These sections include the Kaiparowits Plateau Section (KPS), the Pueblo Reference Section (PRS), and the Bunker Hill Section (BHS) (fig. 20.2).

The detailed chronostratigraphic framework used to correlate between KPS, PRS, and BHS (fig. 20.2) was developed through application of HIRES methods (see Kauffman 1986, 1988a; and Kauffman et al. 1991 for overviews). The methodology depends on four main types of analysis:

1. Biostratigraphy. Based on established molluscan biozonations of Kauffman et al. (1978, 1993), Cobban (1984), and Kennedy and Cobban (1991), ammonite and bivalve taxa documented in bulk sample analyses from the study interval confirm a late Cenomanian through Early Turonian age (Elder 1985, 1987, 1989; Sageman 1985, 1991). Recent advances in biostratigraphic analysis of the Western Interior have resulted in the recognition of up to 12 molluscan assemblage biozones within the study interval (summarized in Kauffman et al. 1993). However, the scheme employed earlier by Cobban (1984), Elder and Kirkland (1985), and Elder (1985, 1991), in which only five major biozones are defined based on total composite range zones of well-known ammonite index taxa, is utilized here (fig. 20.2) because it is most directly comparable to the current European zonation of Kennedy and Cobban (1991). At PRS the Hartland Shale Member corresponds to the Late Cenomanian Metaioceras mosbyense Biozone. The basal beds of the Bridge Creek Limestone Member (e.g., LS1–LS3: fig. 20.2) contain representatives of the Sciponoceras gracile Biozone. The latest Cenomanian Neocardioceras juddii Biozone occurs from marker beds LS4 to LS7, and the earliest Turonian Watinoceras spp. Biozone (including W. devonense Wright and Kennedy and W. coloradoense Cobban) ranges from LS8 to LS11 (fig. 20.2). Above LS11, Mammites nodosoides Biozone taxa have been described from PRS (Cobban 1985; Kennedy and Cobban 1991). The corresponding five biozones of the European Cretaceous (e.g., southern England) include the Calycoceras guerangeri Biozone,
the _Metoicoceras gelsiusianum_ Biozone, the _N. juddii_ Biozone, the _Watinoceras coloradoense_ Biozone, and the _Mammites nodosoides_ Biozone, respectively (Cobban 1984; Kennedy and Cobban 1991).

2. **Physical event units.** Following the work of Hattin (1971), the predominant physical event units that are used for regional correlation of the Greenhorn Limestone include bentonite beds, representing altered volcanic ash fall deposits, and carbonate-rich units, such as limestone or skeletal limestone beds, which commonly represent offshore condensed deposits (e.g., Hattin 1975; Elder 1985, 1987, 1988, 1991; Sageman 1985, 1991). Major bentonite beds that were correlated throughout most of the Western Interior Basin using stratigraphic techniques (e.g., beds A and B of Elder 1988, fig. 20.2) have been tested by chemical fingerprinting methods (see Kowallis et al. 1988), providing independent confirmation of the correlations. They represent the most dependable chronostratigraphic markers for distal to proximal offshore facies. In addition, limestone beds have been shown to grade from central basin distal offshore facies westward into concretion horizons of proximal offshore areas, and subsequently into transgressive lags or marine flooding surfaces on top of prograding parasequence deposits of the seaway’s western margin (Kauffman et al. 1987; Elder et al. 1993). Five such units (FS3–7, fig. 20.2) have been confidently correlated within the study interval (Elder et al. 1993) and provide a set of high-resolution markers that encompass a complete transect from the basin center to the strandline.

3. **Chemostratigraphy.** Within the study interval there are a series of distinctive geochemically defined horizons marked by shifts or spikes in stable isotopic and trace element data. For example, Scholle and Arthur (1980) first recognized a spike in the δ¹³C record of C/T strata that was correlative throughout Europe. Pratt and Threlkeld (1984) and Pratt (1985) later identified this marker in the Western Interior as a 2–4 per mil positive shift in the δ¹³C signature of organic matter spanning about 5 m of strata within the study interval at PRS and BHS (fig. 20.2). Kauffman (1988a) suggested that individual peaks within this excursion could be used for even-finer-resolution correlations. The excursion extends from the base of the _S. gracile_ Biozone into the _Watinoceras_ Biozone and maintains a consistent stratigraphic position relative to biozone boundaries and lithostratigraphic marker beds throughout the west/east transect of the basin. Trace element data presented by Orth et al. (1988) showed similar potential for correlation, with distinct enrichments at several horizons in the lower part of the Bridge Creek Member at PRS (e.g., Mn, Ir). These geochemical markers have since been detected at other Cenomanian/Turonian sections, both within and outside the Western Interior Basin (Orth et al. 1993).

4. **Ecostratigraphy.** Paleoeocological analyses are based on continuous collection of uniform-size bulk samples averaging 10–40 cm in thickness through each stratigraphic section. The resulting data set, including both
biostratigraphic range data and values of total species richness and faunal abundance, are statistically comparable within and between sections. Fossil assemblages are also analyzed for basic taphonomic data (i.e., levels of fragmentation, disarticulation, shell abrasion, and bioerosion), as well as trends in shell density, size distribution, and orientation. These data are used to help distinguish long-term resident community components from short-term event communities and allochthonous biotic elements. Each sample is assigned a resident or event biofacies categorization based on its taphonomic condition, faunal association, trophic group composition, and overall diversity and abundance (e.g., Elder 1989, 1991; Kauffman and Sageman 1990; Sageman 1989; Sageman et al. 1991).

The Hartland Shale and Bridge Creek Limestone Members have long been recognized for their distinctive biotic characteristics. The Hartland Shale at PRS is an interval characterized by finely and evenly laminated, dark calcareous shale with high levels of preserved organic carbon and relatively depauperate faunal assemblages (Kauffman 1977, 1984b; Sageman 1985, 1989, 1991). It is virtually devoid of benthic foraminifera (Eicher and Worstell 1970; Eicher and Diner 1985), contains only very rare burrows, and is dominated by resident communities of epifaunal inoceramid bivalves. These features are best developed in the central axial basin but can be recognized at all localities containing offshore marine strata of the M. moshbyense Biozone. As a result, the Hartland Shale Member has been interpreted as an interval of widespread and prolonged oxygen depletion within the Western Interior Basin (Frush and Eicher 1975; Kauffman 1984a; Sageman 1985, 1989).

In contrast, the overlying lower Bridge Creek Limestone Member is characterized by a shift to highly burrowed pelagic limestone beds interbedded with laminated dark marlstones (interpreted to represent Milankovitch climatic cycles: Barron et al. 1985; Fischer et al. 1985), and contains the highest composite number of species recorded for any part of the Greenhorn Cyclothem (Koch 1977; Elder 1987). In the beds immediately above the lower part of the member, however, evidence of the C/T mass extinction and of the Bonarelli OAE is represented by increased burial of organic carbon in shale beds, significant loss of species (especially molluscan) in a series of extinction "steps," and a widely correlative decrease in diversity and abundance within benthic marine communities (Elder 1989). These events are followed by an initially punctuated and subsequently gradual recovery of marine communities during the Early Turonian (Harries and Kauffman 1990; Harries 1993).

Analysis of Local Bioevents and Ecostratigraphy

Taxonomic, ecological, and sedimentologic data are presented and analyzed for each of the three sections of the west/east transect (figs. 20.3–20.6). For more
extensive presentations of these data the reader is referred to Elder (1987, 1989, 1991, 1985), Sageman (1985, 1989, 1991), Harries and Kauffman (1990), Kauffman and Sageman (1990), Sageman et al. (1991), and Harries (1993). In this paper, plots of species richness and faunal abundance, commonly viewed as proxies for trends in benthic communities, are employed to illustrate bioevents and ecostratigraphic trends (figs. 20.3–20.6). Identified bioevents are categorized following the classification scheme described earlier.

The Kaiparowits Plateau Section (KPS)

The Kaiparowits Plateau Section is located near Wahweap Wash, south-central Utah (fig. 20.2), at the base of the south-facing escarpment of the Kaiparowits Plateau. The study interval includes the Late Cenomanian/Early Turonian parts of the Dakota Formation and lower Tropic Shale, which were deposited in the rapidly subsiding Western Interior foredeep basin (Peterson and Kirk 1977; Gustason 1989). Coal beds occurring at the base of the section represent coastal plain facies of the uppermost part of the middle nonmarine portion of the Dakota Formation (Gustason 1989). They are overlain disconformably by a bioturbated sandy unit and an oyster concretion horizon (FS0, figs. 20.2, 20.3), reflecting the initial marine flooding of the Western Interior sea into southern Utah. The overlying Tropic Shale grades upward from sandy and silty bioturbated mudstones to calcareous shales and contains seven more calcareous concretion or shell lags beds, each of which can be traced westward to transgressive lags overlying upward-coarsening progradational shoreface sequences (Gustason 1989; Elder et al. 1994). These event beds (FS1–7, figs. 20.2, 20.3) represent the marine flooding surfaces of seven parasequences (sensu Van Wagoner et al. 1990) that record relatively short-term, high-frequency fluctuations of the strandline with associated migration of benthic environments. Overall, the study interval at KPS represents a period of progressive deepening from paludal/lagoon to proximal offshore environments.

Based on recognition of key biostratigraphic index taxa, the lower 6.5 m of the Tropic Shale and the underlying Dakota Formation represent the uppermost part of the Late Cenomanian _Metoicoceras mosbyense_ Biozone and correspond to the middle to upper Hartland Shale Member as defined at PRS (fig. 20.2). The base of the overlying interval, equivalent to the base of the Bridge Creek Limestone Member at PRS, is marked by a conspicuous concretion/shell bed (FS2b, figs. 20.2, 20.3) and the first appearance of the _Sciponoceras gracile_ Biozone fauna (Elder 1991). The top of the _S. gracile_ Biozone occurs between 11 and 12 m above the base of the Tropic Shale and is overlain by an interval containing the latest Cenomanian _Neocardioceras juddii_ Biozone fauna (Elder 1991). The Cenomanian/Turonian boundary occurs 19 m above the base of the Tropic Shale and is indicated by the first appearance of _Mytiloides hattini_ Elder, marking the base of the Early Turonian _Watinoceras_ Biozone (Elder 1991).
KPS Bioevents  In figure 20.3 trends in macrofaunal species richness and abundance reflect KPS bioevents and ecozones. Most bioevents identifiable within the study interval are ecological and resulted from rapid migration of benthic environments during eight cycles of transgression and regression of the strandline. Each cycle includes an upward-coarsening progradational phase capped by a discrete marine flooding surface (designated FS0–FS7). Using these flooding surface designations as a guide, the ecostratigraphy of the KPS section is as follows.

FS0  Initial marine flooding at KPS is marked by a colonization bioevent that reflects the local establishment of a distinctive brackish to marine community (fig. 20.3). At the base of the KPS section, the uppermost mappable sandstone bed (and first marine unit) of the Dakota Formation is overlain successively by a thin carbonaceous shale and a 10-cm oyster concretion horizon. The concretion layer reflects the development of a biostrome or shell bed of Flemingostrea prudentia (White), an epifaunal suspension feeder with a preference for shallow brackish to marine waters and soft substrates (Fürsch and Kirkland 1986). Development of the biostrome indicates a local colonization bioevent (ecological diversification) that resulted from a decrease in coarse siliciclastic sedimentation and formation of a biosubstrate in a nearshore muddy marine area with brackish influence (a brackish to marine bay?). The concretion bed can be traced for miles to the west as a transgressive disconformity, in some cases directly overlying coal beds, and clearly reflects the initial marine transgression into the KPS region (initial marine flooding event: fig. 20.3).

FS1 TO FS2A  Increases in species richness and faunal abundance in the lower 4 m of Tropic Shale at KPS reflect colonization and population expansion related to two upward-coarsening parasequences (nearshore parasequences: fig. 20.3). The generalized lithologic description (upsection) for each of these parasequences includes a dark carbonaceous or slightly calcareous laminated shale, overlain by bioturbated silty mudstone with increasing thin, bioturbated to ripple-laminated lower shoreface siltstone/sandstone beds. Flooding surfaces FS1 and FS2a cap the sequences but are not marked by distinct transgressive lag deposits (concretions or shell beds) at the KPS locality. However, continuous updip exposure along the outcrop belt allows regional tracing of parasequences 1 and 2, and correlation of FS1 and FS2a to transgressive lag beds at nearby localities (Gustason 1989; Elder et al. 1994).

The faunal associations in samples spanning the two parasequences reflect a similar succession in each. They are dominated by somewhat brackish (lower bay or estuarine mouth) associations, including trophically diverse infaunal and epifaunal elements (mainly infaunal deposit and suspension-feeding protobranch, corbulid and venerid bivalves, sparse scaphopods, grazing or carnivorous gastropods, and epifaunal suspension-feeding bivalves). Cycles of increas-
Figure 20.3. Bioevents and ecozones at the Kaiparowits Plateau section (KPS) are indicated by trends in species richness and abundance data. Lithologic section and marker beds (M-Beds) are as in figure 20.2. Insets to the right show the relationship of diversification and reduction bioevent horizons (represented by D and R letters) to the time-averaged curve of species richness/abundance data and short-term ecozones. Biostratigraphic zones are indicated at left, with abbreviations as follows: M.m. = Metacoceras mosbyense, S.g. = Sctponoceras gracile, N.j. = Neocadioceras juddii, Wat. = Watinoceras, and M.n. = Mammites nodosoides. Major flooding surfaces are indicated by FS designations. C/T marks the position of the Cenomanian/Turonian boundary.
ing species richness and abundance correlate to trends of increasing shell fragmentation and reach their peaks in the samples just below or at parasequence flooding surfaces FS1 and FS2a. (Note also the faunal peak between the FS1 and FS2a peaks, which is not associated with a widely recognized flooding surface; it may reflect an early pulse of the parasequence 2 progradation.) These cycles reflect trends in benthic colonization and population expansion related to relative shoaling of the parasequences and are interpreted as the result of higher current energy, increased mixing and oxygenation, and greater availability of food resources. Numerous individual colonization bioevents are represented in each cycle, but horizons could not be stratigraphically resolved because of extensive bioturbation. In the samples directly overlying the flooding surfaces, a decline in species richness and abundance, and the occurrence of depauperate faunas (mainly inoceramid, pectinid, pterid, and ostreid bivalves) characteristic of offshore low-oxygen environments and relatively soft substrates reflect reductions in benthic community diversity. These trends, which are much better developed above FS2a than above FS1, are interpreted to reflect rapid deepening and a shift to finer-grained sedimentation, mortality or local emigration of shallow-water brackish forms, and shoreward migration of low-oxygen-tolerant offshore faunas (see “nearshore parasequences” in fig. 20.3).

FS2b to FS3  The first fully marine, offshore flooding surface occurs at 6.5 m above the base of the KPS section (FS2b, figs. 20.2, 20.3) and correlates eastward to LS1 at the base of the Bridge Creek Limestone Member (fig. 20.2). When traced to the west of KPS, this horizon merges with the underlying flooding surface (FS2a) within 10 km, overlies parasequence 2 for about 70 km to its updip pinchout, and continues 90 km further west as a transgressive surface overlying nonmarine sandstones and coal beds of the Dakota Formation (Gustason 1989; Elder et al. 1994). This surface represents the largest landward shift of the strandline within the study interval. Because there is no preserved evidence of a parasequence deposit between this horizon and the underlying parasequence, and because it coalesces for some distance with the underlying flooding surface, the designations 2a and 2b were applied. At the KPS locality, FS2b is a highly complex condensed unit that includes (upsection) an early diagenetic, shell-rich calcareous concretion horizon, a thin horizon of silty calcareous mudstone, and several dense layers of shell material. The interval is marked by a major peak in abundance of whole fossils, shell fragments and fish debris, and the abrupt appearance of highly diverse subtropical to warm temperate marine taxa belonging to the S. gracile Biozone (e.g., numerous molluscs, solitary corals, fodinichnia and domichnia, and abundant planktic foraminifera). These taxa occur mainly as, or associated with, a series of closely spaced or amalgamated colonization surfaces, including horizons with highly abundant surface grazing Leviserithium gastropods, lucinid and arcidi bivalves, and tiny indeterminate oysters. Whereas the abundance and diversity associ-
ated with these colonization events suggests plentiful food resources and favorable benthic conditions, the rapid shifts between distinct associations among successive closely spaced fossil horizons may indicate condensation and/or the presence of disconformities. On some horizons the strong dominance of similarly sized individuals may reflect abrupt mass mortality events (note multiple D/R bioevents, offshore flooding surface 2b, fig. 20.3).

Immediately overlying this fossil-rich zone is a black, organic-rich mudstone unit with dense *Chondrites* burrows followed by a shell-rich layer composed of *Pycnodonte* oysters. Because the *Chondrites* burrow fill consists of sediment from the overlying shell bed, it is possible that burrowing followed deposition of the black mudstone and that the mudstone itself represents a time of low benthic oxygen, almost no benthic habitation, and enhanced preservation of organic matter. The shell bed (FS3), however, contains a moderately diverse fauna in addition to the dominant oysters and has been traced by Gustason (1989) westward to a transgressive lag overlying the third upward-coarsening para-sequence in the marine part of the Dakota Formation (Elder et al. 1994). It appears that the black mudstone represents the deepest phase of the FS2a transgression, that *Chondrites* represent the pioneer colonization bioevent upon shallowing, and that the oyster colonization bioevent is all that is preserved of the subsequent shoaling/flooding event (FS3, fig. 20.3).

Many oyster shell horizons (usually 5–10 cm thick) associated with flooding surfaces along the basin’s western margin consist of a lower biostrome level with shells in life position (representing colonization during the waning stages of progradation). Upon this is superimposed an upper shell lag with disarticulated shells in current stable or chaotic orientations (representing erosion at wave base during development of a ravinement surface). In the case of FS3 the entire unit has the character of a lag deposit and may represent the reworked remains of several colonization events. When this horizon is traced into the basin, it commonly lies directly above the FS2a equivalent, coalesces with the FS2a bed, or is indistinguishable from it. These features support the interpretation of significant condensation and possibly development of disconformities within the FS2a to FS3 interval.

**FS4 to FS7** In the interval overlying FS3 at KPS are four consecutive resistant beds, including fossiliferous concretions, colonization surfaces, and/or shell lags (see offshore parasequences, fig. 20.3). These horizons have been correlated shoreward to four transgressive lags overlying prograding parasequences (Gustason 1989), and basinward to four pelagic limestone beds (Kauffman et al. 1987; Elder 1991; Elder et al. 1994). They are interpreted to represent the offshore expression of the parasequence flooding events. At the KPS locality, each complete cycle includes a 1–2-m-thick unit of variably burrowed claystone or shale representing parasequence progradation, capped by a shelly, carbonate-enriched bed representing the flooding surface.
FS4 is characterized by two distinct short-term colonization bioevents. The lower occurs within an early diagenetic limestone concretion horizon, formed around serpulid worm tubes that colonized a condensed, sediment-starved transgressive surface. The serpulid biostrrome is associated with *Gryphaeostrea* and diverse byssally attached bivalves (e.g., *Phleopteria, Lima*), and shows a modest increase in total faunal abundance and species richness from the previous samples (fig. 20.3). In the bioturbated claystone immediately overlying the concretion bed, a colonization surface dominated by two genera of oysters (*Pycnodonte, Rhynchostreon*) creates the final FS4 abundance peak (fig. 20.3). This oyster biostrome represents the second colonization bioevent associated with flooding of parasequence 4.

In the interval between FS4 and FS5 is a fairly diverse and robust resident faunal association characteristic of the *S. gracile* Biozone along the basin’s western margin (fig. 20.3). Unlike flooding events 1, 2a, 2b, and 3, the late stage of deepening associated with flooding event 4 produced relatively little reduction overall in species richness and abundance. However, changes in biofacies indicate a distinct shift in benthic conditions between FS4 and FS5. Oysters, which dominate in the lower part of this interval, decline in abundance upward; concurrently, the abundance of shallow infaunal deposit-feeders (*Lucina, Drepnanochilus*) increases to a peak just below FS5. These data suggest that infaunal deposit feeders replaced epifaunal oysters because of increasing sedimentation rates and turbidity, and increasing availability of detrital organic matter during progradation of parasequence 5.

FS5 represents an amalgamated diversification bioevent sequence that includes several faunal events. At the base of FS5, a bioturbated limestone concretion contains a diverse assemblage of gastropods and ammonites (e.g., *Sciponoceras, Euomphaloceras, Euspira, Drepnanochilus*). Current-aligned *Sciponoceras gracile* (Shumard) within the concretion suggests sediment bypass/starvation and orientation of biotic elements that thrived during the initial shallow, well-mixed phase of parasequence 5 transgression. Sharp burrow walls indicate that following early diagenetic cementation, diverse infauna (including fodiichnia and domicchia) colonized the shell-rich substrate, producing a second diversification bioevent. A *Pycnodonte* oyster biostrome found immediately above the concretion horizon represents the final colonization event associated with FS5 flooding, resulting in a distinctive spike in faunal abundance at FS5. This spike is followed by a marked decrease in species richness/abundance and a shift toward offshore, low-oxygen-tolerant faunas dominated by a byssate epifaunal bivalve association (*Inoceramus, Phleopteria*). This reduction in diversity reflects the deepest stage of the FS5 flooding event and the landward migration of offshore (low-oxygen) benthic environments.

The character of bioevents at FS6 and FS7 reflects progressive deepening at KPS. Lithologically, the flooding surfaces are marked by beds of resistant, burrowed calcareous shale or mudstone (figs. 20.2, 20.3). The offshore character
of biofacies in the claystone underlying FS6 does not change appreciably through the flooding surface, but a peak in diversity and abundance directly overlies the resistant bed. This horizon lacks the oyster biorite typical of underlying (shallower) flooding surfaces but is dominated by an association of *Inoceramus*, *Phelopteria*, and offshore ammonites (e.g., *Neocardioceras*, *Kamerocrinus*) that marks the peak flooding stage and maximum offshore condensed interval of the parasequence. Similarly, FS7 is marked by a peak in species richness and abundance dominated by the *Inoceramus*, *Phelopteria*, and offshore ammonite association. Faunal abundance drops off rapidly in the samples overlying each flooding surface, and biofacies become progressively dominated by low-diversity associations of generalized and infaunal deposit feeders (*Lucina*, *Drepanochilus*) or epifaunal bivalves (inoceramids and small oysters). These trends reflect diminished benthic oxygen and increased preservation of marine organic matter at KPS. However, unlike the underlying sequences, this pattern of reduced diversity and abundance continues for a considerable distance upsection, including the upper half of the *N. juddii* Biozone and much of the *Watsoniceras* spp. Biozone (fig. 20.3). In this interval, inoceramids and small oysters dominate resident biofacies, and there are only rare colonization events by such infaunal taxa as *Lucina* and *Drepanochilus*.

**KPS Summary** Stratigraphic and faunal data from the KPS locality allow the following conclusions:

1. The section records a late Cenomanian marine incursion across a coastal plain in southern Utah and a series of proximal to medial offshore progradational units and their flooding surfaces (parasequences) that formed as the site progressively deepened toward Early Turonian maximum highstand. A major shift in the character of sediments and faunas occurs midsection (above FS7), where offshore clay-rich facies become dominant and shell-rich flooding surfaces are no longer well developed, suggesting continued deepening to proximal or medial offshore environments that were beyond the perimeter of shallow water shell concentrations.

2. Numerous short-term diversification (D) and diversity reduction (R) bioevents characterize the faunal history of the lower Tropic Shale at KPS. Collectively, they form a pattern of relative D/R cycles that track with a series of seven upward coarsening parasequences in the Dakota Formation. Diversification bioevents are dominantly ecological, and they characterize the shallowest phase of each parasequence cycle (late progradation and early flooding phases), when circulation, benthic oxygenation, nutrient levels, and substrate conditions enhanced opportunities for colonization. Diversification bioevents are commonly complex, amalgamating colonization events that occurred during both relative shallowing and relative deepening periods, and include colonization of transgressive starved and
ravinement surfaces. Diversification of taxa, trophic groups, and adaptive strategies, and increased faunal abundance characterize benthic environments during progressive shoaling and progradation. This effect is enhanced as transgression begins, because of diminished sedimentation rates and initial development of starved flooding surfaces. In many cases benthic communities become dominated by one or two taxa that opportunistically colonize the transgressive ravinement surface, producing distinct abundance peaks. These two types of processes resulting in ecological diversification commonly occur together as a compound event marking KPS flooding surfaces. Reduction bioevents, in contrast, are represented by overall decrease in species richness and abundance because of emigration or localized mortality events, and a shift to offshore biofacies (dominated by low-oxygen-tolerant epifaunal bivalves). They reflect the deepest phases of each parasequence cycle and the furthest landward migration of offshore benthic communities characteristic of oxygen-depleted basinal settings.

3. Plots of species richness and faunal abundance present a time-averaged perspective of faunal change at KPS. Peaks and troughs on the scale of 1–2 m generally correlate with the shallowing and deepening phases of individual parasequences, and these features are bundled in larger relative diversification and diversity reduction zones about 1012 m in thickness (fig. 20.3). Individual peaks and troughs have similar minimum and maximum values within diversification zones (e.g., D2 and D3) and are distinct between diversification and diversity reduction zones (e.g., D3 vs. R3). At each scale the zones are characterized by repetition of similar resident community types and similar multiple bioevents, although taxonomic compositions change through the stratigraphic sequence. Although these short- and long-term ecostratigraphic zones are related to relative sea-level changes and thus appear to reflect normal “faunal tracking” (as described by Brett et al. 1990, and Brett and Baird, paper 10 in this volume), we will demonstrate that they have relatively sharp boundaries that can be correlated at the same stratigraphic level from KPS to BHS. This suggests that the zones reflect more or less synchronous basinwide trends of relative improvement or decline in bentic environments, and thus comprise chronostratigraphically useful ecozones in the Western Interior Basin.

4. The dominant controlling factors for the development of bioevents and ecozones at KPS are interpreted to be (a) levels of bentic oxygenation, reflecting overall water depth, stratification, and mixing intensity; (b) changes in current energy that influenced sediment transport and mixing of the water column; (c) variations in sedimentation rate and resultant changes in substrates, turbidity levels, and transport of land-derived nutrients; and (d) biogenic modification of substrates (e.g., through bioturbation or development of biostromes).
The Pueblo Reference Section (PRS)

Cobban and Scott (1972) established the standard reference section for basinal Cretaceous facies of the Western Interior Seaway in east-central Colorado (see also papers in Pratt et al. 1985). Predominantly medial to distal offshore facies of the Greenhorn and Niobrara Cyclothsms are exposed along escarpments bordering the Arkansas River where it has breached the Rock Canyon Anticline just west of Pueblo, Colorado. The study interval at PRS includes the Hartland Shale and the lower to middle part of the Bridge Creek Limestone Members of the Greenhorn Limestone. The lithostratigraphy and biostratigraphy of these units were introduced earlier under "Geologic Setting" (see also fig. 20.2). Figure 20.4 illustrates the PRS section with species richness and faunal abundance plots and indicates the bioevents and ecozones discussed later.

PRS Bioevents Hartland Shale bioevents are dominantly ecological and reflect rapid changes in benthic oxygen levels and substrate character. Laminated, pyritiferous, olive gray to olive black, C_{org}-rich (3–4 wt. %) Hartland Shale facies are mainly characterized by relatively low-diversity, Inoceramus-dominated resident communities. Inoceramids were well adapted to low oxygen levels (Kauffman 1981, 1984a), possibly through chemosymbiosis (Kauffman 1988b; Kauffman and Sageman 1990; McLeod and Hoppe 1992), and acted as the pioneer species for resident Hartland paleocommunities. Bioevents in the Hartland Shale are mainly expressed as moderate to densely colonized bedding plane surfaces (event communities) of epifaunal benthic bivalves (e.g., *Inoceramus*, Entolium) or less commonly, trace fossils of soft-bodied, deposit-feeding infauna (e.g., *Planolites*, Chondrites). Colonization bioevents reflect brief episodes of benthic circulation and oxygenation, and/or changes in substrate character, and are commonly followed by mass mortality bioevents that suggest rapid deoxygenation and H_{2}S poisoning, or rapid burial.

Bioevents of the Bridge Creek Member at PRS, which is characterized by rhythmic interbedding of highly burrowed micritic limestone beds with laminated, organic-rich shales, include numerous ecological diversification and reduction events. Biofacies of the *Sciponoceras gracile* Biozone represent a significant diversification compared to Hartland Shale faunas, principally through immigration and colonization bioevents. Diversification and reduction bioevents alternate within shale/limestone cycles and reflect regional changes in benthic environments, presumably related to Milankovitch climatic cycles (Barron et al. 1985). In the following sections, PRS bioevents are summarized in ascending stratigraphic order (fig. 20.4).

Entolium Event Communities/Mass Mortality Surfaces The basal 8 m of the Hartland Shale at PRS are characterized by numerous bedding planes covered by single cohorts of highly abundant, small juvenile (1–2-mm-long), thin-shelled *Entolium gregarium* Kauffman and Powell (pectenacea), sepa-
**Figure 20.4.** Bioevents and ecozones at the Pueblo, Colorado, section (PCS) are indicated by trends in species richness and abundance data. Lithologic section and marker beds (M-Beds) are as in figure 20.2. Insets show relationship of diversification and reduction bioevent horizons (represented by D and R letters) to the time-averaged curve of species richness/abundance data and short-term ecozones. In the case of *Inoceramus* and *Entolium* events, the time-averaged curve is a background stipple, whereas the foreground pattern reflects event community abundance levels. Note that different bioevents may be reflected more strongly by species richness or abundance data, as indicated by stipple versus striped patterns. Biostratigraphic zones are abbreviated as in figure 20.3. C/T marks the position of the Cenomanian/Turonian boundary. Diversity trend for “Benthonic (Foram) Zone” inset modified from Eicher and Diner (1985) and Leckie (1985).
rated by thin shale intervals with rare specimens, or lacking *Entolium* (fig. 20.4). These represent opportunistic colonization events or spat falls that occurred during short-term increases in bottom-water oxygenation. Colonization was followed rapidly (weeks-months?) by mass mortality as a result of a rise in the redox boundary to or above the SWI, poisoning by $H_2S$, and/or smothering by thin mud turbidites. These composite bioevents, modeled in the lower right panel of figure 20.4, have regional expression at the same stratigraphic level in the central part of the Western Interior (Colorado to Oklahoma), but individual colonization/mortality surfaces have not been regionally correlated. Although *Entolium gregarium* ranges throughout the study interval, it occurs in exceptional abundance only in this lower to middle Hartland interval. This *Entolium* abundance zone, which represents the best example of a traditionally defined epibole documented within this study, does not correlate with other benthic faunal indicators, and crosses ecozone boundaries that are traceable well beyond its limits.

**Inoceramus Bioevents** A 10-cm-thick, olive gray laminated limestone, 7 m above the base of the Hartland Shale Member at PR5 (marker bed LL1 in fig. 20.4) contains several colonization/mass mortality surfaces representing composite diversification/reduction bioevents related to changes in benthic oxygenation. They are composed of one (predominantly) to two cohorts of *Inoceramus ginterensis* Pergament in or near growth position. Adult-sized *I. ginterensis* (up to 10 cm long) found throughout well-laminated, organic-rich facies of the lower to middle Hartland Shale indicate low-oxygen adaptations for the species. Yet in marker bed LL1 (fig. 20.4), colonization events of *I. ginterensis* were followed within 1 or 2 years by mass mortality, as demonstrated by the strong single size class dominance of juvenile or near-juvenile specimens (0.9 and 1.4 cm long)(Sageman 1989). Lack of evidence for catastrophic burial suggests rapid, extreme oxygen depletion, and/or $H_2S$ poisoning at the SWI. Diversity trends within other samples reflect an additional bioevent type involving *Inoceramus* bivalves in the Hartland Shale. In certain cases, up to three species of *Inoceramus* may be associated with additional byssally attached or cementing taxa (small *Phelopteria*, *Ostrea*, *Pycnodonte*) that were unable to survive on soft, oxygen-depleted calcareous muds but that colonized *Inoceramus* bivalves as shell islands. These represent diversification bioevents made possible by biological interactions.

**Skeletal Limestone Bioevents** At a number of levels within the middle Hartland Shale (SL2, 3 and 4: fig. 20.4), 1–5-cm-thick, olive gray skeletal limestones (calcarenites) are characterized by benthic colonization events reflecting abrupt changes in physical sedimentation. Ripple lamination and scouring suggest that these are storm-generated, density-flow deposits, which also may have been associated with water mass mixing and short-term benthic oxygenation. The major event communities are composed of trace fossils repre-
senting infaunal sediment feeding and dwelling taxa (Planolites, Thalassinoides, and Chondrites burrows) and scattered surface-crawling organisms (Crosopodia). Abundant, fragmented bivalves (mainly Inoceramus) comprising these limestones probably represent locally winnowed or transported material, but larger inoceramid fragments and entire valves, and cementing oysters such as Ostrea suggest short-term colonization of the coarse-grained substrates. Thus colonization bioevents in skeletal limestones probably reflect a combination of factors, including condensation/deposition (development of a firm substrate) and short-term oxygenation.

**Benthic Foraminifer Bioevents** In the uppermost 0.5 m of the Hartland Shale Member, shales become indistinctly burrowed and calcareous benthic foraminifera colonize the central basin for the first time in the Greenhorn Cyclothem (Eicher and Diner 1985; Eicher and Worstell 1970). This initial oxygen-related bioevent of the “Benthonic Zone” (Eicher and Worstell 1970) marks a significant change in substrate and bottom-water conditions in the central Western Interior sea and immediately precedes the beginning of limestone deposition in the central basin (“Benthonic (Foram) Zone,” fig. 20.4). Eicher and Worstell (1970) and Eicher and Diner (1985) document the development of a diverse assemblage of calcareous benthic foraminifers in shale samples of the lower Bridge Creek Member in the central Western Interior Basin, with species richness values rising to 30 species (locally reflecting successive colonization events). Species gradually disappear upsection, and benthic foraminiferal diversity and abundance values reach a minimum in association with well-laminated, organic-rich facies of the *N. juddii* Biozone (fig. 20.4). Although species richness and abundance increase again slightly in the lower Turonian Watinoceras Biozone (Leckie 1985), calcareous benthic foraminifers remain depauperate throughout the Bridge Creek Member, and disappear completely in the overlying Fairport Chalky Shale Member (Eicher and Diner 1985). Because these benthic taxa range throughout the Greenhorn interval in shallower proximal offshore areas (Eicher and Diner 1985), their presence or absence in the central part of the basin is interpreted to reflect ecological controls on colonization and mortality. (Note that the diversity/abundance max of the “Benthonic Zone” corresponds to long-term ecozone D2, fig. 20.4).

**Bioevents in Shale/Limestone Cycles** The Bridge Creek Limestone Member at PRS is characterized by alternating 5–75-cm-thick units of well-laminated, olive gray calcareous shales and marls and 10–50-cm-thick beds of resistant, micritic, gray limestone or marlstone beds (LS1–LS11, fig. 20.2, 20.3). These have been widely interpreted (e.g., Barron et al. 1985; Fischer et al. 1985) to represent changes in sedimentation resulting from alternate phases of Milankovitch climate cycles (characterized predominantly by shifts in evaporation/precipitation balance through changes in monsoonal patterns, or wet/dry cycles). Trends in species richness and abundance, biofacies, and bioevents
suggest a strong correlation between changes in benthic communities and these rhythmic deposition cycles, and a general model is shown by the inset in figure 20.4. Immediately overlying highly burrowed limestone beds, well-laminated to microburrowed, organic-rich shales are characterized by dominance of low-diversity associations of broad, flat, resident epifaunal inoceramids. This shift initially reflects a reduction bioevent in response to development of a softer clay-rich substrate and depletion of oxygen in the bottom water, suggesting enhanced stratification. In contrast, limestone/marlstone beds (especially in the basal Bridge Creek Member) are highly bioturbated, with the density, number of generations, tiering, trophic complexity, and diversity of ichnotaxa (Planolites, Chondrites and Thalassinoides dominant) increasing upward through each carbonate-rich unit (Barron et al. 1985; Elder 1985, 1989, 1991; Kauffman 1988a). A strong correlation between carbonate content and burrow presence, size, and depth of penetration suggests that decrease or cessation of siliciclastic sedimentation and early cementation resulted in firmer carbonate substrates, which in turn encouraged infaunal colonization bioevents. In addition, although higher values of species richness and abundance of aragonitic-shelled ammonites observed in limestone beds may have a slight preservational component, Elder (1989) has correlated these trends into laterally equivalent, nonlimestone facies, suggesting a primary regional ecological signal. Collectively, these events may reflect widespread, short-term changes in community structure in shale/limestone cycles in response to improved benthic oxygen levels, firmer substrate conditions, and greater food availability during times of enhanced mixing.

**PRS Summary** Observations of lithostratigraphic and faunal trends at the PRS locality allow the following conclusions:

1. The Hartland Shale and Bridge Creek Limestone Members at PRS comprise distal offshore facies deposited prior to peak highstand of the second-order Greenhorn Cyclothem in the central Western Interior Basin. Laminated, organic-rich shales of the Hartland Member indicate a predominantly low-energy, low-oxygen depositional environment at PRS. Shale/limestone bedding couplets of the Bridge Creek Member suggest that, as the basin deepened, the response to Milankovitch climate cycles became pronounced, affecting water mass properties and clay and carbonate depositional processes throughout the basin.

2. Local, short-term D/R bioevents are extremely common in the Cenomanian/Turonian sequence at PRS. Diversification bioevents in the Hartland Shale Member include pioneer colonization of muddy substrates, secondary colonization of inoceramid pioneers by small epibionts, and colonization of the substrate by other free-living epifaunal bivalves or small infaunal burrowers, reflecting a gradient of increasing benthic oxygenation and substrate habitability. Reduction bioevents were mainly due
to oxygen decline, \( \text{H}_2\text{S} \) poisoning, and burial by fine-grained sediment, and in many cases followed colonization events within months to 1 or 2 years to produce single-cohort mass mortality surfaces. Storm events are a likely cause for these short-term changes in Western Interior sedimentation and water mass stratification. Similar ecological bioevents characterize the shale/limestone bedding couplets of the Bridge Creek Member at PRS. Diversity reduction events and low-oxygen-tolerant pioneer or opportunistic taxa dominate laminated, organic-rich shaley intervals, suggesting prevalence of a stratified water column. Diversification bioevents resulting in greater trophic complexity, higher overall species richness and abundance values, and more sustained community growth are best developed in the carbonate-rich (limestone/marlstone) lithofacies, suggesting times of greater water column mixing.

3. Overall patterns of species richness and faunal abundance at PRS are similar to KPS: peaks and troughs at a scale of ±1 m associated with limestone/shale cycles resemble the biotic patterns observed in KPS para-sequences, and suggest regional expression of short-term D/R ecozones. D/R bundles at a scale of 3–7 m (intervals R1–D3, fig. 20.4) are also similar to those of KPS, suggesting long-term ecozones. Cross-basin correlation of these biotic patterns is described in a later section on regional ecostratigraphy.

4. Combined sedimentologic, geochemical, and faunal data suggest that climatically driven, short-term fluctuations in benthic oxygen levels (water column stratification, position and variability of redox boundary) and substrate characteristics (supply of siliciclastic versus biogenic sediment, consistency, porosity) controlled benthic communities in the central Western Interior Basin during Cenomanian/Turonian time.

**The Bunker Hill Section (BHS)**

The Bunker Hill section is located in roadcut exposures near the town of Bunker Hill, Russell County, Kansas. The study interval is composed of distal offshore carbonate-enriched lithofacies containing numerous disconformities and condensed zones and reflects deposition on the tectonically stable to slowly subsiding, clastic sediment-starved eastern cratonic platform. The high abundance of fecal pellets and planktic foraminifera and the organic richness of laminated facies throughout the study interval (3–6 wt. %) suggest periods of high productivity within the water column and intensified benthic oxygen deficiency. Underlying the study interval, a single thick bed of cross-laminated skeletal limestone contains fossils of the *Calycoceras canitaurinum* Biozone, suggesting high current energy and significant erosion/condensation of the Lincoln Limestone Member (Sageman and Johnson 1985). A typical *Inoceramus*-dominated *M. mosbyense* Biozone fauna occurs in well-laminated, calcareous to marly shales and thin skeletal limestones in the lower 7.5 m of figure 20.5, and reflects low
benthic oxygen levels and predominantly soft, muddy substrates. The remainder of the section is comprised of burrowed chalky limestones or marlstones interbedded rhythmically with laminated calcareous to marly shales, suggesting deeper water and/or decrease in siliciclastic sedimentation, and periodic development of firmer substrates and higher benthic oxygenation. These rocks contain the standard upsection biozonal sequence of the *S. gracile*, *N. juddii*, *Watinoceras* spp., and *M. nodosoides* biozones (fig. 20.5). Detailed correlation of lithostratigraphic units and biozones from BHS to PRS has been documented by Hattin (1971, 1975), Elder (1988, 1985) and Sageman (1985, 1991) and is represented in figure 20.2. Species richness/abundance plots and models of BHS bioevents are illustrated in figure 20.5 and described later.

**BHS Bioevents** BHS fossil assemblages are generally similar to those of the PRS locality. Inoceramid bivalves numerically dominate the macrofauna (commonly accounting for 98% to 100% of macrofaunal abundance) and reflect the control of bottom-water oxygen and soft substrate characteristics on colonization and benthic mortality. Yet it is commonly difficult to recognize discrete ecological bioevents in BHS laminated shales because of the highly fragmented nature of many fossils (average values of 70% fragmentation/sample are common). These features appear to reflect high current energy, winnowing, and transport of shell material, especially in the lower part of the section, as well as low sedimentation rates and extensive in-place taphonomic alteration of paleocommunities (through chemical and biological degradation of shell material). As a result, colonization/mass mortality surfaces of epifauna like those described from the PRS locality are poorly preserved. Bioevents involving distinct changes in biofacies, such as shifts to soft-bodied infaunal communities commonly associated with lithologic variations, are more readily identifiable as discrete horizons.

**Skeletal Limestone Events** Skeletal limestones in the middle part of the *M. mosbyense* Biozone at BHS are typically about 1 cm thick, wavy to ripple-laminated, and composed of *Inoceramus* prisms, foraminiferal tests, and fish debris (fig. 20.5). The beds are commonly burrowed by *Planolites*, representing brief colonization events following deposition. However, the low diversity and sparse distribution of trace fossils suggest that favorable conditions for infauna were short-lived. Shale samples immediately overlying these skeletal limestones exhibit peak values of faunal abundance and species richness for the *M. mosbyense* Biozone at BHS and are dominated by species of *Inoceramus* and associated shell island taxa (*Phelopteria*, small oysters, and encrusting barnacles), suggesting diversification bioevents due to ecological interactions.

**Shale/Limestone Cycles** Interbedded shale/limestone beds at BHS are lithologically similar to those of the PRS locality and contain many of the same types of bioevents (fig. 20.5). Most limestone beds contain complex cross-
FIGURE 20.5. Bioevents and ecozones at the Bunker Hill section (BHS) are indicated by trends in species richness and abundance data. Lithologic section and marker beds (M-Beds) are as in figure 20.2. Insets show relationship of diversification and reduction bioevent horizons (represented by D and R letters) to the time-averaged curve of species richness/abundance data and short-term ecozones. Note that different bioevents may be reflected more strongly by species richness or abundance data, as indicated by stipple versus striped pattern. Biostratigraphic zones are indicated as in figure 20.3. C/T marks the position of the Cenomanian/Turonian boundary.
cutting traces of both deposit-feeding and sediment-dwelling taxa (including Planolites, Chondrites, and Thalassinoides), representing multiple infaunal colonization events. Limestones commonly have higher overall diversity levels than shales, and the shift from infaunal or mixed infaunal/epifaunal biofacies in limestones to strictly epifaunal communities in shales is interpreted to reflect significant changes in benthic conditions, especially the position of the redox boundary. Laminated shale intervals are typically dominated by one to three species of resident epifaunal Inoceramus bivalves. In many shale samples the presence of rare shell island taxa, such as Phelopteria and small encrusting oysters, suggests limited diversification due to ecological interactions.

BHS Summary Observations of lithostratigraphic and faunal trends at the BHS locality allow the following conclusions:

1. Distal offshore carbonate-enriched lithofacies of the study interval at BHS reflect deposition on the relatively shallow, sediment-starved eastern shelf of the Western Interior Basin. Low rates of sediment supply and subsidence, and/or frequent scouring by storms resulted in significant thinning of the interval through condensation and development of disconformities. Abundant fecal pellets and planktic foraminifera, and high C\textsubscript{org} levels (4–6 wt. %) in many of the BHS mudrocks suggest high productivity. Intensification of benthic oxygen deficiency may have resulted and would explain above-average levels of preserved organic carbon, below-average levels of species richness, and the dominance of low-oxygen-tolerant Inoceramus bivalves throughout the section.

2. As a result of diminished clay input, slow burial and extensive post-mortem alteration, few discrete epifaunal colonization or mass mortality surfaces are preserved at BHS. However, the pervasive occurrence of Inoceramus bivalves, shell fragments, and scattered prisms suggests that ecological diversification and subsequent mortality bioevents were common for these low-oxygen-tolerant opportunists. Infaunal colonization bioevents are associated with deposition of skeletal limestone and chalky limestone beds, and suggest that changes in substrate conditions (grain size, firmness) resulted in improved opportunities for habitation by infaunal burrowers. The trace fossil taxa recorded in these events have been described as pioneer low-oxygen-tolerant forms (Bromley and Ekdale 1984; Savrda and Bottjer 1986). Their absence from adjoining laminated shale facies suggests strong control by substrate characteristics, bottom-water oxygen levels, and redox boundary position on the colonization of infauna. Ecological reduction bioevents (for infauna) are inferred at the sharp boundaries between burrowed and laminated strata.

3. Overall patterns of species richness and faunal abundance at BHS are similar to PRS and KFS: peaks and troughs at a scale of ±1m occur throughout the section but are particularly well developed in association
with limestone/shale cycles, suggesting regional expression of short-term D/R ecozones. D/R bundles at a scale of 3–5 m (intervals R1–D3: fig. 20.5) are also similar to those of PR5 and KPS, suggesting long-term ecozones. Cross-basin correlation of these biotic patterns is described later.

4. The dominant controlling factors for benthic communities at BHS are inferred to be bottom-water and interstitial oxygen levels and the position of the redox boundary, and substrate characteristics, such as grain size, porosity, fluidity, firmness, and organic content.

Analysis of Regional Bioevents and Ecostratigraphy

Understanding the relationships between local bioevents and regional to global trends in ecostratigraphy, biogeography, evolution, and extinction depends upon a detailed regional faunal data base. Although community composition and biofacies vary among different Western Interior depositional settings, the basic trends represented in our west/east transect (fig. 20.6) have been confirmed at more than 25 sites extending north to south from Montana to Texas, and west to east from Utah to Kansas (Elder 1987, 1989; Harries and Kauffman 1990; Sageman 1991). The resulting set of paleoecological patterns (figs. 20.6, 20.7) forms the basis of an ecostratigraphic framework for the C/T study interval. Compilation of taxonomic range data from these and other Western Interior localities (recently summarized in Kauffman et al. 1993) further provides a regional biostratigraphic standard against which published data on C/T faunas of the Gulf Coast, Europe, and other parts of the world (e.g., Stephenson 1952; Wright and Kennedy 1981; Kennedy and Cobban 1991; Nishida et al. 1992) can be compared. Thus biogeographic bioevents and origination/extinction bioevents can be identified and analyzed within the regional ecostratigraphic framework. Figure 20.7 summarizes these data.

Short-Term Ecozones Individual peaks in species richness/abundance data on a ±1-m scale occur throughout the west/east transect of the basin and suggest short-term ecozones (fig. 20.6). Many of these features are associated with lithostratigraphic units (e.g., parasequences, shale/limestone bedding couples), which have been physically correlated using HIRE5 methods (fig. 20.2). For example, detailed analysis of the D2 interval by Elder et al. (1994) resulted in correlation of six such units from Utah to Kansas (FS2a–FS7 = LS1–LS6: fig. 20.2), suggesting a relationship between nearshore parasequence development and the deposition of shale/limestone cycles in the basin. Simple correlation of associated peaks in species richness and abundance (queried lines in fig. 20.6) is problematic, however, because short-term maxima and minima in species richness/abundance of shelly molluscan faunas are not consistently correlative for every bedding couplet across the transect. Peak abundance values at nearshore to proximal offshore sites (such as KPS) commonly occur just below or at a flooding surface bed and represent the effects of shallowing and community
Figure 20.6. Correlation of species richness and abundance data across west/east transect of the Western Interior Basin illustrates ecozones. The cross section is hung on the base of the S. gracile Biozone, which coincides with the LSI marker bed. A thick dashed line and C/T label mark the position of the Cenomanian/Turonian boundary, and a bracket shows the mass extinction interval. Selected lithostratigraphic correlations (thin dashed lines) are shown to illustrate the relative isochronity of ecozone boundaries (compare with fig. 20.1). Long-term ecozones are defined at right, and possible correlations for short-term ecozones are suggested for an interval including the upper Hartland Shale and lower Bridge Creek Limestone Members. Vertical scale varies from west to east (KPS = 43 m, PRS = 26 m, BHS = 16 m).
expansion during progradation combined with sediment cutoff and condensation during the subsequent transgression. In some cases the most closely correlative abundance peaks at offshore sites (such as PRS) occur in shales that are actually stratigraphically higher than the flooding event, whereas the subjacent limestone bed, which is physically traceable to the nearshore flooding surface (Elder et al. 1994), can be relatively low in species richness and abundance of shelly macrofossils. Furthermore, the abundance peak in offshore shale facies is typically dominated by a single faunal group (inoceramid bivalves), and likely reflects opportunistic colonization of muddy substrates under low-oxygen conditions, not improved benthic habitats as indicated by the nearshore trends. Thus short-term faunal abundance peaks that appear closely correlative may reflect disparate local causes and temporally distinct events. Consideration of biofacies data (as represented in fig. 20.1) confirmed that, in fact, relative diversification characterizes the limestones in offshore bedding couplets. Because biofacies integrate body and trace fossil taxa, extent of bioturbation, changes in life habit and trophic structure, as well as community diversity and abundance, they normalize for changes in faunal abundance (or species richness) that are restricted to single genera or families of opportunistic taxa. (Such changes commonly reflect intracomunity competition or niche partitioning, rather than widespread environmental fluctuations.) Short-term ecozones are plotted in figure 20.7 based on a combination of species richness/abundance data and biofacies interpretations (e.g., fig. 8 in Sageman et al. 1991), and result in the correlation of short-term diversification ecozones to limestones and reduction ecozones to shales in offshore facies.

Shale/limestone cycles in the Western Interior Basin have long been interpreted to reflect Milankovitch climatic cyclicity (e.g., Gilbert 1895), and models for their origin are numerous (e.g., Arthur et al. 1985a; Barron et al. 1985; Eicher and Diner 1985; Fischer et al. 1985; Arthur and Dean 1991; Glancy et al. 1993; Pratt et al. 1993). Short-term ecozones within shale/limestone intervals represent a record of the biotic changes associated with these cycles and provide supporting evidence for a link between climate change, sedimentation, and paleoceanography. In Northern Hemisphere climate-model simulations of a warm, ice-free mid-Cretaceous world, one result of orbitally induced variations in solar insolation was variation in patterns of precipitation, expressed as periodic intensification of seasonal storm tracks across the Western Interior region (Barron et al. 1985; Glancy et al. 1993).

During hypothesized “wet” intervals, high freshwater runoff would enhance sediment delivery, stimulating progradation of the shoreface and deposition of mud in the basin, as well as intensify stratification between surface and deeper water masses by increasing density (mainly salinity) contrasts. Reduction intervals dominated by low-oxygen-tolerant inoceramids support this interpretation by indicating soft, muddy substrates and decreased benthic oxygen levels. During “dry” intervals the effect of decreased sediment delivery to the strandline and continuing second-order tectono-eustatic sea-level rise (Kauffman 1977)
would be rapid transgression, resulting in a cutoff of siliciclastic sediment to the basin. In addition, normalization of salinity and/or increase in temperature of surface waters could simultaneously enhance primary productivity (see Eicher and Diner 1985 for alternate view); together these factors would result in limestone deposition. Whereas the breakdown of density stratification would allow greater mixing and potential for benthic oxygenation, decrease in clay sedimentation, concentration of bioclastic material, and the early cementation of carbonate-rich sediments would result in firmer substrates; in both cases increased infaunal diversity would result. Diversification intervals, characterized by abundant deposit-feeding and sediment-dwelling ichnofauna, and/or increased diversity and abundance of other taxa support both sedimentologic and oceanographic predictions. As in the bioevent examples described earlier, the dominant controlling factors for short-term ecozones are inferred to be benthic oxygen levels and substrate characteristics.

**Long-Term Ecozones** In addition to short-term fluctuations in species richness and abundance, “bundles” in species richness/abundance data comprising long-term diversification or reduction zones (long-term ecozones R1–D3: fig. 20.6, 20.7) can be traced across the Western Interior Basin. Relative to biostratigraphic boundaries and bentonite marker beds, the boundaries of these long-term ecozones appear isochronous or nearly so throughout the transect, and thus themselves comprise important bioevent horizons. Yet the characteristics of these intervals vary somewhat from section to section, reflecting the influence of local environments and onshore/offshore environmental gradients. For example, at KPS high species richness and abundance values are found in some intervals (e.g., R2), which are characterized by significantly reduced community development at sites further offshore. The R2 interval coincides with the period of initial transgression into the KPS area, and both lithologic and faunal data

**Figure 20.7.** Using FRAS as a Western Interior standard section, a summary of ecostratigraphic data for the Cenomanian/Turonian study interval is shown. Ecological bioevents ($D_{ec}$ and $R_{ec}$) and short- and long-term diversification (D) or reduction (R) ecozones are replotted from figures 20.3–20.6. (The lengths of $D_{ec}$ and $R_{ec}$ bioevent lines are intended to provide a qualitative reflection of overall species richness/abundance trends and are not scaled.) Short-term ecozones are based on figure 20.6 and data from Elder (1989) and Sageman et al. (1991). In the ecozone columns, solid patterns with letters reflect the ecozones examined in this study; the remaining shaded intervals represent additional short-term ecozones suggested by diversity/abundance data. The stratigraphic positions of biogeographic bioevents are indicated, but $D_{bg}$ and $R_{bg}$ columns are left unscaled as biogeographic analyses of the study interval are still preliminary. (See the text for a discussion of examples.) Origination and extinction data are from Elder (1989), and the position of the OAE II interval is based on the Pratt and Threlkeld (1984) Western Interior $\delta^{13}C$ excursion (fig. 20.1). The relative sea-level curve is based on analysis of transgressive/regressive facies tracts along the western margin of the seaway and is modified from Sageman (1985, 1991) and Elder (1991).
reflect dominance of an estuarine mouth or lower bay community at KPS. The area was too shallow an environment to register the effects of basinal oxygen deficiency. Just below the LS1 datum, however, about a meter of laminated, organic-rich facies is characterized by species richness/abundance values more like those of offshore samples (fig. 20.6), reflecting deepening and the western onlap of the R2 ecozone.

Similarly, species richness and abundance characteristics at BHS reflect regional variations in the ecological response to environmental fluctuations (fig. 20.6). Ecozones R1 and R3 show relatively high abundance values, with maxima similar to those of diversification intervals. Yet consideration of biofacies data reveals that these high values are solely attributable to a single family of taxa, the Inoceramidae, which were extremely opportunistic, low-oxygen-tolerant colonizers that thrived in the carbonate-rich, muddy substrates of the basin’s eastern margin. Thus at BHS, diversity trends and knowledge of biofacies provide important constraints on understanding paleoecological data.

The cross-basin correlation in figure 20.6 reflects several regional trends, such as thinning of the entire section from west to east (long-term ecozones grade from 10 to 3 m in thickness), and development of condensed zones/disconformities at certain horizons (truncation of upper R2 ecozone and condensation of basal D2 ecozone at BHS). Overall, however, long-term diversification and diversity reduction ecozones maintain a consistent character throughout the transect. Reduction ecozones (especially R1 and R2) are dominated by well-laminated, organic-rich shales, low faunal diversity and abundance, and inequitable inoceramid-dominated biofacies. Despite the presence of burrowed limestone beds in ecozone R3 (reflecting overprint of short-term carbonate cycles), levels of burrowing are generally lower, and shales have higher percentages of inoceramid bivalves and higher levels of preserved Corg as compared with shales of ecozones D2 and D3. These factors suggest that oxygen deficiency, which developed particularly during deposition of the shale beds, was more intense during ecozone R3 than during the adjoining D2 and D3 intervals. In contrast, diversification intervals represent overall improvement in benthic oxygenation and substrate habitability, as indicated by increased species richness and abundance, and appearance of relatively diverse infaunal and mixed infaunal/epifaunal biofacies reflecting greater trophic complexity and community equitability. These changes are commonly associated with deposition of coarser-grained and/or more calcareous facies, reflecting the importance of substrate and sediment/water interface conditions on patterns of colonization, and underscoring the linkage between sedimentologic and paleoceanographic controls on benthic ecology.

The correspondence between long-term ecozones and a relative sea-level curve developed from analysis of transgressive/regressive patterns in nearshore facies of the study interval (fig. 20.7) suggests that sea level fluctuations had a secular influence on benthic communities. Diversification is associated with evidence of shallowing and/or rapid transgression at or near the base of each
long-term ecozone (D1, D2, D3). It is suggested that relative shallowing initiates diversification in the basin, primarily through the impact of storms on stratification and the mixing of deep, oxygen-deficient water masses. Diversification persists as relative deepening begins, enhanced by the development of firmer bioclastic substrates in offshore areas, which result from cutoff of siliciclastic sediment and accumulation of bioclastic material during shoreline transgression (e.g., skeletal limestones in the D1 ecozone). As deepening proceeds, however, the eventual reestablishment and/or intensification of stratification results in a return to unfavorable conditions.

Because these fluctuations, which probably represent no more than 10–50 m of relative sea-level rise and fall, occur on a background of progressively rising sea level in the basin, the character of long-term ecozones changes upsection. Whereas the transgressive event associated with the D1 interval resulted in deposition of skeletal limestones in offshore areas, suggesting largely condensation, a similar event at the base of ecozone D2 initiated a significant increase in carbonate production and widespread pelagic limestone deposition, suggesting normal marine circulation and influence of warmer southern (Tethyan) water masses. Apparently, the establishment of open marine circulation and relatively rapid immigration of southern water masses, and/or other oceanographic factors during ecozone D2 were sufficient to dampen the onset of stratification as deepening continued (although the $\delta^{13}$C record suggests that intensification of oxygen deficiency and burial of $C_{\text{org}}$ began in areas outside the Western Interior at this time), and ecozone D2 persists in the central basin through another apparent shallowing cycle (fig. 20.7). During the subsequent deepening pulse, however, the onset of ecozone R3 reflects a return to oxygen-deficient conditions, either through reestablishment or intensification of stratification, and/or expansion and incursion of the oceanic oxygen minimum zone, as suggested by numerous authors (e.g., Arthur et al. 1987; Leckie 1985; Leckie et al. 1991). The next shallowing/deepening cycle corresponds with the cessation of OAE II and the onset of diversification in ecozone D3 (fig. 20.7).

**Biogeographic Bioevents** Support for the interpretation of eustatic changes associated with long-term ecozones is found in biogeographic data. The extent to which diversification or diversity reduction processes result from changes in the biogeographic ranges of taxa, either by immigration or failure to reestablish colonization in previously occupied habitat, reflect changes in migration corridors, or restriction of range resulting from regionally unfavorable conditions, such as oxygen deficiency. Biogeographic events are discernible through comparison of detailed range data within and outside the basin under study. Faunal studies of Cenomanian/Turonian strata in the Texas Gulf Coast (e.g., Stephenson and Reeside 1938; Moreman 1942; Stephenson 1952; Sohl 1967, 1971; Kaufman 1984a; Elder 1987) as well as in England, Germany, and Japan (e.g., Jefferies 1961, 1963; Dhondt 1971; Wright and Kennedy 1981; Kennedy and Cobban 1991; Matsumoto et al. 1991; Nishida et al. 1992) provide a preliminary
comparative data base with which biogeographic events can be assessed for selected Western Interior taxa.

Within the study interval, eurytopic taxa whose stratigraphic ranges in the Western Interior are distinct from those of other areas provide examples of immigration and biogeographic reduction bioevents. For example, *Inoceramus ginterensis* Pergament has been documented in Middle Cenomanian strata in Japan (Matsumoto et al. 1991) but does not occur in the Western Interior until the Late Cenomanian Hartland Shale Member, suggesting an immigration event. Similarly, the ammonite *Calycoceras naviculare* (Mantell) has been documented in beds underlying the *Metoicoceras geslinianum* Biozone in Europe but does not occur until the base of the *Sciponoceras gracile* Biozone in the Western Interior, which is regarded as time equivalent with the *M. geslinianum* Biozone (Kennedy and Cobban 1991). In the case of the pectinid bivalve *Entolium membranaceum* (Nilsson), the opposite pattern is observed. The range of *E. membranaceum* terminates at the top of the *S. gracile* Biozone in the Western Interior Basin but is known to extend into the Maastrichtian in Europe (Dhondt 1971). Similarly, the gastropod *"Cerithiopsis sohli"* Kauffman (name in manuscript), which is present only in the Turonian interval of the Texas Gulf Coast, disappears in the Late Cenomanian *N. juddii* Biozone in the Western Interior Basin.

In each of these cases changes in the biogeographic range of taxa coincide generally with long-term ecozone boundaries. Although the preceding events constitute only a few examples for which accurate data were available, they suggest biogeographic bioevents at the horizons indicated in figure 20.7. Four immigration events (D_\text{bg}\text{; fig. 20.7}) coincide with the onset of long-term diversification ecozones (especially D2 and D3) and probably resulted from a combination of improved benthic conditions due to relative shallowing, and faunal influx associated with subsequent deepening and mixing of northern and southern water masses. Reduction in biogeographic range (R_\text{bg}\text{; fig. 20.7}) is correlated with onset of long-term reduction ecozones (fig. 20.7) and is consistent with the interpretation of intensified regional oxygen deficiency at these times. Thus the dominant controlling factors for biogeographic bioevents were probably changes in basin morphology (size, depth, and water mass inflow/outflow patterns) due to relative sea-level fluctuations, and concomitant changes in the salinity and temperature of surface waters and the oxygen content of deeper water masses in the Western Interior sea.

*Evolution/Extinction Bioevents* The Cenomanian/Turonian boundary interval contains one of the Phanerozoic mass extinctions described by Raup and Sepkoski (1982), and its macrofaunal extinction patterns have been studied extensively (Kauffman 1984b, 1986, 1988; Elder 1985, 1987, 1989). Biostratigraphic range data composited from 18 Western Interior localities by Elder (1989) indicate that 51% of the molluscan taxa documented within the Late Cenomanian (of a total of 84 species) disappear just below or at the C/T boundary. Ammonites and bivalves account for 85% of the species-level extinctions,
and most of these are cosmopolitan taxa (Elder 1989). The mass extinction is expressed as a series of discrete horizons at which taxonomic ranges terminate (reduction bioevents) beginning in the *Sciponoceras gracile* Biozone and extending into the *Watinoceras* Biozone. Elder (1989) numbered the most pervasive extinction horizons 1–6 ($D_{ex}$ bioevents: fig. 20.7). Each extinction bioevent is characterized by loss of diverse molluscan taxa, with progressive loss of shallower-dwelling species and more eurytopic species upsection. The extinctions reach a peak in the core of the OAE II interval (greatest species loss at extinction bioevent 3: fig. 20.7), which also coincides with the onset of reduction ecozone R3. Species loss declines in the overlying interval, with the exception of Early Turonian extinction bioevent 6, which is associated with rapid turnover of surviving and newly radiating biotas following the major extinction episode (Harries and Kauffman 1990).

The study interval is also characterized by a number of origination bioevents in which new taxa appear within narrow stratigraphic horizons ($D_{oe}$ bioevents: fig. 20.7). These events occur dominantly at the base of or within diversification intervals. Speciation events occur at the base of interval D2, with the appearance of the diverse *S. gracile* fauna, and in the Lower Turonian *Watinoceras* Biozone and interval D3, with the first occurrences of *Mytiloides* species (*Inoceramidae*) and various new ammonites representing the recovery following the C/T mass extinction episode (Elder 1989, 1991; Harries and Kauffman 1990; Harries 1991). Trends in origination and extinction thus generally appear to follow the pattern of other bioevents: Diversification is greatest during the shallowest phases of inferred short-term relative sea-level fluctuations, when benthic oxygen levels and conditions for habitation were enhanced, and diversity reduction is highest during short-term deeper phases, when oxygen deficiency was presumably most extreme.

**Discussion: Comparison of Local, Regional, and Global Events**

This study defines a hierarchy of ecostratigraphic units based on the recognition of events ranging from local and/or geologically instantaneous to global and/or temporally long-ranging. The interpretation of events depends on the integration of detailed sedimentological, geochemical, and paleobiological data and the development of a basin-wide, high-resolution event stratigraphic framework. Species richness and faunal abundance data form the basis for ecostratigraphic analysis and are augmented by data on taphonomy, trophic complexity, community equitability, degree of bioturbation, and other factors incorporated into interpretations of resident and event biofacies. These data are correlated across a representative transect of the Western Interior Basin for an interval of Late Cenomanian/Early Turonian strata and are compared with similar but less detailed data from time-equivalent sequences of the Gulf Coast, Europe, and Asia, making possible recognition of local, regional, and global events.
The results of this study suggest that

1. Paleobiological data collected within a high-resolution chronstratigraphic framework from C/T strata of the Western Interior Basin can be used to define a gradient of relative "ecosystem well-being" with definitive endpoints (no living community vs. taxonomically and trophically diverse communities).

2. Paleontological event horizons, or thicker portions of a stratigraphic sequence, can be evaluated in terms of such a gradient and interpreted to represent relative diversification or relative diversity reduction. This study recognized horizons and very thin intervals (bioevents) and two scales of thicker stratigraphic intervals (short- and long-term ecozones).

3. Bioevents and ecozones are the products of colonization, immigration and speciation events (producing diversification), and mass mortality, emigration, and extinction events (producing diversity reduction) that occurred on local, regional, and global scales.

4. Western Interior diversification and diversity reduction events are similar or identical to the ecostratigraphic features (i.e., epiboles and outages) discussed by Brett and Baird (paper 10 in this volume).

5. Based on consideration of modern analogs as well as supporting evidence from sedimentologic and geochemical data, patterns of diversification and diversity reduction can be interpreted in terms of primary physical, chemical, and biological forcing mechanisms, resulting in an integrated reconstruction of paleoenvironments, paleocommunity dynamics, and basin history.

From the Cenomanian/Turonian interval described herein, we have illustrated local and regional colonization and mass mortality bioevents representing from months to years of geologic time, and longer-term sequences of colonization and diversity reduction that are correlative throughout the cross-basin transect, defining ecostratigraphic intervals or ecozones. These ecozones reflect repetitive environmental fluctuations corresponding to inferred Milankovitch climatic cycles (short-term ecozones) as well as longer-term changes in benthic environments that correspond to a record of relative sea-level fluctuations (long-term ecozones). Diversification zones characterize inferred dry-climate phases and the shallowest parts of relative sea-level cycles (including late regression and early transgression), and diversity reduction intervals characterize inferred wet-climate phases and the deepest parts of eustatic cycles (late transgression and early regression). The correspondence between positions and magnitudes of regional biogeographic and worldwide evolution/extinction bioevents and long-term ecozones suggests a relationship between species-level and community-level evolution and/or larval dispersal mechanisms, and changes in regional to global oceanographic factors related primarily to relative sea level.

At all levels of the ecostratigraphic hierarchy the data suggest that benthic communities of the Western Interior Basin were predominantly, if not entirely, controlled by changes in bottom-water oxygen levels and, to a lesser extent,
substrate character; these were the parameters most strongly affected by changes in climate and sea level within the basin. From short-term events representing colonization following storm-induced mixing of a stratified water column in the Hartland Shale Member to widespread diversification reflecting an increase in origination and immigration rates at the base of the Bridge Creek Member (related to a transgressive pulse, increase in carbonate production, and full development of an open marine, well-mixed water column), to the progressive extinction of taxa during a period of global oxygen depletion and organic matter burial, and to the ultimate incursion of oceanic oxygen minimum zone waters in the basin near the C/T boundary, events at all scales of the hierarchy have similar characteristics.

We believe these paleoecological relationships are a direct consequence of the prevailing environmental regime of the mid-Cretaceous world. This was a time of peak Mesozoic global warming and “Greenhouse” conditions (Fischer 1982; Fischer and Arthur 1977), the causes of which have been linked tentatively to increased tectonic and volcanic activity (Fischer and Arthur 1977; Kauffman 1977, 1984a, 1985) and to elevated levels of atmospheric CO₂ (Arthur et al. 1985a, 1985b; Berner 1990; Budyko et al. 1987). The period was characterized by significant reduction in thermal gradients from pole to equator and from the surface to the bottom of world oceans, by a greatly expanded tropics, by apparent lack of permanent polar ice caps, by a global peak highstand of sea level for the Mesozoic, and by extensive development of epicontinental seas marginal to and within cratonic areas (Barron 1983; Barron and Washington 1982; Frakes 1979; Hancock and Kauffman 1979; Haq et al. 1987; Hay 1988; Kauffman 1984a). Oxygen deficiency may have been a prevalent condition in many such basins during the Mesozoic, for a variety of reasons, including basin size, depth, morphology, and connection to oceans. But oxygen deficiency became globally pervasive during the Late Cenomanian sea-level rise event, and appears to have been especially intense in conjunction with the burial of large volumes of organic matter near the C/T boundary (Arthur et al. 1987). Arthur et al. (1987) hypothesized that sea-level change was the driving force for intensified oxygen depletion during the C/T event. Because of flooding of arid, low-latitude regions and the formation of warm, saline bottom waters, large-scale displacement of deep, nutrient-rich oceanic water masses would have greatly stimulated productivity, causing intensification and expansion of midwater oxygen minimum zones.

Under such conditions the most successful communities consisted of organisms that were highly tolerant, specially adapted opportunistic taxa with rapid dispersal mechanisms and extremely wide ranges. These taxa (dominantly molluscs) colonized whenever and wherever possible in a largely physically and chemically controlled marine realm and form the bulk of preserved C/T faunas. The prevalence of ecological bioevents in the study interval (Dₚₑ and Rₚₑ: fig. 20.7) indicates that C/T faunal history was extremely dynamic in the short term, with a near-constant succession of colonization and mortality events in the
benthic realm. As a result, even subtle allocyclic changes in climate and sea level that affected physical/chemical conditions over large areas were recorded consistently by a highly sensitive ecosystem, resulting in a series of chronostratigraphically useful paleontological event horizons and intervals (bioevents and ecozones). The delicately balanced nature of this mid-Cretaceous ecosystem resulted in consistent local, regional, and global paleobiological responses to environmental fluctuations on short and long time scales.

Shallow-water marine environments in the postglacial Holocene world are characterized by high latitudinal temperature gradients, abundant oxygen and nutrients, and highly diverse, patchily distributed communities that are largely biologically accommodated. Under such conditions the relationship between widely distributed communities and changing environmental parameters may be far too complex to result in a consistent biological response, and a modern test of the ecostratigraphic method is difficult. But other intervals of Phanerozoic history (e.g., Silurian, Devonian) were characterized by nonglacially influenced "Greenhouse" conditions similar to those of the mid-Cretaceous. The application of high-resolution ecostratigraphy and a test of environmental sensitivity in the short- and long-term response of Silurian/Devonian communities might provide an important test of the consistency of paleobiological response in physically and chemically controlled ecosystems.

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