

Diversity and Species Abundance Patterns in Late Cenomanian Black Shale Biofacies, Western Interior, U.S.

BRADLEY B. SAGEMAN and CRAIG R. BINA

Department of Geological Sciences, Northwestern University, Evanston, IL 60201

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Questions concerning the application of established biofacies models to mid-Cretaceous black shales prompted a study of diversity characteristics in a fauna from the Late Cenomanian Hartland Shale Member, Western Interior basin. Numerical faunal data are used to assess species abundance patterns, and a new method of analyzing diversity is introduced that incorporates species richness, Shannon index, and equitability into a single plot. In addition, numerical simulations designed to emulate the sampling of species-abundance distributions are used to improve data interpretation. The study illustrates how measured diversity results from the combination of primary ecological controls and sampling effects. Proximal offshore assemblages are characterized by high diversity and log series species-abundance patterns, interpreted as truncated (incompletely sampled) log-normal distributions. Primary ecological controls include variable physical/chemical parameters, biological factors such as predation and competition, and intermediate disturbance frequency. Distal offshore assemblages are characterized by low diversity with patterns of species abundance resembling geometric series. These are interpreted as truncated log-series distributions (sampling effect) that reflect dominance of multiple opportunists, abundant resources in a dysoxic environment, and high disturbance frequency. The data are used to develop an ecological model for diversity levels in basinal black shale facies based on the interplay of recruitment, growth rate, tolerance to low oxygen and sulphide, and disturbance frequency (due to fluctuations of the redox boundary). Although certain taxa (chiefly Inoceramidae) evolved highly opportunistic life strategies to exploit basinal paleoenvironments, it was the unpredictable interaction of these four factors that determined diversity patterns. Analysis of Hartland Shale biofacies illustrates the difficulties in applying a strictly linear relationship between paleo-oxygen levels and diversity.

INTRODUCTION

For over two decades, paleobiologic research in organic carbon-rich facies, commonly interpreted to represent oxygen-deficient paleoenvironments, has been shaped by the Rhoads and Morse (1971) biofacies model. This tripartite scheme (Fig. 1) was developed based upon observations of modern oxygen-deficient environments (i.e., Black Sea, California borderland basins) in which distinct communities (biofacies) are linearly related to specific ranges of dissolved oxygen. These biofacies, and their associated oxygen values, are characterized by two end members, anaer-

obic and aerobic, separated by a dysaerobic transitional zone (Fig. 1A).

Since its publication, there have been a number of modifications or revisions suggested for the Rhoads and Morse (1971) model, recently summarized in Tyson and Pearson (1991). Illustrated in Figure 1B, these include redefinition of the dysaerobic-aerobic boundary based on recognition of shelly faunas at increasingly lower oxygen levels (e.g., Savrda et al., 1984; Thompson et al., 1985), as well as subdivision of the dysaerobic transition along linear gradients in diversity, abundance, trophic structure, and morphologic features of trace and body fossils (e.g., Savrda and Bottjer, 1986, 1987, 1991; Sageman, 1989; Sageman et al., 1991; Wignall and Hallam, 1991). The most significant modifications to the model have come recently, however, and stem from speculations concerning the temporal stability of dysoxic environments (e.g., Oschmann, 1991; Wignall, 1990; Tyson and Pearson, 1991), the relationship between disturbance frequency and adaptive characteristics such as fecundity, growth rate, and body size (e.g., Huston, 1979; Wignall, 1990), and the possibility of nonequilibrium community dynamics due to unusual scenarios of resource utilization (Etter, 1995). The application of these concepts in paleoecological studies has received comparatively little attention (Wignall, 1990; Etter, 1995) and is the focus of this investigation.

The specific questions that our study seeks to address fall into two categories. The first concerns the oxygen-diversity paradigm: (1) Is dissolved oxygen content of bottom waters the dominant controlling factor for benthic communities in organic carbon-rich facies, as Rhoads and Morse (1971)-based models imply, and is the relationship linear? (2) What role do other factors, such as substrate preference, environmental stability, adaptive strategy, competition (or its absence), growth rates, and resource utilization, play in determining the nature of ancient black shale paleocommunities and their resulting biofacies? and (3) If these paleocommunities, which are dominantly composed of now extinct taxa that arose and flourished on a greenhouse Earth, do not conform to equilibrium ecological models, how must we modify our uniformitarian view of ancient diversity patterns? What are the evolutionary-ecological implications for faunas of Paleozoic and Mesozoic (low-oxygen) epiherc seas?

The second category concerns the implications of reinterpreted diversity patterns for reconstructions of basin history: (1) If factors other than oxygen content are important for controlling paleocommunities in paleoenvironments of high organic carbon burial, how does this impact conventional interpretations of ancient oxygen deficiency? and (2) What are the implications of a reinterpreted oxygen-diversity paradigm for models of ancient water-col-

Rhoads and Morse-type Biofacies Model

BIOFACIES	A	No macrofauna; anaerobic sulfur bacteria; laminated sediments.		Predominantly soft-bodied infauna; rare shelly invertebrates; burrowed to bioturbated sediments.				Diverse shelly taxa; epifauna+infauna; bioturbated.		SWI
		Anaerobic		Dysaerobic				Aerobic		
	B	1	2	3	4	5	6	7		SWI
		No macrofauna; anaerobic sulfur bacteria; laminated sediments.		Shelly epifauna and burrowers dominant; laminated to burrowed sediments; subdivisions of dysaerobic gradient defined by trends in morphology, diversity, etc.				Diverse shelly taxa; epifauna+infauna; bioturbated.		
		Anaerobic		Exaerobic	Dysaerobic		?	Aerobic		
O₂	ANOXIC	SUBOXIC		DYSOXIC				OXIC		
(ml/l)	0	0.2		2.0						

FIGURE 1—Using standardized terminology for benthic oxygen concentrations (Tyson and Pearson, 1991), the original Rhoads and Morse (1971) biofacies model (A) is compared to recent revisions (B) in which the dysaerobic zone has been modified (see text for references). Modifications include lowering of the dysaerobic-aerobic boundary, subdivision of the dysaerobic zone, and the definition of new biofacies such as exaerobic (Savrda and Bottjer, 1986).

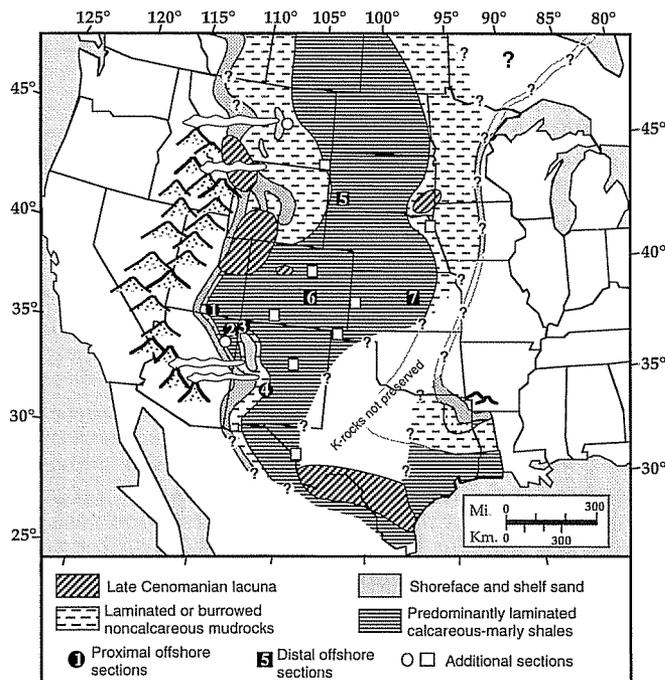


FIGURE 2—Locality map shows paleogeography and distribution of lithofacies for the Late Cenomanian *Metoicoceras mosbyense* Biozone. Proximal offshore localities of study interval are represented by circles, distal offshore localities by squares. Filled symbols with numbers represent measured sections with continuously sampled numerical faunal data. Open symbols without numbers represent additional measured sections used for correlation and supporting faunal evidence. The numbered sections are 1-NBS, 2-BMS5, 3-FCS, 4-CHS, 5-BGS, 6-PHS, and 7-BHS (locality data in Appendix A). Main sources for paleogeographic reconstruction are McNeil and Caldwell (1981), Cobban and Hook (1984), Sageman (1991), Fisher (1991), Elder and Kirkland (1994), Leckie et al. (1994), Sageman and Arthur (1994), and Roberts and Kirschbaum (1995).

umn processes (e.g., water-column circulation vs. stratification)?

In our study, molluscan-dominated fossil assemblages from Cretaceous organic carbon-rich facies of the Western Interior basin were analyzed for patterns of diversity. The sampled fossil assemblages occur in a range of facies from distal offshore organic carbon-rich shales of the Upper Cenomanian Hartland Shale Member, Greenhorn Formation (Colorado, South Dakota and Kansas), to time equivalent proximal offshore deposits (prodelta and equivalents; Danke et al., 1993) of the Tropic and Mancos Shales (Utah and Arizona; Fig. 2). Species richness and fossil abundance data from uniform samples were normalized. These data were used to calculate the Shannon diversity index and equitability index for each sample. Analysis of trends in species richness, Shannon index, and equitability of the Upper Cenomanian samples allow an evaluation of species-abundance distributions in low-oxygen paleocommunities of the Western Interior that are independent of previously established biofacies (Rhoads and Morse-type) schemes. To improve our understanding of the diversity data, we also performed some simple numerical models emulating the sampling of species-abundance distributions in benthic communities. The results of these analyses provide evidence for evaluation of the oxygen-diversity paradigm, and offer insight concerning the interpretation of water-column processes in the Western Interior basin during Late Cenomanian time.

GEOLOGICAL BACKGROUND

During the Cenomanian and Turonian, foreland basin subsidence and tectonoeustatic sea-level rise resulted in widespread marine flooding of the Western Interior U.S. (Kauffman, 1984; Fig. 2). Among the strata that accumulated in the resulting depositional basin, the Greenhorn

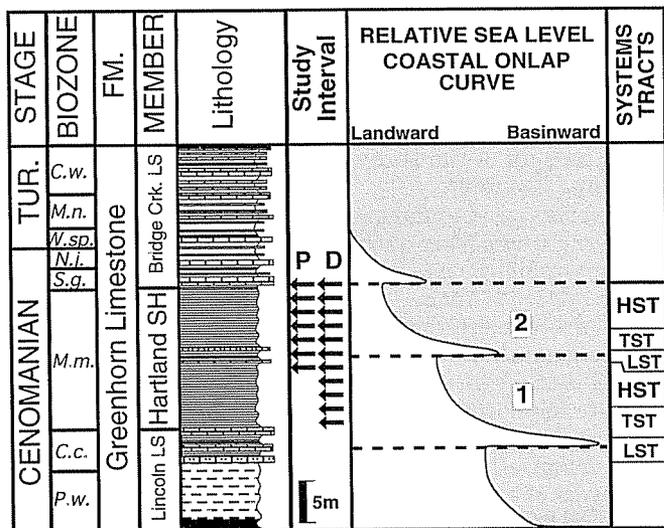


FIGURE 3—Generalized stratigraphic column for the Greenhorn Limestone, central Western Interior Basin, illustrating position of Hartland Shale Member. Study interval at distal offshore sites (D) is ~16 meters in thickness and corresponds to the *Metacoceras mosbyense* Biozone (abbreviated *M.m.*; biozonation from Cobban, 1984; Elder, 1985; Kennedy and Cobban, 1991). The study interval at proximal offshore western localities (P) includes the upper half of the *M. mosbyense* Biozone in shales and mudstones of the Tropic Shale (Utah) and Mancos Shale (Arizona and New Mexico). Approximately 50 standardized samples were collected from the study interval at each distal offshore section, and about half that number at each proximal offshore section (Fig. 2). Relative sea-level curve and systems tract designations are modified from Sageman (1991).

Formation is renowned for its organic carbon-rich shales and limestone-marlstone cycles (e.g., Pratt et al., 1985). The Hartland Shale, the middle member of the Greenhorn Formation (Fig. 3), is one of the most widespread units of organic carbon-rich strata in the basin. It corresponds to the *Metacoceras mosbyense* Biozone (Fig. 3) and is characterized by finely and evenly laminated, pyritiferous, dark calcareous shale with high levels of preserved organic carbon (3–4 wt. %) and relatively depauperate faunal assemblages (Kauffman, 1977, 1984; Sageman, 1985, 1989, 1991). In the central part of the basin, these assemblages are virtually devoid of benthic foraminifera (Eicher and Worstell, 1970; Eicher and Diner, 1985), contain only very rare burrows, and are dominated by resident epifaunal inoceramid bivalves. Although these biofacies are replaced by increasingly diverse assemblages in strata representing marginal marine environments, they virtually dominate the fine-grained (proximal to distal offshore) marine facies of the *M. mosbyense* Biozone. As a result, the Hartland Shale Member (HSM) has commonly been interpreted to record an interval of widespread and prolonged oxygen depletion in the Western Interior sea due to density stratification of the water column (Frush and Eicher, 1975; Kauffman, 1984; Sageman, 1985).

In a study of HSM stratigraphy and paleoecology, Sageman (1989, 1991) analyzed in detail seven sections spanning marginal marine to distal offshore depositional environments (Fig. 2). The results of this study document a broad spectrum of Hartland biofacies, ranging from barren, laminated, organic carbon-rich strata, through mono-

specific *Inoceramus* bivalve communities in laminated strata, to relatively diverse molluscan assemblages in highly burrowed strata. In addition, evidence of common benthic colonization and mass-mortality events are believed to represent episodes of short-term oxygenation and oxygen depletion in the basin during Hartland Shale deposition. As a result, the HSM fauna provides an ideal opportunity to test hypotheses pertaining to the dysaerobic transition.

METHODOLOGY

The HSM data set represents a total of 273 samples comprising over 23,000 specimens and 245 taxa. To produce this data set, the study interval was logged at a resolution of 1 cm at each of the 7 localities indicated in Figure 2 (filled symbols). Standardized bulk samples averaging about 0.01 m³ were collected continuously through the sections (the equivalent average decompacted sediment volume would equal about 0.07 m³ assuming a 1:7 compaction ratio). The thickness of the sampled interval was varied systematically from west to east (50 cm to 10 cm, respectively) to account for changes in sedimentation rates. These rates, which vary from 4.5 to 1.4 cm/ky respectively, were determined using biozone boundary ages interpolated between dated volcanic ash beds (Kauffman et al., 1993). An average of 14 ky for the duration of each sample was calculated from the sedimentation rates.

The collections were made in marine mudrocks that show similar levels of fossil preservation and taphonomic alteration, and the faunas are dominantly molluscan. Calcareous shell material is very well-preserved and aragonitic shells occur as molds or periostracal films. Because patterns of ammonite diversity and abundance are found to cross facies in the Greenhorn Limestone, it is believed that, despite some taphonomic loss, primary (ecological) trends in the aragonitic taxa are retained (e.g., Elder, 1989). Although bivalve shells are commonly disarticulated, corresponding valves are found close together in many cases (in rare instances “butterflies” are observed). Overall fragmentation levels are high, but in most cases the fragments are large enough to permit identification. Corrosion levels are quite low and there is no evidence of sorting or preferred orientation. Since the HSM samples represent time-averaged collections, the impact of patchy or clumped distributions on diversity estimates should be minimized.

In the laboratory, each bulk sample was carefully split along bedding planes and its fossil content recorded. These observations included taxonomic identifications and counts of all fossil material visible by eye or 10x hand lens. Body fossils from large bivalves to large ostracods were counted. These counts included both whole specimens and fragments; articulated valves and fragments that could be determined as belonging to the same individual were counted as unit occurrences. In samples for which two or more species of a genus were associated with fragments identifiable only to that genus, the fragment abundance value was added proportionally to the species abundance values. Where possible, individual burrows were counted as an estimate of soft-bodied infauna. In cases where burrows (or body fossils) were difficult to count individually because they were too numerous, an

abundance ranking system was used. These rankings were later converted to equivalent numerical values in order to calculate diversity indices (see below).

Faunal abundance data may be difficult to interpret for many taxonomic groups and paleoenvironmental settings because the relationship of such numbers to the original community can be obscured by differential taphonomic loss, introduction of exotic taxa, and faunal mixing (e.g., Dodd and Stanton, 1990). However, recent observations on the preservation potential of modern molluscan communities indicate they show the highest fidelity to original communities (Kidwell and Flessa, 1996). In addition, our taphonomic analysis indicates that losses were relatively few and more or less similar in the basinal paleoenvironments where fine-grained mudrocks accumulated. HSM taphonomic characteristics recall the "disturbed-neighborhood communities" described by Scott (1974) and would fall somewhere between taphofacies 4, 6, and 7 of Speyer and Brett's (1988) taphofacies model for Paleozoic epicontinental seas (indicating low to moderate sedimentation rates, low turbulence, and a range of possible oxygenation levels). Based on this, we assume that changes in the relative abundance of fossils in standardized samples of the Hartland Shale can be interpreted to reflect a reasonable record of relative changes in the original benthic populations.

Although species richness (S) provides an important measure of diversity trends in paleocommunities, ecologists commonly express diversity data as a measure of the relative proportion of species in a sample, for which abundance data are necessary. Such analyses moderate the effects of very rare and very abundant species on total diversity values and allow more reasonable comparisons of community characteristics among different populations and regions (or facies). Two of the most widely employed calculations of this type include the Shannon index (H') and equitability or evenness (e). The Shannon index is expressed as

$$H' = \sum (n_i/N) \ln(n_i/N),$$

where n_i is the abundance of each taxon in a sample, N is the total abundance of the sample, and \sum is performed from $i=1$ to S , with S equal to the species richness of the sample. Equitability can then be calculated as

$$e = H'/\ln S$$

(Dodd and Stanton, 1990; Magurran, 1988). Although the Shannon index incorporates a measure of evenness automatically, it can be useful to plot e separately (see below). Unlike S and e , which decrease and increase, respectively, at low abundance levels, the H' statistic is comparatively unaffected by relative sample size (Gibson and Buzas, 1973) except at very low abundances (e.g., Wignall, 1990). Samples with abundance values below a minimum level and samples with only 1 species (and thus H' and e values of 0) were omitted from the analysis.

The Shannon index is based on two assumptions: (1) individuals are randomly sampled from infinitely large populations; and (2) all species of the community are represented in the samples (Pileou, 1975). The first condition is generally valid for time-averaged fossil assemblages in marine mudstone facies. Based on the taphonomic arguments given above, we assume that the second condition is

reasonably met for a study of *relative* diversity trends, especially in fossil assemblages from slowly accumulating, well-laminated strata where soft-bodied infauna were commonly diminished or absent. A doubling of sample size was tested in some of the well-laminated facies that comprise the bulk of the study and did not appreciably alter measured diversity.

Proportional abundance indices make no assumptions about the underlying species-abundance distributions of the populations being sampled (Magurran, 1988), but they can be related to them. In general, diverse, biologically accommodated communities that exist under conditions of environmental stability ("equilibrium species") will have high H' and e values and species-abundance distributions that are log normal (Sanders, 1968; May, 1975; Hughes, 1986). In contrast, communities that exist under physically or chemically stressful conditions, and/or experience low levels of environmental stability ("opportunistic species") will have low H' and e values and species-abundance distributions that are log series or geometric series (May, 1975; Hughes, 1986). In addition to these factors, sampling effects can influence the observed distribution (Hughes, 1986). Overall, H' values range between 1 and 3.5 and rarely exceed 4.5 in natural communities (Magurran, 1988, and references therein).

DATA ANALYSIS

The data analyzed in this study include samples from localities representing a gradient of depositional environments within the HSM and time-equivalent strata. These include proximal offshore, poorly to moderately calcareous mudrocks of the western foredeep (sites 1–4, Fig. 2), distal offshore, hemipelagic calcareous mudrocks of the central basin region (sites 5 and 6), and distal offshore, chalky mudrocks of the eastern stable platform (site 7). During deposition of the HSM, fluctuations in relative sea level (Fig. 3) caused tracking of the benthic communities (cf. Brett and Baird, 1996), so that lateral gradients in biofacies also occur stratigraphically. These are mainly expressed as variations in faunal diversity and abundance in the distal offshore sites, but include major changes in community structure at more onshore localities (Sageman et al., 1996). The HSM data set includes samples representing two cycles of relative sea-level change (Fig. 3). Note that definitive lowstand deposits and sequence boundaries are poorly developed in the HSM due to: (1) active subsidence of the foreland basin; (2) a net deepening trend during deposition; and (3) the small scale of the mid-HSM relative sea-level fall event (Sageman, 1991, 1996). However, Sageman (1996) interpreted skeletal limestone beds of the middle Hartland Shale to represent a relative lowstand.

Hartland Shale Member Biofacies

Samples of the HSM analyzed in this study range from barren, well-laminated shales to bioturbated mudstones containing taxonomically and trophically diverse fossil assemblages. Molluscan taxa dominate throughout the member and include bivalves, cephalopods, and gastropods, in order of decreasing relative importance. Suspension-feeding inoceramid bivalves (e.g., *Inoceramus pictus*,

I. ginterensis, etc.) comprise the bulk of faunal abundance, especially in distal offshore samples. Additional bivalve taxa include members of the Pectinidae, Ostreidae, and Pteriidae, which may colonize as epibionts on the inoceramids or occur as free-living epifauna (Sageman, 1989; Sageman et al., 1991). Ammonites are also common in distal offshore biofacies of the Hartland Shale. Most of these ammonite taxa were interpreted by Kirkland (1990) and Batt (1993) to represent nektobenthonic scavenger-predators. They are included in the analysis of diversity based on the assumption that they reflect environmental conditions in the water column, and that they may be trophically dependent (in part) on the benthic community.

In proximal offshore regions, inoceramids also occur in laminated, relatively organic carbon-rich facies (i.e., transgressive and early highstand deposits), but decrease in dominance. During late highstand intervals, and in the sections closest to shore, other taxonomic, trophic, and life-habit groups appear. These include infaunal deposit- and suspension-feeding bivalves (e.g., nuculids, corbulids), grazing gastropods, scaphopods, and echinoids, suspension-feeding solitary corals and annelids (*Serpula*), acrothoracic barnacles (*Scapellum*), scavenging crustaceans, and even boring sponges (*Clione*), resulting in high-diversity assemblages ($S_{\max} = 46$). Ichnofaunas documented in the HSM range from microbioturbation (Pratt, 1984) in the predominantly laminated distal offshore facies to diverse fodinichnia, pascichnia, and domichnia in proximal offshore silty mudrocks. Common ichnotaxa include *Planolites*, *Chondrites*, *Teichichnus*, *Zoophycos*, and *Thalassinoides*.

In previous analyses of the Hartland Shale data set, taxonomic composition, life habit, trophic strategy, dominance and diversity, and relative species diversity and abundance were used to assign biofacies categories and subdivisions to the samples (Sageman, 1989, 1991; Sageman et al., 1991; Arthur and Sageman, 1994; Fig. 4). The biofacies were categorized according to dominantly infaunal (deposit feeders, suspension feeders, or mixed) and dominantly epifaunal (mostly suspension feeders; some grazers, scavengers, and carnivores) end members (Fig. 4). The samples showed a continuous gradient from no metazoan taxa, to monospecific or paucispecific infaunal or epifaunal biofacies, to diverse mixed infaunal-epifaunal assemblages. Seven subdivisions were identified, largely based on trophic structure (Sageman, 1989; Sageman et al., 1991), and the standard Rhoads and Morse (1971) conventions were applied (anaerobic biofacies, aerobic biofacies, and five intermediate or dysaerobic biofacies). The assignment of a given biofacies to the dysaerobic category was based mainly on analogy, and placement of the boundaries was necessarily somewhat subjective.

Although the HSM biofacies model interprets a linear relationship between benthic diversity and oxygenation, as did similar models developed independently from studies of Jurassic to Miocene organic carbon-rich facies (i.e., Savrda et al., 1991; Wignall and Hallam, 1991), it specifically emphasized several additional factors: (1) the definition of distinct infaunal and epifaunal biofacies; (2) the dominance of epifaunal biofacies attributed to a boundary condition (physical, chemical, or biological) at the sediment-water interface; and (3) the dominance of relatively short-term colonization and mortality events.

In Figures 5 through 7, values of species richness (S), Shannon index (H') and equitability (e) calculated for each of the HSM samples are presented in a series of cross plots that represent a novel method for illustrating fossil-diversity data. Plots of H' vs. S and e vs. S (Figs. 5 and 6) show the variance in H' and e statistics for a given S value, and reflect variations in the relative abundance of species among samples with the same S value. By plotting e directly against H' (Fig. 7), these characteristics can be illustrated in one plot. In addition, the rate of change in e relative to H' for samples of a given S value, and for samples representing a range of S values, is depicted. In the following sections we develop the H' - e crossplot method.

Species Richness Crossplots

In Figure 5, H' vs. S and e vs. S plots for samples from the three distal offshore sections are shown (sites 5, 6, and 7 in Fig. 2). These sections represent the central basin and eastern platform where water depth, environmental stability, and oxygen deficiency are assumed to have been greatest. Here the sections include two cycles of relative sea-level change with a sea-level fall event corresponding to the middle HSM (Fig. 3). The samples contain monospecific to low-diversity fossil assemblages dominated by taxa that have been interpreted as specially adapted, low oxygen-tolerant species (Sageman et al., 1991). The plots in Figure 5 show the following trends: (1) overall, S values in distal offshore samples (Fig. 5) range from 1 to 11 spp. (for comparison, the highest S value in the proximal offshore samples is 46 spp.); (2) two groups of samples are defined in the distal offshore data (distinguished by shaded areas in Figs. 5A and 5B). Samples with S values < 6 spp. exhibit a range of H' values with an upper limit of 1.38 (Fig. 5A). For the categories from S = 2 to 6 spp., the average H' value doubles (from 0.41 to 0.83), as does the maximum H' value, suggesting a trend of increasing H' . However, there is much variance in the values of H' for a given S value; (3) samples with S > 6 were less common in the distal offshore data, and had average H' values significantly higher than the samples with S < 6 (ranging from 1.04 to 2.08). Unlike the samples with S < 6, these samples showed no cases with an H' value less than 1.04; (4) the plot in Figure 5B shows a wide range in e values (0.03 to 1.0) for samples with 2 to 6 spp., including many with e approaching 1.0. Samples with S > 6 have no e values close to 1.0, but also have none below 0.5; (5) unlike the samples with S < 6, there is an apparent trend of increasing e with increasing S for samples with S > 6 in the distal offshore data set.

In Figure 6, H' vs. S and e vs. S plots for the four proximal offshore localities are shown. These sites represent a gradient of increasingly shallower depositional environments, and the sampled interval ranges from one lowstand to the next in a retrogradational (overall deepening) sequence (cycle 2 in Fig. 3). The samples include fossil assemblages with characteristics similar to those of the distal offshore sections, but also show evidence of major changes in community structure, trophic complexity, and diversity. Examination of these plots show that the maximum values for S and H' are much greater in proximal offshore sections (S = 46; $H' = 2.91$), reflecting samples with significantly higher diversity levels. Four main groups of samples can be defined in the plots. Group 1 is a set of low-

Rhoads and Morse-type Biofacies Model for Greenhorn Formation

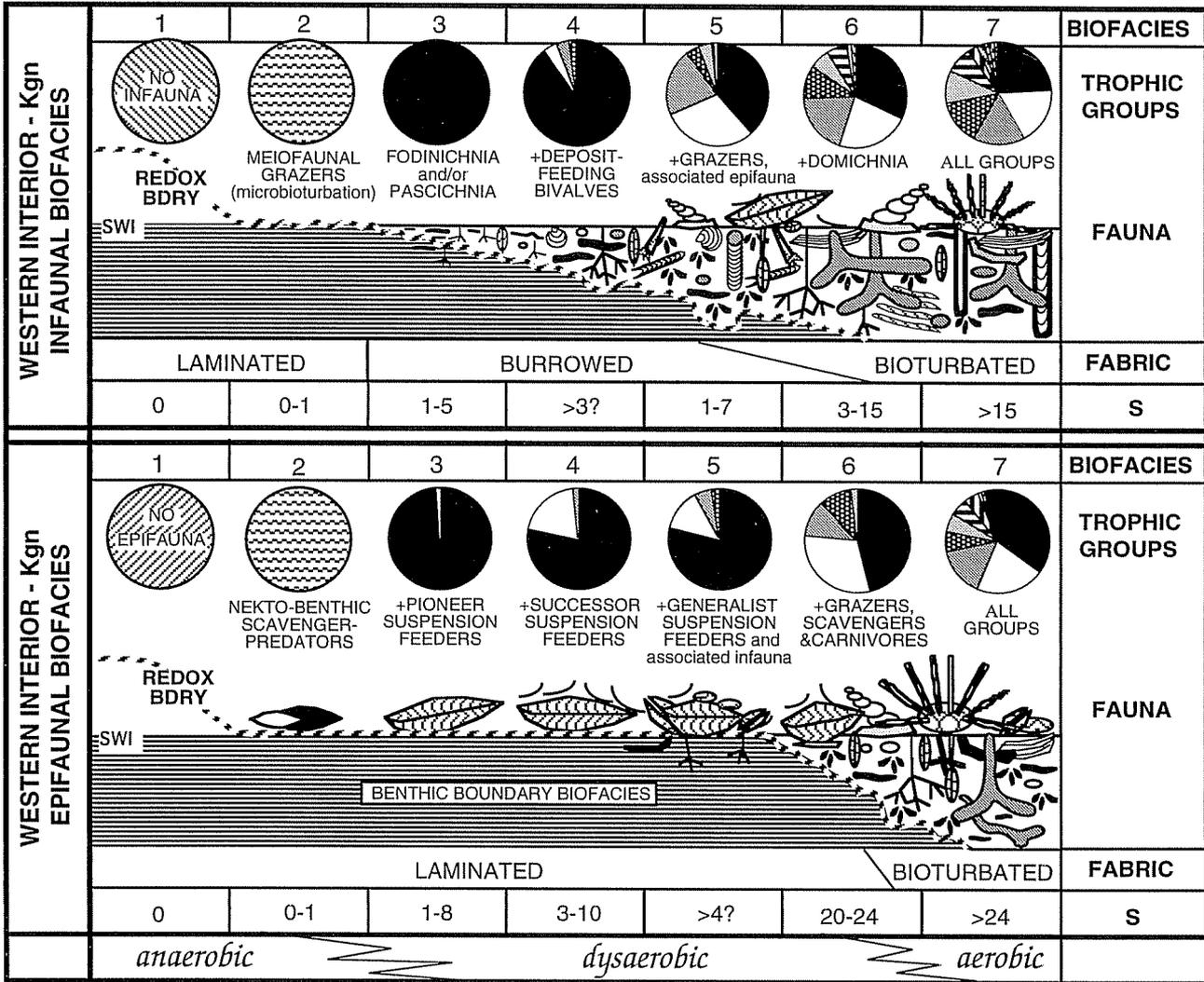


FIGURE 4—Biofacies model developed for Greenhorn Formation, Western Interior Basin, based mainly on HSM data (Sageman, 1989, 1991). The model defines biofacies first by life habit, establishing dominantly infaunal and dominantly epifaunal end members. Seven subdivisions of each end member were then defined based on taxonomic composition and trophic characteristics. Using these subdivisions, HSM samples were categorized and average values for species richness and percent trophic type tabulated. The pie charts thus represent averaged trophic diversity for each biofacies level, and they are additive. Species richness and trophic complexity increase more or less linearly, and this was interpreted to reflect a linear increase in paleo-oxygen levels.

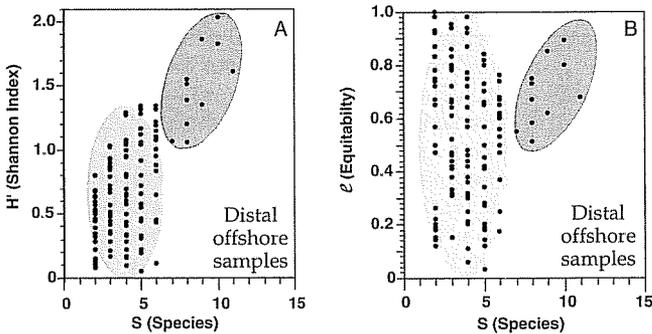


FIGURE 5—Crossplots of (A) species richness (S) vs. Shannon index (H') and (B) species richness (S) vs. equitability (e) for distal offshore sites. Two groups of data points described in the text are illustrated with shading.

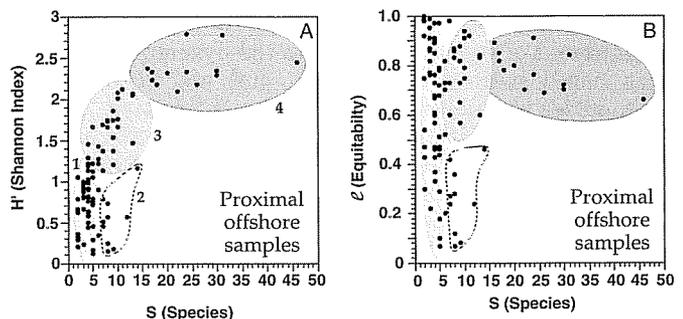


FIGURE 6—Crossplots of (A) species richness (S) vs. Shannon index (H') and (B) species richness (S) vs. equitability (e) for proximal offshore samples. Four groups of data points described in the text are illustrated with shading.

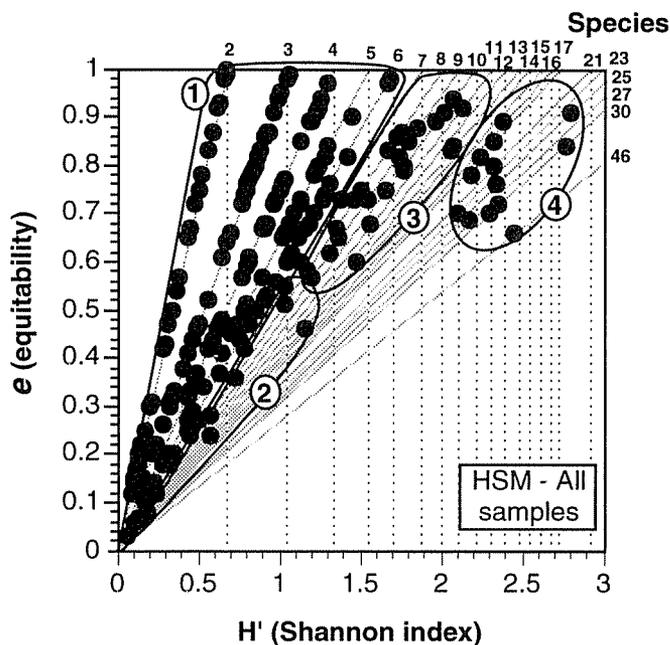


FIGURE 7—Crossplots of Shannon index (H') vs. equitability (e) for all HSM samples. Lines corresponding to species values between $S=2$ and $S=46$ are shown. The four groups of samples discussed in the text are designated.

diversity samples with characteristics similar to those of distal offshore samples with $S < 6$ (relatively low S and H' values, a trend of increasing H' with increasing S [i.e., steady increase in H'_{max} for successive S value], and a very wide range of e values among the samples). Unlike the distal offshore samples, however, values of H' and e are not as dense or continuous in the low S range, and the highest H' value is 2.36 instead of 1.39. Group 2 samples (dashed outline, Fig. 6) are characterized by moderate S values (between 6 and 15 spp.), but they are highly inequitable with e values ranging from 0.5 to less than 0.1, and corresponding H' values less than 1.04. Group 3 also includes samples with moderate S (6 to 15 spp.), but H' values range from 1.38 to 2.08, and e values are generally high (> 0.5). Group 4 samples have the highest diversity, defined by S values from 15 to 46 spp., H' values that level off between about 2.08 and 2.91 (for a given change in S there is now relatively little change in H'), and e values between 0.6 and 0.9.

H' vs. e Crossplot

By crossplotting e against H' directly, many of the features illustrated in Figures 5 and 6 can be redefined. In this type of plot (Fig. 7), samples of constant S value plot as straight lines (of slope $1/\ln S$) that intersect the $e = 1.0$ line at $H' = \ln S$. At the lowest S value for which e values are defined ($S = 2$), it can be seen that, for a given change in H' , there is a correspondingly large change in e . As the S value of a sample increases, the change in e for a given change in H' decreases. We have included all the HSM samples in the H' - e crossplot in order to illustrate the H' - e characteristics of the previously defined sample groups. Group 1 includes samples of low species richness that plot

along S lines from 2 to 6 spp. The main feature of these samples is the relatively continuous series of e values, with H' values ranging from 0.07 to 1.39. Group 2 includes inequitable samples of moderate species richness that plot along S lines between 6 and 15 spp., characterized by low H' (< 1.59) and e values (< 0.6). Group 3 samples have moderate species richness and high equitability and plot along a narrow range of S lines from 7 to 15 species. Their e values range from 0.6 to about 0.92, with H' values from 1.32 to 2.22. Group 4 includes diverse samples that plot in a broad field of S values from 15 to 46 species. They are characterized by e values from 0.6 to 0.9 and H' values from about 2.08 to 2.91. While samples plotting in Groups 1 through 3 characterize both distal and proximal offshore sites, samples with Group 4 characteristics are only found in proximal offshore sites.

Interpretation of Diversity Data

Among the H' - e characteristics of the HSM data set that we seek to explain are the broad equitability range of samples with very low species richness in Group 1, the low equitability values of samples with moderate species richness in Group 2, and the high diversity of a few samples in Group 4 (e.g., $S=46$). In the discussion below, we consider the faunal characteristics and potential controls on each of the diversity-defined groups and relate them to species abundance patterns in the original populations. Seven representative samples have been chosen to illustrate the diversity groups (Fig. 8; see also Appendix B for faunal lists).

Group 1 is dominated by assemblages with low species richness (2–6 spp.), in which species of *Inoceramus* are most abundant. These occur mainly in distal offshore, laminated, organic-rich shales (late TST and most of HST; Fig. 3) and include secondary elements such as small pectinid, pteriid, and ostreid bivalves (in order of relative abundance), and rare ammonites. Most of these are truly “low-diversity” samples (with H' and e values below about 1.04 and 0.6, respectively) that have a species-abundance distribution resembling the geometric series (Fig. 8A). Some of them, however, are characterized by low H' but high e values due to the subequal abundance of a few species of dominant *Inoceramus* (Fig. 8B).

Size-frequency distributions of bivalves on many bedding-plane surfaces in these samples show strong, monospecific, single size-class dominance, interpreted to represent a pattern of event colonization (Sageman, 1989). In fact, some distal offshore samples are entirely monospecific and, thus, were not included in the H' - e analyses (when $S=1$, H' and $e = 0$). In other distal offshore low-diversity samples, pectinids (*Entolium gregarium*), which are tiny, paper-thin, and almost certainly juvenile, greatly exceed the inoceramids in abundance. These cases clearly represent the mass mortality of a recent spatfall (Sageman, 1989), and result in extremely low H' and e values. The distal offshore regions of the Western Interior Basin have been widely interpreted as deep, quiet-water environments with extremely low levels of dissolved oxygen (in part, based on the aforementioned faunal characteristics). Under such conditions, particulate organic matter in suspension would provide an abundant food source to filter feeders, and large mobile predators would be limited. Ac-

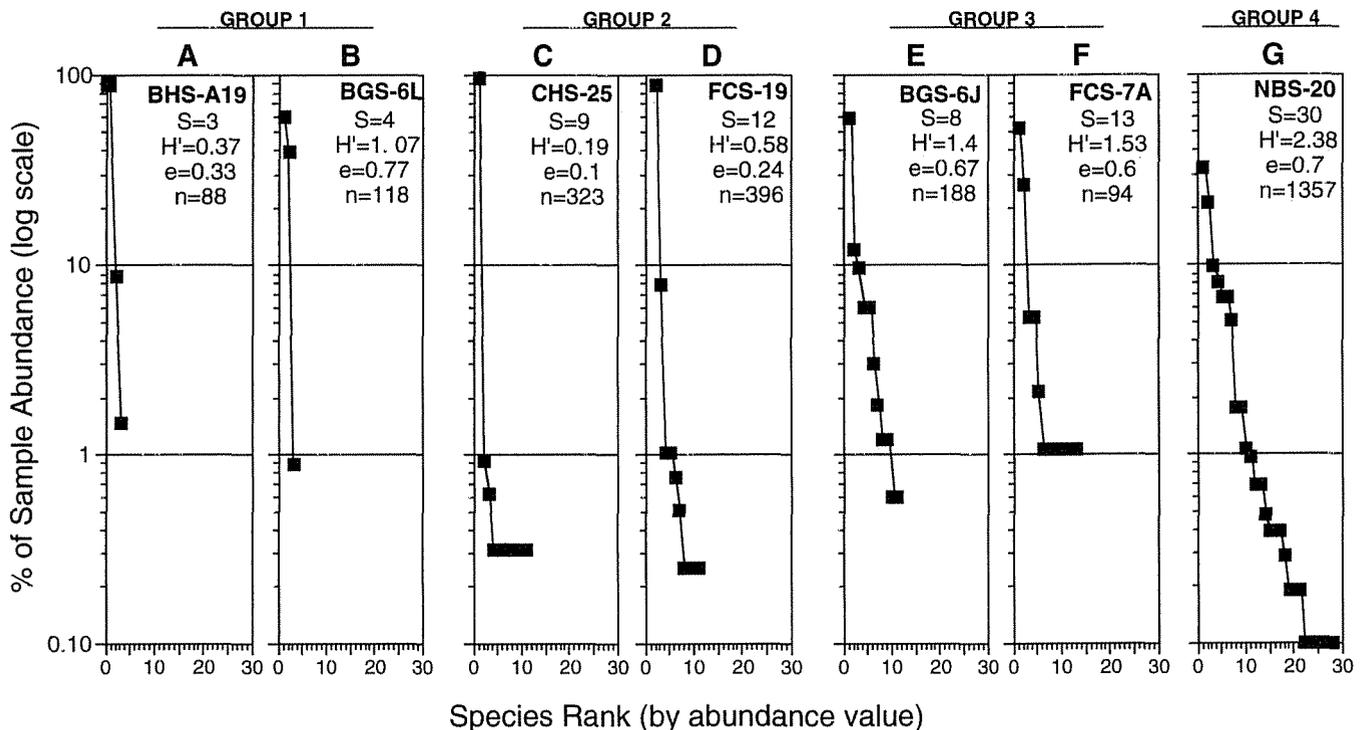


FIGURE 8—Representative species abundance plots from each of the four sample groups. The plots show percent abundance for species of each sample, ranked from most to least abundant. The plots include sample labels and data on S, H', e and n (total sample abundance). The order from most to least proximal site is NBS, FCS, CHS, BGS and BHS.

cordingly, oxygen has been viewed as the dominant control on diversity.

Data points representing proximal offshore sites that plot within low-diversity Group 1 include samples from burrowed mudstones where rare body fossils and a few scattered ichnotaxa were identified, and mudstone samples where high dominance resulted from a single highly abundant taxon in the assemblage. The taxonomic composition of assemblages from this group (e.g., the *Plicatula* assemblage, the *Pycnodonte* assemblage) is distinct from time-equivalent counterparts at distal and more proximal sites. Thus, they do not appear to merely represent poor samples of the latter, but rather transitional stages between the dominant distal and proximal offshore communities. The *Pycnodonte* assemblage characterizes the shallowest facies representing rapidly transgressing environments. Dominance of a cemented epifaunal life style suggest that substrate, current energy, and disturbance frequency (e.g., storms) may have been important controls. In contrast, the *Plicatula* assemblage occurs in proximal offshore facies characterized by laminated sediment fabric and increased organic carbon (OC) levels and probably represents a community of taxa with broader tolerances to periods of low oxygen.

Group 2 includes samples with moderate species richness but extremely low equitability (Fig. 8C and D). These samples are relatively uncommon, and they result from the extreme abundance of a single taxon in an otherwise moderately species-rich assemblage (that is, a Group 3 assemblage). In the case of sample CHS-25 (Fig. 8C), H'-e characteristics reflect the dominance of *Entolium* bivalves in an assemblage that includes infaunal and epifaunal bi-

valves, ammonites, and large burrowers (represented by the ichnotaxa *Planolites* and *Thalassinoides*). This sample is time-equivalent with Group 1 samples from the distal offshore area that are also dominated by *Entolium*, indicating that this "paper pecten" was a widely distributed opportunist. But the associated taxa are more similar to a proximal offshore Group 3 assemblage than those of the distal offshore. The impact of paper pectens on the equitability of otherwise moderately diverse assemblages has been observed in Jurassic black shales as well. Although Duff (1975) interpreted the pectinids to represent pseudoplankton, Wignall (1990, 1994) argues for a benthic life style. In another Group 2 case (sample FCS-19, Fig. 8D), a diverse community that includes epifaunal and infaunal suspension-feeding bivalves, gastropods, ammonites, and serpulid worms, is dominated by *Pycnodonte* oysters, which occur in a thin, dense bed (344 specimens counted) within the sample interval. Development of the oyster bed probably resulted when a rapid marine flooding event (parasequence scale) at a more onshore site produced short-term changes in sedimentation and substrate consistency in the FCS region (e.g., Elder et al., 1994). Colonization by oysters strongly skewed the equitability of a sample that otherwise would have had Group 3 characteristics.

Group 3 includes samples with moderate species richness (6–15 spp.) from both distal and proximal offshore environments. The distal offshore samples are associated with the middle HSM, where monotonous laminated shales are replaced by moderately laminated to sparsely burrowed calcareous mudstones interbedded with skeletal limestones. Sageman (1996) has interpreted these facies

to represent the offshore expression of a minor sea-level lowstand (Fig. 3). Although the faunas are largely unchanged in terms of overall taxonomic composition from subjacent and superjacent Group 1 samples, S increases and the distribution of abundance among component species is shifted toward a more equitable pattern (Fig. 8E), possibly reflecting a log-series distribution (which approximates a straight line: Hughes, 1986). There is no change in the average size of bivalve specimens in these samples, and no evidence of other ecological changes (predation, food sources, etc.). The most significant difference in some samples seems to be the presence of an infauna (albeit restricted). Changes in the distal offshore depositional environment associated with the middle HSM lowstand that could have affected diversity patterns include changes in circulation (greater/more frequent mixing of oxygen to the benthic zone) and in substrate (grain size, consistency, pore-water chemistry).

Samples from proximal offshore sites with Group 3 characteristics are similar to Group 3 samples from distal offshore environments; they both basically represent more equitable versions of local Group 1 communities (Fig. 8F). In many of these cases, however, new taxa occupying previously unrepresented life habits and trophic strategies contribute to an increase in diversity (e.g., sample FCS-7A; see Appendix B). Again, a significant difference between Groups 1 and 3 is the establishment of infauna, reflecting the importance of substrate as a control. However, these samples have characteristics that are intermediate between low-diversity, dominantly epifaunal Group 1 and high-diversity, mixed infaunal/epifaunal Group 4 of the proximal offshore samples. They appear to represent significant changes in physical/chemical conditions, availability of resources, competitive interactions, and probably niche diversity.

Group 4 samples are characterized by high species richness and high equitability. They represent the most diverse assemblages that occur within the HSM data set, and include numerous infaunal and epifaunal bivalves, gastropods, scaphopods, ammonites, echinoids, and corals, as well as ichnotaxa representing fodinichnia, pascichnia, and domichnia (e.g., *Planolites*, *Chondrites*, *Thalassinoides*, *Arenicolites*). The distribution of species abundances approximates a log-series distribution in the rank abundance plot (Fig. 8G). Increased diversity probably reflects a broader range of physical/chemical conditions relative to organism-tolerance levels (higher O_2 , lack of H_2S , diverse substrates, abundant food, etc.). In addition, at least three of the highest diversity samples represent offshore condensed units in which sedimentation rates were greatly reduced. These samples reflect time-averaging of faunas over a significantly longer period than standard samples. The high S , high H' values occur in samples that correlate westward to a transgressive surface extending over 150 km in a landward direction (Elder et al., 1994). In this case, condensation probably resulted in "overprinting" of several different benthic communities (from lowstand to early transgressive) to produce exceptional species richness ($S=46$ spp.).

Species Abundance Simulations

To analyze possible influences on the species abundance patterns observed in the HSM, we developed a simple nu-

merical model. The model allowed simulation of different diversity patterns that then could be sampled randomly, emulating the effects of preservational and sampling biases. To create the synthetic populations, we generated a random data set of sample characteristics for each of 5000 samples. The samples were characterized by S values and species-abundance distributions that represent a range of possible ecological scenarios. The design of the model populations was based on observations of modern communities where large species-rich populations (representing favorable conditions) have distributions of species abundance that tend toward a log normal distribution, and species-poor communities (typically representing the most unfavorable conditions) tend to produce log-series or geometric series (May, 1975; Hughes, 1986; Magurran, 1988).

In the models, we simulate time-averaged mudrock fossil assemblages by employing a random sampling protocol upon idealized population distributions. For each model, we generate 10 random populations from identical distributions. We randomly extract 500 samples from each of these 10 populations, yielding 5000 random samples. The H' and e characteristics of these 5000 samples are calculated and plotted for each model as in Figure 7, and a rank-abundance plot is constructed as in Figure 8. Each individual model is characterized by three parameters chosen to represent a continuum of possible species-abundance distributions: the number of "background species" in the population; the number of "weak opportunistic species"; and the number of "strong opportunistic species" (these terms are defined below). Each individual species, of any type, contains a number of individuals randomly selected from a normal (Gaussian) probability distribution characterized by a mean, m , and a standard deviation, s , a distribution that we will write as $N(\mu, \sigma)$. Each individual species, then, will be characterized by its own particular values of μ and σ .

For our purposes, each of our simple background species is characterized by a mean μ and a standard deviation σ , where each μ value is randomly selected from $N(1000, 500)$ and σ randomly chosen from $N(100, 100)$. Thus, a background species will have roughly on the order of 1000 individuals in the total population, with some significant variation between different background species. A weak opportunist is simply a species whose membership exceeds that of a typical background species by about an order of magnitude. Thus, the mean number of individuals μ of a weak opportunistic species is chosen from $N(10000, 5000)$ while σ is chosen from $N(1000, 1000)$. Similarly, a strong opportunist is a species whose membership exceeds that of a typical background species by about two orders of magnitude. Thus, the mean number of individuals μ of a strong opportunistic species is chosen from $N(100000, 50000)$ and σ from $N(1000, 1000)$. From the large populations thus created, individual random samples are collected. The number of individuals in each sample is chosen randomly from $N(80, 4)$, so that each sample contains roughly 80 individuals. The total S value of a sample, which is an important determinant of its ultimate $H'-e$ character, is a product of random sampling from a distribution in the models. In nature, however, S_{tot} and the composition of background vs. opportunistic species in a population are directly controlled by environmental and ecological constraints.

The modeling results may be summarized as follows. Populations dominated entirely by background species are characterized by high diversity and equitability. Samples from such populations show the high H' and e values char-

acteristic of Group 4 samples (Fig. 9A). Furthermore, their abundance-ranking of species (Fig. 9A) exhibits a pattern similar to that of a truncated log-normal population distribution (approximates a sigmoid curve: Hughes, 1986).

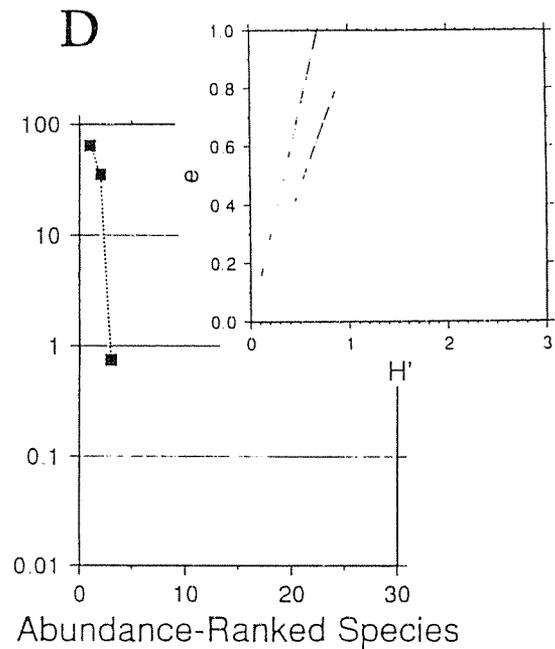
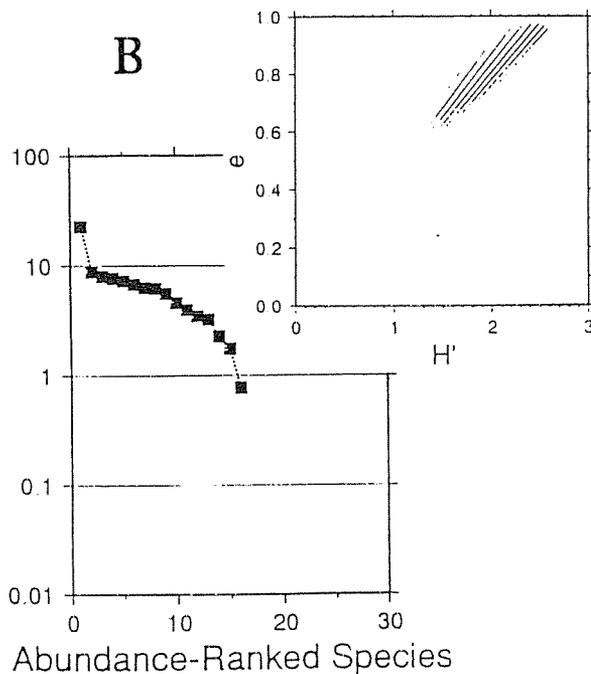
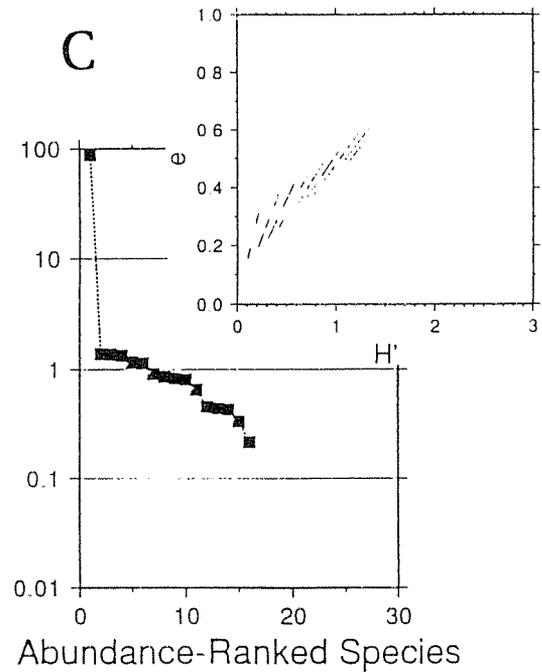
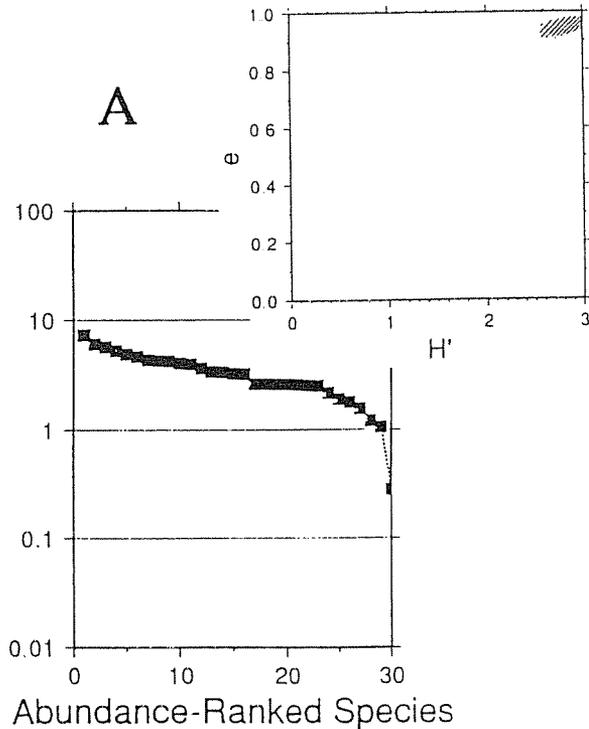


FIGURE 9—Numerical model results include H' - e plots and abundance-ranked species plots for 5000 samples chosen from populations characterized by: (A) solely a large number [30] of background species (characteristics strongly resemble Group 4 samples); (B) a moderate number [15] of background species and a single [1] weak opportunistic species (characteristics strongly resemble Group 3 samples); (C) a moderate number [15] of background species and a single [1] strong opportunistic species (characteristics strongly resemble Group 2 samples); and (D) a small number [1] of background species relative to a larger number [2] of strong opportunistic species (characteristics strongly resemble Group 1 samples).

When a weak opportunist is added to the population, e and H' values extend to simultaneously smaller values, exhibiting characteristics similar to those of Group 3 samples (Fig. 9B). Their abundance-ranked species pattern begins to adopt a high-abundance spike, reflecting the dominant taxon characteristic of log-series or geometric population distributions. This is superposed upon the truncated log-normal distribution of the rarer background species (Fig. 9B). As the fortitude of the opportunist is increased from weak to strong, e and H' all migrate to lower values, and the characteristics of Group 2 samples (low e at moderate H') appear (Fig. 9C). The abundance-ranking pattern now clearly exhibits the dominance spike (Fig. 9C). Finally, as multiple opportunists are added to the population in numbers rivaling or exceeding those of the background species, the more unusual properties of Group 1 samples (high e at low H') appear (Fig. 9D). The abundance-ranking pattern has now shifted completely to the steep aspect of a geometric series distribution and the number of rare species is very low (Fig. 9D).

DISCUSSION

The study of black shale biofacies represents an effort to understand the adaptive characteristics of species and communities as they approach and exceed the limits of survival in what are interpreted to be oxygen-deficient environments. Applications of this work range from improving our understanding of the early (and ongoing) evolution of life under oxygen-poor conditions (Rhoads and Morse, 1971) to increased knowledge of the causes and consequences of natural and anthropogenic eutrophication (Tyson and Pearson, 1991). These processes are predicted to intensify in association with future global warming, underscoring the importance of studying black shales deposited during ancient greenhouse events.

The faunas of the HSM represent an ecosystem that developed during the mid-Cretaceous greenhouse in the shallow Western Interior epicontinental sea. Although prior study of these faunas (Sageman, 1991) allowed a categorization of biofacies based on the Rhoads and Morse (1971) model and employing a linear oxygen-diversity paradigm (Fig. 4), the key observations from the HSM pertaining to adaptation at the limits of survival concerned the high frequency and short duration of benthic colonization events, the influence of substrate on benthic faunas, and the role of sediment-water interface conditions as a boundary to infaunal, but not epifaunal colonization (Sageman, 1989; Sageman et al., 1991). These results added to the growing body of work indicating that many ancient epicontinental black shales were not deposited under long-term stable low-oxygen conditions, but were more likely representative of environments that were relatively dynamic (e.g., Hallam, 1987; Wignall, 1990; Tyson and Pearson, 1991).

Although water-column stratification continues to be viewed as an important process in the development of ancient black shales, many studies are now seeking to assess the relative role of seasonal or longer-term changes in the flux of metabolizable organic matter to the substrate in controlling redox conditions (e.g., Pederson and Calvert, 1990). Paralleling these developments, there have been notable modifications in the ecological interpretation of

faunas of modern and ancient low-oxygen environments. For example, in addition to the observations that led to a redefinition of dysoxic communities in the 1980's (e.g., Savrda et al., 1984; Thompson et al., 1985), there is recent evidence of cephalopods exploiting low-oxygen habitats (Boutilier, et al., 1996), and cases of large mobile epifauna at 0.0 ml/L O_2 beneath the Peru upwelling zone (M.A. Arthur, pers. comm. based on observations from submersible dives). These data indicate that many invertebrate taxa may be extremely tolerant of oxygen deficiency, especially where it is temporally variable and associated with low sulfide levels.

Environmental stability or disturbance frequency is considered to be an important determinant of diversity and dominance in modern communities (e.g., Whittaker, 1975; Valentine, 1971; May, 1975; Connell, 1978; Huston, 1979), and is emerging as one of the central ecological issues for low-oxygen paleoenvironments (e.g., Kauffman, 1981; Wignall and Myers, 1988; Sageman, 1989; Savrda and Bottjer, 1991; Tyson and Pearson, 1991; Wignall, 1990, 1994). In fact, a new oxygen-related biofacies has even been specifically devoted to it (the poikiloaerobic biofacies of Oschmann, 1991). Although there has been debate concerning the effects of stability on community diversity (Bretsky and Lorenz, 1970; Eldredge, 1974; Pielou, 1975; Huston, 1979; Pimm, 1984; Frontier, 1985), low environmental stability is generally believed to result in low diversity by favoring r-selected eurytopic species or opportunists (Levinton, 1970; Valentine, 1971; Huston, 1979). Dominance is high because these taxa represent pioneers in a community succession that never has the opportunity to develop much beyond the pioneer stage, as environmental perturbations repeatedly reset the ecological clock (Pielou, 1975; Whittaker, 1975). The pioneers are characterized by rapid reproduction, wide dispersal, and large numbers of offspring.

If applied to the Western Interior basin, this model would suggest increasing instability along a deepening environmental gradient. However, an alternate interpretation to account for diversity patterns in ancient epicontinental black shales has been proposed. This nonequilibrium model suggests that chemosymbiosis in taxa adapted to low oxygen and the presence of H_2S (e.g., Kauffman, 1988; McLeod and Hoppe, 1992) accounts for the pattern of diversity in some black shales (Etter, 1995). Although this hypothesis may be plausible, isotopic data used to argue for chemosymbiosis in Cretaceous inoceramids has been questioned (Grossman, 1993), features commonly associated with other chemosymbiotic bivalves are lacking (Cavanuagh, 1985; Seilacher, 1990), and there is no independent evidence to directly support a chemosymbiotic strategy, such as the detection of symbiont bacteria within host bivalves.

Summary of HSM Results

The purpose of this study was to consider alternate ecological scenarios for the diversity patterns of organic carbon-rich facies by analyzing species abundance data from the Hartland Shale Member. To investigate species-abundance patterns we developed a method for analyzing diversity data that incorporates the separate measures of species richness, Shannon index, and equitability into a

single plot (Figs. 5–7). This approach is valuable because samples can be grouped according to patterns of diversity and equitability that are independent of biofacies interpretations based on the linear oxygen-diversity paradigm (e.g., Fig. 4). Representative rank abundance plots can then be constructed for selected groups (Fig. 8), thus facilitating comparisons between fossil species-abundance distributions and established species-abundance models. The HSM results indicate a gradient from samples with log-series characteristics (Fig. 8G) to samples resembling a geometric series (Fig. 8A). The major factor determining the character of intervening samples (Fig. 8B–F) appears to be the number and relative abundance of dominant species.

To aid in the interpretation of the diversity data, we developed a simple numerical model. The purpose of the model was to simulate the effects of variable species-abundance distributions on *measured* diversity. Thus, the model was designed to allow manipulation of species abundance patterns to test hypotheses for different population characteristics, which were then randomly sampled to emulate the sampling effects inherent in preservation and data collection. What was significant about the model was not the illustration of predictable end members in a continuum of species abundance distributions, but the ability to test for abundance distributions most likely to produce high e , low S , and low H' values when randomly sampled. This effort highlighted the importance of variations in relative strength and number of dominant species in a population, and turned our attention toward an explanation for multiple co-existing opportunistic species, which are an unlikely occurrence in equilibrium models of community development. Furthermore, the modeling confirmed Hughes' (1986) suggestion that sampling effects can produce a truncated log-normal pattern, that depending on the proportion of species not sampled, can resemble a log-series distribution.

Ecological Interpretation

There has been considerable debate in the ecological literature concerning the interpretation of species abundance models for natural communities (Magurran, 1988). The main factors that influence measured diversity are primary ecological controls and sampling effects. Hughes (1986) provided a cogent summary of the different species-abundance models in a paper on marine benthic communities. Starting with the log-normal model, many workers have concluded that multiple physical, chemical, and biological factors operating in complex, species-rich communities with large numbers result in a normal distribution of species abundance (Preston, 1948; May, 1975; Whittaker, 1975). Such communities are thought to represent stable or equilibrium conditions where biological competition plays a large role in determining diversity patterns. However, sampling effects tend to produce a truncated log-normal pattern as fewer of the rare species in a community are counted (e.g., Preston, 1948) and, depending on where the sampling limit falls relative to the mode of a normal distribution, the truncated log normal can approximate a log-series distribution (Hughes, 1986). Furthermore, Hughes (1986) indicated that the truncated log-normal and log-series distributions may, in fact, reflect small, pioneer, or stressed communities. Such communities are typically associated with the geometric series, which is

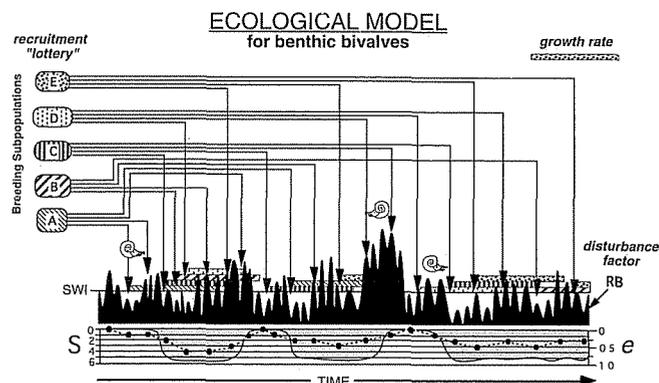


FIGURE 10—Ecological model for development of low-diversity, high-equitability biofacies in the HSM includes three components: (1) Recruitment lottery—breeding subpopulations A-E (left side of diagram). Recruitment is represented by lines with arrows; (2) Growth rate/tolerance—bars representing colonization and growth of recruits (along bottom of diagram) are keyed to subpopulations A-E by fill patterns. Time progresses from left to right in figure; (3) Disturbance factor—fluctuations of the redox boundary above SWI represented by black fill. Species richness (S) represented by dashed line and equitability (e) by shaded curve.

based on the niche preemption hypothesis (May, 1975); when resources are severely limiting and species are recruited at regular intervals, the dominant species are thought to utilize a major fraction of the resources, the next dominant the same fraction of the remaining resources, and so on, resulting in a geometric decline in species abundance.

The major problem with this and other hypotheses to account for species-abundance distributions is that they are not constrained by specific ecological criteria (Pileou, 1975). For example, in the case of marine benthic communities, if recruitment is random rather than regular, the same conditions as described above for a geometric series would lead to a log series (Hughes, 1986). Hughes (1986) attempted to address this problem by developing a “dynamics model” in which species-abundance patterns of marine benthic communities are determined by ecologically realistic parameters, such as recruitment potential (number of dispersing immigrants or fecundity of established individuals), survival potential (relative to disturbance frequency), and gregariousness (relating growth rates among recruits to established conspecifics). Hughes (1986) found that this model matched the predictions of the intermediate disturbance hypothesis (Connell, 1978; Huston, 1979), and provided a better descriptor for a wide range of natural communities.

Building on Hughes' (1986) model, we propose that the observed pattern of diversity in the offshore assemblages of the HSM is a consequence of interactions between three independent ecological factors: (1) the “lottery” of larval production and dispersal from different breeding subpopulations representing separate species of low-oxygen tolerant opportunistic bivalves; (2) the relationship between age, size, and tolerance to low O_2/H_2S of bivalve taxa (controlled largely by growth rate); and (3) the frequency and intensity of redox boundary (RB) fluctuations above the SWI. Our model is illustrated in Figure 10. Breeding subpopulations A through E are depicted on the left side of the figure. Recruitment of larvae within the basin through

time is depicted along the bottom of the figure. Dominance of recruitment from any given subpopulation is random, resulting in a recruitment "lottery." The survival of recruits is determined by tolerance to oxygen deficiency and the presence of H_2S , which varies with organism age and size. Although small or juvenile organisms may be more tolerant of low oxygen because of lower respiratory demands and greater surface area to volume ratios (Shumway et al., 1983), they are more susceptible to sulfide than adults (Thurberg and Goodlett, 1979; Groenendaal, 1980; Shumway et al., 1983). We hypothesize that the major cause of environmental instability (and benthic mortality) is fluctuation of the redox boundary above the SWI, which based on the apparent age structure of most HSM communities (Sageman, 1989), must have occurred on a scale of years to 10's of years. In our model, the major cause of mortality is prolonged H_2S exposure, as low oxygen levels and short-term exposure to H_2S (sufficient to kill *Entolium* bivalves) do not appear to affect most inoceramids.

As a result of interplay between the breeding population "lottery," larval dispersal/colonization and growth rate, tolerance limits of juveniles and adults, and the frequency and intensity of RB fluctuations, multiple species of opportunistic bivalves can colonize and cohabitate for periods of time, resulting in fossil assemblages with high e , low S , and low H' values (Fig. 10)—the characteristics of many Group 1 samples.

A final factor in explaining the measured diversity patterns of the HSM are sampling effects. Based on our discussion, the log-series pattern in high-diversity, proximal offshore samples may be interpreted as a truncated log normal distribution. Similarly, the geometric series pattern in low-diversity, distal offshore samples probably reflects a truncated log-series distribution. Although physical/chemical conditions may have been limiting, it is unlikely that any species could dominate either food (particulate organic matter was abundant), living space (only very rare bedding planes suggest crowding), or oxygen. Hence, niche preemption is unlikely. Lastly, the steepness of the curves in Figure 8 are probably a consequence of both the dominance of r -selected, opportunistic taxa in offshore Western Interior communities, and the fact that time-averaged collections can record brief colonization events of these taxa within samples dominated by "background species" with less extreme abundance characteristics.

Evolutionary and Paleoenvironmental Significance

The ecological model described above leads to a possible explanation of diversification patterns observed in Western Interior inoceramid lineages. These taxa have been described as having high rates of speciation (Kauffman, 1978). Was diversification favored in organisms living at or near the limits of survival, in deep basinal paleoenvironments? Although a tendency toward speciation should not be unexpected given our three assumptions (small breeding subpopulations, rapid turnover rates, and unpredictable, unstable environments), the fact that deeper, quieter regions of the basin are a locus of instability is in marked contrast to the conventional time-stability view of marine communities (Sanders, 1968). The mechanism for disturbance is biogeochemical, and its effect is stochastic as a consequence of the unpredictable interaction between recruitment, organism-

growth rates and tolerance levels, and redox fluctuations. In addition, biogeochemical factors may account for spatial heterogeneity of the SWI and the isolation of subpopulations (geographic differences in organic loading of the substrate may have caused variations in the position of the redox boundary in space as well as time).

A further implication of the model pertains to the Cenomanian-Turonian (C-T) extinction event, which occurred less than 0.5 myr after deposition of the HSM. Whereas 51% of total molluscan taxa in the Western Interior were affected during this event, 92% of the inoceramids went extinct (Elder, 1989). Valentine (1971) hypothesized that abundant resources and high disturbance frequencies lead to major extinctions. Although we believe the HSM was characterized by just these conditions, extinction did not occur until later. In fact, the extinction event followed a change in the character of disturbance. The rhythmic alternation of lime-marl sedimentation on 20 to 100 ky time scales, which entailed fluctuations in substrate consistency, OC fluxes to the benthic zone, and bottom-water and pore-water redox conditions (e.g., Elder, 1989; Sageman et al., 1997), followed HSM deposition and occurred up to and during the C-T extinction event. These factors may have caused the nature of disturbance to change from a *transient* level favoring speciation to a *persistent* level where extinction events outpaced speciation, thus defining a critical ecological threshold.

A final consideration concerns interpretation of the history of the Western Interior basin during Late Cenomanian time. It was a broad, shallow seaway with extremely low bathymetric gradients, restricted connections to oceanic water masses, and water depths from 50 to about 200 m in offshore areas (Sageman and Arthur, 1994; Sageman, 1996). Features of the HSM such as high OC content, laminated sediment fabric, abundant disseminated pyrite, and low faunal diversity have typically been used to argue for stable density stratification of the water column (Kauffman, 1977, 1984; Pratt, 1984). Yet the basin had a warm, temperate to subtropical climate with abundant precipitation and frequent storms that could mix oxygenated waters to significant depths (Kauffman, 1984; Pratt, 1984; Upchurch and Wolfe, 1993; Ludvigson et al., 1994; Witzke and Ludvigson, 1994; Winn et al., 1987). In addition, it had high freshwater input that delivered fine-grained sediment and terrestrial nutrients to the basin (Pratt, 1984), but surface waters were never brackish (Eicher and Diner, 1985, 1989). Finally, it had high productivity levels (based on nannofossil fertility indicators) and, thus, a significant flux of OC to the sediment (Sageman, 1991; Bralower, 1988).

Based on our ecological model, the data from the HSM can be interpreted to indicate that oxygen levels fluctuated sporadically in the water column, and that the redox boundary was confined to a zone within or just above the SWI. In Berner's (1981) geochemical classification of environments, the HSM might represent a "post-oxic nonsulphidic anoxic" environment. Whether this condition resulted from rapid re-stratification following storm events, or was simply due to fluctuations in organic loading of sediments due to productivity blooms following mixing of riverborne or *in situ* nutrients to the surface is not known. However, the latter model (where productivity provides sufficient OC to drive sediments and pore waters anoxic

due to bacterial decomposition, but frequent mixing of the water column maintains sufficient oxygenation to prevent accumulation of sulfide) provides a better mechanism to explain the evidence from the HSM. If so, the Western Interior sea was a biogeochemically dynamic system. This view of epicontinental seas has been strongly supported in recent papers on modern and ancient oxygen-deficient environments (Tyson and Pearson, 1991). Although there are no good modern analogs for epiherc seas with the size and configuration of the Western Interior, similar biogeochemical processes probably occur in the modern Santa Monica Basin, where oxygenated water masses episodically "leak in" across the sill, preventing the stable development of euxinic conditions (Pratt, pers. comm., 1996).

CONCLUSIONS

(1) Late Cenomanian distal offshore assemblages from the Western Interior basin have diversity characteristics that probably reflect a truncated log-series pattern of species abundance among species-poor fossil populations. Ecological analysis and diversity simulations indicate that a combination of sampling bias and the dominance of single to multiple opportunistic species in an environment of high disturbance frequency best explains the pattern. In contrast, Late Cenomanian proximal offshore assemblages have log-series abundance patterns that are interpreted as truncated log-normal distributions representing samples of large, species-rich populations. These probably reflect normal marine, level bottom, soft substrate communities that were controlled by a variety of environmental and biological factors (salinity, temperature, oxygen, food type and availability, predation, competition), and may represent intermediate levels of disturbance.

(2) The relationship between biofacies and interpreted benthic oxygen concentrations may be complex. Numerical diversity data define a continuous gradient in diversity for HSM samples. Thus, sharp delineation of dysaerobic and aerobic biofacies based strictly on H' and e values is difficult. Distal offshore assemblages interpreted as high-disturbance biofacies dominated by opportunistic species most likely represent a relatively broad range of paleo-oxygen levels. They are not exaerobic biofacies, as this designation implies a specific range of (very low) oxygen levels, but are more similar to Wignall's (1994) redefinition of Oschmann's (1991) poikiloaerobic biofacies. Although the Rhoads and Morse (1971) biofacies model has served as an excellent general framework for categorizing low-oxygen faunas, its use as a direct proxy for paleo-oxygen levels must be exercised with caution.

(3) Absolute oxygen content may not be as important a controlling factor for benthic communities in ancient black shale environments as is its variability (transient or persistent relative to ecological time scales). Transient disturbances, largely in the form of H_2S at the SWI, may have been the major factor influencing diversification patterns in shallow epicontinental basins like the Western Interior. Persistent disturbances, including changes in redox conditions and substrates, may have provided an important mechanism for extinction among taxa adapted to life at the limits of survival. This mechanism may have acted at a larger scale also. For example, the Inoceramidae were among the dominant inhabitants of broad, shallow epicon-

tinental seas during the Mesozoic, and the entire family went extinct at the end of the Cretaceous in conjunction with the loss of those environments.

(4) Finally, the lack of direct modern analogs for both the dominant taxa and the basinal settings that characterized ancient greenhouse periods underscores the need for innovative analysis of integrated physical, chemical, and biological data sets to ensure correct paleoenvironmental and ecological reconstructions (Bottjer et al., 1995). The ecological arguments presented herein not only contribute to a new view of the Western Interior sea as a dynamic paleoenvironment, but also present a hypothesis to explain relationships between climatic events, oceanographic processes, and the ecology and evolution of molluscan communities.

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REFERENCES

- ARTHUR, M.A., and SAGEMAN, B.B., 1994, Marine black shales: A review of depositional mechanisms and environments of ancient deposits: *Annual Reviews Earth and Planetary Science*, v. 22, p. 499-552.
- BATT, R., 1993, Ammonite morphotypes as indicators of oxygenation in a Cretaceous epicontinental sea: *Lethaia*, v. 26, p. 49-63.
- BERNER, R.A., 1981, A new geochemical classification of sedimentary environments: *Journal of Sedimentary Petrology*, v. 51, p. 359-365.
- BOTTJER, D.J., CAMPBELL, K.A., SCHUBERT, J.K., and DROSER, M.L., 1995, Paleocological models, non-uniformitarianism, and tracking the changing ecology of the past: *in* Bosence, D.W.J., and Allison, P.A., eds., *Marine Paleoenvironmental Analysis From Fossils*: Geological Society of London, Special Publication no. 83, p. 7-26.
- BOUTILIER, R.G., WEST, T.G., POGSON, G.H., MESA, K.A., WELLS, J., and WELLS, J.M., 1996, Nautilus and the art of metabolic maintenance: *Nature*, v. 382, p. 534-536.
- BRALOWER, T.J., 1988, Calcareous nannofossil biostratigraphy and assemblages of the Cenomanian-Turonian boundary interval: Implication for the origin and timing of oceanic anoxia: *Paleoceanography*, v. 3, p. 275-316.
- BRETSKY, P.W., and LORENZ, D.M., 1970, An essay on genetic-adaptive strategies and mass extinctions: *Geological Society of America Bulletin*, v. 81, p. 2449-2456.
- BRETT, C.E., and BAIRD, G.C., 1996, Epiboles, outages, and ecological evolutionary bioevents: Taphonomic, ecological, and biogeographic factors: *in* BRETT, C.E., and BAIRD, G.C., eds., *Paleontological Events: Stratigraphic, Ecological and Evolutionary Implications*: Columbia University Press, N.Y., p. 249-284.
- CAVANAUGH, C.M., 1985, Symbiosis of chemoautotrophic bacteria and marine invertebrates from hydrothermal vents and reducing sediments: *Bulletin of the Biological Society of Washington*, v. 6, p. 373-388.
- COBBAN, W.A., 1984, Mid-Cretaceous ammonite zones, Western Interior, United States: *Bulletin Geological Society of Denmark*, v. 33, p. 71-89.
- COBBAN, W.A., and HOOK, S.J., 1984, Mid-Cretaceous molluscan biostratigraphy and paleogeography of southwestern part of Western Interior, United States: *in* WESTERMANN, G.E.G., ed., *Jurassic-Cretaceous Biochronology and Paleogeography of North America*: Geological Association Canada, Special Paper 27, p. 257-271.
- CONNELL, J.H., 1978, Diversity in tropical rain forests and coral reefs: *Science*, v. 199, p. 1302-1310.

- DAHNIKE, B.M., SAGEMAN, B.B., and KAUFFMAN, E.G., 1993, Trace fossil distribution patterns in Cretaceous facies of the Western Interior basin, North America: *in* CALDWELL, W.G.E., and KAUFFMAN, E.G., eds., *Cretaceous Evolution of the Western Interior basin, North America: Geological Association of Canada, Special Publication 39*, p. 585–620.
- DODD, J.R., and STANTON, R.J., 1990, *Paleoecology, Concepts and Applications*, 2nd ed.: Wiley Interscience, New York, 559 p.
- DUFF, K.L., 1975, Paleoecology of a bituminous shale: The Lower Oxford Clay of central England: *Palaeontology*, v. 18, p. 443–482.
- EICHER, D.L., and DINER, R., 1985, Foraminifera as indicators of water mass in the Cretaceous Greenhorn Sea, Western Interior: *in* PRATT, L.M., KAUFFMAN, E.G., and ZELT, F.B., eds., *Fine-grained Deposits and Biofacies of the Cretaceous Western Interior Seaway: Evidence of Cyclic Sedimentary Processes: Society of Economic Paleontologists and Mineralogists, Fieldtrip Guidebook no. 4*, Tulsa, p. 60–71.
- EICHER, D.L., and DINER, R., 1989, Origin of the Cretaceous Bridge Creek cycles in the Western Interior, United States: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 74, p. 127–146.
- EICHER, D.L., and WORSTELL, P., 1970, Cenomanian and Turonian foraminifera from the Great Plains, United States: *Micropaleontology*, v. 16, p. 269–324.
- ELDER, W.P., 1985, Biotic patterns across the Cenomanian-Turonian extinction boundary near Pueblo, Colorado: *in* PRATT, L.M., KAUFFMAN, E.G., and ZELT, F.B., eds., *Fine-grained Deposits and Biofacies of the Cretaceous Western Interior Seaway: Evidence of Cyclic Sedimentary Processes: SEPM Field Trip Guidebook no. 4*, p. 157–169.
- ELDER, W.P., 1989, Molluscan extinction patterns across the Cenomanian-Turonian stage boundary in the Western Interior of the United States: *Paleobiology*, v. 15, p. 299–320.
- ELDER, W.P. and KIRKLAND, J.I., 1994, Cretaceous paleogeography of the southern Western Interior region: *in* CAPUTO, M., and PETERSON, J., eds., *Mesozoic Systems of the Rocky Mountain Region, U.S.: Rocky Mountain Section—Society Sedimentary Geology (SEPM) Special Publication*, p. 415–440.
- ELDER, W.P., GUSTASON, E.R., and SAGEMAN, B.B., 1994, Correlation of basinal carbonate cycles to nearshore parasequences in the Late Cretaceous Greenhorn Seaway, Western Interior: *Geological Society of America, Bulletin*, v. 106, p. 892–902.
- ELDREDGE, N., 1974, Stability, diversity, and speciation in Paleozoic epeiric seas: *Journal of Paleontology*, v. 48, p. 540–548.
- ETTER, W., 1995, Benthic diversity patterns in oxygenation gradients: an example from the Middle Jurassic of Switzerland: *Lethaia*, v. 28, p. 259–270.
- FISHER, C.G., 1991, Calcareous nannofossil and foraminifera definition of an oceanic front in the Greenhorn Sea (Late Middle through Late Cenomanian), northern Black Hills, Montana and Wyoming: *Paleoceanographic implications: Unpublished Ph.D. Thesis, University of Colorado, Boulder*, 325 p.
- FRONTIER, S., 1985, Diversity and structure in aquatic ecosystems: *Annual Reviews of Oceanography and Marine Biology*, v. 23, p. 253–312.
- FRUSH, M.P., and EICHER, D.L., 1975, Cenomanian and Turonian foraminifera and paleoenvironments in the Big Bend region of Texas and Mexico: *in* CALDWELL, W.G.E., ed., *The Cretaceous System in North America: Geological Association of Canada, Special Paper 13*, p. 277–301.
- GIBSON, T.G. and BUZAS, M.A., 1973, Species diversity: Patterns in modern and Miocene foraminifera of the eastern margin of North America: *Geological Society of America Bulletin*, v. 84, p. 217–238.
- GROENENDAAL, M., 1980, Tolerance of the lugworm (*Arenicola marina*) to sulphide: *Netherlands Journal of Sea Research*, v. 14, p. 200–207.
- GROSSMAN, E.L., 1993, Evidence that inoceramid bivalves were benthic and harbored chemosynthetic symbionts, Comment and Reply: *Geology*, v. 21, p. 94–96.
- HALLAM, A., 1987, Mesozoic marine organic-rich shales: *in* BROOKS, J., and FLEET, A.J., eds., *Marine Petroleum Source Rocks: Geological Society, London, Special Publication 26*, p. 215–261.
- HUGHES, R.G., 1986, Theories and models of species abundance: *American Naturalist*, v. 128, p. 879–899.
- HUSTON, M., 1979, A general hypothesis of species diversity: *American Naturalist*, v. 113, p. 81–101.
- KAUFFMAN, E.G., 1977, Geological and biological overview: Western Interior Cretaceous Basin: *Mountain Geologist*, v. 13, p. 75–99.
- KAUFFMAN, E.G., 1978, Evolutionary rates and patterns among Cretaceous Bivalvia: *Philosophical Transactions Royal Society London, ser. B*, v. 284, p. 277–304.
- KAUFFMAN, E.G., 1981, Ecological reappraisal of the German Posidonienschiefer (Toarcian) and the stagnant basin model: *in* GRAY, J., BOUCOT, A.J., and BERRY, W.B.N., eds., *Communities of the Past: Hutchinson Ross, Stroudsburg*, p. 311–381.
- KAUFFMAN, E.G., 1984, Paleobiogeography and evolutionary response dynamic in the Cretaceous Western Interior Seaway of North America: *in* WESTERMANN, G.E.G., ed., *Jurassic-Cretaceous Biochronology and Paleogeography of North America: Geological Association of Canada, Special Paper 27*, p. 273–306.
- KAUFFMAN, E.G., 1988, The case of the missing community: Low-oxygen adapted Paleozoic and Mesozoic bivalves (“flat clams”) and bacterial symbioses in typical Phanerozoic seas: *Geological Society of America, Abstracts with Program*, v. 20, p. A48.
- KAUFFMAN, E.G., SAGEMAN, B.B., ELDER, W.P., KIRKLAND, J.I., and VILLAMIL, T., 1993, Cretaceous molluscan biostratigraphy and biogeography, Western Interior Basin, North America: *in* CALDWELL, W.G.E., and KAUFFMAN, E.G., eds., *Evolution of the Western Interior Basin: Geological Association of Canada, Special Paper 39*, p. 397–434.
- KENNEDY, W.J., and COBBAN, W.A., 1991, Stratigraphy and interregional correlation of the Cenomanian-Turonian transition in the Western Interior of the United States near Pueblo, Colorado, a potential boundary stratotype for the base of the Turonian stage: *Newsletters in Stratigraphy*, v. 24, p. 1–33.
- KIDWELL, S.M., and FLESSA, K.W., 1996, The quality of the fossil record: Populations, species, and communities: *Annual Reviews of Earth and Planetary Science*, v. 24, p. 433–464.
- KIRKLAND, J.I., 1990, The paleontology and paleoenvironments of the Middle Cretaceous (Late Cenomanian–Middle Turonian) Greenhorn Cyclothem at Black Mesa, Northeastern Arizona: *Unpublished Ph.D. thesis, University of Colorado, Boulder*, 1320 p.
- LECKIE, D.A., BHATTACHARYA, J.P., BLOCH, J., GILBOY, C.F., and NORRIS, B., 1994, Cretaceous Colorado/Alberta Group of the western Canada sedimentary basin: *in* MOSSOP, G., and SHETSEN, I., compilers, *Geological Atlas of the Western Canada Sedimentary Basin: Canadian Society of Petroleum Geologists, Calgary*, 510 p.
- LEVINTON, J.S., 1970, The paleoecological significance of opportunistic species: *Lethaia*, v. 3, p. 69–78.
- LUDVIGSON, G.A., WITZKE, B.J., GONZALEZ, L.A., HAMMOND, R.H., and PLOCHER, O.W., 1994, Sedimentology and carbonate geochemistry of concretions from the Greenhorn Marine Cycle (Cenomanian-Turonian), eastern margin of the Western Interior Seaway: *in* SHURR, G.W., LUDVIGSON, G.A., and HAMMOND, R.H., eds., *Perspectives on the Eastern Margin of the Cretaceous Western Interior Basin: Geological Society America Special Paper 287*, p. 145–174.
- MAGURRAN, A.E., 1988, *Ecological Diversity and its Measurement: Princeton University Press, Princeton*, 179 p.
- MCLEOD, K.G., and HOPPE, K.A., 1992, Evidence that inoceramid bivalves were benthic and harbored chemosynthetic symbionts: *Geology*, v. 20, p. 117–120.
- MCNEIL, D.H., and CALDWELL, W.G.E., 1981, Cretaceous rocks and their foraminifera in the Manitoba Escarpment: *Geological Association of Canada, Special Paper 21*, 439 p.
- MAY, R.M., 1975, Patterns of species abundance and diversity: *in* CODY, M. L., and DIAMOND, J. M., eds., *Ecology and Evolution of Communities: The Belknap Press of Harvard University Press, Cambridge and London*, p. 81–120.
- OSCHMANN, W., 1991, Anaerobic-poikiloaerobic-aerobic: A new facies zonation for modern and ancient neritic redox facies: *in* EINSELE, G., RICKEN, W., and SEILACHER, A., eds., *Cycles and Events in Stratigraphy: Springer-Verlag, Berlin*, p. 565–571.
- PEDERSON, T.F., and CALVERT, S.E., 1990, Anoxia vs. productivity: What controls the formation of organic-carbon-rich sediments and sedimentary rocks?: *American Association Petroleum Geologists Bulletin*, v. 74, p. 454–466.

- PILEOU, E.C., 1975, Ecological diversity: Wiley, New York, 165 p.
- PIMM, S.L., 1984, The complexity and stability of ecosystems: *Nature*, v. 307, p. 321–326.
- PRATT, L.M., 1984, Influence of paleoenvironmental factors on the preservation of organic matter in middle Cretaceous Greenhorn Formation near Pueblo, Colorado: *American Association of Petroleum Geologists Bulletin*, v. 68, p. 1146–1159.
- PRATT, L.M., KAUFFMAN, E.G., and ZELT, F.B., eds., 1985, Fine-grained deposits and biofacies of the Cretaceous Western Interior Seaway, Evidence of cyclic sedimentary processes: *Society of Economic Paleontologists and Mineralogists, Field Trip Guidebook no. 4*, 249 p.
- PRESTON, F.W., 1948, The commonness and rarity of species: *Ecology*, v. 29, p. 254–283.
- RHOADS, D.C., and MORSE, J.M., 1971, Evolutionary and ecologic significance of oxygen-deficient marine basins: *Lethaia*, v. 4, p. 413–428.
- ROBERTS, L.N.R., and KIRSCHBAUM, M.A., 1995, Paleogeography of the Late Cretaceous of the Western Interior of Middle North America—Coal distribution and sediment accumulation: *U.S. Geological Survey Professional Paper 1561*, 115 p.
- SAGEMAN, B.B., 1985, High-resolution stratigraphy and paleobiology of the Hartland Shale Member: Analysis of an oxygen-deficient epi-continental sea: in PRATT, L.M., KAUFFMAN, E.G., and ZELT, F.B., eds., *Fine-Grained Deposits and Biofacies of the Cretaceous Western Interior Seaway: Evidence of Cyclic Sedimentary Processes: Society of Economic Paleontologists and Mineralogists, Fieldtrip Guidebook no. 4*, p. 112–121.
- SAGEMAN, B.B., 1989, The benthic boundary biofacies model: Hartland Shale Member, Greenhorn Formation (Cenomanian) Western Interior, North America: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 74, p. 87–110.
- SAGEMAN, B.B., 1991, High-resolution event stratigraphy, carbon geochemistry, and paleobiology of the Upper Cenomanian Hartland Shale Member (Cretaceous), Greenhorn Formation, Western Interior, U.S.: Unpublished Ph.D. thesis, University of Colorado, Boulder, 572 p.
- SAGEMAN, B.B., 1996, Lowstand tempestites: Depositional model for Cretaceous skeletal limestones, Western Interior, U.S.: *Geology*, v. 24, p. 888–892.
- SAGEMAN, B.B., and ARTHUR, M.A., 1994, Early Turonian paleogeographic/paleobathymetric map, Western Interior, U.S.: in CAPUTO, M., and PETERSON, J., eds., *Mesozoic Systems of the Rocky Mountain Region, U.S.: Rocky Mountain Section—Society of Sedimentary Geology (SEPM) Special Publication*, p. 457–470.
- SAGEMAN, B.B., RICH, J., ARTHUR, M.A., and DEAN, W.E., 1997, Evidence for Milankovitch periodicities in Cenomanian-Turonian lithologic and geochemical cycles, Western Interior U.S.: *Journal Sedimentary Research*, Vol. 67, No. 2, March, 1997, p. 285–301.
- SAGEMAN, B.B., WIGNALL, P.B., and KAUFFMAN, E.G., 1991, Biofacies models for black shales: Tools for paleoenvironmental analysis: in EINSELE, G., RICKEN, W., and SEILACHER, A., eds., *Cycles and Events in Stratigraphy*: Springer-Verlag, Berlin, p. 542–564.
- SAGEMAN, B.B., KAUFFMAN, E.G., HARRIES, P.J., and ELDER, W.P., 1996, Cenomanian-Turonian bioevents in the Western Interior Basin: Contrasting scales of local, regional and global events: in BRETT, C.E., and BAIRD, G.C., eds., *Paleontological Events: Stratigraphic, Ecological, and Evolutionary Implications*: Columbia University Press, N.Y. p. 285–312.
- SANDERS, H.L., 1968, Marine benthic diversity: A comparative study: *American Naturalist*, v. 102, p. 243–282.
- SAVRDA, C.E., and BOTTJER, D.J., 1986, Trace fossil model for reconstruction of paleo-oxygenation in bottom waters: *Geology*, v. 14, p. 3–6.
- SAVRDA, C.E., and BOTTJER, D.J., 1987, The exaerobic zone, a new oxygen-deficient marine biofacies: *Nature*, v. 327, p. 54–56.
- SAVRDA, C.E., and BOTTJER, D.J., 1991, Oxygen-related biofacies in marine strata: An overview and update: in TYSON, R.V., and PEARSON, T.H., eds., *Modern and Ancient Continental Shelf Anoxia: Geological Society of London, Special Publication 58*, p. 201–220.
- SAVRDA, C.E., BOTTJER, D.J., and GORSLINE, D.S., 1984, Development of a comprehensive oxygen-deficient marine biofacies model: Evidence from Santa Monica, San Pedro, and Santa Barbara basins, California continental borderland: *American Association of Petroleum Geologists Bulletin*, v. 68, 1179–1192.
- SAVRDA, C.E., BOTTJER, D.J., and SEILACHER, A., 1991, Redox-related benthic events: in EINSELE, G., RICKEN, W., and SEILACHER, A., eds., *Cycles and Events in Stratigraphy*: Springer-Verlag, Berlin, p. 525–541.
- SCOTT, R.W., 1974, Bay and shoreface benthic communities in the Lower Cretaceous: *Lethaia*, v. 7, p. 241–252.
- SEILACHER, A., 1990, Aberrations in bivalve evolution related to photo- and chemosymbiosis: *Historical Biology*, v. 3, p. 289–311.
- SHUMWAY, S.E., SCOTT, T.M., and SHICK, J.M., 1983, The effects of anoxia and hydrogen sulphide on survival, activity and metabolic rates in the Coot Clam, *Mulina lateralis* (Say): *Journal of Experimental Marine Biology and Physiology*, v. 71, p. 135–146.
- SPEYER, S.E., and BRETT, C.E., 1988, Taphofacies models for epeiric sea environments: Middle Paleozoic examples: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 63, p. 225–262.
- THOMPSON, J.B., MULLINS, H.T., NEWTON, C.R., and VERCOUTERE, T.L., 1985, Alternative biofacies model for dysaerobic communities: *Lethaia*, v. 18, p. 167–179.
- THURBERG, F.P., and GOODLETT, R.O., 1979, Impact on clams and scallops. Part 2. Low dissolved oxygen concentrations and surf clams—a laboratory study: in SWANSON, R.L., and SINDERMAN, C.J., eds., *Oxygen Depletion and Associated Benthic Mortalities in New York Bight, 1976: National Oceanographic and Aeronautical Administration, Professional Paper 11*, p. 277–280.
- TYSON, R.V., and PEARSON, T.H., 1991, Modern and ancient continental shelf anoxia: An overview: in TYSON, R.V., and PEARSON, T.H., eds., *Modern and Ancient Continental Shelf Anoxia: Geological Society of London, Special Publication 58*, p. 1–24.
- UPCHURCH, G.R., and WOLFE, J.A., 1993, Cretaceous vegetation of the Western Interior and adjacent regions of North America: in CALDWELL, W.G.E., and KAUFFMAN, E.G., eds., *Evolution of the Western Interior Basin: Geological Society of Canada, Special Paper 39*, p. 243–282.
- VALENTINE, J.W., 1971, Resource supply and species diversity patterns: *Lethaia*, v. 4, p. 51–61.
- WHITTAKER, R.H., 1975, *Communities and ecosystems*. 2nd ed.: Macmillan, New York. 385 pp.
- WIGNALL, P.B., 1990, Benthic palaeoecology of the late Jurassic Kimmeridge Clay of England: *The Palaeontological Association, Special Paper 43*, London, 74 p.
- WIGNALL, P. B., 1994, *Black shales: Claredon*, Oxford. 127 p.
- WIGNALL, P.B., and HALLAM, A., 1991, Biofacies, stratigraphic distribution and depositional models of British onshore Jurassic black shales: in TYSON, R.V., and PEARSON, T.H., eds., *Modern and Ancient Continental Shelf Anoxia: Geological Society of London, Special Publication 58*, p. 291–309.
- WIGNALL, P.B., and MYERS, K.J., 1988, Interpreting benthic oxygen levels in mudrocks: A new approach: *Geology*, v. 16, p. 452–455.
- WINN, R.D., BISHOP, M.G., and GARDNER, P.S., 1987, Shallow-water and sub-storm-wave-base deposition of Lewis Shale in Cretaceous Western Interior Seaway, south-central Wyoming: *American Association of Petroleum Geologists Bulletin*, v. 71 (7), p. 859–881.
- WITZKE, B.J., and LUDVIGSON, G.A., 1994, The Dakota Formation in Iowa and the type area: in SHURR, G.W., LUDVIGSON, G.A., and HAMMOND, R.H., eds., *Perspectives on the Eastern Margin of the Cretaceous Western Interior Basin: Geological Society of America Special Paper 287*, p. 43–78.

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APPENDIX A

Locality data for sections numbered in Figure 2.

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- 1) NBS—Nipple Butte Section, Wahweap Wash, Kane County, Utah
Lone Rock Quadrangle, Utah-Arizona, 1981 Edition, 1:24,000
LAT 37° 4 0' LONG 111° 35 0'
 - 2) BMS5—Black Mesa Section #5, Yale Point, Navajo County, Arizona
Sweathouse Peak Quadrangle, Arizona, 1968 Edition, 1:24,000
LAT 36° 20 92' LONG 109° 49 10'
 - 3) FCS—Four Corners Section, Red Wash, San Juan County, New Mexico
Rattlesnake, New Mexico-Colorado, Quadrangle, 1937, reprint 1949, 1:62,500
LAT 6° 48 43' LONG 108° 55 61'
 - 4) CHS—Carthage Hartland Section, near Carthage town site, Socorro County, New Mexico
Canon Agua Buena, New Mexico, Quadrangle, 1981 Edition, 1:24,000
LAT 33° 53 08' LONG 106° 44 87'
 - 5) BGS—Black Gap Section, near Hot Springs, Pennington County, South Dakota
Hot Springs, South Dakota, Quadrangle, 1950 (Revised 1979) Edition, 1:24,000
LAT 43° 27 0' LONG 103° 22.0'
 - 6) PHS—Pueblo Hartland Section (PHS), Rock Canyon Anticline, Pueblo County, Colorado
Northwest Pueblo, Colorado, Quadrangle, Revised 1970 and 1974 Editions, 1:24,000
LAT 38° 16 0' LONG 104° 43 0'
 - 7) BHS—Bunker Hill Section, Bunker Hill, Russell County, Kansas
Dorrance NW, Kansas, Quadrangle, 1967 Edition, 1:24,000
LAT 38° 55 35' LONG 98° 42 36'
-

APPENDIX B

Numerical faunal data for samples plotted in Figure 8.

Sample	Taxa	Abund (indiv.)	S (spp.)	H'	e
BHS-A-19	<i>Inoceramus ginterensis</i>	79			
	<i>Phelopteria minuta</i>	6			
	<i>Inoceramus tenuistriatus?</i>	3			
	moderately laminated	—			
	TOTAL	88	3	0.39	0.353
BGS-6L	<i>Inoceramus tenuistriatus?</i>	48			
	<i>Phelopteria minuta</i>	44			
	<i>Inoceramus</i> sp. aff. <i>I. tenuis</i>	19			
	<i>Neocardioceras?</i> sp.	1			
	moderately well-laminated	—			
TOTAL	112	4	1.07	0.77	
CHS-25	<i>Entolium</i> sp.	311			
	<i>Plicatula</i> sp. cf. <i>P. ferryi</i>	3			
	<i>Inoceramus pictus?</i>	2			
	<i>Planolites</i>	2			
	<i>Callistina?</i> sp.	1			
	<i>Pycnodonte</i> sp.	1			
	ammonite indet.	1			
	ostracod unident.	1			
	<i>Thalassinoides</i>	1			
	poorly-moderately laminated	—			
TOTAL	323	9	0.23	0.106	
FCS-19	<i>Pycnodonte</i> sp. aff. <i>P. kellumi</i>	344			
	<i>Plicatula</i> sp. cf. <i>P. ferryi</i>	31			
	<i>Turritella</i> sp.	4			
	<i>Serpula intricata</i>	4			
	<i>Exogyra</i> sp. aff. <i>E. acroumbonata</i>	3			

APPENDIX B

Continued.

Sample	Taxa	Abund (indiv.)	S (spp.)	H'	e
	<i>Solemya obscura</i>	2			
	<i>Inoceramus</i> sp.	1			
	<i>Gryphaeostrea</i> sp.	1			
	<i>Lucina</i> sp.	1			
	gastropod indet.	1			
	<i>Alloecioceras</i> sp.	1			
	burrowed	—			
	TOTAL	393	11	0.55	0.23
BGS-6J	<i>Inoceramus ginterensis</i>	88			
	<i>Inoceramus tenuistriatus?</i>	27			
	<i>Phelopteria minuta</i>	25			
	<i>Inoceramus</i> sp. aff. <i>I. tenuis</i>	16			
	<i>Phelopteria quadrate</i> sp. aff. <i>P. minuta</i>	5			
	<i>Phelopteria quadrate</i> sp. (rugate)	3			
	<i>Neocardioceras?</i> sp.	2			
	<i>Borissiakoceras?</i> sp.	1			
	moderately well-laminated	—			
	TOTAL	167	8	1.40	0.674
FCS-7A	<i>Pycnodonte</i> sp. aff. <i>P. kellumi</i>	48			
	<i>Plicatula</i> sp. cf. <i>P. ferryi</i>	25			
	<i>Plicatula</i> sp. cf. <i>P. hydrotheca</i>	5			
	<i>Astarte</i> n. sp.	5			
	<i>Metoicoceras</i> sp. cf. <i>M. mosbyense</i>	2			
	<i>Pycnodonte</i> sp. cf. <i>P. kellumi</i>	1			
	<i>Psilomya</i> sp. cf. <i>P. concentrica</i>	1			
	<i>Rhynchostreon levis</i>	1			
	<i>Geltena?</i> sp.	1			
	<i>Cerithiopsis</i> sp.	1			
	<i>Turritella</i> sp.	1			
	<i>Gyrodes</i> sp. cf. <i>G. tramitensis</i>	1			
	<i>Cadulus praetenuis</i>	1			
	<i>Calycoceras</i> sp. cf. <i>C. naviculare</i>	1			
	moderately bioturbated	—			
	TOTAL	94	14	1.52	0.578
NBS-20	<i>Pycnodonte newberryi</i>	354			
	<i>Pseudomelania</i> sp. (<i>Levicerithium?</i>)	335			
	<i>Lucina</i> sp. aff. <i>L. linearia</i>	203			
	<i>Nemodon</i> sp.	141			
	<i>Chondrites</i> sp.	60			
	<i>Borissiakoceras</i> sp.	34			
	<i>Rhynchostreon levis</i>	30			
	<i>Planolites</i> sp.	22			
	<i>Phelopteria</i> sp. cf. <i>P. minuta</i>	14			
	<i>Calycoceras naviculare</i>	14			
	<i>Psilomya</i> sp. aff. <i>P. concentrica</i>	12			
	<i>Trochocyathus (Platygyathus)</i> sp.	11			
	<i>Plicatula</i> sp. cf. <i>P. ferryi</i>	10			
	<i>Psilomya</i> sp. aff. <i>P. elongata</i>	8			
	<i>Gryphaeostrea</i> sp.	8			
	<i>Anomia?</i> sp.	8			
	<i>Inoceramus</i> sp.	5			
	<i>Thalassinoides</i> sp.	5			
	<i>Pseudocalyoceras</i> sp. (F)	4			
	<i>Nuculana</i> sp. cf. <i>N. mutuata</i>	4			
	<i>Geltena</i> sp.	4			
	<i>Turritella</i> sp.	3			
	<i>Parmicorbula</i> sp.	2			
	<i>Sexta</i> n. sp. aff. <i>S. navicula</i>	2			
	<i>Callistina</i> sp. aff. <i>C. alta</i> (juv.)	2			
	<i>Ostrea</i> sp.	2			
	<i>Dentalium</i> sp. aff. <i>D. sublineatum</i>	1			
	bioturbated	—			
	TOTAL	1298	27	2.10	0.636